

Seed augmentation has a limited effect on species diversity of sand-dwelling ants

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ABSTRACT

Enrichment experiments can provide useful information on the coexistence mechanisms by which resources are shared among species within an assemblage. In this study, we examined the effect of artificial seed augmentation on the diversity of seed-eating ant species at the Mash'abim Sands Nature Reserve in the Negev Desert in Israel. In a two-year experiment, the foraging activity of the different ant species was observed at two-month intervals, during both night and day, in nine plots that were enriched daily with millet and sunflower seeds. Each plot was divided into 20 stations. The nine plots were randomly assigned to each of three seed-enrichment treatments: no seed addition (control); addition of seeds that were available only for ants (Ant); or addition of seeds that were available for both ants and rodents (Ant+Rod). Eight seed-eating ant species were observed at the baits, three of which were specialist seed-eaters, and the other five were generalist species. The results reveal no significant effect of seed augmentation on ant species diversity. However, there was a trend of increase in diversity in the Ant compared to the control plots during the day. This increase contradicts the hypothesis that seed-enrichment in deserts would lead to decreased ant species diversity due to increased inter-specific or inter-taxon competition due to increased territoriality of either the dominant ant or rodent species, respectively. Our finding agrees with a growing number of studies in ants that revealed either an increase or no change in diversity following artificial resource augmentation.

KEYWORDS: ants, granivory, Negev Desert, seed enrichment, species diversity

INTRODUCTION

Food availability can limit the abundance and distribution of animal taxa on both local and regional scales (MacArthur, 1972; Rosenzweig and Abramsky, 1993; Wright et al., 1993). On the regional scale, animal productivity, i.e., the rate of conversion of resources

to biomass per unit area per unit time (Waide et al., 1999), and diversity correlate with primary productivity in a wide variety of taxa and exhibit varying response patterns (e.g., Currie, 1991; Waide et al., 1999; Mittelbach et al., 2001; Ziv and Tsairi, 2004). On the local scale, manipulation of productivity (defined here as gross primary productivity) can provide useful information on coexistence mechanisms by which resources are shared among species within an assemblage (Wright et al., 1993). Studies that examined the effect of artificial augmentation of resources on local communities in various taxa revealed contradicting results of either increase, decrease, or no change in species diversity following the addition of resources (e.g., Rosenzweig, 1971; Abramsky, 1978; Brown and Munger, 1985; Diehl and Feissel, 2001; Acuña et al., 2008).

In this study, we examined the effect of food addition on seed-eating ant species in a desert region. Ants offer a good model for examining diversity–productivity responses since they are sensitive to environmental changes and have stationary nesting habits that allow for resampling over time (Hölldobler and Wilson, 1990; Alonso and Agosti, 2000). In addition, studying ant-diversity responses to resource augmentation is particularly interesting in desert environments, in which resources are scarce and seed-eating ants have been shown to be food-limited (e.g., Bernstein, 1975; Davidson, 1977; Segev, 2010). Therefore, any increase in seed availability could have a significant effect on the energetic efficiency of foraging and can be readily translated into fitness. Although ant assemblages have been shown to respond to local-scale resource augmentation in varying ways, they have mainly exhibited either a positive response (Deslippe and Savolainen, 1994; Kaspari and Valone, 2002) or no response (Davidson et al., 1985; Munger, 1992; Jean-Philippe Lessard, unpublished data).

Several hypotheses have been put forward to explain the observed increase in ant species diversity with resource augmentation (e.g., Kaspari et al., 2003; Sanders et al., 2007). The “abundance–extinction mechanism” (Pimm et al., 1988) asserts that increased resource availability can support larger average population sizes, thus decreasing the probability of a demographic extinction of each species. Within the time frame of enrichment experiments, support for this hypothesis could be provided if higher site productivity is shown to support higher average population sizes and hence higher species diversity. Alternatively, the “sampling mechanism” suggests that a positive association between resource enrichment and species diversity could be due to a mere sampling effect (Preston, 1962). Accordingly, increased site productivity results in an increase in the number of individuals in the local assemblage, which may enable the sampling of more species.

