

## Assembly rules for New England ant assemblages

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Community assembly rules specify patterns of species co-occurrence and morphology dictated by interspecific competition. We collected data on the occurrence of ground-foraging ant species in 22 ombrotrophic bogs and adjacent forest plots of New England to test two general assembly rules: reduced co-occurrence of species among communities, and even spacing of body sizes of species within communities. We used null models to generate random communities unstructured by competition and evaluated patterns at regional and local spatial scales. At the regional scale, species co-occurrence in forests, but not bogs, was less than expected by chance, whereas, at the local scale, co-occurrence in both habitats was not different from random. At the regional scale, spacing of body size distributions was random (in bogs) or aggregated (in forests). At the local scale, body size patterns were weakly segregated in bogs, but random or weakly aggregated in forests. In bogs, size ratio constancy was accompanied by greater generic diversity than expected. Although assembly rules were originally developed for vertebrate communities, they successfully explained some patterns in New England ant assemblages. However, the patterns were contingent on spatial scale, and were distinctly different for bog and forest communities, despite their close proximity and the presence of many shared species in both assemblages. The harsh physical conditions of bogs may act as a habitat filter that alters community assembly rules.

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1990, Holway 1998), and the existence of chemical warfare (Andersen et al. 1991). We sampled ant communities across north-central New England (regional scale) and used data collected within small sampling grids at each site to analyze species co-existence at the local scale. At both spatial scales, we used a battery of null model algorithms to test for patterns of non-random co-occurrence and body size overlap.

## Materials and methods

### Ant sampling and body size measurements

We censused ants in 22 high-grade, undisturbed bogs and their surrounding forests in northern New England (Vermont, Massachusetts, and Connecticut). Sites were spread across the states and spanned three degrees of latitude (42–45° N). At each site, we established two 5 × 5 grids of 25 pitfall traps spaced 2 m apart (64 m<sup>2</sup>). One grid was located in the center of the bog, and one in the adjacent forest, < 100 m away. Each pitfall trap consisted of a 95 mm diameter plastic cup, filled with 20 mm of dilute soapy water. A similar trap design has proven effective in other regional surveys of ant faunas (Andersen 1997, Gotelli and Arnett 2000). Traps were buried so that the upper lip of each trap was flush with the surface of the substrate, and left in place for 48 hours during dry weather. Trap contents were fixed in the field in 95% EtOH. At each site, two complete ant surveys were conducted, separated by approximately 42 days. The same grids were re-sampled in the second survey. We started sampling on 2 June 1999 and finished on 29 August 1999. Pitfall trapping was supplemented with baiting, leaf-litter surveys, and hand collecting. Full details of sampling procedures are given in Gotelli and Ellison (2002).

We used Weber's length (Brown 1953), the distance from the anterodorsal margin of the pronotum to the posteroventral margin of the propodeum (Longino 1997), as a simple measure of ant body size. For every species collected within a habitat at a site, we measured the index on six randomly selected workers, or the maximum number that were collected, whichever number was smaller. Queens and morphologically aberrant individuals were not measured. We did not distinguish between major and minor workers in the genus *Crematogaster*. We calculated a mean Weber's length for each species at a site, and then averaged these values to create a single index of body size for each species collected within a habitat. Our null model analyses did not incorporate body size variation within species (Losos 1990), which was small compared to variation among species and genera (e.g. *Crematogaster* vs *Lasius*).

### Regional and local scales of analysis

We analyzed species co-occurrence and body size overlap at two distinct spatial scales: regional and local. At the regional scale, co-occurrence data were organized as a presence-absence matrix for each habitat. Each row of the matrix was a different species, each column was a different site ( $n = 22$ ), and the entries were the presence or absence of a species at a site. Data from all collection methods (pitfall traps, baits, leaf-litter samples, hand collection) were combined to construct this presence-absence matrix.

At the local scale, we constructed presence-absence matrices for the pitfall grid data only. Each row of the matrix was a different species, and each column was a different pitfall trap ( $n = 25$ ) within the grid. Thus, 44 presence-absence matrices were constructed for analysis at the local scale, 22 from bogs and 22 from forests. We analyzed the early and the late-season grid data separately. A few grids could not be analyzed because fewer than two species were collected.

