ORIGINAL
ARTICLE

Assembly rules of ground-foraging ant assemblages are contingent on disturbance, habitat and spatial scale

Nathan J. Sanders[1]*, Nicholas J. Gotelli[2], Sarah E. Wittman[2], Jaime S. Ratchford[3]†, Aaron M. Ellison[4] and Erik S. Jules[3]

[1]*Department of Ecology and Evolutionary Biology, 569 Dabney Hall, University of Tennessee, Knoxville, TN 37996, USA,* [2]*Department of Biology, University of Vermont, Burlington, VT 05405, USA,* [3]*Department of Biological Sciences, Humboldt State University, Arcata, CA 95521, USA and* [4]*Harvard University, Harvard Forest, 324 North Main Street, Petersham, MA 01366, USA*

ABSTRACT

Aim A major endeavour of community ecology is documenting non-random patterns in the composition and body size of coexisting species, and inferring the processes, or assembly rules, that may have given rise to the observed patterns. Such assembly rules include species sorting resulting from interspecific competition, aggregation at patchily distributed resources, and co-evolutionary dynamics. However, for any given taxon, relatively little is known about how these patterns and processes change through time and vary with habitat type, disturbance history, and spatial scale. Here, we tested for non-random patterns of species co-occurrence and body size in assemblages of ground-foraging ants and asked whether those patterns varied with habitat type, disturbance history, and spatial scale.

Location Burned and unburned forests and fens in the Siskiyou Mountains of southern Oregon and northern California, USA.

Methods We describe ground-foraging ant assemblages sampled over two years in two discrete habitat types, namely *Darlingtonia* fens and upland forests. Half of these sites had been subject to a large-scale, discrete disturbance – a major fire – in the year prior to our first sample. We used null model analyses to compare observed species co-occurrence patterns and body-size distributions in these assemblages with randomly generated assemblages unstructured by competition both within (i.e. at a local spatial scale) and among (i.e. at a regional scale) sites.

Results At local spatial scales, species co-occurrence patterns and body-size ratios did not differ from randomness. At regional scales, co-occurrence patterns were random or aggregated, and there was evidence for constant body-size ratios of forest ants. Although these patterns varied between habitats and years, they did not differ between burned and unburned sites.

Main conclusions Our results suggest that the operation of assembly rules depends on spatial scale and habitat type, but that it was not affected by disturbance history from fire.

Correspondence: Nathan J. Sanders, Department of Ecology and Evolutionary Biology, 569 Dabney Hall, University of Tennessee, Knoxville, TN 37996, USA. E-mail: nsanders@utk.edu

†Present address: Jaime S. Ratchford, Department of Rangeland Ecology and Management, Oregon State University, Corvallis, OR 97331, USA.

INTRODUCTION

A common theme in studies of community assembly and biogeography is that local assemblages are composed of a set of species with co-adjusted niches that partition limited resources

(Diamond, 1975; Chase & Leibold, 2003). This theory predicts that among assemblages competing species should co-occur less than expected by chance (Diamond, 1975), and that within assemblages species should differ in body size (Hutchinson, 1959) to reduce overlap in resource use and allow for species

coexistence (MacArthur & Levins, 1967; Schoener, 1974; Dayan & Simberloff, 2005). Alternatively, the 'aggregation model of coexistence' (Hanski, 1981; Inouye, 1999) suggests that intraspecific aggregation of competitors at patchily distributed resources can facilitate coexistence without species having to avoid one another other by spatial segregation or reduced body-size overlap (Ives, 1988).

Early reviews found only weak evidence for segregated patterns of co-occurrence among birds (Schluter & Grant, 1984), and suggested that competition may not structure avian assemblages. However, a recent meta-analysis of published presence–absence matrices found evidence for species segregation that is consistent with the hypothesis that competition and niche-partitioning structure species assemblages (Gotelli & McCabe, 2002). In a similar fashion, early meta-analyses also found weak evidence for regular spacing of body sizes within assemblages (Simberloff & Boecklen, 1981). However, a more recent review of dozens of studies found that the body sizes of close competitors often differ in such a way as to reduce competition (Dayan & Simberloff, 2005).

Both species co-occurrence patterns and body-size distributions can depend on the spatial scale of analysis (Hanski, 1982; Dayan & Simberloff, 1994; Levin, 1992; Gotelli & Ellison, 2002; Jenkins, 2006). For example, at regional (for example across communities) spatial scales, body-size distributions and species co-occurrence patterns might be aggregated if climate acts as a filter to limit the pool of potentially colonizing species. At local scales, however, behavioural modifications (Cerdá et al., 1998) and fine-scale resource partitioning (Albrecht & Gotelli, 2001) might act to promote coexistence among species.

Most of these studies, regardless of scale, have assumed that communities are in an equilibrium state, and there has been little consideration of whether co-occurrence or body-size overlap patterns are stable in time or vary in space. If disturbance removes species from an assemblage (or at least dramatically reduces their abundance), assembly processes may be restarted. This observation suggests two predictions. First, among sites, co-occurrence patterns in undisturbed assemblages should be non-random if competition acts to affect species distributions, but in disturbed assemblages co-occurrence patterns should tend towards randomness (Gotelli & Arnett, 2000; Sanders et al., 2003; Badano et al., 2005). Second, within sites, body-size distributions should be regularly spaced in undisturbed habitats if competition acts to structure communities, but body-size distributions in disturbed habitats need not necessarily be regular, especially if species sorting acts to shape body-size distributions. Taken together, this suggests that assembly rules, namely the processes that cause non-random coexistence patterns and body-size distributions, can vary with scale and depend on disturbance history.

Here we examine 32 ground-foraging ant assemblages occurring in four distinct habitat types – burned fens, burned upland forests, unburned fens, and unburned upland forests – in the Siskiyou Mountains of southern Oregon, USA. Half of the sites burned before our sampling began. We use these data to test the following three predictions.

