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ORIGINAL ARTICLE

María Natalia Lescano · Alejandro G. Farji-Brener

Exotic thistles increase native ant abundance through the maintenance of enhanced aphid populations

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Abstract Exotic species change the structure and composition of invaded communities in multiple ways, but the sign of their impact on native species is still controversial. We evaluated the effects of the thistles *Carduus thoermeri* and *Onopordum acanthium*—two of the most abundant exotic plant species in disturbed areas of the Patagonian steppe—on the native tending ant assemblage. Exotic thistles showed an increased number of plants with aphids and had greater aphid density than native plants. Since native tending ants were present only in plants with aphids, their abundance was higher in infested thistles than in native plants. Path analyses confirmed that ant activity depended more on aphid density than on thistle traits. Our results suggest that the presence of exotic thistles in disturbed areas of NW Patagonia indirectly benefit the native ant assemblage through the maintenance of an increased aphid population. This illustrates how the impact of exotic on native species can depend on the ecological context.

Keywords Aphids · Ants · Facilitative interactions · Exotic species · Thistles

Introduction

Exotic species often modify invaded communities and ecosystems. Several studies have examined the negative impacts of exotic species at population, community and ecosystem levels (Daehler and Strong 1993; Simberloff 1995; Parker et al. 1999). In particular, invasive alien plants can inhibit the establishment and growth of native species following disturbance (Flory and Clay 2010), modify the activity of pollinators (Morales and Aizen 2002; Bartomerus et al. 2008) or immobilize soil nitrogen, leaving fewer nutrients available for native species (Ehrenfeld et al. 2001). Although research on plant invasion processes has focused traditionally on the negative effects on the native biota, sometimes aliens can have beneficial effects on native species (Sax et al. 2005; Rodriguez 2006). For example, exotic woody species may allow the regeneration of native understory plants in areas of heavy degradation (Lugo 2004; Fischer et al. 2009), or the presence of an exotic plant can buffer native insect populations from fluctuations in the availability of their hosts (Shapiro 2002). Therefore, the study of how and when exotic species may facilitate the performance of native populations could be useful for the full understanding of community dynamics.

Facilitative interactions between exotic plants and native biota occur widely, and can have cascading effects across trophic levels as well as the potential to restructure communities (Sax et al. 2005; Jensen and Six 2006; Rodriguez 2006; Stuble et al. 2010). Diverse mechanisms have been proposed to explain how exotic plants facilitate native species. For instance, invasive plants can (1) modify the abiotic conditions or create novel habitats (French and Major 2001; Ehrenfeld 2003), (2) serve as refuges from parasitoids and/or predators (Fox and Eisenbach 1992; Gratton and Welter 1999) and (3) supply limiting resources to higher trophic levels increasing native populations (Richardson et al. 2000; French and Major 2001; Novotny et al. 2003; Rodriguez 2006). Particularly, the availability of new resources may stimulate novel mutualistic interactions in the invaded community. For example, exotic flowering plants may attract native flower visitors (Memmot and Waser 2002) and invasive fleshy fruits may attract local frugivores (Sallabanks 1993; Gosper and Vivian-Smith 2006). Moreover, these positive effects on native fauna can spread along trophic chains altering the mutualistic interactions at other trophic levels (Farji-Brener et al. 2009).

Ant–plant mutualism is one of the most extended animal–plant interactions in terrestrial biological communities (Rico-Gray and Oliveira 2007). In direct ant–

M. N. Lescano (✉) · A. G. Farji-Brener
Lab Ecotono, CRUB-Universidad Nacional del Comahue,
INIBIOMA-CONICET, Pasaje Gutiérrez 1125,
8400 Bariloche, Argentina
E-mail: natilescano@comahue-conicet.gob.ar

