Moisture enhances the positive effect of leaf-cutting ant refuse dumps on soil biota activity

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Abstract Soil biota activity in arid lands is often limited by the availability of water and organic matter. We experimentally explored whether small changes in soil moisture affect the activity of soil biota in external refuse dumps of the leaf-cutting ant *Acromyrmex lobicornis*, one of the most important sources of organic matter in a semi-arid land of north-western Patagonia. We estimated CO_2 consumption in refuse dumps and in adjacent, non-nest soil samples at two moisture levels, after 48 and 72 h. Soil biota activity, estimated by respiration rates, was up to 160 times greater in refuse dumps than in adjacent, non-nest soils. Activity of soil biota in non-nest soil did not change through time and was not affected by moisture. Conversely, soil biota increased their activity in refuse dump samples only at high moisture condition after 72 h. As the activity of microorganisms is key for soil nutrient generation and availability, refuse dumps may be considered as 'islands of fertility' for plants. This effect may be especially important after sporadic spring rainfalls, when the beneficial effect of refuse dumps on soil biota is enhanced. In addition, as refuse dumps generate several times more CO_2 than non-nest soils, nest areas may be considered also as hot spots of CO_2 emissions. These results illustrate the potential importance of ant nests for nutrient cycling, maintenance of plant cover and carbon balance in arid ecosystems.

Key words: *Acromyrmex lobicornis*, ant debris, arid ecosystem, Patagonia, soil fertility.

INTRODUCTION

The activity of soil fauna and microbes (hereafter, soil biota) is key for the maintenance of life. Soil biota decomposes organic matter into available nutrients for plants, which are the base of the food chain in all terrestrial systems (Swift *et al.* 1979). Throughout their role in organic matter turnover, soil biota has major control over the carbon cycle, nutrient availability, and, consequently, on plant growth and community structure (Bardgett 2005). Therefore, knowing which factors affect soil biota activity is crucial to better understand the ecological processes of every habitat.

In arid lands the activity of soil microorganisms is strongly limited by the availability of water and organic matter (Schlesinger *et al.* 1990; Davidson *et al.* 2000). Several experiments showed that CO_2 production declines as water content falls below field capacity (Orchard & Cook 1983; Doran *et al.* 1991). Also, soil biota requires organic matter as food source to grow and reproduce. The relative low abundance of vegetation cover and animal biomass typical of arid lands

restricts the availability of soil organic matter, limiting the activity of soil biota (Mun & Whitford 1989; Satti *et al.* 2003). Accordingly, the low concentration of soil nutrients in desert soils has been partially attributed to the low amount of organic matter, which results in low rates of mineralization (Fisher *et al.* 1990). Thus, the study of how the availability of water and organic matter affects the activity of soil biota has important implications for the maintenance of vegetation in dry regions (Schlesinger *et al.* 1990).

Ant nests affect the abundance of soil organic matter in many arid ecosystems through several processes (Bestelmeyer & Wiens 2003; Ginzburg *et al.* 2008). Ants concentrate the organic matter they forage on around the nests, which may lead to an increase in the abundance and richness of soil biota in the vicinities of ant nests (Wagner *et al.* 1997; Dauber & Wolters 2000; Boulton *et al.* 2003; Boulton & Amberman 2006). As soil biota decomposes the organic matter into mineral nutrients, areas near ant nests are often richer in soil nutrient content than adjacent soils (Wagner *et al.* 1997; Petal 1998). Therefore, plants established in ant-nest areas often show a higher performance than in non-nest soils (Rissing 1986; Whitford & DiMarco 1995; Brown & Human 1997; Wagner 1997). For this reason, ant nests are considered to be

'islands of fertility' playing a critical role as a source of soil heterogeneity in desert ecosystems (Dean *et al.* 1997; Wagner 1997). However, the accumulation of organic waste piles is one of the most drastic ways in which ants affect soil biota, nutrient cycling and plant cover.

