Strong influence of regional species pools on continent-wide structuring of local communities

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There is a long tradition in ecology of evaluating the relative contribution of the regional species pool and local interactions on the structure of local communities. Similarly, a growing number of studies assess the phylogenetic structure of communities, relative to that in the regional species pool, to examine the interplay between broad-scale evolutionary and fine-scale ecological processes. Finally, a renewed interest in the influence of species source pools on communities has shown that the definition of the source pool influences interpretations of patterns of community structure. We use a continent-wide dataset of local ant communities and implement ecologically explicit source pool definitions to examine the relative importance of regional species pools and local interactions for shaping community structure. Then we assess which factors underlie systematic variation in the structure of communities along climatic gradients. We find that the average phylogenetic relatedness of species in ant communities decreases from tropical to temperate regions, but the strength of this relationship depends on the level of ecological realism in the definition of source pools. We conclude that the evolution of climatic niches influences the phylogenetic structure of regional source pools and that the influence of regional source pools on local community structure is strong.

Keywords: regional species pool; community assembly; phylogenetics; tropical niche conservatism; diversity gradients; Formicidae

1. INTRODUCTION

The relative importance of ecological and evolutionary processes on the structure of local communities remains an open question. While a growing number of studies integrate phylogenetic methods into ecological studies in an attempt to examine the interplay of ecology and evolution, a framework for disentangling the influence of these two processes is still lacking (but see [1]). As an example, the Tropical Niche Conservatism hypothesis posits that many clades originated in the warm and wet tropics, and that dispersal and diversification into cold and dry climatic regions have been both recent and evolutionarily challenging [2]. As fewer clades have been able to overcome this challenge, average phylogenetic relatedness of species in a local community is expected to be higher in tropical climates relative to communities in temperate climates [3,4]. However, geographical variation in the relative importance of ecological mechanisms that mediate coexistence in communities could also produce this same pattern of phylogenetic community structure along climatic gradients [5,6].

Studies assessing the influence of broad-scale evolutionary processes on the structure of communities have been either narrow in their geographical span or used broadly defined assemblages rather than communities of co-occurring species. As an example, tests of phylogenetic niche conservatism at broad spatial extents often use coarse-grain grid cells as sampling units that range in size from entire counties to $1 \times 1°$ latitudinal–longitudinal grid cells, not local communities of interacting species [3,4,7,8]. Alternatively, test of phylogenetic niche conservatism in fine-grained studies of what most ecologists would call local communities are often restricted to a set of geographically clustered communities (e.g. [4,9–11]), and often ignore how geographical variation in climate or evolutionary history might influence which ecological factors prevail during community assembly. If ecologists aim to understand the interplay of ecological and evolutionary processes on local communities, then clearly local communities need to be the unit of study and sampling should cover a broad geographical extent [5,12–15].

The definition of source pools has a strong influence on understanding which particular processes shape the structure of local communities [11,16]. Studies that examine whether local communities are non-random subsets of the regional species source pool have, for the most part, defined source pools arbitrarily. To address this

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problem, we consider a suite of increasingly restrictive and ecologically realistic source pool definitions, ranging from a source pool that simply contains all species found in the study, to a source pool that incorporates much of the empirical structure of species distributions [17]. Evaluating this range of source pools allows us to assess the statistical robustness of the results, but more importantly provides a framework for interpreting the causes of phylogenetic community structuring.

Here, we assess the interplay of climatic niche evolution, regional source pools and local interactions on continent-wide patterns of phylogenetic community structure and species density in ants. We do this using a molecular phylogeny (resolved at the genus-level) that includes 592 species coupled with data from 292 local communities of co-occurring ant species in North America spanning 50° of latitude and 60° of longitude. Specifically, we (i) define source pools in four different ways and for each community, (ii) assess the relative influence of regional source pools and local interactions on both phylogenetic community structure and species density (i.e. the number of species per unit of area), and (iii) examine which factors might underlie systematic variation in community structure along climatic gradients.

