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Reports

Invasive ants alter the phylogenetic structure of ant communities

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Abstract. Invasive species displace native species and potentially alter the structure and function of ecological communities. In this study, we compared the generic composition of intact and invaded ant communities from 12 published studies and found that invasive ant species alter the phylogenetic structure of native ant communities. Intact ant communities were phylogenetically evenly dispersed, suggesting that competition structures communities. However, in the presence of an invasive ant species, these same communities were phylogenetically clustered. Phylogenetic clustering in invaded communities suggests that invasive species may act as strong environmental filters and prune the phylogenetic tree of native species in a nonrandom manner, such that only a few closely related taxa can persist in the face of a biological invasion. Taxa that were displaced by invasive ant species were evenly dispersed in the phylogeny, suggesting that diversity losses from invasive ant species are not clustered in particular lineages. Collectively, these results suggest that there is strong phylogenetic structuring in intact native ant communities, but the spread of invasive species disassembles those communities above and beyond the effect of simple reductions in diversity.

Key words: *biological invasions; community phylogenetics; community structure; Formicidae.*

Introduction

Recent studies have taken advantage of the increasing availability of phylogenetic data to infer assembly processes from the taxonomic composition of local communities (e.g., Slingsby and Verboom 2006, Kraft et al. 2007, Swenson et al. 2007). Because ecological niches tend to be phylogenetically conserved (Swenson et al. 2006, Johnson and Stinchcombe 2007), examining the extent to which co-occurring species are related can provide insights into the ecological processes shaping communities (but see Losos 2008). Phylogenetic clustering (i.e., coexisting species are more closely related than expected by chance) can arise if habitats filter species. This results in a set of closely related species whose traits allow them to persist in a particular habitat (Cavender-Bares et al. 2004). Alternatively, phylogenetic evenness (i.e., coexisting species are more distantly related than expected by chance) might arise if competitive exclusion reduces co-occurrence among closely related species (Slingsby and Verboom 2006). If community structure arises by neutral processes, or if the opposing forces of habitat filtering and interspecific competition counteract one another, then phylogenetic structure may appear random (Kraft et al. 2007).

The spread of invasive species can also offer insights into the mechanisms controlling community assembly. In a recent study, Strauss et al. (2006) used community phylogenetics in the context of biological invasions to investigate susceptibility of native plant communities to invasion by introduced grass species. They found that introduced grasses were more likely to become established if the native community lacked taxa closely related to the introduced species.

Invasive ant species provide some of the best evidence that competitively dominant species can affect biodiversity and alter species composition (Holway et al. 2002), and alter patterns of species co-occurrence (Gotelli and Arnett 2000, Sanders et al. 2003). In this study, we describe the effects of invasive ant species on the phylogenetic structure of native ant communities at both local and regional scales to infer the processes underlying community assembly.

We examined the phylogenetic structure of intact and invaded ant communities through a meta-analysis of 12 published studies for which phylogenetic information for the taxa in the intact and invaded ant communities is available. We asked three questions: (1) Do intact ant communities exhibit nonrandom phylogenetic structure? (2) Does phylogenetic structure change in the presence of an invasive species? (3) Are species that become locally extinct in the presence of an invasive ant species a phylogenetically nonrandom subset of the intact community?

Methods

We compiled data on the composition of ant communities by searching Web of Science and Google Scholar using the key words ants, invasive, invasion, community, richness, diversity, and structure on 30 November 2007. From this search we selected studies that (1) explicitly compared invaded and un-invaded

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(i.e., "intact") communities, and (2) used standardized, quantitative sampling methods (Longino and Colwell 1997) to quantify ant community structure in both the invaded and intact sites. Only 12 studies met those criteria (Appendix A).

Invaded sites were those in which the invasive ant species was at least twice as abundant as in intact sites, and intact sites were those in which the invasive species was either absent or very uncommon relative to the invaded sites. Locally extinct taxa were defined as those species that were recorded in intact sites but were absent from the invaded sites. However, the degree to which sampled communities are accurate estimates of actual community composition depends on sampling efficiency and techniques (Longino and Colwell 1997). In our study, the absence of a species in a sample suggests that it is either absent from the sampled community or not abundant enough to be detected in it (e.g., Morrison 2002).