Conversely, a potential decrease in ant species diversity following resource augmentation could be the result of increased competition due to the dominance of species that are competitively superior in exploiting the augmented resources or are more aggressive in guarding them (“competitive structure mechanism”: MacArthur, 1972; Rosenzweig, 1995). This hypothesis is supported by the fact that ant community structure can be highly affected by dominant ant species (e.g., Hölldobler and Wilson, 1990; Morrison, 1996; Sanders and Gordon, 2003). An alternative explanation is the “inter-taxon competition mechanism” (Rosenzweig and Abramsky, 1993), according to which ant species diversity decreases due to asymmetric competition with rodents that are more proficient

seed foragers (Brown and Davidson, 1977; Davidson et al., 1984). This mechanism is mainly relevant in desert communities in which ants and rodents are the two key granivorous taxa (Brown et al., 1986).

The objective of this study was to examine the effect of a two-year seed enrichment experiment on an ant assemblage within a desert region. Specifically, two questions were addressed: (1) Would seed addition affect the foraging activity and diversity of seed-eating ant species in the study region? and (2) If such a response exists, which of the above-mentioned mechanisms might explain the observed pattern? Uncoupling the effects of these mechanisms can be achieved with appropriate indices and enrichment techniques. For example, if ant species diversity increases with the addition of seeds, distinguishing between the “sampling mechanism” and “abundance–extinction mechanism” is possible using Fisher’s α , an index that estimates species diversity while removing the sampling artifact (Fisher et al., 1943; Kaspari et al., 2003; Sanders et al., 2007). On the other hand, if a decrease in ant species diversity is exhibited with the addition of seeds, the “competitive structure mechanism” could be distinguished from the “inter-taxon competition mechanism” by comparing ant species diversity between plots in which seed enrichment is only available for ants, and plots in which seeds are available for both ants and rodents.

MATERIALS AND METHODS

Study site

The study was conducted at the Masha’bim Sands Nature Reserve (31°00’N/34°43’E) in the Negev Desert in Israel. Mean annual precipitation in this region is 110 mm, and rain is limited to the winter season (November–March). Average summer-maximum and winter-minimum temperatures are 33.5° and 6° C, respectively (Israeli Meteorological Service data). The area is characterized by long east-to-west stretches of dunes that are separated by valleys and provide three habitat types: semi-stabilized dunes, stabilized sands, and rocky hillsides. To reduce the effect of habitat heterogeneity, the study was restricted to the stabilized dunes on which vegetation varies from open grassland, sparsely covered with annuals, to shrubland with patches of perennials, such as *Retama raetam*, *Lycium shawii*, and *Artemisia monosperma*.

Experimental design

At the beginning of 2001, nine 1-ha plots were established at least 30 m apart. Each plot comprised 20 uniformly distributed 0.3 m³ seed enrichment stations. The plots were randomly assigned to each of three seed enrichment treatments (three plots per treatment) in which seeds were either not added (control) or added, but were made available only for ants (Ant), or for both ants and rodents (Ant+Rod). In the Ant plots, each regularly enriched station was protected by a 40 cm³ enclosure constructed of 10 mm² wire mesh, with the bottom half covered in sand placed in an aluminum tray, ensuring that ants were

the only granivorous taxon able to enter the station. In the Ant+Rod plots, the regularly enriched stations were not enclosed, but deployed in the open field. Enrichment comprised a daily addition of 4 g of millet and broken sunflower seeds supplied at sunset in order to prevent seed intake by diurnal seed-eating birds prior to ant activity. Seeds of both types were used as they vary in size, and thus may be selected by ant species of different sizes.

Ant species diversity was compared between the treatments by monitoring the foraging activity of the different species at the experimental baits. Since ant species that nest in the regularly enriched plots (the Ant and Ant+Rod treatments) may become habituated to the location of the 20 regularly enriched stations, foraging activity was also measured at six randomly placed baits in each of the Ant, Ant+Rod, and control plots. The baits were protected by enclosures similar to those in the Ant plots, and were activated only when no enrichment was provided in the regular stations. These baits were observed at two-month intervals during the year 2002 (a total of five sampling days) in which each plot was visited during both night and day. Seeds were placed at sunset for a baiting period of three consecutive days to allow their detection by species with low resource discovery rates. On the third day, ant sampling was initiated 3 and 9–12 hrs following placement of baits. The number of individuals of each species that occupied the baits for a fixed period of two minutes was counted. Individuals were identified to species level on site, and in cases of uncertainty, they were collected and identified in the lab, following Kugler (1984).