2. METHODS

(a) *Community composition dataset*
We used ant species composition data from 54 published studies and 292 communities (figure 1a) in the North American ant database (www.antmacroecology.org/projects.html). We included communities (i) that have been sampled using one or more of a combination of the following techniques [18]: pitfall trapping, leaf-litter extraction, baiting or visual surveys (note that we included six studies from species-poor communities in northern Canada that used only visual surveys), (ii) where sampling was not limited to particular trophic levels or taxonomic groups (e.g. the study did not focus on only seed-harvesting ants or only on ants in a single genus), and (iii) where each community within the study had a total of at least 10 samples (e.g. 10 pitfall traps, 10 leaf-litter samples or 10 baits). Information on the sampling area covered was not available for many studies, but we nonetheless excluded studies that clearly consisted of species list for broad regions. Among the studies for which the size of the sampling grain was available, the largest grain sampled was 2.7 km^2, but for most studies, the grain was smaller than 0.1 km^2. In addition, the species density of ants (i.e. the number of species per unit of area) among communities did not correlate with the size of the sampling grain in a global study using similar community data for ants [19]. We further excluded studies conducted in highly disturbed anthropogenic habitats (e.g. road-sides) because it is unclear how high-levels anthropogenic disturbance might interfere with the ecological and evolutionary processes shaping ant communities. Finally, because a previous study showed that invasive ant species can alter the phylogenetic structure of ant communities [20], we excluded communities in which any invasive ant species was present in any of the samples.

(b) *Climatic dataset*
We included the variables minimum temperature of the coldest month and annual precipitation to describe variation in
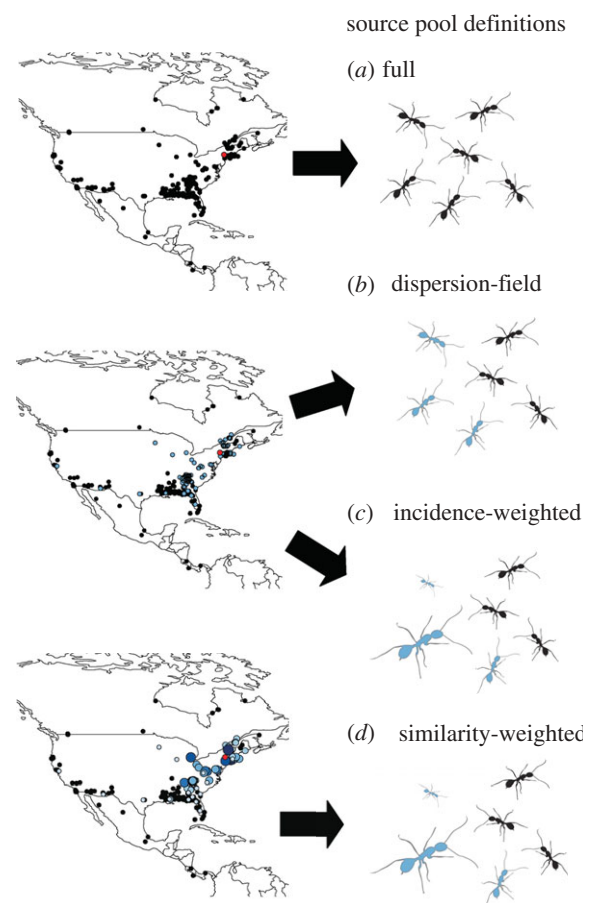

Figure 1. Map showing geographical placement of analysed communities and associated definitions of the source pool for analyses of phylogenetic community structure. The source pool for a given focal community (red dot) includes either (a) all the species recorded in North America (black dots) or (b–d) all species recorded in the dispersion-field (blue dots). Using (d) the community similarity-weighted definition of the source pool, communities sharing many species with the focal community (big, dark blue dots) are more likely to have a species present in the focal community than communities sharing fewer species (small, light blue dots). The relative size of ant symbols indicates whether (a,b) the probability of any species being present in the focal community was equal to any other species or (c,d) dependent on its incidence in the dispersion field.

the 'tropicality' of climate and climatic niches. Climate influences many attributes of ant community structure and has been shown to explain a large proportion of geographical variation in ant abundance [21,22], species density [19,21,22] and species composition [23]. Recent global studies have shown that temperature and precipitation account for a large portion of the variation in ant species density, whether among ground foraging ant assemblages [19] or canopy species [24]. One possible explanation is that evolutionary constraints on ecological traits such as cold and/or drought tolerance could play a central role in explaining the relative paucity of ant species in these regions.

For each community in the database, we extracted values for two climatic variables (minimum temperature of coldest month and annual precipitation) by overlaying the geographical coordinate for each community with climatic data layers obtained from WorldClim (v. 1.4; http://www.worldclim.org/). The data layers in WorldClim are generated through

interpolation of average monthly climate data from weather stations at 1 km spatial resolution.

