Positive ecosystem engineering effects of the ant *Atta vollenweideri* on the shrub *Grabowskia duplicata*

Beatriz Sosa & Alejandro Brazeiro

Abstract

Question: How does the ant *Atta vollenweideri* indirectly affect the shrub *Grabowskia duplicata*? Does environmental modification induced by nest building affect the life history and population structure of this dominant shrub?

Location: Halophytic savanna of western Uruguay, South America.

Methods: We compared the density of three shrub size classes, seedlings, saplings and adults, among patches created by ant nest building and in non-modified areas. We studied key soil properties for plant growth in both live nests and non-modified areas. We performed a greenhouse experiment to study the effects of soils (live nest versus non-modified area) on shrub germination probability. We also assessed vegetative propagation by measuring the incidence of root suckers and clonal offshoots in live nests and non-modified areas through a field survey.

Results: Seedling-size class was more abundant on live nests than in non-modified areas, suggesting that environmental conditions of this type of habitat (i.e. increased sodium and moisture content of soil, and decreased soil compaction) could facilitate shrub recruitment. We did not find any effects of soil type (live nests versus non-modified areas) on shrub germination probability. However, the vegetative propagation incidence was higher in the environment with live nests.

Conclusions: We found a strong indirect relationship between the ant *A. vollenweideri* and the shrub *G. duplicata*. This relationship seems to be mediated by an allogenic engineering process, i.e. soil bioturbation caused by nest building. The environmental conditions of live nests seem to facilitate shrub recruitment, mainly by increasing vegetative propagation.

Keywords: Ant nests; Bioengineering; Clonal reproduction; Germination; Indirect interaction; Population structure.

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Introduction

Animal–plant interactions are an important topic in community ecology (e.g. Morin 1999), although this has only recently begun to develop as a distinct ecological subdiscipline (Smallwood 2001). This research area has traditionally emphasized direct, consumption-related interactions such as herbivory, frugivory, pollination and some kinds of animal-mediated seed dispersal (Hunter et al. 1992). Nevertheless, indirect interactions can also be important and widespread.

The recent emergence of the ecosystem engineering concept has shed light on a multiplicity of indirect animal–plant interactions (Wright et al. 2002, 2003; Bruun et al. 2005; Davidson & Lightfoot 2006; Jouquet et al. 2006), suggesting that they are pervasive in nature. In this context, Jones et al. (1994) distinguished two types of process, autogenic and allogenic. Autogenic engineers create, maintain or modify habitats by means of their presence, as is the case of coral reefs or trees. Conversely, allogenic engineers change the environment by transforming living or non-living material from one physical state to another via their activities (e.g. dam building by beavers, rock splitting via tree root growth). Animal engineers affecting resource availability or environmental conditions relevant for plant germination, growth, reproduction or survival, probably cause major indirect animal–plant interactions in nature.

In the context of allogenic engineering, soil-modifying animals are critically important for plants because the soil encompasses key resources for their development in terrestrial ecosystems (Brussaard 1998; De Deyn et al. 2003). Soil invertebrates are known to have indirect positive effects on plant populations by increasing the availability of limiting resources, as well as providing safe sites for recruitment. In tropical rain forests, ant nests of the genus *Atta* provide open, nutrient-rich, litter-free sites for forest regeneration (Farji-Brener & Illes 2000). In Venezuelan tropical savannas, *A. laevigata* nests provide nutrient-rich, fire-safe sites for woody plant species (Farji-Brener & Silva 1995). In Patagonia (Argentina), *A. lobicornis* nests play an important role in plant recruitment, mainly during

the driest periods (Farji-Brener & Ghermandi 2004). In African savannas, nests of the termite *Macrotermes michaelseni* provide flood-safe sites allowing plant recruitment (Dangerfield et al. 1998).

