Effect of harvester ants of the genus *Pogonomyrmex* on the soil seed bank around their nests in the central Monte desert, Argentina

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Abstract. 1. The abundance and composition of soil seed banks is a key determinant of plant community structure. Harvester ants can remove huge quantities of preferred seeds close to the nest affecting composition and spatial distribution of plants.

2. In the central Monte desert (Argentina) ants of the genus *Pogonomyrmex* have high seed removal rates, especially of the five main grasses. The aim of this study was to establish if their foraging activity affects spatial patterns of the soil seed bank around their nests. Our hypotheses were: (1) removal by ants decreases seed abundance of preferred species in the soil; and (2) the effect varies in time.

3. Soil seed abundance was assessed at different distances from *Pogonomyrmex* nests in the litter and in bare soil at the beginning, the middle, and the end of the season (late spring-early autumn).

4. A lower seed abundance of preferred species was observed close to the nest in the litter at the end of the season. Non-preferred species showed no distance gradient.

5. The lower foraging activity and seed consumption at the beginning of the season could explain the temporal variation of the spatial effect. This was only observed in the litter, probably because of the higher removal frequency in this substrate.

6. Colonies of *Pogonomyrmex* spp. could enhance the heterogeneity of soil seed banks in the central Monte desert from the summer to the beginning of the autumn. Implications for vegetation dynamics depend on the degree to which seed density limits perennial grasses recruitment after ant activity season.

Key words. Argentina, community ecology, granivory, *Pogonomyrmex*, top-down effects.

Introduction

In arid and semi-arid ecosystems, seeds constitute the most frequent life form of many plant species (Kemp, 1989). They accumulate in the soil surface forming seed banks and remain viable through long periods of time (Baker, 1989). Thus, the abundance and composition of soil seed banks is a key determinant of the plant community structure (Nelson & Chew, 1977; Reichman, 1984; Kerley, 1992; Guo *et al.*, 1998; Marone *et al.*, 2000; Gutiérrez & Meserve, 2003; Kelt *et al.*, 2004).

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Seeds are generally not homogeneously distributed in the soil. Spatial patterns vary both vertically with soil depth and horizontally across the surface (Simpson *et al.*, 1989; Guo *et al.*, 1998). The horizontal pattern is usually related to the distribution of microhabitat types with more seeds in natural depressions and under trees and shrubs than in the open areas between woody vegetation (Nelson & Chew, 1977; Reichman, 1984; Chambers & MacMahon, 1994; Marone & Horno, 1997; Guo *et al.*, 1998; Marone *et al.*, 2004). This pattern is partly caused by the spatial distribution of adult plants and the influence of abiotic and biotic factors, such as wind, which redistributes the seeds (Marone *et al.*, 1998a), and the presence of granivores, which may have high consumption rates (Mull & MacMahon, 1996; Pirk & Lopez de Casenave, 2006).

The most common granivores in desert ecosystems (i.e. birds, rodents, and ants) can exert a significant impact on soil seed abundance (Whitford, 1978; Brown *et al.*, 1979; Crist & MacMahon, 1992; Mull & MacMahon, 1996; Marone *et al.*, 1998b; Azcárate & Peco 2006), which in turn affects plant abundance (Brown *et al.*, 1979; Inouye *et al.*, 1980; Samson *et al.*, 1992; Heske *et al.*, 1993; Guo *et al.*, 1995). Moreover, their selective consumption of seeds and the selection of foraging patches can modify composition and spatial distribution of the vegetation (Inouye *et al.*, 1980; Samson *et al.*, 1992; Espigares & López-Pintor, 2005). The effects of granivores on seeds (top-down effects), however, may be influenced by seed abundance, which reciprocally affects the ecology and behaviour of consumers (bottom-up effects). Therefore, it is useful to have information on how seed abundance, distribution, and composition affect granivores to more accurately predict their effects on seed resources (Pirk *et al.*, 2009; Pol *et al.*, 2011).

Harvester ants can remove huge quantities of seeds, but this removal usually represents less than 10% of the total seed production (Pulliam & Brand, 1975; Whitford, 1978; MacMahon *et al.*, 2000). However, they can have a dramatic impact on preferred species (Whitford, 1978; Reichman, 1979; Pirk & Lopez de Casenave, 2006) of which they can remove up to 100% of available seeds (Crist & MacMahon, 1992). Harvester ant effects on seeds, however, are not always negative: some ants may accidentally disperse seeds (a dispersal system called dyszoochory) by abandoning them on the way to the nest, forgetting them in underground granaries, or mistakenly reject them intact on middens (Rico-Gray & Oliveira, 2007).

Ants are central-place foragers, i.e. they carry their forage to the nest. Consequently, seed collection is restricted to foraging areas relatively close to the nest and around trails (Crist & MacMahon, 1992; Mull & MacMahon, 1996). A few studies have explored the magnitude of the effect of seed consumption by ants on the soil seed bank around the nest. In a shrub-steppe of North America, *Pogonomyrmex occidentalis* (Cresson) has an effect on seed abundance, although it is restricted to certain microhabitats (Mull & MacMahon, 1996) and is very low compared with other granivores (Anderson & MacMahon, 2001). In the Negev desert of Israel, granivory by *Messor ebeninus* (Santschi) reduces seed species richness on trails, with important temporal variations (Nicolai & Boeken, 2012). Thus, harvester ants can influence spatial distribution of seeds around their nests but the effects depend on the study systems and particular species (e.g. their foraging strategy and colony size). Colony density and distribution are important in determining the effects at a broader scale; e.g. a lower effect is expected if colonies are scarce or an effect concentrated in certain areas if colonies show an aggregated pattern. Understanding the effects of ant consumption on soil seeds in relation to their nests and their density and distribution is crucial to have a complete picture of the different factors affecting soil seed bank spatial patterns in arid areas.

