

Niche filtering rather than partitioning shapes the structure of temperate forest ant communities

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Summary

1. An ever-increasing number of studies use tools from community phylogenetics to infer the processes underlying the assembly of communities. However, very few studies simultaneously use experimental approaches to characterize the ecological niches of species and directly assess the importance of these structuring processes.

2. In this study, we developed an experimental approach for quantifying the use of four types of food resources and three habitat templates in temperate forest ant assemblages. We then used null models to assess whether niches overlapped more or less than expected by chance. Finally, we integrated comparative phylogenetic methods with experimental data on niche use to assess the degree of phylogenetic signal in several key components of the niche.

3. We found that niche filtering, rather than partitioning, was the predominant structuring force. Niche filtering resulted from conservatism in habitat niches in evolutionary time and limitations in the availability of food resources in ecological time.

4. Our study thus supports the idea that similarities in niches among species, rather than the differences, drive the assembly of ant communities.

Key-words: community structure, co-occurrence, environmental filtering, niche overlap, null models, phylogenetic niche signal, resource availability

Introduction

The ‘niche’ is at the core of much of community ecology (Chase and Leibold 2003), though it can be vexing to define precisely. Most ecologists might agree, however, that a niche includes conditions in the physical environment and resource availability as important axes of ecological space. It has long been argued that the differences among species in their niches (or niche partitioning) promote coexistence in a variety of ecological communities (McKane *et al.* 2002; Levine & HilleRisLambers 2009). An alternative explanation is that the similarities, rather than the differences, among species allow them to persist in local communities – a process sometimes referred to as ‘niche filtering’ (Mouillot *et al.* 2005; Carnicer *et al.* 2008; Mouchet *et al.* 2010). The relative importance of niche partitioning and niche filtering might vary with spatial scale and depend on evolutionary processes such as niche conservatism and ecological factors such as habitat-driven

context dependency or the availability of limiting resources. To date, however, surprisingly few field studies have experimentally explored how these evolutionary and ecological processes might interact to mediate the relative importance of niche filtering and partitioning in promoting coexistence in local communities.

Traditionally, ecologists have directly quantified the niche use of species to ask whether niches overlap more or less than expected (MacArthur 1958; Pianka 1974; Gotelli, Graves & Rahbek 2010). If the niches of species overlap less than expected by chance, then niche partitioning is generally assumed to determine community membership. Alternatively, if niches overlap more than expected by chance, then niche filtering (a.k.a., environmental filtering) rather than niche partitioning is often invoked as a structuring mechanism. However, because quantifying niche filtering and partitioning in the field can be an arduous task, ecologists have increasingly turned to community phylogenetics to infer the processes that might structure local communities and detect the influence of niche partitioning and niche filtering (Webb *et al.* 2002; Cavender-Bares *et al.* 2009). In this approach, the

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phylogenetic distances among co-occurring species in local communities are compared with the phylogenetic distances among species in null communities that are constructed from sampling randomly from the regional species pool (Webb *et al.* 2002). The community phylogenetic approach, however, provides at best only indirect measures of the predominant structuring process and relies on the key assumption that niches are conserved (Losos 2008).

Niche conservatism posits that many ecological traits remain unchanged (or at least change slowly) through evolutionary time and, consequently, closely related species are ecologically more similar than are distantly related ones. Alternatively, if niches are evolutionarily labile, then there should be no or very little correlation between ecological similarity and phylogenetic distances among species. A handful of (mostly observational) studies have found evidence that closely related species share similar niches, whereas other studies (again, mostly observational) suggest that niche similarity or dissimilarity is largely independent of phylogenetic relatedness (Losos *et al.* 2003; Losos 2011). Only a few experimental studies have directly quantified niche use and tested the assumptions that closely related species are ecologically more similar and compete more intensely than do more distantly related species (Burns & Strauss 2011; Violle *et al.* 2011).

Relating niche use or overlap to phylogenetic relationships can be challenging for still another reason: some attributes of the niche may be evolutionary conserved whereas others are more labile. As a result, the correlation between ecological similarity and phylogenetic relatedness might be specific to particular traits or niche components (Ackerly, Schwilk & Webb 2006; Silvertown *et al.* 2006a, b). Nevertheless, identifying which attributes of the niche are conserved can help uncover how evolutionary processes mediate ecological interactions and shape contemporary patterns of community structure (Rabosky *et al.* 2011). For example, one might expect high levels of conservatism in habitat niches to be associated with high level of overlap in the use of these same habitat templates (Southwood 1988) in ecological time, which would point to the importance of niche filtering (Cavender-Bares, Keen & Miles 2006). Alternatively, strong conservatism of habitat niches combined with a high level of evolutionary lability along other niche axes (e.g. food resource acquisition strategies) might promote niche divergence and facilitate coexistence in species assemblages (Silvertown *et al.* 2006b). Such a scenario would support the dual importance of niche filtering and partitioning in shaping local communities. Detailed knowledge of the autecologies of species and phylogenetic relationships among them is thus essential to infer assembly processes (Losos 1992).

