

Ecological engineering by a native leaf-cutting ant increases the performance of exotic plant species

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Received: 1 July 2009 / Accepted: 9 February 2010 / Published online: 24 February 2010
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Abstract Numerous mechanisms are proposed to explain why exotic plants successfully invade natural communities. However, the positive effects of native engineers on exotic plant species have received less consideration. We tested whether the nutrient-rich soil patches created by a native ecological engineer (refuse dumps from the leaf-cutting ant *Acromyrmex lobicornis*) increase the performance of exotic more than native plants. In a greenhouse experiment, individuals from several native and exotic species were planted in pots with refuse dumps (RDs) and non-nest soils (NNSs). Total plant biomass and foliar nutrient content were measured at the end of the experiment. We also estimated the cover of exotic and native plant species in external RDs from 54 field ant nests and adjacent areas. Greenhouse plants showed more biomass and foliar nutrient content in RDs than in NNS pots. Nevertheless, differences in the final mean biomass among RD and NNS plants were especially great in exotics. Accordingly, the cover of exotic plants was higher in field RDs than in adjacent, non-nest soils. Our results demonstrated that plants can benefit from the enhanced nutrient content of ant RDs, and that *A. lobicornis* acts as an ecosystem engineer, creating a substrate that especially increases the performance of exotics. This supports the fluctuating resource hypothesis as a mechanism to promote

biological invasions, and illustrates how this hypothesis may operate in nature. Since ant nests and exotic plants are more common in disturbed than in pristine environments, the role of ant nests in promoting biological invasions might be of particular interest. Proposals including the use of engineer species to restore disturbed habitats should be planned with caution because of their potential role in promoting invasions.

Keywords *Acromyrmex lobicornis* · Ants · Biological invasions · Ecological engineers · Fluctuating resource hypothesis · Soil disturbance

Introduction

Understanding the mechanisms that determine the successful invasion of a community by exotic plants is of theoretical and applied interest. Invasive species offer excellent opportunities to study basic demographic and community processes, such as the importance of morphological/physiological traits to population growth (Parker et al. 1999) and the relevance of biological interactions structuring species assemblages (Shea and Chesson 2002). Furthermore, exotic plants are a source of worldwide environmental change, altering ecosystem processes, harming native species and natural communities, and causing plant and animal extinctions (Clavero and García-Berthou 2005). Recognizing how exotic plants become successful invaders may thus provide useful information for ecological theory and conservation practices.

Many diverse and interacting mechanisms have been proposed to explain why exotic plants successfully invade natural communities (reviewed by Catford et al. 2009). However, one mechanism that has received less

Communicated by Bryan Foster.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-010-1589-1) contains supplementary material, which is available to authorized users.

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consideration is the facilitative impact that native ecological engineers may have on the performance of exotic plants. Although all organisms interact with their physical environment, some of them considerably change the environmental conditions and resource availability via nontrophic interactions in ways that affect the performance and distribution of other species (“ecological engineers,” sensu Jones et al. 1994, 1997). However, if these environmental changes benefit the performance of exotic more than native species, the process of ecological engineering may promote biological invasions. This positive effect of native engineer species on exotic species has only recently been recognized as a possible mechanism of biological invasions (Badano et al. 2007).

Leaf-cutting ants are probably one of the most notable examples of ecological engineers because of their high capacity to alter the environment where they live (Correa et al. 2010). Ants move an extraordinary quantity of soil to construct and maintain their nests, cut a large amount of vegetation, and deposit large piles of organic waste around the nest area (Farji-Brener and Illes 2000). Specifically, the deposition of this novel, nutrient-rich substrate on the soil surface substantially affects the abundances and performances of other species (Farji-Brener and Illes 2000). These organic waste or refuse dumps (hereafter, RDs) are a product of the process of plant degradation by the ant mutualistic fungus, and in some leaf-cutting ant species are located in external piles. These RDs are several times richer in organic carbon and nutrients than adjacent soils, generating nutritive patches around the nest area that affect plant distribution and abundance (Farji-Brener and Illes 2000). Exotic plants may differ in their requirements compared with natives and, as such, increments in soil resources have the capacity to increase their invasive potential (Daehler 2003; Siemann and Rogers 2007).

Hence, if exotic species respond better than natives to the presence of RDs, the creation of enriched soil patches by leaf-cutting ants may promote the success of biological invasions.

