

Ant interactions with native and exotic seeds in the Patagonian steppe: Influence of seed traits, disturbance levels and ant assemblage

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Abstract Invasive plants may establish strong interactions with species in their new range which could limit or enhance their establishment and spread. These interactions depend upon traits of the invader and the recipient community, and may alter interactions among native species. In the Patagonian steppe we studied interactions of native ant assemblages with seeds of native and exotic plants, and asked whether ant–seed interactions differ with seed types and disturbance levels and whether the amount and type of ant–seed interactions can be predicted if both ant and seed traits are known. To characterize and quantify ant–seed interactions, we offered baits with large seeds of *Pappostipa speciosa* (native) and

medium-sized elaiosome-bearing seeds of *Carduus thoermeri* (exotic), near and far from a road (high vs. low disturbed areas), and compared ant abundance and composition between areas. Interaction frequency was the highest for *C. thoermeri* seeds far from the road. Composition of ants interacting with *C. thoermeri* in these areas differed from that near the road and from that interacting with native seeds. Ant composition and abundance were similar between areas, but some species interacted more with exotic seeds in low disturbed areas. Ant foraging type predicted ant–seed interactions since the abundance of seed harvesters was positively correlated to interactions with *P. speciosa*, and that of generalists and predators, with interactions with *C. thoermeri*. The high interaction of ants with exotic seeds in low invaded areas suggests that ant activity could influence plant invasion, either by predated or dispersing seeds of invasive plants.

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Introduction

The spread of exotic plants has changed the composition, structure and functioning of many ecosystems worldwide (Williamson 1996; Mack et al. 2000). During the invasion process numerous biotic and abiotic factors affect the establishment and dominance

of exotic plants in recipient communities (Mitchell et al. 2006). In particular, exotic plants may set up strong interactions with resident species which can either limit their establishment and spread (e.g. with competitors, pathogens, herbivores; Levine et al. 2004) or contrarily, facilitate it (e.g. with seed dispersers, pollinators, Richardson et al. 2000). These new interactions depend upon the invader traits and the recipient community and may alter previously established interactions among native species (Pearson and Callaway 2003; Traveset and Richardson 2006). The study of the nature and strength of these interactions is relevant to understand any invasion process and its impact on the community.

Animals may play an important role in the plant invasion process through their interactions with exotic seeds (Blaney and Kotanen 2001; Pearson et al. 2014a). For example, granivorous ants can remove important amounts of seeds of exotic species (Blaney and Kotanen 2001; French and Major 2001; Vilà and Gimeno 2003). Granivorous ants generally select seeds based on their traits. For instance, they prefer seeds with high nutrient content, low concentration of secondary compounds, bigger sizes as long as their own size allows it and elongate morphology (Kelrick et al. 1986; Crist and MacMahon 1992; Azcárate et al. 2005; Pirk and Lopez de Casenave 2010). Due to their high selectivity, their seed consumption could not only affect plant abundance, but also vegetation composition (Inouye et al. 1980; Samson et al. 1992; Espigares and López-Pintor 2005). A high predation of exotic seeds may reduce granivores' pressure upon native seeds increasing native plant abundance. However, granivores' effects on plant abundance depend upon many factors, such as the amount of seeds removed and the life history of the plants (Louda and Potvin 1995) so the outcome is usually difficult to predict.

Ants can also act as seeds dispersers, through a process called myrmecochory, particularly when seeds bear nutritious structures (i.e. elaiosomes). After consuming the lipid-rich elaiosome, intact seeds are discarded inside or near their nests, where they avoid parental competition and predation, and soils are usually enriched (Rico-Gray and Oliveira 2007). Ants involved in this type of interaction are usually generalists and carnivorous, but granivorous ants can also disperse seeds accidentally (diszoochory), when they drop them on the way to their nests, discard viable seeds in their middens or leave them behind in inner

chambers (granaries) when they abandon their nests (MacMahon et al. 2000). Therefore, the level and type of ant–seed interactions (i.e. dispersal or predation) may depend on the characteristics of the ant assemblage (e.g. ant size and relative abundance of granivorous, predator and generalist ant species) and of seed traits (i.e. presence of elaiosome, size, chemical composition). Information on both ant and seed traits may help to predict ants' responses to newly introduced species, important to managing plant invasions especially at initial stages.

In northern Patagonia (Argentina), exotic plants comprise about 20% of total species (Zuloaga et al. 1999). Roadsides in the Patagonian steppe present high abundance of invasive species, decreasing with distance from the road (Margutti et al. 1996), and are considered key areas for their dispersal (Farji-Brener and Ghermandi 2008). Disturbance caused by roads usually affects composition and abundance of ants (DeMers 1993; Stiles and Jones 1998) and it can also affect their foraging activity since road disturbance affects resource types and abundance (Forman and Alexander 1998). Therefore, the level and type of ant–seed interactions may vary between high and low disturbed areas, with important implications for plant invasions. So far, no studies have addressed the identity of ants interacting with seeds in the area, let alone in high versus low invaded sites.

In this study we evaluate and compare the interactions between ants and seeds of the exotic *Carduus thoermeri* (Asteraceae) and the native *Pappostipa speciosa* (Poaceae), near and far from a road (i.e. high vs. low disturbed areas) in the Patagonian steppe. *Carduus thoermeri* and *P. speciosa* are the most abundant exotic and native species in the study area, respectively. *Carduus thoermeri*'s seeds are smaller than *P. speciosa*'s seeds (3.9 vs. 7.9 mg) and the base of the floral style has been considered an elaiosome (Pemberton and Irving 1990; Alba-Lyn and Henk 2010). We studied via seed offer experiments: (a) the composition of ants interacting with seeds, (b) the frequency of these interactions and (c) ants' foraging behaviour towards seeds, and compared these variables between seed types and areas (near vs. far from roads). We also quantified and compared ant abundance and composition, and plant cover and composition, near and far from roads. We asked the following questions: (a) Do ant–seed interactions differ with seed type and disturbance levels? If they do, are

differences explained by differences in ant composition and abundance and/or by differences in ant behaviour towards seeds? (b) Can the amount and type of ant–seed interactions be predicted if ant composition and traits (i.e. their foraging type and size) and seed traits (i.e. seed size and presence of elaiosome) are known? We predict that ant–seed interactions will be overall higher for *C. thoermeri* because these seeds will attract a wider range of ant species (mostly generalists, carnivorous, but also granivorous) due to their smaller size and the presence of elaiosome, whereas *P. speciosa* will attract mostly granivorous ants and bigger species. We also expect variations in these interaction levels between sites in response to different ant abundance and composition. In particular, we expect different frequency of interactions and foraging behaviours towards seeds close and far from the road due to road-associated disturbance.