In this study, we report on a field experiment aimed at elucidating the relative roles of niche filtering and niche partitioning in structuring temperate forest ant assemblages at local and regional scales. We argue that the

integration of niche analyses in the field, phylogenetic analyses and manipulative experiments can elucidate the interplay between evolutionary and ecological processes and identify the mechanisms that ultimately assemble ecological communities. Specifically, we provided five food resource types in each of three habitat templates to characterize the niches of 18 ant species across 20 temperate forest sites in the south-eastern USA. To test for the relative importance of niche filtering and partitioning, we first estimated the degree of niche overlap among all species in these assemblages. We then asked whether the amount of niche overlap between species pairs was related to the frequency with which they co-occurred in local assemblages. We predicted that if niche filtering was the predominant structuring mechanism, then niche overlap would be higher than expected if species were randomly assigned to particular niches. We then examined whether the amount of niche overlap among species pairs was related to the phylogenetic similarity among species.

Materials and methods

STUDY SYSTEM

We conducted this study at 20 sites within the Great Smoky Mountain National Park in East Tennessee, USA, from June to August 2009, during the time of peak ant activity in this system (Dunn, Parker & Sanders 2007). All sites (100 m²) were between 400 and 800 m elevation in mixed hardwood forests and were away from trails, recent obvious human disturbance and roadways. Additionally, sites were at least 1 km from one another. Common tree species at the sites included *Liriodendron tulipifera*, *Acer rubrum*, *Quercus rubra*, *Betula lenta*, *Carya alba*, *Oxydendrum arboretum*, *Halesia carolina* and *Robinia pseudoacacia*. Common shrub species included *Alnus serrulata*, *Acer pensylvanicum*, *Acer saccharum* and *Viburnum acerfolium*. Temperatures at these sites range from c. 4 to 24 °C annually, and mean annual precipitation is 1200 mm, with most rainfall occurring during the late winter and late summer (Busing, Stephens & Clebsch 2005; Fridley 2009).

Given their ubiquity, abundance and diversity, numerous investigators have focused on the assembly of ant communities (Lach, Parr & Abbott 2009; Cerda, Arnan & Retana 2013). Early work focused on the role of interspecific competition in shaping communities (Fellers 1987; Savolainen & Vepsäläinen 1988), whereas more recent work has focused on trade-offs (Parr & Gibb 2012; Stuble *et al.* 2013). Some of the most classic work on the relationships among coexistence, niche use and community structure in ants has been carried out in temperate forests in the eastern USA (Lynch, Balinsky & Vail 1980; Lynch 1981; Fellers 1987; Herbers 1989; Gotelli & Ellison 2002). Most previous investigators have relied on one of the tried and true methods of ant community ecology – observing ants recruit to and compete for a concentrated resource such as a clump of tuna or dollop of honey on a 7.62 × 12.7 cm card. While this is of course artificial, it does not differ substantially from how ants typically encounter resources naturally; for instance, a forager might discover a dead mouse or a dense patch of aphids or cache of seeds. In this study, we use concentrated resources in 50-mL centrifuge tubes (see Study Design below), which has proven to be an informative

approach (Kaspari, Yanoviak & Dudley 2008; Kaspari, Chang & Weaver 2010; Kaspari *et al.* 2012; Stuble *et al.* 2013). In this system, the ants are generally omnivores (Lessard, Dunn & Sanders 2009a) and generally active at about the same time during the year (Dunn, Parker & Sanders 2007).

STUDY DESIGN

We visited each of the 20 sites between 12:00 and 15:00 on sunny or mostly sunny days. At each site, we placed five types of liquid food resources in each of three habitat templets. We focused on liquid food resources so that observed patterns of resource use were not affected by the texture, shape or size of the resource, but depended on only the type of resource (Kaspari, Yanoviak & Dudley 2008). The food resources were placed in 50-mL Fisher Scientific polypropylene centrifuge tubes, which contained 10 mL of one of the following solutions (water/volume): H₂O (distilled water, as a control), 1% NaCl, 20% CHO (cane sugar), 20% amino acid (unflavoured whey protein isolate) and lipids (extra virgin olive oil). The liquid resources were prepared by pouring 10 mL of solution into each polypropylene tubes and then placing a cotton ball *c.* 5 cm into each tube in order to absorb the liquid and keep it from draining out of the tube. We chose these resource types because they were all frequently used by a variety of ant species, but there were some indication from previous studies that species differentially use carbohydrates, proteins and sodium (Yanoviak & Kaspari 2000; Sanders & Gordon 2003; Kaspari, Yanoviak & Dudley 2008; Kaspari *et al.* 2012).