In the central Monte desert some studies provide evidence that autumn-winter granivores, mainly birds, might have major qualitative as well as quantitative impacts on soil-seed reserves (Marone *et al.*, 1998b; Marone *et al.*, 2008). The impact of seed consumption on seed banks in spring and summer, when ants are the most important granivores (Lopez de Casenave *et al.*, 1998), remains unexplored. Ant species of the genus *Pogonomyrmex* show relatively high seed removal rates (6×10^4 and 5×10^4 seeds per colony, for *P. rastratus* (Mayr) and *P. mendozanus* (Cuezzo & Claver), respectively; Pirk & Lopez de Casenave, 2006) throughout their foraging season (late spring-early autumn). These two species, as well as *P. inermis* (Forel) consume seeds on the soil at an average distance of 4 m from the nest entrance (Pol *et al.*, 2011). The three species concentrate their consumption on five main grasses, *Aristida* spp., *Pappophorum* spp., *Trichloris crinita*, *Digitaria californica*, and *Stipa ichu* (Pirk *et al.*, 2004, 2009; Pirk & Lopez de Casenave, 2006) of which at least *Aristida* spp. and *Pappophorum* spp. are also highly preferred (Pirk & Lopez de Casenave, 2011). Seeds carried to the nest are found in granaries (Nobua-Behrmann *et al.*, 2010) from where ants consume them. *Pogonomyrmex inermis* accumulates bracts and seed remains in external middens where no intact seeds were found, whereas *P. rastratus* does not accumulate discarded material around the nest (Pirk *et al.*, 2007). This suggests that these species behave exclusively as seed predators. Therefore, these ants could significantly reduce seed abundance of these species near their nests. Also, as foraging activity (Pol & Lopez de Casenave, 2004), seed removal rates (Pirk & Lopez de Casenave, 2006) and diet (Pirk & Lopez de Casenave, 2006; Pirk *et al.*, 2009) of these species vary throughout the season, their spatial effect on the seed bank may vary in time. More precisely, in a previous study we found that when preferred seeds are scarce (at the beginning of the season) *P. rastratus* changes its diet whereas *P. inermis* reduces its foraging activity, indicating bottom-up effects of resources on consumers which could attenuate potential top-down effects at this time of the season (Pirk *et al.*, 2009).

The aim of this study was to establish if ant foraging activity affects spatial patterns of the soil seed bank around their nests in the central Monte desert. We tested two hypotheses: (1) removal by *Pogonomyrmex* spp. ants significantly decreases seed abundance of preferred species in the soil; and (2) the intensity of this effect varies in time. Therefore, we expected a lower seed abundance of preferred species in the soil near the nest entrance, where most ant activity takes place, than at higher distances but no such difference in non-preferred species. We also expected a more marked pattern at the end of the summer, as bottom-up effects may attenuate effects of ants on seeds at the beginning of the season. Finally, we discuss the effect at a broader scale using data on colony density and distribution of the studied species.

Materials and methods

Study area

The study was carried out at the Biosphere Reserve of Ñacuñán (34°03′S–67°54′W), located in the central portion of the Monte desert, Mendoza Province, Argentina. The main habitat of the reserve, where this study took place, is the open woodland of *Prosopis flexuosa* where individuals of this species and of *Geoffroea decorticans* are scattered within a matrix of perennial

tall shrubs (>1 m height, mostly *Larrea divaricata*, but also *Condalia microphylla*, *Capparis atamisquea*, *Atriplex lampa* and *Larrea cuneifolia*), low shrubs (*Lycium* spp., *Junellia aspera* and *Acantholippia seriphioides*), and perennial grasses (e.g. *Trichloris crinita*, *Pappophorum* spp., *Sporobolus cryptandrus*, *Aristida* spp., *Digitaria californica*, and *Setaria leucopila*). Annual forb cover (e.g. *Chenopodium papulosum*, *Phacelia artemisioides*, and *Parthenium hysterophorus*) is highly variable from year to year.

Ñacuñán's climate is dry and temperate with marked seasonality. The mean annual temperature is 15.9 °C (1972–2004) and the mean annual rainfall is 342 mm (1972–2004) with high inter-annual variation. Seventy five per cent of the annual rainfall occurs in spring and summer (October–March).

Soil seed abundance and composition in Ñacuñán is very variable in space and time (Marone & Horno, 1997; Marone *et al.*, 1998a, 2004). In general, forb seeds enter the bank in spring, shrub seeds from late spring to early summer, and grass seeds from early summer to fall (Marone *et al.*, 1998a). As a consequence, the greatest accumulation occurs in winter whereas the minimum occurs at the beginning of the summer (Marone & Horno, 1997). As regards spatial patterns, forb seeds enter the bank through the microhabitats located beneath the canopy of trees and tall shrubs, and remain there after redistribution. Most grass seeds, in contrast, enter the bank through bare-soil and under-grass microhabitats, and reach more even distributions after secondary dispersal, especially because of important losses owing to granivory and wind redistribution in bare soil (Marone *et al.*, 2004). Therefore, seed abundance differs between different types of substrates. Seeds that reach areas with litter are not easily removed by the wind or the water and become trapped. Consequently, seed abundance in litter is higher than in bare soil (Marone *et al.*, 2004; Milesi, 2006).

