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Good ant, bad ant? Soil engineering by ants in the Brazilian Caatinga differs by species

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ABSTRACT

It is commonly acknowledged that ants improve the hydraulic properties of soils in which they build their nests. To date, however, most studies of such soil modifications have focused on one ant species and one type of ecosystem, rather than investigating how different ant species affect different types of land cover within the same landscape. Our study focused on modifications to water infiltration and surface texture of Haplic Luvisols by two ant species—one of them present only in a forest and the other present only in a pasture. These two sites are located near each other in the Caatinga, a tropical dry forest region of Brazil, and have similar climatic conditions and soil type. We found that in the forest site, soils undisturbed by ant activity already showed water infiltration 13 times higher than the similarly undisturbed soils of the pasture site; and that the ant *Dinoponera quadriceps* more than doubled water infiltration in their nest annular zones compared with the surrounding forest areas. In addition, *D. quadriceps* increased clay content in their mound soils by 50% compared with the soils of the surrounding forest. In contrast, at the pasture site, the leaf-cutter ant *Atta laevigata* had a mixed effect on water infiltration: compared with pasture matrix soils, their nest-building activities led to a threefold increase in infiltration of the mound soils, but a threefold decrease in the nest annular zones. In addition, compared with the pasture matrix, *A. laevigata* almost doubled sand content in their mounds—which explains the comparatively high infiltration rates. These results suggest that the contrasting soil modifications by the two species could lead to amplifying feedbacks in opposite directions: an ant species that depends on healthy forests is improving water infiltration and soil texture (and thus increasing water available to plants) in its environment, while another ant species that is known to profit from disturbances is having the opposite effect.

1. Introduction

Ants (Hymenoptera, Formicidae) are present in most terrestrial environments (Wilson, 1971) and play important roles in the functioning of ecosystems—as key species in trophic webs, as seed dispersers, and as soil engineers (Lobry de Bruyn and Conacher, 1990; Folgarait, 1998; Leal et al., 2007; Styrsky and Eubanks, 2007). Soil-engineering ants are those that modify or create habitat for other species, including plants, by altering the soil inside and around their nests. Ants and other ecosystem engineers (sensu Jones et al., 1994) have been shown to increase their activity in the latter stages of secondary forest succession (Colloff et al., 2010), which can facilitate community recovery (Bonachela et al., 2015; Brener and Silva, 1995; Moutinho et al., 2003). In semiarid regions, ants and other soil fauna—such as termites and rodents—have been shown to increase the spatial heterogeneity of soil and to promote diversity by creating habitats for disturbance-dependent plants (Reichman and Seabloom, 2002). In a modeling study, Bonachela et al. (2015) showed that the presence of termite mounds can both increase the resilience of drylands in the face of climate change and reduce their threshold of recovery from a desertified state. The authors also point out that their results are “applicable to mounds of diverse species and architectures, provided nutrient and/or water availability is elevated either on the mound proper or in the annular zone around the mound.”

Soil modifications by ants are often disproportionately large relative to their biomass and can last long after the colony is no longer active (Baxter and Hole, 1967; Bucher, 1982; Lobry de Bruyn and Conacher, 1990; Jonkman, 1978). These modifications include: (i) bioturbation, or soil turnover, as the process of ant nest construction and tunnel digging brings sediment from lower soil layers to the surface, mixing the soil and sometimes even creating a distinct new horizon (Baxter and Hole, 1967; Lobry de Bruyn and Conacher, 1994a, 1994b: Cammeraat et al., 2002); (ii) modification of soil structure and creation of macropores, which lowers bulk density and thereby can enhance water

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infiltration (Cammeraat and Risch, 2008; Colloff et al., 2010; Eldridge, 1993; Lobry de Bruyn and Conacher, 1994a); and (iii) alteration of soil organic carbon and nutrient content, which can happen either directly, through waste disposal (Brener and Silva, 1995; Haines, 1975) or indirectly, through activity that increases soil infiltration and aeration and consequently promotes root development and microbial activity (Dean and Yeaton, 1993; Lei, 2000; Whitford, 1988). Ant mounds can also act as runoff sinks, altering the distribution of nutrients and water in the soil and sometimes creating islands of fertility and elevated moisture (Cammeraat et al., 2002; Eldridge, 1993; Lobry de Bruyn and Conacher, 1990). This process is particularly important in semiarid environments, where water availability is limited and heavy rains concentrated over a short period of time can generate high runoff volumes (Ludwig et al., 2005; Wilcox et al., 2003). In such environments, soil modified by ant activity can offer enhanced conditions for plant germination, growth, and survival (Briese, 1982; Carlson and Whitford, 1991; Dean and Yeaton, 1993; Eldridge, 1994; Whitford, 1988).

The Caatinga is a semiarid region in Brazil that is home to some of the largest areas of tropical dry forest in the world. Like most tropical dry forests, it is threatened by desertification as a consequence of anthropogenic disturbances and climate change (Araújo et al., 2008; Ribeiro-Neto et al., 2016; Santos et al., 2014). Anthropogenic disturbances such as intensive grazing and browsing by livestock often result in compaction of the soils, leading to lower infiltration and higher runoff rates, with a consequent decrease in primary productivity (Ludwig et al., 2005; Wilcox et al., 2003). In contrast, soil modifications by ants and other soil engineers might have the opposite effect: by increasing water infiltration on and around their nests, they might locally foster primary productivity, increasing the resilience of these forests (Bonachela et al., 2015). Many of the Caatinga forests are secondary forests, at different stages of succession (Leal et al., 2005), and the region also includes abandoned lands (pastures and agricultural fields) that have the potential for recovery to a forested state (and thereby the reestablishment of ecosystem functionality). While the process of recovery of soil hydraulic properties, such as infiltration, might take several decades (Leite et al., 2017), it could be accelerated by the activity of ants and other soil engineers. A number of studies have investigated how ants modify soil hydraulic properties in semiarid landscapes, but most have focused on one species of ant and one type of land cover (Cammeraat and Risch, 2008; Cammeraat et al., 2002; Carlson and Whitford, 1991; Dean and Yeaton, 1993; Eldridge, 1994; Rissing, 1988), and few have evaluated soil modifications by different species and/or considered the effects of these modifications on native cover versus degraded land (Colloff et al., 2010; Lobry de Bruyn and Conacher, 1994a, 1994b).

