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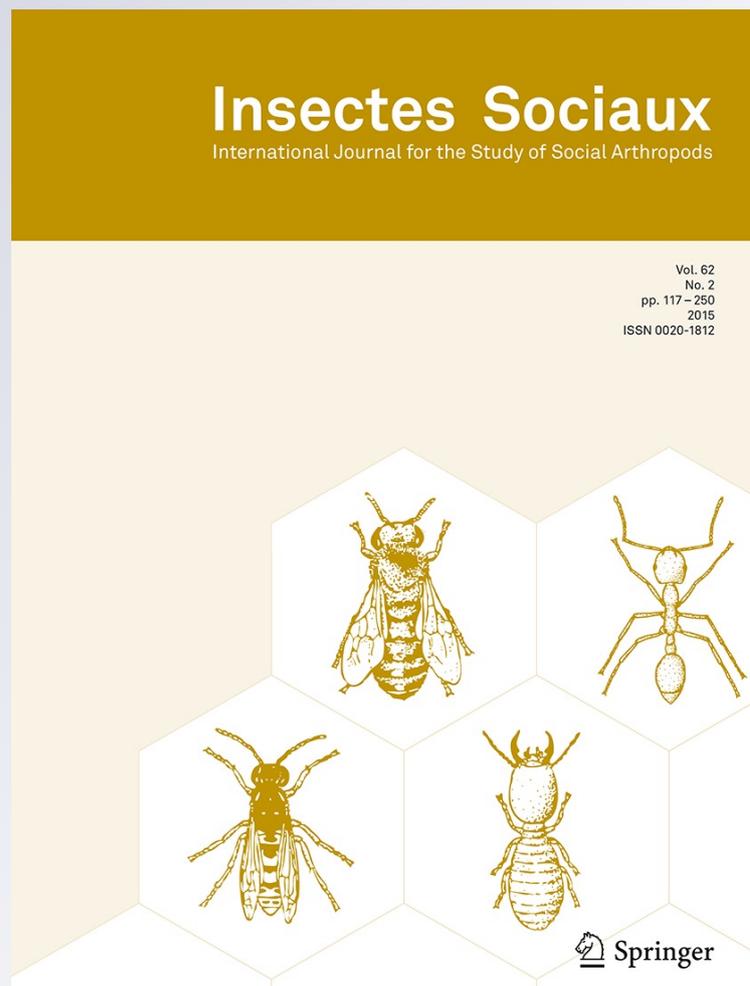
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# Outcomes of competitive interactions after a natural increment of resources: the assemblage of aphid-tending ants in northern Patagonia

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**Abstract** Ant-aphid relationships provide excellent opportunities to study how changes in resource availability may affect the outcome of competitive interactions. Variations in soil fertility may affect host plant quality, with concomitant effects on aphid abundance and the amount/quality of aphid honeydew. This may determine the intensity at which tending ants defend aphids against natural enemies and competing ants. In a shrub-steppe of northern Patagonia, aphid-infested thistles naturally grow on contrasting fertility substrates: organic waste piles of leaf-cutting ants (refuse dumps) and nutrient-poor steppe soils. Thistles growing on refuse dumps have much larger aphid colonies than thistles growing on steppe soils. We took advantage of the co-occurrence in the field of plants with contrasting aphid density to study the effect of natural variation in food availability (aphid density) on aphid-tending ant species richness and agonistic interactions among them. Enhanced aphid density did not promote the coexistence of aphid-tending ant species. Although all ant species are potential colonizers of the study plants, thistles were often monopolized by a single ant species, regardless

of aphid density. Field experiments showed that increased aphid density did not modify aggressiveness toward an intruder ant, nor the probability of coexistence between two rival ant species after the invasion of a host plant. We discuss several hypotheses to explain why increased resource availability does not necessarily reduce competitive interactions in ant-aphid relationships.