plant interactions, plants often offer nesting space and/or food rewards to ants. In exchange, ants frequently act as dispersal or pollinator agents or protect plants from herbivores, competitors and pathogens (see review in Rico-Gray and Oliveira 2007). Sometimes, ecological interactions between ants and plants are mediated by third species such as hemipterans and lepidopteran larvae (Cuautle et al. 1999; Pierce et al. 2002). In Hemiptera-mediated mutualism, hemipterans provide ants with carbohydrate-rich honeydew, the waste product of their sugar-rich diet of plant sap (Cushman and Whitham 1989; Cushman and Addicott 1991; Del-Claro and Oliveira 2000). In return, ants defend them from predators and parasitoids (Way 1963; Hölldobler and Wilson 1990) and exhibit increased aggressiveness towards other arthropods on plants (Way 1963; Floate and Whitham 1994; Styrsky and Eubanks 2010). This ant behaviour potentially protects plants from other, more damaging herbivores (Ito 1991; Cushman et al. 1998; Kaplan and Eubanks 2005). In certain ecological contexts, exotic plants may offer more resources than native plants, either directly (e.g. by providing rewards or refuge), or indirectly (e.g. via aphids), enhancing native ant populations (Jensen and Six 2006). Accordingly, recent reviews highlight the high faunal diversity and abundance associated with invasive plants (Sax et al. 2005; Rodriguez 2006).

In north-western Patagonia, the thistles *Onopordum acanthium* and *Carduus thoermeri* are two of the most abundant exotic plant species in disturbed steppe areas (Farji-Brener and Ghermandi 2008). These thistles are usually infested by aphids, which in turn are tended by several native ant species (Farji-Brener et al. 2009). Preliminary field observations suggest that this plant–aphid–ant relationship rarely occurs in other abundant native plant species in the study area. The majority of the native steppe flora is not infested by aphids, with few plant species showing reduced aphid abundance (M.N.L., field observation). In this study, we evaluate the impact of exotic thistle species on the native tending ant assemblage. Particularly, we address whether the presence of exotic thistles increases the abundance of native ants through the maintenance of abundant aphid populations.

Materials and methods

Study site

We conducted our study in the eastern border of the Nahuel Huapi National Park, located in north-western Patagonia, Argentina (41°S, 72°W). The mean annual temperature is 8°C and the mean annual precipitation is 600 mm. In the study area, the maintenance of road verges is a frequent soil disturbance that allows the presence of a mixture of exotic and native plant species (Farji-Brener and Ghermandi 2000). The dominant native vegetation includes species such as *Stipa speciosa*, *Imperata condensata*, *Senecio filaginoides*, *Mulinum spinosum*, *Baccharis salicifolia*, *Oenothera odorata* and *Solidago chilensis*. Exotic species are represented mainly by *Bromus tectorum*, *Onopordum acanthium*, *Carduus thoermeri*, *Lactuca serriola*, *Conium maculatum* and *Verbascum thapsus* (see Correa 1969–1998 for a full description of the vegetation in the region). The study area was a belt of approximately 100 × 5,000 m within a large portion of disturbed steppe along a main road. Roadside habitats are considered a good scenario for the study of biological invasions because of the simultaneous occurrence of exotic and native plant species (Safford and Harrison 2001; Gelbard and Harrison 2003).

Preliminary field observations, carried out for $\sim$120 h from December to March, on $\sim$150 individuals of each of the most representative plant species in this area (7 native and 6 exotic), allowed us to identify plant species colonised by aphids during the growing season. In the study area, *Carduus thoermeri and Onopordum acanthium* (exotic), plus *Oenothera odorata* and *Baccharis salicifolia* (native) were the species in which the frequency of individuals infested by aphids was much higher than in other species. Therefore, these species were selected for this study.

Exotic and native focal plant species

Carduus thoermeri (Nodding or Musk thistle) and *Onopordum acanthium* (Scotch thistle) (Asteraceae: Cardueae) are two of the most abundant exotic plant species in the study area (Farji-Brener and Ghermandi 2000, 2008) and are considered serious weeds worldwide (Shea and Kelly 1998; Qaderi et al. 2002). Both species are biennial, monocarpic herbs capable of colonizing several types of habitats (Shea et al. 2005). During the 1st year these plants form a flat basal rosette and during the 2nd year, they produce a single or several high stems with a high number of inflorescences. Plants die after seed dispersal.

Our focal native plants species were *Oenothera odorata* (perennial herb) and *Baccharis salicifolia* (evergreen shrub). They were the only representative native species in the study area that showed aphids and tending ants. *O. odorata* is a resprouter species that initially forms a flat rosette, and then produces an elongated stem and several secondary lateral ones. This plant species grows to 60–90 cm high and their leaves are linear to oblanceolate, with slightly corrugated margins. *B. salicifolia* is a branched shrub that reaches 1–2 m in height; it has many small and oblanceolate leaves (Correa 1969–1998). Both exotic and native plant species were interspaced in the study area.

