A shift in seed harvesting by ants following Argentine ant invasion

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A SHIFT IN SEED HARVESTING BY ANTS FOLLOWING ARGENTINE ANT INVASION

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ABSTRACT. – The effect of Argentine ant (*Linepithema humile*) invasion on the dispersal - predation balance of non-myrmecochorous seeds by ants and vertebrates is analyzed. Three Papilionaceae, *Calicotome spinosa, Psoralea bituminosa*, and *Spartium junceum*, were studied. The seeds were made available in field trials during 48 hour periods using ant and vertebrate exclusions in zones invaded by *L. humile* and non-invaded zones. The Argentine ant invasion resulted in the displacement of most of the native ant species, including the single seed predator ant in the non-invaded zone, *Messor bouvieri*. Consequently, the level of seed removal by ants was lower in the invaded zone for the three seed species. This could produce two opposite effects for the plant: a positive reduction of seed predation and a negative loss of seed dispersal due to diszoochory (the seed dispersal performed by seed eating ants). The three studied species suffered different intensities of seed removal by ants in the non-invaded zone, so they would be affected to varying degrees after the invasion. The level of seed removal by vertebrates was lower than seed removal by ants and was similar in the invaded and non-invaded zones and for the three seed species.

INTRODUCTION

Invasions by non-native ants are an ecologically destructive phenomenon affecting both continental and island ecosystems throughout the world (Williams 1994, Holway *et al.* 2002). The Argentine ant (*Linepithema humile* Mayr) is a well documented example. Native to south of the Parana River in Argentina (Tsutsui *et al.* 2001), this well known invasive species (McGlynn 1999) has been introduced in various zones of the world due to human commercial activities (Hölldobler & Wilson 1990, Suarez *et al.* 2001). The widely reported competitive displacement of native ants caused by invasive ants (Hölldobler & Wilson 1990, Porter & Savignano 1990, Williams 1994, Hoffmann *et al.* 1999, Holway *et al.* 2002) is also well documented in its case, and worldwide *L. humile* has decimated native ant faunas where it has been introduced (Cammell *et al.* 1996, Human & Gordon 1997, Suarez *et al.* 1998, Holway 1999, Gómez & Oliveras 2003, Sanders *et al.* 2003). These reductions in the diversity and abundance of native ants resulting from ant invasions give rise to a variety of direct and indirect effects on non-ant taxa of both animals and plants (Holway *et al.* 2002).

The key role of ants in the seed dispersal processes of many plants worldwide is now unquestionable. Therefore, changes in the composition of ant assemblages could alter these ant-seed relations, drastically affecting the seed dispersal process. If the alteration of the native ant community is a consequence of the introduction of an exotic, highly competitive species, the impact on the seed dispersal process and the subsequent reproductive success of the plant will depend on the ability of the invasive

ant to assume the role of the displaced native ant species (Lach 2003). Some studies have focused on the impact of Argentine ant invasion on the seed dispersal process of myrmecochorous seeds (Bond & Slingsby 1984, Quilichini & Debussche 2000, Christian 2001, Carney *et al.* 2003, Gómez & Oliveras 2003, Gómez *et al.* 2003). The results obtained vary and in some cases the Argentine ants seem capable of dispersing some seeds, although certainly not to the same extent as native ants (Quilichini & Debussche 2000, Gómez & Oliveras 2003), so it seems clear that the invasion may negatively affect the seed dispersal process of most myrmecochorous species. However, the effect on non-myrmecochorous seeds is still unknown. Here, the impact could be different. Despite the omnivorous character of *L. humile* (Newell & Barber 1913), seeds are not included in its diet (Human *et al.* 1998). Its documented attraction to seeds (Bond & Slingsby 1984, Midgley & Bond 1995, Carney *et al.* 2003) and even transport of these seeds (Quilichini & Debussche 2000, Gómez & Oliveras 2003) includes only myrmecochorous species where the lipid rich elaiosome attached to the seed is the only attractive element, whereas non-myrmecochorous seeds are unlikely to be used by this species. In fact, among the known harvester ant species, Dolichoderines are absent (Hölldobler & Wilson 1990).