In addition to providing safe sites for recruitment, ants could alter the relative importance of sexual and asexual reproduction in plant life histories by modifying the soil environment. In spite of the fact that the relative importance of sexual reproduction relative to vegetative propagation depends on environmental conditions (Prati & Schmid 2000; Villegas 2001), the role of ants and other soil invertebrates on plant reproductive strategies has been little studied. It was predicted that in a heterogeneous environment, branching probability would be higher in patches containing more nutrients, light or density of competitors (Sutherland & Stillman 1988). In agreement with this prediction, we expect that soil allogenic engineers like ants would be able to affect the incidence of vegetative propagation by creating new soil patches.

In this study we provide evidence of a strong indirect interaction between the ant *A. vollenweideri* Forel and the shrub *Grabowskia duplicata* Arn. that appears to be related to an improvement in vegetative propagation when the shrub is growing on living nests of this ant. *A. vollenweideri* is an herbivorous farming ant, endemic to South America (Bonetto 1959). It is largely distributed in the Chaco region, including southern Brazil and Bolivia, northern Argentina, eastern Paraguay and western Uruguay. This species builds large, conspicuous nests of up to 1 m in height and 9 m in diameter (Brazeiro et al. 2005). The subterranean component of these nests reaches approximately 5 m in depth and contains a complex system of tunnels and chambers, including chambers for farming, waste disposal and a queen shelter (Jonkman 1980). When the queen of the colony dies, the nest structure persists in the landscape, showing different stages of decay that can be classified as dead nests and ponds. Dead nests are collapsed convex promontories of about 50 cm in height and ponds are depressions of about 50 cm in depth that are generated by the complete collapse of dead nests. Therefore, nest building by *A. vollenweideri* generates three different patch types in the landscape, live nests (LN), dead nests (DN) and ponds (P), which are embedded in a matrix of non-modified areas (NMA) (Brazeiro et al. 2005).

The aim of this study was to assess the indirect effects of the ant *A. vollenweideri* on the shrub *G. duplicata*, driven by the modification of soil properties as a consequence of nest building. We focused on live nests, where *G. duplicata* recruitment could

be facilitated. Thus, in order to search for the underlying engineering mechanisms, we studied key soil properties (i.e. sodium content, moisture and bulk density) for plant growth and also evaluated population processes linked with reproductive strategies (i.e. seed germination and asexual propagation) both in live nests and in non-modified areas.

Methods

Study site

Fieldwork was conducted in western Uruguay in the Department of Río Negro (32°52′S, 58°02′W; Fig. 1). This region is characterized by mean annual precipitation of 1244 mm and mean annual temperature of 18°C (Dirección Climatológica y Documentación 1996). The study site is an area of about 5 ha, which belongs to a system of halomorphic savannas scattered along the Uruguay River (Fig. 1). This is a relict landscape in Uruguay, where grasslands are the dominant ecosystem. Given its physiographic characteristics, it could be associated with the Espinal Phytogeographical Province distributed in Argentina (Cabrera & Willink 1980).

The tree stratum is dominated by "algarrobo" *Prosopis nigra* (Griseb.) Hieron. (Fabaceae), "ñandubay" *P. affinis* Spreng. (Fabaceae), "quebracho blanco" *Aspidosperma quebracho-blanco* Schltdl. (Apocynaceae) and "chañar" *Geoffroea decorticans* (Gillies ex Hook. & Arn.) Burkart (Fabaceae). The herb stratum is dominated by *Selaginella sellowii* Hieron. (Selaginellaceae), *Evolvulus sericeus* Sw. (Convolvulaceae) and *Tripogon spicatus* (Nees) Ekman (Poaceae). Preliminary work in the study area showed that *G. duplicata* is the dominant shrub in the system (Sosa 2007). This shrub belongs to the Solanaceae family and is classified as a halomorphic species (Yansen 2008). In Uruguay, its distribution is restricted to the halomorphic savanna systems of Western Uruguay (Grela 2004).