Aphids

Three aphids (Hemiptera: Aphididae) species inhabit the study area, *Brachycaudus cardui* (Linnaeus 1758), *Aphis* *fabae* (Scopoli 1763) and *Uroleucon aeneum* (HilleRis Lambers 1939). All species belong to the tribe Macrosiphini, are gregarious and show high rate of population increase. Non-winged (most abundant) and winged individuals are produced, and their reproduction is viviparous and parthenogenetic. *A. fabae* and *B. cardui* are cosmopolitan, polyphagous and host-alternating species (Fischer et al. 2001). *U. aeneum* is of Palaearctic origin but naturalized in Argentina (Carvalho et al. 1998; Ortego et al. 2004). They live on different plants, especially on numerous genera of Asteraceae (Carvalho et al. 1998). While *A. fabae* and *B. cardui* are nearly always tended by ants, *U. aeneum* only occasionally is (M.N.L., field observation).

Ants

In the study area aphids are tended by four native ant species: *Dorymyrmex tener*, *D. wolffuegeli* (Dolichoderinae), *Brachymyrmex patagonica* (Formicinae) and *Solenopsis richteri* (Myrmicinae). The species of genus *Dorymyrmex* are generalist predators that live and forage in open soil and under rocks (Kusnezov 1953). These ants have been observed feeding on protein or carbohydrate baits, showing an opportunistic behaviour (Farji-Brener et al. 2002; Masciocchi et al. 2010). *B. patagonica* nests in a variety of habitats, especially in soil under stones, in leaf litter or under piles of dead wood (MacGown et al. 2007) and their colonies have many individuals. The diet of this ant species consists mainly of honeydew from various insects and other food sources (Dash et al. 2005; MacGown et al. 2007). *S. richteri* nests in open areas and is an omnivorous species that feeds on honeydew, plant exudates, other insects, spiders and oils from seeds (Kemp et al. 2000).

Methodology

In order to evaluate the effect of exotic thistle species on the native ant assemblage, we compared the abundance of aphid and tending ant populations between flowering field plants of native and exotic focal plants. This comparison was carried out during the growing seasons (spring–summer) of 2008–2009 and 2009–2010. To determine the occurrence of aphid and tending ant populations on focal plants, we measured presence/absence of aphids and tending ants in a total of 640 plants (160 individuals per species). We used chi-square tests to determine whether the presence of aphids and ants depended on the plant species.

To examine the effect of exotic thistles on aphid density, we randomly selected 132 plants with aphids (40 individuals per species, but 12 of *O. odorata* because we did not find more individuals of this species with aphids and/or ants in the study area). We estimated mean aphid density (aphids cm^{-2} plant^{-1}) from ten digital photos per plant. The photos were distributed randomly along the entire plant. In all sampled plants and on the same day when aphid density was measured, we also estimated ant activity by counting the number of ants tending aphids during 1 min (ants/min). This measure was repeated five times on each plant. We then calculated the mean number of ants/min for each plant. We compared the response variables (aphids/cm^2 and ants/min) between the four plant species using Kruskal–Wallis tests followed by a post-hoc Dunn's test. We employed this non-parametric test because all response variables were unbalanced with zero-inflated data. Also, to determine whether the number of tending ant species associated with the abundance of aphids, we employed a Spearman non-parametric correlation.