The effect of organic debris accumulation by ants on soil nutrients and plant performance partially depends on colony size, ant activity, durability of nests and the amount of debris generated. Ants that build large, long-lived nests and produce high amounts of organic matter will affect soil conditions and plant performance more intensively and constantly than ants with small colonies, short-lived nests and with a low organic matter production. Leaf-cutting ants are one of the most important sources of soil organic matter and nutrients worldwide, including arid lands (Farji-Brener & Tadey 2009). They form colonies with thousands or millions of workers occupying a single, stable nest for 10–20 years (Fowler *et al.* 1986) and collect large amounts of vegetation from an extensive area (Wirth *et al.* 2003; Costa *et al.* 2008). This collected material is used as substrate for growing fungus gardens in nest chambers, and ants feed the brood on structures produced by the fungi. The waste material product of 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 (i.e. 'fertility islands') (Farji-Brener & Illes 2000; Farji-Brener & Tadey 2009). This high availability of nutrients usually increases plant abundance, diversity, and productivity and accelerates nutrient cycling around the nest area (Lugo *et al.* 1973; Haines 1978; Farji-Brener & Silva 1995; Farji-Brener & Illes 2000; Moutinho *et al.* 2003; Farji-Brener & Ghermandi 2004).

Previous studies showed that the accumulation of organic matter by leaf-cutting ants also increases soil biota abundance, enhancing soil mineralization rates (Farji-Brener 2010; Sousa-Souto *et al.* 2012). For example, in tropical areas, nutrient cycling is faster in refuse dumps from leaf-cutting ants than in adjacent soils (Haines 1978; Hudson *et al.* 2009). However, little is known about how moisture affects this positive effect of leaf-cutting ants on soil biota, especially in arid lands where rainfall is scarce. Small and short water pulses could stimulate soil microbial activity in dry ecosystems, particularly in soil micro-sites with high abundance of organic matter like ant refuse dumps (González-Polo & Austin 2009). In this study we experimentally explored whether small changes in soil moisture affected the activity of soil biota in external refuse dumps of the leaf-cutting ant *Acromyrmex lobicornis* compared with non-nest soils in a semi-arid land of north-western Patagonia. As refuse dumps

harbour more soil biota and have higher water retention capacity than adjacent soils (Farji-Brener & Ghermandi 2004; Farji-Brener 2010), we expected small increments in moisture to enhance the soil biota activity mainly in refuse dumps.

METHODS

Study area and ant species

The total sampling area (~400 km^2) includes habitats ranging from the semi-arid steppe at the eastern (driest) border of the Nahuel Huapi National Park (41°S, 72°W) to the south of the Monte desert region, near the town El Chocón, Neuquén province (39°S, 68°W), Argentina. This area represents the driest environment of northern Patagonia, with a mean annual precipitation between 80 and 400 mm concentrated mainly in autumn and winter. The mean annual temperature is between 8 and 15°C, but soil temperatures can reach a minimum of –13°C in winter and a maximum of 65°C in summer (Farji-Brener 2000; Tadey & Farji-Brener 2007; Farji-Brener & Tadey 2012). The dominant vegetation is characterized by xerophytic scrublands, herbs, forbs, and biannual plant species typical of the Patagonian steppe and Monte desert such as *Stipa speciosa*, *Mulinum spinosum*, *Imperata condensata*, *Baccharis pingraea*, *Larrea cuneifolia*, *Larrea divaricata*, *Monttea aphylla*, *Bougainvillea spinosa*, *Chuquiraga erinacea*, *Prosopis alpataco* and *Atriplex lampa* (Correa 1979–1999). Bare soil represents approximately 50% of the soil surface.

Acromyrmex lobicornis (Emery) is the only leaf-cutting ant species inhabiting north-western Patagonia (Farji-Brener & Ruggiero 1994), and its nests are key components of this habitat. The vicinities of *A. lobicornis* nests harbour a greater density of soil biota, higher content of soil nutrients, and greater density and richness of plants than adjacent, non-nest soil areas (Farji-Brener & Ghermandi 2000, 2004; Farji-Brener 2010). The nests of *A. lobicornis* reach depths of 1 m, and on the soil surface the ants construct a mound of twigs, soil and dry plant material, which may reach up to 1 m high and 1 m wide. Inside this mound, the ants grow the fungus on which the ant larvae feed. Discarded organic material from the fungus culture, dead ants and debris are removed from the internal fungus garden to the soil surface, creating a refuse dump. This refuse material is deposited in a few large and flat piles on the soil surface near the mound, which makes it accessible to nearby plants and seeds (Farji-Brener 2000).