Although leaf-cutting ants have been proposed as ecological engineers (Wirth et al. 2003; Correa et al. 2010), studies of their effects under this conceptual framework, including their potential impact on exotic plant species, are still lacking (e.g., absent in the review of Hastings et al. 2007). Earlier evidence suggests that engineering activities by leaf-cutting ants may promote biological invasions. Ant nest areas are often colonized by exotic plant species in Brazilian savannas (Coutinho 1982), arid Argentinean woodlands and Patagonian steppes (Farji-Brener and Ghermandi 2000, 2004). However, these examples are mostly anecdotal, and the underlying mechanism by which leaf-cutting ants may promote biological invasions has never been formally tested (but see Farji-Brener and Ghermandi 2008). In this work, we documented the effect of RDs on the performance of the most common native and exotic species of a semi-arid steppe of north-western Patagonia. Specifically, we experimentally tested whether the performance of plants in high-nutrient patches created by a native ecological engineer (the leaf-cutting ant *Acromyrmex lobicornis*) depends on the species’ origin. In addition, we measured the relative cover of exotic and native plants in field nest-sites and adjacent control sites.

Materials and methods

Study site, plant and leaf-cutting ant species

For this study, we selected 14 plant species, seven natives and seven exotics (Table 1). All of them are highly

Table 1 Origin, life form and family of each plant species used in this study

Species name	Symbol	Family	Origin	Life form
<i>Bromus setifolius</i>	BS	Poaceae	Native	Grass, P
<i>Coniza lechleri</i>	CL	Asteraceae	Native	Herb, A, B
<i>Chenopodium ambrosioides</i>	ChA	Chenopodiaceae	Native	Herb, A, B
<i>Euphorbia serpens</i>	ES	Euphorbiaceae	Native	Herb, P
<i>Poa lanuginosa</i>	PL	Poaceae	Native	Grass, P
<i>Senecio filaginoides</i>	SF	Asteraceae	Native	Shrub
<i>Stipa speciosa</i>	SS	Poaceae	Native	Grass, P
<i>Bromus tectorum</i>	BT	Poaceae	Exotic	Grass, A
<i>Conium maculatum</i>	CM	Apiaceae	Exotic	Herb, B
<i>Carduus nutans</i>	CN	Asteraceae	Exotic	Herb, B
<i>Lactuca serriola</i>	LS	Asteraceae	Exotic	Herb, B
<i>Onopordon acanthium</i>	OA	Asteraceae	Exotic	Herb, B
<i>Rumex acetosella</i>	RA	Polygonaceae	Exotic	Herb, P
<i>Verbascum thapsus</i>	VT	Scrophulariaceae	Exotic	Herb, B

A annual; B bi-annual;
P perennial. See Correa (1969–
1998) for further information

abundant in our area of interest, the driest part of Nahuel Huapi National Park, Argentina (41°S, 72°W), and are representative of the local flora (Farji-Brener and Ghermandi 2000, 2004; see also Correa 1969–1998). They represent ~70% of the cover and 90% of the seed bank abundance of the plant assembly in the study area (Farji-Brener and Ghermandi 2000, 2004). The mean annual temperature in this area is 8°C and the mean annual precipitation is approximately 600 mm. *A. lobicornis* Emery is the only leaf-cutting ant species that inhabits Patagonia. The geographical range of *A. lobicornis* includes several different biomes, but in the study area it is more abundant in the driest region of the national park, especially near road borders where natives and exotic plant species are both common (Farji-Brener and Ghermandi 2000, 2008). *A. lobicornis* nests reach depths of 1 m, and externally show a conical mound of twigs, soil and dry plant material. Refuse dumps are located on the soil surface near the mound in a few large piles, and they are up to 8 times richer in nutrients than the adjacent non-nest soil (Farji-Brener and Ghermandi 2000, 2008; see also S1 in the “[Electronic Supplementary Material](#),” ESM).