Materials and methods

Study area

The study was conducted at the eastern border of the Nahuel Huapi National Park, located in northwestern Patagonia, Argentina (41°S, 72°W). Mean annual temperature is 8 °C and mean annual rainfall is about 600 mm. Sampling was performed at eight sites, at least 2 km apart, along 40 km of National Road 237, at 40–80 km from San Carlos de Bariloche. We established two sampling grids per site, one near the road (5–10 m from it) and the other one far from it (>100 m). Exotic species decline in their abundance with distance from the road (Farji-Brener 1996). Grids were rectangular (90 × 10 m) and parallel to the road. Twenty sampling stations were established per grid, each every 10 m (320 stations altogether).

Seed-carrying ant assemblages

To identify ant species that interact with seeds, we offered seeds of *Pappostipa speciosa* (Poaceae) and *Carduus thoermeri* (Asteraceae), the most abundant native and exotic species, respectively, in the study area (G Pirk, Online Resource Table 1). Baits were offered in January–February 2011 at the peak of ant activity (Lopez de Casenave et al. 1998; Folgarait and Sala 2002). Seeds were collected during the previous

season and stored in paper bags in dark and dry conditions. *Pappostipa speciosa* seeds are fusiform cariopses, of about 1.5 cm long and 0.13 cm wide, whereas *C. thoermeri* seeds are achenes of around 0.43 cm long and 0.16 cm wide. Sound seeds of both species were selected under a stereoscope, avoiding hand contact. Groups of 20 seeds of *P. speciosa* and 40 seeds of *C. thoermeri* (both ~160 mg) were placed in Petri dishes in the field. We offered the same mass instead of the same number of seeds to assure a similar amount of visual and odour cues for both species. Petri dishes were placed at each sampling station flush with the soil surface. Two soil ramps were fixed to aid ants in entering and exiting the dishes. Each seed type was offered separately on two non-consecutive days, in a random order. The experiments took place on days of similar temperature and humidity conditions and light wind.

Seeds were offered 1 h before the observations to allow ants to discover the baits at the onset of their activity period. Stations were visited 4 times (around 8:30, 10:30, 17:00 and 19:00) during each sampling day (no ants were observed at midday and night). At each station we recorded the number and species of ants that were displaying the following five behaviours during a 1-min observation period: (a) ignore: ants did not interact with the seeds; (b) inspect: ants contacted the seeds with their mandibles, antennae or legs but did not move them; (c) manipulate: ants grabbed or tried to grab the seeds with their mandibles and moved them in place, (d) carry: ants grabbed and moved the seeds from one place to another inside the dishes and (e) remove: ants grabbed the seeds and carried them out of the dishes. We considered ants to be interacting with seeds when they manipulated, carried or removed seeds during the observation period. When <5 seeds were left, dishes were replenished; the frequency of seed reposition was considered an indirect estimation of seed removal. Individuals of ant species that could not be identified in the field were collected and taken to the laboratory, where they were identified with the aid of existing taxonomic keys (Snelling and Hunt 1975; Kusnezov 1978) and a reference collection (Laboratorio Ecotono, INIBIOMA, CONICET-UNCOMA).

Total ant assemblages and vegetation composition

To determine the ant assemblages near and far from the road at each site, epigeal ants were collected using five pitfall traps per grid ($N = 80$). They consisted of plastic containers (9 cm deep, 8 cm wide) buried flush with the soil surface. Propylene glycol (40%) was poured inside them and a few inodorous detergent drops were added to break surface tension. Traps remained open for 7 days (21–28 February 2011) and then covered and taken to the laboratory where ants were extracted, counted and identified under a stereoscopic microscope. Species were classified into foraging groups (i.e. seed harvesters, cultivators of fungi, generalized foragers and generalized foragers/predators) as in Fergnani et al. (2013), and based on Kusnezov (1959) and Brown (2000). They were also classified according to their size (i.e. head width): small (<0.6 mm), medium (0.6–1.5 mm) and large (>1.5 mm).

In order to characterize vegetation and to quantify invasive plant abundance close and far from the road at each site, we assessed species cover in 1 m² squares centred at each sampling station, adding 5 more stations per grid at both extremes (i.e. 25 m² total sampled area per grid) in January–February 2012. When a species could not be identified in the field, individuals were collected and identified to species in the laboratory with the aid of existing keys and plant collections.

Data analyses

In order to characterize ant assemblages interacting with both types of seeds, we calculated species richness (i.e. number of species) and composition (i.e. proportion of each species) of ants that manipulated, carried or removed seeds of *C. thoermeri* and *P. speciosa* per grid. Also, we estimated frequency of ant–seed interactions, as the percentage of stations with ant–seed interactions (for total ants and for each species separately), and then averaged this proportion across the four daily visits. Additionally, we estimated frequency of seed reposition per site as the number of times dishes were replenished during the sampling day. Species richness, frequency of interactions and of seed reposition were compared between offered seed types and distance from the road using a two-way ANOVA block design per variable, with sites as

random blocks. In this and in all subsequent analyses, ANOVA assumptions were tested and if not met, variables were transformed (e.g. squared root or log-transformed), or otherwise non-parametric tests were used. In order to compare interaction levels of each individual ant species with each seed type between distances, we used Wilcoxon matched pair tests. A Principal Component Analysis (PCA) was used to characterize and compare the composition of ants interacting with seeds at each grid and an Analysis of Similarities (ANOSIM) to determine if ant composition differed between distances and seed types.

