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Complex foraging ecology of the red harvester ant and its effect on the soil seed bank

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ABSTRACT

Granivory is an important interaction in the arid and semi-arid zones of the world, since seeds form an abundant and nutritious resource in these areas. While species of the genus *Pogonomyrmex* have been studied in detail as seed predators, their impact on seed abundance in the soil has not yet been explored in sufficient depth. We studied the impact of the harvesting activities of the ant *Pogonomyrmex barbatus* on seed abundance in the soil of the Zapotitlán valley, Mexico. We found that *P. barbatus* activity significantly impacts the abundance of seeds in the soil, which is lower in the sites where *P. barbatus* forages than it is in sites with no recorded foraging. We also found that *P. barbatus* distributes intact seeds of three tree species, two of which are nurse plants, and could consequently be promoting the establishment of these species. Using tools derived from graph theory, we observed that the ant-seed interactions exhibit a nested pattern; where more depredated seed species seem to be the more spatially abundant in the environment. This study illustrates the complex foraging ecology of the harvester ant *P. barbatus* and elucidates its effect on the soil seed bank in a semi-arid environment.

1. Introduction

Granivorous ants are dominant in the soil of various arid and semi-arid ecosystems of the world (Hölldobler and Wilson, 1990; Taber, 1998; MacMahon et al., 2000). These eusocial organisms are very effective seed predators since they can direct members of their own colony towards zones where the seeds are abundant, thus removing large quantities of seeds over a short period of time (Mares and Rosenzweig, 1978; Brown et al., 1979; Davidson et al., 1984; Parmenter et al., 1984; Hölldobler and Wilson, 1990; Mull and MacMahon, 1997; García-Chávez et al., 2010).

With more than 60 species, the genus *Pogonomyrmex* is dominant in the arid and semi-arid ecosystems of the American continent (Smith, 1969; Hölldobler and Wilson, 1990; Taber, 1998; MacMahon et al., 2000; Mackay and Mackay, 2002). The patterns of activity and foraging of *Pogonomyrmex* suggests that these ants directly impact seed abundance in the soil (Taber, 1998; MacMahon et al., 2000; Pol and De Casenave, 2004; Pirk and De Casenave, 2006). By foraging from a central point (Oster and Wilson, 1978; Hölldobler and Wilson, 1990), it could be expected that *Pogonomyrmex* would concentrate its foraging activity around the colony, reducing the local abundance of the resources on which it depends, in contrast to sites in which it does not forage, where these resources would be expected to be more abundant.

Some seeds stored by these ants are extracted and placed in the waste-heap, which is located at a specific site of the colony mound. These seeds are discarded in an undamaged state, perhaps because they do not fulfill the requirements of the colony (Rissing, 1986) or because of seasonal fluctuations in the availability of other seeds; in contrast the husks of consumed species are placed here too (MacMahon et al., 2000; Guzmán-Mendoza et al., 2012).

This set of discarded seeds can germinate and establish as seedlings, but are then immediately removed by the ants themselves. On abandonment of a colony, however, these seeds can then establish undisturbed (Smith, 1969; Clark and Comanor, 1975; Porter and Jorgensen, 1988; Wu, 1990). In addition of being predators of seeds, these ants can also therefore accidentally disperse them (MacMahon et al., 2000).

The genus *Pogonomyrmex* has been the subject of much study in North America (Taber, 1998; MacMahon et al., 2000); however, few studies have been conducted in the intertropical arid zones (e.g., Belchior et al., 2012; Guzmán-Mendoza et al., 2012). One of the most important semi-arid ecosystems of Mexico is the region of Tehuacán – Cuicatlán, where *Pogonomyrmex barbatus* (Smith 1858) is one of the dominant ant species in the soil (Ríos-Casanova et al., 2006). Through

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field experiments, it has been shown that seed predation in the Valley of Tehuacán – Cuicatlán is conducted mainly by ants, especially *P. barbatus* (García-Chávez, 1998; García-Chávez et al., 2010), and that this process change between vegetal associations (García-Chávez et al., 2010). However, due to the experimental nature of the studies that evaluated predation of some focal plants, it is not known to what extent the granivorous activity of *P. barbatus* affects naturally dispersed seeds of different species present in the soil of this ecosystem (García-Chávez et al., 2010).

Guzmán-Mendoza et al. (2012) found that *P. barbatus* has a wider trophic niche in the dry season compared to the rainy season, due to differences in resource availability. These same authors also report that *P. barbatus* plays an important role in the maintenance of the trophic network in this ecosystem, since it transports different types of food resources (e.g., fruits, seeds, twigs, leaves, flowers and invertebrates of different groups) to the interior of the colony. Indeed, there is growing evidence that harvester ants not only rely on seeds, it seems that they also include invertebrates in their diets to redress specific colony requirements (Whitford and Jackson, 2007; Belchior et al., 2012). For this reason, furthering the knowledge of the trophic ecology of *P. barbatus* and its impact on plant communities, as well as studying the seed-ant interaction, are priorities since this could provide us with important information concerning the functioning of these communities. Indeed, there is little information currently available in this regard (but see, Crist and MacMahon, 1992) and most of the information that does exist is merely anecdotal.

