Ecol Res (2009) 24: 139–145
DOI 10.1007/s11284-008-0491-3

ORIGINAL ARTICLE

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Small-scale disturbances spread along trophic chains: leaf-cutting ant nests, plants, aphids, and tending ants

Received: 31 October 2007 / Accepted: 29 February 2008 / Published online: 17 April 2008

Abstract Small-scale disturbances caused by animals often modify soil resource availability and may also affect plant attributes. Changes in the phenotype of plants growing on disturbed, nutrient-enriched microsites may influence the distribution and abundance of associated insects. We evaluated how the high nutrient availability generated by leaf-cutting ant nests in a Patagonian desert steppe may spread along the trophic chain, affecting the phenotype of two thistle species, the abundance of a specialist aphid and the composition of the associated assemblage of tending ants. Plants of the thistle species *Carduus nutans* and *Onopordum acanthium* growing in piles of waste material generated by leaf-cutting ant nests (i.e., refuse dumps) had more leaves, inflorescences and higher foliar nitrogen content than those in non-nest soils. Overall, plants in refuse dumps showed higher abundance of aphids than plants in non-nest soils, and aphid colonies were of greater size on *O. acanthium* plants than on *C. nutans* plants. However, only *C. nutans* plants showed an increase in aphid abundance when growing on refuse dumps. This resulted in a similar aphid load in both thistle species when growing on refuse dumps. Accordingly, only *C. nutans* showed an increase in the number of ant species attending aphids when growing on refuse dumps. The increase of soil fertility generated by leaf-cutting ant nests can affect aphid abundance and their tending ant assemblage through its effect on plant size and quality. However, the propagation of small-scale soil disturbances through the trophic chain may depend on the identity of the species involved.

Keywords *Acromyrmex lobicornis* · Ants · Aphid · Bottom-up effects · Fertilizer effect · Soil disturbances · Thistle · Trophic cascades

Introduction

Small-scale disturbances caused by animals are common landscape components in several terrestrial ecosystems, and may affect vegetation dynamics and diversity (Heske et al. 1993; Doak and Loso 2003). This generally occurs because of significant changes in soil resource availability (Huston 2004), which may differentially affect growth, morphology and performance of plant species (Bazzaz 1996; Diemer and Schmid 2001). Invasive or weed species are particularly efficient in exploiting such altered soil patches (Funk and Vitousek 2007). There is substantial evidence that changes in the phenotype of plants growing on disturbed (and often nutrient-enriched) microsites may influence the distribution and abundance of the associated insect herbivores (bottom-up effects, Hunter and Price 1992; Stiling and Rossi 1997). For instance, plants showing increased height, a greater number of branches or enhanced foliar nitrogen are more likely to sustain larger populations of herbivorous insects (Root 1973; Coley and Barone 1996; Helms and Hunter 2005). Furthermore, the direct impact of variations in plant quantity and quality on insect herbivores may cascade up through higher trophic levels, including predators and parasitoids (Siemann 1998; Stiling and Moon 2005). For example, plants with higher foliar quality have larger leaf galls that suffer lower parasitism (Cattell and Stiling 2004). To our knowledge, however, few studies have addressed whether small-scale soil disturbances by animals may affect higher trophic levels through bottom-up cascades (Wilby et al. 2001). Here we examine how the

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high nutrient availability generated by leaf-cutting ant nests in a desert steppe may spread along the trophic chain, affecting the phenotype of two exotic plant species, the abundance of an introduced specialist aphid species and the associated assemblage of native tending ants species.

Leaf-cutting ant nests are recognized as small-scale soil disturbances with a substantial impact on plant assemblages (Farji-Brener and Illes 2000). When leaf-cutting ants build and maintain their nests, they cover the ground with large quantities of excavated soil, clearing the area of vegetation and modifying resource availability through the deposition of organic wastes originated from their fungal gardens (Wirth et al. 2003). These specific disposal areas (refuse dumps) are several times richer in nutrients than the adjacent soils, thus generating nutrient hot-spots around the nest area, where plant abundance, diversity and productivity are increased (Farji-Brener and Illes 2000; Moutinho et al. 2003; Wirth et al. 2003; Farji-Brener and Ghermandi 2004). Plants that grow on refuse dumps often show greater biomass and tissue quality than plants on non-nest soils (Sternberg et al. 2006). These changes in plant quantity and quality could generate concomitant changes in the abundance of herbivorous insects and associated arthropods. This possibility remains unexplored.