We placed the centrifuge tubes in one of three habitat templets within each site: on the ground, on shrubs and on the trunks of trees. Previous work in tropical systems suggested strong niche partitioning among habitat templets (Torres 1984; Yanoviak & Kaspari 2000). We placed ground centrifuge tubes horizontally on the leaf litter surface. Shrubs were classified as species <3 m in height and <50.8 mm in diameter. We placed the centrifuge tubes on shrubs on branches (i.e. horizontally but often with a slight angle) of deciduous species at a height of *c.* 2 m from the ground. We positioned the centrifuge tubes horizontally on the trunks of trees at *c.* 2 m from the ground. Trees were, on average, 20 cm diameter at breast height. The centrifuge tubes for shrub and tree were affixed using adhesive Velcro[®] Brand industrial strength adhesive straps that held them in place on their respective substrates. At each site, samples were randomly drawn out of bags and placed every 10 m on corresponding substrate, systematically alternating among tree, shrub and ground. At each site, there were 75 centrifuge tubes (3 habitat templets × 5 resource types × 5 replicates) and 1500 total samples (75 tubes per site × 20 sites) across the study. After the tubes were placed, we waited for 3 h before retrieving them. Upon retrieval, we collected the tubes and screwed the cap on before returning the tubes to the laboratory so that all individuals in the tubes could be identified and enumerated. Voucher specimens are deposited in the collection of NJ Sanders at the University of Tennessee.

While the experimental approach we employed is frequently used (Yanoviak & Kaspari 2000; Sanders & Gordon 2003; Kaspari, Yanoviak & Dudley 2008; Kaspari, Chang & Weaver 2010; Kaspari *et al.* 2012; Stuble *et al.* 2013), it does come with a couple of caveats. Most notably, this approach assumes that if a species recruits more to one particular resource over the others, *ceteris paribus*, that resource is 'limiting' in the environment because if it were readily available, ants would not recruit as

intensively to the resource tube with that resource. The second caveat is that ants or other taxa (e.g. beetles, spiders, etc.) might competitively displace ants from the tubes, thereby influencing the apparent foraging behaviour of particular ant species. As with many ecological experiments, though, we are unsure what happens at our sample locations while we were not looking; however, we did make frequent rounds to observe the resource tubes during the entire 3-h sampling period.

ANALYSES

Patterns of niche use

To examine whether community-level recruitment (and indicator of resource limitation) varied among the 12 habitat templet × food resource combinations (note that we eliminated all niche categories comprising H₂O since no ant species was ever recorded in the H₂O only tubes), we calculated the % hits for each habitat templet × food resource combination (Kaspari, Yanoviak & Dudley 2008). That is, for each of the 12 combinations (ignoring the H₂O resources), we tallied the proportion of tubes, out of five, in which an ant was collected to obtain the % hits for that habitat templet × food resource combination, for a given site. We then used a two-way analysis of variance (ANOVA) with habitat templet, food resource and their interaction as factors in the model, with % hits as the response variable.

Niche overlap

We used null model analyses (EcoSim version 7.0, Gotelli & Entsminger 2004) to test the hypothesis that ant species partition habitat templets and food resources. We created matrices in which each column in the matrix was a niche represented by a combination of habitat templet and food resources ($n = 12$), and each row was a species. Each entry in the matrix was the number of centrifuge tubes in which a species was recorded for a given habitat templet × resource combination. We conducted the analyses at both the regional (across all 20 sites) and local (at each site separately) scale. At the regional scale, we tallied the number of tubes in which a species was recorded for each of the 12 niche categories, across all sites. We thus had a single matrix for which we tested the null hypothesis that niche overlap in the observed matrix was less than the random expectation. The matrix was reshuffled 1000 times to generate a distribution of random expectations for niche overlap. In such an analysis, niche overlap is considered to be significantly lower than the null expectation if the observed value of niche overlap falls in the lower 5% of the tail of the distribution. Niche overlap was estimated using Pianka's index (Pianka 1973). Pianka's index quantifies the symmetrical overlap among a set of discrete categories (e.g. the combination of habitat templets and resource types) for a pair of species and ranges from 0 (indicating no overlap) and 1 (complete overlap). We selected the options niche breadth retained and zero states retained in EcoSim as these lead to more conservative and more realistic estimates of randomly generated values of niche overlap. At the local scale, we repeated the same procedure, but we created a separate matrix for each site and ran the analyses separately for each site. We then computed a standardized effect size (hereafter 'SES') of niche overlap for each site, which controls for among-site differences in niche overlap that might be due to differences in the number of species present

at a site. We tested whether local niche overlap is lower than expected by chance using each SES as an observation in a one-sample *t*-test. An average SES that was significantly lower than zero would indicate less niche overlap than expected by chance.