**Keywords** Aggressive behavior · Ant communities · Competitive interactions · Resource availability

## Introduction

The role of resource competition in structuring communities is often linked to a key assumption: limited resource availability (Davis et al. 1998; Ray and Sunquist 2001; Gebauer et al. 2002; Luiselli 2006; Rees 2013; Chang and Smith 2014). This may be tested by evaluating the outcome of competitive interactions when resource availability varies (e.g., Wilson and Tilman 1993). Since competition is a negative interaction for all the competitors, an increase in the limiting resource should reduce the level of dominance and aggressive behavior, allowing the use of surplus resources by subordinate species (Wilson 1988; Ribas et al. 2003). For example, the intensity with which the hummingbird *Lampornis clemenciae* excluded competing species from its territory was reduced when nectar availability in artificial feeders was unlimited (Powers and McKee 1994). However, increments of limiting resources do not necessarily reduce competitive interactions. Dominant species may show rapid numerical responses to this new scenario, incrementing their abundance, and thus keeping subordinate species outcompeted (e.g., Matthiessen et al. 2010; Tsvuura and Kirkman 2013). Moreover, if

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behaviors of dominant species were selected under competitive environments, transient resource increments would not necessarily reduce the intensity of resource defense (Vepsäläinen and Savolainen 1990; Cerdá et al. 1998). The outcome of interspecific competition in a context of increased resource availability could depend on the response behavior of interacting species.

Ant-aphid relationships provide excellent opportunities to study how changes in resource availability may affect the outcome of competitive interactions. In this mutualistic interaction, aphids supply honeydew, an energy-rich food resource, and in exchange for it ants defend them from other ants, predators, and parasitoids (Rico-Gray and Oliveira 2007; Moreira and Del-Claro 2005; Del-Claro and Oliveira 2000). Honeydew is a valuable and renewable food resource that may increase ant colony fitness (Styrsky and Eubanks 2007; Helms and Vinson 2002; Davidson et al. 2003). It is expected that ant species will compete intensely and tend to monopolize plants with aphids (Blüthgen et al. 2000; Wimp and Whitham 2001; Blüthgen and Fiedler 2004). The attractiveness of aphids for tending ants depends on various factors (e.g., proximity of ant colonies to host plants with aphids, availability of other food sources), and host plant quality may be a particularly important factor (Cushman 1991 and references therein). Host plant quality may affect the nutritional content of honeydew (Douglas 2003), and plants with enhanced quality may sustain larger aphid populations (e.g., Lescano et al. 2012), which in turn leads to a greater amount of honeydew available for ants. Summarizing, host plant quality, through changes in the quality and/or quantity of honeydew, may affect the attractiveness of aphids for tending ants, influencing the intensity with which ants defend them against natural enemies and other competing ants (Oliveira and Del-Claro 2005; Blüthgen and Fiedler 2004; Wimp and Whitham 2001).

In northern Patagonia, tending ants are found in thistles that naturally grow on substrates of varying quality, which is reflected in the density of aphid colonies. Thistles growing on refuse dumps (organic waste piles generated by the leaf-cutting ant, *Acromyrmex lobicornis*) are larger and have greater concentration of foliar nutrients than those on the nutrient-poor typical steppe soils (Farji-Brener and Ghermandi 2008; Farji-Brener et al. 2009). This enhanced plant quantity/quality leads thistles to sustain higher aphid densities, which means more honeydew available for tending ants (Farji-Brener et al. 2009; Lescano et al. 2012). In this system, a previous study showed that ant species tend to monopolize and defend the aphid-infested thistles growing on nutrient-poor steppe soils, suggesting that competition plays an important role in the structure of the aphid-tending ant assemblage (Lescano et al. 2014). The presence of thistles with increased resources (higher aphid density) could alter the competitive interactions among ants. The