Honeydew-producing aphids are herbivorous insects that often develop mutualistic associations with ant species. Ants collect and consume honeydew excreted by aphids as waste product of plant sap ingestion and, in return, protect them from predators and parasitoids (Buckley 1987). Changes in plant quality and biomass may influence the abundance of aphids and alter the quantity and/or quality of the honeydew that they produce, thus affecting ant behavior (Córdova-Yamauchi et al. 1998) and the number of attendant ants (Styrsky and Eubanks 2006). The latter may also translate into a greater number of tending ant species because species richness is an increasing function of total individual abundance (Srivastava and Lawton 1998). Therefore, the enhanced soil quality generated by leaf-cutting ant nests may bring about a cascade of effects in the community of associated insect species (Stiling and Moon 2005).

In northern Patagonia, Argentina, the nest of the leaf-cutting ant *Acromyrmex lobicornis* is a frequent soil disturbance that improves soil quality (Farji-Brener and Ghermandi 2000, 2004). External refuse dumps from *A. lobicornis* nests are richer in organic carbon and nutrients, and have higher water retention capacity than adjacent soils (Farji-Brener and Ghermandi 2000, 2004; Tadey and Farji-Brener 2007). Two exotic Scotch thistle species, *Carduus nutans* and *Onopordum acanthium*, are frequently associated with the refuse dumps of *A. lobicornis*. These plant species are commonly infested by the aphid *Brachycaudus cardui*, which is attended by, at least, four different native ant species: *Dorymyrmex tener*, *D. richteri*, *Brachymyrmex patagonica* and *Solenopsis richteri*. We took advantage of this ecological scenario to evaluate whether the input of nutrients from ant refuse dumps affects plant quantity and quality, and whether this effect spreads along the trophic chain affecting aphid populations and the associated tending ant assemblage. Specifically, in plants of both thistle species that naturally grow on refuse dumps and adjacent soils, we measured (1) plant height and the number of leaves and inflorescences, (2) the content of foliar nitrogen in leaves and stems, (3) the abundance of aphids and (4) the number of ant species tending aphids. If this system is resource-limited (i.e., regulated by bottom-up forces), we expected that plants on refuse dumps would show greater size and tissue quality, larger aphid populations and increased abundance or richness of tending ant species than those on non-nest soils.

Materials and methods

Study site and species

The study was conducted at the eastern (driest) border of the Nahuel Huapi National Park, located in northern Patagonia, Argentina (41° S, 72° W). Sampling was performed in roadside steppes along 50 km of both sides of the road 237 (~50 ha), the main access to the national park, where both thistles and leaf-cutting ants are very abundant. The mean annual temperature in this area is 8°C and the mean annual precipitation is approximately 600 mm. The dominant vegetation is a mix of native species typical of Patagonian steppes (e.g., *Stipa speciosa*, *Mulinum spinosum*, *Imperata condensata* and *Plagiobothrys tinctorius*), and exotic herbs (e.g., *Bromus tectorum*, *O. acanthium*, *C. nutans* and *Verbascum thapsus*) (Correa 1969–1998).

Acromyrmex lobicornis (Formicidae: Attini) is the only leaf-cutting ant species that inhabits Patagonia. The geographical range of *A. lobicornis* includes several different biomes (Farji-Brener and Ruggiero 1994), but in the study area is more abundant close to roads (Farji-Brener 2000). Nests of *A. lobicornis* may reach a depth of 1 m and a height and width of 1 m, and externally consist of a mound of twigs, soil and dry plant material. Organic debris is removed from the internal fungus garden and dumped on the soil surface near the mound in a few large piles (refuse dumps). The refuse dump of *A. lobicornis* is richer in nutrient content than non-nest soils (Farji-Brener and Ghermandi 2000, 2004; Tadey and Farji-Brener 2007).