We collected samples of refuse dump and adjacent, non-nest soils in 19 mature *A. lobicornis* nests (mounds of ~60 cm of diameter) during the spring and summer of 2011. We performed our sample collection in spring because it is the season of highest soil biota activity. Soil biota activity is strongly limited during winter because of low temperatures, and also during summer because of extremely high temperatures and water scarcity. Nests (one nest = one colony) were at least 10 m apart from each other. This distance ensures the independence of the effect of each nest on soil biota activity. In each nest, we collected 500 g from the external refuse dump and three replicate cores (10 cm wide × 10 cm deep)

of approximately 200 g from adjacent non-nest soil site 2–6 m away. Control (non-nest soil) samples were randomly collected regardless of the presence of vegetation; however, most of them were obtained from bare soil. The samples were pooled as one sample for each site and treatment (i.e. refuse dump and non-nest soil). Therefore, we analysed a total of 19 refuse dumps and 19 non-nest soil composite samples ($n = 19$ sites). All the samples were maintained at 4°C and transported to the laboratory. In the lab, soil and refuse samples were stored for about 6 months in dry conditions. Ten days before starting the experiment, we pre-incubated all samples at 15°C as recommended by Franzluebber et al. (1996). At the same time, we adjusted the water capacity of both soil and refuse dump samples. The measure of moisture in the beginning of the pre-incubation period allowed us to corroborate – and eventually adjust – moisture values throughout the experiment. Each refuse dump and non-nest soil sample from the same site was divided in two subsamples of 200 cm³, which represented ~200 g for soil, and ~50 g for refuse dumps. Each subsample was placed in a container of 10×20 cm, and randomly assigned to one of two moisture levels: high (30 mL) or low (10 mL). These moisture levels are equivalent to 9 and 3 mm of precipitation, respectively, and were selected to represent the amount of rainfall in a moderately wet or dry spring week (see Farji-Brener & Ghermandi 2004 for details). Samples were watered only once, at the beginning of the experiment. Soil biota activity was estimated through their respiration rate (i.e. CO_2 consumption).

To assess CO_2 changes in refuse dump and non-nest soil substrates, the samples were incubated in sealed flasks at 25°C with vials containing NaOH, where CO_2 was trapped. Blanks were also incubated. After 48 and 72 h of incubation the remaining NaOH was titrated with HCl after addition of excess $BaCl_2$. This analysis was performed once. To assess the respiration rate, we applied the equation: *mg of $CO_2 = (B − S) \star N \star E$* (Anderson 1982), where B = mL of acid needed to titrate the NaOH in the blank vials; S = mL of acid needed to titrate the NaOH in the sample vials; N = normality of the acid; E = 22, equivalent weight to express as CO_2. The normality used for soils was NaOH and HCl 0.5 N, and for refuse dumps was NaOH 2 N and HCl 1 N. The CO_2 production rate (mg of CO_2 C kg⁻¹ dry matter h⁻¹) was calculated as the cumulative CO_2 change during the incubation period in all samples for 48 and 72 h (see Lerch et al. 1992; Iannotti et al. 1994; Leconte et al. 2009 for methodological details).

Differences between treatments in the activity of soil biota (i.e. respiration rate) were analysed by a 2×2 factorial, repeated measures ANOVA. Both moisture (M) with two levels (high and low) and substrate (S) with two levels (refuse dump and non-nest soil) were considered as fixed factors. Time (measures performed at 48 and 72 h) was the repeated measure. We included all interactions in the model (i.e. M⋆S, S⋆T, M⋆T and M⋆S⋆T). The response variable was the emission of CO_2 (in g) per 100 g of dry substrate, which is a proxy for microorganism activity. Tukey contrasts were used for all post-hoc comparisons. All response variables were examined to meet ANOVA assumptions and transformed when necessary. All analyses were performed using Statistica software (StatSoft Inc., Tulsa, Oklahoma).