We described foraging behaviour of ants with high interaction levels (>4%; Table 1) and evaluated if frequency of different behaviour types differed between distances and offered seeds. To do so, we calculated the percentage of stations per visit in which ants displayed each of the five recorded behaviours and then averaged this proportion across visits. We then performed a three-way ANOVA block design per ant species, with sites as random blocks and type of behaviour, distance and seed type offered as fixed factors. Tukey's contrasts were used when differences were significant.

To compare abundance of ant species in pitfall traps, the proportion of traps in which each species was present (i.e. the frequency of occurrence) was calculated per grid. This variable was preferred to number of individuals per species because the latter may overestimate abundance because ants are central place foragers and traps may gather a high number of individuals if they are located close to the nest entrance. However, occurrence could not be used to analyse total ant abundance since all traps contained ants. Because three traps were lost to livestock trampling or were cracked, we used number of ants per trap and not total abundance among traps, as our measure of ant abundance. Finally, species richness was defined as the number of species collected per grid, and because the total number of ants differed, a rarefaction was performed before the species richness analysis. Total ant abundance, species occurrence and richness were compared between distances with a one-way ANOVA block design and species composition with PCA and ANOSIM. Occurrence of each species was compared between distances using Wilcoxon matched pair tests.

To determine if ant foraging type and size could be good predictors of ant interactions with different seed

Table 1 Mean (±SE) percentage of Petri dishes with individuals of each ant species interacting with *Pappostipa speciosa* and *Carduus thoeimeri* seeds, and mean (±SE) percentage of pitfall traps where each ant species was found near and far from the road ($N = 8$ per distance) in northwestern Patagonia, Argentina

Ant species	Ant size/foraging type	Seed offer experiments				Pitfall traps			
		<i>Pappostipa speciosa</i>		<i>Carduus thoeimeri</i>		<i>Pappostipa speciosa</i>		<i>Carduus thoeimeri</i>	
		Near	Far	Near	Far	Near	Far	Near	Far
Dolichoderinae									
<i>Dorymyrmex antarcticus</i> Forel	M/GFP	0	0.16 ± 0.16 (1)	0 a	10.78 ± 4.18 (5) b	33.12 ± 1.24 (5)	4.17 ± 1.49 (5)		
<i>Dorymyrmex minutus</i> Emery	M/GFP	0	0	0	0.16 ± 0.16 (1)	10.00 ± 5.34 (3)	29.17 ± 10.61 (5)		
<i>Dorymyrmex tener</i> Mayr	M/GFP	1.88 ± 1.00 (3)	0.94 ± 0.31 (5)	4.69 ± 1.90 (5)	10.94 ± 4.18 (6)	79.40 ± 8.47 (8)	62.50 ± 15.78 (6)		
<i>Dorymyrmex wolffhuegeli</i> Forel	M/GFP	0	0	1.09 ± 0.93 (2)	0	17.50 ± 5.90 (5)	12.50 ± 6.48 (3)		
Formicinae									
<i>Brachymyrmex patagonica</i> Mayr	S/GF	0	0	0	0	51.78 ± 11.72 (7)	45.83 ± 7.60 (8)		
<i>Camponotus distinguendus</i> Spinola	M, L/GF	0	0	0	0	0	2.50 ± 2.50 (1)		
<i>Lasiophanes valdiviensis</i> Forel	M/GF	0	0.16 ± 0.16 (1)	0	0.31 ± 0.31 (1)	10.00 ± 5.34 (3)	7.50 ± 3.66 (3)		
Myrmicinae									
<i>Acromyrmex lobicornis</i> Emery	M, L/CF	0.16 ± 0.16 (1)	0	0.47 ± 0.23 (3)	0	35.00 ± 12.39 (5)	15.00 ± 8.23 (3)		
<i>Pheidole spininodis</i> Mayr	M/SH	0	0	0.62 ± 0.47 (2)	0	20.00 ± 11.34 (3)	7.50 ± 5.26 (2)		
<i>Pogonomyrmex carbonarius</i> Mayr	L/SH	4.22 ± 1.92 (5)	2.66 ± 1.97 (4)	0.16 ± 0.16 (1)	0.31 ± 0.31 (1)	37.50 ± 13.33 (5)	25.00 ± 10.52 (4)		
<i>Solenopsis richteri</i> Forel	M, S/GF	0	0	0	0.47 ± 0.47 (1)	25.00 ± 25.00 (1)	25.00 ± 25.00 (1)		
<i>Solenopsis</i> sp.	M, S/GF	0	0	0	0.31 ± 0.20 (2)	10.00 ± 5.34 (3)	5.00 ± 3.27 (2)		

Ant size was determined according to head width: small (S: <0.6 mm), medium (M: 0.6–1.5 mm) and large (L: >1.5 mm)

Foraging types follow Fergani et al. (2013): generalized foragers and predators (GF), generalized foragers (GFP), cultivators of fungi (CF) and seed harvesters (SH)

Number of study sites with each species present is indicated between brackets

Different letters indicate significant differences between distances from the road for each ant species (Wilcoxon matched pair test; $P < 0.05$)

types, we correlated frequency of occurrence of seed harvesters (SH), cultivators of fungi (CF), generalized foragers (GF) and generalized foragers and predators (GFP) in pitfall traps with interaction levels with each seed type recorded at each grid ($N = 16$). We performed the same analysis considering ant size, i.e. small (S), medium (M) and large (L) species.

In order to evaluate the effect of distance from the road on vegetation, we calculated percentage cover and species richness of exotic, native and total plants in every grid and analysed each variable with a one-way ANOVA block design, with distance from the road as a fixed factor (near, far) and sites as random blocks. To compare plant composition between distances, we performed an ANOSIM with Bray–Curtis similarity index.

