Pogonomyrmex cunicularius as the keystone disperser of elaiosome-bearing *Jatropha excisa* seeds in semi-arid Argentina

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Abstract

Myrmecochory or seed dispersal by ants is often described as a diffuse mutualism, because many of the ant species that function as partners are considered to be similar in terms of the frequency and consequences of their interactions. In this work, we test this assumption by conducting ant community surveys and seed removal experiments in six study sites located within a semi-arid region of northwest Argentina. At each site, we characterized the ant assemblage that interacted with the seeds of *Jatropha excisa* Griseb. (Euphorbiaceae), an ant-dispersed native shrub. Our results demonstrate that seed removal was dominated by one species, *Pogonomyrmex cunicularius* Mayr (Hymenoptera: Formicidae: Myrmicinae), which was responsible of 84% of the observed seed removal events. Although several ant species were attracted to the elaiosome-bearing seeds of *J. excisa*, seed removal did not depend on ant community composition (species richness and ant activity) but was significantly influenced by the abundance of *P. cunicularius*. Its physical, behavioral, and ecological attributes are common with other ant species that have been characterized as keystone seed dispersers in other regions of the world. Nest feeding with marked seeds revealed that once *P. cunicularius* ants consume the elaiosomes, seeds are left inside the nests undamaged and at an appropriate depth for emergence. Our results support the hypothesis that myrmecochory is often an unevenly diffuse mutualism (i.e., one partner species is particularly important) and that at a local scale *P. cunicularius* is the keystone seed disperser of *J. excisa*.

Introduction

Myrmecochory, or seed dispersal by ants, is ecologically important and geographically widespread (Beattie, 1985; Rico-Gray & Oliveira, 2007). True myrmecochory involves the dispersal by ants of seeds bearing a lipid-rich appendage called an elaiosome. Myrmecochory is successful for the plant when ants collect and transport the seeds to their nests, where they consume the elaiosome without damage to the embryo. The seeds are then discarded inside the nest into nest chambers or outside into the refuse piles (Beattie & Culver, 1981). Myrmecochory has been described as a mutualism, with the ants benefiting from the nutritive

resources of the elaiosome and the plant profiting from the seed dispersal by ants (e.g., Beattie, 1985). The dispersal-related benefits for plants include (1) reduction in parent–offspring conflict and sibling competition, (2) avoidance of seed predators, (3) enhancement of seed germination, (4) avoidance of fire, and (5) relocation of the seeds to more favorable microsites (i.e., the nest) for survival, germination, and plant establishment (reviewed in Giladi, 2006).

The elaiosome contains mainly lipids but also proteins, carbohydrates, and vitamins (Fischer et al., 2008). Many studies have shown that seed disperser ants are specially attracted by the lipid components of the elaiosomes (e.g., Midgley & Bond, 1995; Pizo & Oliveira, 2001; Gammans et al., 2005; Boulay et al., 2006; Pfeiffer et al., 2010), which either are of important nutritional value or function as

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releaser of seed-carrying behavior in ants (Marschall et al., 1979; Brew et al., 1989; Skidmore & Heithaus, 1998). Nevertheless, this attractiveness is non-selective, and the elaiosomes have a large range of potential consumers among ants (Beattie & Hughes, 2002). In turn, ants do not need a clear morphological specialization for seed dispersal and elaiosome consumption, myrmecochorous seeds comprise only a minor portion of their diet, and the studies that tested for a net benefit to the ant colony as a result from this interaction are not conclusive (Morales & Heithaus, 1998; Marussich, 2006; but see Gammans et al., 2005).

As a result, myrmecochory has been generally considered a good example of diffuse mutualism, in which plant dispersal depends on a gallery of non-specific partners (Beattie & Hughes, 2002). However, this traditional view is now being reconsidered because, although several ant species are attracted to the elaiosome-bearing seeds, at the local scale, seed dispersal is in fact provided by a small subset of the ant community (Giladi, 2006). In Australia, seed dispersal is dominated by *Rhytidoponera* species (Gove et al., 2007), in the temperate deciduous forests of North America, species of the genus *Aphaenogaster* are the main removers of the seeds of ant-dispersed herbs (Smallwood & Culver, 1979; Zelikova et al., 2008; Ness et al., 2009), and in the Iberian Peninsula, *Camponotus cruentatus* (Latreille) and *Formica lugubris* Zetterstedt are the main seed dispersers of the myrmecochore *Helleborous foetidus* L. (Manzaneda & Rey, 2009). These studies have provided evidence that myrmecochory is, at least in these regions, not a diffuse mutualism, but one in which only a few (often in the order of one or two) ant species are disproportionately important for the interaction, dominating the seed dispersal process. Gove et al. (2007) termed this type of mutualism 'unevenly diffuse' and called the dominant ant seed remover species the 'keystone mutualist'.