Niche overlap and co-occurrence

We tested whether niche overlap was greater for species that do not frequently co-occur than for those that co-occur at many sites. We estimated pairwise species co-occurrence using a species by site matrix and by computing the total number of draught-board combinations (Gotelli 2000). We then estimated pairwise niche overlap distances using Pianka's index (see above section). We created three matrices of niche overlap: habitat templet, food resource and habitat templet \times food resource. We examined the relationship between co-occurrence and niche similarity using Mantel's test, which returns the Pearson correlation coefficient (*r*). We compared the observed *r* value to 1000 randomly generated values. In such an analysis, if the observed correlation coefficient falls in the lower 5% of the tail of the distribution, then the relationship between niche overlap and co-occurrence is significant. A positive relationship indicates that species with similar niches are more likely to co-occur, suggesting that niche filtering predominates. A negative relationship would suggest that similar species are less likely to co-occur, lending support to the idea niche partitioning is more important.

Niche overlap and phylogenetic distance

We tested whether niche overlap was greater for closely related species than for distantly related species. We used the same procedures as in Lessard *et al.* (2009b, 2012) to construct a species-level molecular phylogeny based on the genus-level phylogeny constructed by Brady *et al.* (2006). Species were added within genera as basal polytomies (see Supporting information for details). We used this phylogenetic tree to estimate pairwise interspecific phylogenetic distances among all possible species pairs in our data set. We then used Mantel's test to ask whether there was a correlation between niche overlap and phylogenetic distance (Warren, Glor & Turelli 2008). A positive relationship or no relationship would suggest convergence (i.e. lability) in the evolution of niches whereas a negative relationship would indicate some degree of niche conservatism (Losos *et al.* 2003).

Phylogenetic signal in niche use

Because the previous approach gives only a general picture of the relationship between phylogenetic distance and niche similarity, we also examined whether the use of particular niche categories was related to the proximity of species in the phylogeny. We considered each habitat templet, food resource and habitat templet \times food resource category as a trait and % hits in resource tubes as trait values. For each species, the % hit was calculated as the number of hits in one category (e.g. Ground) divided by the total number of hits across all niche categories (e.g. Ground + Shrub + Tree; $n = 3$ for habitat templet, $n = 4$ for resources). We assessed the degree to which there was phylogenetic signal in niche use (i.e. closely related taxa have similar trait values for a given niche category) of ant species using the *K* statistic (Blomberg, Garland & Ives 2003) implemented in the

PICANTE package (Kembel *et al.* 2010) in R (R Development Core Team, 2010). *K* quantifies the degree of phylogenetic signal using a Brownian motion-like model of trait evolution (i.e. using % hits for a given niche category as trait values). Values of *K* near 1 indicate that the distribution of % hits values across the phylogeny perfectly fits expected values given a Brownian-like model of trait evolution. Values near zero 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 $K > 1$ indicate that phylogenetic signal is greater than expected by a Brownian-like model of trait evolution and suggest strong niche conservatism (Losos 2008). The use of incomplete phylogenies and the inclusion of missing species as basal polytomies (such as the one used in our study) lead to biases in the estimation of *K*. We therefore used a rarefaction-based approach (Davies *et al.* 2012), which reduces biases in the estimation of *K*. We (A) randomly trimmed down all polytomies in the phylogeny to include only one species, (B) calculated *K* for the newly created 'trimmed phylogeny' and (C) repeated steps A and B 1000 times to generate a distribution of rarefied *K* values for each niche category.

Results

In total, we collected 7408 individual workers from 19 species in nine genera (Table S1, Supporting information). The total % hits (i.e. how many resource tubes had foragers in them out of the total placed) varied from 19 to 35% across all sites. Species richness varied from 3 to 11 among sites. The total hits exhibited by particular ant species was strongly and positively related to the number of sites at which it occurred ($R^2 = 0.62$, $n = 19$, $P < 0.0001$). *Aphaenogaster rudis*, *Nylanderia faisonenensis* and *Temnothorax longispinosus* exhibited the highest % hits and also occurred at the highest number of sites. *A. rudis* had the highest % hits on the ground (53%; that is, of the 500 resource tubes placed on the ground, 284 of them had at least one *A. rudis* forager in it), and *Lasius alienus* (22%) had the highest % hits on shrubs and *T. longispinosus* (39%) on trees. Species-specific per cent of hits on particular food resources was generally proportional to the total number of tubes and sites in which they were recorded. For all food resource types, *A. rudis* had the highest number of hits.