Shrub population abundance

To assess the effect of *A. vollenweideri* nests on *G. duplicata* populations at the patch level, we sampled the shrub abundance in nine replicates in each of the three types of ant nest (LN, DN and P) as well as in NMA. Unfortunately, we could not find nine comparable P patches, as planned in the sampling design, and had to work with seven replicates of this patch type. This yielded a total of 34 replicates of shrub abundance, randomly selected in the
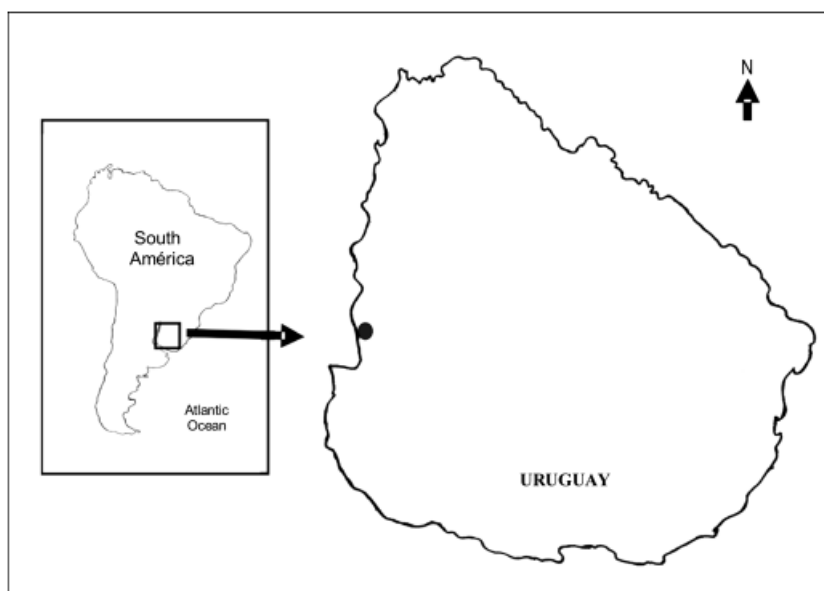
Fig. 1. Study site location (32°52′49.5″S; 58°02′37.0″W).

landscape. In the case of NMA, we only included sites more than 10 m from the nearest nest. To sample the abundance of *G. duplicata* we set 5×5-m plots, where shrubs were counted and their heights measured. Shrubs were classified into size classes on the basis of maximum height according to Barberis et al. (2002): seedlings < 30 cm, saplings between 30 and 60 cm and adults > 60 cm.

We evaluated the hypotheses that the ant patches facilitate *G. duplicata* development and hence we expected to find: (1) an abundance increment of *G. duplicata* on the ant patches (LN, DN and P) when compared with non-modified areas; (2) an effect of the ant patches on *G. duplicata* population structure when compared with non-modified areas. We also evaluated the hypothesis that recruitment of *G. duplicata* is facilitated on LN, thus we expected to find more shrub seedlings on LN than in NMA. We tested these hypotheses by performing pair-wise planned comparisons; this test provides better power against Type I errors and guarantees a more logical interpretation of the outcome than a posteriori comparisons (Underwood 1997).

To compare *G. duplicata* abundance among NMA, LN, N and P, we transformed this variable (Log $x+1$) to meet the assumption of homogeneity of variances and then performed a one-way ANOVA to assess the main effect and three pair-wise planned comparisons (NMA versus LN, NMA versus DN and NMA versus P) for variance homogeneity.

G. duplicata abundance by size class (seedlings, saplings and adults) was also compared. In this case, the assumption of homogeneity of variance was not

met so we used Welch's test, a robust alternative when variances are unequal (Zar 1984; Johnson 1995), then performed three pair-wise planned comparisons (NMA versus LN, NMA versus DN and NMA versus P) adjusted for unequal variances.

We also estimated the response of the *G. duplicata* population to ant patches at the landscape level by simulating virtual landscapes with and without ant patches. We first estimated the incidence of ant patches in the landscape by surveying the area occupied by each type of nest in three transects of 200×10 m, randomly set in the study area. On average, the estimated incidence and percentage area occupied by each patch type (in parentheses) per hectare were: 36 (9%) DN, 20 (5%) P and 16 (4%) LN. The total area occupied by ant patches was 18% per hectare.