Carduus nutans (Nodding or Musk thistle) and *O. acanthium* (Scotch thistle) (Asteraceae: Cardueae) are common along roadsides but they are especially abundant on refuse dumps of *A. lobicornis* nests (Farji-Brener and Ghermandi 2000). Both species are biennial, monocarpic herbs with remarkable capacities for colonization and dispersal, which confer them the status of invasive species in a number of regions (Shea et al. 2005). Seedlings of these thistle species emerge in spring, develop into a flat rosette and spend the first year in this stage. In the next year, the thistles bolt and produce a single or several tall stems with numerous purple inflorescences. Plants die after flowering and there is no vegetative reproduction. The thistle aphid, *Brachycaudus cardui* (Aphididae: Macrosiphini) is a common herbivore of both plant species in the study area and in other temperate regions (Trumble and Kok 1982; Desrochers et al. 1988). Aphid colonies are located beneath leaves, on stems and at the inflorescence bases. *Brachycaudus cardui* is a myrmecophilous species (Fischer et al. 2001) and in the study area is attended by at least four native ant species: *D. tener*, *D. richteri* (Dolichoderinae), *Brachymyrmex patagonica* (Formicinae) and *Solenopsis richteri* (Myrmicinae).

Methodology

We evaluated the effect of refuse dumps of *A. lobicornis* nests on plant size and tissue quality, aphid infestation, and the number of ant species attending aphids. Sampling was carried out in flowering field plants of *C. nutans* and *O. acanthium* naturally established on refuse dumps and non-nest soils during the growing seasons (spring and summer) of 2003–2005. All sampled plants were 1–2 m tall.

We measured the content of nitrogen (N) in ten plants of *C. nutans* and ten plants of *O. acanthium* from non-nest soils and refuse dumps (20 plants in total for each species). Plants from refuse dumps were selected from different ant nests (one plant per nest). Plants from non-nest soils were randomly selected in adjacent areas by selecting random angle measurements from 0 to 360° and random distances between 5 and 10 m using the algorithm proposed by Skalski (1987). A sample of leaves and stems was randomly taken from each plant (~500 g), oven-dried in the laboratory to constant weight and ground to a fine powder. The concentration of N was determined by the Kjeldahl method using block digester (Bigham 1996), and expressed as percentage of dry weight.

We estimated the relative abundance of aphids per plant in a total of 106 plants, 44 of *C. nutans* (30 from non-nest soils and 14 from refuse dumps) and 62 of *O. acanthium* (39 from non-nest soils and 23 from refuse dumps). Plants from refuse dumps were selected from different ant nests; plants from non-nest soils were randomly selected in adjacent areas as described above. Plant height was measured in all individuals. The relative abundance of aphids was expressed as the percentage of plant surface (stems, leaves and inflorescence bases, the feeding sites of colonies of *Brachycaudus cardui*) covered by aphids, visually estimated according to the following categories: 0 (0%), 1 (<25%), 2 (25–50%), 3 (50–75%) and 4 (>75%). Sampling consisted in recording the relative abundance of aphids (0–4) during 1 min on ten randomly selected leaves, stems and inflorescence bases of each plant. These measurements were averaged to obtain the infestation level of each individual plant. We also counted the number of ant species attending aphids during 5 min per plant. Sampling was performed between 10 and 19 h in sunny days. In a sample of 42 plants of *C. nutans* (21 from refuse dumps and 21 from non-nest soils) and 46 plants of *O. acanthium* (23 from refuse dumps and 23 from non-nest soils) we also measured the total number of leaves and inflorescences per plant.

The foliar N content, number of leaves, number of inflorescences, mean relative abundance of aphids and the number of attending ant species were compared between plants of *C. nutans* and *O. acanthium* in refuse dumps and non-nest soil using ANCOVAS. Substrate (non-nest soils and refuse dumps) and plant species (*C. nutans* and *O. acanthium*) were considered fixed factors and plant height was used as covariate. All response variables were examined for normality and heterogeneity of variances and transformed when necessary. Response variables that did not meet these assumptions (e.g., ant richness) were analyzed by non-parametric ANCOVA using ranks (Zar 1999). Duncan post hoc comparison of means was employed when ANCOVA results were statistically significant. Additionally, to determine whether the number of tending ant species was associated with the abundance of aphids, we employed a Spearman non-parametric correlation.