PATTERNS OF NICHE USE

The % hits varied significantly among the four resource types and three habitat templates (Table 1, Fig. 1; Table S2, Supporting information). Across habitat templates, carbohydrates appeared to be most limiting resource (mean % hits \pm SE = 61% \pm 3), followed by oils (39% \pm 3), amino acids (29% \pm 3) and NaCl (16% \pm 3). The % hits also varied among habitat templates (Table 1): more than half of the resource tubes on the ground were hit by foraging ant species (62% \pm 2), whereas only ~25% of resource tubes on shrubs (25% \pm 2) and trees (22% \pm 2) attracted foragers. However, the interaction between resource type and habitat templet was significant

Table 1. The effects of habitat templet, food resource and their interaction on the % hits

Source	d.f.	SS	F	P
Habitat templet	2	7.73	88.22	<0.0001
Resource type	3	6.44	49.02	<0.0001
Habitat templet × Resource type	6	1.58	6	<0.0001

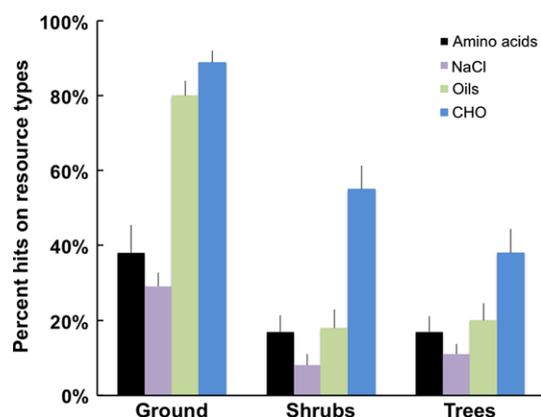


Fig. 1. The effects of food resources and habitat templet on recruitment by ants. Bars indicate, for each niche category, the per cent of tubes of a given category (\pm SE) with at least one ant individual.

(Table 1), suggesting that resource use or limitation in ant communities is not independent of habitat templet.

NICHE OVERLAP

At regional scales (i.e. among all sites), species overlapped more in their use of particular habitat templet × food resource combinations than expected by chance (Fig. 2a, Pianka's index observed = 0.37, mean Pianka's index random = 0.29, $P < 0.0001$). At local scales (i.e. within sites), however, standardized niche overlap indices did not differ significantly from the random expectation (Fig. 2b, mean SES = 0.23 ± 0.21 ; one-sample t -test, d.f. = 19, $P = 0.23$).

NICHE OVERLAP AND CO-OCCURRENCE

Species that co-occurred at many sites overlapped more in their use of particular niches than did species that rarely co-occurred (Fig. 3a, $r = 0.27$, $P = 0.02$). Overlap in habitat templets alone was not related to the degree of co-occurrence among sites ($r = 0.12$, $P = 0.23$). However, overlap in food resource was positively related to the degree of co-occurrence among sites ($r = 0.34$, $P = 0.008$).

NICHE OVERLAP AND PHYLOGENETIC DISTANCE

Overall, niche overlap was negatively related to the degree of phylogenetic relatedness (Fig. 3b, $r = -0.22$, $P = 0.02$). Overlap in the use of particular habitat templets alone

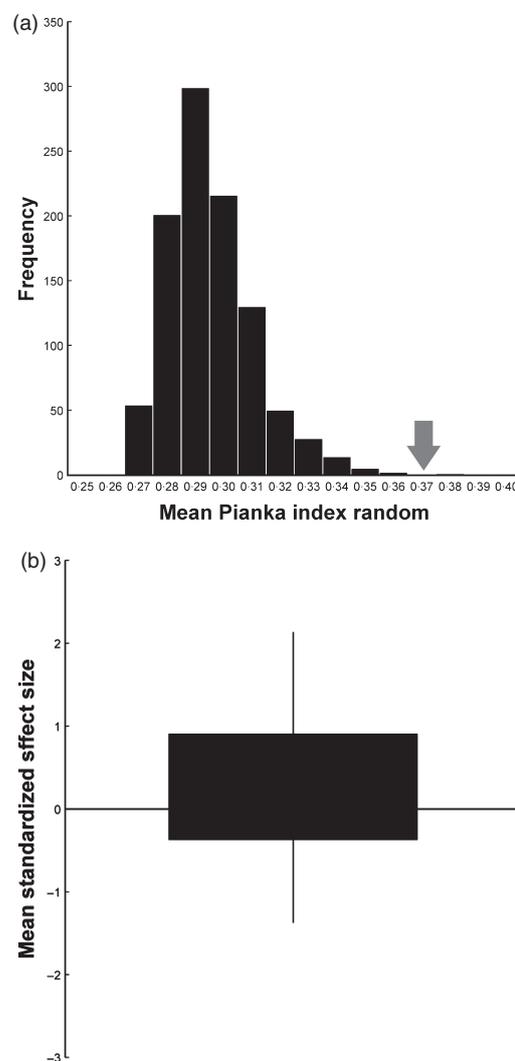


Fig. 2. Niche overlap at (a) regional and (b) local scales. The top panel shows the frequency distribution of random niche overlap values relative to the observed value for the regional assemblage. The observed value (0.37) is indicated with a grey arrow. The bottom panel shows the mean standardized effect size (SES) of local niche overlap across 20 sites. The boxplots show the 25th and 75th percentile of SES values. [Correction added on 14 Feb 2014 after first online publication: grey arrow added to part (a) and caption amended.]

was negatively related to the degree of phylogenetic relatedness ($r = -0.18$, $P = 0.04$), but overlap in food resource was not related ($r = -0.06$, $P = 0.28$).