surplus of resource (aphid honeydew) could diminish the intensity of defensive behavior by dominant ants. This could promote the invasion of the more valuable thistles (with high aphid density) by competing, formerly subordinate ant species, thus encouraging the coexistence of different species in a host plant. The co-occurrence in the field of plants with contrasting aphid density is particularly adequate to study how changes in resource availability affect aphid-tending ant species richness and agonistic interactions among them. We carried out field measurements and experimental manipulations to address these issues. According to the general idea that a limited supply of a common resource is key to allow competitive interactions, we expected (1) a lower frequency of aggressive behaviors in ants inhabiting thistles with high aphid density compared to those on thistles with low aphid density, independent of ant species identity, (2) a higher frequency of ant invasions from thistles with low aphid density to thistles with high aphid density than in the opposite direction, and (3) in the case of invasions, a higher frequency of ant coexistence on thistles with high aphid density.

## Materials and methods

This study was carried out during the growing season (December 2010–February 2011) at the eastern edge of the Nahuel Huapi National Park, located in NW Patagonia, Argentina (41°S, 71°W). The climate of the region is cold (mean annual temperature 8 °C), and rainfall is concentrated in autumn–winter. The study area is crossed by the Limay River and Route 237, and the vegetation corresponds to an herbaceous-shrub steppe (Correa 1969). In this region, four native ant species, *Dorymyrmex tener*, *D. wolffuegeli*, *Brachymyrmex patagonica*, and *Solenopsis richteri*, have mutualistic relationships with the aphid *Brachycaudus cardui* (Lescano et al. 2012). The main hosts plants in this mutualism are two exotic thistle species, *Onopordum acanthium* and *Carduus thoermeri*, which naturally grow in two contrasting substrates: nutrient-rich refuse dumps (organic waste piles of the leaf-cutting ant *Acromyrmex lobicornis*; Farji-Brener and Ghermandi 2000, 2008) and nutrient-poor steppe soils (Satti et al. 2003). Thistles growing on refuse dumps have higher leaf-nutrient content and are larger than those growing on adjacent soils. Aphid density in thistles established on refuse dumps was ~200 % higher than in those growing on steppe soils, and this aphid density rise was associated with a ~120 % increase in the activity of aphid-tending ant species (Lescano et al. 2012). Ant species in this assemblage co-occur in the same patches and colonize host plants regardless of their relative abundance in the area, resulting in competition for thistles with aphids (Lescano et al. 2014).

### Impact of resource availability on the aphid-tending ant assemblage

First, we evaluated the effect of increased resource availability (aphid density) in host plants on the structure of the aphid-tending ant assemblage. We used aphid density as a measure of resource availability for tending ants because it is often associated with the quantity of honeydew available to ants (Dixon 1998). We sampled 143 flowering plants (41 and 32 individuals of *O. acanthium* growing on refuse dumps and soil, respectively, and 39 and 31 individuals of *C. thoermeri* growing on refuse dumps and soil, respectively), which were in their second (final) year of life and had a height of 1–2 m. The selected thistles were at least 10 m apart, thus reducing the chance to observe ant workers from the same colony in different host plants, and were located within an area where we previously documented that the home ranges of ant species overlap and interspecific competition plays a relevant role structuring the ant assemblage (Lescano et al. 2014). Thistles on refuse dumps and thistles on soils were assigned to the high aphid density and low aphid density treatments, respectively, based on their actual aphid density (number of aphids per cm<sup>2</sup>, mean  $\pm$  SE) as reported by Lescano et al. (2012) for the same plants on refuse dumps (*O. acanthium*:  $30.9 \pm 1.3$ ; *C. thoermeri*:  $23.2 \pm 2.3$ ) and on adjacent soils (*O. acanthium*:  $12.6 \pm 2.2$ ; *C. thoermeri*:  $7.1 \pm 1.0$ ). In each focal plant, we determined the identity of the resident ant species. When there were several species, we counted the number of workers of each ant species (five min per plant) and classified ant species as dominant or subordinate according to their worker abundance. We used  $\chi^2$  tests to analyze whether the number of aphid-tending ant species per host plant varied with thistle condition (high or low aphid density).