We simulated a landscape of 1 ha with a quadrat pixel size of 5×5 m, as also used in the field observations. A lattice of 400 cells of 5×5 m was therefore generated. We classified cells as LN, DN, P or NMA according to the estimated incidence per hectare. We then assigned abundance values to each cell by re-sampling with replacement from the survey data according to the patch it represented (LN, DN, P, NMA). Following this procedure, we created four lattice sheets, one for total abundance and one for abundance of each size class (seedlings, saplings and adults). Landscapes without ant patches were created using the same procedure, but assuming that all cells were NMA. We iteratively ($n = 10,000$) re-calculated *G. duplicata* total abundance and abundance by size class by running the Monte Carlo module of Pop

tools in Excel software (Microsoft Office v 2003, Microsoft Corporation).

From Monte Carlo outputs we obtained mean total abundance and mean abundance by size class of *G. duplicata*, as well as the variances. We plotted mean abundance and its standard deviation in simulated landscapes with and without ant nests. Significant differences were considered when standard deviation intervals did not overlap. Given the high number of iterations used, the estimated confidence intervals were narrower than the standard deviation intervals. Consequently we preferred to use standard deviations as a more robust method to detect significant differences.

Soil modifications by live ant nests

To evaluate the effects of ant nests on soil properties, we took paired samples at LN and NMA, using a randomized block design with nine replicates. Three soil properties were assessed: sodium concentration, moisture and bulk density.

Soil sodium level was measured in winter (2005) when the availability of this cation is expected to be very low due to leaching and runoff caused by high precipitation. Samples were taken in the surface layer (15-cm depth) using a cylindrical corer of 5-cm diameter. Soil sodium levels were analysed using an atomic absorption spectrophotometer at the Soil Laboratory of Facultad de Ciencias (Universidad de la República, Uruguay).

Bulk density and soil moisture content were analysed in the summer (2006), when soil moisture content is more critical for vegetation. For each replicate, three subsamples were taken using a cylindrical corer of 5-cm diameter and 10-cm depth. These samples were kept wrapped with aluminium foil, carried to the laboratory and weighed before and after oven drying for 48 h at 100°C. Bulk density was calculated by dividing sample dry weight by sample volume. Moisture content was calculated as the difference between the initial and final weight after oven drying. We assessed the effects of LN on soil properties by performing one-way ANOVA.

Soil type effects on shrub germination and vegetative propagation

In order to explore how *G. duplicata* recruitment is improved under the environmental conditions of LN, we analysed the effect of soil type on shrub germination in a greenhouse experiment. *G. duplicata* has two classes of seed, small (mean weight: 1.0 mg) and big (mean weight: 2.2 mg) that also clearly differ in their shapes and endocarp positions. We sowed 16 seeds in each pot, with six replicates per treatment. The experiment was carried out for 3 months in a controlled environment (25°C, light–dark regime of 12 h). Seeds were watered daily to field capacity. Seeds showing radicles longer than 1 mm were considered as germinated. Germination probability was calculated as the percentage of germinated seeds in each replicate.

An $Arcsin\sqrt{x}$ transformation of this variable was carried out to meet the assumptions of normality and homogeneity of variances. We compared the effects of soil type (LN soil versus NMA soil) and seed size (big versus small) on *G. duplicata* germination probability by performing a factorial two-way ANOVA (soil type×seed size).

To compare *G. duplicata* clonal reproduction between LN and NMA, we dug around the main stem of randomly selected saplings and adult shrubs (30–80-cm high) and recorded the presence of root suckers and clonal offshoots. A total of 10 individuals were evaluated, five located in LN and the remaining five in NMA. Differences in root sucker and clonal offshoot occurrence between LN and NMA were evaluated using a chi-square test.

Results

Shrub population response to ant nests

Atta vollenweideri patches affected the abundance of *G. duplicata* plants ($F_{3,29} = 15.2$, $P < 0.0001$) (Fig. 2a). The contrast from planned comparisons showed that shrub abundance was higher in LN ($t_{29} = -3.87$ $P = 0.001$) and DN ($t_{29} = 6.4$ $P = 0.000$) than in NMA. However, we did not detect significant differences between P and NMA ($t_{29} = 1.6$ $P = 0.1$).

