

Leaf-Cutting Ant Nests and Soil Biota Abundance in a Semi-Arid Steppe of Northwestern Patagonia

by

Alejandro G. Farji-Brener

ABSTRACT

The availability of organic matter and the abundance of soil biota responsible for their decomposition and mineralization often limit vegetation growth. I examine whether leaf-cutting ant nests affect the abundance of soil micro-organisms in a semi-arid steppe of NW Patagonia. External refuse dumps from *Acromyrmex lobicornis* nests contained between 1-2 orders of magnitude more bacteria and fungi than adjacent, non-nest soils. Since these taxa are responsible for the major fraction of the mineralization occurring in soils, they may be responsible for the high nutrient content in ant refuse dumps documented in earlier works. Ant nest sites should be considered not only as hot spots of plant diversity and abundance, but also as a source of soil improvement biota.

Key words: ants, bacteria, fungi, soil disturbance, soil fertility, Patagonia.

INTRODUCTION

Soil nutrients often limit plant establishment, growth and reproduction in arid ecosystems (Mun & Whitford 1989, Satti *et al.* 2003). For example, total nitrogen storage is relatively low in deserts compared with other regions (Post *et al.* 1985). The low concentration of soil nutrients in desert soils have been partially attributed to the low amount of organic matter, which results in low rates of mineralization (Fisher *et al.* 1990). Therefore, the distribution of organic matter and the abundance of soil biota responsible for chemical transformations can have important implications for vegetation maintenance in dry regions (Schlesinger *et al.* 1990).

Ant nests affect the abundance of soil organic matter in many arid ecosystems (Bestelmeyer & Wiens 2003). Ants concentrate the organic matter

they forage around their nests as food stocking and waste products. This accumulation of organic matter may lead to an increase in the abundance and richness of soil biota. Previous research showed that soil biota was more abundant and functionally diverse in ant nests than control soils (Wagner *et al.* 1997, Daubers & Wolters 2000, Boulton *et al.* 2003, Boulton & Amberman 2006). Soil biota decomposes the organic matter into mineral nutrients making nest areas richer in soil nutrient concentrations than adjacent non-ant nest soils (Petal 1998, Wagner *et al.* 1997, 2004). Consequently, plants often show a better performance when they grow near ant-nests than away from them (Rissing 1986, Whitford & DiMarco 1995, Brown & Human 1997, Wagner 1997). For this reason, ant nests are considered as an important source of heterogeneity in desert ecosystems (Dean *et al.* 1997).

To what extent ants affect soil properties and the vegetation will partially depend on colony size, ant activity and durability of nests. Ants that build large, long-lived nests and produce high amounts of organic matter will affect more soil conditions than ants with small colonies, short-lived nests and with a low organic matter production. Leaf-cutting ants are considered as one of the most important sources of soil nutrient patches (Farji-Brener & Illes 2000). They form colonies with more than 10^6 workers occupying a single, stable nest for 10-20 years (Fowler *et al.* 1986) and collect large quantities of vegetation from a large area (Costa *et al.* 2008). This collected material is used as substrate for fungus culturing in underground nest chambers. The fungi grow on this plant substrate and parts of the fungal colonies are used to feed the developing ant brood. The waste material obtained from the fungal decomposition is removed from the fungus gardens to specific external or internal disposal areas (hereafter, refuse dumps). These refuse dumps are several times richer in organic carbon and nutrients than the adjacent soils, generating nutritive hot spots around the nest area (Farji-Brener & Illes 2000). This high availability of nutrients usually increases plant abundance, diversity, productivity and accelerates nutrient cycling around the nest area (Lugo *et al.*, 1973, Haines 1978, Farji-Brener & Silva 1995b, Farji-Brener & Illes 2000, Moutinho *et al.* 2003, Farji-Brener & Ghermandi 2004).

The soil biota is mostly responsible for chemical transformations in the soil. Therefore, the high soil nutrient content in leaf-cutting ant nests suggests that they also alter the abundance of biotic agents responsible for

decomposition and mineralization, such as bacteria and fungi. As discussed above, soil micro-organisms typically occur at elevated densities in nests of other ant species (Wagner *et al.* 1997, Daubers and Wolters 2000, Boulton *et al.* 2003, Boulton & Amberman 2006). To our knowledge, no previous study has addressed whether soil micro-organisms are also increased in leaf-cutting ant nests, although these nests are considered as a major source of soil fertility in arid regions (Farji-Brener & Ghermandi 2000, 2008; Tadey & Farji-Brener 2007).