We further categorized these 12 studies into regional-scale studies (Ward 1987, Porter and Savignano 1990, Human and Gordon 1997, Holway 1998, Suarez et al. 1998, Gotelli and Arnett 2000, Sanders et al. 2003, Ipser et al. 2004, King and Tschinkel 2006, Wetterer et al. 2006, Abbott et al. 2007, Garnas et al. 2007) and local-scale studies (Ward 1987, Suarez et al. 1998, Gotelli and Arnett 2000, Sanders et al. 2003, Ipser et al. 2004, Wetterer et al. 2006). Regional-scale studies were those in which the author(s) provided a single list of species collected from some number of invaded sites and a single list of species from some number of intact sites. A region varied in size from 32 ha (Porter and Savignano 1990) to a 2000-km transect that spanned several eastern U.S. states (Gotelli and Arnett 2000). In contrast, local-scale studies were those studies in which the author(s) provided lists of ant species from replicated samples of the invaded and intact communities. In these local-scale studies, the sampling area ranged from 50 to 200 m^2. We pooled intact and invaded sites separately in each of the six local-scale studies so that we could examine the impacts of invasive ants on phylogenetic structure at regional scales for these studies as well. We also used these 12 pooled data sets to determine which taxa were displaced in each study. Because not all studies had locally extinct taxa, we used only seven data sets to form locally extinct taxa subsets for the community phylogenetic analyses.

Testing for phylogenetic structure

We examined phylogenetic structure of ant communities at the genus level using the phylogeny proposed by Brady et al. (2006; see Appendix B). Unfortunately, a robust species-level phylogeny of the ants does not yet exist. For the analyses here, that means that for an entire genus to be displaced, all of the species in this genus would have to be displaced. Therefore, our metric of the effect of invasive species on the phylogenetic structure is conservative. We note that the only previous study that examined changes in community phylogenetic structure as a consequence of invasive species (Strauss et al. 2006) employed a similar strategy of using a genus-level phylogeny because a species-level phylogeny was not available. We explored the consequences of including species as terminal taxa by creating trees where members of the same genus were modeled as terminal and basal polytomies (see Appendix B for details; results listed in Appendix C). However, analyses of tree topologies that included these unrealistic extremes yielded phylogenetic patterns that were uninformative. Hereafter we present the results from only genus-level analyses. Fig. 1 illustrates an example of the phylogenetic patterns for California ant communities in the presence and absence of the invasive Argentine ant *Linepithema humile* (Ward 1987).

We estimated the phylogenetic structure of each community from the 12 studies using two indices: mean phylogenetic distance (MPD) and mean nearest neighbor distance (MNND; Webb et al. 2002). MPD estimates the average phylogenetic relatedness between all possible pairs of taxa in a local community. MNND estimates the mean phylogenetic relatedness between each taxon in a community and its nearest relative (see Appendix D for further details on null community construction).

We then calculated measures of standardized effect sizes of each estimate of phylogenetic structure to facilitate comparisons among studies. The net related index (NRI) estimates the standardized effect size for MPD values, and the nearest taxon index (NTI) estimates standardized effect size for MNND values (Webb et al. 2002). These two standardized indices describe the difference between average phylogenetic distances in the observed and randomly generated null communities, standardized by the standard deviation of phylogenetic distances in the null communities (see Webb et al. 2008 and Appendix B for details). We tested whether the average NRI and NTI values in invaded and intact sites differed from one another using paired t tests and whether either differed from zero using one-sample t tests. In all analyses and comparisons, the invasive species is not included in the phylogeny.

Testing for differences in species and generic richness

We also examined whether ant species richness and generic richness differed between intact and invaded communities. We estimated local species richness (species density) for intact and invaded communities by averaging the number of species recorded across sites in each study and regional species richness as the total number of species recorded in all of the intact or invaded sites. We also estimated the relative proportion of displaced taxa by subtracting the number of taxa recorded in invaded sites from the number recorded in intact sites and dividing that difference by the number of taxa recorded in intact sites. We tested for differences in the absolute number and relative proportion of native species and