A. vollenweideri patches also affected the population structure of *G. duplicata* (Fig. 2). Adult size class was affected (Welch test: $W_{3,13.4} = 14.28$ $P < 0.0001$), and adults were more abundant on LN ($t_{10} = -3.1$ $P = 0.01$), DN ($t_8 = 6.0$ $P = 0.000$) and P ($t_7 = 2.6$ $P = 0.03$) than in NMA. We also detected significant variations in seedling size class (Welch test: $W_{3,14.5} = 3.69$, $P = 0.03$): seedlings were more abundant on LN than on NMA ($t_{10} = -3.0$ $P = 0.01$). In the case of saplings, no significant differences were observed among the patch types (Welch test: $W_{3,1.4} = 2.3$ $P = 0.1$).

Simulations suggested that the abundance of *G. duplicata* at the landscape level was notably enhanced by the presence of patches generated by *A. vollenweideri* nests (Fig. 3). Simulated landscapes
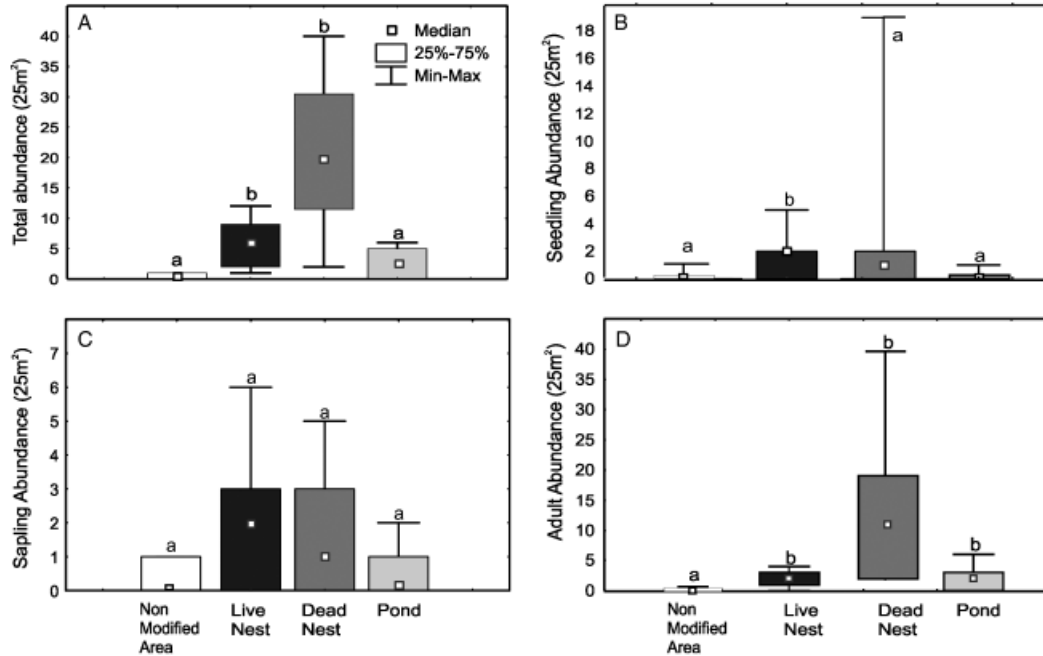
Fig. 2. Effects of *A. vollenweideri* nests on *G. duplicata* abundance. (a) Total abundance, (b) Seedling abundance, (c) Sapling abundance, (d) Adult abundance. Different letters above the bars indicate significant differences for the comparison between NMA and corresponding ant patches (LN, DN and P).
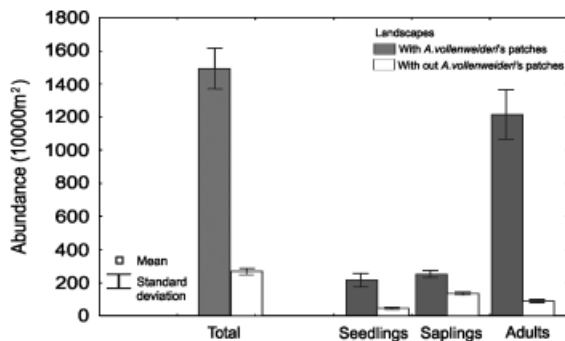
Fig. 3. *G. duplicata* abundance in simulated landscapes with and without *A. vollenweideri* patches.