In order to evaluate the effect of enhanced resource availability (aphid density) on the competitive interactions among the aphid-tending ant species, we conducted two field experiments using the three numerically dominant ant species (*B. patagonica*, *D. tener*, and *S. richteri*; Lescano et al. 2014). First, we performed a “confrontation” experiment to determine if the level of aggressiveness displayed by the resident ant species to an intruder species varies with the quantity of resources in the host plant. We conducted sets of trials where an individual ant from a low aphid density thistle (“intruder”) was carefully placed on thistles, with high or low aphid density, dominated by a different resident ant species. The three dominant ant species were used in this experiment both as intruder and resident. We recorded the behavior of the resident ant individuals during 5 min (or until the intruder ran away from the plant or was killed). The behavior of the resident ants was classified into categories representing different degrees of aggressiveness (based upon Dimarco et al. 2010): 0 (no

aggression, the residents ignore the intruder without making contact), 1 (slight interaction, the residents make antennal contact and touch the body to the intruder), 2 (mild aggression, the residents pursue the intruder until it leaves from the plant), 3 (moderate aggression, one or more residents bite/prick/sting the intruder), and 4 (severe aggression, the resident killed the intruder). We performed 122 sets of trials, 21 in high aphid density thistles and 101 in low aphid density thistles and used  $\chi^2$  tests to determine whether ant aggressiveness varied with aphid density. Second, to determine whether resource availability (aphid density) on host plants affects (1) the probability of invasion by another ant species and (2) the coexistence between ant species in the invaded thistle, we facilitated the invasion between ant colonies located on nearby thistles. To do this, we sought pairs of neighboring thistles (less than 1.5 m apart) occupied by different tending ant species and connected each pair using sisal yarn, thus creating artificial bridges between plants. Previous experimental studies have documented that ants can use artificial bridges connecting neighboring vegetation to invade a plant (e.g., Davidson et al. 1988; see photo in the electronic supplementary material A). The experiment had two treatments: (a) high—low aphid density pairs ( $N = 9$ ) and (b) low—low aphid density pairs ( $N = 31$ ). The number of replicates for each treatment depended on the availability plant pairs meeting these conditions. One week after connecting each pair of plants, we documented the occurrence of invasion from the plant previously occupied by other ant species and, when invasion actually took place, we checked whether resident and intruder species coexisted. We counted the number of ants per species and considered coexistence to occur when the relative abundance of subordinate species was greater than 0.10 (i.e., 10 % of the total number of ant workers). We recorded the direction in which invasion occurred in the high—low aphid density treatment (the direction of invasion in the low—low aphid density was immaterial for our objective). We used a Chi square test to determine whether the coexistence after ant invasion depended on aphid density.

### Results

Aphids *Brachycaudus cardui* on the thistles *Carduus thoermeri* and *Onopordum acanthium* were tended by four ant species: *Dorymyrmex tener*, *D. wolffuegeli*, *Brachymyrmex patagonica*, and *Solenopsis richteri*. Host plants were usually monopolized by one of these ant species ( $\approx 65$  % of cases), and coexistence occurred in nearly 25 % of the sampled thistles. The number of ant species per thistle was independent of aphid density. Thus, the proportion of plants with 0, 1, 2, and 3 resident ant species was similar between thistles growing on refuse dumps (high aphid density) and

those growing on adjacent soils (low aphid density) ( $\chi^2 = 4.53$ ,  $df = 3$ ,  $P = 0.2$ , Fig. 1). Overall, regardless of aphid density, the two most abundant ant species were *B. patagonica* and *D. tener*, either as the monopolizing or the numerically dominant species. *S. richteri* rarely monopolized a host plant but it was frequently the dominant species, while *D. wolffuegeli* was usually a subordinate species (Fig. 2; see also supplementary material B).