Results

Seed-carrying ant assemblage

Ten out of the 12 species detected in the pitfall traps interacted with the seeds (Table 1). Altogether more ant species interacted with *Carduus thoermeri* than with *Pappostipa speciosa* seeds as expected (10 vs. 5 species, Table 1), but the number of interacting ant species per site did not vary with seeds offered or distance from the road (Fig. 1). The species most interacting with *P. speciosa* was the large seed

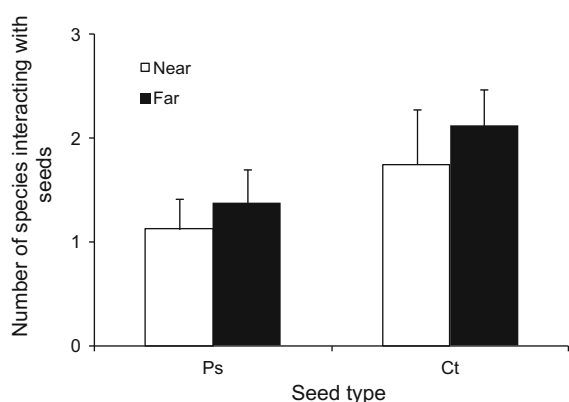


Fig. 1 Mean (+SE) number of ant species interacting with seeds of *Pappostipa speciosa* (Ps) and *Carduus thoermeri* (Ct) in grids established near (open bars) and far (black bars) from the road ($N = 8$ per distance) in northwestern Patagonia, Argentina. Differences between distances and seed types were not significant (two-way ANOVA)

harvester *Pogonomyrmex carbonarius*, while the medium-sized generalists and predators of the genus *Dorymyrmex* highly interacted with *C. thoermeri* (Table 1).

According to the PCA, composition of ants interacting with *C. thoermeri* in grids far from the road was variable and different from the others grids. Grids separated mainly along the first component, where the ones to the negative values were characterized by *Solenopsis richteri*, *Solenopsis* sp. and *Dorymyrmex tener*, while those to the positive values were *D. antarcticus* and *Lasiophanes valdiviensis* (Fig. 2). Composition of ants interacting with *C. thoermeri* near the road and with *P. speciosa* near and far was similar as grids tended to ordinate together. ANOSIM showed that composition of ants interacting with *P. speciosa* did not differ between distances ($R = 0.05$, $P = 0.25$), but that of ants interacting with *C. thoermeri* did ($R = 0.19$, $P = 0.03$).

Frequency of ant–seed interactions depended on distance from the road and species offered (distance \times species interaction was significant; $F_{(1,21)} = 19.34$, $P < 0.01$, ANOVA). It was much higher for *C. thoermeri* in the grids far from the road ($P < 0.05$, Tukey's comparisons; Fig. 3a). By the end of the day, 18 and 10% of dishes with *P. speciosa* and 22 and 60% with *C. thoermeri* near and far from the road, respectively, had shown ant–seed interactions in any one time. When individual ant species were analysed, *D. antarcticus* showed higher frequency of interactions in grids far than near the road but only with *C. thoermeri* ($P = 0.043$, Wilcoxon matched pair test; Table 1). Frequency of seed reposition followed the same pattern as frequency of interactions; it depended on distance and species offered (distance \times species interaction was significant; $F_{(1,21)} = 8.5$, $P = 0.008$, ANOVA) and was much higher for *C. thoermeri* in the grids far from the road ($P < 0.05$, Tukey's comparisons; Fig. 3b).

Distance from the road influenced behaviour of *D. antarcticus* towards *C. thoermeri* seeds ($F_{(1,63)} = 36.9$, $P < 0.01$): proportion of dishes with different behaviour types were much lower near the road, where only ants ignoring or inspecting the seeds were observed (Fig. 4a). Also, all behaviour types occurred in similar proportions ($F_{(4,63)} = 0.7$, $P = 0.58$) and did not depend on distance (distance \times behaviour interaction was not significant; $F_{(4,63)} = 0.6$, $P = 0.68$, ANOVA). In contrast to *D.*

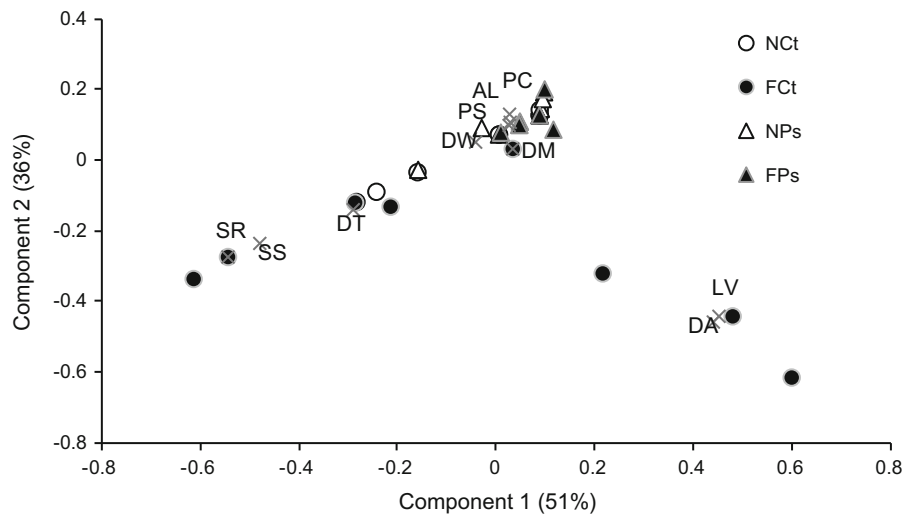


Fig. 2 Ordination of ant species (cross symbol) and grids near (N, white) and far (F, black) from the road in northwestern Patagonia, Argentina, according to composition of ants interacting with seeds of *Carduus thomeri* (Ct, circles) and *Pappostipa speciosa* (Ps, triangles) along components 2 versus 1 of the PCA. The percentage of variation explained by each

