

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

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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

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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

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

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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 \times 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 \times 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 \times habitat type. This reshuffling was done 1000 times in *ECO-SIM* 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 \times habitat type combinations are statistically different in their observed C-scores. In other words, some disturbance category \times 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

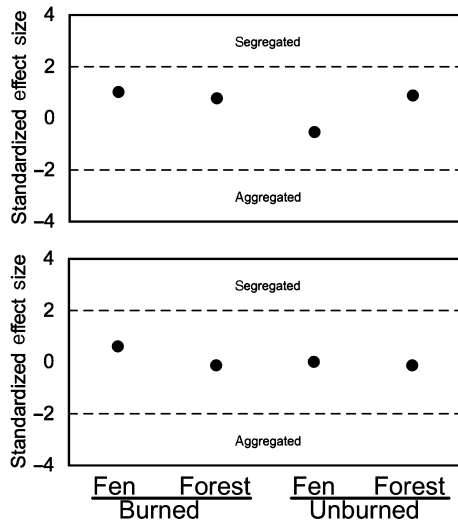


Figure 3 Meta-analysis for local-scale co-occurrence patterns in 2003 and 2004. The symbols represent the average standardized effect size $(I_{obs} - I_{sim}) / s_{sim}$, where I_{obs} is the C-score of the observed assemblage, I_{sim} is the C-score of the 5000 simulated assemblages, and s_{sim} is the standard deviation of the null assemblages. The dashed lines represent 1.96 standard deviations, the approximate level of statistical significance ($\alpha \leq 0.05$).

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 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.

Site	2003				2004			
	Fen		Forest		Fen		Forest	
	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
	4	0.742	0.285	0.707	0.430			

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 \times habitat type combination indicated strong differences among combinations in co-occurrence patterns in 2004 ($\alpha = 0.009$; 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 ($\alpha = 0.42$).

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 \times disturbance category \times 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).

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

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,

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,

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