Although ants are abundant and diverse in desert ecosystems (Hölldobler & Wilson, 1990; MacKay & MacKay, 2002) and myrmecochory is especially common in arid Australia (Berg, 1975; Beattie, 1985) and South Africa (Bond & Slingsby, 1983), in the deserts of South and North America true myrmecochory seems to be rare and has only been reported for a handful of plant species (O'Dowd & Hay, 1980; Bullock, 1989; Boyd, 1996; Ness & Bressmer, 2005; Marussich, 2006; Leal et al., 2007). Here, we describe for the first time myrmecochory in a semi-arid region of northwest Argentina while focusing on the removal and dispersal of a native ant-dispersed shrub, *Jatropha excisa* Griseb. (Euphorbiaceae). First, we characterize at six study sites the ant-disperser assemblage that was attracted to the elaiosome-bearing seeds of *J. excisa*, and we describe their interactive behavior toward the seeds. Second, we test the hypothesis that seed dispersal by ants is an unevenly diffuse

mutualism, which depends on one keystone mutualist. Therefore, we expect that variances in seed dispersal rates across the study sites will be positively related to variances in the abundance of a particular ant species and not to variances of the overall ant species community composition. Additionally, we followed the movements of marked *J. excisa* seeds within the nests of the main seed remover ant species of this study, *Pogonomyrmex cunicularius* Mayr (Hymenoptera: Formicidae: Myrmicinae). By doing this, we could find out the final location of the seeds once they were transported into the nest as well as their level of damage caused by ant manipulation.

Materials and methods

Study site

Field work was carried out at six sites located within a 1 600-km² area in the La Rioja province of northwest Argentina (distance between sites: 5–46 km; Table 1). This area is located within the northern portion of the Monte Desert biome and is characterized as an open shrubland dominated by *Larrea cuneifolia* Cav. (Zygophyllaceae) ('jarillal') (Abraham et al., 2009). Leguminosae (Fabaceae), Cactaceae, and Zygophyllaceae are the most speciose families in the area. Climate is semi-arid to arid, showing a marked seasonal and daily rhythm. Average annual temperature is 16.6 °C, and annual rainfall ranges from 145 to 380 mm, almost exclusively limited to the summer months (from December to March) (Anillaco Meteorological Station, data from 1999 to 2008). During the summer, ground insolation is high and soil surface temperatures may reach more than 60 °C (A Aranda-Rickert, unpubl.). Soils are typically low in organic matter and nutrients, particularly phosphorous and nitrogen (Abraham et al., 2009).

Although the six study sites shared a major part of their plant species composition, they differ in other aspects such as elevation, soil texture, percentage of plant cover, topography, and presence/absence of *J. excisa* (Table 1). Sites PH, PHE, ANJ, and SPP (see Table 1 for site abbreviations) represent typical Monte Desert habitats, whereas sites SP and CAR show a different physiognomy. The SP site has lower vegetation cover, possibly because water is less available, thus representing harsher environmental conditions. In contrast, the CAR site represents a transition between the Monte Desert and the Dry Chaco biomes, with larger amounts of summer rains and a denser plant cover.

Plant species

Jatropha excisa is a perennial, obligate seeding shrub endemic to northwest Argentina and Bolivia (Lourteig &

Table 1 Locations and brief description of the study sites within a semi-arid region of northwest Argentina

Location (abbreviation)	Coordinates	Elevation (m a.s.l.)	Habitat type	*Jatropha excisa* presence
Puerta de Huaco 1 (PH)	28°50′S, 66°39′W	927	Semi-arid – Monte Desert	−
Puerta de Huaco 2 (PHE)	28°54′S, 66°39′W	699	Semi-arid – Monte Desert	+
Anjullón (ANJ)	28°42′S, 66°56′W	1389	Alluvial fan – Monte Desert	+
Señor de la Peña (SP)	28°47′S, 66°53′W	1263	Arid – Monte Desert	−
Señor de la Peña Piedemonte (SPP)	28°46′S, 66°45′W	945	Piedmont – Monte Desert	+
Carrizal (CAR)	29°03′S, 66°41′W	669	Ecotone Monte Desert – Dry Chaco	+

O'Donnell, 1943). The species has a diplochorous seed dispersal system, which combines ballistic dispersal in a first step with dispersal by ants in a second step (Aranda-Rickert & Fracchia, 2010). Fruits are tricarpellate capsules with each carpel containing one seed. The seeds of *J. excisa* are considerably large for myrmecochorous seeds, with a mean ± SD fresh diaspore mass of 60.7 ± 11.8 mg. The elaiosome is conspicuous, whitish, and firmly attached to the micropyle of the seed, comprising ca. 4% of the total diaspore fresh mass. Seeds have a hard coat and a smooth surface. Dispersal of *J. excisa* seeds occurs during the summer season, with a peak in January–early February and again in March–early April (A Aranda-Rickert, unpubl.). Field observations revealed that seed shedding of *J. excisa* occurs synchronously across the populations here studied and that the phenology of seed setting overlaps with an overall seed production of shrubs and forbs (Marone et al., 1998). *Jatropha excisa* was the only myrmecochorous plant (i.e., with elaiosome-bearing seeds) in the study sites.

Experimental design

Within each of the six sites, five replicate 100-m transects, placed at least 2 km from roads and separated by at least 100 m, were randomly established. Transects consisted of 10 points (10-m spacing), each point representing a sampling unit (50 points per site). Trials were conducted during the summer of 2010 (January and February), coinciding with the peak of the overall ant activity (A Aranda-Rickert, unpubl.).

Characterization of the ant community

At each site, we estimated ant species richness and ant abundance by pitfall trapping. Ants were sampled at each point of transects (50 points per site). Pitfall traps consisted of 4-cm-diameter plastic cups (30 ml volume) partially filled with propylene glycol, which has been shown to neither significantly attract nor repel ants and effectively capture ground-foraging ants (Andersen, 1991; Bestelmeyer, 2000). Pitfall traps were buried flush with the soil surface and left for a period of 72 h. All traps were operated simultaneously. Contents were sorted and identified

to species or genus using Kusnezov (1963, 1978), Fernández (2003), and Cuezzo & Claver (2009).