antarcticus which practically only interacted with *C. thomeri* seeds, *Dorymyrmex tener*'s behaviour was analysed simultaneously for *P. speciosa* and *C. thomeri* seeds since it highly interacted with both seed types (Table 1). Behaviour differed with species offered (species \times behaviour interaction was significant; $F_{(4,133)} = 3.1$, $P = 0.02$, ANOVA), with lower removal and seed carrying of *P. speciosa* than *C. thomeri* seeds ($P < 0.05$, Tukey's comparisons; Fig. 4b, c). Distance from the road also affected ant behaviour (distance \times behaviour interaction was significant; $F_{(4,133)} = 3.1$, $P = 0.02$, ANOVA), with lower removal close to the road than far from it ($P < 0.05$, Tukey's comparisons). The most common behaviour towards seeds of both species was ignoring them, and was significantly higher than all other behaviours ($P < 0.05$, Tukey's comparisons). The behaviour of *P. carbonarius* did not vary with distance from the road (distance \times behaviour interaction was not significant; $F_{(4,133)} = 0.72$, $P = 0.58$, ANOVA) but differed with species offered (species \times behaviour interaction was significant; $F_{(4,133)} = 5.6$, $P = 0.0003$, ANOVA) mainly because seed carrying and removal were higher for *P. speciosa* than for *C. thomeri* seeds ($P < 0.05$, Tukey's comparisons) (Figs. 4d, 5e).

component is indicated between brackets. (References: AL = *Acromyrmex lobicornis*, DA = *Dorymyrmex antarcticus*, DM = *D. minutus*, DT = *D. tener*, DW = *D. wolffhuegeli*, LV = *Lasiophanes valdiviensis*, PC = *Pogonomyrmex carbonarius*, PS = *Pheidole spininodis*, SR = *Solenopsis richteri*, SS = *S. sp.*)

Total ant assemblages and vegetation composition

Altogether 18,944 ants of 12 native species belonging to three subfamilies and eight genera were found in pitfall traps in all study sites (Table 1). All of them except for *Brachymyrmex patagonica* and *Camponotus distinguendus*, interacted with seeds during offer experiments.

Mean (\pm SE) ant abundance per trap did not differ between distances from the road (194.2 ± 62.1 and 282.0 ± 172.4 , near and far from the road, respectively; $F_{(1,7)} = 0.30$, $P = 0.6$, ANOVA), nor did occurrence of any of the species ($P > 0.05$ in all cases, ANOVA; Table 1). Species richness was similar between distances (3.3 ± 0.6 and 3.4 ± 0.8 , near and far from the road, respectively; $F_{(1,7)} = 0.01$, $P = 0.9$, ANOVA). The PCA showed that grids near the road did not separate from grids far from it according to ant composition (Fig. 5). Also, ANOSIM showed no differences in ant composition near and far from the road ($R = -0.052$, $P = 0.65$).

When we performed correlations to find out if interaction levels of each seed type were related to abundance of different foraging groups, we found a significant and positive correlation between interaction levels with *C. thomeri* and abundance of

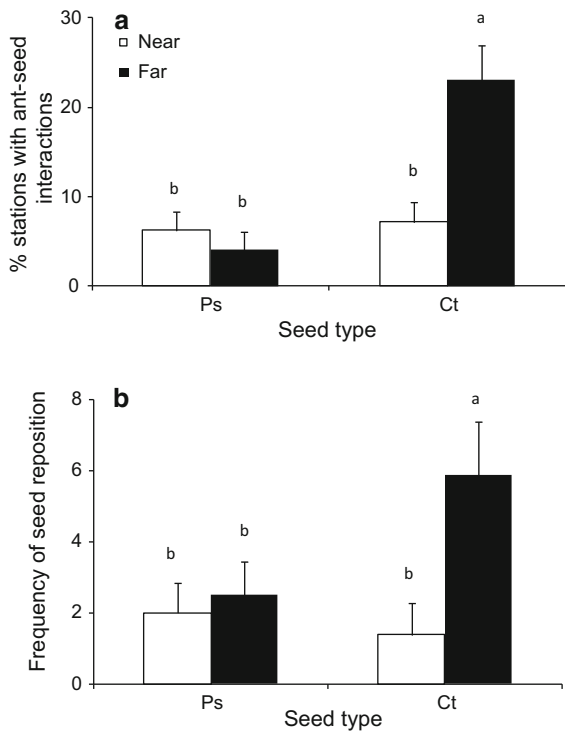
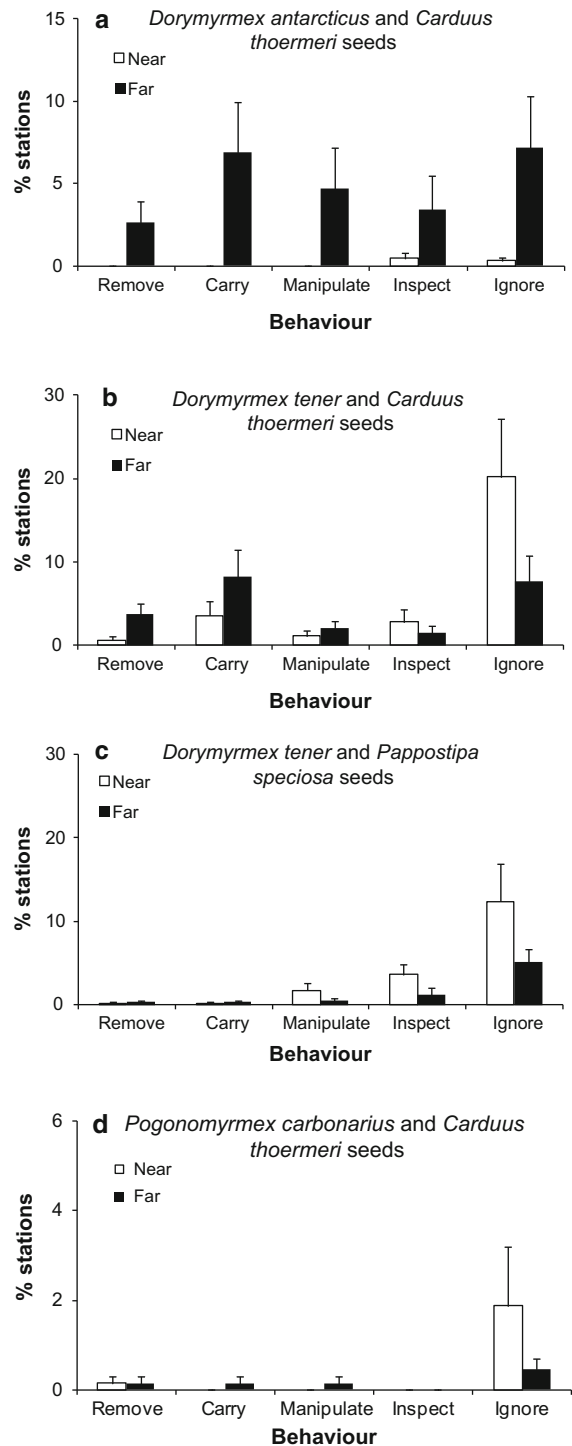