1. At local scales, body-size distributions and co-occurrence patterns will be segregated if species coevolve in response to competition with one another.
2. At regional scales, body-size distributions and co-occurrence patterns will be aggregated if the environment acts as a filter to limit the distribution of species.
3. In disturbed sites, co-occurrence patterns and body-size distributions will be random if disturbance acts to reset the assembly process.

Ants are an ideal taxon to use to test for community assembly patterns because a substantial body of work suggests that ant assemblages are broadly structured by competition (Hölldobler & Wilson, 1990). Evidence for competition in ant assemblages includes behavioural dominance hierarchies (Vepsäläinen & Pisarski, 1982; Perfecto, 1994; Sanders & Gordon, 2003), territoriality (Fox et al., 1985), chemical defence (Andersen et al., 1991), spatial mosaics (Jackson, 1984; Ryti & Case, 1984, 1992), dominance–diversity relationships (Andersen, 1992), competition–colonization tradeoffs (Holway, 1999), co-occurrence patterns (Gotelli & Arnett, 2000; Gotelli & Ellison, 2002), and the dramatic collapse of native ant communities in the presence of introduced species that are superior competitors (Holway et al., 2002). The occurrence of conspicuous interference competition between ant species that use similar resources is a good indicator that resources are limiting, either currently or in the evolutionary past (Connell, 1980), because if resources were not limiting it seems unlikely that ants would engage in costly interference. Because ant colonies (at least those of the species in our assemblages) are fairly sedentary once established, interspecific competition should also lead to non-random spatial patterns within assemblages.

METHODS

Defining the species pool

We sampled ant assemblages in fens and adjacent forests in the Siskiyou Mountains near the Oregon–California border during June–August of 2003 and July–August 2004, one and two years after a large-scale disturbance, the 202,000-ha Biscuit Fire that burned from August to September 2002 (Fig. 1). Mesic fens are dominated by the carnivorous plant *Darlingtonia californica*, and are botanically distinct from the surrounding arid upland forests where *D. californica* is absent (Whittaker, 1960). We sampled 16 paired forest–fen plots (a total of 32 ant assemblages); eight of the pairs were in areas that burned during the fire, and eight were not (Fig. 2). The paired plots were selected based on four criteria: (1) the plots had been undisturbed by recent human activity; (2) the fen plots were large enough to contain an 8 × 8 m sampling plot (see below); (3) forest plots were located at least 50 m away from the fen boundary in a direction that placed the plot at approximately the same elevation, slope and aspect as the fen plot. Paired plots were, on average, *c.* 21 km (range = *c.* 5 to *c.* 60 km) from the nearest other paired plot, so the plots can be viewed
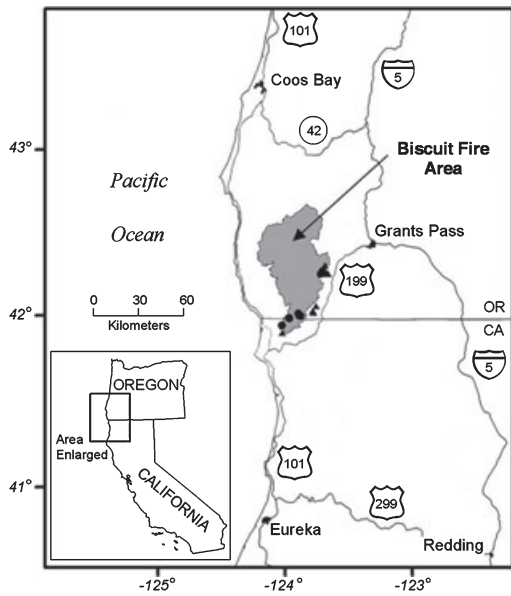
Figure 1 Map of the study region. Each symbol indicates one of the 16 sites. Recall that at each site, we sampled in a fen habitat and the adjacent upland forest. In the figure, circles represent sites that burned during the Biscuit Fire, and triangles represent sites that did not burn.

as independent units. Paired forest–fen plots were selected to minimize spatial clustering – the burned sites were not all adjacent to one another and the unburned sites were not adjacent to one another (Fig. 1). For more details of the sites, see Ratchford *et al.* (2005).

At each of the 32 plots, we established an 8 × 8 m sampling grid in 2003 and sampled ants at 25 bait stations (arranged in a 5 × 5 grid with 2-m spacing). Because ant species may differ in diurnal phenology, we visited baits nine times throughout a single day in both 2003 and 2004 to obtain a more complete sample of the myrmecofauna. Because the sampling grids for a pair of fen–forest plots were at least 50 m from one another, it is

unlikely that workers from the same nests were detected in the forest and fen sampling grids. Bait stations were 7.6 × 12.7 cm index cards stocked with both 5.5 g of tuna and a cotton ball soaked in honey water. We did not use pitfall traps because pitfalls flooded in the fens and could not be dug into the rocky soil in the upland forests. We used multiple bait stations, two resource types, and direct sampling (i.e. hand collecting and searching of a plot; Bestelmeyer *et al.*, 2000) in all of the plots; only one ant species, *Lasius flavus* (Fabricius), was found by direct sampling that did not occur at the bait stations. Thus, we are confident that our sampling techniques adequately assessed ant assemblages in these plots (Ratchford *et al.*, 2005). Voucher specimens are deposited at the University of Tennessee in Knoxville. Nomenclature follows Bolton (1994, 2003). For full details of the sampling strategy, see Ratchford *et al.* (2005).

All of our subsequent analyses of these data assume that the collection data accurately reflect species occurrences and absences and are not heavily influenced by sampling errors (undetected species or false presences). Our results suggest that our sampling procedures minimized these kinds of errors.