Soil seed abundance

Soil seed abundance was assessed at different distances from *Pogonomyrmex* nests in Ñacuñán's open woodland on three occasions: at the beginning (October 2004), the middle (December 2004), and the end (April 2005) of ants' activity season. Only active colonies which were at least 20 m away from other *Pogonomyrmex* colonies were sampled. This was done in order to avoid studying colonies whose foraging areas overlapped, and thus to be able to attribute the observed patterns to a single colony. Once a colony was found, the absence of other active colonies was confirmed within a 20-m radius circular area around its entrance during periods of high ant activity on two different days per sampling occasion. In October, we randomly chose active colonies in the study area which fulfilled these requirements ($N = 8$; six *P. inermis*' and two *P. rastratus*' colonies). In December another *P. rastratus* colony was added ($N = 9$). In April, however, three *P. inermis*' and one *P. rastratus*' colonies were not sampled because they were inactive or active neighbouring colonies were found within 20 m of their entrance ($N = 5$).

On each sampling occasion, a 20-m transect, centred at the nest entrance of each colony, was laid at a random direction. In December and April this direction was changed at least $\pm 15°$

with respect to previous occasions to avoid resampling. Soil samples were extracted at two positions within three distance ranges on both sides of the nest entrance. These ranges represent different foraging situations (Pol *et al.*, 2011): close to the nest (at <0.5 m and 1 m from the nest entrance; light foraging), medium distance (at 2 and 4 m; intense foraging), and far from the nest (at 7 and 10 m; almost no foraging). At each position two samples were taken from bare soil and two from litter owing to the high heterogeneity in seed abundance among these substrates. Thus, a total of 48 samples per colony were obtained, except for some cases in which only one type of substrate was present. Each sample comprised a circular area of 64 cm², 0.5 cm deep. This depth was chosen because only surface seeds are available to several granivorous ant species (Reichman, 1979; Crist & MacMahon, 1992; Mull & MacMahon, 1996). Moreover, about 80% of the preferred grass seeds are found in the upper 1 cm of soil at Ñacuñán (Marone *et al.*, 2008). A Petri dish cover was used as a sampler. Its open side was pushed into the soil and then a metal scoop was pushed carefully under the bottom edge to isolate the contained soil. Samples were stored in plastic containers and taken to the laboratory where they were sieved under water pressure with a mesh of 0.27 mm, small enough to prevent the smallest grass seeds found in the seed bank of Ñacuñán from passing through the sieve (Marone & Horno, 1997). Seeds of the preferred species (*Aristida* spp., *Pappophorum* spp., *Trichloris crinita*, *Digitaria californica*, and *Stipa ichu*) found in the samples were identified and counted under a stereoscopic microscope. In April, all seeds present in the samples were identified and counted. Only sound seeds, i.e. those that did not crumble when probed with forceps (Mull & MacMahon, 1996), were considered in this study.

Statistical analyses

Abundance (seeds m⁻²) of sound seeds of *Aristida* spp., *Pappophorum* spp., *Trichloris crinita*, *Digitaria californica*, and *Stipa ichu*, was calculated for each distance range and for bare soil and litter separately. To obtain this variable, we averaged seed density of the two positions within each distance range at each side of the transect, for every colony on every occasion. Abundance of non-preferred seeds, total seed abundance, the proportion of preferred/total seeds, and seed diversity (Shannon–Wiener index) were estimated likewise for April samples.

We adjusted a linear mixed model for each variable per sampling occasion using the nlme package in R. Nests were considered randomised blocks, transects were included as a random factor nested within nests, and distance (near, medium or far from the nest), substrate (bare soil or litter), and species (*P. rastratus* or *P. inermis*) were fixed factors. As distance data are spatially correlated, we modelled the correlation structure using an exponential correlation model which has been found to fit spatial correlation data in varied applications well and is recommended for cases where data are not equidistant (Schabenberger & Pierce, 2002). However, models lacking this correlation structure were the ones with the best adjustment (as indicated by AIC and BIC values), and thus, are the ones we report here. Variables were square-root, reciprocal or log-transformed when

needed to achieve homogeneity of variances. Tukey's contrasts were performed when fixed factors or their interaction were significant.

Results

The seed density of preferred species was higher in the litter than in bare soil on the three sampling occasions (Fig. 1; Table 1). Distance from the nest entrance affected seed density only in April, but its effects depended on substrate type (i.e. there was a significant substrate × distance interaction; Table 1). Densities were the highest in litter samples far from the nest, but they were similar among distances in bare soil (Fig. 1c). Seed density also depended on ant species in April (Table 1). It was higher in *P. inermis* than in *P. rastratus*' nests (480.4 ± 80.4 vs. 151.4 ± 47.2 seeds m^{-2}) but general patterns were the same for both species (i.e. all interactions of distance, substrate, and species were not significant; Table 1).

When species-specific patterns were analysed, October seed density did not vary with distance from the nest in any of the five preferred species and it was higher in the litter than in bare soil (Fig. 2a–e; Table 2). Seed abundance of *S. ichu* was higher in *P. rastratus*' than in *P. inermis*' nests (29.3 ± 12.4 vs. 6.0 ± 25.6; Table 2), this was mainly due to a higher density of seeds in the litter of *P. rastratus*' nests (substrate × species interaction was marginally significant, $P = 0.07$). In December, distance had a significant effect on *S. ichu* seed abundance but depended on substrate type (i.e. substrate × distance interaction was significant; Table 3), with a much higher seed density in the furthest distance in the litter (Fig. 2j). Seed abundance of all species except for *Aristida* spp. was higher in the litter (Fig. 2f–j; Table 3). In April, there was an effect of distance on seed density of *Digitaria californica* and *S. ichu*, and the effect was also marginally significant ($P = 0.07$) for *T. crinita* (Fig. 2k–o; Table 4). In *D. californica* and *T. crinita*, the furthest distance differed from the closest distance from the nest, but in *S. ichu*, it also differed from the medium distance (Tukey's contrasts, $P < 0.05$). All species had higher densities in the litter.