Seed removal experiments

To describe the ant-disperser assemblage and estimate the site-level seed removal rate, we used the elaiosome-bearing seeds of *J. excisa*. At the time of our experiments, *J. excisa* seeds were maturing at the study sites; therefore, fresh seeds were obtained from mature capsules, stored at 4–5 °C in paper bags and used within 3 days for the trials.

At each site, and along three of the five 100-m transects described for pitfall trapping, we placed seed depots every 10 m, each consisting of a 7 × 5 cm white card anchored with nails to the ground (30 depots per site). Five fresh *J. excisa* seeds were placed on each depot. The observations were carried during the morning between 10:00 and 12:00 hours or during the afternoon between 16:00 and 18:00 hours. Pilot observations showed that a large proportion of seeds were removed during these hours by diurnal ant species. Seed removal trials were conducted three times, on days representative of the time of the year and within 1 week of the pitfall trapping sessions. A total of 2 700 seeds were offered at the six sites (5 seeds × 3 trials = 15 seeds per depot, 150 per transect, 450 per site).

Once the seeds were deposited, each depot station was observed for 5 min at 15-min intervals for up to 90 min (i.e., six times). During each 5-min observation, the ant species and number of individuals per species present on the card were recorded, as well as their interactive behavior toward the seeds. A total of 3 240 5-min observations were made at the six study sites (30 depots × 6 observations × 3 replications = 540 observations per site). Every time a dispersal event occurred, we measured the dispersal distance and destination (nest or lost). For ant species with recruitment strategies, unique dispersal events were those that involved a new depot or a new nest, regardless of how many times a single colony exploited a particular depot. For ant species with an individual foraging strategy, we considered each dispersal event as a unique event, assuming that each individual ant discovered the depot independently from other individuals of the same colony. All ant

species observed interacting with the seeds were collected, preserved, and identified to species using the same references as for the pitfall trap data.

To characterize the interactive behavior of the ants attracted to the *J. excisa* seeds, ant species were assigned to one of four functional groups [modified from Manzaneda et al. (2007) and Boulay et al. (2007)]: (1) legitimate dispersers, an ant that removes the seed from the depot; (2) elaiosome predator, an ant that partially or completely predates the elaiosome without transporting the seed; (3) mixed behavior, an ant that behaves indistinctly (i.e., seed removal and elaiosome consumption records were similarly represented); and (4) indifferent to diaspores, an ant that just antennates or examines seeds, but neither removes nor consumes elaiosomes.

Seed removal was monitored after the 90-min sessions. The number of seeds removed in each depot was counted and used as an estimate of dispersal success. A seed was considered removed when it was not found within a radius of 50 cm from the seed depot. As it was previously demonstrated that *J. excisa* seeds are removed only by ants, it was not necessary to use vertebrate exclusion cages (Aranda-Rickert & Fracchia, 2010). Under the assumption that seeds from different depots along the same transect were removed by ants belonging to different colonies owing to the 10-m distance between depots, each individual seed depot was treated as an independent replicate.

Ant species collected at depots were characterized by body size and recruitment strategy. Total length was measured in 10 individuals using a dissecting microscope with a micrometer and was calculated as the sum of the head length, the Weber's length (length of mesosoma in lateral view), and the petiole and gaster length. For polymorphic species (e.g., *Pheidole* spp.), we considered only the minor workers, as these were the ones that predominantly transported the seeds.

Ant nest excavations

During February 2010, we followed the fate of the *J. excisa* seeds that were transported to the nests of *P. cunicularius* ants, as this ant species removed the majority of the offered seeds during the seed removal experiments. At the PH site, six *P. cunicularius* nests were located by following returning workers. Fresh *J. excisa* seeds were marked with a small dot of enamel white paint, allowed to dry, and placed on the ground at 15-cm distance from the nest entrances. Each nest was offered 20 seeds. Nests were observed until all seeds were carried inside (approximately after 30 min). The seed movement within the nest was followed over a 15-day period: 2, 7, and 15 days after the seeds were offered. Two of the six nests were randomly selected and excavated. A pit was dug next to the colony, and chambers

were progressively exposed in their horizontal aspect. During each excavation, we noted the number and location of the marked *J. excisa* seeds inside the nest. Where seeds were found, we measured the depth of the chamber floor from the surface. The contents of each chamber were stored in separate containers and further analyzed in the laboratory, for overlooked seeds. Prior to the excavation, we also searched for marked seeds around the nest entrance. All recovered seeds were examined under a stereoscopic microscope in order to check damages caused by ant manipulation.

Data analysis

Species richness, species abundances, and ant activity (total number of workers of all species) in pitfall traps were summed for each transect. We used the transects rather than the pitfall traps as the unit of analysis in order to reduce the wide variance in capture rates owing to differences in the proximity of traps to nests. Transect values (n = 5 per site) were used to compare species richness and species abundances between sites using nested analysis of variance (ANOVA), with transects nested within sites. When differences were significant, Tukey's honestly significant difference (HSD) test was used for pairwise post-hoc comparisons. For those variables that did not meet normality assumptions, data were log-transformed. Occurrence was the percentage of pitfall traps in which a given species was collected per site.