Aphid density did not influence the agonistic interactions within the aphid-tending ant assemblage. The introduction of an intruder individual produced a moderate attack response by the resident, independent of whether the host plant had high or low aphid density ( $\chi^2 = 9.73$ ,  $df = 4$ ,  $P = 0.95$ ; Fig. 3). The resident ant species bit/pricked/stung the intruder (moderate aggressive behavior) in 48 % of the cases (10/21 and 48/101 trials in high and low aphid density, respectively) and occasionally, the intruder died as a result of a severe attack (2/21 and 14/101 trials in high and low aphid density, respectively). Intruder ants were rarely ignored (no attack by the resident ants was observed in 1/21 and 8/101 cases in high and low aphid density, respectively).

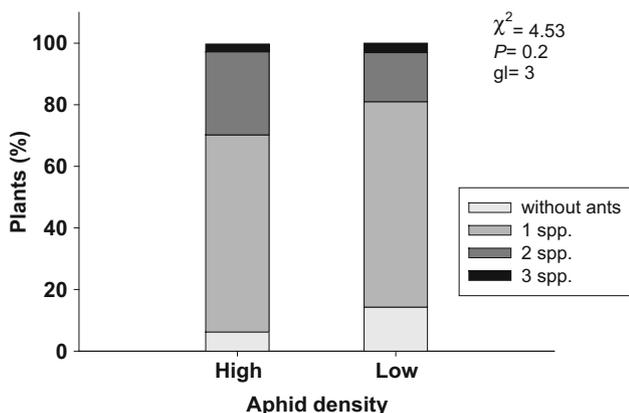
Artificial bridges between thistles with different ant species allowed the invasion of a plant previously occupied by another species (3 out of 9 pairs of high—low aphid density; 20 out of 31 pairs of low—low aphid density). Aphid density influenced the direction in which the ant species moved. In the high—low pairs, all invasions were from plants with low aphid density to plants with high aphid density. On the other hand, aphid density did not influence the coexistence of different ant species after the invasion ( $\chi^2 = 0.73$ ,  $df = 1$ ,  $P = 0.39$ ). We observed species coexistence in 3 and 11 invaded plants with high and low aphid

density, respectively, and in 9 low aphid density plants, the resident ant was excluded by the intruder.

## Discussion

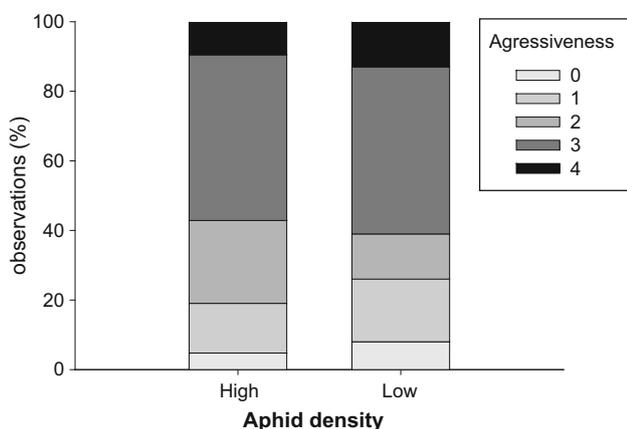
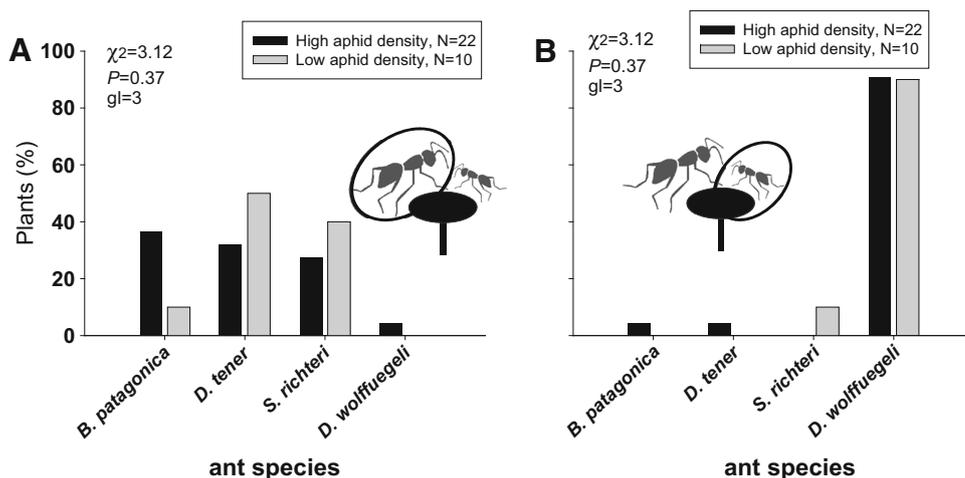
Contrary to the expectation that increased resources would reduce the strength of competitive interactions, our results suggest that resource availability in host plants (aphid density) does not influence competitive interactions among the native aphid-tending ant assemblage in northern Patagonia. Enhanced aphid abundance often affects positively ant foraging efficiency, and hence colony growth (Davidson 1998; Davidson et al. 2003; Helms and Vinson 2008; Yanoviak and Kaspari 2000). Other factors besides aphid abundance, such as the nutritional demands of the ant colony and the proximity and abundance of alternative food sources, may be affecting the attractiveness of the aphid-plant system for tending ants (Cushman 1991). Here, we showed that the increased aphid density did not promote the coexistence of aphid-tending ant species. Despite all ant species are potential colonizers of the study plants, thistles were often monopolized by a single ant species, regardless of aphid density. Field experiments showed that increased aphid density does modify neither aggressiveness toward an intruder ant nor the probability of coexistence between two rival ant species after the invasion of a host plant. These results are opposite to the expectation that aggressive behavior between competing species decreases when resource levels are high (Powers and McKee 1994). The monopolization and defense of host plants independent of aphid density could be explained by several non-exclusive hypotheses: (1) diet-dependent behavior, (2) valuable but transient resources, (3) rapid population response, (4) honeydew quality or production, and (5) evolutionary-fixed behaviors. We discuss each of them below.