In dry areas of Patagonia, the combined effects of scarce rainfall, poor soils, and overgrazing have produced important reductions in vegetation cover and soil fertility (Bisigato & Bertiller 1997, Mazzarino *et al.* 1998; Satti *et al.* 2003, Tadey 2006). Therefore, any factor that increases soil fertility will have relevant ecological consequences. The leaf-cutting ant *Acromyrmex lobicornis* Emery is considered a key species in these arid regions because it enhances soil fertility and plant performance (Farji-Brener & Ghermandi 2000; 2008). This ant species dump their nutrient-rich organic waste in external piles. Adjacent plants can thus access these nutrients, improving their growth, seed production and abundance (Farji-Brener & Ghermandi 2008). All these facts, together with the evidence from other ant species (see above), suggest that leaf-cutting ant nests should affect soil biota. Here we characterize the effects of nests of the leaf-cutting ant *A. lobicornis* on the abundance of soil micro-organisms (bacteria and fungi) in a semi-arid steppe of northwestern Patagonia, Argentina.

METHODS

This study was performed in a semi-arid steppe located at the East (driest) border of the Nahuel Huapi National Park, Argentina (41°S, 72°W). The mean annual temperature is 8°C and the mean annual precipitation is approximately 600 mm. The dominant vegetation of the study area is a mix of native species typical from Patagonian steppes (e.g., *Stipa speciosa*, *Mulinum spinosum*, *Imperata condensata*, *Plagiobothrys tinctorius* and *Baccharis pingraea*), and some exotics (e.g., *Bromus tectorum*, *Onopordon acanthium*, *Carduus nutans* and *Verbascum thapsus*) (Correa 1969-1998). *Acromyrmex lobicornis* is the leaf-cutting ant species with the widest latitudinal range that occurs in Argentina, reaching from subtropical areas in southern Brazil

and Bolivia (23° S) to Patagonia (44° S) (Farji-Brener & Ruggiero 1994). *A. lobicornis* occurs in a broad range of plant communities but is especially common in dry regions, and is the only leaf-cutting ant species living in Patagonia (Kusnezof 1978, Farji-Brener & Ruggiero 1994). *A. lobicornis* nests reach depths of 1 m, and on the soil surface the ants build a mound of twigs, soil and dry plant material. Inside this mound, ants tend the fungus on which the ant larvae feed. Organic waste is removed from the internal fungus garden and dumped onto the soil surface. This refuse dump is up to 80 times richer in nutrient content than adjacent non-nest soils (Farji-Brener & Ghermandi 2000, 2008).

I studied the content of soil micro-organisms (bacteria and fungi) in refuse dumps and adjacent non-nest soils from 10 adult *A. lobicornis* nests located within an area of ~ 2 ha. The nests were at least 10 m apart. Populations of bacteria and fungi were sampled in the late spring (October-December) of 2001. In each nest, I collected three replicate cores (10 cm wide x 10 cm deep) from the organic waste pile and a paired non-nest soil site 2-6 m away. Non-nest soil samples were randomly collected regardless of the presence of vegetation; however, most of them were obtained from bare soil. The three samples were gathered into one sample for each site and treatment (i. e., refuse dump and non-nest soil). Therefore, I analyzed a total of 10 refuse dumps and 10 non-nest soil compound samples ($n = 10$ sites). All the samples were transported to the laboratory and maintained at 4°C upon processing. Sub-samples of 20 g were removed and weighed in the laboratory for their analysis. Filamentous fungi, yeasts and total bacteria abundance were measured in each case per duplicate and incipient colonies were counted in nutritive agar plates following Parkinson (1994) and Zuberer (1994), respectively. Abundance data of bacteria and fungi were estimated per gram of substrate. Response variables were expressed as colony forming units per gram (CFU/ g). The CFU/g of bacteria and fungi were analyzed in each case using paired t-tests. Data were log transformed to meet parametric assumptions.