Non-myrmecochorous seeds are only collected by species of a particular guild of ants known as harvester ants which regularly consume seeds as part of their diet. As opposed to disperser ants, harvester ants feed on the seeds themselves (Hölldobler & Wilson 1990). These ants are important seed predators in arid and semi-arid regions of the world, including dry open Mediterranean biotopes.

Wherever they occur, they are capable of inflicting severe seed losses (Andersen 1991) and are often serious grain pests (Hölldobler & Wilson 1990, Andersen 1990, Taber 1998). Moreover, seed predation and other activities of harvester ants could have an effect on the composition and structure of plant communities (Briese 1982, Nowak *et al.* 1990, MacMahon *et al.* 2000, Anderson & MacMahon 2001, Rey *et al.* 2002). Therefore, we expect that the displacement of native ants after invasion will reduce the impact of harvester ants on seeds in invaded areas, thus resulting in a reduction of the number of seeds lost by predation. This could enhance the reproductive effectiveness of these species, and thus potentially alter the structure of the plant community.

This study analyses the impact of the invasion of the Argentine ant on the removal of the non-myrmeco-chorous seeds of three long-lived perennial Mediterranean plants. Specifically we analyze if the level of seed removal by granivorous ants and vertebrates is altered after the invasion. We also discuss the potential impact of the invasion on non-myrmecochorous species.

METHODS

Study area: The study was carried out in summer 2003 in the Serra Llonga, in the southern edge of the Gavarres Massif, near the village of Castell d'Aro (NE Spain) (41° 49' N, 3° 00' E). The study area is 4 km from the Mediterranean coast. The climate of this region is Mediterranean subhumid, with 627 mm of annual rainfall, a minimum temperature in January ($7.2°C$) and a maximum in July ($22.6°C$). In this area we can found invaded and non-invaded zones separated by the invasion front. The Argentine ant distribution in the study area is concentrated principally in those zones next to urbanized areas from where its access and subsequent expansion in less-altered areas started. Both study zones are situated at elevations of 200 to 300 m.a.s.l. and vegetation is open cork oak secondary forests dominated by *Quercus suber* (L.), *Q. ilex* (L.), *Erica arborea* (L.), *Cistus mon - speliensis* (L.), *C. salvifolius* (L.), and *Arbutus unedo* (L.). The relative proximity, as well as the similar characteristics of vegetation, face, slope, and altitude of the study zones allow us to assume that the composition of the native ant community previous to the invasion in the now invaded zones would have to be very similar to that found in the non-invaded zone.

Plant species: In this study we used the seeds of three long-lived perennial Papilionaceae present in the study area: *Calico - tome spinosa* (L.), *Psoralea bituminosa* (L.), and *Spartium junceum* (L.). The three species produce seeds without an elaiosome, so they are not adapted to myrmecochorous seed dispersal. However, these seeds are collected and consumed by harvester ant species. All seeds are of small size, thick coated, and their masses are: (mean ± SE) *C. spinosa* = 8.47 ± 0.35 mg (n = 200), *P. bituminosa* = 13.76 ± 0.29 mg (n = 100), and *S. junceum* = 14.66 ± 0.22 mg (n = 150). Fruit maturation and seed dehiscence of the three species occur generally throughout

July. The seeds used in the trials were obtained collecting mature fruits or directly from the plant in the field. The fruits were transported to the laboratory in paper bags and were left there until dried and dehisced, when the seeds were then obtained. The seeds were handled with forceps throughout the trials.

Ant species: Previous studies performed in the same area (Gómez & Oliveras 2003, Gómez *et al.* 2003) and recent visual inspections of the study zones where the trials were performed allowed verification that the ant community in the invaded zone was highly dominated by the Argentine ant. No harvester ant species were observed within the invaded zone. In the non-invaded zone the ant community was much diverse and one harvester ant species was detected, *Messor bouvieri* Bondroit. Some trails of this species were observed, mainly in the most open sites and in the paths.