In April, seed density of non-preferred species did not vary with distance from the nest and it was higher in the litter than in bare soil (Fig. 3a; Table 5). The proportion of preferred/total seeds in the soil differed with distance from the nest (Table 5). It was higher further than at a medium distance or close to the nest (Tukey's contrasts, $P < 0.05$; Fig. 3b). There was also a species effect, with a higher proportion of preferred/total seeds in *P. inermis*' nests (0.28 ± 0.04 for *P. inermis* and 0.11 ± 0.05 for *P. rastratus*). Finally, seed diversity differed between substrates but depended on species and distance (i.e. distance × substrate and substrate × species interactions were significant; Table 5). Diversity was lower in the bare soil than in the litter, but the lowest at a medium distance from the nest (Tukey's contrasts, $P < 0.05$; Fig. 3c). Also, it was the lowest in the bare soil for *P. rastratus* (0.92 ± 0.14 and 1.86 ± 0.14 in bare soil and litter, respectively, for *P. rastratus*; 1.33 ± 0.12 and 1.71 ± 0.12 in bare soil and litter, respectively, for *P. inermis*; Tukey's contrasts, $P < 0.05$).
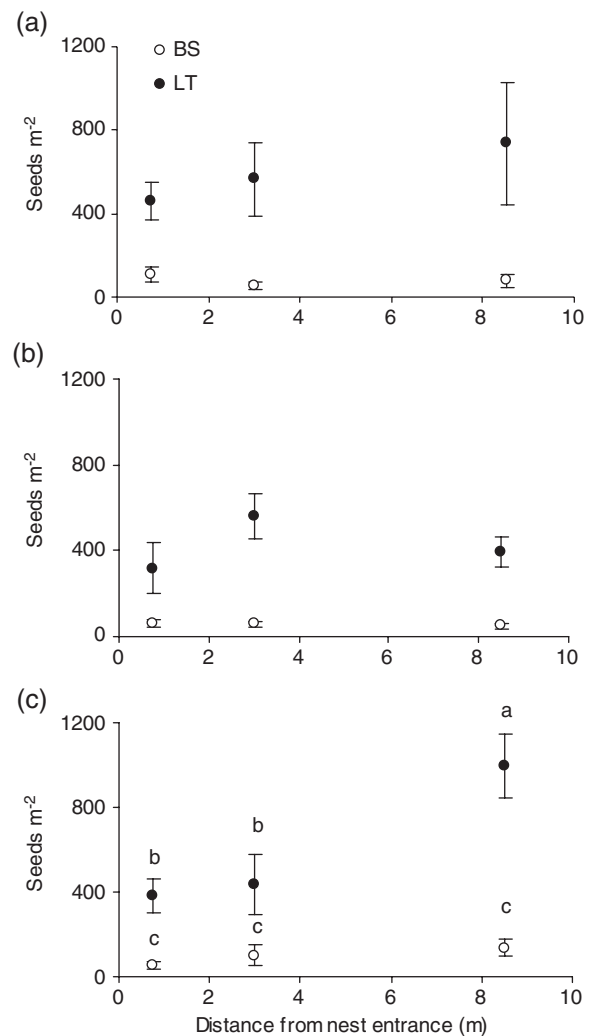
Fig. 1. The mean (±SE) seed density (seeds m^{-2}) of preferred seeds at different distances (m) from *Pogonomyrmex rastratus* and *P. inermis*' nest entrances in litter (LT; black circles) and bare soil (BS; open circles) in (a) October ($N = 8$ colonies), (b) December ($N = 9$), and (c) April ($N = 5$). When the substrate × distance interaction is significant, different letters indicate significant differences with Tukey's contrasts ($P < 0.05$). See Table 1 for more statistical results.

Discussion

The foraging activity of *P. rastratus* and *P. inermis* appears to affect seed abundance in the soil in the central Monte desert. A lower seed abundance of the most preferred species by both harvester ants was observed close to the nest entrance, where most of the foraging activity takes place, agreeing with our first hypothesis. Moreover, this effect varied in time as it was only evident at the end of the season, after most foraging activity had taken place, supporting our second hypothesis.

The temporal variation of the spatial effect of ants on the seed bank could be explained by analysing the temporal dynamics of seed removal. During mid-spring (i.e. October–November), the foraging activity is low (Pol & Lopez de Casenave, 2004) and

Table 1. Results of fixed factors in linear mixed models for seed density of preferred seeds at different distances (0–1, 2–4, and 7–10 m) from *Pogonomyrmex rastratus* and *P. inermis*' nest entrances in two substrates (litter and bare soil) in October, December, and April soil samples.

Source	d.f.	October F	October P	December F	December P	April F	April P
Distance	2	0.22	0.80	0.71	0.49	14.62	**<0.01**
Substrate	1	36.79	**<0.01**	13.35	**<0.01**	107.27	**<0.01**
Species	1	0.23	0.65	0.23	0.65	23.73	**0.02**
Distance × substrate	2	0.32	0.73	0.97	0.38	4.38	**0.02**
Distance × species	2	0.17	0.85	0.37	0.69	0.26	0.77
Substrate × species	1	1.82	0.18	1.96	0.17	1.66	0.20
Distance × substrate × species	2	0.14	0.87	0.50	0.61	0.30	0.74

Statistically significant results ($P < 0.05$) are shown in bold. Random factors (nest and transect) were not significant except for nest in April.

diet includes a lower proportion of seeds and a higher proportion of vegetative plant structures and invertebrates (Pirk & Lopez de Casenave, 2006; Pirk *et al.*, 2009). In fact, during the season when this study took place (2004–2005), seed proportion in the diet of these two species was lower in October than during the rest of the season (61% vs. >85% for *P. rastratus* and 64% vs. >95% for *P. inermis*, in October vs. the rest of the season, respectively, G. I. Pirk *et al.*, unpublished). The absence of an effect in October could be a result of a low consumption rate, determined by a low activity of the colonies, and by a lower proportion of seeds in the diet.