including NMA with ant nests (LN, DN and P) at their natural frequency showed higher abundance of *G. duplicata* than simulated landscapes without ant patches (NMA only). In engineered landscapes, *A. vollenweideri* patches contributed to 82% of *G. duplicata* offshoot abundance. In fact, *G. duplicata* abundance in the engineered landscape was on average seven times the abundance estimated in the non-modified landscape. Our results also suggest that the height distribution of *G. duplicata* was affected by *A. vollenweideri* nests. In landscapes with ant nests, the adult size class was dominant, while non-modified landscapes were dominated by the sapling size class.

Ant nest effects on soil properties

The comparison between LN and NMA indicated that *A. vollenweideri* modifies soil properties through nest building. Soil bulk density was higher ($F_{1,15} = 5.1$, $P = 0.03$) in NMA (mean $\pm$ SD: $1.53 \pm 0.14 \, g \, cm^{-3}$) than in LN (mean $\pm$ SD: $1.37 \pm 0.13 \, g \, cm^{-3}$), indicating less compacted soils on LN. Moisture content was higher ($F_{1,15} = 13.24$, $P = 0.01$) on LN ($0.10 \pm 0.02\%$) than NMA ($0.07 \pm 0.01\%$). Important sodium level differences were observed between LN and NMA ($F_{1,16} = 51$, $P < 0.001$). On average, the soil sodium in LN ($17.59 \pm 3.45 \, mEq.100 \, g^{-1}$ soil) was almost one order of magnitude higher than in NMA (2.51 ± 0.97 mEq. $100 \, g^{-1}$ soil).

Soil type effects on shrub germination and vegetative propagation

The greenhouse experiment showed that germination probability in LN soils ($24.0 \pm 8.7\%$) tends to be lower than in NMA soils ($30 \pm 13\%$), but the difference was not statistically significant ($F_{1,20} = 2.35$, $P = 0.15$). This confirmed that *G. duplicata* was able to germinate in soils with a very high sodium content, and that it was not significantly affected by an increase in sodium concentration at the level observed in LN.
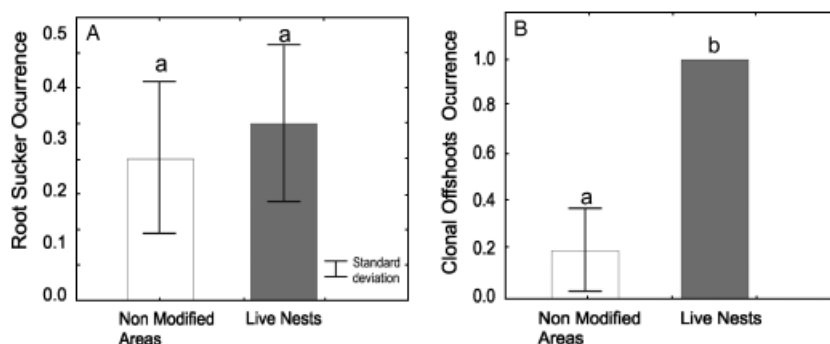
Fig. 4. Effects of *A. vollenweideri* nests on *G. duplicata* vegetative propagation. (a) Root sucker occurrence and (b) Clonal offshoot occurrence of *G. duplicata* in live nests and non-modified areas. Different letters above the bars indicate significant differences ($P < 0.05$).

On the other hand, seed size, the other factor analysed in the greenhouse experiment, affected shrub germination probability ($F_{1,20} = 7.9$, $P = 0.01$). Small seeds had higher germination responses than bigger seeds. The interaction between soil type and seed size was not statistically significant ($F_{1,12} = 1.6$, $P = 0.20$).