Species co-occurrence at the local scale

We used null model analyses (Gotelli & Graves, 1996) to examine species co-occurrence patterns. We constructed presence–absence matrices for each site in 2003 and 2004, with species as rows ($n = 1$ to 12 species), and bait locations within the site as columns ($n = 25$ baits). If a species was detected at a bait during any of the nine observations, it was counted as occurring at that bait, regardless of whether it was actually foraging or not. In each year, 32 presence–absence matrices were thus constructed (2 habitat types × 2 disturbance regimes × 8 replicates). However, a few of the matrices could not be analysed because only one species was collected at the site (2003: 3 burned fens and 4 unburned fens could not be analysed; 2004:2 unburned fens and 1 unburned fen could not be analysed).
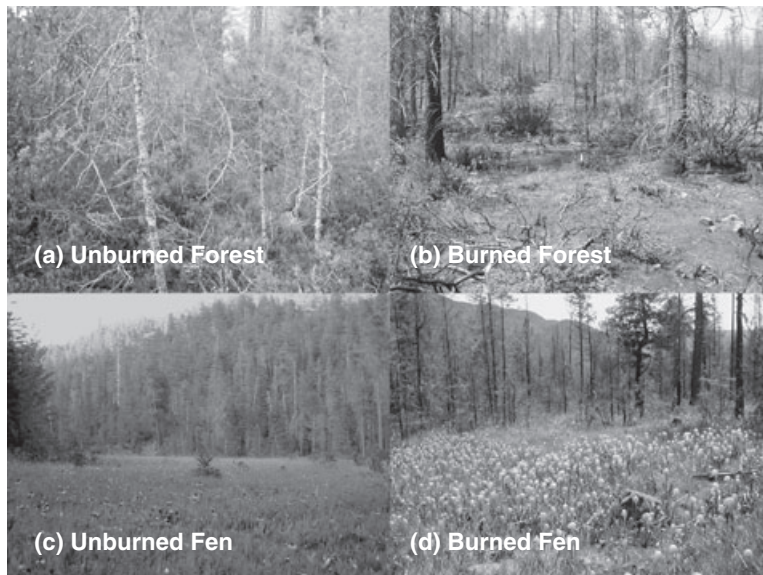
Figure 2 The four habitat types in which ants were sampled.

We used the C-score of Stone & Roberts (1990) to quantify co-occurrence patterns. If one species in the pair always occurs with the other, the C-score for that pair is 0. The C-score is larger for species pairs that show less co-occurrence. The C-score for the assemblage is the mean of all the C-scores for species pairs within an assemblage. Observed C-scores are compared with those generated from 5000 randomly constructed assemblages (using null models in EcoSim version 7.0: Gotelli & Entsminger, 2005). For an assemblage that is structured by competition, the mean C-score, averaged across all unique pairs of species, should be significantly larger than expected by chance. C-scores that are not significantly larger than expected by chance indicate random species distributions among sites; C-scores that are smaller than expected by chance indicate species aggregation.

For co-occurrence analysis at the local scale, we used a fixed-equiprobable null model (SIM2 in Gotelli, 2000) to generate the randomly constructed assemblages. In this null model, row sums are fixed, so that each species occurs with the same frequency in the randomly constructed assemblages as in the observed assemblages. Preserving row totals further safeguards against sampling that may have overlooked especially rare species. In SIM2, column totals are not fixed. This model treats each site (i.e. bait location) as being equally suitable for a species.

Because we analysed 64 co-occurrence matrices for looking at local-scale patterns, it may be more informative to compare results across sampling periods and habitats. Thus, we calculated standardized effect size (SES) (Gurevitch et al., 1992), which measure the number of standard deviations that each of the observed indices is above or below the mean index of the simulated null assemblages. It is calculated as $(I_{obs} - I_{sim})/S_{sim}$, where I_{obs} corresponds to the index for the observed assemblage, I_{sim} corresponds to the index for the null assemblages, and S_{sim} is the standard deviation of the null assemblages. Assuming a normal distribution of deviations, c. 95% of the SES values should fall between −2.0 and 2.0. Values larger than c. 2.0 indicate non-random species segregation, and values lower than −2.0 indicate non-random species aggregation.

Body size at the local scale

As in other studies (Gotelli & Ellison, 2002; Nipperess & Beattie, 2004), we used Weber's length (Brown, 1953) as a measure of ant body size. Weber's length is the distance from the anterodorsal margin of the pronotum to the posteroventral margin of the propodeum, and it is correlated with other morphological characteristics of ants (Nipperess & Beattie, 2004; Weiser & Kaspari, 2006). For each species in our sample, we measured Weber's length on six randomly selected individuals, and we used the average of these six samples as the value for each species (we did not consider body-size variation within species or among populations). For three species (*Myrmica incompleta*, *Camponotus laevigatus* and *Solenopsis molesta*), we measured only two specimens from

our collections and at least two other specimens from the collection at the California Academy of Sciences.

To examine body-size ratios at local scales, we first calculated the difference in the log-transformed Weber's lengths of adjacent species (the pair of species most similar to one another in size that occurred in the same assemblage). The variance in these segment lengths (σ_{sl}^2) for an entire assemblage is an index of the constancy of size ratios between species ordered by body size (Poole & Rathcke, 1979). We compared the observed variance in each assemblage with the variance of 1000 randomly constructed assemblages consisting of the same number of species drawn from the regional species pool. If competition affects body-size ratios, the observed σ_{sl}^2 should be smaller than expected by chance because the body-size ratios of adjacent species will be very similar to one another. In the extreme case, if the body-size ratio of adjacent species is constant, then $\sigma_{sl}^2 = 0$.

We used three null models to generate assemblages with random body-size distributions drawn from the regional species pool: an equiprobable source-pool model, an occurrence-weighted source-pool model, and an abundance-weighted source-pool model. In the equiprobable source-pool model, species are drawn randomly and with equal probability from the regional species list. Once a species is drawn, it cannot be selected again for a particular null assemblage. In the occurrence-weighted source-pool model, null assemblages are also created by drawing species randomly from the regional pool, but the probability of drawing a particular species is proportional to the number of sites at which that species occurred in the regional pool. Similarly, the abundance-weighted source-pool model constructs null assemblages by drawing species randomly from the regional species list, with the occurrence probabilities set proportional to the total abundance of the species in the region (i.e. the total number of baits at which it was detected in its habitat). Occurrence and abundance data were segregated by forest or habitat, but pooled across years and burn classes.