To analyze body size overlap at the regional scale, we used the list of all species collected from bog or forest habitats, combining data from all sites, times, and sampling methods. At the local scale, we used the list of species collected from a particular site (all trapping method and times combined) and compared body size distributions to those expected from random colonization from the regional source pool. Again, some sites could not be analyzed because at least three species are necessary to test for constancy in body size ratios.

We used simple indices to describe the pattern of co-occurrence and species body size overlap. These were trap(to)-544.5(datices)-543.-447oEalartrap(to) datnu-590.5(datasse]TJ

munity contains the same number of species as the original community (fixed column total), and each species occurs in the same frequency as in the original community (fixed row total; Connor and Simberloff 1979). This algorithm has good statistical properties (low frequency of Type I and Type II errors) when tested against random and structured matrices (Gotelli 2000). We created the random matrices by a swapping algorithm, in which the original matrix is shuffled through repeated swapping of random submatrices (Stone and Roberts 1990, Manly 1995). Similar results were obtained with an unbiased version of Sanderson et al's. (1998) knight's tour algorithm, in which an empty matrix is filled randomly one cell at a time (Gotelli and Entsminger 2001b).

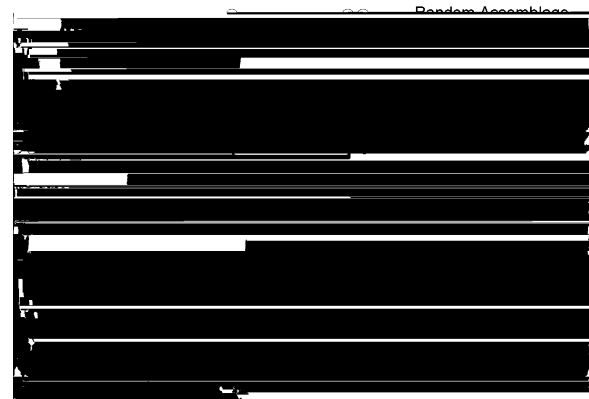
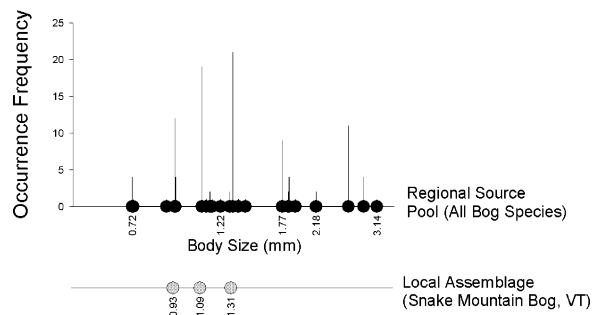
*F*

In this null model, only the row sums are fixed, and the columns (= sites) are treated as equiprobable. Thus, each species occurrences are randomly re-shuffled within each row of the matrix. This null model treats all of the sites as equally suitable for all species (Haukisalmi and Henttonen 1998), and was applied only at the local scale of analysis.

In this null model, the column totals are fixed, so that each site in the null community contains the same number of species as each site in the original community. However, the occurrence frequency of each species is proportional to the total abundance in pitfall traps summed across all sites within a habitat and all sampling periods. For the small number of species that did not occur in pitfall traps, we assigned an abundance weight of 1, corresponding to a rare species that was represented by only 1 individual in a pitfall trap.

**Body size overlap analysis**

To test the hypothesis that body size ratios show constant spacing, we first plotted body sizes on a log<sub>10</sub> scale, and then calculated the difference between adjacent species. We calculated the variance in these segment lengths ( $\sigma_{s_i}^2$ ) as an index of constancy in body size



strains possible body sizes of species in the null assemblage to those represented by species in the region as a whole.

*O*  
 In this null model, species are also drawn randomly from the regional species list, but the relative probability that a species is drawn is proportional to the number of sites in which it occurred.

*A*  
 In this null model, species are also drawn randomly from the regional species list, but the relative probability that a species is drawn is proportional to its total abundance from the pitfall trap collections within a habitat, summed across all sites and sampling periods. Species that were not represented in pitfall traps were assigned an abundance of 1 for the purposes of calculating weights.