Attraction of ants to seeds: The seeds of the three studied species are all included in the diet of *M. bouvieri* as workers were often observed carrying them to the nests, and broken coats of these seeds were frequently found in refuse piles of the nests. On the other hand, these seeds are presumably neither transported nor consumed by the Argentine ant, seeing that *L. humile* workers did not show any attraction to the seeds of any of the three species and never tried to take and carry them to nests, as we observed in offers made in the field (no transport response in n = 50 seeds offered by each plant species).

Seed removal trials: Seeds were prepared with four different treatments to discriminate between the roles of ants and vertebrates with regard to seed removal: 1) vertebrate exclusion, where seeds were placed in a Petri dish covered by a wire mesh (8 mm inner diameter), so that ants had access to the seeds but vertebrates (birds during the day and rodents at night) did not; 2) ant exclusion, where seeds were fixed with a colourless (and odourless to humans when dry) glue in a Petri dish, so vertebrates could remove the seeds but ants could not; 3) total exclusion, which consisted of a combination of the two exclusion treatments described above, so neither ants nor vertebrates could remove the seeds (used to prove the effectiveness of the exclusion methods); and 4) control, where seeds were placed in a Petri dish and were accessible to both ants and vertebrates. The trial consisted of 100 Petri dishes (9 cm in diameter), 25 for each treatment, placed at 2 meter intervals along a transect. The four treatments were alternatively arranged along the transect. All experiments were done within one week of the normal period of seed dispersal. Two transects (one in the invaded zone and one in the non-invaded zone) were established for each plant species. Ten seeds of each plant species (but five for *P. bituminosa* due to lower seed availability) were placed in each Petri dish. Thus, a total of 1000 seeds of each plant species (500 for *P. bituminosa*) per zone were used in the trials. The frequencies of seed removal were checked at sunset and sunrise at both sites during a 48 hour period.

Data analysis: The number of removed seeds per dish after the 48 hours of exposure in the field was compared between zones for each seed species and each treatment using the Mann-

Whitney U-test. On the other hand, comparisons between seed species were done with the Kruskal-Wallis H-test, and there the proportion of removed seeds per dish was used because of the different number of seeds per sample unit used in the three species. Data were not transformed in the analyses. All analyses were performed using SPSS package for Windows version 11.5 (SPSS Inc).

RESULTS

Exclusion effectiveness

No seeds were removed from dishes with the total exclusion treatment (Table I), so the exclusion methods used were effective – wire mesh effectively stopped removal of seeds by vertebrates and glue had the same effect on ants. Therefore, the total exclusion treatment was not included in the analyses.

Seed removal by ants

After 48 hours of exposure in the field, seed removal from the Petri dishes treated for vertebrate exclusion was significantly lower in the invaded zone than in the non-invaded zone for the three plant species ($C. spinosa$, $U = 89.0$, $df = 1$, $P < 0.001$; $P. bituminosa$, $U = 233.5$, $df = 1$, $P < 0.05$; $S. junceum$, $U = 180.5$, $df = 1$, $P < 0.01$) (Table I). The total percentage of seed removal by ants for the three seed species was 3.0% (n = 625 seeds) in the invaded zone and 32.0% (n = 625 seeds) in the non-invaded zone. Seed removal by ants occurred during both diurnal and nocturnal periods in the non-invaded zone whereas in the invaded zone the few seeds were mainly removed during night periods (Fig. 1A). The mean proportion of seeds removed by ants was significantly different between the three seed species in the non-invaded zone ($H = 11.381$, $df = 2$, $P < 0.01$), seeds of $C. spinosa$ being the most removed (46.4%, n = 250) and seeds of $P. bituminosa$ the least removed (12%, n = 125) (Table I). In the invaded zone no significant differences in the proportion of seeds removed between the three species were detected ($H = 1.591$, $df = 2$, $P = 0.451$).