RESULTS

Soil biota activity, estimated by their respiration rates, differed according to substrate, moisture level, time and their interactions. First, microorganisms from refuse dump samples had higher respiration rates than those from non-nest, control soils (0.56 ± 0.03 vs. 0.0035 ± 0.003 g of CO_2 per 100 g, respectively, $F_{1,72} = 283$, $P < 0.0001$, mean $\pm$ SE). Soil biota also showed greater activity at higher than at lower moisture level (0.32 ± 0.003 vs. 0.24 ± 0.003 g of CO_2 per 100 g of substrate, respectively, $F_{1,72} = 5$, $P = 0.027$, mean $\pm$ SE), and after 72 than after 48 h (0.30 ± 0.003 vs. 0.26 ± 0.003 g of CO_2 per 100 g of substrate, respectively, $F_{1,72} = 11.6$, $P = 0.001$, mean $\pm$ SE). The interactions between substrate, moisture and time showed that soil biota strongly increased their activity only in refuse dump samples under high moisture condition after 72 h (Fig. 1). Soil biota in non-nest soil samples did not change their activity through time or between moisture treatments (Fig. 1).

DISCUSSION

Our results demonstrate that the presence of external refuse dumps from leaf-cutting ants greatly increases the activity of soil biota in arid lands of north-western Patagonia, and reveal that small quantities of water enhance this effect. First, respiration rates in refuse dumps were up to 160 times higher than in control soil samples. This increased microorganism activity agrees with previous reports of a higher abundance of soil biota in ant nest soils (Wagner et al. 1997; Dauber
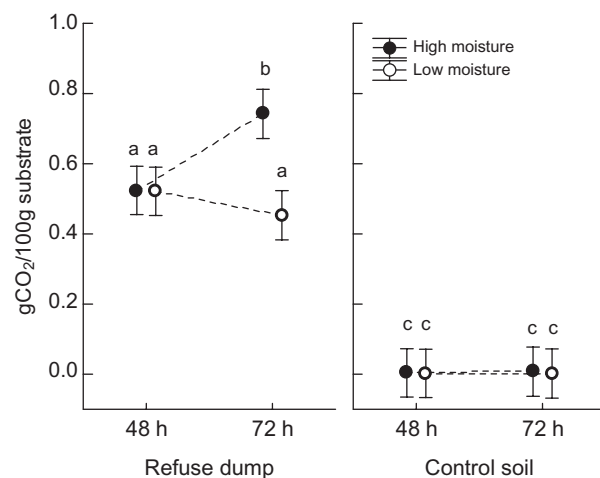

Fig. 1. Soil biota activity (estimated as CO_2 production) in refuse dumps of the leaf-cutting ant *Acromyrmex lobicornis* and in adjacent non-nest soils (control), at two moisture levels (mean $\pm$ SE). Different letters represent significant statistical differences ($P < 0.05$, Tukey post-hoc test).

& Wolters 2000; Boulton *et al.* 2003; Boulton & Amberman 2006), including refuse dumps from leaf-cutting ants (Farji-Brener 2010; Sousa-Souto *et al.* 2012). Second, and as expected, soil biota in refuse dumps increased their activity with modest increments in moisture (Orchard & Cook 1983; Doran *et al.* 1990; Huxman *et al.* 2004). However, the positive effect of moisture on soil biota activity depended on elapsed time and substrate origin. After 48 h, respiration rate of soil microorganisms was similar between moisture treatments. However, after 72 h, soil biota in refuse dumps at high moisture had respiration rates 25% higher than at low moisture. Increased moisture in non-nest soils did not affect biota activity, probably because this substrate naturally harbours a lower abundance of microorganisms and/or has poor water retention capacity. Conversely, refuse dumps are known to harbour higher abundance of soil biota and water retention capacity than non-nest soils (Farji-Brener & Ghermandi 2004; Farji-Brener 2010). Therefore, moisture increases the soil biota activity only in refuse dumps. This suggests that sporadic spring rainfalls, despite their short duration, can greatly improve the positive effect of refuse dumps of leaf-cutting ants on soil biota activity.