Data analysis

The effect of treatment on species diversity was tested using repeated-measures ANOVA with two within-subject factors: diel patterns of activity (visits during the night and day) and sampling days. Overall sample size consisted of 90 observations (3 plots \times 3 treatments \times 2 visits per day \times 5 sampling days). Species diversity was measured by counting the observed number of species per plot. However, since this measurement is strongly affected by the number of individuals per sample (Gotelli and Colwell, 2001), Fisher's α index was also used as it is not affected by sample size (Rosenzweig, 1995). Since ants are colony-forming organisms, Fisher's α was estimated on the basis of the number of occurrences at the baits rather than the number of individuals for each species. The repeated-measures ANOVA assumption of circularity was tested using Mauchly's test of sphericity and was found to be valid for the within-subjects factors (Von-Ende, 2001). In addition, since the Ant+Rod treatment was only suitable for examining the "inter-taxon competition mechanism", a planned comparison contrast test was conducted between Ant and control plots in order to examine the validity of the other mechanisms that were suggested to explain the response patterns in ant species diversity to resource augmentation.

To further examine the sampling artifact, the relationship between Fisher's α values and number of species in a plot was evaluated using a linear regression. A nonsignificant relationship between these variables indicates that a sampling artifact could not be excluded as an explanation for differences in species number within plots as well as among the different treatments (see also Kaspari et al., 2003; Sanders et al., 2007).

Following an increase in resource availability, it is possible that interference competition and territoriality could increase or decline (see Rosenzweig and Abramsky, 1993; Rosenzweig, 1995): e.g., on the scale of the plot, species-richness would increase, whereas on the scale of the bait, species-richness would decrease, due to increase in species territoriality. This was examined by exploring the relationship between species richness at plots and species richness at baits. The average species number at baits was therefore regressed against the average species number at plots for each treatment separately. Slopes with higher values indicate higher increase in species richness at plots with increasing species richness at baits, which may indicate an increase in territoriality at baits. The slopes of these linear regression analyses were compared among the different treatments using ANCOVA, with average species number in plots as the dependent variable, treatment as the factor, and average species number in baits as the covariate. A significant interaction between the treatment and the covariate would suggest significant differences between the slopes. Species number at baits, species number at plots, and Fisher's α measurements were all log transformed to meet the assumptions of normality and homogeneity of variances (Zar, 1998). Statistical analyses and graphs were conducted using SPSS 15 (SPSS Inc., Chicago, IL) and SigmaPlot 11 (Systat Inc., San Jose, CA).

RESULTS

Eight seed-eating ant species were observed collecting the seeds at the baits. Three of these were specialist seed-eaters: *Messor arenarius*, *Messor ebeninus*, and *Messor aegyptiacus*. The other five species were generalist seed-eaters: *Crematogaster inermis*, *Monomorium salomonis*, *Monomorium pharaonis*, *Pheidole pallidula*, and *Temnothorax arenarius*. Most of these species were observed in all treatments.

No significant differences were observed in ant species number among the different treatments (repeated-measures ANOVA: $F_{2,6} = 0.713$, $P = 0.53$; Fig. 1A) (Table 1). The species number was significantly higher during the day compared to night (repeated-measures ANOVA: $F_{1,6} = 42.58$, $p < 0.001$; Fig. 1A) and also differed among days (repeated-measures ANOVA: $F_{4,24} = 8.05$, $p < 0.001$). The interaction between these two variables was also significant (repeated-measures ANOVA: $F_{4,24} = 6.17$, $p < 0.001$). However, interactions between any of the within-subject factors and the treatment effect were not significant (Table 1). A contrast test for the difference between Ant and control plots revealed a difference for the daytime (though not significant, $P = 0.086$) and no significant difference for the nighttime ($P = 0.986$). This indicates that the number of ant species in the daytime was slightly higher in the Ant plots compared to the control (Fig. 1A).