(c) Constructing the phylogeny

A robust species-level phylogeny for ants does not yet exist, therefore, we used a published genus-level phylogeny [25]. This genus-level phylogeny is based on a Bayesian analysis of seven nuclear loci (5988 bps). Using this published tree as a topological constraint (as in Lessard *et al.* [20]), we estimated branch lengths with maximum likelihood under a $GTR + I + \Gamma$ model of sequence evolution on the concatenated sequence data using the program PAUP* [26]. An ultrametric tree was obtained using penalized likelihood [27] with a smoothing parameter selected via cross validation as implemented in the program r8s [28]. We used a single fixed age constraint at the base of the tree to generate the ultrametric tree (cf. Lessard *et al.* [20]). We assigned each species in our dataset to a genus present in the phylogeny following common practices in community phylogenetics [3,4,29]. We included species as terminal taxa in the phylogeny by creating trees where members of the same genus were modelled as terminal and basal polytomies (see electronic supplementary material, appendix S1). Because the outcome of these analyses did not depend on which approach we used to resolve polytomies across the phylogenetic tree, we present only the results obtained from using the phylogeny wherein species were introduced as basal polytomies. Using this approach, all species in the polytomy (i.e. genus) are equally divergent to one another as they are to the sister genus.

As this published phylogeny [25] does not include all of the ant genera that occurred in our community dataset, we substituted 17 genera in the community dataset with nearest genera present in the phylogeny (following Lessard *et al.* [20]). We substituted closely related genera based on phylogenetic and taxonomic information available in the primary literature (electronic supplementary material, appendix S2 for a list of substituted taxa and for references). Two genera (*Adelomyrmex* and *Mycocepurus*) were not replaceable owing to lack of a close relative in the phylogeny. For genera in our analysis represented by two species in the published phylogeny [25], we chose the species that occurred in North America. If the genus was polyphyletic or paraphyletic, we chose the branch of the phylogeny that represented a species or genus in North America.

(d) Estimating the strength of phylogenetic niche signal

We quantified climatic envelopes by calculating the arithmetic mean values of the minimum temperature of the coldest month and precipitation for each species in the database. Though we examined the consequence of using other measures of central tendency to quantify climatic envelopes, we focus on the mean because the median, minimum and maximum values yielded qualitatively similar results.

For any given species, the number of occurrence in the database varied from 1 to 121 (see electronic supplementary material, figure S2). Therefore, we ran separate analyses excluding species with few occurrences (i.e. less than 2, less than 3 or less than 4) and found that removing species with few occurrence records did not affect our conclusions. We thus retain the poorly sampled species in our analyses. These mean climatic values were then used to represent broad-scale climatic niches as traits in analyses of phylogenetic signal. In addition, we used the first principal

component from a principal component analysis (PCA) on the correlation matrix to represent the overall climatic niche of each species. The first principal component explained 69 per cent of the variation in the climatic data.

We assessed the degree to which there is a phylogenetic signal in the climatic envelope of species (i.e. closely related taxa have similar broad-scale climatic niches) of ant species using the K statistic [30] implemented in the PICANTE package [31] in R [32]. K quantifies the degree of phylogenetic signal using a Brownian motion-like model of trait evolution (i.e. using mean values of climatic variables as traits). Values of K near 1 indicate that the distribution of broad-scale climatic niches across the phylogeny perfectly fit expected values given a Brownian-like model of trait evolution. Values near 0 indicate a lack of phylogenetic signal, which is to say that traits are less related to phylogenetic position than expected from Brownian-like model of trait evolution. Values of K greater than 1 indicate that phylogenetic signal is greater than expected by a Brownian-like model of trait evolution and indicate strong niche conservatism [33]. We assessed statistical significance by permuting the climatic data across the tips of the phylogeny 10 000 times and comparing the observed value of K (K_{obs}) with the distribution of randomly generated values of K (K_{null}). For phylogenetic signal to deviate significantly from the null expectation, K_{obs} had to be in the upper 2.5 per cent (two-tailed test) of the null distribution.