### Generic diversity

We used a rarefaction analysis (Simberloff 1970, Hurlbert 1971) to test the hypothesis that generic diversity within local communities is higher than expected by chance. Because genera differ significantly from one another in body size, such a pattern of increased generic diversity might be associated with non-random spacing of body sizes. We drew species randomly and equiprobably from each regional source pool to estimate the expected number of genera represented in local communities (Gotelli and Colwell 2001). For each local community, we made 100 random draws of an equivalent number of species, and then calculated the average as the expected number of genera in a random assemblage. Within bogs and within forests, we then tabulated the number of assemblages for which the observed generic diversity was greater than expected, and assessed the distribution of values with a binomial probability test.

## Results

### Community composition

In total, just over 10 000 individual ants were collected,

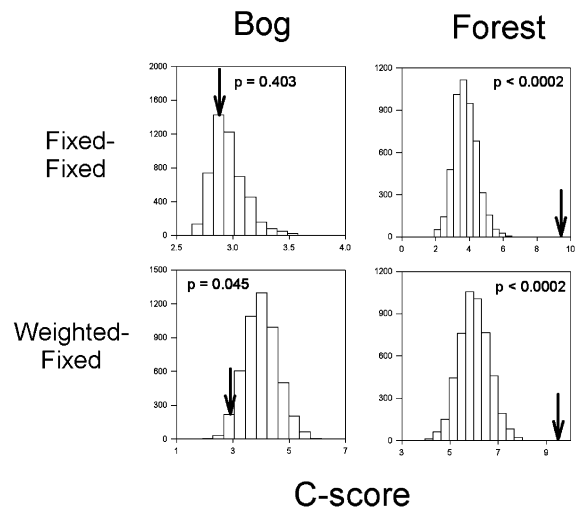


Table 1. Meta-analysis of effect sizes for co-occurrence patterns at the local scale. "Lower tail" and "Upper tail"

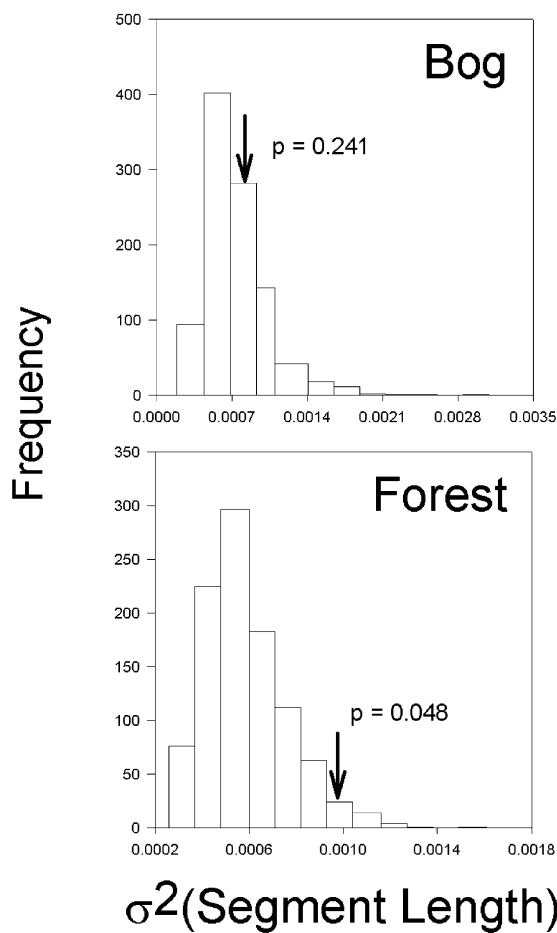


Fig. 3. Body size overlap patterns at the regional scale of analysis. The histograms give the frequencies of simulated variance in segment length ( $\sigma_{si}^2$ ), a measure of the constancy of size ratios of adjacent species (Fig. 1). For both the habitats, the null model is one in which species body sizes are distributed randomly and uniformly (log scale) between the endpoints of the largest and smallest observed species in the assemblage. Arrows indicate observed variances, with associated tail probabilities. Communities structured by interspecific competition should exhibit unusually small variances, corresponding to relatively constant body size ratios and an even spacing of species body sizes on a logarithmic scale.

then subtle “habitat checkerboards” may cause species segregation that is not necessarily related to competition (Gotelli and McCabe 2002). Bog species richness was less predictable among sites (Gotelli and Ellison 2002), and there was little evidence at the regional scale of non-random co-occurrence of bog species.