Seed removal by vertebrates

Vertebrates removed a lower number of seeds than ants in the two study zones (Table I). The total percentage of seeds removed from the Petri dishes treated for ant exclusion for the three seed species was 0.2% (n = 625 seeds) in the invaded zone and 5.1% (n = 625 seeds) in the non-invaded zone. The intensity of seed removal was not significantly different between zones for any of the three plant species ($C. spinosa$, $U = 300.0$, $df = 1$, $P = 0.317$; $P. bituminosa$, $U = 312.5$, $df = 1$, $P = 1.000$; $S. junceum$, $U = 286.0$, $df = 1$, $P = 0.274$) (Table I). The presence of broken seed coats in dishes and the removal of all seeds during night periods (Fig. 1B) evidence that rodents, and not birds, were the main seed predators. The three seed species were removed to a similar extent for the two study zones ($H = 5.391$, $df = 2$, $P = 0.067$) (Table 1).

Control experiments

Seed removal from unprotected dishes was significantly lower in the invaded zone than in the non-invaded zone for $C. spinosa$ ($U = 147.5$, $df = 1$, $P < 0.05$) and $P. bituminosa$ ($U = 221.5$, $df = 1$, $P < 0.05$), but not significantly different for $S. junceum$ ($U = 299.5$, $df = 1$, $P = 0.775$) (Table I). The total percentage of seeds removed for the three species was 16.6% (n = 625) in the invaded zone and 33.8% (n = 625) in the non-invaded zone. The mean proportion of seeds removed from unprotected dishes was significantly different between the three seed species in the non-invaded zone ($H = 8.946$, $df = 2$, $P < 0.05$), seeds of $C. spinosa$ being the most often removed (49.2%, n = 250) and seeds of $P. bituminosa$ the least often removed (17.6%, n = 125) (Table I). In the invaded zone no significant differences in the proportion of seeds removed between the three species were detected ($H = 4.875$, $df = 2$, $P = 0.087$) (Fig. 1C).

DISCUSSION

To our knowledge, this study is the first to reveal the alteration of the dispersal process of non-myrmeco-

Table I. Number of seeds removed from each of the four treatments and the three seed species after the 48 hours of exposure in the field in the invaded and the non-invaded zones.

	Invaded zone				Non-invaded zone			
	Vertebrate exclusion	Ant exclusion	Control	Total exclusion	Vertebrate exclusion	Ant exclusion	Control	Total exclusion
Calicotome spinosa [a]	9	0	33	0	116	2	123	0
Psoralea bituminosa [b]	1	0	8	0	15	0	22	0
Spartium junceum [a]	9	1	63	0	69	30	66	0