A potential major abundance of ants on thistles might be the consequence of certain plant characteristics attractive to ants or simply the result of an enhanced aphid population. To discriminate between these two potential effects of each exotic thistle species, we counted the total number of inflorescences and leaves per focal thistle plant on the same day when aphid density and ant activity were estimated. Inflorescences of thistles can attract ants directly because they host small insect prey or provide nectar, while leaves may act as shelters against the high midday temperatures of the study area, allowing them to continue active for longer periods. The correlation between two variables often represents a composite measure of direct and indirect effects (Legendre and Legendre 2004). We discriminated between direct (i.e. plant features) and indirect (i.e. aphid abundance) effects of thistles on the activity of ants using structural equation models (SEM; Shipley 2000). This methodology was developed originally as a way to partition the variation from observational data into causal and non-causal components (Mitchell 2001). We constructed a general model in which we could partition the net effect of thistles on ant activity into direct and indirect effects. The variables in the model were number of leaves (NL), number of inflorescences (NI), aphid density (AD) and ant activity (AA). We proposed that leaves of thistles may affect ants (1) indirectly, through their effect on aphids, which in turn directly influences ant activity; and (2) directly, by providing refuge to ants. Additionally, inflorescences can also affect ant activity (1) indirectly, by sustaining aphids; or (2) directly, because they could attract ants as explained above. Path coefficients were computed using standardized variables. The fit of the model with the data was evaluated via SEM using chi-square and associated probabilities (higher P values indicated a better fit; Shipley 2000). However, path coefficients can also be calculated as standardized regression coefficients with conventional least squares regression procedures when statistically significant chi-square values suggest poor fit to the model. Although this technique does not allow the evaluation of the overall goodness-of-fit of the covariance structure of the model to the data, it is useful to summarize relationships among a set of variables in a coherent way (Vázquez and Simberloff 2004). The value of the indirect effects of a particular plant trait on ant activity was estimated by multiplying the respective path coefficients of the pathway proposed. For example, the indirect effect of NL on AA through AD was obtained as the product of NL-AD and the AD-AA path coefficients.

Results

The presence of aphids differed significantly among the plant species studied ($\chi^2 = 238$, *df*: 3, $P < 0.0001$; Fig. 1a); the occurrence of aphids was higher in exotic plant species than in natives. While only a small number of observed native plants had aphids (7.5% of *O. odorata* and 26.9% of *B. salicifolia* plants), most observed exotic thistles supported aphids (80% of *O. acanthium* and 72.5% of *C. ithoermeri* plants). Tending ants were present only in plants with aphids. When only plants with aphids were analysed, the presence of tending ants also differed significantly among plant species ($\chi^2 = 167$, *df*: 3, $P < 0.0001$; Fig. 1b); the percentage of plants with tending ants was higher in exotic species than in natives. Tending ants were present in 87.5% of *C. thoermeri* and in all *O. acanthium* plants with aphids, while only 25% of *O. odorata* and 16% of *B. salicifolia* plants with aphids had tending ants. On the other hand, the relative abundance of aphids was significantly different among plant species ($H = 97.4$ *df*: 3, $P < 0.001$). Exotic plants showed up to 28 times more aphids/cm^2 than natives (Fig. 2a). Accordingly, the abundance of tending ants was significantly different among plant species ($H = 84.1$ *df*: 3, $P < 0.001$); it was higher in exotic thistles than in native plants (Fig. 2b). Exotic plants showed 51 times more ant activity than native plants.

Throughout the field sampling period we found only one aphid species per native plant species (Fig. 3). On the other hand, two or three aphid species were observed per exotic plant species in the study area; *B. cardui* was the most frequent in both thistles (present in 80% and 87.5% of individuals of *C. thoermeri* and *O. acanthium*, respectively). The other two aphid species also colonized *C. thoermeri,* but only *A. fabae* was present in *O. acan-*