Seed removal at each site was calculated as the proportion of seeds removed from each seed depot. Here, we summed the number of seeds removed per depot across the three trials (5 seeds × 3 trials = 15 seeds per depot and 150 seeds per transect) and used each depot as an independent replicate (n = 30 depots per site). A Kruskal–Wallis one-way ANOVA followed by a Mann–Whitney pairwise comparison test with Bonferroni correction was used to compare seed removal across sites, because data did not meet the assumption of normality even after an arcsine $\sqrt{x}$ transformation.

A general linear mixed model (GLMM) was used to examine the influence of ant species richness, ant activity, *P. cunicularius* abundance, and *Camponotus mus* Roger (Hymenoptera: Formicidae: Formicinae) abundance in pitfall traps on the arcsine $\sqrt{x}$-transformed proportion of seeds removed from depots. Transects and sites were treated as random factors. We included both the main seed remover (*P. cunicularius*) and the main seed predator (*C. mus*) ant species as predictors of seed removal in the model. Finally, we used simple linear regressions to examine the relationship between the significant variables in the model and the average proportion of seeds removed per site. All data were tested for normality and log- or

arcsine √x-transformed prior to analyses. All statistical analyses were performed using the STATISTICA 7 software package (StatSoft, Tulsa, OK, USA).

Results

Characterization of the ant community

Overall, 30 ant species belonging to nine genera and four subfamilies (Myrmicinae, Dolichoderinae, Formicinae, and Pseudomyrmecinae) were collected from the pitfall traps in the six sites. Sites showed variation in species richness at the transect scale ($F_{5,24} = 9.15$, $P<0.0001$) (Table 2). Species richness did not differ significantly between sites PH, PHE, ANJ, and SPP (Tukey's HSD test: $P>0.5$ for all comparisons). On the other hand, sites SP and CAR showed the lowest and the highest number of species among all sites, respectively (Tukey: $P<0.05$ for all comparisons), although neither of them harbored site-exclusive ant species.

Pogonomyrmex cunicularius was the most abundant ant species in terms of the number of individuals sampled across the study area. It occurred at five of the six study sites and made up 37.1% of the individual ants collected at all sites (total n = 8 383). The other most common ant species were *C. mus* (19.3% of total individual ants collected at the six sites), *Forelius chalybaeus* Emery (Dolichoderinae) (13.2%), and *Pheidole bergi* Mayr (Myrmicinae) (7.4%). At the five sites where *P. cunicularius* was recorded as present, at least one individual was found in each pitfall trap. At the transect scale, the abundance of *P. cunicularius* (all sites pooled) was significantly higher than the abundances of the other three most common ant species (ANO-
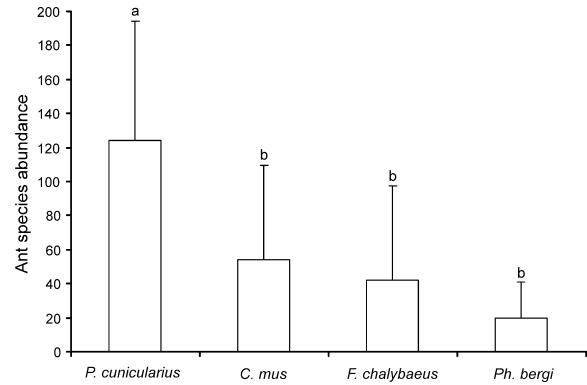

Figure 1 Mean (+ SD) number of individuals per transect for the four most common ant species (*Pogonomyrmex cunicularius*, *Camponotus mus*, *Forelius chalybaeus*, and *Pheidole bergi*) collected from pitfall traps at five study sites in northwest Argentina. Data are pooled from the five sites where *P. cunicularius* was collected; n = 5 transects, 50 pitfall traps per site. Different letters denote significant differences between sites (ANOVA followed by Tukey's HSD test: P<0.001).

VA on log-transformed data: $F_{3,24} = 14.73$, $P<0.001$; Tukey: $P<0.001$ for all comparisons) (Figure 1).

The abundance of *P. cunicularius* (mean number of individuals per transect) was significantly different between sites (ANOVA on log-transformed data: $F_{5,24} = 135.87$, $P<0.001$) (Table 2). Besides site SP, where the species was not present, site CAR showed the lowest abundance values among the six sites (Tukey: CAR vs. PH, PHE, and ANJ: $P<0.005$; CAR vs. SPP: $P = 0.29$), whereas highest abundances were found in sites PH, PHE, ANJ,

Table 2 Ant species richness, ant activity, and abundance of *Pogonomyrmex cunicularius* at the six study sites in northwest Argentina. Data were obtained from pitfall traps opened for 72 h (n = 50 per site)

	PH	PHE	ANJ	SP	SPP	CAR
Species richness	14	15	15	11	14	19
Mean spp. per transect ± SD (n = 5)	13 ± 1.58b	13 ± 2.54b	12.2 ± 2.16b	7.8 ± 2.38a	12.2 ± 2.49b	18.2 ± 1.92c
Ant activity	2341	1584	1390	422	1119	1527
P. cunicularius worker abundance	818	832	705	0	555	196
P. cunicularius abundance (mean ± SD) (n = 5)	163.6 ± 56.85a	166.4 ± 76.18a	141 ± 64.9a	0	111 ± 48.82ab	39.2 ± 13.73b
P. cunicularius occurrence (%) (n = 50)	100	100	100	0	100	100