RESULTS AND DISCUSSION

Refuse dumps contained higher abundance of soil micro-organisms than adjacent, non-nest soils. The mean (\pm SE) abundance of bacteria was 2 orders of magnitude higher in refuse dumps than adjacent, control soils ($1.9 \times 10^9 \pm$

1.0×10^8 CFU/g versus $1.0 \times 10^7 \pm 3.4 \times 10^6$ CFU/g, respectively, $t = 11.1$, $df = 9$, $P < 0.001$). The mean (\pm SE) abundance of fungi was also superior in refuse dumps than in non-nest soils ($1.2 \times 10^7 \pm 6.6 \times 10^6$ CFU/g versus $1.5 \times 10^5 \pm 3.6 \times 10^4$ CFU/g, respectively, $t = 6.4$, $df = 9$, $P < 0.001$).

Nests of *A. lobicornis* were associated with high abundance of soil micro-organisms. Refuse dumps contained between 1-2 orders of magnitude more bacteria and fungi than adjacent, non-nest soils. Previous studies showed that refuse dumps from *A. lobicornis* nests increased soil organic matter, soil nutrient content and neighboring plants abundance and reproduction (Farji-Brener & Ghermandi 2000, 2004, 2008). Since micro-organisms are the decomposers responsible for over 90% of the mineralization occurring in soils (Lavelle & Spain 2001), the high abundance of bacteria and fungi in refuse dumps is likely to be the responsible for the high nutrient content found in this substrate (Farji-Brener & Ghermandi 2000, 2008). Thus, the findings of this work complete the missing link between the higher content of organic matter in leaf-cutting ant nest sites and its exploitation by the neighboring vegetation. Briefly, ants concentrate plant material through foraging and generate a huge amount of organic waste. This organic waste favors the reproduction and abundance of soil biota, offering food and adequate microclimatic conditions for decomposers. Previous research showed that refuse dumps presented more stable temperatures and higher water retention than control soils (Farji-Brener & Ghermandi 2004). Finally, soil biota decomposes the organic matter into soil nutrients available for plants, which can access and employ these nutrients enhancing their abundance and reproduction (Farji-Brener & Ghermandi 2008). The distribution of organic matter and the abundance of soil biota responsible for chemical transformations are ecologically important in the maintenance of vegetation in dry regions (Schlesinger *et al.* 1990).

However, there are other possible explanations for this pattern. Ants could track areas with high concentration of organic matter and soil biota, rather than cause them. Nevertheless, there are several lines of evidence that suggest that ants are responsible for changes in soil organic matter and soil biota. First, the accumulation of organic matter is evident in many ant species (Wagner *et al.* 1997 and references therein), including leaf-cutting ants (Farji-Brener & Illes 2000). Second, ants actively accumulate organic debris over time; soil

editor's note: we would suggest adding a figure or table summarizing the results to this section.

organic matter and nutrient content is higher in older than in incipient ant nests (Wagner *et al.* 2004). Third, the reverse is also true: when ant nests die or are abandoned by the colony, the elevated concentration of soil fertility declines (Hudson *et al.* 2009). Finally, soil biota and nutrients show higher abundance in external organic waste piles, a substrate that is directly generated by the ants (Farji-Brener & Ghermandi 2008). All these facts, together with the lack of evidence that leaf-cutting ants prefer patches of soils with higher contents of organic matter for nest founding, strongly suggest that ants and their activities are the cause of the high abundance of soil organic matter, soil biota and soil nutrient content typically associated with their nest sites.

In arid regions, shrubs are recognized as micro-sites of higher soil fertility (Bestelmeyer & Schooley 1999). Soil biota often shows higher abundance around roots and in the litter accumulated beneath shrubs, while open spaces or bare soils exhibit lower biological activity. The results of this study reinforce the idea that ant nest sites (including those from leaf-cutting ants) are an additional and important source of soil fertility in arid regions (Wagner *et al.* 1997, Farji-Brener & Ghermandi 2000, Tadey & Farji-Brener 2007). These results may also have implications for conservation and restoration. From a conservation point of view, leaf-cutting ant nests should be considered not only as hot spots of plant diversity and abundance (Farji-Brener & Ghermandi 2000), but also as a source of soil improvement biota. From a restoration perspective, refuse dumps could be employed as a cheap and renewable fertilizer to improve soil quality in low-fertility, overgrazed arid sites.