Ant refuse dumps are not the only source of organic matter in arid lands. Several studies demonstrated that plant debris also increases soil biota activity, microbial biomass, and decomposition rates in Patagonian desert soils. For example, soil under plant-covered patches had 2–8 times more microbial biomass and 2–3 times more soil respiration than adjacent, inter-canopy areas (Abril *et al.* 2009; González-Polo & Austin 2009; Prieto *et al.* 2011). However, in ant refuse dumps soil respiration rates could be 160 times higher than in control, non-nest soils. Plants may cover larger areas than leaf-cutting ant nests within a region, but ant nests have a stronger effect than plants on activity of soil biota. Therefore, leaf-cutting ants could play a key role as source of organic matter affecting soil biota activity in arid lands.

This enhanced soil biota activity in refuse dumps of leaf-cutting ants may be relevant for at least for two reasons. First, refuse dumps may act as nutritive hot spots (i.e. islands of fertility) helping plant establishment and success. If microorganisms are more active in external refuse dumps than in adjacent non-nest soils, then decomposition of organic matter into nutrients available for plants should be faster and more abundant around ant nest areas. Several studies support this idea, showing that refuse dumps from leaf-cutting ants have up to 80 times more nutrient content (Farji-Brener & Illes 2000; Farji-Brener & Tadey 2009) and up to 98 times faster nutrient flow than adjacent non-nest soils (Haines 1978). Accordingly, plants often germinate, grow and reproduce better in refuse dumps than in adjacent non-nest soils

(Farji-Brener & Ghermandi 2008; Farji-Brener *et al.* 2010; Cerdá *et al.* 2012). Moreover, this positive effect of refuse dumps on plants may be enhanced by the presence of sporadic rainfalls in spring, the growing season of almost all plants in temperate habitats. Second, leaf-cutting nest areas may act as potential hot spots of CO_2 emission by increasing the decomposition of organic matter. The activity of soil biota is responsible for much of small-scale cycling of carbon (Lenoir *et al.* 2001). As several ecosystems have a balanced carbon budget (Raich & Potter 1995; Malhi *et al.* 1999), small changes in efflux may affect the final result of the carbon cycle. Here we demonstrated that refuse dumps from *A. lobicornis* generate 160 times more CO_2 than adjacent non-nest soils, even under low moisture conditions. The impact level of these emissions, however, may depend on the density and covered area of nests. *A. lobicornis* may reach up to 43 nests per hectare in the study area (Farji-Brener 2000). As a single ant nest (including refuse piles) may cover an estimated of 1 m^2, a simple calculation suggests that the 0.43% of the area generates, at least, 160 times more CO_2 than the surroundings. Even though these values appear relatively small, they are still important for understanding a complete picture of the carbon balance in arid lands. Another recent study also demonstrated that nests from the leaf-cutting ant *Acromyrmex balzani* significantly increase CO_2 emissions in Brazil (Sousa-Souto *et al.* 2012). Although the present values (and those reported in Sousa-Souto *et al.* 2012) may account for a relatively small portion of the total soil CO_2 emission, they are still important. This is particularly true considering that leaf-cutting ant nests proliferate across human-modified landscapes, which are ever-increasing worldwide (Wirth *et al.* 2007).

In summary, we found that the presence of refuse dumps from the leaf-cutting ant *A. lobicornis* enhances the activity of soil biota in arid regions of Patagonia, and demonstrated that a small quantity of water enhances this effect. As soil biota activity is key in making soil nutrients available to plants, refuse dumps may be considered as 'islands of fertility' in which plants can germinate and grow better than in surrounding areas. Several insects generate 'islands of fertility' through different processes. For example, termite mounds, through their effect on soil shape, water retention and nutrient accumulation, form small refuges for savanna tree species that seem less adapted to fire, have lower nutrient availability and suffer more from water stress than typical savanna trees (Van der Plas *et al.* 2013). Seed-dispersal ants may create 'islands of fertility' by soil disturbances and seed catching that affect plant distribution and productivity in herbaceous prairies (Hobbs 1985). Here we demonstrated that leaf-cutting ants create 'islands of soil fertility' for plants in this temperate desert through their positive effect on soil biota activity, which enhance soil

nutrients availability, plant abundance and plant reproduction (Farji-Brener & Ghermandi 2004, 2008). In addition, refuse dumps generate several times more CO_2 than non-nest soils. Thus, nest areas may be considered also as hot spot of CO_2 emissions. These results illustrate the potential importance of ant nests to nutrient cycling, the maintenance of plant cover and the carbon balance in arid regions.

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