Species co-occurrence at the regional scale

At the regional scale, we again used C-scores and null models to assess patterns of species co-occurrence for each disturbance category for each habitat type in each year. The regional-scale co-occurrence data were organized as eight separate presence–absence matrices, with species as rows and sites as columns. The separate matrices represented the eight combinations of disturbance × habitat × year. For each analysis, there were eight sites, and the number of species varied from 6 to 21.

At this spatial scale, we used two null models, namely SIM2, the fixed-equiprobable model that was used for the local-scale co-occurrence analyses, and SIM9, a fixed-fixed model. Both of these null models correspond to colonization models in which species colonize sites randomly with respect to one another, but not necessarily randomly with respect to the sites. Unlike SIM2, in which sites are treated as equiprobable, both row totals and column totals are fixed within sites and among

species in SIM9, which maintains differences among sites and among species. Gotelli (2000) suggests that SIM9 is appropriate for analysing co-occurrence patterns of species from 'island lists' (faunistic or floristic surveys from island archipelagos; for example Connor & Simberloff, 1979), whereas SIM2 is suitable for comparing standardized samples that have been collected in areas of homogenous habitats. Comparing the observed co-occurrence patterns with different null models that incorporate different degrees of randomness can also identify how changing the model assumptions affects the results (Hilborn & Mangel, 1997). In diagnostic tests, both SIM2 and SIM9 showed low probabilities of Type I errors (Gotelli, 2000).

We also tested whether species co-occurrence patterns differed among the possible combinations of disturbance categories and habitat types (disturbance × habitat type) in 2003 and 2004. We first assembled all of the data from each year in a single matrix, with rows as species, and the 32 columns as sites. An additional row contained the column label – the disturbance category × habitat type classification of the site. To construct a null assemblage, we reshuffled the column labels, so that each sample was randomly reassigned to a particular disturbance category × habitat type. This reshuffling was done 1000 times in EcoSim 7.0. Note that only the column labels were reshuffled, not the underlying presence–absence data. After the reassignment, we calculated the C-score for each column, and then computed the variance in the C-score among columns. If the observed variance is significantly larger than expected by chance, the disturbance category × habitat type combinations are statistically different in their observed C-scores. In other words, some disturbance category × habitat type combinations have relatively large C-scores and some have relatively small C-scores, relative to a random assignment of samples. This analysis does not ask whether C-scores differed from random. Rather, it tests a subtly different pattern, namely whether C-scores differed among disturbance category × habitat type classifications.

Body size at the regional scale

At regional scales, we analysed the observed body-size distributions in two ways. First we examined the observed body-size distributions in each disturbance category × habitat type combination in both 2003 and 2004. Then we examined the body-size distributions of species occurring in forests and fens (regardless of whether they were burned or unburned) to test whether habitat type, regardless of disturbance history, might shape body-size distributions at regional scales. For both sets of analyses, we compared the observed body-size distributions with body-size distributions generated by randomly sampling from three *a priori* parametric distributions: uniform, normal, and log-normal. In all cases, the parameters for the distributions (minimum and maximum for the uniform distribution, and mean and variance for the normal distributions) were estimated from the data themselves.

RESULTS

The species pool

In total, we collected 125,280 ants in 26 species and 14 genera. An analysis of variance with habitat type, disturbance history, and their interaction as predictors indicated that forest plots (mean species richness = 7.0, range = 2–12) had more than twice as many ant species as did fen plots (mean species richness = 2.5, range = 1–6) ($F_{1.56} = 74.49$, $P < 0.0001$). There was no main effect of fire on ant species richness across habitat types ($F_{1.56} = 0.72$, $P = 0.40$). There was, however, a significant interaction between disturbance and habitat on ant species richness ($F_{1.56} = 5.41$, $P = 0.02$). Within fens, species richness was higher in burned plots (mean species richness = 3.0, range = 1–6) than in unburned plots (mean species richness = 2.0, range = 1–5). In contrast, species richness was higher in the upland forest in unburned plots (mean species richness = 8.2, range = 5–12) than in burned plots (mean species richness = 5.7, range = 2–9). Ratchford *et al.* (2005) provide more detail on the responses of individual ant species to habitat and fire.

### Species co-occurrence at the local scale

Within sites, we predicted that species co-occurrence patterns would be segregated if competition structures communities. However, species assemblages appeared to be random subsets of the overall species pool. We also predicted that co-occurrence patterns would be random in disturbed sites relative to intact sites; however, we found no evidence for either aggregated or segregated co-occurrence patterns in any habitat type or in either year (Fig. 3).

Body size at the local scale

At local scales, we predicted that body-size distributions would be evenly spaced if competition acts to structure communities. We also predicted that, if competition structures communities and disturbance resets the assembly process, body-size distributions should be random in disturbed sites. Contrary to that prediction, body-size distributions were evenly spaced only at a single site – the burned forest at site 1 in 2003 (Table 1). In all other sites for which sufficient data were available for analysis, body-size distributions were not distinguishable from random expectation.