Fig. 3 Mean (+SE) percentage of Petri dishes with ants interacting with seeds (a), and mean (+SE) frequency of seed reposition during a sampling day (b) in offer experiments with seeds of *Pappostipa speciosa* (Ps) and *Carduus thoermeri* (Ct) in grids established near (open bars) and far (black bars) from the road ($N = 8$ per distance) in northwestern Patagonia, Argentina. Different letters indicate significant differences ($P < 0.05$, Tukey's comparisons)

generalized foragers and predators and a marginal positive correlation between abundance of seed harvesters and interactions with *P. speciosa* (Table 2). As for ant size, correlations between all size classes and seed types were non-significant.

A total of 59 plant species were identified in the study area, out of which 14 (23%) were exotic (Online Resource Table 1). Exotic species cover was almost four times higher near the road than far from it, whereas native and total species cover was similar between distances (Online Resource Fig. 1). Also, exotic species richness was higher near than far from the road but native and total richness were similar in both distances (Online Resource Fig. 1). Vegetation composition differed between distances (Global $R = 0.32$; $P = 0.007$, ANOSIM). Among native species *Pappostipa speciosa*, *Imperata condensata*, *Mulinum spinosum* and *Senecio bracteolatus* had the



highest cover, both near and far from the road. *Carduus thoermeri*, *Bromus tectorum*, *Verbascum thapsus* and *Rumex acetosella* were the exotic species with the highest cover close to the road, and the latter

Fig. 4 Mean (+SE) percentage of stations where ants displayed different behaviours towards offered seeds in grids established near (*open bars*) and far (*black bars*) from the road ($N = 8$ per distance) in northwestern Patagonia, Argentina. **a** *Dorymyrmex antarcticus* with *Carduus thoermeri* seeds, **b** *D. tener* with *C. thoermeri* seeds, **c** *D. tener* with *Pappostipa speciosa* seeds, **d** *Pogonomyrmex carbonarius* with *C. thoermeri* seeds and **e** *P. carbonarius* with *P. speciosa* seeds. See text for statistical results

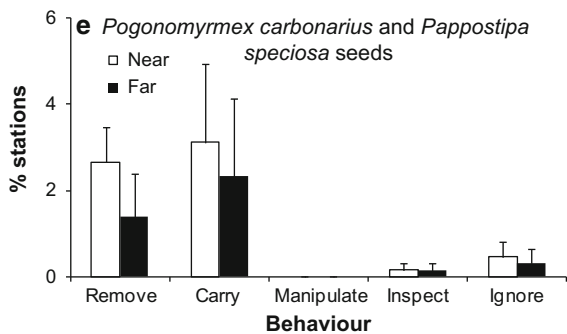


Fig. 4 continued

was the most abundant one far from the road (Online Resource Table 1). Ten out of the 14 exotic species found have been classified as highly invasive in northwestern Patagonia (Speziale and Ezcurra 2011). In our study, most exotic species (~80%) occurred in

more than one site (Online Resource Table 1) and since invasion process requires distant dispersal (Richardson et al. 2000), they are likely to be invasive in the study area. All in all, grids established close to the road presented higher invasive species abundance and a different species composition than grids >100 m from the road.

Discussion

This study shows that most ant species in the study area within the Patagonian steppe are capable of interacting with seeds. Also, that the frequency of ant–seed interactions depends upon distance from the road and seed type offered. The elaiosome-bearing seeds of the exotic *Carduus thoermeri* attracted more ant species than those of the native grass, *Pappostipa speciosa*, and reached the highest interaction levels but only far from the road. Also, seed traits and composition of ant assemblages in terms of foraging type may be good predictors of ant–seed interactions.

Except for *Camponotus distinguendus* and *Brachymyrmex patagonica*, all species found in the study sites interacted with seeds: they manipulated, carried or removed the seeds of the exotic *Carduus thoermeri* and the native *Pappostipa speciosa* from dishes. As

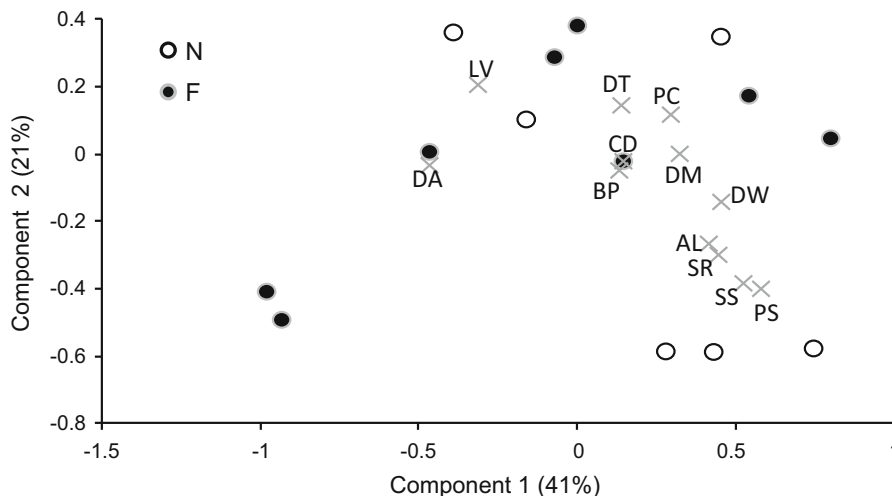


Fig. 5 Ordination of ant species (*cross symbol*) and grids near (N, *white*) and far (F, *black*) from the road in northwestern Patagonia, Argentina, according to composition of ants (frequency of occurrence of each species) in pitfall traps along components 2 versus 1 of the PCA. The percentage of variation explained by each component is indicated between brackets.