At the beginning of the summer (i.e. December), ant activity is higher than in spring (Pol & Lopez de Casenave, 2004) and the diet is concentrated on *S. ichu* seeds (Pirk *et al.*, 2009), the only C3 grass in the study site, whose seed production starts earlier than C4 grasses (Pol *et al.*, 2010). More precisely, in December 2004 *P. inermis* carried 72% and *P. rastratus* 86% *S. ichu* seeds (seeds were manually collected in 4 and 3 colonies, respectively; G. I. Pirk *et al.*, unpublished). During this period, no distance effect was detected when all preferred species were considered, but *S. ichu* seeds were significantly less abundant close to the nest. At the end of the summer ant activity decreases but the diet includes almost exclusively seeds of *Pappophorum* spp., *Aristida* spp., *T. crinita*, *D. californica*, and *Stipa ichu* (Pirk & Lopez de Casenave, 2006; Pirk *et al.*, 2009; see also Pol *et al.*, 2011). The high consumption of these seeds from mid-summer on resulted in a detectable effect in the soil seed bank in April, when a lower abundance of seeds was observed closer to the nest entrance. This trend was also observed in three of the five species when analysed individually.

Ant effects were only observed in the litter and not in the bare soil. The three species of the genus *Pogonomyrmex* present in Ñacuñán collect seeds more frequently from the litter than from the bare soil (75%, 61%, and 78% of punctual sites where seeds were taken by foragers of *P. rastratus*, *P. mendozanus*, and *P. inermis*, respectively, had litter; Pol, 2008), which explains the observed results. An alternative explanation, although not an exclusive one, is related to the horizontal redistribution of seeds. Although most grass seeds enter the bank through

open microhabitats with less litter cover (out of the influence of trees and shrubs), its abundance soon achieves more even distributions across microhabitats, mainly owing to the action of the wind, which would accumulate the seeds in areas under the canopy of trees and shrubs, with abundant litter (Marone *et al.*, 1998a). This way, if seed consumption had an effect on bare soil, it would be transient and difficult to observe because of a significant horizontal redistribution.

There is strong evidence that the observed decrease in seed abundance at the end of the season is a result of ant removal. In contrast, the species which are more affected on each occasion are the ones most consumed by these ants. Moreover, in April samples, when all species of seeds were analysed, the proportion of preferred/total seeds showed a distance gradient, whereas we found no gradient in non-preferred species. On the other hand, Pol *et al.* (2011) found that *P. rastratus* and *P. inermis* average foraging distance from the nest to the foraging site ranged from 3 to 4 m, and most foraging events (>80%) occurred within a radius of about 7 m. Precisely, the greater differences in seed abundance detected in April occurred between the close (0–1 m) and medium (2–4 m) distance ranges from the nest, and the furthest one (7–10 m), which is beyond the 'average' ants' influence. Finally, effects were only noticeable in the litter, where most foraging by these ants occurs.

In spite of the evidence supporting that ant activity causes seed bank patterns around the nest, other alternative explanations are worth analysing, such as a lower density of plants (and in turn a sparse seed rain) near the nest. Nevertheless, *Pogonomyrmex* spp. in Ñacuñán do not produce a free-vegetation disc around the nest entrance as other species in North America (MacMahon *et al.*, 2000). In fact, the *P. rastratus* nesting microhabitat has ~40% grass and ~25% forb and shrub cover (Pol, 2001). Grass cover at random points is very similar (~35%; R. G. Pol, pers. comm.), discarding a facilitation effect. Moreover, in April non-preferred species showed no distance gradient, suggesting that seed rain is not associated with nests. Also, a lower frequency of adult grasses of preferred species was not observed close to the nest (0.6 ± 0.1, 0.3 ± 0.1 and 0.4 ± 0.1, close, at a medium distance and far from the nest respectively; data taken in four colonies pooling grass species). Rodent and bird activity is relatively low during spring–summer in the central Monte desert (Lopez de Casenave *et al.*, 1998) and there is no evidence that their seed consumption may be associated with ant nests.