PHYLOGENETIC SIGNAL IN THE USE OF NICHES

Using a rarefaction-based version of Blomberg's K (Davies *et al.* 2012), we tested for phylogenetic signal in the % hits for each niche category (Fig. S1, Supporting information). We found increasing phylogenetic signal in the use of habitat templets from ground (median $K = 28$) to shrub (median $K = 41$) and trees (median $K = 59$) (Fig. S3, Supporting information). For resources, phylogenetic signal was strongest for salt (median $K = 0.81$) and oil (median $K = 0.77$).

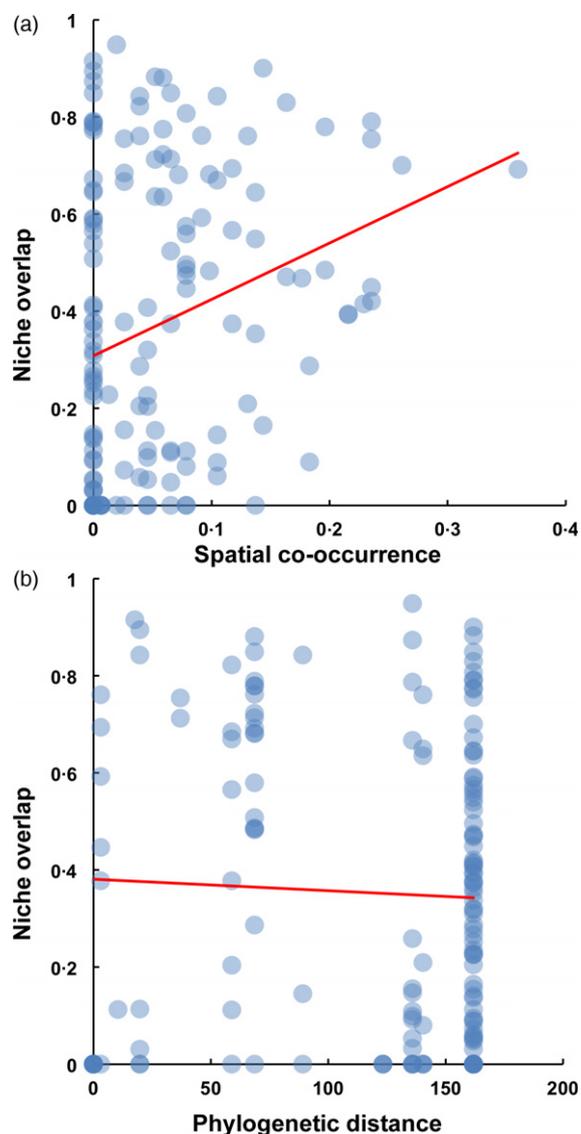


Fig. 3. Relationship between pairwise species niche overlap and (a) the degree of spatial co-occurrence and (b) phylogenetic distance at the regional scale.

Discussion

The most salient result of this study is that co-occurring ant species tend to use the same habitats and be limited by the same resources – that is, they occupy the same niches. As a result, niche filtering rather than niche partitioning appears to structure ant assemblages in temperate forests in the south-eastern United States. At first glance, this experimental result contradicts decades of research that has sought to explain the assembly of ant communities by searching for niches that must be partitioned (Culver 1974; Fellers 1987; Parr & Gibb 2010). In fact, numerous studies provide compelling evidence that niche partitioning occurs in some ant communities (Retana & Cerdá 2000; Albrecht & Gotelli 2001), with species partitioning niches both spatially and temporally (Albrecht & Gotelli 2001; Stuble *et al.* 2013), based on food type

(Sanders & Gordon 2003) or food size (Davidson 1977), or among habitat templates (Yanoviak & Kaspari 2000). More recent studies, however, have highlighted the lack of niche differences (Andersen 2008; Stuble *et al.* 2013) and the importance of environmental or niche filtering (Machac *et al.* 2011; Lessard *et al.* 2012) and biogeographic history (Lessard *et al.* 2012).