(e) Estimating the degree of phylogenetic community structure

We estimated the phylogenetic structure of each community by calculating the net relatedness index (NRI) for each community. The NRI measures the mean phylogenetic distance between all pairs of taxa in a community, relative to the mean phylogenetic distance of the species in the source pool. In particular, this standardized index is a measure of the difference between the mean phylogenetic distance in the observed community relative to randomly generated null communities, standardized by the standard deviation of mean phylogenetic distances among null communities [34]. Positive values of NRI indicate phylogenetic clustering whereas negative values indicate phylogenetically even dispersion.

(f) Constructing source pools

Deviations between observed and null communities have been interpreted as a signal of habitat or abiotic filtering (phylogenetic clustering) or competition (phylogenetically evenly dispersed [5,9,11,16]; but see [35]). However, the definition of the source pool affects both the observed degree of phylogenetic clustering and the interpretation of the pattern [11,36]. When using a definition of the source pool that includes all species in North America, deviations between observed and null are likely to result from processes operating at broad spatial and temporal scales [11,15,37]. Using a more ecologically realistic definition, deviation from null communities would instead be interpreted as the result of processes operating at finer spatial scales [11,15,37]. For example, consider a tree-fall gap plant community in a southeastern temperate forest in North America. The source pool for that gap community could consist of all North American species, or all of the southeastern temperate forest species, or all of the tree-fall gap species in the region. When the source pool is narrowly defined as all tree-fall gap

species in the region (i.e. the regional source pool), any significant community structure is likely to be caused by local interactions between the plant species and their biotic and abiotic environment.

Rather than arbitrarily choosing a definition of the source pool, we explore four explicit definitions; each of them sheds slightly different light on the processes of interest (figure 1). We consider the *full source pool*, *dispersion-field source pool*, *incidence-weighted source pool* and *community similarity-weighted source pool*. These source pool definitions differ in (i) species composition and (ii) the probability of sampling a particular species. For all four definitions, we constructed regional source pools for each of the 292 communities and used these source pools to estimate the net relatedness index. For each focal community and each definition of the source pool, we generated 1000 null communities, each of which had the same number of species as the observed (focal) community. All analyses and null models were implemented in R (see electronic supplementary material, appendix S3).

The widest source pool definition was the full source pool, which contained all species found in the study. This is the source pool definition that has been most commonly used for analyses of phylogenetic community structure (figure 1*a*). The composition of the full source pool is determined by the study extent (i.e. the continent of North America) and is thus partly arbitrary.

A more ecologically motivated description of regional source pools is constituted by assemblage dispersion fields [17]. The dispersion field of a focal community is found by overlaying the ranges of all species found at the community. Dispersion fields provide a spatial representation of both the size and, importantly, the distribution in space of the region across which species in the focal community have dispersed at some point in their history [17]. The dispersion-field source pool contains all species that occur at least once within the dispersion field, i.e. in communities that share at least one species with the focal community (figure 1*b*). The rationale behind this source pool definition is that if, for example, two species (A and B) occupy a single focal community (X), then A could theoretically occupy all of B's communities and vice versa, such that the dispersion field for 'community X' is all locations occupied by species from that community.

Empirical communities are typically dominated by a few widespread species [38]. To incorporate and assess the effect of dominance [39,40], we also created an incidence-weighted source pool (figure 1*c*), which had the same species composition as the dispersion-field source pool, but where the probability of sampling each species was weighted by its incidence in the dispersion field.

As illustrated by assemblage dispersion fields [17,41], empirical communities share more species with nearby and ecologically similar communities than with distant and ecologically dissimilar communities (figure 1*d*). In a probabilistic framework, a species that occurs in several communities that share 20 species with the focal community is more likely to be part of the community's source pool than a species that occurs in a community that only shares a single species [39]. This observation was incorporated by the community similarity-weighted source pool, which weights the probability of sampling a species by the compositional similarity between the communities it occupies and the focal cell, as well as its incidence in the source pool. The algorithm chooses a random community in the dispersion field,

weighted by the number of shared species. It then picks a random species from that community.

Note that there is a tradeoff between ecological realism and statistical power in the construction of source pools [39,42,43]. A source pool definition that is too wide (includes a large region and/or many species) will overestimate the number of species that could actually colonize a community. The probability that a null community will be different from the empirical community is high when drawn from too large a source pool (increasing type I error rate). On the other hand, a source pool that is constrained to be more similar to the empirically observed communities will produce a smaller variety of null communities and thus reduce the power to detect statistical pattern (increasing type II error rate).