Our results differ from those on other harvester ants. In a shrub-steppe in Wyoming (U.S.A.), seed abundance was higher away from foraging trails of *P. occidentalis*, but *Bromus tectorum* seeds were more abundant close to the nest probably owing to facilitation effects (Mull & MacMahon, 1996). In the Negev Desert (Israel), although seed removal by *M. ebeninus* reduces availability along trails, seed dispersal from plants on nests has a greater influence on seed availability than granivory (Nicolai & Boeken, 2012). In contrast to these species, nests of *P. rastratus* and *P. inermis* in the Monte desert are just a small hole in the ground with similar plant cover as the rest of the environment (R. G. Pol, pers. comm.), forager abundances are relatively low (Nobua-Behrmann *et al.*, 2013), and they lack conspicuous foraging trails (*P. rastratus* is an exclusive solitary
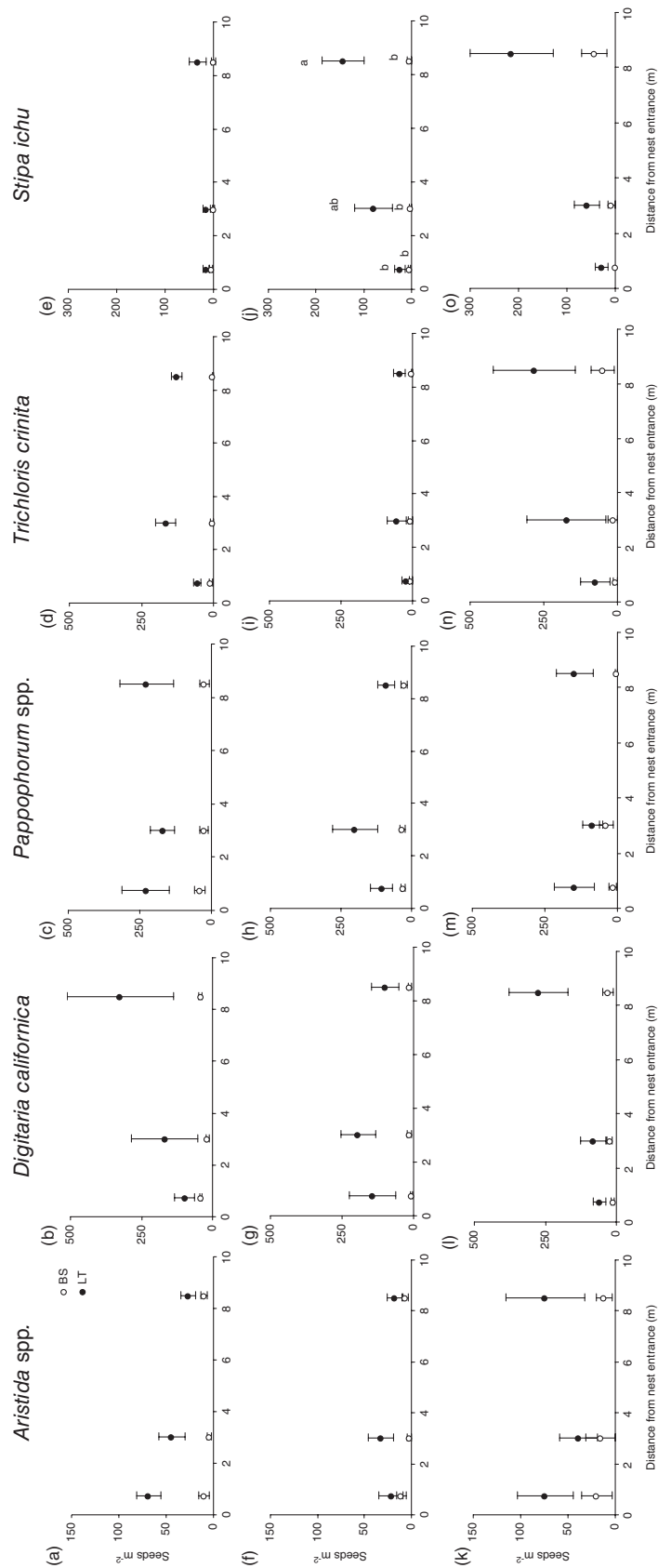
Fig. 2. The mean (±SE) seed density (seeds m^{-2}) of *Aristida* spp., *Digitaria californica*, *Pappophorum* spp., *Trichloris crinita*, and *Stipa ichu* at different distances (m) from *Pogonomyrmex rastratus* and *P. inermis*' nest entrances in litter (LT; black circles) and bare soil (BS; open circles) in (a–e) October ($N = 8$ colonies), (f–j) December ($N = 9$), and (k–o) April ($N = 5$). When the substrate × distance interaction is significant, different letters indicate significant differences with Tukey's contrasts ($P < 0.05$). See Tables 2–4 for more statistical results.

Table 2. Results of fixed factors in linear mixed models for seed density of the five species of preferred seeds at different distances (0–1, 2–4, and 7–10 m) from *Pogonomyrmex rastratus* and *P. inermis'* nest entrances in two substrates (litter and bare soil) in October soil samples.

Source	d.f.	*Aristida* spp.		*Digitaria californica*		*Pappophorum* spp.		*Trichloris crinita*		*Stipa ichu*	
		F	P	F	P	F	P	F	P	F	P
Distance	2	1.21	0.30	1.32	0.29	0.20	0.82	0.16	0.85	1.05	0.35
Substrate	1	6.61	**0.01**	5.48	**0.02**	29.21	**<0.01**	14.5	**<0.01**	11.66	**<0.01**
Species	1	4.06	0.09	1.32	0.29	0.99	0.36	0.64	0.43	7.23	**0.01**
Distance × substrate	2	1.51	0.23	0.58	0.56	0.02	0.98	0.90	0.41	2.51	0.09
Distance × species	2	0.50	0.61	1.27	0.29	0.08	0.92	1.41	0.32	0.54	0.58
Substrate × species	1	0.11	0.74	1.73	0.19	0.64	0.43	0.07	0.79	3.30	0.07
Distance × substrate × species	2	0.17	0.85	0.05	0.95	0.14	0.87	0.13	0.88	1.13	0.12

Statistically significant results ($P < 0.05$) are shown in bold. As for random factors (nest and transect), only nest was significant for *Aristida* spp., *Trichloris crinita*, and *Stipa ichu*.

Table 3. Results of fixed factors in linear mixed models for seed density of the five species of preferred seeds at different distances (0–1, 2–4, and 7–10 m) from *Pogonomyrmex rastratus* and *P. inermis'* nest entrances in two substrates (litter and bare soil) in December soil samples.