ACKNOWLEDGMENTS

This work was partially supported by grants from CONICET (PIP 5110) and FONCyT (PICT 25314), Argentina. Comments from M. Larva Tadey improved the manuscript.

REFERENCES

- Bestelmeyer, B. T. & J. Wiens. 2003. Scavenging ant foraging behavior and variation in the scale of nutrient redistribution among semi-arid grasslands. *Journal of Arid Environments* 53: 373-386.
- Bestelmeyer, B. T. & R. Schooley. 1999. The ants of the southern Sonoran desert: community structure and the role of trees. *Biodiversity and Conservation* 8: 643-657.
- Bisigato, A. & M. Bertiller. 1997. Grazing effects on patchy dryland vegetation in northern Patagonia. *Journal of Arid Environments* 36: 639-653.

- Boulton, A. & K. Amberman. 2006. How ant nests increase soil biota richness and abundance: a field experiment. *Biodiversity and Conservation* 15: 69-82.
- Boulton, A., B. Jaffe & K. Scow. 2003. Effects of a common harvester ant (*Messor andrei*) on richness and abundance of soil biota. *Applied Soil Ecology* 23: 257-265.
- Brown, M., & K. Human. 1997. Effects of harvester ants on plant species distribution and abundance in a serpentine grassland. *Oecologia* 112: 237-243.
- Correa, M. N. 1969-1998. Flora Patagónica. 7 Vols. Instituto Nacional de Tecnología Agropecuaria, Buenos Aires.
- Costa, A., H. Vasconcelos, E. Vieira-Neto & E. Bruna. 2008. Do herbivores exert top-down effects in Neotropical savannas? Estimates of biomass consumption by leaf-cutter ants. *Journal of Vegetation Science* 19: 849-854.
- Dauber, J. & V. Wolters. 2000. Microbial activity and functional diversity in the mounds of three different ant species. *Soil Biology and Biochemistry* 32: 3-99.
- Dean, W., S. Milton & S. Klotz. 1997. The role of ant-mounds in maintaining small-scale patchiness in dry grasslands in Central Germany. *Biodiversity and Conservation* 6: 1292-1307.
- Farji-Brener, A. G. & L. Ghermandi. 2008. Leaf-cutting ant nests near roads increase fitness of exotic plant species in natural protected areas. *Proceedings of the Royal Society - Series B*. 275: 1431-1440.
- Farji-Brener, A. G. & L. Ghermandi. 2004. Seedling recruitment in the semi-arid Patagonian steppe: facilitative effects of refuse dumps of leaf-cutting ants. *Journal of Vegetation Science* 15: 823-830
- Farji-Brener, A. G. & L. Ghermandi. 2000. The influence of nests of leaf-cutting ants on plant species diversity in road verges of northern Patagonia. *Journal of Vegetation Science* 11: 453-460.
- Farji-Brener, A. G. & A. Illes. 2000. Do leaf-cutting ant nests make 'bottom up' gaps in neotropical rain forests? A critical review of the evidence. *Ecology Letters* 3: 219-227.
- Farji-Brener, A. G. & J. Silva. 1995a. Leaf-cutting ant nests and soil fertility in a well-drained savanna in western Venezuela. *Biotropica* 27: 250-253.
- Farji-Brener, A.G. & J. Silva. 1995b. Leaf-cutting ants and forest groves in a tropical parkland savanna of Venezuela: facilitated succession? *Journal of Tropical Ecology* 11: 651-669.
- Farji-Brener, A.G. & A. Ruggiero. 1994. Leaf-cutting ants (*Atta* and *Acromyrmex*) inhabiting Argentina: patterns in species richness and geographical ranges sizes. *Journal of Biogeography* 21: 535-43.
- Fisher, F.M., D. Freckman & W. Whitford. 1990. Decomposition and soil nitrogen availability in Chihuahuan desert field microcosms. *Soil Biology and Biochemistry* 22: 241-249.
- Fowler, H., L. Forti, V. Da-silva & N. Saes. 1986. Population dynamics of leaf-cutting ants, in: Logfren, S., Vandermeer, R. (Eds.), *Fire and Leaf-cutting Ants: Biology and Management*, Westview Press, Boulder, Colorado, pp. 123-145.