Means in a row followed by different letters are significantly different (Tukey's HSD test: P<0.05).
Species richness: total number of species; ant activity: total number of individuals of all ant species; *P. cunicularius* worker abundance: total number of individuals per site; *P. cunicularius* abundance: mean number of individuals collected per transect at each site; *P. cunicularius* occurrence: percentage of pitfall traps where at least one individual was collected per site. See Table 1 for site abbreviations.
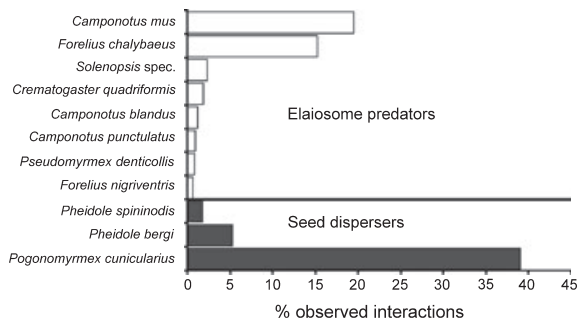
Figure 2 Percentage total observed interactions between ants and seeds of *Jatropha excisa* for each of 11 ant species in northwest Argentina. Above the horizontal line (white bars) are shown those species which behaved as elaiosome predators, and below it are shown the seed disperser species (black bars) (n = 832 interactions).

and SPP, with no significant differences between them (Tukey: P>0.5 for all comparisons).

Characterization of the ant-disperser assemblage and ant interactive behavior

A total of 832 ant–seed interactions involving 11 species were registered during 3 240 5-min observations at the six sites. From them, 387 (46.5%) corresponded to dispersal events, 410 (49.3%) to elaiosome predation, and 35 (4.2%) to ambiguous behaviors (Figure 2, Table 3). No mixed behavior was observed.

Three myrmicine ant species behaved as legitimate dispersers. One species, *P. cunicularius*, was responsible for the majority of the removal events, accounting for 84.0% (325 from 387) of the observed seed transports. The other two species, *Ph. bergi* and *Pheidole spininodis* Mayr, accounted for 11.4 and 4.7% of the records, respectively. Seven ant species behaved as elaiosome predators, and the most frequent were *C. mus* and *F. chalybaeus* (45.4 and 36.5% of the records, respectively). The other five species contributed in similar percentages to the total observed elaiosome predator behaviors (Figure 2, Table 3). Only one species, *Pseudomyrmex denticollis* Emery, showed an ambiguous behavior, acting both as an elaiosome predator and indifferently.

The three seed-dispersing species transported the seeds to their nests, and we never observed that the seeds were dropped or lost during transport. *Pogonomyrmex cunicularius* and the two *Pheidole* species differed in the method of seed holding during transportation, as well as in their distance of transport, foraging strategies, and body size (Table 3). *Pogonomyrmex cunicularius*, a large solitary forager species, carried the seeds individually, holding them with their mandibles high above the soil (Figure 3). The

average dispersal distance that seeds were carried was in the range of 7.5 m, and the maximal observed distance was up to 18 m (Table 3). In contrast, both *Pheidole* species carried the seeds cooperatively, in groups of 5–15 individuals, dragging them along the soil surface by reverse walking. For these *Pheidole* species, the seed-carrying distances were considerably shorter (approximately 1 m) compared to *P. cunicularius*.

Whereas in seed-dispersing ants, the initial antennation after discovering the seed was always followed by an almost immediate transport of the seed, elaiosome predators were never observed trying to drag the seeds. Instead, they stayed on the card and ate the elaiosome in situ. Body size alone does not explain the capability of being a disperser or an elaiosome predator, because large and small ant species are included in both functional groups (Table 3).

Seed removal

Pooling data from the six sites, ants removed a total of 1 425 (52.8%, n = 2 700) *J. excisa* seeds after 90 min of the beginning of the experiment. The number of seeds removed significantly differed between the six sites (Kruskal–Wallis test: $H_{5,174} = 102.2$, P<0.001) (Figure 4). Sites PH, ANJ, PHE, and SPP showed no significant differences in the number of seeds removed per depot (77.6, 75.1, 68.9, and 66.0% of 15 offered seeds per depot removed, respectively; Mann–Whitney test: P>0.1 for all comparisons). In contrast, at the SP and CAR sites, seed removal was significantly lower (Mann–Whitney test: P<0.001 for all comparisons). At site SP, ants removed 20.7% of the offered seeds, whereas at site CAR, removal was slightly higher (25.1%) but not significantly different from the SP site (Mann–Whitney test: P = 0.93).

The results of the GLMM analysis showed that the only variable that significantly influenced seed removals was the abundance of *P. cunicularius* (Table 4). Simple linear regressions demonstrated a positive and significant relationship between *P. cunicularius* abundance and the average proportion of seeds removed per site ($F_{1,5} = 9.43$, $r^2 = 0.70$, P = 0.037, n = 6) (Figure 5). Ant species richness, total ant activity, and *C. mus* abundance were not significantly related to the number of seeds removed (P = 0.99, 0.18, and 0.98, respectively).

Ant nest excavations

Pogonomyrmex cunicularius nests were on average 56.9 cm deep, harbored ca. 600 workers, and contained a mean number of 13.3 chambers, mostly concentrated in the upper portion of the nest (n = 6 nests). The nests have a unique entrance surrounded by a characteristic 20-cm-diameter disk made of coarse soil particles and lack an external refuse dump.