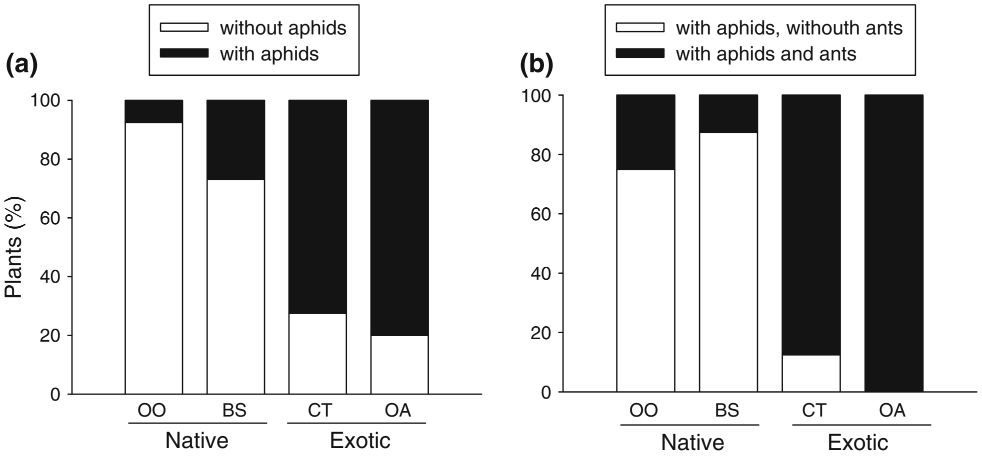

Fig. 1 Occurrence of aphid and tending ant populations on *Oenothera odorata* (*OO*), *Baccharis salicifolia* (*BS*), *Carduus thoermeri* (*CT*), and *Onopordum acanthium* (*OA*). **a** Percentage of plants with and without aphids ($n = 160$ individuals per species). **b** Percentage of aphid-infested plants with and without ants ($n = 40$ individuals per species, but $n = 12$ for *O. odorata*)

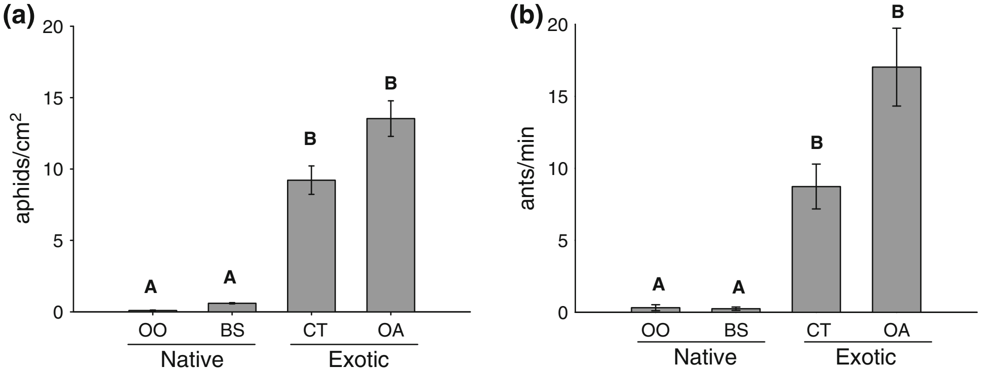

Fig. 2 Abundance of aphid and ant populations on focal plants: *Oenothera odorata* (*OO*, native), *Baccharis salicifolia* (*BS*, native), *Carduus thoermeri* (*CT*, exotic), and *Onopordum acanthium* (*OA*, exotic). **a** Mean of aphid density (aphids/cm^2) per plant (±SE). **b** Mean of ant activity (ants/min) per plant (±SE). Different upper case letters imply statistically significant differences ($P < 0.001$, Kruskal–Wallis tests, Dunn's test post-hoc comparisons); $n = 40$ individuals per species, but $n = 12$ for *O. odorata*

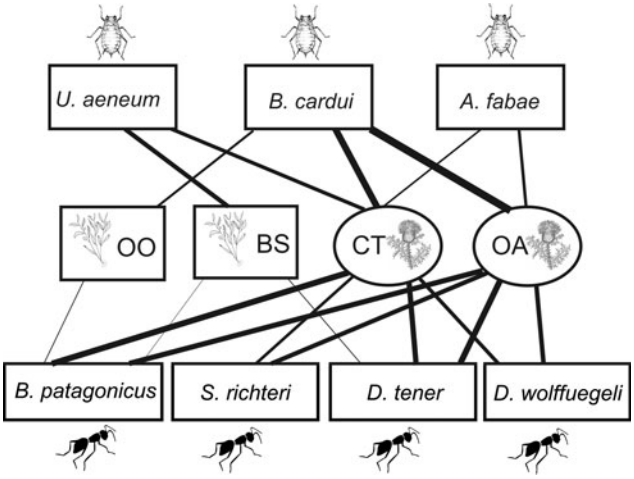

Fig. 3 Schematic representation of the relationship of aphids and ants with the focal plants, *Oenothera odorata* (*OO*), *Baccharis salicifolia* (*BS*), *Carduus thoermeri* (*CT*), and *Onopordum acanthium* (*OA*). The link thickness is proportional to the frequency of the relationship. *Oval boxes* Exotic plant species