- Haines, B. 1978. Element and energy flows through colonies of the leaf-cutting ant, *Atta colombica*, in Panama. *Biotropica* 10: 270-277.
- Hudson, T., B. Turne, H. Herz & J. Robinson. 2009. Temporal patterns of soil nutrient availability around nests of leaf-cutting ants (*Atta colombica*) in secondary moist tropical forest. *Soil Biology and Biochemistry* 41: 1088-1093.
- Kusnezov, N. 1978. Hormigas Argentinas: Claves para su Identificación. Miscelanea 61, Tucuman, Argentina.
- Lavelle, P. & A. Spain. 2001. *Soil Ecology*. Kluwer Scientific Publications, Amsterdam.
- Lugo, A., E. Farnworth, D. Pool, P. Jerez & G. Kaufman. 1973. The impact of the leaf cutter ant *Atta colombica* on the energy flow of a tropical wet forest. *Ecology* 54: 1292-1301.
- Mazzarino, M., M. Bertiller, C. Sain, P. Satti & F. Coronato. 1998. Soil nitrogen dynamics in northeastern Patagonia steppe under different precipitation regimes. *Plant and Soil* 202: 125-131.
- Moutinho, P., D. Nepstad & E. Davidson. 2003. Influence of leaf-cutting ant nests on secondary forest growth and soil properties in Amazonia. *Ecology* 84: 1265-1276.
- Mun, H. T. & W. Whitford. 1989. Effects of nitrogen amendment on annual plants in the Chihuahuan desert. *Plant and Soil* 120: 225-232.
- Parkinson, D. 1994. Filamentous fungi. *In*: Weaver, R.H., Angle, J.S., Bottomley, P.S. (Eds.), *Methods of soil analysis. Part II: Microbiological and biochemical properties*. Soil Science Society of America, Inc. Madison, pp 119-144.
- Petal, J. 1998. The influence of ants on carbon and nitrogen mineralization in drained fen soils. *Applied Soil Ecology* 9: 271-275.
- Post, W., J. Pastor, P. Zinke & A. Stangenberger. 1985. Global patterns of soil nitrogen storage. *Nature* 317: 613-616.
- Rissing, S.W. 1986. Indirect effects of granivory by harvester ants: plant species composition and reproductive increase near ant nests. *Oecologia* 68: 231-234.
- Satti, P., M. Mazzarino, M. Gobbi, F. Funes, L. Roselli & H. Fernández. 2003. Soil N dynamics in relation to leaf-litter quality and soil fertility in northwestern Patagonian forests. *Journal of Ecology* 91: 173-181.
- Tadey, M. 2006. Grazing without grasses: effects of introduced livestock on plant community composition in an arid environment in northern Patagonia. *Applied Vegetation Science* 9: 109-116.
- Tadey, M. & A. G. Farji-Brener. 2007. Indirect effects of exotic grazers: livestock decreases the nutrient content of refuse dumps of leaf-cutting ants through vegetation impoverishment. *Journal of Applied Ecology* 44: 1209-1218.
- Shlesinger, W. H., J. Reynolds, G. Cunningham, L. Huennenke, W. Jarrell, R. Virginia & W. Whitford. 1990. Biological feedbacks in global desertification. *Science* 247: 1043-1048.
- Wagner, D. 1997. The influence of ant nests on *Acacia* seed production, herbivory and soil nutrients. *Journal of Ecology* 85: 83-93.
- Wagner, D., J. Jones & D. Gordon. 2004. Development of harvester ant colonies alters soil chemistry. *Soil Biology and Biochemistry* 36: 797-804.

- Wagner, D. M. Brown & D. Gordon. 1997. Harvester ant nests, soil biota and soil chemistry. *Oecologia* 112: 232-236.
- Whitford, W. G. & R. DiMarco. 1995. Variability in soils and vegetation associated with harvester ant (*Pogonomyrmex rugosus*) nests on a Chihuahuan desert watershed. *Oecologia* 20: 169-173.
- Zuberer, D. A. 1994. Recovery and enumeration of viable bacteria. *In*: Weaver, R.H., Angle, J.S. and Bottomley P.S. (Eds.), *Methods of soil analysis. Part II: Microbiological and biochemical properties*. Soil Science Society of America, Inc. Madison pp.119-144.