Results

Thistle plants growing on nutrient-rich refuse dumps showed clear differences in plant quality and size, aphid infestation, and ant richness, compared to those growing on non-nest soils. However, the strength of some of the effects of refuse dumps varied between the thistle species. Plant height (cm, mean ± SE) was similar within refuse dumps (*C. nutans*: 151 ± 6; *O. acanthium*: 147 ± 6) and outside of them (*C. nutans*: 130 ± 5; *O. acanthium*: 127 ± 7). Plants of *C. nutans* and *O. acanthium* in refuse dumps had more leaves, inflorescences and higher foliar N content than those in non-nest soils, even after controlling for plant height (Table 1, Fig. 1a–c). While this pattern was similar for both thistle species, the effect of these changes in plant phenotype on the relative abundance of aphids was different between plant species. Overall, plants in refuse dumps showed higher abundance of aphids than plants in non-nest soils, and aphid colonies were of greater size on *O. acanthium* plants than on *C. nutans* plants (Fig. 1e, Table 1). However, the main pattern found was that only *C. nutans* plants showed an increase in aphid abundance when growing on refuse dumps compared to plants in non-nest soils (significant substrate × plant species interaction in the ANCOVA, Table 1, Fig. 1e). This resulted in a similar aphid load in both thistle species when growing on refuse dumps. Accordingly, only in *C. nutans* was there an increase in the number of ant species attending aphids when growing on refuse dumps (Table 1, Fig. 1d). Whereas throughout field sampling we found the four

Table 1 Results of the ANCOVA of the number of inflorescences, number of leaves, foliar nitrogen, aphid abundance, and the number of tending ant species in *C. nutans* and *O. acanthium* plants growing in non-nest soils and refuse dumps

Source of variation	*df*	MS	*F*	*P*-value
Inflorescences				
Plant height (covariate)	1	7791.5	33.3	0.002
Species	1	292	1.25	0.27
Substrate	1	5276.7	22.6	< 0.001
Species × substrate	1	7.7	0.03	0.86
Error	83	233.7		
Leaves				
Plant height (covariate)	1	44194.5	22.8	< 0.001
Species	1	2187.5	1.1	0.29
Substrate	1	43864.7	22.7	< 0.001
Species × substrate	1	4.3	0.002	0.96
Error	83	1933.9		
Foliar nitrogen				
Plant height (covariate)	1	1.7	1.2	0.43
Species	1	0.0008	0.0013	0.97
Substrate	1	11	17.2	< 0.001
Species × substrate	1	0.04	0.06	0.81
Error	36	0.64		
Aphid abundance				
Plant height (covariate)	1	2.7	2.2	0.15
Substrate	1	24.5	19.7	< 0.001
Species	1	10.5	8.4	0.004
Substrate × species	1	7.6	6.2	0.01
Error	101	1.2		
Ant species				
Plant height (covariate)	1	0.001	0.01	0.99
Substrate	1	1.6	5.4	0.02
Species	1	0.1	0.2	0.67
Substrate × species	1	0.9	3.14	0.07
Error	101	0.29		

tending ant species described for the study area, the maximum number of ant species attending aphids in a sampled plant was three. Refuse dump plants of *C. nutans* had, on average, one more ant species than non-nest soil plants; but *O. acanthium* plants showed a similar number of attending ant species independently of the substrate where they grew (Fig. 1d). Overall, the number of ant species was positively associated with the relative abundance of aphids ($R_s = 0.37$, $n = 106$ plants, $P < 0.001$). On the other hand, neither aphid abundance nor the number of ant species per plant was affected by plant height (Table 1).