Most ecologists (and picnickers) are aware that many ant species forage on the ground and for sugar-based resources, which is what our experiment demonstrated. If recruitment to resources is an estimate of limitation (as suggested by Kaspari, Yanoviak & Dudley 2008), then our results suggest that carbohydrates limit ants in these temperate forests. Interestingly, however, resource use varied among habitat templates (i.e. there was a significant food resource \times habitat template interaction). CHO resources received the most hits across all habitat templates, and NaCl received the fewest. For reasons we are unable to explain, the % hits on oils dropped from $\sim 80\%$ on the ground to $<20\%$ on other habitat templates. Regardless of the specific details, this result of habitat-dependent responses to resources contrasts with two previous studies on resource use and habitat templates in ants. First, Yanoviak and Kaspari (2000) found that total ant activity in tropical forests was higher on protein baits than on carbohydrate baits, but the responses of ants to food resources did not vary between habitat templates (ground foraging vs. foraging in tree canopies, in their case). Secondly, based on patterns of visitations at salt baits, Kaspari, Yanoviak and Dudley (2008) argued that ants are more limited by salt (NaCl) than by other nutrients. The differences between the results from our experiment and these two previous experiments might arise because, at geographic scales, ants are not equally limited everywhere by the same set of nutrients. In fact, Kaspari, Yanoviak and Dudley (2008) demonstrated geographic variation in salt limitation that appears to be driven by proximity to the ocean. Our results suggest that ants in our system are only moderately limited by NaCl (i.e. relative to all other resources), even though our sites are more than 500 km from the ocean (the source of NaCl deposition). It could be the case that sodium deposition in the southern Appalachians is higher than expected given its distance from the ocean. Comparable experiments, replicated at numerous sites, could disentangle relative limitation of various resources (Kaspari, Yanoviak & Dudley 2008; Adler *et al.* 2011).

Ants in these forests apparently do not coexist within local assemblages (i.e. $\sim 50 \times 50$ m plots) by partitioning niches (Stuble *et al.* 2013). Instead, niches do not overlap any more or less than expected at local scales and niches overlap more than expected at regional scales. Scale-dependent differences in the importance of ecological processes are likely the norm rather than the exception (Ricklefs 1987; Levin 1992). Several studies suggest that environmental filtering plays a more important role regionally, whereas competitive exclusion and niche

partitioning predominate locally (Kembel & Hubbell 2006; Kraft, Valencia & Ackerly 2008). In ants, the predominance of ecological processes seems to vary with scale as well. Body-size distributions of ant species in the genus *Rhytidoponera* in Australia were evenly dispersed at small spatial scales, but the magnitude of overdispersion decreased at larger spatial scales (Nipperess & Beattie 2004). Similarly, body-size distributions of forest and bog ant assemblages in New England were random or aggregated at regional scales, but more evenly distributed in bog habitats at local scales (Gotelli & Ellison 2002). Sanders *et al.* (2007) found that co-occurrence patterns among ant species in the Siskiyou mountains were aggregated at regional scales but random at local scales. Together, these studies, and the results of our experiment reported here, indicate that the processes that shape ant communities depend on spatial scale and likely vary among ecosystems. That is, the forces that structure ant assemblages in deserts need not be the same as those operating in temperate forests (Schemske *et al.* 2009).

We examined the degree to which phylogenetic distances explained among-species differences in niche use. Most tests of phylogenetic signal are observational, but there are some exceptions. For example, Burns and Strauss (2011) were perhaps the first to experimentally demonstrate that closely related plant species are more similar and compete more intensively than distantly related species. Similarly, Violle *et al.* (2011) manipulated bacterial communities and found stronger density-dependent effects among closely related species than distantly related ones. Again in experimental bacterial communities, Peay, Belisle and Fukami (2011) documented stronger priority effects among closely related species as a result of greater overlap in food resource use. Here, we found that closely related ant species exhibited similar patterns in their use of niches, and in particular, habitat templates. This is not to say, however, that competition was necessarily more intense among closely related species of ants because they tended to use the same microhabitats. Nevertheless, the negative relationship between phylogenetic distance and habitat niche overlap suggests that habitat templates, or the life-history traits associated with the use of particular habitat templates, might be evolutionary conserved in ants (Losos *et al.* 2003; Warren, Glor & Turelli 2008).

A growing number of studies show phylogenetic signal of habitats, and more generally of abiotic niches, might influence the assembly of communities (Cavender-Bares, Keen & Miles 2006; Wiens *et al.* 2006). In ants, previous studies have documented significant phylogenetic signal in the climatic niches and composition of local assemblages (Machac *et al.* 2011; Lessard *et al.* 2012). In our study, we found increasing strength of phylogenetic signal in the use of habitat templates from ground to shrubs and trees (Fig. S1, Supporting information). Consistent with our results, it has been suggested that the ancestral habitat of ants is in the soil and on the ground and that the

evolution of life on plants has been challenging and recent (Ward 2010). We further found stronger phylogenetic signal in the use of salt and oil than that of sugar and amino acid.