Table 3 Ant species that interacted with *Jatropha excisa* seeds at six study sites in northwest Argentina

Functional group	Species (subfamily)	Body size range (mm) (n = 10)	No. individuals (range)[1]	Behavior[2]	% total observed interactions (n = 10) (per functional group in parentheses)	Dispersal distance (m) (mean ± SD) (range in parentheses)
Seed disperser	*Pogonomyrmex cunicularius* Mayr (Myrmicinae)	9.0–9.5	1–3	IT	39.06 (83.97)	7.77 ± 4.54 (n = 30) (0.95–18.2)
	Pheidole bergi Mayr (Myrmicinae)	3.0–3.6	5–15	RT	5.28 (11.36)	1.2 ± 0.96 (n = 25) (0.3–4.1)
	Pheidole spininodis Mayr (Myrmicinae)	3.0–3.5	1–6	RT	2.17 (4.67)	0.84 ± 0.58 (n = 14) (0.32–2.6)
Elaiosome predator	*Camponotus mus* Roger (Formicinae)	7.5–9.0	1–7	GRS	26.97 (45.41)	–
	Camponotus blandus Smith F. (Formicinae)	8.0–13.0	1–3	GRS	1.17 (4.06)	–
	Camponotus punctulatus Mayr (Formicidae)	8.0–8.5	1–3	GRS	0.96 (2.29)	–
	Forelius chalybaeus Emery (Dolichoderinae)	2.5–3.5	5–36	MRS	15.26 (36.49)	–
	Forelius nigriventris Forel (Dolichoderinae)	2.5–3.6	4–32	MRS	0.72 (1.72)	–
	Solenopsis spec1 (Myrmicinae)	2.2–2.4	3–15	MRS	2.28 (5.45)	–
	Crematogaster quadriformis Roger (Myrmicinae)	3.4–4.0	5–20	MRS	1.92 (4.59)	–
Ambiguous	*Pseudomyrmex denticollis* Emery (Pseudomyrmecinae)	6.2–8.3	1–3	IS/IN	4.21 (100)	–

Ant species are organized in functional groups according to their type of interaction with the seeds and characterized with respect to their body size, recruitment, or individual strategy when interacting with seeds, behavior toward seeds, and percentage of observed interactions (n = 832). Mean ± SD dispersal distances are given only for ant seed dispersers.

[1]Number of individual ants per seed depot after 90 min of experiment.

[2]Behavior when interacting with seeds: IT, individual transport; RT, recruitment and transport; IS, individual in situ elaiosome consumption; GRS, group recruitment and in situ elaiosome consumption; MRS, mass recruitment and in situ elaiosome consumption; IN, indifferent.

Figure 3 A *Pogonomyrmex cunicularius* ant transporting an elaiosome-bearing seed of *Jatropha excisa*.

Over the 15-day period of the experiment, we recovered 100 seeds from a total of 120 seeds offered (mean number of recovered seeds per nest = 16.6 of 20 offered). A total of 10 seeds were found outside the nests and over the nest mound. Two days after the seeds were offered, 74.3% of the recovered seeds were found in the deepest chambers, which were located at an average distance of 48.5 cm from the surface. These chambers concentrated the brood and the majority of the callows (young workers) of the colony. We also found some seeds (17.1%) inside chambers located at a depth between 40 and 30 cm. These chambers contained also brood and callows but in lower number than the deepest chambers. An additional 8.6% of the seeds were rejected outside the nest.
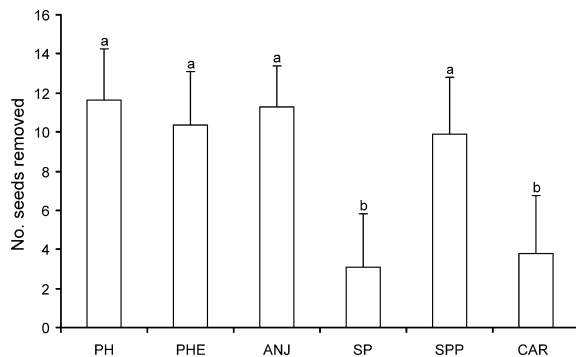

Figure 4 Seed removal by ants among the six sites within a region of northwest Argentina (see Table 1 for explanation of acronyms). Bars show the mean (+ SD) number of seeds removed from each seed depot after 90 min, pooling data from three trials (15 seeds per depot, 30 depots per site). Different letters denote significant differences among sites (Kruskal–Wallis followed by Mann–Whitney pairwise comparison test: $P<0.001$).

After 7 and 15 days of offering the seeds, no difference was found regarding the location of the seeds inside the nests. From the total recovered seeds, 87.7% were found inside the superficial chambers of the nest. These chambers were situated at an average depth of 5.8 cm and contained, besides the marked seeds, a considerable amount of rests of arthropods corpses and a few seeds of other plant species. No *J. excisa* seed was found in the brood chambers. The rest of the seeds were found outside the nest (10.8%), and one seed was found in an intermediate chamber.

All the seeds that were recovered inside the nest had their elaiosome completely removed. Seeds recovered outside the nests had their elaiosome either consumed or intact in equal percentages. A more detailed examination of the seeds revealed that while consuming the elaiosomes, ants scratched the testa of the seeds, especially in the micropyle where the elaiosome was attached. No recovered seed showed its embryo exposed nor consumed.