Similar to the findings for species number, no significant differences were observed in Fisher's α among the different treatments (repeated-measures ANOVA: $F_{2,6} = 0.367$, $P = 0.708$; Fig. 1B) (Table 1). Ant species diversity was significantly higher during the day compared to the night (repeated-measures ANOVA: $F_{1,6} = 41.69$, $p < 0.001$; Fig. 1B) and it also differed among days (repeated-measures ANOVA: $F_{4,24} = 7.19$, $p < 0.001$). The interaction between these two variables was also significant (repeated-measures

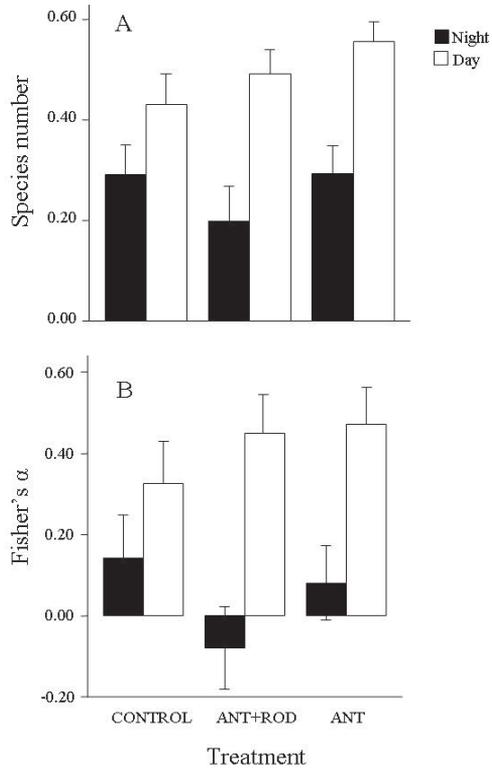


Fig. 1. Log species number (A) and log Fisher's α (B) (mean \pm SE), measured at the Ant, Ant+Rod and control plots, during night and day.

Table 1

Results of a repeated-measures ANOVA for the effects of treatment, sampling day and diel activity (night/day) on ant species number and Fisher's α

Source of variation	df	Log species number			Log Fisher's α		
		MS	F	p	MS	F	p
<i>Between-subjects</i>							
Treatment (T)	2	0.053	0.713	0.528	0.061	0.367	0.708
Error	6	0.074			0.167		
<i>Within-subjects</i>							
Sampling day (S)	4	0.276	8.044	< 0.001	0.839	7.186	< 0.001
Diel activity (D)	1	1.21	42.575	< 0.001	3.047	41.681	< 0.001
S \times D	4	0.127	6.167	< 0.001	0.389	5.130	< 0.005
T \times S	8	0.046	1.326	0.278	0.100	0.859	0.563
T \times D	2	0.049	1.734	0.254	0.230	3.145	0.116
T \times S \times D	8	0.013	0.633	0.742	0.056	0.742	0.654

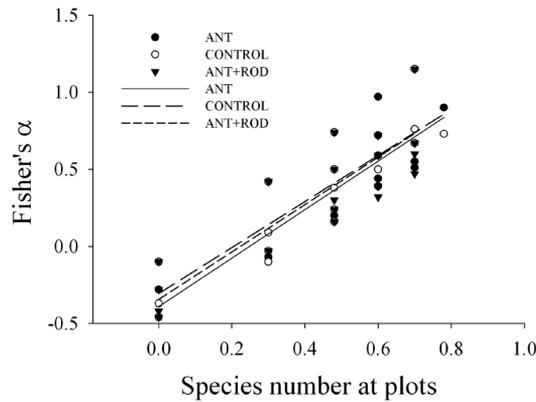


Fig. 2. The relationship between log number of species at plots and log Fisher's α , for the Ant, Ant+Rod and control treatments.

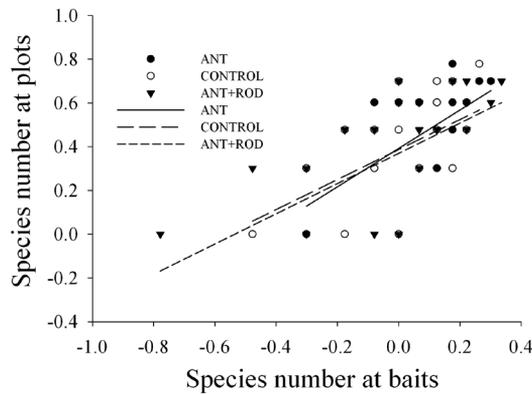


Fig. 3. The relationship between log number of species at baits and log number of species at plots for the Ant, Ant+Rod, and control treatments.

ANOVA: $F_{4,24} = 5.13$, $p < 0.005$), but the interactions between all the within-subject factors and the treatment effect were not significant (Table 1). A contrast test for the difference between Ant and control plots revealed no significant difference between day ($P = 0.291$) and night ($P = 0.661$).