Greenhouse experiment

To determine whether the nutrient-rich RD differentially affects the performance of exotic and native plant species, we designed a greenhouse experiment. Seeds of the 14 plant species were collected in the field from ~10 of individuals per species established in non-nest soils (hereafter NNSs) throughout the study area. Seeds of all species were set to germinate in commercially available organic soil in a greenhouse. Germinated seeds (first leaves just emerged) were removed and immediately planted into individual pots (one per pot). Pots were plastic containers 15 cm in diameter by 15 cm deep with RD or NNS as substrate. RD samples were collected in the field from ten selected *A. lobicornis* nests, and NNS samples from nearby non-nest sites. In the lab, RD samples from the ten nests were mixed between them, as well as control soil samples from the ten adjacent non-nest sites. Seedlings of each species were randomly allocated to a RD or NNS pot, with a total of 20 replicates per species (10 per substrate). The total number of pots was 280 (20 × 14 plant species), 140 per substrate (RD and NNS). Pots were randomly placed within the greenhouse and watered every 2 days until the end of the experiment (end of the growing season 2006). Planted individuals were maintained alone in each pot (i.e., seedlings from the seed bank were harvested when they emerged). Mortality was very low (~1%); almost all the seedlings remained alive until the end of the experiment. After 16 weeks, all plants were harvested and the root and shoot lengths (hereafter, leaves) measured, washed and

oven-dried at 50°C for 4 days before weighing. Also, in a random selection of five leaves per plant (5 plants per species per treatment), we measured the content of foliar nitrogen (N) and phosphorus (P). Total N was determined by a CN analyzer (Flash EA 112, Thermo Electron Corp.) Ashes were determined by weight loss at 550°C. Phosphorus was extracted from the ashes with conc. HCl and determined by the ascorbic–molybdate method (Richards 1993). Foliar N and P contents were expressed as percentage of dry weight.

Data analysis

Leaf and root dry biomass (in g) and foliar contents of N and P (in %) were analyzed using a mixed-model ANOVA. Fixed factors were substrate (RD or NNS) and origin (native or exotic), while species (nested within origin) was included as a random factor. Plant species was considered a random rather than a fixed factor because our interest was in testing for the effect of RD on the growth of native and exotic plant species in general, rather than answering the more restricted question of whether refuse dump had an effect on these particular 14 species. Tukey post hoc comparisons of means were employed when ANOVA results were statistically significant ($P < 0.05$). A series of *t* tests for each plant species comparing its performance between RD and NNS soils was also employed. All response variables were examined to meet ANOVA assumptions and transformed when necessary.

Field measures

To determine whether RD differentially affects the performance of exotic and native plant species in field conditions, we analyzed the data from surveys of plant diversity that we performed in the study area between 1996 and 2003 (see Farji-Brener and Margutti 1997; Farji-Brener and Ghermandi 2000, 2004). During this sampling period, we measured the cover of plant species in RDs from 54 adult nests of *A. lobicornis* and adjacent NNS sites. Sampling was carried out during the summer, when identification of annual plants is likely. Plant cover was measured in each RD and NNS site in a 2 × 2 m plot subdivided into 400 cells of area 10 × 10 cm. Refuse dumps were located at the centers of the RD plots, and each RD plot was paired with an NNS plot in a randomly selected paired non-nest site 2–4 m away from the nest and parallel from the route border (source of exotic propagules). Species cover was calculated as the number of cells in which a species was present over the total number of cells. All species were categorized as exotic or native. We then summed the cover of all the exotic and native species in each plot and calculated the exotic/native ratio (E/N) for each RD and its

paired NNS site. $E/N > 1$ corresponds to exotic plant dominance, while $E/N < 1$ corresponds to native plant dominance. We compared the E/N ratio between the RD and nearby NNS plots with a paired t test ($n = 54$ pairs).

Results

The type of substrate, plant species, and the interaction between origin and substrate all affected plant growth (S2 in the “ESM”). Plants in RD pots grew better than plants in NNS pots, and species differed in their final biomass. Nevertheless, final leaf and root biomass in RD plants were especially great for exotics compared to natives (statistically significant interaction of origin \times substrate, Fig. 1; see also S5 in the “ESM”). While natives showed ~ 2 times greater mean leaf biomass and 1.3 times more mean root biomass in RDs than in NNSs (with the exception of ChA, see Table 2), exotics showed means of 3.5 and 5.6 times more leaf and root biomass in RDs than in NNSs, respectively. Almost all of the exotic species studied ($\sim 80\%$) showed significantly higher final biomass in RDs compared with NNSs, but less than half of the native species studied ($\sim 35\%$) showed the same trend (Table 2).