Species co-occurrence at the regional scale

At regional scales, we predicted that species co-occurrence patterns would be aggregated if the environment acts as a filter to limit the distribution of species and segregated if competition structures communities, and that both body-size and co-occurrence patterns would not differ from random in disturbed sites. There was no evidence of species segregation among sites in any habitat type or in either year (Table 2).
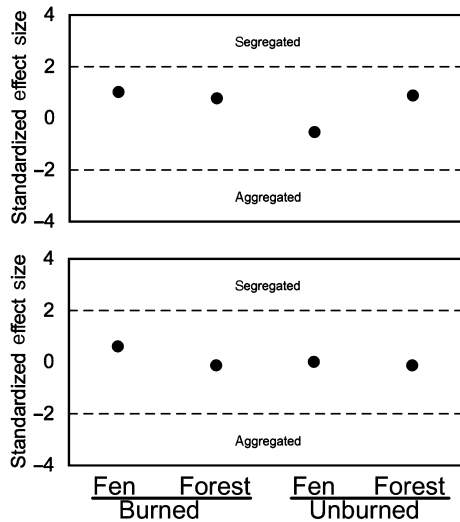
Figure 3 Meta-analysis for local-scale co-occurrence patterns in 2003 and 2004. The symbols represent the average standardized effect size $(I_{obs} - I_{sim})/S_{sim}$, where I_{obs} is the C-score of the observed assemblage, I_{sim} is the C-score of the 5000 simulated assemblages, and S_{sim} is the standard deviation of the null assemblages. The dashed lines represent 1.96 standard deviations, the approximate level of statistical significance ($P \leq 0.05$).

However, the fixed-equiprobable model (SIM2) indicated species aggregation (small C-score), especially in burned and unburned fens in 2003 and in unburned forests in 2004. The analysis of disturbance category × habitat type combination indicated strong differences among combinations in co-occurrence patterns in 2004 ($P = 0.009$; burned fens C-score = 0.722, unburned fens C-score = 1.200, burned forests C-score = 2.121, unburned forests C-score = 1.444), but not in 2003 ($P = 0.42$).

Body size at the regional scale

At the regional scale, we predicted that body-size distributions would be aggregated if the environment acts as a filter or evenly spaced if competition structures communities. There was little evidence of reduced body-size overlap within each year × disturbance category × habitat type combination (Table 3). In burned forests in 2003 and unburned forests in 2004, the uniform null model indicated a reduced overlap of body sizes. Ignoring the disturbance category, there was no evidence for non-random body-size distributions in fens (Table 4). However, the analyses for forests indicated slight evidence of reduced body-size overlap (Table 4).

Table 1 Results of the local-scale body-size analyses. The values in the cells represent the lower tail probability of detecting non-random body-size distributions. Values < 0.05 indicate even spacing of body sizes in observed assemblages. The symbol '●' indicates that that there were not enough species in the assemblage to analyse. Note that in only three cases (the same burned forest site in 2003) was there evidence of non-random body-size distributions within assemblages.

| | 2003 | | | | 2004 | | | |
| | Fen | | Forest | | Fen | | Forest | |
Site	Unburned	Burned	Unburned	Burned	Unburned	Burned	Unburned	Burned
Equiprobable source pool								
1	●	0.197	0.668	0.037	●	0.377	0.683	0.962
2	●	0.286	0.878	0.290	●	●	0.873	0.629
3	●	●	0.703	0.338	●	0.283	0.704	0.430
4	●	0.279	0.459	0.845	●	●	0.481	●
5	0.908	0.366	0.916	0.540	0.993	0.695	0.892	0.723
6	●	●	0.786	0.920	●	●	0.777	0.335
7	●	0.795	0.546	0.558	●	0.795	0.567	0.429
8	●	●	0.465	0.803	●	●	0.488	0.415
Abundance-weighted source pool								
1	●	0.200	0.680	0.026	●	0.353	0.698	0.955
2	●	0.715	0.744	0.274	●	●	0.878	0.637
3	●	●	0.761	0.315	●	0.266	0.670	0.425
4	●	0.712	0.506	0.841	●	●	0.485	●
5	0.901	0.615	0.912	0.527	0.930	0.694	0.876	0.727
6	●	●	0.682	0.942	●	●	0.803	0.358
7	●	0.180	0.764	0.536	●	0.784	0.540	0.417
8	●	●	0.453	0.763	●	●	0.485	0.434
Occurrence-weighted source pool								
1	●	0.187	0.695	0.037	●	0.337	0.322	0.961
2	●	0.693	0.754	0.279	●	●	0.860	0.645
3	●	●	0.720	0.334	●	0.273	0.681	0.390
4	●	0.716	0.544	0.836	●	●	0.483	●
5	0.952	0.602	0.900	0.521	●	0.662	0.883	0.683
6	●	●	0.704	0.898	●	●	0.789	0.334
7	●	0.228	0.801	0.552	●	0.825	0.506	0.386
8	●	●	0.444	0.773	●	●	0.490	0.407

Year	Burn	Habitat	C-score	Mean of simulated	P(observed > expected)	SES
Fixed-equiprobable (SIM2)						
2003	Burned	Fen	0.909	1.286	0.983	−2.379
	Unburned	Fen	0.800	1.307	0.944	−1.734
	Burned	Forest	1.883	1.891	0.571	−0.041
	Unburned	Forest	1.143	1.161	0.643	−0.207
2004	Burned	Fen	0.722	1.013	0.932	−1.482
	Unburned	Fen	1.200	1.176	0.564	0.108
	Burned	Forest	2.121	2.102	0.534	0.077
	Unburned	Forest	1.444	1.737	0.967	−2.088
Fixed-fixed (SIM9)						
2003	Burned	Fen	0.909	0.958	0.853	−0.825
	Unburned	Fen	0.800	0.796	0.484	0.034
	Burned	Forest	1.883	1.907	0.676	−0.444
	Unburned	Forest	1.143	1.159	0.690	−0.581
2004	Burned	Fen	0.722	0.796	0.824	−0.760
	Unburned	Fen	1.200	1.198	0.816	0.022
	Burned	Forest	2.121	2.099	0.384	0.240
	Unburned	Forest	1.444	1.402	0.201	0.809

Table 2 Regional-scale co-occurrence patterns. The first three columns indicate the sampling year, the disturbance history, and the habitat type. The observed C-score is the C-score calculated from the observed assemblages, and the simulated C-score is the mean C-score for 5000 randomly assembled communities. *P* is the one-tail probability that the observed index was greater than expected by chance. An SES (standardized effect size) > 2 indicates segregation, and an SES < −2 indicates significant species aggregation.