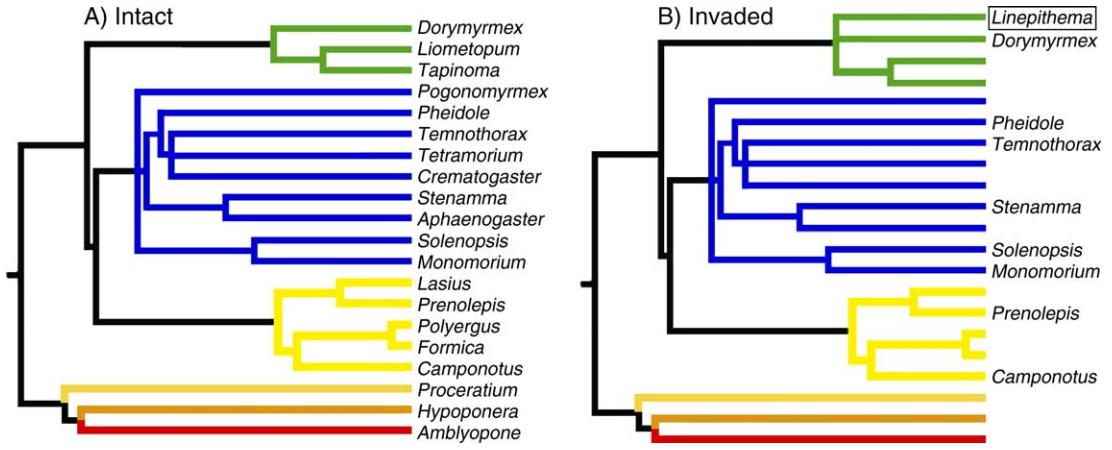

FIG. 1. Example of regional-scale phylogenetic structure of intact California ant communities vs. those invaded by the Argentine ant *Linepithema humile* (Ward 1987). (A) Intact communities are phylogenetically evenly dispersed; (B) invaded communities are phylogenetically clustered. Colored branches indicate different ant subfamilies: green, Dolichoderinae; blue, Myrmecinae; light yellow, Formicinae; dark yellow, Proceratiinae; orange, Ponerinae; red, Amblyoponinae. The phylogenetic position of the invader *Linepithema* is indicated by the black rectangle.

genera in intact and invaded sites, at both local and regional scales, using paired *t* tests and one-sample *t* tests.

Testing for differences in phylogenetic diversity

We assessed whether there were differences in phylogenetic diversity between intact and invaded sites using Faith's index in PHYLOCOM (Webb et al. 2008). We tested that phylogenetic diversity was higher in intact than invaded sites using paired *t* tests for the regional-scale studies and Wilcoxon tests for local-scale studies.

RESULTS

Regional-scale studies

At the regional scale, phylogenetic structure of intact ant communities differed significantly from random. Intact ant communities tended to be phylogenetically evenly dispersed (NRI = −0.41, $P = 0.01$; NTI = −0.06, $P = 0.40$; Fig. 2A, B; Appendix E). In contrast, in the presence of invasive species the phylogenetic structure of ant communities tended to be clustered (NRI = 0.78, $P = 0.02$; NTI = 0.59, $P = 0.04$; Fig. 2A, B; Appendix E). Finally, ant genera that were displaced showed a pattern opposite of the pattern represented by the species that persisted: they were significantly evenly dispersed in the phylogeny (NRI = −0.92, $P < 0.003$; NTI = −0.68, $P = 0.03$; Fig. 3).

The phylogenetic structure of paired invaded and intact sites differed from one another (NRI, paired $t = 1.95$, $n = 12$ studies, $P = 0.04$; NTI, paired $t = 2.09$, $n = 12$, $P = 0.03$). Although at regional scales the mean number of species in intact and invaded communities differed (intact, 26.58 ± 5.08 species [mean ± SE]; invaded, 17.67 ± 4.93 species; paired $t = -5.72$, $n = 12$, $P < 0.0001$), the number of genera did not (intact, 12.5 ± 1.62 genera; invaded, 10.67 ± 1.75 genera; paired $t = -1.08$, $n = 12$, $P = 0.15$). Similarly, the proportional

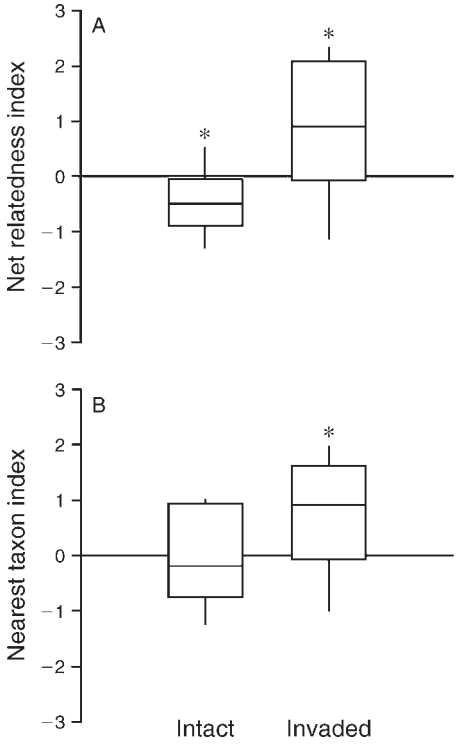

FIG. 2. Phylogenetic structure of intact and invaded ant communities pooled for 12 studies listed in Appendix E. Boxplots showing (A) NRI and (B) NTI values. The line at the center of each box shows the median. The boundary of the box closest to zero indicates the 25th percentile, and the boundary of the box farthest from zero indicates the 75th percentile. Whiskers above and below the box indicate the 90th and 10th percentiles. Positive NRI and NTI values indicate phylogenetic clustering, whereas negative values indicate phylogenetic evenness. Asterisks indicate significant departure from the null expectation of no phylogenetic structure ($P \leq 0.05$).