The proportion of plants with root suckers did not differ significantly between LN and NMA ($\chi^2 = 0.06$, $P = 0.8$). However, the proportion of plants with clonal shoots was higher in LN ($\chi^2 = 6.67$, $P < 0.0001$) (Fig. 4). In fact, in LN plots all the shrubs with root suckers presented clonal growth.

Discussion

Shrub population response to ant nests

Our results showed that *A. vollenweideri* nests locally affect the abundance pattern of the shrub *G. duplicata*. In LN and DN, the total abundance of shrubs increased when compared with NMA. Scaling up these local effects through simulations, we found important population effects at the landscape level. In the engineered landscape, the patches generated by nest building occupied only 18% of the studied area, but they support 82% of the shrub population, indicating that they are key microhabitats for *G. duplicata*.

Simulations also suggested changes in population structure at the landscape level. Under engineered landscapes, the shrub population was dominated by the adult size class, while non-modified landscapes were dominated by saplings. This change in the abundance population structure should respond to differences in underlying demographic processes, like sapling and adult survival or shrub growth rate.

The high habitat dependence of *G. duplicata* should generate strong coupling between shrub po-

pulation dynamics and patch dynamics driven by nest building and the following decay processes. The colonization rate of *A. vollenweideri* colonies could be determining the number of LN patches available in the landscape to be colonized by *G. duplicata*, and therefore its abundance and spatial distribution. Our results suggest that under the environmental conditions generated by nest building, *G. duplicata* recruitment could be facilitated. Recruitment facilitation could represent the main mechanism coupling the dynamics of the shrub population with patch dynamics of the nests.

Soil property modifications by nest building

In this study, we observed important edaphic modifications in *A. vollenweideri* live nests: increased soil sodium concentration and moisture content, and reduced soil compaction (i.e. lower bulk density).

The soil sodium content in LN was not only higher than the value expected for superficial layers ($1.4\,mEq.100\,g^{-1}$ soil) in halophytic soils of Uruguay, but also twice as high as the content expected for deeper layers (8.3–$8.7\,mEq.\,100\,g^{-1}$ soil) (Duran 1991). These results are likely a consequence of ant bioturbation, which is known to annually affect up to $1.1\,ton\,ha^{-1}$ of soil (Bucher & Ziccardi 1967). Deep excavation (to 5-m depth, Jonkman 1980) by *A. vollenweideri* during nest building brings soil particles rich in sodium to the surface, thus increasing the sodium concentration in surface soil. While hydrological processes associated with sodium movement, such as runoff and leaching are expected to reduce its accumulation on the soil surface, soil bioturbation would counteract such processes. Ant nests could be regarded as powerful ion pumps that redistribute sodium and other ions across the soil profile. Such mechanisms, linked with runoff, are

also able to horizontally move part of the sodium concentrated in LN to surrounding areas, affecting sodium distribution in the landscape.

Soil bulk density is lower on *A. vollenweideri* nests than in NMA, indicating less compacted soils, as reported for other ant nests (e.g. Blomqvist et al. 2000; Dostál et al. 2005). These findings are usually explained by the digging activity of ants, which loosens the soil structure (Woodell & King 1991). A loose soil structure, together with the creation of tunnels and chambers, generally increases evaporation leading to lower moisture in nest soils relative to non-modified areas (Blomqvist et al. 2000). However, nest soils in our study had a higher moisture content than NMA, despite lower compaction. This unexpected result could be a consequence of decreased evaporation on nest soils due to formation of saline crusts at the nest surface, as observed in the field.

In summary, nest building by *A. vollenweideri* modifies soil parameters that are important for plant development. Sodium increases osmotic pressure and pH and can trigger soil toxicity (Buckman & Brady 1977). High sodium levels in *A. vollenweideri* nests would increase the osmotic pressure, therefore reducing plant water absorption. However, the higher moisture content of LN relative to NMA could reduce this stress, thus favouring halophytic species adapted to deal with sodium toxicity. Finally, soil compaction could affect seed germination and root development.