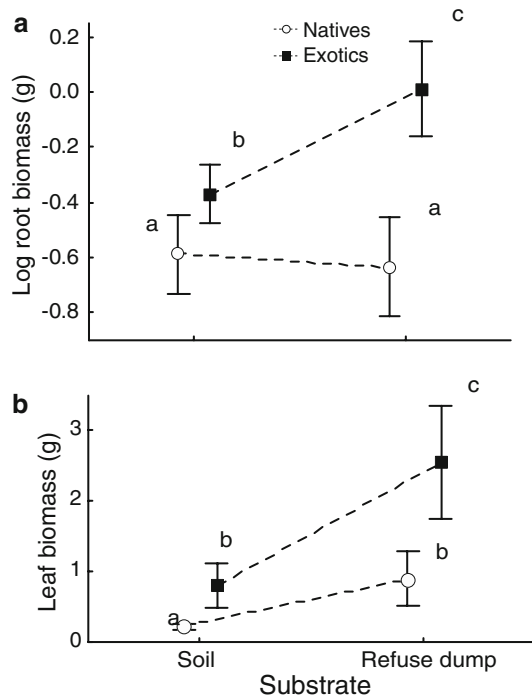


Fig. 1 Dry weights (g) of **a** roots and **b** leaves of native and exotic plant species grown in refuse dumps of the leaf-cutting ant *Acromyrmex lobicornis* and control soils under greenhouse conditions (see S5 in the “ESM”). Values are mean \pm SE ($n = 10$ plants per treatment per species, 14 plant species; a total of 280 plants). Different letters indicate statistically significant differences ($P < 0.05$). See S2 in the “ESM” for ANOVA results

Moreover, only natives showed the opposite trend (i.e., more root biomass in NNS soils, Table 2). On the other hand, the variations of foliar N and P contents depended on the plant species, substrate and origin (only for P) (S3 in the “ESM”). Overall, plants in RDs showed higher percentage N and P foliar contents than plants in NNSs (for N: 2.5 ± 0.2 vs. 1.5 ± 0.1 , respectively; for P: 0.31 ± 0.01 vs. 0.24 ± 0.02 , respectively, mean ± 1 SE). However, this increase in RD plants was similar in native and exotic species for both foliar nutrients (i.e., nonsignificant interaction of origin \times substrate, S3 and S4 in the “ESM”). Field estimations of exotic and native cover in RD and NNS sites followed the same trend found in our greenhouse experiment. Overall, exotics showed more cover than

Table 2 Leaf and root dry weights (g) of the 14 plant species in refuse dumps (RDs) and non-nest soils (NNSs); values are mean \pm SE ($n = 10$ plants per treatment)

Species	Origin	Refuse dump	Non-nest soil	RD/NNS	<i>P</i>
Leaves					
BS	N	1.05 \pm 0.27	0.29 \pm 0.03	3.6	0.01
CL	N	0.15 \pm 0.05	0.17 \pm 0.03	0.9	0.75
ChA	N	3.35 \pm 0.68	0.30 \pm 0.06	11.7	<0.01
ES	N	0.18 \pm 0.05	0.03 \pm 0.01	6	<0.01
PL	N	0.19 \pm 0.06	0.18 \pm 0.03	0.9	0.81
SF	N	0.31 \pm 0.10	0.35 \pm 0.08	0.9	0.74
SS	N	0.11 \pm 0.04	0.08 \pm 0.01	1.4	0.74
BT	E	2.57 \pm 0.61	0.67 \pm 0.09	3.8	<0.01
CM	E	0.24 \pm 0.06	0.15 \pm 0.01	1.6	0.21
CN	E	0.52 \pm 0.18	0.12 \pm 0.01	4.3	0.02
LS	E	2.31 \pm 0.38	0.65 \pm 0.10	3.6	0.02
OA	E	1.84 \pm 0.36	0.48 \pm 0.01	3.8	<0.01
RA	E	2.13 \pm 0.38	0.46 \pm 0.12	4.6	<0.01
VT	E	6.20 \pm 1.70	2.44 \pm 0.77	2.5	<0.01
Roots					
BS	N	1.25 \pm 0.25	0.94 \pm 0.15	1.3	0.89
CL	N	0.20 \pm 0.06	0.55 \pm 0.12	0.4	0.03
ChA	N	2.61 \pm 0.41	0.54 \pm 0.10	4.8	<0.01
ES	N	0.13 \pm 0.03	0.03 \pm 0.01	4.3	0.01
PL	N	0.19 \pm 0.04	0.31 \pm 0.07	0.6	0.26
SF	N	0.54 \pm 0.31	0.72 \pm 0.19	0.7	0.11
SS	N	0.08 \pm 0.04	0.25 \pm 0.07	0.3	<0.01
BT	E	3.79 \pm 1.07	0.79 \pm 0.14	4.8	0.02
CM	E	0.33 \pm 0.07	0.36 \pm 0.04	0.9	0.25
CN	E	0.72 \pm 0.24	0.24 \pm 0.10	3	0.05
LS	E	0.60 \pm 0.16	0.79 \pm 0.14	0.7	0.30
OA	E	2.24 \pm 0.50	0.33 \pm 0.07	6.8	<0.01
RA	E	2.03 \pm 0.37	1.03 \pm 0.19	2	0.02
VT	E	37.6 \pm 18.7	1.80 \pm 0.52	20.9	0.03