Discussion

The first finding of the present study is that within an area of northwest Argentina, seed dispersal activity of experimentally placed *J. excisa* seeds is dominated by one ant species, *P. cunicularius*. Variation in *P. cunicularius* abundance explained about 70% of the variation in the proportion of seeds removed at each site. At the six sites, the number of seeds that were removed from depots increased with increasing abundance of *P. cunicularius*, with the lowest values at the site where this ant species was absent. Our results support the hypothesis that myrmecochory is often an unevenly diffuse mutualism (i.e., one partner species is particularly important) (Gove et al., 2007) and that, at least at a local scale, *P. cunicularius* is the keystone seed disperser of *J. excisa* seeds. The low level of partner diversity for myrmecochory found here and in similar studies (Gove et al., 2007; Zelikova et al., 2008; Manzaneda & Rey, 2009; Ness et al., 2009) well compares with that observed in more specialized mutualisms, such as those involving pollinators and ants protecting plants (Wheelwright & Orians, 1982; Blüthgen et al., 2007), suggesting that the view of myrmecochory as a predominantly generalized interaction should be re-evaluated.

Ness & Morin (2008) have suggested that keystone seed dispersers may tend to be those species that are most abundant in local communities. Vázquez et al. (2007) have also pointed out that species abundance determines the frequency of interspecific interactions. Indeed, in our study area, *P. cunicularius* was the most abundant ant species: when present, and at the times of the day when this ant species is active, they can be seen virtually everywhere. Neither total ant worker abundance (total ant activity) nor

Table 4 Results of the general linear mixed model examining the influence of ant species richness, ant activity, *Pogonomyrmex cunicularius* abundance, and *Camponotus mus* abundance in pit-fall traps on the arcsine √x-transformed proportion of seeds removed from depots at six sites in northwest Argentina

Factor	d.f.	MS	F	P
P. cunicularius abundance	1	1.302	16.177	0.0012
C. mus abundance	1	0.026	0.331	0.57
Ant activity	1	0.183	2.273	0.15
Species richness	1	0.079	0.991	0.34
Error	14	0.080		

Transects (n = 5) and sites are treated as random factors. The second- and third-order interactions are not shown because they were not significant in any case

species richness accounted for any of the variation in the number of seeds removed.

It is worth noting that the presence of *J. excisa* was always related to the presence of *P. cunicularius* ants, but this relationship was not symmetrical, as site PH harbored the ant but not the plant. It remains a possibility that the environmental requirements of *P. cunicularius* are the same as for the plant, so they spatially coincide but they are not dependent on each other. The presence of the ant
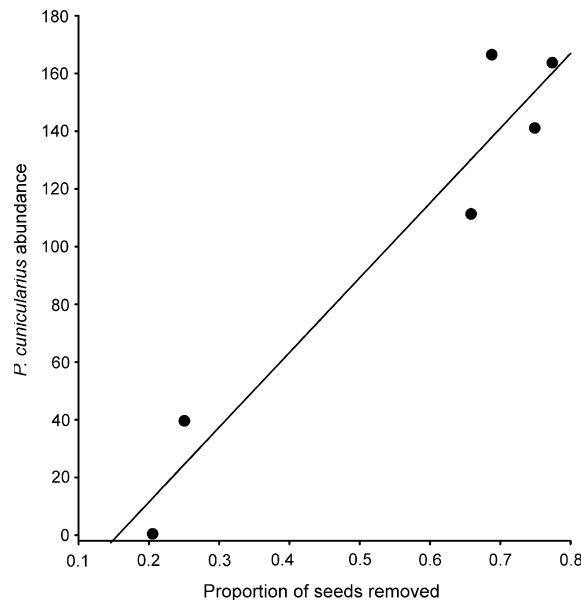

Figure 5 Relationship between the average proportion of seeds removed (15 seeds per depot, 30 depots per site) and the abundance of *Pogonomyrmex cunicularius* (mean number of individuals per transect; n = 5) in pitfall traps at six sites within a region of northwest Argentina.

but not the plant could mean that the plant has not yet colonized this site, but may be able to, by means of dispersal events such as flash floods. After one or more individuals have arrived, the interaction with the ants could then improve the successful establishment of the population within that site.

Elaiosome predation by ants occurred at all sites and with approximately the same frequency as seed dispersal. Moreover, more than twice as many ant species acted as cheaters (= elaiosome predators) than as dispersers. Ant species behaving as cheaters were characterized by both small and large body sizes, with both mass and group recruitment. Elaiosome predation was dominated by *C. mus*, a large-bodied, group recruiter ant that monopolized the seed depots with aggressive behaviors. The other common ant species found predating the elaiosome was *F. chalybaeus*, a small-bodied mass recruiter, and also a behaviorally dominant ant species. Small-sized dominant ants that recruit massively to forage have been reported as elaiosome consumers in other studies (Gove et al., 2007; Manzaneda et al., 2007; Castro et al., 2010). In contrast, other species of *Camponotus* have been found to behave either as legitimate seed dispersers (Leal et al., 2007; Zelikova & Breed, 2008; Manzaneda & Rey, 2009) or as indifferent to myrmecochorous seeds (Castro et al., 2010).