Discussion

The bottom-up hypothesis states that organisms on each trophic level are limited by the resources available from the level below. Hence, an increase in the quantity or quality of resources at basal levels should propagate along the trophic chain and indirectly support greater populations at upper levels (Hunter and Price 1992). We found that the effect of small-scale soil disturbances enhancing resource availability can spread along the trophic chain through their effects on plants, but the extent of this influence depends on the identity of the plant species involved. Individuals of both thistle species established in ant refuse dumps showed 100–300% more leaves and inflorescences and 100% more foliar N than those established in non-nest soils. However, this enhanced plant size and quality was associated with an increase in the relative abundance of aphids only in *C. nutans*. Accordingly, the number of ant species that tended aphids per plant increased in refuse dump plants only in this thistle species.

Both plant species increased their size and improved their tissue quality when growing on refuse dumps. Recent studies demonstrated that plants can benefit from leaf-cutting ant refuse dumps because they exploit the high nutrient content of this substrate (Farji-Brener and Ghermandi 2004; Sternberg et al. 2006). This study supports these evidences, suggesting that additional sources of nitrogen are available for plant growth and reproduction due to the activity of *A. lobicornis*. Moreover, our results suggest that both plant species are nutrient-limited in this habitat (Satti et al. 2003). However, these changes in plant attributes were associated with an increment in aphid abundance only in *C. nutans*.

In non-disturbed conditions (i.e., non-nest soils), *O. acanthium* plants supported greater aphid populations than *C. nutans*, which suggests that *O. acanthium* is a better host than *C. nutans* for the aphid *Brachycaudus cardui*. This pattern appears to be unrelated with differences in size, number of inflorescences and leaves, or the content of foliar N between these plant species; an