(g) *Statistical analyses*

We were interested in the average phylogenetic structure of ant communities and whether it varied depending on the definition of the source pool. We thus compared mean net relatedness index values for all 292 ant communities and for each of the four definitions of the source pool using ANOVA.

To examine the potential relationships between spatial variation in phylogenetic community structure and contemporary climate, we used generalized linear modelling in JMP v. 8.0 (SAS, 2008) using an identity link function. Net relatedness index was the response variable and mean minimum temperature of the coldest month (hereafter minimum temperature), mean annual precipitation (hereafter precipitation) and an interaction term (i.e. minimum temperature × precipitation) were predictors. Then, we tested whether the relationship between NRI and climate depends on the definition of the source pool by including 'source pool definition', as well as interaction terms (i.e. minimum temperature × source pool definition and precipitation × source pool definition), as factors in the model. A significant interaction term would suggest that the strength of the relationship between NRI and climate depends on the definition of the source pool.

We further examined the relationship between species density and phylogenetic structure (i.e. net relatedness index) using linear regressions. Finally, to assess the relationship between climate and species density, we ran a generalized linear model (using the same climatic variables listed above) using a Poisson distribution and a log link function.

To examine whether the relationship between phylogenetic community structure and climate varied with the definition of the source pool, we ran a separate generalized linear model of climate variables on net relatedness index values generated with each of the source pool definitions. We used adjusted r^2 to examine how well these different source pool definitions affected model performance. We did not use Akaike information criterion (AIC) because net relatedness index (the response variable) values differed depending on which null models we used to create null communities.

We further examined how local species density related to source pool richness. We estimated source pool species richness using the dispersion-field source pool (figure 1). Thus, all species included in the dispersion-field source pool of a community were included in our estimate of the source pool richness. We evaluated whether local species density increases linearly with source pool richness or whether it reaches a plateau at high levels of source pool richness. We

tested for the linearity of the relationship between species density and source pool richness by comparing the fit (using AIC) of linear and quadratic models.

3. RESULTS

Regardless of source pool definition, the phylogenetic structure of ant communities was, on average, clustered ((mean NRI $\pm$ s.e., t-statistic) full source pool: 0.95 ± 0.10, $t = 9.95$, $p < 0.0001$; dispersion-field source pool: 0.51 ± 0.07, $t = 7.07$, $p < 0.0001$; incidence-weighted source pool: 0.50 ± 0.08, $t = 6.43$; community similarity-weighted source pool: 0.28 ± 0.06, $t = 4.72$; $n = 292$, $p < 0.0001$). In addition, ant communities were more phylogenetically clustered when we used the full source pool definition than with any other definitions of the source pool (ANOVA: $F_{3,1167} = 13.16$, $p < 0.0001$; figure 2a).

The relationship between the species density of local communities and the size of the source pool was better fit by a polynomial model ($r^2 = 0.54$, d.f. $= 292$, $p < 0.0001$, AIC $= 973.77$) than by a linear model ($r^2 = 0.49$, d.f. $= 292$, $p < 0.0001$, AIC $= 1003.01$), but the polynomial model described a U-shaped rather than a hump-shaped relationship (figure 2b). The residuals of the relationship between local species density and source pool richness were positively related to net relatedness indices ($r^2 = 0.10$, d.f. $= 292$, $p < 0.0001$, AIC $= 605.03$), indicating that after controlling for the size of the source pool, ant communities are more species poor in phylogenetically clustered communities than in phylogenetically evenly dispersed communities (figure 2c).

Mean minimum temperature, precipitation and minimum temperature $\times$ precipitation all accounted for variation in the phylogenetic community structure of the ant assemblages examined here. Net relatedness index was negatively related to both minimum temperature and annual precipitation (see electronic supplementary material, table S1 and figure 3). In other words, colder regions and drier regions had ant communities that drew from relatively few lineages, given their diversity. The same climatic variables that were correlated with NRI also accounted for 16 per cent variation in species density (electronic supplementary material, table S2), but phylogenetic community structure was not related to species density (see electronic supplementary material, figure S3).