Table 3 Results of the regional-scale body-size analyses. The values in the cells represent the lower tail probability of detecting non-random body-size distributions. Values ≤ 0.05 indicate even spacing of body sizes in observed assemblages. Significant values are in bold.

	2003				2004			
	Burned		Unburned		Burned		Unburned	
	Fen	Forest	Fen	Forest	Fen	Forest	Fen	Forest
Uniform	0.13	**0.01**	0.19	0.21	0.57	0.30	0.29	**0.03**
Normal	0.24	0.06	0.28	0.22	0.45	0.30	0.45	0.09
Log-normal	0.44	0.09	0.39	0.43	0.70	0.52	0.42	0.12

Table 4 Results of the regional-scale body-size analyses. The values in the cells represent the lower tail probability of detecting non-random body-size distributions. Values ≤ 0.05 indicate even spacing of body sizes in observed assemblages. Significant values are in bold.

Distribution	Fen sites	Forest sites
Uniform	0.112	**0.013**
Normal	0.203	**0.050**
Log-normal	0.349	0.088

DISCUSSION

We found random patterns of co-occurrence at local scales in both habitat types, whether burned or unburned, in both 2003 and 2004 (Fig. 3). In contrast, many other studies have shown that competition affects interspecific spatial patterns among nests (Levings & Traniello, 1981; Ryti & Case, 1988; Sanders & Gordon, 2004) and the spatial distribution of foragers (Room, 1971; Majer, 1972; Fellers, 1987; Savolainen & Vepsäläinen,

1988; Andersen & Patel, 1994; Albrecht & Gotelli, 2001; but see Gotelli & Ellison, 2002) within communities. Because the local-scale data come from observations at baits, where the effects of behavioural interactions should be most pronounced, it is surprising that we found no evidence of spatial segregation. There are two candidate explanations for the random co-occurrence patterns at local scales. First, if ants are good dispersers at small spatial scales, then perhaps there is just random mixing of all species in a local patch. This seems unlikely because the foraging distances of many species in these habitats, especially the subordinate species, are only *c.* 1–2 m from the nest (Wittman, unpublished data), and we did not see nests throughout each site. Second, because we 'lumped' counts of ants at two resource types on baits from nine observations throughout the day, we may not have been able to detect the effects of competition at this scale, especially if species partition resource type, entire baits, or show temporal partitioning (Albrecht & Gotelli, 2001). However, there is little evidence in this system that different ant species differentially used the two bait types offered (Wittman, unpublished data). Future studies (Wittman, unpublished data) will address the potential effects of niche partitioning, detailed behavioural interactions and priority effects on the patterns documented here.

Co-occurrence patterns in recently burned plots did not differ from those in unburned plots. In a study similar to ours (although it deals with time since disturbance rather than just with disturbance), Badano *et al.* (2005) found that ant assemblages on newly emerged islands tended to show random co-occurrence patterns, but that assemblages on 'old' islands showed less co-occurrence than expected by chance. Badano *et al.* (2005) suggest that assemblages on the newly emerged islands had not had enough time to become structured. However, we saw no difference in co-occurrence between disturbed and undisturbed ant assemblages in 2003 and 2004,

Table 5 Summary of null model analyses of ant assemblages across spatial scales, habitats, and years.

Year	Burn	Habitat	Co-occurrence	Body-size overlap
Local scale				
2003	Burned	Fen	Random	Random
2003	Unburned	Fen	Random	Random
2004	Burned	Fen	Random	Random
2004	Unburned	Fen	Random	Random
2003	Burned	Forest	Random	Random
2003	Unburned	Forest	Random	Random
2004	Burned	Forest	Random	Random
2004	Unburned	Forest	Random	Random
Regional scale				
2003	Burned	Fen	Aggregated	Random
2003	Unburned	Fen	Aggregated	
2004	Burned	Fen	Aggregated	
2004	Unburned	Fen	Random	
2003	Burned	Forest	Random	Segregated
2003	Unburned	Forest	Random	
2004	Burned	Forest	Random	
2004	Unburned	Forest	Aggregated	

nor did we see less co-occurrence in 2003 (when ants might have been responding to disturbance rather than to competition) than in 2004, suggesting that disturbance did not affect co-occurrence patterns in these assemblages. An alternative possibility is that two years since disturbance is not enough time for the signature of competition to be detected.

In the few cases for which assemblage structure was non-random, co-occurrence patterns were aggregated (Table 5), not segregated as predicted by assembly rules predicated on competition. A recent meta-analysis (Gotelli & McCabe, 2002) indicated that non-random species segregation is the rule, especially in ants (e.g. Cole, 1983; Gotelli & Arnett, 2000; Gotelli & Ellison, 2002; Sanders et al., 2003). In contrast to the habitat types in other studies, the extremely wet fens and extremely hot open forests (mean July max temperature = 32.2°C) in the Siskiyou Mountains may impose strong habitat filters on the pool of colonizing species. As a result, species occurrences are aggregated in a few tolerable sites. Species segregation is perhaps more likely among distinct habitat areas or even for habitat islands in which dispersal is limited.

We also found no evidence for competition among species reflected in body-size distributions at local scales. At regional scales, segregated body-size patterns in forests (but not fens) suggest the working of competition-based assembly rules in this habitat. Our results mirror analyses of size distributions in European bumblebees (Hanski, 1982; Ranta, 1982) and desert rodents (Dayan & Simberloff, 1994) that also indicated that species were overdispersed at regional but not at local scales.

Why might body-size distributions be evenly spaced at regional but not at local scales? Dayan & Simberloff (1994) argue that coevolution among competing species is more likely at regional than at local scales. Thus, at local scales species

might not coevolve in response to one another; instead, they may simply partition time or resources. That is, the evolutionary pressure is not substantial enough to lead to morphological change at local scales, especially when individuals could just modify their foraging behaviour or activity cycles in response to competition (Cerdá et al., 1998; Sanders & Gordon, 2003).

Two recent studies on ant assemblages contrast with our results. Nipperess & Beattie (2004) found that 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. Similarly, Gotelli & Ellison (2002) found that 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.