At the local scale, there was no evidence for reduced co-occurrence in either habitat, no matter which null model was used. This result is similar to patterns documented for coral reef fishes, in which communities appeared to be organized by competition at large spatial scales (Anderson et al. 1981; but see Bellwood and Hughes 2001), but appeared random when analyzed at small spatial scales (Sale and Williams 1982, Sale 1984, Findley and Findley 1985). These results are surprising for ants because there is substantial evidence for competitive structure at small spatial scales (Levings and Traniello 1981, Fellers 1987, Rytı and Case 1992, Punttila et al. 1996). Our results could possibly reflect the kind of data that were used (pitfall trap catches) rather than the spatial scale per se. Pitfall catches may have revealed the spatial pattern of randomly foraging workers, whereas the spatial distribution of nest entrances (Rytı and Case 1984, Cushman et al. 1988) or the occurrence of species at food resources (Holway 1998, Albrecht and Gotelli 2000) might have reflected stronger spatial partitioning. However, most baits remained empty during the sampling period (N.J. Gotelli and A.M. Ellison, unpubl. data), suggesting that food resources were not limiting at a local scale. Moreover, pitfall traps captured over 75% of all species recorded, and we believe it is unlikely the results would have changed with other sampling methods, such as baits.

Only a few other studies have used null model analyses to investigate ant community structure. Simberloff (1983) used an equiprobable regional species pool and re-analyzed the harvester ant data of Davidson (1977); he found no evidence for the hypothesis that similar species could not co-exist unless they differed in foraging mode (group vs individual). In ant assemblages of prairie grasslands, niche overlap in bait utilization was

Table 2. Meta-analysis of effect sizes for body size overlap patterns at the local scale. Data organized as in Table 1. Communities with constant body size ratios should frequently reject the null hypothesis in the lower tail, and the meta-analysis pattern would be an effect size significantly less than 0.0.

Model	SD of	t	p	Bonferonni
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Table 3. Expected and observed ant generic diversity in bogs and forests. For each local assemblage ( $n = 22$ ), the expected and observed number of genera based on random draws of species from the regional source pool. Entries are the number of local assemblages for which the observed number of genera was greater than the expected number. The binomial test is for the null hypothesis that deviations above and below the expected number of general occurred with equal frequency.

Habitat	Observed number of genera > expected	Observed number of genera < expected	Binomial test
Bog	16	6	0.026
Forest	10	12	0.738

Table 4. Summary of null model analyses of bog and forest assemblages at regional and local spatial scales.

	Co-occurrence		Body size overlap	
	Bog	Forest	Bog	Forest
Regional scale	Random or weakly aggregated	Segregated	Random	Weakly aggregated
Local scale	Random	Random	Weakly segregated	Random

less than expected by chance, although the patterns varied seasonally and diurnally (Albrecht and Gotelli 2000). In the eastern United States, regional co-occurrence of both forest and open field ant assemblages was less than predicted by the fixed-fixed null model, although this pattern broke down in the presence of the invasive red fire ant, *S. v. f.* (Gotelli and Arnett 2000).

The best examples of reduced body size overlap have come from detailed analyses of North American desert rodents (Bowers and Brown 1982, Brown and Nicoletto 1991), Middle Eastern mammalian carnivores (Dayan et al. 1989, 1990, 1992), Caribbean *A.* lizards (Haefner 1988, Losos 1990, 1995), Galapagos Island finches (Schluter and Grant 1984, Schluter et al. 1985), and North American stickleback fishes (Schluter and McPhail 1992).

Fewer examples exist for invertebrates assemblages, which are often described as unsaturated with many empty niches (Lawton and Strong 1981, Rohde 1991; but

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