The absence of a reduction in monopolization and aggressive behaviors in thistles with high aphid density could be related to food nutritional quality. The aggressive defense of food is a prevalent mechanism in animals, particularly in nectar feeders (Nagamitsu and Inoue 1997). Honeydew, as nectar, is a carbohydrate-rich food, and several studies in ant species suggest a positive relationship between carbohydrate content in the diet and aggressive behavior and territoriality (Davidson 2005; Davidson et al. 2003; Grover et al. 2007; Ness et al. 2009; Palmer et al. 2008). The excess of carbohydrates in ants is often invested in N-free or C-based semiochemicals or allelochemicals involved in foraging and defense (Davidson 1997, 1998). However, aphid-tending ant species inhabiting thistles with high aphid density were not more aggressive than those inhabiting thistles with low aphid density. We observed moderate or severe aggression by the resident ant in 60 % of



**Fig. 1** Percentage of thistles with aphids occupied by different number of aphid-tending ant species (0, 1, 2, and 3 species). Bars correspond to thistles growing on refuse dumps (high aphid density;  $N = 80$  plants) and on adjacent soils (low aphid density;  $N = 63$  plants)

**Fig. 2** Percentage of host plants occupied by the four aphid-tending ant species being **a** dominant species and **b** subordinate species in thistles growing on refuse dumps (high aphid density) and on adjacent soils (low aphid density). We compared the frequencies for each ant species between high and low aphid density plants using  $\chi^2$  test



**Fig. 3** Percentage of observations of the different aggressiveness degrees displayed by the resident aphid-tending ants after the arrival of an intruder ant, in thistles growing on refuse dumps (high aphid density) and on adjacent soils (low aphid density). The aggressiveness degree was measured in categories ranging from 0 (no aggression) to 4 (kill the intruder). See further details in “Materials and methods”

the clashes in both thistle groups. Therefore, the idea that increased C-based food intensifies ant aggressiveness does not fully explain the results found. It seems that the mere presence of aphids, regardless of their density, triggers ant aggressive behavior at a rather fixed level.