The definition of the source pool affected the degree to which the variation in net relatedness index was explained by climate (see electronic supplementary material, tables S1 and S3). The interaction term 'minimum temperature $\times$ source pool definition' in the full model was statistically significant ($x^2 = 21.34$, d.f. $= 15$, $p < 0.0001$), indicating that the strength of the relationship between NRI and minimum temperature depends on the definition of the source pool. When using the full source pool definition climate explained three times more variation in net relatedness index than when using the *similarity-weighted source pool* definition and two times more variation than when using the *dispersion-field* or *incidence-weighted source pool* definitions (see electronic supplementary material, table S1). The degree of phylogenetic clustering (using the full source pool definition) was not related to local species density ($r^2 = 0.01$, $n = 292$, $p = 0.1$).
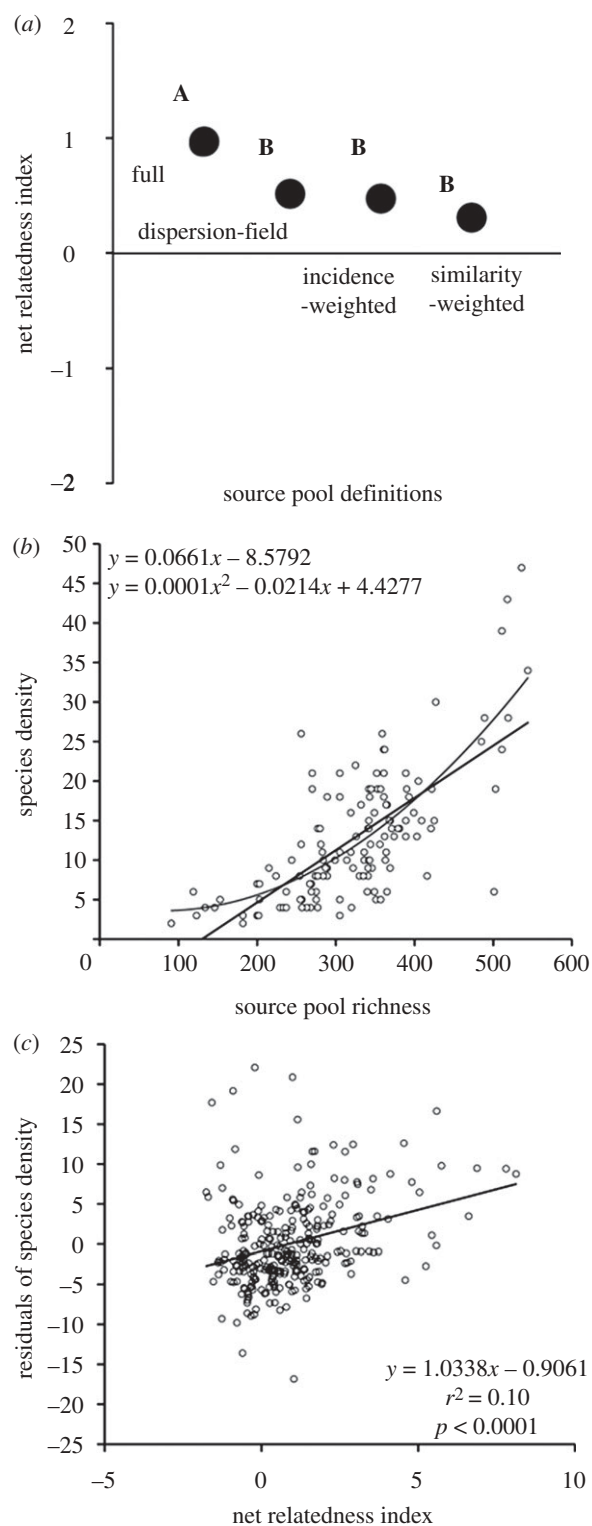