(References: AL = *Acromyrmex lobicornis* DA = *Dorymyrmex antarcticus*, DM = *D. minutus*, DT = *D. tener*, DW = *D. wolffhuegeli*, LV = *Lasiophanes valdiviensis*, PC = *Pogonomyrmex carbonarius*, PS = *Pheidole spininodis*, SR = *Solenopsis richteri*, SS = *S. sp.*)

Table 2 Spearman correlation coefficients (r_s) and their statistical significance (P) between frequency of occurrence of different ant foraging types and sizes in pitfall traps and antinteraction levels with *Pappostipa speciosa* and *Carduus thoermeri* seeds ($N = 16$) in northwestern Patagonia, Argentina

	<i>Pappostipa speciosa</i>		<i>Carduus thoermeri</i>	
	r_s	P	r_s	P
Ant foraging type				
Seed harvesters	0.46	0.07	−0.01	0.98
Generalized foragers	0.05	0.86	−0.23	0.39
Generalized foragers and predators	−0.15	0.58	0.54	0.03
Cultivators of fungi	0.25	0.35	−0.04	0.88
Ant size				
Small	−0.17	0.52	−0.25	0.36
Medium	0.07	0.79	0.39	0.14
Large	0.41	0.11	−0.01	0.99

Significant ($P < 0.05$) and marginally significant ($P < 0.08$) correlations are indicated in bold

expected, granivorous ants were the ones which most interacted with *P. speciosa* seeds. In fact, the only species of the genus *Pogonomyrmex* present in the area, the large *Pogonomyrmex carbonarius*, frequently visited *P. speciosa* baits where it was practically only seen removing or carrying the seeds. *Pogonomyrmex* species usually have marked preference for grass seeds (Pirk and Lopez de Casenave 2011), and in particular *P. speciosa* is the most common seed in the diet and the most preferred one for *P. carbonarius* in the area (L Aput and G Pirk, unpublished data). As for *C. thoermeri*, generalists and predators of the genus *Dorymyrmex* (*D. tener* and *D. antarcticus*) were the ones which most interacted with these seeds. The presence of a structure, which has been considered as an elaiosome (Pemberton and Irving 1990) in *C. thoermeri* seeds could cause the attention of *Dorymyrmex* spp. on these seeds. In general, the fatty acid composition of elaiosomes resembles more that of insects than of seeds (Hughes et al. 1994), therefore recruiting carnivorous and omnivorous ants. This constitutes an adaptive advantage for plant species since these ants are only interested in the elaiosome, leaving the seeds undamaged (Carroll and Janzen 1973). However, the composition and role of this structure in *C. thoermeri* still needs to be studied. In contrast to what was observed in *P. speciosa* baits, *Dorymyrmex* spp. mostly ignored the seeds. These generalist and predator ants (Kusnezov 1959; Brown 2000) probably consume a great variety of other food resources (e.g. Lescano and Farji-

Brener 2011). However, the large number of workers in the dishes resulted in a high frequency of interactions.

The frequency of ant–seed interactions depended on distance from the road as expected, but only for *C. thoermeri*. Ant interactions with seeds of *C. thoermeri* were the highest far from the road, i.e. in areas of low invasive species abundance. Meanwhile, interaction frequencies with seeds of *P. speciosa* near and far from the road and with *C. thoermeri* seeds close to the road were similar and much lower. The composition of interacting ants was also similar in these three cases and differed from that interacting with *C. thoermeri* far from the road. As mentioned above, *Pogonomyrmex carbonarius* was responsible for most interactions with *P. speciosa* while *Dorymyrmex tener* was for those with *C. thoermeri*. However, far from the road *D. antarcticus* also highly interacted with *C. thoermeri* seeds and several other species also did but in only one or two of the eight sampled sites (*Lasiophanes valdiviensis*, *Pheidole spininodis* and two species of the genus *Solenopsis*). Thus, although interacting species richness per site was not higher, total array of species interacting with *C. thoermeri* far from the road was richer. The higher frequency of ant–seed interactions with *C. thoermeri* far than close to the road cannot be attributed to differences in ant composition and abundance between areas since pitfall traps sampling showed no differences.

Contrary to our expectations, ant composition, richness and abundance were similar near and far

from the road. Many studies have reported that disturbance caused by road construction and maintenance benefits some ant species because roadsides provide suitable conditions for colony establishment (DeMers 1993; Pirk et al. 2004). However, no differences were observed in the ant assemblages or the occurrence of individual species in areas close to the road and more than 100 m from it in this area of the Patagonian steppe. Disturbance associated with roads clearly affected vegetation since invasive species cover and richness were higher near the road and vegetation composition differed between areas. Also, temperature at ground level was on average 1.5 °C higher near than far from the road (data recorded with data loggers during pitfall trap collection). The fact that ants were not affected leads us to think that these differences were not high enough to affect colony establishment. Although areas far from the road suffer less road disturbance they are subjected to other types of disturbance, such as livestock trampling and grazing. Sites were chosen to minimize this type of disturbance following visual cues (e.g. tracks, signs of overgrazing, dung) but the area altogether has been affected by livestock for decades, which has proven to influence the structure of ant communities (Bestelmeyer and Wiens 1996; Claver et al. 2014). Also, grids close to the road were established at 5–10 m from it excluding areas directly denuded by road construction and maintenance. In fact, total plant cover, which is a key driver of ant diversity in some environments (Lassau and Hochuli 2004; Fergnani et al. 2013), was similar close and far from roads. Thus, since differences in ant assemblages do not explain differences in ant interactions with *C. thoermeri* seeds between areas close and far from the road, other factors, such as differences in ant behaviour between areas may explain this pattern.