Significant differences according to the t test are shown in **bold**. See Table 1 for species names and S2 in the “ESM” for ANOVA results
N Native; E exotic

natives in almost all the sampling sites (i.e., $E/N > 1$) because, in the study area, *A. lobicornis* is more frequent in disturbed habitats where exotics are dominant (Farji-Brener and Ghermandi 2000, 2008). Nevertheless, the E/N ratio was higher in RD sites than in nearby NNS sites (3.8 ± 0.6 vs. 1.8 ± 0.6 , mean (± 1 SE), respectively, $n = 54$, $t = 3.8$, $P < 0.001$, Fig. 2). In particular, the exotic plant species employed in the greenhouse experiment also showed more cover in field refuse dumps than in control, non-nest soils (S6 in the “ESM”).

Discussion

Our results demonstrate that the leaf-cutting ant *A. lobicornis* acts as an ecological engineer through the creation of a novel substrate that alters the performance of plants, especially if they are exotics. While other studies have suggested that leaf-cutting ants may act as ecological engineers affecting vegetation patterns (Farji-Brener and Illes 2000; Wirth et al. 2003; Correa et al. 2010), few works have experimentally tested this hypothesis, and none have specifically linked that idea with the likelihood of biological invasions. Using a representative number of plant species of the study area, we experimentally demonstrated that exotics gain $\sim 100\%$ more leaf and root biomass than natives when both kinds of species grow in RDs, suggesting that leaf-cutting ant nests may promote the invasion of exotic plants. Our field measurements of exotic and native plant cover also support this hypothesis. These results are of both theoretical and applied interest. They (1) confirm that plants can benefit from the enhanced nutrient content of external ant RDs; (2) support the fluctuating resource hypothesis as a mechanism to promote biological invasions; and (3) provide arguments to discuss the potential role of ecological engineers in conservation and restoration practices.

Recent studies have shown that plants can access and benefit from the high nutrient content of leaf-cutting ant RDs (Moutinho et al. 2003; Sternberg et al. 2007;

Farji-Brener and Ghermandi 2008). However, these studies tested this positive effect in only a few plant species. We experimentally showed that RDs improved the performance of a large number of plant species, suggesting that leaf-cutting ant nests have the potential to broadly influence plant assemblages. Moreover, the positive effect of this native ecological engineer on plants was stronger in exotic than in native species, which supports the fluctuating resource hypothesis (FRH) as a mechanism of biological invasions. The general idea of the FRH is that resource addition acts to reduce the effects of competition by the native community, thereby facilitating the success of the invader (Davis et al. 2000). We demonstrated that even in the absence of competition (e.g., plants growing alone), an increase in soil nutrient content improves the growth of exotics more than natives. This supports the previous idea that invasive plant species, by virtue of particular morphological and/or physiological traits, may use soil nutrients more efficiently and thus outcompete co-occurring natives (D’Antonio et al. 1998; Daehler 2003; Suding et al. 2004; Zou et al. 2007). Other studies have also showed that an increase in soil nutrients can promote exotic plant colonization (Burke and Grime 1996; Davis and Pelsor 2001; Brooks 2003). However, these studies often employed commercial fertilizers, which is unrealistic because in nature nutrient patches are likely associated with decomposing organic matter. We thought that our experiment with RDs more realistically illustrates how the FRH may operate in nature.