Environmentally mediated effects on *G. duplicata* recruitment

Our greenhouse experiment demonstrated that under the same light, moisture and temperature conditions, soil type (LN versus NMA) does not affect the germination probability of *G. duplicata*. The seeds of this shrub were not significantly affected by the sodium concentration in LN. Hence, soil sodium content did not limit shrub recruitment at live nests of *A. vollenweideri*.

On the other hand, our field observations supports that, at LN, recruitment is mainly driven by asexual propagation facilitated in less compacted and more humid soils. *G. duplicata* was able to produce root suckers at the same level in both LN and NMA, but the capability of root suckers to generate offshoots increased in the less compacted soils of live nests. Thus, the increased shrub seedling abundance in LN seems to be the result of increased vegetative propagation. Positive effects of ant nests on belowground biomass were also reported for *Carex arenaria*, which develops shorter internodes and more shoots on ant mounds than in the surrounding matrix (Blomqvist et al. 2000). These authors suggested that *C. arenaria* colonizes the nests vegetatively. In our system, however, we did not observed *G. duplicata* ramets around the nests. Therefore, we do not expect nests to be vegetatively colonized by *G. duplicata* ramets occurring in the surrounding area. *G. duplicata* fruits are small drupes that are likely dispersed by birds. Thus, shrub recruitment may be determined by seed arrival mediated by frugivorous birds using the big nests, either as a perch or a feeding site on ants. After establishment, saplings and adult individuals would take advantage of the less compacted and more moist soils that facilitate root development and production of clonal offshoots.

New questions and perspectives

In our biological model, an interesting and poorly explored issue is highlighted, which is the possible effects of ecosystem engineering on the mode of reproduction in plants, i.e. sexual or clonal. In the ant–shrub system studied here, it seems that both reproductive strategies occur. Through shrub sexual reproduction and seed dispersal, the live nests of *A. vollenweideri* would be colonized, and after establishment, new shrubs are produced by both sexual and asexual propagation, although we expect asexual propagation to become dominant. The engineering-mediated changes in the reproductive mode of plants may have important implications in genetic population structure and therefore in evolutionary processes.

Another interesting issue that needs more research is the effect of the affected organism on the engineer population. Jones et al. (1994) suggested that feedbacks in the relationship between the engineer and the affected species could generate an asymmetric interaction $(0/-, 0/+)$. However, in our biological model, *G. duplicata* could have negative feedbacks to the ant population by altering the fungal symbiont environment.

The fungus, probably *Leucocoprinus gongylophorus* (Stradling & Powell 1986), has strict demands for high humidity and temperatures between 25°C and 30°C for growth (Quinlan & Cherrett 1978; Powell & Stradling 1986). With restricted temperature tolerance and high relative humidity demands, the *A. vollenweideri* symbiont appears to set the limits within which optimal colony growth rates can be achieved. For leaf-cutting ants, temperature is a powerful variable predicting the occurrence and density of Paraguayan and Argentinean species (Farji-Brener 1994). Our study area is located in the southernmost range of distribution of *A. vollenweideri* and therefore temperature could represent a key limiting factor for

colony growth, particularly in winter. On live nests (LN), temperature could be affected by the high density of *G. duplicata*. The shrub canopy could increase light interception and thus reduce live nest temperature. Additionally, root development could damage tunnels and openings affecting nest ventilation and consequently temperature. Root respiration could also modify gas concentration ratios (CO_2, O_2) inside nests.

In conclusion, if the above hypothetical feedbacks actually occur, *G. duplicata* could negatively affect the *A. vollenweideri* colony and eventually be responsible for its destruction. If *G. duplicata* affects ant colony survival, then this shrub would indirectly modify the patch dynamics in the landscape. Population dynamics of engineering species and associated patch dynamics have been explored using modelling (e.g. Gurney & Lawton 1996; Hui et al. 2004; Wright et al. 2004). However the potential feedbacks of the species affected by the engineer and the consequences for patch dynamics have been less studied.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Picture S1. Savanna landscape with *Atta vollenweideri* live nest
Picture S2. *Atta vollenweideri* live nest with *Grabowskia duplicata*
Picture S3. *Atta vollenweideri dead* nest covered with *Grabowskia duplicata*

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