[a] n = 250 seeds per exclusion treatment (10 seeds/dish)
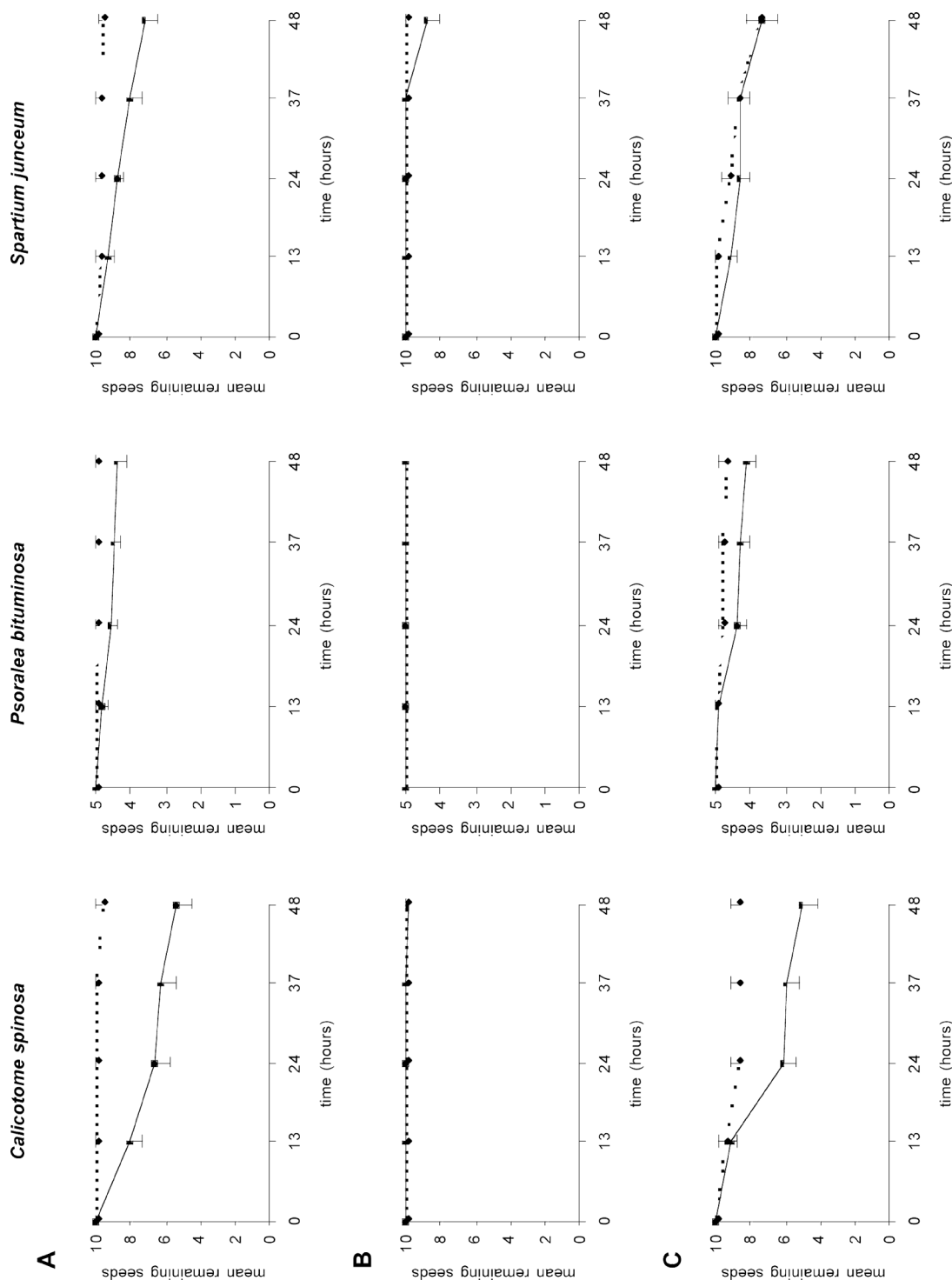[b] n = 125 seeds per exclusion treatment (5 seeds/dish)

Fig. 1. Mean (± SE) of seeds removed per sample by ants from dishes treated for vertebrate exclusion (file A), dishes treated for ant exclusion (file B), and the control dishes (file C), during the 48 hours of exposure in the field for each plant species (in separated rows). The broken lines show the zone invaded by *L. humile* and the solid lines show the non-invaded zone.

chorous seeds after Argentine ant invasion. The displacement of the native seed harvester ant species caused by the Argentine ant invasion is the most probable cause for the reduction of the number of seeds taken by ants observed in the invaded zone. This fact will probably imply a reduction of the number of seeds predated by harvester ants. The responsible for the few (19 of 625) seeds removed from the dishes treated for vertebrate exclusion in the invaded zone is unknown. It seems improbable that

it was *L. humile* due to its unlikely attraction to non-myrmecochorous seeds, but other crawling insects could also be attracted to the seeds. In this sense, some studies have shown the paper of carabid beetles as seed predators (Westerman *et al.* 2003, Honek *et al.* 2003), although we do not know about their presence in our study area.

The intensity of seed removal by harvester ants in our non-invaded study zone is low if compared with studies performed in different habitats (Andersen 1991, Haase *et*

al. 1995, Kaspari 1996, MacMahon *et al.* 2000). This could be due to a lower number and abundance of harvester ants in our area (pers obs) because seed harvesting is mostly a phenomenon of more open and arid habitats (Andersen 1991, Andersen *et al.* 2000). In fact, in the non-invaded study zone the non-myrmecochorous seeds were removed entirely by a single species, *M. bouvieri*, whose period of maximum activity is in the autumn (Cros *et al.* 1997) and whose presence is mainly concentrated in the most open areas and on paths. Thus, the low occurrence of harvester ants in our area seems unlikely to be capable of causing severe damage to plants. However, in other habitats harvester ants remove an impressive volume of seeds and are capable of inflicting severe seed losses (Andersen 1991). Therefore, the disappearance of harvester ants in these habitats could have more drastic consequences.