In summary, our results indicate that the operation of assembly rules depends on spatial scale, and that there is little consistency in the modification of assembly rules by disturbance history or habitat type (Table 5). The search for universal laws in ecology continues, especially for those that structure communities (Tilman, 2004; Lawton, 1999; Hubbell, 2001; but see Simberloff, 2004). However, our results suggest that many assembly rules might be both temporally dependent and spatially contingent (Drake, 1990; Chase, 2003; Fukami, 2004; Connolly et al., 2005).

REFERENCES

Albrecht, M. & Gotelli, N.J. (2001) Spatial and temporal niche partitioning in grassland ants. *Oecologia*, **126**, 131–141.

Andersen, A.N. (1992) Regulation of momentary diversity by dominant species in exceptionally rich ant communities of the Australian seasonal tropics. *The American Naturalist*, **140**, 401–420.

Andersen, A. N., Blum, M.S. & Jones, T. H. (1991) Venom alkaloids in *Monomorium* "rothsteini" *forel* repel other ants: is this the secret to success by *Monomorium* in Australian ant communities? *Oecologia*, **88**, 157–160.

Andersen, A. N. & Patel, A. D. (1994) Meat ants as dominant members of Australian communities: an experimental test of their influence on the foraging success and forager abundance of other species. *Oecologia*, **98**, 15-24.

Badano, E.I., Regidor, H.A., Nunez, H.A., Acosta, R. & Gianoli, E. (2005) Species richness and structure of ant communities in a dynamic archipelago: effects of island area and age. *Journal of Biogeography*, **32**, 221–227.

Bestelmeyer, B.T., Agosti, D., Alonso, L.E., Brandao, C. R. F., Brown, W. L., Delabie, J. H. C. & Silvestre, R. (2000) Field techniques for the study of ground-dwelling ants: an overview, description, and evaluation. *Ants: standard methods for measuring and motoring biodiversity.* (ed. by D. Agosti, J. D. Majer, L. E. Alonso & T. R. Schultz), pp. 122–144. Smithsonian Institution Press.

Bolton, B. (1994) *Identification guide to the ant genera of the world.* Harvard University Press, Cambridge, MA.

Bolton, B. (2003) Synopsis and classification of Formicidae. *Memoirs of the American Entomological Institute*, **71**, 1–370.

Brown, W.L. (1953) Revisionary studies in the ant tribe Dacetini. *American Midland Naturalist*, **50**, 1–137.

Cerdá, X., Retana, J. & Cros, S. (1998) Prey size reverses the outcome of interference interactions of scavenger ants. *Oikos*, **82**, 99–110.

Chase, J.M. (2003) Community assembly: when should history matter. *Oecologia*, **136**, 489–498.

Chase, J.M. & Leibold, M.A. (2003) *Ecological niches: linking classical and contemporary approaches.* University of Chicago Press, Chicago, IL.

Cole, B. J. (1983) Assembly of Mangrove ant communities: patterns of geographical distribution. *Journal of Animal Ecology*, **52**, 339–347.

Connell, J.H. (1980) Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos*, **35**, 131–138.

Connolly, S.R., Hughes, T.P., Bellwood, D.R. & Karlson, R.H. (2005) Community structure of corals and reef fishes at multiple scales. *Science*, **309**, 1363–1365.

Connor, E.F. & Simberloff, D. (1979) The assembly of species communities: chance or competition? *Ecology*, **60**, 1132-1140.

Dayan, T. & Simberloff, D. (1994) Morphological relationships among coexisting heteromyids: an incisive dental character. *The American Naturalist*, **143**, 462–477.

Dayan, T. & Simberloff, D. (2005) Ecological and community-wide character displacement: the next generation. *Ecology Letters*, **8**, 875–894.

Diamond, J.M. (1975) Assembly of species communities. *Ecology and evolution of communities* (ed. by M.L. Cody and J.M. Diamond), pp. 342–444. Harvard University, Cambridge, MA.

Drake, J.A. (1990) Communities as assembled structures – do rules govern pattern? *Trends in Ecology & Evolution*, **5**, 159–164.

Fellers, J. H. (1987) Interference and exploitation in a guild of woodland ants. *Ecology*, **68**, 1466–1478.

Fox, B.J., Fox, M.D. & Archer, E. (1985) Experimental confirmation of competition between two dominant species of *Iridomyrmex* (Hymenoptera: Formicidae). *Australian Journal of Ecology*, **10**, 105–110.

Fukami, T. (2004) Assembly history interacts with ecosystem size to influence species diversity. *Ecology*, **85**, 3234–3242.

Gotelli, N.J. (2000) Null model analysis of species co-occurrence patterns. *Ecology*, **81**, 2606–2621.

Gotelli, N.J. & Arnett, A.E. (2000) Biogeographic effects of red fire ant invasion. *Ecology Letters*, **3**, 257–261.

Gotelli, N.J. & Ellison, A.M. (2002) Assembly rules for New England ant assemblages. *Oikos*, **99**, 591–599.

Gotelli, N.J. & Entsminger, G.L. (2005) *EcoSim: Null models software for ecology. Version 7.* Acquired Intelligence Inc. & Kesey-Bear, Jericho, VT. http://garyentsminger.com/ecosim.htm. 7.0 edn.

Gotelli, N.J. & Graves, G.R. (1996) *Null models in ecology.* Smithsonian Institution Press, Washington, DC.

Gotelli, N.J. & McCabe, D.J. (2002) Species co-occurrence: a meta-analysis of J. M. Diamond's assembly rules model. *Ecology*, **83**, 2091–2096.

Gurevitch, J., Morrow, L.L., Wallace, A. & Walsh, J.S. (1992) A meta-analysis of competition in field experiments. *The American Naturalist*, **140**, 539–572.

Hanski, I. (1981) Coexistence of competitors in a patchy environment without predation. *Oikos*, **37**, 306–312.