difference in the number of species was greater than zero (one-sample $t = -1.76$, $n = 12$, $P < 0.0001$), but the proportional difference in the number of genera was not (one-sample $t = -0.07$, $n = 12$, $P = 0.31$).

At the genus level, there was no difference in phylogenetic diversity between intact and invaded sites (intact $= 0.135 \pm 0.013$, invaded $= 0.116 \pm 0.016$; paired $t = -1.23$; $n = 12$; $P = 0.12$). At the species level, there was also no difference in phylogenetic diversity between intact and invaded sites (intact $= 0.131 \pm 0.015$, invaded $= 0.116 \pm 0.019$; paired $t = -0.94$; $n = 12$; $P = 0.18$).

Local-scale studies

The phylogenetic structure of local intact communities was idiosyncratic. Phylogenetic structure was clustered in one study, evenly dispersed in three, and random in two (Appendix F). Further, neither the number of species (paired $t = 0.55$, $n = 12$, $P = 0.30$) nor the number of genera (paired $t = -0.44$, $n = 12$, $P = 0.34$) differed between intact and invaded communities at local scales. Phylogenetic diversity was higher in intact communities in two studies, higher in invaded communities in one study, and not different in three.

Discussion

We found that the phylogenetic structure of intact ant communities at the regional scale differed significantly from random: coexisting genera were, on average, more distantly related than expected from a random assignment of taxa to communities (Fig. 1). Although intact communities were phylogenetically evenly dispersed as estimated by NRI, their structure was random as estimated by NTI. Because NRI is sensitive to deeper clade-level patterns of phylogenetic structure, even dispersion as measured by the NRI index indicates that genera from a few disparate lineages co-occur in intact communities.

Under the assumptions of niche conservatism, an evenly dispersed pattern of phylogenetic structure suggests that competition shapes the structure of uninvaded communities by preventing species that are closely related from coexisting with one another (Kraft et al. 2007). An alternative explanation for even phylogenetic dispersion is that it may reflect the effects of habitat filtering (Cavender-Bares et al. 2004) if important ecological traits reflect ecological convergence, rather than niche conservatism (Kraft et al. 2007). Additionally, facilitation might cause communities to appear phylogenetically evenly dispersed (Valiente-Banuet and Verdu 2007). However, both the habitat filtering and the facilitation mechanisms seem implausible for ant assemblages. Habitat filtering is unlikely to be operating here because most genera recorded in these studies have large geographic ranges and are not strong habitat specialists. For example, most of the genera found in Sanders et al.'s (2003) study of the impacts of *Linepithema humile* on native ants in California were also represented in Gotelli and Arnett's (2000) study of impacts of *Solenopsis invicta* in the eastern United States. Facilitative interactions between ant species have not been documented in the communities analyzed here, but they have been documented in desert ant assemblages (Davidson et al. 1984). Clearly, the role of positive, indirect, and facilitative interactions in shaping ant assemblages deserves more attention.

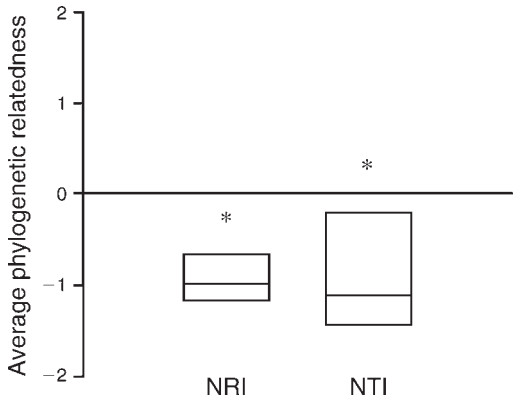

Fig. 3. Mean phylogenetic relatedness of extinct species subset for seven regional-scale studies. Phylogenetic relatedness is estimated using mean NRI and NTI values. Asterisks indicate means that are significantly different from zero.