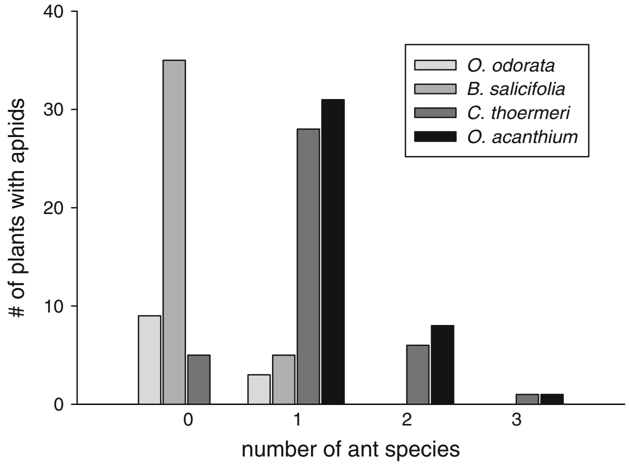

Fig. 4 Relationship between the number of plants with aphids, the number of ant species attending aphids per plant, and the host plant species of the aphids

thium. The four ant species were observed tending the three aphid species, but the number of ant species per plant depended on plant species. While all native plants showed only one ant species tending aphids, the 23% of thistles showed two or three aphid-tending ant species per plant (Fig. 4). The two most abundant ant species were *Brachymyrmex patagonica* (49%) and *Dorymyrmex tener* (39%). *Dorymyrmex wolffuegeli* was found sharing the plant with other ant species and, usually, was the subordinate species (in 94% of the plants with *D. wolffuegeli* observed). Additionally, the abundance of tending ants was positively associated with the abundance of aphids ($R_s = 0.44$, $P < 0.0001$, $N = 80$).

Although our data did not fit well into the proposed model (chi-square values were high and $P < 0.05$), the path analysis did summarize well the relationships among thistles, aphids and ants (Fig. 5a, b). In general, ant activity was influenced more by the direct and positive effect of aphid density than by direct or indirect effects via plant traits. However, the strength and sign of indirect effects differed among plant species. In *O. acanthium*, the number of inflorescences and of leaves had both indirect effects on ant density but with opposite signs. The number of leaves influenced aphid density positively, and thus, positively affected ant activity. However, the number of inflorescences had a negative effect on aphid density, thus negatively affecting ant activity. In *C. thoermeri*, the number of leaves had a significant but negative effect on aphid density, having an indirect and negative effect on the activity of ants, although it had a direct and positive effect on ant activity (Fig. 5b).

Discussion

Exotic plant species are known to have a wide variety of negative impacts on native biota (Mack et al. 2000; Grosholz 2002; Levine et al. 2003; Vilà and Weiner 2004). However, exotic plants may also facilitate the performance of native organisms when they, directly or

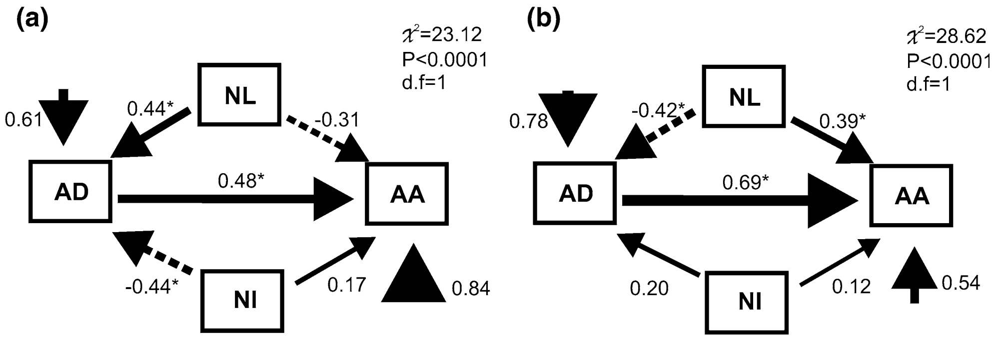

Fig. 5 Path analysis of the relationships between thistle traits (*NL* number of leaves, *NI* number of inflorescences), aphid density (*AD*) and ant activity (*AA*). *One headed arrows* Direct causal effects. Coefficients are given for each path, and their value is also represented by arrow line thickness (the thicker the arrow, the higher coefficient value). *Continuous lines* Positive effects, *dashed lines* negative effects, *asterisks* significant path coefficients ($P < 0.05$), *vertical arrows* unexplained variability. The adequacy of models was evaluated based on model χ^2 and associated *P* values. **a** *Onopordum acanthium*, **b** *Carduus thoermeri*