There are, however, some concerns about the argument that external ant RDs can promote biological invasions. First, exotics grew better than natives in RDs but did not show higher foliar N and P contents. The concentration of foliar nutrients is a function of foliar re-absorption and re-localization rather than merely a result of root uptake (Larcher 1995). Thus, the extra nutrients absorbed by the plants can be diluted into new tissue, and so they do not necessarily closely reflect its difference in size. Second, we did not measure plant fecundity directly, and thus the superior performance of exotics could be speculative. However, plant size is widely considered a good estimator of fecundity because, within a species, larger plants often produce more seeds (Horvitz and Schemske 2002 and references therein). It is very plausible that the high difference in plant size found here will generate comparable differences in seed production. Accordingly, some of the species studied here show 2–4 times more biomass and an equivalent increase in seed production when grown in field RDs (Farji-Brener and Ghermandi 2008). Third, our selection of native and exotic plants species may have biased our results. For example, the native selected pool contains more perennials and fewer biennials than the exotic pool. Differences in the effect of RDs on plant

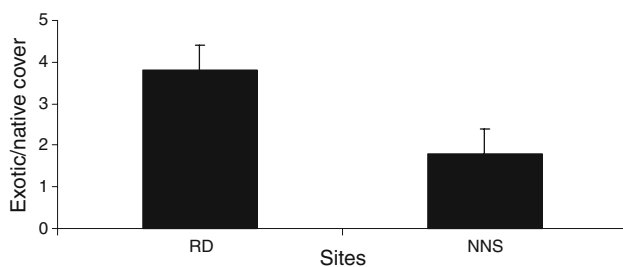


Fig. 2 Ratio of exotic to native plant cover in field refuse dumps (RD) of the nests of the leaf-cutting ant *Acromyrmex lobicornis* and adjacent, non-nest soils (NNS) ($n = 54$ sites, $t = 3.8$, $P < 0.001$). Values are mean ± 1 SE

biomass may thus reflect differences in life strategies rather than origins (Meiners 2007). As explained earlier, we selected this species pool for our greenhouse experiment because they are highly representative of the plant assembly of the study area. In this manner, we attempted to replicate under greenhouse conditions as closely as possible what could happen under natural conditions. In other words, including an equal representation of life strategies in the native and exotic pools should have increased our precision, but may have decreased our accuracy (i.e., a nonrepresentative picture of what occurs in the study area). Therefore, further studies with an expanded species pool are needed to confirm the generality of the RD–plant origin relationship. Finally, our main results are from a greenhouse experiment. This approach offers many practical advantages over field-based measurements, such as better control of treatments and extrinsic factors, but it might also restrict the ability to apply the experimental results to natural communities (Gibson et al. 1999). For example, in the field, RD natives may outcompete exotics, exotics may facilitate the establishment of natives rather than inhibit it, and exotics may be more heavily harvested by the ants than the natives. However, two lines of evidence suggest that the stronger positive effect of RDs on exotic plants that we found under greenhouse conditions also occurs in nature. First, our field data confirms that exotic plants are relatively more abundant in RDs than in nearby NNSs. This result discards the hypotheses that natives restrict exotics, and that exotics may facilitate the establishment of natives. Second, leaf-cutters avoid contact with their RDs because they harbor microorganisms that are dangerous to ants and their symbiotic fungus (Currie et al. 1999). Consequently, leaf-cutting ants usually do not attack plants growing on RDs (Farji-Brener and Sasal 2003). This suggests that the better performance of exotics found in the greenhouse also occurs in natural situations, despite interactions between plants and the risk of ant herbivory. Moreover, the stronger effect of RDs on exotic plants can persist after the colony dies; abandoned nest sites also showed more exotic plant cover than nearby control plots (Farji-Brener and Ghermandi 2000). Once established in RDs, several exotic species produce a vast number of seeds that fall by gravity, germinating and establishing at the same site where the parent grew (Farji-Brener and Ghermandi 2008). This positive feedback can maintain the dominance of exotics at a site even after the colony had died or abandoned the nest.

The positive effect of *A. lobicornis* as an ecological engineer on the performance of exotic plants may also occur in other leaf-cutting ant species and at larger spatial scales. The creation of nutrient-rich soil patches by different species of leaf-cutting ants is a widely known, well-documented phenomenon in tropical, subtropical and temperate American environments (Farji-Brener and Illes 2000; Moutinho

et al. 2003; Farji-Brener and Ghermandi 2008), even for those species that show underground refuse chambers (Farji-Brener and Silva 1995; Moutinho et al. 2003). Furthermore, nest densities show up to a 30-fold increase in disturbed habitats, where exotic plants are often abundant (Farji-Brener and Illes 2000; Farji-Brener 2001; Vasconcelos et al. 2006; Wirth et al. 2007). Since the likelihood of exotic plant invasion strongly depends on propagule pressure (Von Holle and Simberloff 2005), the fact that ant nests are hyperabundant in habitats with plenty of exotic plants enhances their role in promoting biological invasions.