The aim of this study was to describe the complex foraging ecology of the harvester ant *Pogonomyrmex barbatus* (Hymenoptera: Formicidae) and to evaluate their effect on soil seed bank in the semiarid region of Zapotitlán, Mexico. Specifically, we addressed the following questions: i) What food items are used by *P. barbatus*? ii) What is the foraging area of the nests of *P. barbatus*? iii) What is the impact of *P. barbatus* on plant richness and seed abundance within its foraging area? and iv) What is the structure of the trophic interactions involving *P. barbatus*? For the latter of these questions, we used tools derived from network theory to understand the complex structure of the intra-populational use of the food resource of *P. barbatus*.

2. Materials and methods

2.1. Study area

We conducted this study on the southern slope of the San Juanero hill (18°19′39″ N; 97°27′27″ O), located within the limits of the Helia Bravo Hollis botanical garden, in the municipality of Zapotitlán Salinas, Puebla, Mexico. The garden has an area of 100 ha and is located within the Zapotitlán valley, which is in turn contained within the Tehuacán–Cuicatlán Biosphere reserve. The mean altitude is 1400 m asl. Annual mean precipitation is 376 mm and the mean temperature is 20.7 °C. The rainy season lasts from June to September, with high levels of inter-annual predictability (Valiente, 1991). The vegetation corresponds to crassicaule scrub (Rzedowski, 1978). The plant association corresponds to “tetechera”, with the columnar cactus *Neobuxbaumia tetetzo* and the spiny shrubs *Prosopis laevigata*, *Mimosa luisana*, *Parkinsonia praecox* and *Vachellia constricta* comprising the dominant species (Zavala-Hurtado, 1982).

2.2. *Pogonomyrmex barbatus* Smith (1858)

This is a granivorous ant of the subfamily Myrmicinae (Supplemental material 1, Supplemental material 2). Its geographic distribution ranges from the central United States to the warm subhumid areas of the state of Oaxaca in Mexico (Taber, 1998). The length of individual workers is 8–10 mm. These ants construct a crater-shaped mound, free of vegetation, on the surface of the soil. This can measure up to 50 cm in height and up to 5 m in diameter (P. Luna pers. obs. Supplemental material 3); it is covered with gravel that the workers extract from the interior of the nest, organic material transported from the surroundings or waste from feeding activities. Moreover, the colonies of this species can live up to 15 years, and can house up to 15,000 workers (Wagner and Gordon, 1999). These ants are found in different ecosystems, ranging from arid zones and pastures to forests of pine, pine-oak and oak (Hölldobler, 1976; Hölldobler and Wilson, 1990; Taber, 1998; Mackay and Mackay, 2002).

2.3. Activity area

To estimate the area of activity of the colonies, we followed 15 ants from each, at a distance of 1.5 m in order not to disturb their behavior, from when they left the mound to the site where they collected an object. We recorded the distance from this point to the entrance of the colony and take the azimuth of this straight line. We projected these data on a Cartesian plane, transforming the data from polar (distance and azimuth) to Cartesian (x,y) coordinates in order to form a cloud of points. We then connected the external points to form a convex polygon (White and Garrot, 1990). The interior of this polygon was defined as the area with activity and the area outside the polygon as that without activity. This criterion was used for the following sections.

In order to determine the number of ants that should be followed in order to estimate the area of activity, we first calculated the area of the polygon that forms three points, then that of four points and so on until reaching the polygon with twelve points. The area of the polygon increases with increased number of points of localization, but after a certain number the area size reached the asymptote, which we considered the appropriate sampling size for estimating area of activity, which was six ants. In order to be more certain in terms of the validity of the sample, we decided to follow 15 ants per colony, making sure that they travelled to all four cardinal points.

2.4. Diet of *P. barbatus*

Between the 27th of June and the 27th of August 2015, we studied 12 *P. barbatus* colonies. In order to control the effect of size (number of individuals per colony), we worked with colonies that presented mounds of an average diameter (± SE) of 1.1 (± 0.11) m, since they are the most abundant. We characterized the material transported to the colony, capturing all ants that returned to the mound with an object (see Pirk and De Casenave, 2006; Belchior et al., 2012). Each colony was sampled in four 20-min periods between 9:00 and 18:00 h on different days, from the 1st to the 24th of July. All seeds collected were identified to the smallest taxonomic level possible with the help of a guide of plants for the region (Weller, 2010) and a reference collection created by us during sampling. Invertebrates and their fragments were identified to the smallest taxonomic level possible with the help of taxonomic keys available in the literature relevant to each group. The plants and the invertebrates and their fragments were stored in jars and transported to the Population Ecology laboratory of the Facultad de Ciencias Biológicas of the Benemérita Universidad Autónoma de Puebla.

2.5. Richness and abundance of seeds in the soil

In order to estimate the richness and abundance of seeds in the soil in each colony, we took a soil sample from the area with activity and another from the area without activity. It should be noted that the soil sample from the area with activity was taken at an approximate distance of 12 m from the entrance of the colony, since this is where most ant activity was recorded in all twelve colonies (histogram inserted into Fig. 1). Moreover, and in order to be more certain of the low activity of ants in the relevant sites, one-minute counts were conducted. These counts generally found null or very low activity, represented by one or two ants. The soil samples were taken in quadrants of 25 × 25 cm and