For our study, we selected a number of soil physical properties that can directly affect water availability to plants (bulk density, water infiltration, and texture and examined how those soil properties are modified by two ant species, both commonly found in Brazilian Caatinga landscapes but normally under different types of land cover. The first ant species is *Dinoponera quadriceps* Santschi (Ponerinae), which is both a predator of other invertebrates and an important seed disperser (Asher et al., 2013; Leal et al., 2007; Leal et al., 2014b). These ants are extremely sensitive to anthropic disturbances such as grazing and harvesting of firewood (Leal et al., 2014b) and are found mainly in areas covered with native vegetation, which in our study region consists primarily of tropical dry forest. We investigated the effects of *D. quadriceps* on the soils of a mature forest site in which the occurrence of nests was approximately 40/ha. The second species is the leaf-cutter ant *Atta laevigata* Smith (Myrmicinae), most commonly found in open and disturbed areas such as abandoned pastures and roadsides (Leal et al., 2014a; Siqueira et al., 2017; Wirth et al., 2007). We investigated the effects of *A. laevigata* on the soils of a recently abandoned pasture in which we found two nests of this ant species (one active and one abandoned) and no nests of *D. quadriceps.*

We hypothesized that the soils in the mounds and annular zones of both the ant species of our study would show lower soil bulk densities and higher water infiltration than the surrounding soils, which would agree with the results reported by most other studies on the effects of ants on soil physical properties (Cammeraat and Risch, 2008; Lobry de Bruyn and Conacher, 1990; Whitford and Eldridge, 2013). Further, since ant mounds are normally composed of soil particles from the deeper layers of the nest construction site (Whitford and Eldridge, 2013), we also hypothesized that the ant mounds and their annular zones would have a higher clay content, because the soils of our study region—like those of many other semiarid regions—have accumulated clays in the B horizon. Since clay has higher water-holding capacity than sand, the combination of these hypothesized soil modifications could mean higher water availability for plants in proximity to the ant nests.

2. Study sites

Our study was carried out during June, July, and October of 2015, in two sites (2.5 km apart) within the municipality of Serra Talhada, PE Brazil: a pastureland and a Caatinga forest that has not been cleared since at least 1960. The climate is semiarid with monthly temperatures ranging between 23 °C and 27 °C and mean annual rainfall (based on measurements from the period 2000–2014) of 608 mm (Appendix 1). Most of the precipitation occurs between December and May, mainly in the form of short but intense rainfall events. The soils at both sites are Haplic Luvisol (Food and Agriculture Organization, 2014), developed over crystalline rocks during the late Tertiary through a widespread pediplanation (Ab'Sáber, 1977). Preliminary surveys (Pessoa, 2015—unpublished data have found that these soils are weakly structured, rocky, and shallow (approximately 40 cm), with a sandy loam texture in the A horizon (0–15 cm) and a distinctly argillic B horizon (15–30 cm). The native vegetation of the Caatinga has been modified by centuries of slash-and-burn clearing, normally followed by rudimentary agriculture and/or grazing (Coimbra Filho, 1996; Leal et al., 2005). It currently includes shrublands of varying densities and areas of seasonally dry forest (composed mainly of deciduous trees 7–15 m in height and sparsely distributed). The main woody plants are legumes (Fabaceae) within the sub-families Caesalpinioideae, Mimosoideae, and Faboideae, as well as a large number of Euphorbiaceae and Cactaceae (Sampaio et al., 1995).

The pasture site is an area of 5 ha that was cleared of its original forest cover in the 1960s, cultivated with cotton until the 1980s, and intensely grazed until 2014 (see Appendix 2). At the beginning of our study, there were clear signs of degradation, such as the formation of rills and gullies on the lower elevations. Nine months prior to our study, grazing had ceased and the area lay fallow. This is a traditional land use strategy, adopted by most landowners in the region. The fallow period can last from a few years to decades, and allows for natural soil recovery through forest regrowth (Leite et al., 2017). We recorded two leaf-cutter ant (*A. laevigata*) nests in the area, one active and one abandoned. Each nest consists of a network of thousands of spherical chambers interconnected by tunnels. The chambers are used for specific purposes such as taking care of the brood, cultivating their fungus gardens, or dispose of their waste. The loose soil that is generated during nest excavation is piled up at the surface, creating enormous mounds that can contain several tons of bioturbated soils. The area surrounding each mound (annular zone) is constantly cleaned by the ants and is practically bare of vegetation (Moreira et al., 2004). The mounds of the two nests within our pasture site were similar in size—an area of approximately 80 m^2, a height between 0.5 and 1 m, and an annular zone that extended 3–5 m beyond the mound and covered approximately 170 m^2. The active mound had no vegetation cover and had clear signs of crusting (Fig. 1); the abandoned mound had some islands of vegetation in a matrix of bare soil resembling that of the surrounding pasture. There were approximately 20 open entrances, 10–20 cm in diameter, in the active nest, whereas most of the entrances