On the other hand, we have to take into consideration the possible positive effect of seed harvester ants on seeds, known as diszoochory. Rissing (1986) demonstrated that granivorous ants can have a beneficial effect upon the seeds they remove. Moreover, Retana *et al.* (2004) have recently documented the potential positive effect of the harvester ant *Messor bouvieri* on seed dispersal of the non myrmecochorous Mediterranean perennial herb, *Lobularia maritima* (L.). Consequently, the displacement of harvester ants due to the Argentine ant invasion will result in the disappearance of this beneficial effect on those seeds really dispersed by these species. From the point of view of the plant, the loss of this seed dispersal mechanism would be a negative effect of the Argentine ant invasion.

The three seed species studied were not equally removed by ants in the non-invaded zone. Consequently, they will not be equally affected in the short-term. Seeds of *C. spinosa*, the most removed ones, would benefit most by the disappearance of harvester ants. Despite the most removed seed species was the lightest one (*C. spinosa*), seed weight is unlikely to explain these differences in seed removal as the other two seed species are not so much heavier as to make their transport by *M. bouvieri* difficult (pers obs). In fact, Willott *et al.* (2000) documented a strong preference of *M. bouvieri* for large seeds. Moreover, Hensen (2002) documented the ability of *M. bouvieri* to carry seeds up to 95.9 mg. Seed size would also not explain the different removal rates as the three seeds have similar sizes and can be easily grasped by *M. bouvieri* workers. Thus, other factors and not seed weight or size are responsible for the differences in removal rates between the three seed species by *M. bouvieri* in the non-invaded zone. Harvester ants usually collect a variety of seed species at different rates (Briese 1982, Hölldobler & Wilson 1990, MacMahon *et al.* 2000, Rey *et al.* 2002), related to the physical and chemical characteristics of the seeds (Davidson 1982), seed availability (Crist & MacMahon 1992, Milton &

Dean 1993, Willott *et al.* 2000), and the size of the ant species (Davidson 1982, Kaspari 1996). Kaspari (1996) found that small seeds are harvested by a greater variety of ants than large seeds, and Rodgerson (1998) showed that species with weaker seeds experienced much higher levels of seed predation. Therefore, we expect that those plants with lighter and/or weaker seeds, which are more likely to be more removed and eaten by harvester ants, would benefit in a greater extent than those with heavier and/or stronger seeds after the disappearance of harvester ants.

The level of seed loss due to rodents was low in the study area. Studies performed in other areas of the world have documented much higher levels of seed predation by rodents (Heithaus 1981, Turnbull & Culver 1983, Bond & Breytenbach 1985, Anderson & MacMahon 2001, Rey *et al.* 2002). This does not necessarily mean that the population of rodents is low in the area covered in this study, but that perhaps the seeds used were not preferred by rodents and/or because the rodents' activity is usually patchy (Turnbull & Culver 1983, Rey *et al.* 2002, Saba & Toyos 2003). Due to the competition between rodents and harvester ants for limited seed resources, the disappearance of this guild of ants from an area could cause an increase in the population of rodents due to the greater number of seeds made available, as observed by Brown *et al.* (1979) and Davidson *et al.* (1984). Nonetheless, in our study area the disappearance of the native harvester ants after the Argentine ant invasion does not seem to have affected the rodent population, as no significant differences in seed removal from the dishes treated for ant exclusion were detected between the invaded and the non-invaded zones.

In conclusion, the countervailing forces of predation and dispersal as general phenomena in harvesting ant – seed interactions were shifted following the Argentine ant invasion. However, the effect will vary according to habitat (presence and density of harvester ants and rodents) and seed characteristics (size, weight, toughness). Further work could reveal us the long-term consequences of this alteration on the reproductive success of the affected species and the impact on the whole plant community.

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