Another possible explanation why increased resources do not relax agonistic interactions may be the particular value of thistles on refuse dumps, which might be lost to a rival ant colony. The lifespan of ant colonies largely exceeds that of thistles, which are bi-annual plants and are not always infested by aphids. This makes aphid-infested thistles an ephemeral food source for ants. Moreover, thistles that sustain large aphid colonies are an unusual resource because they depend on the existence of refuse dumps of the leaf-cutting ant *Acromyrmex lobicornis*, which are present in low density in the study area (Farji-Brener 2000). Thus, thistles

with aphids, and particularly those with high aphid density (growing on refuse dumps), are highly valuable but transient resources by which this ant assemblage may compete intensely. We showed that access facilitation led to the invasion of a host plant previously occupied by a rival ant species, resulting—in some cases—in resident ant exclusion. If invasions of host plants by nearby ant colonies are common in nature, ants should defend their host plants regardless of aphid density. This hypothesis is somewhat weakened by the fact that coexistence of more than two ant species in a single host plant was not rare (20–30 % of sampled plants), suggesting that invasions not always lead to monopolization.

The competitive dynamics of interacting species may depend on the capacity of dominant species to respond to changes in food availability. If dominant species have the capacity to rapidly derive the surplus of resources to increase their own density, it may lead to maintain aggressive behaviors and dominance. This numerical response may result in aphid density becoming a limiting resource again, thus hindering the activity of subordinate species in high aphid density plants. In a previous study in this system, we found that enhanced aphid populations resulted in increased ant activity in refuse dump thistles (Farji-Brener et al. 2009; Lescano et al. 2012). This increase in tending ant activity in high aphid density plants depended on ant identity regardless of their abundance in the surroundings. Further experimental approaches are needed to validate the hypothesis of rapid population response.

The observed results could be partly explained by unmeasured factors, such as variations in aphid honeydew quantity or quality. We used aphid density as an estimate of food availability (honeydew) for tending ants because aphid abundance is often positively associated with ant colony fitness (Helms and Vinson 2002; Davidson et al. 2003). However, changes in host plant quality may impact not only

on aphid abundance but also on the quantity and/or quality of excreted honeydew (Cushman 1991; Dixon 1998; Douglas 2003). Honeydew production is a consequence of aphids' poor nutrient diet (Douglas 2006). It could be conceived that individuals whose diet is closer to their nutritional requirements would excrete less honeydew and/or honeydew of lesser quality, i.e., with a relatively lower proportion of carbohydrates. This would compensate the increased number of aphids, for a relatively constant total resource quantity and/or quality across thistles differing in aphid density, hence explaining why ant competition did not vary. We did not measure whether honeydew production or quality varied between thistles growing on different substrates, but this is not unlikely given that tissue quality of thistles changes when growing on refuse dumps (Farji-Brener et al. 2009).

Finally, the identity of the dominant ant species may explain why increased resources did not reduce competitive interactions. If aggressive behaviors of certain ant species were selected under competitive environments, transient increments in food density would not necessarily modify these evolutionary-fixed behaviors. As discussed above, thistles with high aphid density are transient food sources. The low spatiotemporal predictability in aphid availability may hamper the modification of the hypothetically idiosyncratic or fixed defensive behavior of some ant species. For example, regardless of aphid density, *B. patagonica* usually monopolized host plants and on occasions coexisted with *D. wolffuegeli* but almost never did it with *D. tener* or *S. richteri*. Also, regardless of aphid density, when ant species coexisted, *D. wolffuegeli* was generally the subordinate species (see supplementary material B) and the strongest fighting occurred between *B. patagonica* and *S. richteri* (see supplementary material C).

Summarizing, our results show that the tending ant species in the ant-aphid-thistle system are highly territorial and exhibit strong aggression against competitor ants, independent of increments in the density of their food resource. These behaviors, unexpected under the assumption that increased resource availability should relax competitive interactions, may be explained by both host plant characteristics and intrinsic features of ant species in this assemblage.

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