Figure 2. (*a*) North American ant communities ($n = 292$) are phylogenetically clustered. Letters indicate significant differences (Tukey–Kramer HSD; $p < 0.001$) in the mean ($\pm$s.e.) net relatedness index of North American ant communities among source pool definitions. Owing to their small size, error bars are hidden behind the dots. (*b*) The number of species recorded in a community (i.e. species density) is positively related to the number of species in the dispersion-field Akaike information criterion (AIC) source pool. (*c*) The residuals of the local species density–source pool species richness relationship are negatively related to the degree of phylogenetic clustering: after controlling for differences in the size of the source pool, phylogenetically clustered communities are more species-poor than phylogenetically evenly dispersed communities.
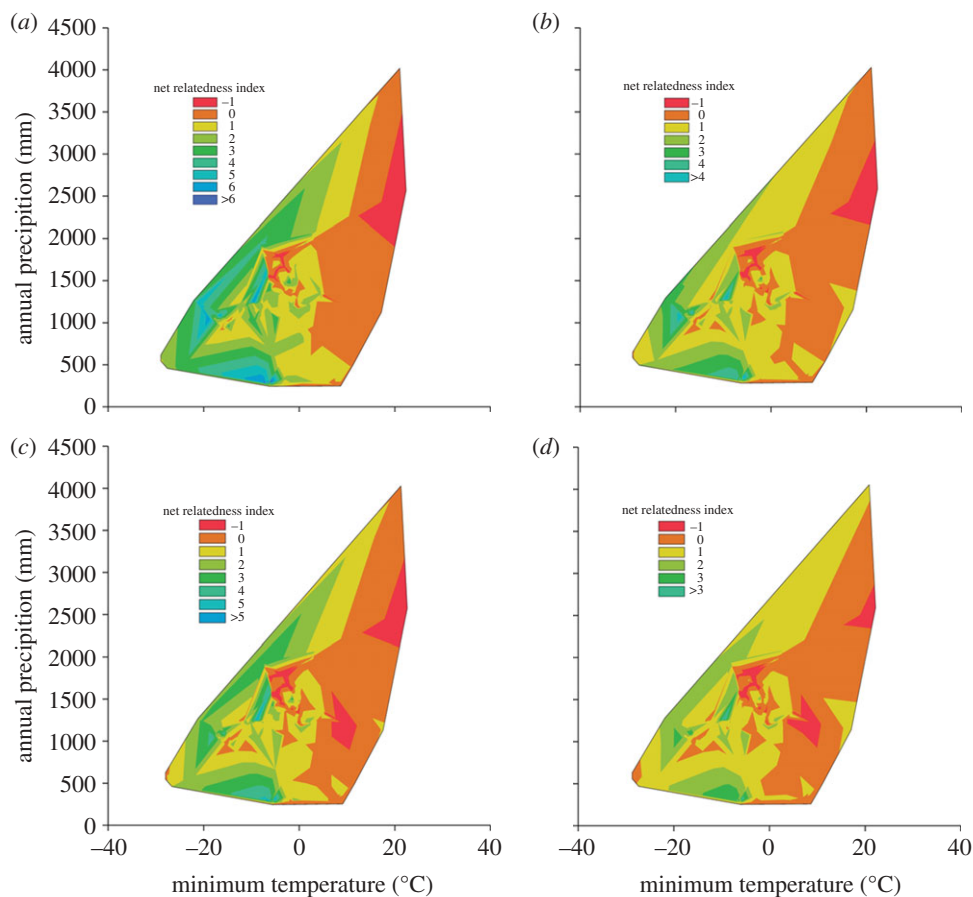
Figure 3. Temperature and precipitation interact to shape the phylogenetic structure of ant communities. Contour plots show variation in phylogenetic community structure along two climatic axes (i.e. minimum temperature of the coldest month and annual precipitation) for 292 North American ant communities. Colours indicate phylogenetic structure using the (*a*) full source pool, (*b*) dispersion-field source pool, (*c*) incidence-weighted source pool and (*d*) community similarity-weighted source pool to estimate net relatedness index values.

Broad-scale climatic niches of closely related ant species were, on average, more similar to one another than expected from a random assignment of broad-scale climatic niches to the tips of the phylogenetic tree (electronic supplementary material, figure S4). Mean minimum temperature ($K = 0.29$, $p < 0.0001$) and mean precipitation ($K = 0.21$, $p < 0.0001$) across the range of ant species were more likely to be similar for close relatives than for distantly related ones. In addition, the first principal component of average minimum temperature and annual precipitation also showed a phylogenetic signal ($K = 0.25$, $p < 0.0001$). However, because K was never greater than 1, the tempo and mode of evolution in the climatic niches of ants are not consistent with niche conservatism [33].

4. DISCUSSION

Our continent-wide analysis of 292 local communities of North American ants demonstrates a general tendency for phylogenetic clustering. The degree of clustering decreases with increasing levels of ecological realism in the definition of source pools, but is always present, regardless of the source pool used. This phylogenetic clustering also increases as one goes from tropical to more temperate communities, with cold and dry communities being the most clustered, though this effect also weakens as the definition of the source pool becomes

more ecologically realistic. Taken together, our results suggest that the non-random evolution of climatic niches shapes the phylogenetic structure of regional source pools, and attributes of regional source pools contribute much of the variation in phylogenetic structure and species density among ant communities.