Source	d.f.	*Aristida* spp.		*Digitaria californica*		*Pappophorum* spp.		*Trichloris crinita*		*Stipa ichu*	
		F	P	F	P	F	P	F	P	F	P
Distance	2	0.11	0.89	0.22	0.80	1.37	0.26	0.20	0.82	8.61	**<0.01**
Substrate	1	1.72	0.19	5.06	**0.03**	5.12	**0.03**	10.11	**<0.01**	47.80	**<0.01**
Species	1	0.63	0.45	0.59	0.47	0.06	0.81	0.11	0.75	0.20	0.67
Distance × substrate	2	1.87	0.16	0.02	0.98	0.84	0.44	0.47	0.63	9.22	**<0.01**
Distance × species	2	2.45	0.09	0.31	0.74	0.60	0.55	1.66	0.20	1.51	0.23
Substrate × species	1	0.26	0.61	0.09	0.76	0.54	0.47	0.16	0.69	0.01	0.93
Distance × substrate × species	2	0.30	0.74	0.31	0.73	0.91	0.41	0.33	0.72	0.45	0.63

Statistically significant results ($P < 0.05$) are shown in bold. As for random factors (nest and transect), nest was significant in all species except for *Aristida* spp., and transect was significant in *Digitaria californica*, and *Trichloris crinita*.

foraging species and *P. inermis* uses a group-foraging strategy with limited recruitment; Pol, 2008). Thus, areas with low seed abundance are localised surrounding the nest entrance, rather than associated with trails as in other species.

Both the composition and the size of the soil seed bank in the central Monte desert are highly heterogeneous among microhabitats (Marone *et al.*, 2004), like in other deserts (Kemp, 1989; Chambers & MacMahon, 1994). Grass seeds predominate under grasses and in natural depressions of the soil whereas forb seeds accumulate under trees and tall shrubs (Marone *et al.*, 2004). Our study shows that *P. inermis* and *P. rastratus* reduce the abundance of preferred seeds in the litter in areas surrounding the nest entrance, adding another layer of heterogeneity at a similar spatial scale. Data of colony density, distribution, and temporal stability are crucial to integrate those spatial patterns. Colony density in the open woodland during the summer is around 15

Table 4. Results of linear mixed models for seed density of the five species of preferred seeds at different distances (0–1, 2–4, and 7–10 m) from *Pogonomyrmex rastratus* and *P. inermis'* nest entrances in two substrates (litter and bare soil) in April soil samples.

Source	d.f.	*Aristida* spp.		*Digitaria californica*		*Pappophorum* spp.		*Trichloris crinita*		*Stipa ichu*	
		F	P	F	P	F	P	F	P	F	P
Distance	2	0.79	0.46	3.12	**0.05**	0.17	0.85	2.83	0.07	6.02	**<0.01**
Substrate	1	12.73	**<0.01**	12.29	**<0.01**	32.81	**<0.01**	10.73	**<0.01**	10.73	**<0.01**
Species	1	0.01	0.94	1.88	0.26	1.26	0.34	0.91	0.41	0.91	0.41
Distance × substrate	2	0.33	0.72	2.67	0.08	1.39	0.26	1.33	0.27	1.23	0.30
Distance × species	2	1.81	0.18	0.35	0.70	2.34	0.11	0.86	0.43	0.86	0.43
Substrate × species	1	2.84	0.10	0.52	0.47	0.28	0.60	0.43	0.52	0.43	0.52
Distance × substrate × species	2	0.43	0.66	0.37	0.69	1.17	0.32	0.16	0.85	0.16	0.85

Statistically significant results ($P < 0.05$) are shown in bold. As for random factors (nest and transect), only nest was significant for *Aristida* spp., *Trichloris crinita*, and *Pappophorum* spp.
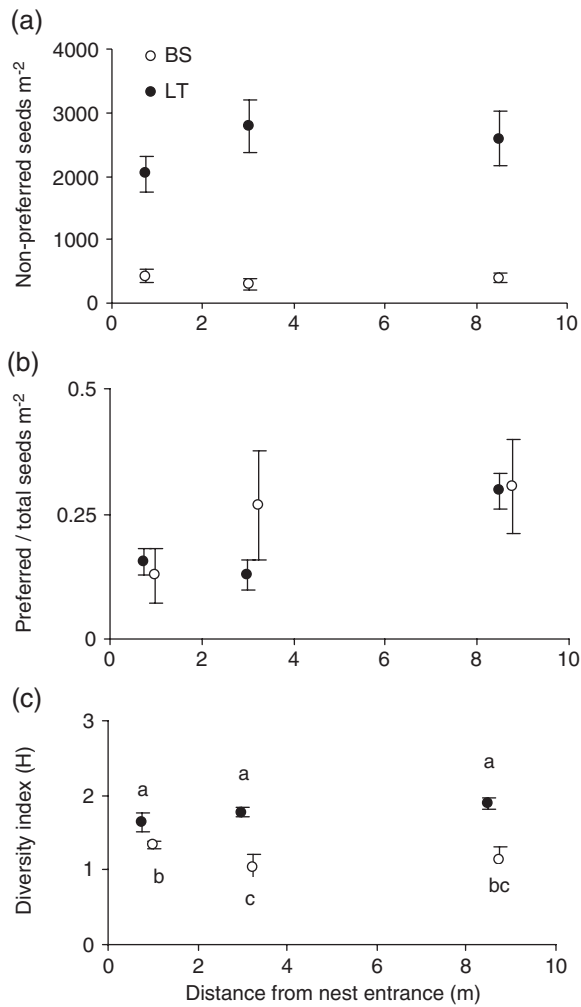
Fig. 3. The mean (±SE) seed density (seeds m^{-2}) of non-preferred seeds (a), proportion of preferred/total seeds (b), and seed diversity (Shannon–Wiener index, H) (c) at different distances (m) from *Pogonomyrmex rastratus* and *P. inermis*' nest entrances in litter (LT; black circles) and bare soil (BS; open circles) in April ($N = 5$ colonies). When the substrate × distance interaction is significant, different letters indicate significant differences with Tukey's contrasts ($P < 0.05$). See Table 5 for statistical results.