The relationship between log species number at plots and log Fisher's α revealed a significant positive relationship for all treatments (Ant: $F_{1,28} = 113.33$, $r^2 = 0.80$, $p < 0.001$; control: $F_{1,28} = 92.97$, $r^2 = 0.77$, $p < 0.001$; Ant+Rod: $F_{1,28} = 133.52$, $r^2 = 0.83$, $p < 0.001$; Fig. 2). This suggests that the effect of sampling on ant species richness can be eliminated. The slopes for the linear relationship between log species number at baits and log species number at plots did not differ significantly between the treatments (ANCOVA: treatment \times species number in baits, $F_{2,84} = 0.274$, $P = 0.761$; Fig. 3). This

suggests that the rate of increase in species richness at plots with increasing species richness at baits is similar between treatments.

DISCUSSION

On both the local and regional scales, resource availability can regulate ant species diversity (e.g., Davidson, 1977; Kaspari et al., 2000; Arnan et al., 2007). In this study, we examined the effect of food augmentation on the diversity of seed-eating desert ants using a two-year enrichment experiment. Similar to the findings of several other studies (Davidson et al., 1985; Munger, 1992; Jean-Philippe Lessard, unpublished data), the results of this experiment revealed no significant effect of seed augmentation on species diversity (Fig. 1). Such a lack of effect could be attributed to the ability of ant colonies to cache food resources for long periods of time (Hölldobler and Wilson, 1990), which might mitigate any short-term effect of seed augmentation. This can be particularly true for harvester ants, such as *Messor* spp., which comprise three of the eight seed-eating ant species in our study region. In addition, it is possible that other regulatory factors, such as the availability of nest sites, could prevent an increase in ant species diversity even if the increased availability of resources potentially enables it (Kaspari, 1996; Andersen, 2000). Alternatively, it is also possible that seed augmentation may increase the size rather than the number of ant colonies.

Although only a trend, the number of ant species during the day was higher in the Ant compared to the control plots (Fig. 1A). It is possible that this increase in species diversity following seed augmentation was not significant due to the small sample size and hence weak statistical power of the test (i.e., five sampling days and three plots per treatment). This increase can be attributed to two different, not mutually exclusive, mechanisms: the “sampling mechanism” and the “abundance–extinction mechanism”. The results of this study suggest that the observed pattern cannot be exclusively explained by the “sampling mechanism”, which attributes diversity increase to increased sampling, because the relationship between Fisher’s α and the number of species per plot was significant for all treatments (Fig. 2). Conversely, this trend may imply that the “abundance–extinction mechanism” (Pimm et al., 1988) occurs in this desert-ant assemblage. Assuming that foraging activity at the baits is correlated with ant colony density, this trend suggests that the enriched plots support higher population densities than the control plots. This is consistent with other studies that were conducted in desert regions, which found that food availability can limit ant species diversity (e.g., Bernstein, 1975; Davidson, 1977; Marsh, 1986; Segev, 2010).

The results of this study agree with a growing number of studies showing that local food addition does not lead to a decrease in ant species diversity and abundance (e.g., Davidson et al., 1985; Munger, 1992; Kaspari and Valone, 2002). According to the findings, competition within the ant taxon and between ants and rodents did not affect ant species diversity in response to seed augmentation in this study region. Interspecific competition is known to be one of the main factors affecting the organization of ant

communities (e.g., Hölldobler and Wilson, 1990; Davidson, 1998; Sanders and Gordon, 2003). However, the slight increase in species diversity exhibited at the Ant, compared to the control plots (Fig. 1), and the insignificant effect of treatment on the relationship between species numbers at baits and plots (Fig. 3), suggest that food addition did not increase territoriality of the ant species on these two spatial scales. Similarly, while competition between ants and rodents is known to be important in the desert region (Brown and Davidson, 1977; Brown et al., 1986), the results of this and other desert studies suggest that inter-taxon competition does not lead to a decrease in ant species diversity following seed addition (Davidson et al., 1985; Brown et al., 1986).

In conclusion, various resource-augmentation experiments have revealed contradicting results of either increase, decrease, or no change in species diversity. Interestingly, although it has been suggested that in general species diversity will decrease with experimental increase of productivity (see Rosenzweig, 1995), a growing body of evidence from ant studies, including the present one, has failed to demonstrate such a pattern. Further studies examining the effect of enrichment along resource gradients, as well as using different organisms that differ in their ability to store food, are still needed.

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