In summary, through experimental and field measurements, we have documented that (1) leaf-cutting ants can act as ecosystem engineers by the creation of patches of a nutrient-rich substrate around their nests (RDs), and that (2) the presence of an RD enhances plant performance, mostly in exotic species, and thus may promote biological invasions. Our findings reinforce the novel idea that native ecological engineers may promote biological invasions through the creation of nutrient-rich soil patches (Badano et al. 2007). Furthermore, they suggest that, besides leaf-cutting ants, other native ecological engineers that increase the availability of soil nutrients, such as other ant species, termites, plants and mammals (see Crooks 2002; Wright and Jones 2004 for examples), also have the potential to promote biological invasions if exotic propagules are abundant.

Our results imply that the design of conservation strategies should consider the potential effects of native ecological engineers on invaders. In disturbed environments where exotic propagules are abundant, ecological engineering that enhances or creates nutrient hotspots such as ant nests can act as a source of weeds (Farji-Brener and Ghermandi 2008). Conversely, in more pristine environments dominated by native vegetation, they might reduce the chance of plant invasions through the increase of native plant abundance (but see Levine 2000). Given that disturbed and secondary environments are currently expanding (Wirth et al. 2007), their role in promoting biological invasions may be more widespread than their ability to increase biotic resistance. Therefore, proposals to use engineer species to restore disturbed habitats (Byers et al. 2006) should be planned with caution because of their potential role in promoting invasions.

Acknowledgments This research was partially funded by CONICET (PIP 5110) and ANPCyT (PICT 25314), Argentina. We thank Irene Khavin, Cameron Naficy, and three anonymous reviewers for their useful comments.

References

- Badano E, Villaroel E, Bustamante R, Marquet P, Caviares L (2007) Ecosystem engineering facilitates invasions by exotic plants in high-Andean ecosystems. *J Ecol* 95:682–688