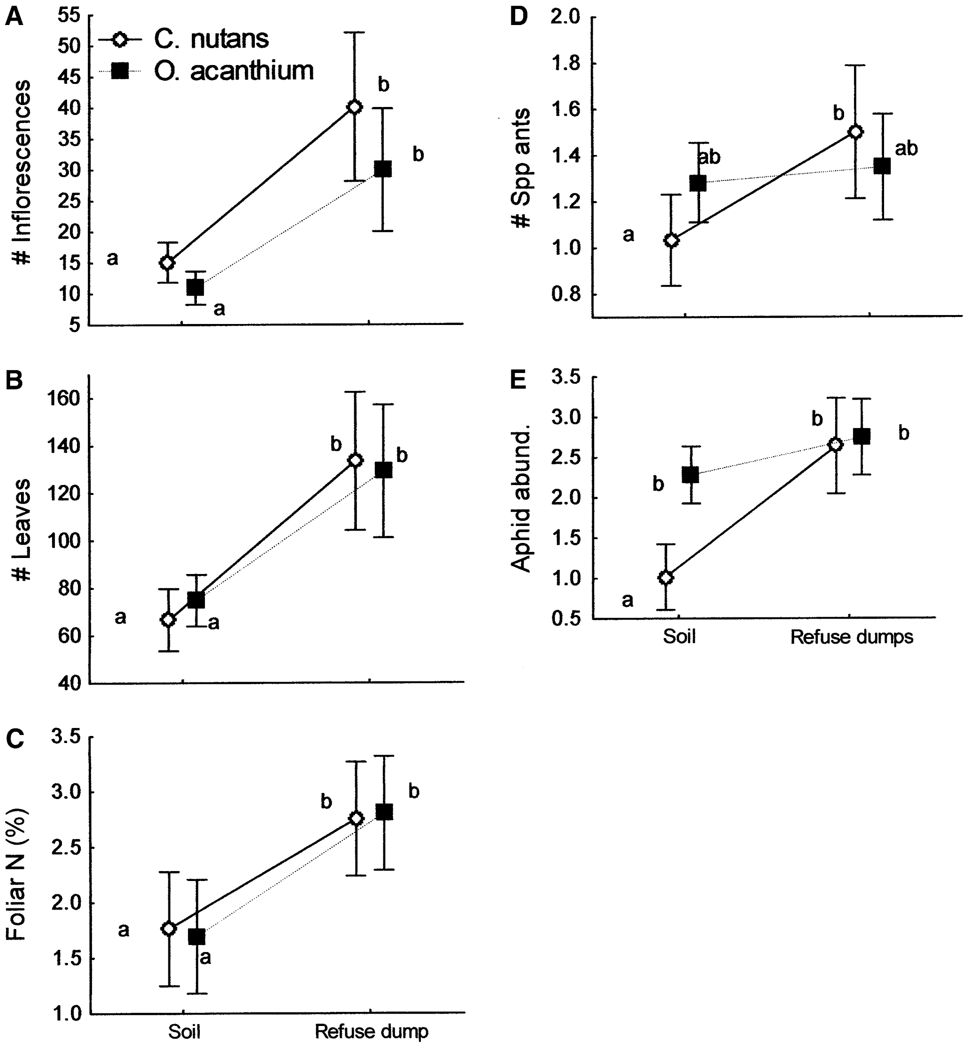

Fig. 1 Number of inflorescences, number of leaves, content of foliar Nitrogen (N), relative abundance of aphids and number of tending ant species in plants naturally growing in non-nest soils (Soil) and refuse dumps of the leaf-cutting ant *Acromyrmex lobicornis*. Different *lowercase letters* imply statistically significant differences. Values shown are mean ± SE. See Table 1 for ANCOVA results

increase in these plant attributes did not involve an increment in aphid abundance (Fig. 1e). Enhanced aphid growth on *O. acanthium* could be explained by particular plant traits not measured in this study, which may confer aphids a better protection against environmental hazards. Aphids often select feeding sites within plants that reduce their mortality risk such as the undersurface of leaves or inflorescences or less exposed stem parts (Dixon 1998; Gianoli 1999; Gonzáles et al. 2001). Compared with *C. nutans*, *O. acanthium* have larger leaves and rougher stems, and it is clearly more hairy. We might speculate that these differences in plant morphology may offer *Brachycaudus cardui* a better protection against high temperatures, which are common in mid summer in the Patagonian desert steppe. However, this hypothesis needs additional field work to be verified. While plant morphology appears to play an important role in the performance of *Brachycaudus cardui* on *O. acanthium*, enhanced plant size and tissue quality appears to influence aphid performance in *C. nutans*. Thus, plants of *C. nutans* in refuse dumps showed similar aphid loads as plants of *O. acanthium*. This suggests that increased plant size and quality as a result of growing on refuse dumps enhance the host value of *C. nutans* for aphids; which then attain levels similar to those that *O. acanthium* exhibits naturally. The latter, in turn, does not modify its suitability as host when growing on refuse dumps.

Changes in the relative abundance of aphids influenced their tending ant assemblage. In theory, larger aphid populations may sustain more ant individuals and/or species (Styrsky and Eubanks 2006; Rico-Gray and Oliveira 2007). As expected, we found more tending ant species in plants with a greater aphid load. This could be related to an increase in aphid abundance and/or changes in honeydew quantity/quality (Stadler et al. 2002; Styrsky and Eubanks 2006). We did not measure whether honeydew quality or production varied between plant species and growing substrates. Consequently, we presently lack evidence to propose a causal link between aphid population size and the richness of tending ant species.

We suggest that higher trophic levels such as tending ants are affected by changes in soil nutrient availability through its effect on plants and aphids. Further evidence is needed, however, to support this statement. A better understanding of the dynamics of the populations within the studied community would be gained if a closer follow-up during the whole growth season is undertaken. Furthermore, experimental manipulation of plant traits, microclimatic conditions and the abundance of aphids should be carried out to identify the mechanisms underlying the detected patterns. Nevertheless, the extensive field sampling carried out and the use of unmanipulated wild populations confer reliability to the evidence obtained, and suggest that the effect of small-scale soil disturbances on higher trophic levels operate within the range of conditions that occur naturally.

Summarizing, we provide comparative and associative evidence that the increase of soil fertility generated by leaf-cutting ant nests can affect aphid abundance and their tending ant assemblage through its effect on plant size and quality. This illustrates how abiotic factors such as soil nutrient availability may indirectly influence ant–hemipteran interactions (Styrsky and Eubanks 2006). However, the strength of this 'trophic cascade effect' partly depends on the relevance of particular plant attributes for aphid performance. Thus, the propagation of small-scale soil disturbances through the trophic chain may depend on the identity of the species involved.

Acknowledgments This research was partially funded by PICT # 25314, Fondo Nacional de Ciencia y Tecnología (FONCyT), Argentina.

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