Table 5. Results of linear mixed models for seed density of non-preferred seeds, proportion of preferred/total seeds, and seed diversity (Shannon–Wiener index, H) at different distances (0–1, 2–4, and 7–10 m) from *Pogonomyrmex rastratus* and *P. inermis*' nest entrances in two substrates (litter and bare soil) in April soil samples.

Source	df	Non-preferred seeds		Preferred/total seeds		Seed diversity	
		F	*P*	*F*	*P*	*F*	*P*
Distance	2	0.35	0.71	4.07	**0.02**	0.87	0.42
Substrate	1	129.38	**<0.01**	0.31	0.58	62.74	**<0.01**
Species	1	0.01	0.97	11.34	**0.04**	0.63	0.48
Distance × substrate	2	2.07	0.14	0.74	0.48	3.97	**0.03**
Distance × species	2	1.25	0.30	1.71	0.19	1.55	0.22
Substrate × species	1	1.97	0.17	1.41	0.24	11.34	**<0.01**
Distance × substrate × species	2	1.05	0.36	1.16	0.32	1.10	0.34

Statistically significant results ($P < 0.05$) are shown in bold. As for random factors (nest and transect), only nest was significant for seed diversity.

colony effect would be the most relevant one, and would generate more evenly distributed patches of reduced abundance of preferred seeds (i.e. foraging areas around each nest).

If the spatial pattern generated by the ants was synchronised with high germination rates (which in Ñacuñán have a peak during warm months and is positively associated with rainfall; Marone *et al.*, 2000), a lower proportion of preferred species would be expected close to the nests. Several studies have concluded that harvester ant predation can affect annual plant densities in different systems (Inouye *et al.*, 1980; Samson *et al.*, 1992; Espigares & López-Pintor, 2005). In general, an increase in plant density and a variation in composition of species have been observed after ant removal. In contrast to annual plants, whose recruitment is mostly limited by seed supply, recruitment in stable populations of long-lived perennials often seems to be limited by the availability of safe sites (Putwain *et al.*, 1968; Grice & Westoby, 1987; Andersen, 1989). Consequently, recruitment patterns of perennial plants are relatively complex and the meaning of seed loss is very difficult to establish at the population level (Andersen, 1989). In a recent study, Marone *et al.* (2008) found that in the central Monte desert, in spite of moderate-to-high seed predation by birds during autumn–winter, the number of grass seeds that remains in the soil in spring would not limit seed germination and seedling recruitment. In contrast, safe-site availability and drought may be important factors limiting grass recruitment. Thus, in order to fully understand the implications of ant seed consumption on vegetation dynamics, it would be necessary to study if seed density in the soil actually limits the recruitment of perennial grasses after the harvester ant activity season.

Ants and seeds are affected reciprocally. This means that not only can ants reduce seed densities and affect composition and distribution of the remaining seeds through their selective consumption (i.e. top-down effects), but conversely, seed availability (i.e. its abundance, distribution, composition and quality) could affect consumers' ecology and behaviour (i.e. bottom-up

and 5 nests ha^{-1} for *P. rastratus* and *P. inermis*, respectively (R. G. Pol *et al.* unpublished). In addition to the very low colony density of *P. inermis*, in this study we show that overall seed density around *P. inermis*' nests in April was higher than that of *P. rastratus*, suggesting a lower foraging intensity, probably owing to their lower forager abundance (47 and 77 foragers per colony for *P. inermis* and *P. rastratus*, respectively; Nobua-Behrmann *et al.*, 2013). However, *P. inermis*' effect on the seed bank could be more relevant when their colony distribution is considered: their colonies tend to aggregate in clay-rich patches (F. A. Milesi, unpublished). Thus, their foraging would be more intense in particular areas, or more heterogeneous at a bigger scale. In contrast, *P. rastratus* colonies are more homogeneously distributed (F. A. Milesi, unpublished) so the individual

effects). Previous studies have shown that seed abundance in the environment can affect these ants' diet, particularly at the beginning of the season, when preferred seeds are still scarce (Pirk *et al.*, 2009; Pol *et al.*, 2011). As mentioned above, ants tend to carry items other than seeds, and among seeds, a higher proportion of shrub and forb seeds (i.e. non-preferred species). The flexibility observed in the diet of these species could mitigate top-down effects during periods of low resource abundance, as a less flexible diet would determine the highest effect on seed reserves when the most preferred species are scarce (Crist & MacMahon, 1992). Thus, in this system, bottom-up effects seem to prevail in spring whereas top-down effects are more important during the summer and the beginning of the autumn. This change is associated with grass seed production patterns which are tightly linked to rainfall patterns (Pol *et al.*, 2010). Thus, precipitation has a very important role in ant–seed interactions.

In conclusion, we found that harvester ants affect spatial patterns of soil seed banks in the Monte desert, but the intensity of these effects are linked to temporal dynamics of ant activity and seed phenology. Ants reduce seed abundance of preferred species close to the nest, creating patches of similar composition associated with nests within the open woodland. The extent to which this patterns translate into vegetation patterns needs to be explored taking into account that preferred grasses are perennial species.

Acknowledgements

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