Overall, we found more compelling evidence for a phylogenetic signal in habitat niches than in food resource niches. It may be generally true that those traits governing the distribution of species among assemblages (a.k.a., the β niche) tend to be more conserved than those associated with resource use and coexistence within assemblages (a.k.a., α niche) (Silvertown *et al.* 2006a,b; Emerson & Gillespie 2008; but see Rabosky *et al.* 2011). Losos *et al.* (2003) argued that niche conservatism could be overcome when the intensity of competition is high and when species have a long co-evolutionary history of ecological interactions. In such a scenario, some of the niche components are evolutionary conserved (e.g. microhabitats), and divergence in other niche components (e.g. the type of food resource) can facilitate coexistence among sympatric species. Here, we found evidence that, although habitat niche similarity was correlated with phylogenetic distance, food resource niches were not. Therefore, our results did not indicate that divergence in the use of food resources has evolved as a means to facilitate coexistence. In fact, species that used similar food resources tended to co-occur more often than did species that used different resources, suggesting that resource filtering, rather than partitioning, shapes the composition of ant assemblages (Kaspary *et al.* 2012). It might be the case that the availability of particular food resources, or a mix of food resources, has a strong influence on which species are able to maintain populations at any given site.

CAVEATS

We provide evidence that membership in local communities depends on niche filtering rather than niche partitioning, and this filtering resulted from conservatism in habitat niches in evolutionary time and limitations in the availability of food resources in ecological time. However, we realize that the interpretations of our results rely on the assumptions that (i) our experimental approach (and our use of artificial resources) accurately characterizes the niches of all the species in a local community and (ii) the quantification of phylogenetic niche signal is not biased by the lack of resolution in our phylogeny. Several factors could affect the frequency with which a species is detected in a particular niche category. Not all of the ant species that occur at any given site recruit to 50-mL Falcon tubes filled with liquid resources; some species are specialized predators (e.g. *Strumigenys* spp.) whereas others are fungus growers (e.g. *Trachymyrmex*). It is possible, for example, that behaviourally dominant species might displace subordinate species from food resources during the course of the experiment. This could explain the relatively high use of NaCl by *Camponotus pennsylvanicus* and *Prenolepis imparis* (data not shown), both of which are behaviourally

dominant in this system (Lessard, Dunn & Sanders 2009a; Stuble *et al.* 2013). However, the high number of tubes deployed in our study and especially the number of tubes that went unoccupied indicates that it should be possible for subordinate species (which exhibit higher frequency of occurrence) to discover tubes that are unused by dominant species. The number of unoccupied tubes also suggests that we are estimating the fundamental niches (i.e. the niche of the species in the absence of interactions) rather than the realized niches (i.e. the niche of these species, in the presence of competitors, at least for these two resource axes). The genus-level resolution of our phylogeny may reduce our ability to quantify accurately phylogenetic signal. Davies *et al.* (2012) showed that unresolved phylogenies could inflate estimates of phylogenetic signal such as the one we used in the current study (i.e. Blomberg's K). We therefore used a rarefaction-based approach developed by Davies *et al.* (2012) that yields estimation of K that compares favourably with K values derived from complete phylogenies.

Summary

The signature of evolutionary history and broad-scale climatic gradients can be detected even at very small spatial grains (Ricklefs 1987; Pärtel, Laanisto & Zobel 2007; Harrison & Cornell 2008; Lessard *et al.* 2012). Processes operating at broad temporal and spatial scales thus interact with those operating at local scales and occurring in ecological time to shape community structure. Taken together, our results suggest that both evolutionary conservatism of habitat niches and ecological filtering mediated by food resource availability jointly determine community composition. A growing body of evidence suggests that niche differences might not be necessary for species to coexist in local assemblages. Much uncertainty persists, however, because the predominant ecological processes shaping community structure often vary from place to place (Lawton 1999), or along environmental gradients (Chase 2007; Kikvidze, Suzuki & Brooker 2011). The lack of geographic replication in local studies hinders the development of synthetic theories that account for the role of both evolutionary and ecological processes. Future studies should focus on improving our knowledge of species autecology and function, integrating phylogenetic analyses with experiments (Weber & Agrawal 2012) and replicating local studies across biogeographic regions that differ in evolutionary history. Such integration might ultimately reveal the forces that structure ecological communities, and why those forces vary (or do not) from place to place on the planet.

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Supporting Information

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

Table S1. Occurrence (number of hits) of ant species in each habitat templet by food resource niche categories.

Table S2. Results from Tukey HSD tests on mean differences in % hits among types of food resources and by habitat templet.

Fig. S1. Test of phylogenetic signal (i.e., phylogenetic independent contrast) on the % hits on particular habitat templets (a) and for food resources (b).