Behaviour of some ant species towards seeds differed with seed type and distance from the road. *Dorymyrmex antarcticus* interacted with *C. thoermeri* seeds only in low disturbed areas, while close to the road it only ignored or inspected seeds in a few sites but did not remove, manipulate or carry them. As for *D. tener*, removal of *C. thoermeri* seeds was higher far from the road. The lower interaction of *D. antarcticus* and *D. tener* with *C. thoermeri* seeds close to the road could be explained by different factors. In high disturbed areas (i.e. near the road) *C. thoermeri*'s cover is higher than in low disturbed areas (i.e. far

from the road; G Pirk, Online Resource). Thus, ants may find plenty of seeds in these areas (individuals produce ~4000 to 30,000 seeds per plant during the summer; Farji-Brener and Ghermandi 2008). This high abundance of seeds may satiate ants (Heithaus et al. 2005; Bologna and Detrain 2015) making them lose interest in baits. In fact, there is a negative association between ant interaction levels and *C. thoermeri* cover in the studied grids (Spearman $R: -0.77, P < 0.001, N = 16$; G Pirk, unpublished data). *Pogonomyrmex carbonarius*, specialized in *P. speciosa* seeds, behaved similarly in both areas, with similar abundance of *P. speciosa*. Another non-exclusive explanation could be that invasive plants provide more valuable resources than seeds to these generalist ants. A recent study showed that exotic thistles *C. thoermeri* and *Onopordum accanthium* host a greater aphid density than native plants which increases the abundance of tending ants including *Dorymyrmex* spp. (Lescano and Farji-Brener 2011). Alternatively, taking into account that frequency of interactions of ants with *P. speciosa* was similar to that with *C. thoermeri* in high invaded areas, what may actually be happening is that interactions of ants with *C. thoermeri* seeds are not lower in high invaded areas but especially high in low invaded ones. This could be because ants are commonly attracted to novel resources and in low invaded areas *C. thoermeri*, which is practically absent, could be considered one. Other studies have shown high responses of ants to baits of seeds presented for the first time (e.g. Medel and Vásquez 1994; Folgarait and Sala 2002). Studies which confirm if ant assemblages in the Patagonian steppe are especially attracted to novel resources could be revealing since this particular behaviour may limit or disperse invasive seeds upon their arrival in non-invaded areas.

The frequency of ant interactions matched seed reposition frequency implying that where ants were seen manipulating and carrying seeds in dishes, they were removing them too. However, seed removal does not necessarily equal seed predation. Seeds transported by ants may actually be dispersed by them. In the case of *P. speciosa*, seeds are most likely predated as *P. carbonarius*, responsible for most removal, belongs to a genus which typically take seeds to the nests and store them for later consumption (MacMahon et al. 2000). Thus, ant granivory may be in part responsible of the nil or low seed banks of this species

found in Patagonian steppe (Ghermandi 1997; Pazos and Bertiller 2008), which has indeed been attributed to predation as well as to a low burial capacity due to the large seed size (González et al. 2010). As for *C. thoermeri*'s seeds, the base of the floral style, like in other species of the genus, has been proposed to be an elaiosome, specialized food bodies which may aid seed dispersal (Pemberton and Irving 1990). Although ant removal of these seeds has previously been assumed to be dispersal (Alba-Lyn and Henk 2010), the function or attractiveness of this small structure has not been tested. Seed dispersal would involve that ants consume the lipid-rich elaiosome, not damaging the seed. Some authors have raised awareness on the interpretation of seed removal of *Carduus* spp. since they consider that the actual fate in offer experiments is uncertain (Jongejans et al. 2015) and that the two processes (i.e. predation and dispersal) may be co-occurring. In our study, if we consider that removed seeds are actually consumed, this may cause a reduction in recruitment and population spread especially in low invaded areas. Seeds arriving from high invaded sites, probably transported by animals or wind, could be predated by ants and remain little in the soil, and thus, having less chance of establishing. Conversely, the opposite scenario would be that none of the seeds are consumed and that ants favour the spread of this species. In the open Caldén (*Prosopis caldenia*) forests of Argentina, Pearson et al. (2014b) found that ants (*Pheidole* spp.) removed nearly all *Carduus nutans* seeds from depots but only few that emerged from the nests were viable, suggesting that although many introduced plant species bear elaiosomes their influence on invader success depends on the specific recipient community. Therefore, knowledge of how a particular ant species handles seeds of a particular plant species is essential information for understanding the fate of the seeds and the outcome for different types of plants. In this case, more detailed studies on the fate of *C. thoermeri* seeds after ant removal and the role of the base of the floral style need to be carried out to confirm if ants exert resistant to invasion of this species in the Patagonian steppe and also how they behave towards other invasive species lacking elaiosomes.

In this study we show that seeds from exotic plants establish strong interactions with native ants in the Patagonian steppe. A relevant question to ask is whether one can predict the type and strength of

interactions that newly introduced species will establish with native species upon arrival. Here, we found that knowledge of some seed traits and of abundance and composition of ant foraging groups may be good predictors of these interactions. Namely, the abundance of seed harvesters in our study sites (including areas both close and far from the road) was positively correlated to interactions with *P. speciosa* seeds, while the abundance of generalist foragers and predators, to interactions with *C. thoermeri* seeds. This trend was found even when there were some differences in ant behaviour of some species close and far from the road, and the range of site to site variation in ant composition was not large. Ant size was not a good predictor of ant–seed interactions, probably because in the ant assemblages there are other large species which practically did not interact with the large seeds (e.g. *Acromyrmex lobicornis*) and several medium-sized species which did not interact with *C. thoermeri* seeds. Thus, information on the foraging types of the ants present in an ant assemblage could help to predict the ant–seed interactions of newly introduced species. For example, a newly introduced grass may suffer more predation where seed harvesters are more abundant, but generalist ants will probably not interact with it. This type of information is important to manage and understand plant invasions, especially at initial stages.

Finally, although the ant assemblages in the Patagonian steppe are relatively poor in species, most of them are capable of interacting with seeds. The especially high interaction of generalist ants with exotic seeds in sites with low abundance of invasive plants is revealing. A closer look into the fate of removed seeds of *C. thoermeri* and other exotic species could shed more light into the role of ants in invasion process.

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