Hanski, I. (1982) Structure in bumblebee communities. *Annales Zoologici Fennici*, **19**, 319–326.

Hilborn, R. & Mangel, M. (1997) *The ecological detective: confronting models with data.* Princeton University Press, Princeton, NJ.

Hölldobler, B. & Wilson, E.O. (1990) *The ants.* The Belknap Press of Harvard University Press, Cambridge, MA.

Holway, D.A. (1999) Competitive mechanisms underlying the displacement of native ants by the invasive Argentine ant. *Ecology*, **80**, 238–251.

Holway, D.A., Lach, L., Suarez, A.V., Tsutsui, N.D. & Case, T.J. (2002) The causes and consequences of ant invasions. *Annual Review of Ecology and Systematics*, **33**, 181–233.

Hubbell, S.P. (2001) *The unified neutral theory of biodiversity and biogeography.* Princeton University Press, Princeton, NJ.

Hutchinson, G.E. (1959) Homage to Santa Rosalia or Why are there so many kinds of animals? *The American Naturalist*, **93**, 145–158.

Inouye, B.D. (1999) Integrating nested spatial scales: implications for the coexistence of competitors on a patchy resource. *Journal of Animal Ecology*, **68**, 150–162.

Ives, A.R. (1988) Aggregation and the coexistence of competitors. *Annales Zoologici Fennici*, **25**, 75–88.

Jackson, D.A. (1984) Ant distribution patterns in a Cameroonian cocoa plantation: investigation of the ant mosaic hypothesis. *Oecologia*, **62**, 318–324.

Jenkins, D.G. (2006) In search of quorum effects in metacommunity structure: species co-occurrence analysis. *Ecology*, **87**, 1523–1531.

Lawton, J.H. (1999) Are there general laws in ecology? *Oikos*, **84**, 177–192.

Levin, S. A. (1992) The problem of pattern and scale in ecology. *Ecology*, **73**, 1943–1967.

Levings, S.C. & Traniello, J.F.A. (1981) Territoriality, nest dispersion, and community structure in ants. *Psyche*, **88**, 265–319.

MacArthur, R.H. & Levins, R. (1967) The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist*, **101**, 377–385.

Major, J.D. (1972) The ant mosaic in Ghana cocoa farms. *Bulletin of Entomological Research*, **62**, 151–160.

Nipperess, D.A. & Beattie, A.J. (2004) Morphological dispersion of Rhytidoponera assemblages: the importance of spatial scale and null model. *Ecology*, **85**, 2728–2736.

Perfecto, I. (1994) Foraging behavior as a determinant of asymmetric competitive interactions between two ant species in a tropical agroecosystem. *Oecologia*, **98**, 184–192.

Poole, R.W. & Rathcke, B.J. (1979) Regularity, randomness, and aggregation in flowering phenologies. *Science*, **203**, 470–471.

Ranta, E. (1982) Species structure of North European bumblebee communities. *Oikos*, **38**, 202–209.

Ratchford, J.S., Wittman, S.E., Jules, E.S., Ellison, A.M., Gotelli, N.J. & Sanders, N.J. (2005) The effects of fire, local environment, and time on ant assemblages in fens and forests. *Diversity and Distributions*, **11**, 487–497.

Room, P.M. (1971) The relative distributions of ant species in Ghana's cocoa farms. *Journal of Animal Ecology*, **40**, 735–751.

Ryti, R.T. & Case, T.J. (1984) Spatial arrangement and diet overlap between colonies of desert ants. *Oecologia*, **62**, 401–404.

Ryti, R. & Case, T.J. (1988) Field experiments on desert ants: testing for competition between colonies. *Ecology*, **69**, 1993–2003.

Ryti, R.T. & Case, T.J. (1992) The role of neighborhood competition in the spacing and diversity of ant communities. *The American Naturalist*, **139**, 355–374.

Sanders, N.J. & Gordon, D.M. (2004) The interactive effects of climate, life history, and interspecific neighbours on mortality in a population of seed harvester ants. *Ecological Entomology*, **29**, 632–637.

Sanders, N.J., Gotelli, N.J., Heller, N. & Gordon, D.M. (2003) Community disassembly by an invasive species. *Proceedings of the National Academy of Sciences USA*, **100**, 2474–2477.

Savolainen, R. & Vepsäläinen, K. (1988) A competition hierarchy among boreal ants: impact on resource partitioning and community structure. *Oikos*, **51**, 135–155.

Schluter, D. & Grant, P.R. (1984) Determinants of morphological patterns in communities of Darwin's finches. *The American Naturalist*, **123**, 175–196.

Schoener, T.W. (1974) Resource partitioning in ecological communities. *Science*, **185**, 27–39.

Simberloff, D. (2004) Community ecology: is it time to move on? *The American Naturalist*, **163**, 787–799.

Simberloff, D. & Boecklen, W. (1981) Santa Rosalia reconsider: size ratios and competition. *Evolution*, **35**, 1206–1228.

Stone, L. & Roberts, A. (1990) The checkerboard score and species distributions. *Oecologia*, **85**, 74–79.

Tilman, D. (2004) Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invastion, and community assembly. *Proceedings of the National Academy of Sciences USA*, **101**, 10854-10861.

Vepsäläinen, K. & Pisarski, B. (1982) Assembly of island ant communities. *Annales Zoologici Fennici*, **19**, 327–335.

Weiser, M.D. & Kaspari, M. (2006) Ecological morphospace of New World ants. *Ecological Entomology*, **31**, 131–142.

Whittaker, R.H. (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, **30**, 279–338.

SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online:

Table S1. A regional-scale site × species matrix showing the species detected at each of the sites.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365–2699.2007.01714.x (This link will take you to the article abstract).

Please note: Blackwell Publishing are not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article

BIOSKETCH

Nathan J. Sanders studies the community ecology of ants, biological invasions, and how biotic and environmental factors influence ecological communities across spatial scales. He is an assistant professor at the University of Tennessee.

Editor: Jon Sadler