Elaiosome consumption without seed dispersal can be envisioned as a negative interaction from the plant's point of view, as the reward (the elaiosome) is consumed without the benefit of the transport of the seeds to the ant nests (Giladi, 2006; Boulay et al., 2007). Additionally, the gnawing of small pieces of the elaiosome may lead to a reduction in seed attractiveness, even when the elaiosome is not completely consumed (Castro et al., 2010). Therefore, this behavior may influence further interactions with other ant species, ultimately with a negative effect on the dispersal process (Boulay et al., 2007).

Not all seed removals are favorable dispersal events. The quality of dispersal depends on the particular ant species that takes the seed. The two major ant species that removed the *J. excisa* seeds differed substantially in a series of features. *Pheidole bergi* is a recruiter and small-bodied ant, able to transport seeds cooperatively only 1 m on average. This genus has been reported repeatedly as a seed disperser in a variety of habitats (Hughes & Westoby, 1992; Espadaler & Gómez, 1996; Leal et al., 2007), although it has also been categorized as a poor disperser or a 'low-quality' disperser. This is mainly attributable to short transport distances and high rates of embryo damage (Hughes & Westoby, 1992). Therefore, the capability of *Ph. bergi* to act as a legitimate seed disperser should be further assessed.

On the other hand, *P. cunicularius* shares several features with those ant species categorized as 'high-quality' and keystone seed dispersers in other localities, such as *Aphaenogaster* spp. or *Rhytidoponera* spp. (Gove et al., 2007; Ness et al., 2009). *Pogonomyrmex cunicularius* are locally abundant, solitary and long-distance foragers, large-sized, and behaviorally subordinated ants that inhabit transient and shallow nests and have an omnivorous scavenging diet (Kusnezov, 1963; A Aranda-Rickert, unpubl.). All these ant traits have been related to a high quality of seed dispersal (Giladi, 2006; Gove et al., 2007). We concur with Rico-Gray & Oliveira (2007), who suggested that the cumulative effects of several ant traits and behaviors, rather than a single trait, is what determines that a certain ant species will behave as a 'high-quality' seed disperser. Conversely, plant traits related to seed dispersal by ants should match ant traits of 'high-quality' disperser ants. Seed and elaiosome sizes (Garrido et al., 2002; Alcántara et al., 2007), elaiosome chemistry (Boulay et al., 2006), fruiting and dissemination phenologies (Oberrath & Bohning-Gaese, 2002; Guitián & Garrido, 2006), and rates and modes of seed presentation (Hughes & Westoby, 1992; Oberrath & Bohning-Gaese, 2002; Boulay et al., 2007) are all plant traits that may determine the dispersal success of a myrmecochorous plant under a specific ant's community.

The excavation of *P. cunicularius* nests showed that within the first 48 h of being transported to the nests, the elaiosomes are fed to the brood. Once the elaiosome is consumed, seeds are vertically transported to the uppermost chambers of the nest, where the waste material is deposited. Because the hard coat of the *J. excisa* seeds prevents their damage by the ants' mandibles (Rodgerson, 1998), the embryo of the seeds remained intact after the elaiosome was consumed, whereas the scarification of the seed coat and/or the removal of the elaiosomes may improve their germination as it does in other species (Hutchinson & Ashton, 1979; Horvitz, 1981; Ohkawara, 2005).

The deposition of the seeds in the inside waste chambers suggests that seeds without the elaiosome are considered waste material. We discard the possibility of these seeds to be used as food because *Pogonomyrmex* harvesting ants store the seeds that will be later consumed in granary chambers usually situated in the deepest part of the nest (Tschinkel, 1999). The final deposition of the seeds inside the nest rather than in external refuse dumps is considered to be more advantageous for plants, because to be buried gives the best conditions for germination (Beattie & Culver, 1982; Gibson, 1993), whereas those expelled outside run the risk of post-dispersal predation and environmental disruption (Beattie, 1985; Giladi, 2006). However, if seeds are buried too deep, seedlings may never reach the soil surface. Maximum seedling emergence depth scales allometrically with seed weight (Bond et al., 1999), and for the *J. excisa* seeds, this predicted depth is 10.8 cm. Therefore, the average depth (5.8 cm) at which the seeds were found inside the *P. cunicularius* nests certainly allows their emergence as seedlings.

Interestingly, the same pattern of specialization found in our study, in which true myrmecochory is limited to the *J. excisa* plants, has been found in regions where ant-mediated seed dispersal is fairly common, as is the case of southwest Australia and eastern North America (Berg, 1975; Beattie & Culver, 1981). Moreover, the autecology of the main seed disperser ant of this study, *P. cunicularius*, is strikingly similar to that of the main seed disperser ant species described for these regions, mainly *Rhytidoponera violaceae* (Forel) (Lubertazzi et al., 2010) and *Aphaenogaster rudis* Enzmann (Ness et al., 2009). This raises the question about the possible evolutionary pathway that has lead to the relationship between *P. cunicularius* ants and *J. excisa* plants in northwest Argentina.

We conclude that seed dispersal of *J. excisa* in our study region was not a function of the entire ant fauna but instead was largely driven by one ant species, *P. cunicularius*. Its high local abundance, colony organization, and morphological and behavioral traits all likely contribute to the role that these ants play as the keystone seed disperser of a myrmecochorous plant in northwest semi-arid Argentina. Further studies will be conducted to explore whether *P. cunicularius* dispersal services to *J. excisa* remains constant across the plant distribution range or alternatively, other ant species functionally replace it, as well as to confirm that such specialization is a species-level trait rather than a mere attribute of local populations where *J. excisa* grows.

Acknowledgements

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