indirectly, increment the availability of resources in the invaded area. This appears to be the case for some exotic plants in the arid region of north-western Patagonia. The typical native plant species of the Patagonian steppe rarely maintain large aphid populations and thus are poorly attractive to native tending ants. However, disturbed areas such as road verges are often colonized by exotic thistles, which are typically aphid-infested. We demonstrated that aphid density on thistles was up to 28 times more than that on native plant species. Although previous studies documented that aphids can colonize the native plant genera studied here (*Oenothera*: Hughes and Bazzaz 2001; Rakauskas 2004; Johnson 2008; *Baccharis*: Delfino and Buffa 1996; Delfino 2005; Fagundes et al. 2005), in the study area this native species sustain very small aphid populations. Since tending ants are associated with aphids, this increased aphid density on exotics thistles impacts on the native ant assemblage.

Exotic thistles showed 51 times more tending ant activity and increased ant richness than native plants. Tending ants were only rarely associated with native plants. Several lines of evidence suggest that this enhanced ant activity on thistles depends more on the abundance of aphid populations than on specific thistle traits. First, ants were positively associated with aphid density. Second, the direct effect of aphids on ant activity was stronger than the indirect effect of thistles on ant activity via aphids. Third, plants without aphids or with a low abundance of aphids were not attractive to ants; especially if nearby thistle plants infested by aphids were present.

Aphids, via their honeydew, represent a stationary and renewable food resource for ants (Carroll and Janzen 1973). The strong dependence of the ants on aphids on the exotic plants suggested by the results of the path analyses was confirmed by our field observations (~120 h), which showed that ants on focal plants were tending aphids and rarely searching for other insect prey and/or plant reward. This is consistent with evidence showing that enhanced aphid abundance often positively affects ant performance, including sexual reproduction and colony expansion (Davidson 1998; Yanoviak and Kaspari 2000; Helms and Vinson 2002; Davidson et al. 2003). Therefore, our results suggest strongly that, in the study area, exotic plants positively affect the native ant assemblage through the maintenance of an enhanced aphid population.

Although exotic plants might have a positive direct effect on native fauna (Memmot and Waser 2002; Jensen and Six 2006), sometimes their main impact is indirect (Farji-Brener et al. 2009). Indirect effects on higher trophic levels have been reported in various terrestrial systems. For example, Johnson (2008) show that plant genotype had a bottom-up effect effects on tritrophic interactions; Teder and Tammaru (2002) found that the variability in host plant quality induced indirect effects on performance of parasitoids, through their effects on herbivores. In this study, the enhanced ant activity and richness on thistles were poorly related with the direct effect of these plants on ant populations but strongly related with aphid density (Fig. 5). The effect of thistles on ants was thus mainly an indirect, bottom-up effect via aphids. The effect of exotic plants enhanced aphid populations may also occur in other exotic plant species and in other disturbed habitats. For example, in perturbed California grasslands, native aphids preferred exotics annuals as hosts and experienced higher fecundity on them (Malmstrom et al. 2005). However, the indirect consequences of this exotic-native interaction on the native ant assemblage have not been deeply explored. As far as we know, our study is the first to document this pattern.

As discussed earlier, exotic species may facilitate natives in certain ecological circumstances. For example, it has been reported that a nitrogen-fixing exotic woody plant facilitates growth, reproduction and recruitment of two native herbaceous species by improving soil conditions mainly in highly stressful sand dune prairies (Shumway 2000). Also, an invasive tree facilitates endemic understory species in managed tropical forests (Fischer et al. 2009). Our results suggest that, in the Patagonia steppe, where native species are rarely infested by aphids, the presence of exotic thistles in disturbed areas play an important role for the native ant assemblage via the maintenance of an enhanced aphid population. This illustrates how, under certain ecological contexts, exotic plant species might indirectly and positively affect native organisms at higher trophic levels through bottom-up, cascade effects.

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