In the presence of invasive species the phylogenetic structure of ant communities tended to be clustered. This is consistent with the prediction that invasive species prune the phylogenetic tree of native species in a nonrandom manner, such that only a few closely related taxa can subsist in the face of biological invasion. Another possibility to account for phylogenetic clustering in invaded communities is that some other factor, such as disturbance, affected both the phylogenetic structure of the invaded community and their susceptibility to invasion (King and Tschinkel 2006). However, at least for several studies in our database, both the invaded and intact sites were relatively undisturbed and yet the structure of the native ant community still differed between intact and invaded sites. Although disturbance affects native ant communities and can increase the probability that invasive species become established, one study in our analysis (Sanders et al. 2003), and one recent study by Tillberg et al. (2007), used pre- and post-invasion data in sites that had not been disturbed, and still found strong impacts of invasive species on native ant communities.

On average, the phylogenetic structure of intact and invaded ant communities differed even though genus-level richness did not. The lack of a difference in genus-level richness indicates that the differences in the phylogenetic structure between invaded and intact sites arose from shifts in community composition rather than from simple reductions in the number of genera in invaded communities. Similarly, Sanders et al. (2003) found differences in the structure of intact ant communities and invaded communities, even though the

number of species did not differ between invaded and intact communities. Although ant invasions did not alter the number of genera present, other studies have documented a decline in native ant species richness in the presence of invasive species (Holway et al. 2002). However, even in those studies, there is evidence that changes in species composition cannot be accounted for simply by species losses (Gotelli and Arnett 2000, Sanders et al. 2003).

The relative importance of habitat filtering and competition on community assembly can vary with spatial scale (Kembel and Hubbell 2006). Here, although the phylogenetic structure of intact ant communities at the regional scale was evenly dispersed, results at the local scale were inconsistent, with examples of even, random, and clustered patterns. Our findings are similar to other studies that have documented differences in phylogenetic structure at different spatial scales (e.g., Kembel and Hubbell 2006, Swenson et al. 2006). Why might the phylogenetic structure of ant communities be scale dependent? Dayan and Simberloff (1994) argued that long-term responses of species to interspecific competition are more likely to be detected at regional scales than at local scales, perhaps because competing species might avoid competition at local scales by partitioning time, space, and resources. Another study of ant community structure has also detected nonrandom community structure at regional, but not local, spatial scales (Gotelli and Ellison 2002).

The ant genera that were displaced were significantly evenly dispersed in the phylogeny. Our results contrast with results from previous studies on plants in which extinct taxa were more related than expected by chance (Willis et al. 2008). If displaced taxa were evenly dispersed in the phylogeny, then how could it be that the remaining communities were phylogenetically clustered? One possibility is that all subfamilies have an equal probability of losing at least one genus. But, because some subfamilies have perhaps only one genus, displacement of that genus strongly affects the topology of the remaining tree (see Fig. 1). As an example, when a species in the genus *Neivamyrmex* (usually the only representative of the Ecitoninae) is displaced, then there are likely to be drastic changes in phylogenetic structure.

If the phylogenetic structure of the displaced taxa were clustered, it would be consistent with the hypothesis that displaced taxa share traits that make them more vulnerable to displacement following the spread of an introduced species. Two possibilities are that invasive species displace specialists (e.g., seed dispersers, Suarez et al. 1998; or specialist predators) or primitive lineages (Ward 1987), perhaps because these groups are locally rare even in intact communities. But our results suggest that identifying which species will be displaced by invasive species may be challenging. In addition, and in contrast to Strauss et al.'s (2006) analysis of invasive plants, we found no association between the position of the invader in the phylogeny and the phylogenetic structure of the community it invades (J.-P. Lessard, *unpublished results*). Nevertheless, the phylogenetic reorganization of invaded ant communities suggests that invasive ants act as strong structuring agents and can affect community membership. Documenting which morphological, behavioral, and/or ecological traits are conserved in the ant phylogeny and which of those traits allow resident species to persist following the spread of an invader offers exciting venues for future research.

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APPENDIX A

Literature sources for data on community composition of invaded and intact ant assemblages (*Ecological Archives* E090-186-A1).

APPENDIX B

Constructing the phylogeny (*Ecological Archives* E090-186-A2).

APPENDIX C

Phylogenetic structure results using polytomies (*Ecological Archives* E090-186-A3).

APPENDIX D

Constructing the null communities (*Ecological Archives* E090-186-A4).

APPENDIX E

Regional-scale results (*Ecological Archives* E090-186-A5).

APPENDIX F

Local-scale results (*Ecological Archives* E090-186-A6).