Ant communities in North America are, on average, phylogenetically clustered. Considering four definitions of the source pool did not affect our conclusion regarding the mean phylogenetic structure of these ant communities, which indicates that this result is statistically robust. While communities were phylogenetically clustered independent of source pool definition, the source pool definition affected the degree to which a community was clustered [11,36]. Communities were more phylogenetically clustered when the source pool included all species (i.e. the full source pool) than with definitions incorporating greater levels of ecological realism. In particular, the phylogenetic structure of ant communities appeared significantly less clustered when the source pool included mainly species with high ecological affinity to the focal community and high incidence in the dispersion field—those species that are likely to disperse and establish in the focal community. This result is consistent with the hypothesis that the observed phylogenetic clustering results largely from processes operating over broad temporal and spatial scales [11,15,37], and which shape the phylogenetic structure of regional

source pools. Note, however, that differences in the magnitude of phylogenetic clustering using different source pool definitions may also, at least partially, result from differences in statistical power (see §2*f*).

The linear relationship between the species density of local ant communities and the species richness of associated source pools (defined as the dispersion-field source pool) also lends support to the hypothesis that the effects of broad-scale processes trickle down to local communities [15,44,45]. Moreover, after controlling for differences in the size of the source pool among communities, phylogenetic clustering accounted for an additional 10 per cent of variation in ant species density among communities. Therefore, the species richness of source pools may influence the number of species in a community, but other processes (e.g. habitat filtering) operating at finer spatial scales account for additional variation in local species density. Inferring exactly which ecological processes underlie this covariation in phylogenetic structure and species density will entail conducting geographically replicated manipulative experiments (e.g. [46]) and detailed observational local studies (e.g. [47]).

While source pools account for much of the variation in ant phylogentic community structure and species density, the relationship between phylogenetic community structure and climate implies that the ecological processes that mediate species coexistence in temperate communities might differ from those in tropical communities [48]. For example, one possibility is that abiotic filtering predominates in cold climates, and interspecific competition predominates in more climatically benign environments at low latitudes and elevations [5,6]. For the ant communities examined here, there was only a weak relationship between climate and community phylogenetic structure when using the most restrictive and ecologically realistic definition of the source pool. Therefore, differences in ant community phylogenetic structure along climatic axes result largely from differences in the phylogenetic structure of regional species pools. Thus, elucidating the factors driving geographical variation in the phylogenetic structure of ant communities entails exploring which biogeographical, historical and evolutionary factors shape the phylogenetic structure of regional species pools [3,4,49].

By shaping regional species pools, stasis in the evolution of climatic niches could lead to systematic variation in both the phylogenetic structure and species density of communities from tropical to temperate regions [2]. Consistent with this hypothesis, ant species that persist in extremely cold and dry environments are largely from derived clades in the phylogeny and most species in basal clades are absent from extremely cold and dry regions (electronic supplementary material, figure S4). However, broad-scale climatic niches in North American ants show less evolutionary stasis than expected under strong niche conservatism [33]. Therefore, increased phylogenetic clustering along a tropical–temperate climatic gradient does not result solely from stasis in the evolution of climatic niches [4]. In addition, ant species density does not decrease as phylogenetic clustering increases, which would be expected if conservatism of climatic niches drove spatial variation in ant species density [3]. Our study thus supports the view that evolutionary processes other than conservatism of climatic niches

(e.g. time for speciation, rapid niche evolution following key innovations) underlie the tropical–temperate gradient in phylogenetic community structure and species density [49].

In conclusion, although the reigning paradigm in ant ecology is that competition is the main determinant of community structure [50,51], here we show that broad-scale variation in the abiotic environment exerts a strong influence on continent-wide structuring of ant communities. By considering several explicit definitions of the source pool with increasing degree of ecological realism [11], we find support for the hypothesis that the phylogenetic structure and species density of communities are determined by broad-scale processes that have shaped regional species pools. However, our findings further indicate that at least some of the variation in community structure among ant communities depends on local interactions operating within, rather than among, regional source pools. Understanding the forces that drive spatial variation in the structure of communities will require gaining a better understanding of the interplay between the factors that govern community assembly in evolutionary time (e.g. the formation of source pools) and those which mediate species coexistence in ecological time.

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