- Brooks M (2003) Effects of increased soil nitrogen on the dominance of alien plants in the Mojave Desert. *J Appl Ecol* 40:344–353
- Burke M, Grime JP (1996) An experimental study of plant community invasibility. *Ecology* 77:776–790
- Byers J, Cuddington K, Jones C, Talley T, Hastings A, Lambrinos J, Crooks J, Wilson W (2006) Using ecosystem engineers to restore ecological systems. *Trends Ecol Evol* 21:493–500
- Catford J, Jansson R, Nilsson C (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Divers Distrib* 15:22–40
- Clavero M, García-Berthou E (2005) Invasive species are a leading cause of animal extinctions. *Trends Ecol Evol* 20:110
- Correa M (1969–1998) Flora Patagónica, vol 7. INTA, Buenos Aires
- Correa M, Silva P, Wirht R, Tabarelli M, Leal I (2010) How leaf-cutting ants impact forests: drastic nest effects on light environment and plant assemblages. *Oecologia* 162:103–115
- Coutinho L (1982) Aspectos ecológicos de savana no cerrado. Os murundus de terra, as características psamofíticas das espécies de sua vegetação e sua invasão pelo Capim Gordura. *Rev Bras Biol* 42:147–153
- Crooks J (2002) Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos* 97:153–166
- Currie C, Scott J, Summerbell R, Malloch D (1999) Fungus-growing ants use antibiotic-producing bacteria to control garden parasites. *Nature* 398:701–704
- D'Antonio C, Hughes R, Mack M, Hitchcock D, Vitousek P (1998) The response of native grasses to the removal of invasive exotic grasses in the seasonally dry Hawaiian woodland. *J Veg Sci* 9:699–712
- Daehler C (2003) Performance comparisons of co-occurring native and alien invasive plants: implications for conservation to agricultural weeds. *Biol Conserv* 84:167–180
- Davis M, Pelsor M (2001) Experimental support for a resource-based mechanistic model of invasibility. *Ecol Lett* 4:421–428
- Davis M, Grime J, Thompson K (2000) Fluctuating resource in plant communities: a general theory of invasibility. *J Ecol* 88:528–534
- Farji-Brener AG (2001) Why are leaf-cutting ants more common in early secondary forests than in old-growth tropical forests? An evaluation of the palatable forage hypothesis. *Oikos* 92:169–177
- Farji-Brener AG, Ghermandi L (2000) The influence of nests of leaf-cutting ants on plant species diversity in road verges of northern Patagonia. *J Veg Sci* 11:453–460
- Farji-Brener AG, Ghermandi L (2004) Seedling recruitment in the semi-arid Patagonian steppe: facilitative effects of refuse dumps of leaf-cutting ants. *J Veg Sci* 15:823–830
- Farji-Brener AG, Ghermandi L (2008) Leaf-cutting ant nests near roads increase fitness of exotic plant species in natural protected areas. *Proc R Soc B* 275:1431–1440
- Farji-Brener AG, Illes A (2000) Do leaf-cutting ant nests make “bottom up” gaps in neotropical rain forests? A critical review of the evidence. *Ecol Lett* 3:219–227
- Farji-Brener AG, Margutti L (1997) Patterns of plant species in relation to *Acromyrmex lobicornis* nest-mounds on roadside vegetation in northwest Patagonia. *Int J Ecol Environ Sci* 23:37–47
- Farji-Brener AG, Sasal Y (2003) Is dump material an effective small-scale deterrent to herbivory by leaf-cutting ants? *Ecoscience* 10:151–154
- Farji-Brener AG, Silva J (1995) Leaf-cutting ant nests and soil fertility in a well-drained savanna in western Venezuela. *Biotropica* 27:250–253
- Gibson J, Connolly J, Hartnett D, Weidenhamer J (1999) Designs for greenhouse studies of interactions between plants. *J Ecol* 87:1–16
- Hastings A, Byers J, Crooks J, Cuddington K, Jones C, Lambrinos J, Talley T, Wilson W (2007) Ecosystem engineers in space and time. *Ecol Lett* 10:153–164
- Horvitz C, Schemske D (2002) Effects of plant size, leaf herbivory, local competition and fruit production on survival, growth and future reproduction of a neotropical herb. *J Ecol* 90:279–290
- Jones C, Lawton J, Shachar M (1994) Organisms as ecosystem engineers. *Oikos* 69:373–386
- Jones C, Lawton J, Shachar M (1997) Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78:839–841
- Larcher W (1995) Physiological plant ecology, 3rd edn. Springer, New York
- Levine JM (2000) Species diversity and biological invasions: relating local process to community pattern. *Science* 288:852–854
- Meiners SJ (2007) Native and exotic plant species exhibit similar population dynamics during succession. *Ecology* 88:1098–1104
- Moutinho P, Nepstad D, Davidson E (2003) Influence of leaf-cutting ant nests on secondary forest growth and soil properties in Amazonia. *Ecology* 84:1265–1276
- Parker I, Simberloff D, Lonsdale W, Goodell K, Wonham M, Kareiva P, Williamson M, Von Holle B, Moyle P, Byers J, Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biol Invasions* 1:3–19
- Richards JE (1993) Chemical characterization of plant tissue. In: Carter MR (ed) Soil sampling and methods of analysis. Canadian Society of Soil Science, Pinawa, pp 115–139
- Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. *Trend Ecol Evol* 17:170–176
- Siemann E, Rogers W (2007) The role of soil resources in an exotic tree invasion in Texas coastal prairie. *J Ecol* 95:689–697
- Sternberg L, Pinzon M, Moreira M, Moutinho P, Rojas E, Herre A (2007) Plant use macronutrients accumulated in leaf-cutting ant nests. *Proc R Soc B* 274:315–321
- Suding K, LeJeune K, Seastedt T (2004) Competitive impacts and responses of an invasive weed: dependencies on nitrogen and phosphorus availability. *Oecologia* 14:526–535
- Vasconcelos H, Vieira-Neto E, Mundim F, Bruna E (2006) Roads alter the colonization dynamics of a keystone herbivore in Neotropical savannas. *Biotropica* 38:661–665
- Von Holle B, Simberloff D (2005) Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology* 86:3212–3218
- Wirth R, Herz H, Rye I, Beyschlag W, Hölldobler B (2003) Herbivory of leaf-cutting ants. Springer, Berlin
- Wirth R, Meyer S, Almeida W, Araujo M, Barbosa V, Leal I (2007) Increasing densities of leaf-cutting ants (*Atta* spp.) with proximity to the edge in a Brazilian Atlantic forest. *J Trop Ecol* 23:501–505
- Wright J, Jones C (2004) Predicting the effects of ecosystem engineers on patch-scale species richness from primary productivity. *Ecology* 85:2071–2081
- Zou J, Rogers W, Siemann E (2007) Differences in morphological and physiological traits between native and invasive populations of *Sapium sebiferum*. *Funct Ecol* 21:721–730