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Does Atta laevigata (Smith, 1858) act as Solanum lycocarpum seed dispersers?

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Abstract

Ants can act as seed dispersers, modifying their distribution, affecting the reproductive success and the vegetation spatial structure. The leaf-cutting ants function, as dispersers of non-myrmecochorous plants, is little known. This work aimed to evaluate descriptively the Atta laevigata interaction with Solanum lycocarpum diaspores. The observations were carried out, throughout 10 days, in a secondary fragment of Semidecidual Seasonal Forest in Ivinhema, MS. To determine the removal rate, 500 seeds were taken from ripe fruits, dried, labeled and distributed in groups ranged from five to 50 seeds, totaling 100 seeds per foraging trail. Groups of 30 seeds with pulp were also distributed every 1.0 m on the trails. Individuals of different sizes presented different interactions to the fruits and seeds, smaller workers carried pulp or seeds separately, medium workers carried seeds with pulp or cleaned them before carry to the nest and the largest workers carried the seeds to the nest. Atta laevigata acted primarily as predators, with few seeds discarded. Their actions may interfere in the native vegetation regeneration, with a significant role in removing S. lycocarpum seeds, a pioneer species, and in population control for this species by the severe predation of seeds. However, the remaining 1.6% of intact seeds allows germination, with A. laevigata acting as a seed disperser over short distances for this species, favoring the S. lycocarpum dispersion.

Introduction

Seeds dispersal consist in a displacement process of these propagules from the parent plant to different locations, fundamental to the cycle of life of plant species (Cordeiro & Howe, 2003), especially in tropical environments (Howe & Miriti, 2004). Regarding the zoochorous dispersal, ants are considered the main invertebrate seed dispersers in terrestrial ecosystems, a process known as myrmecochory (Stiles, 1980; Beattie, 1985). Acting as primary (Courtenay, 1994) and also secondary (Roberts & Heithaus, 1986; Kaspari, 1993) dispersers, ants can markedly change the seeds distribution, affecting not only the reproductive success, but also the spatial structure of plant populations.

Studies reported that ants are capable of carrying a large number of seeds, and the dispersion distance provided by the ant fauna is considered a potential benefit to the plants (Andersen, 1998). However, some authors report that this process is carried out mainly by a small group of species in the ant community (Santos, 2007; Zelikova & Breed, 2008).

Harper et al. (1970) and Dalling & Hubbell (2002) emphasize that the dispersion advantage only becomes effective when the seed is deposited into a suitable microenvironment for the establishment of new plant. Moreover, the dispersion of seeds can provide, for plants species, reduced parasites and predators attack sand intraspecific competition after germination (Janzen, 1970), the colonization of new habitats (Howe & Smallwood, 1982) and the influence on recruitment patterns of plant species in tropical ecosystems (Farji-Brener & Silva, 1996; Böhning-Gaese et al., 1999; Passos & Oliveira, 2002). In this matter, Moutinho et al. (2003) and Passos & Oliveira (2004) emphasize the importance of ants to carry the seeds to places known as more favorable for germination, such as their nests.



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Behavioral and ecological studies on ants foraging contribute to the understanding of seed dispersal by them in the environment (Endringer, 2011). Aspects, such as abundance, deposition place and seed characteristics (weight and presence of pulp or elaiosome), are also important in studies that seek to investigate the consumption activities and removal of seeds by those species (Reader, 1993; Edwards & Crawley, 1999).

Diaspores dispersal by ants is a relevant process also for non-myrmecochorous plants, without pulp or elaiossome (Farnese et al., 2011), but the leaf-cutting ants function as seed dispersal agents of these species, is still little known (Leal & Oliveira, 1998; Smith et al., 2007; Bieber et al. 2011). It is known that leaf-cutting ants play an important role in secondary seed dispersal of *Solanum lycocarpum* (Courtenay, 1994), but these ants act as primary dispersers of the diaspore of this plant at short distances? Based on the hypothesis the existence of this interaction, it was verified that researches showing this dispersion behavior are lacking. Neither is it known if seeds with pulp are more removed than seeds without pulp. Thus, the aim of this work was to describe the interaction role of *Atta laevigata* (Smith, 1858) with the diaspores of *S. lycocarpum*.

Material and methods

Solanum lycocarpum is a shrubby species, with ramified stems, cylindrical, woody, fistulous branches, a little crooked and covered with dense starry hair (Corrêa, 1984). It presents a continuous bloom pattern, according to the Newstrom et al. (1994) classification, producing few flowers per individual during the year, but at flowering peak, there is a production increase of these structures (Oliveira Filho & Oliveira, 1988). The fruit is a berry, greenish even when mature and produce numerous dark gray, reniform, flat seeds (Almeida et al., 1998). The fruit production is early, the amount produced varies depending on the plant age and each fruit produces an average 1.200 seeds. The most of the seeds has an average of 6.00 to 7.00mm in length and 5.58 to 5.08 in width 5.08mm and 1.50 to 2.10mm thick (Castelani et al., 2008).

This work was carried out at the edge of a secondary fragment of Semidecidual Seasonal Forest, with typical formation of biome transition vegetation, Cerrado-Atlantic Forest, located a rural area in Ivinhema, State of Mato Grosso do Sul, Brazil (22°16'43''S, 53°48'47"W). The fragment consisted of vegetation resulting from regeneration processes, once the primary vegetation was removed for eucalyptus planting, which was afterwards removed for marketing, approximately 15 years before this work, thus, most trees from this vegetation, had height around 5 meters. In the study period, the area was being cleared again to be subdivided into small farms.

At early May 2013, fifteen days before sampling, this fragment underwent a burning process by anthropic action, thus creeping plants and small bushes that lined the fragment edges were destroyed.

For ant nest location, some of the individuals of A.

laevigata foraging in *S. lycocarpum* bushes were followed while they move in the trails. The straightdistance between bushes and nests 1, 2, 3, 4 and 5 was 0.96 (under a bush); 5.94; 6.10; 10.47 and 19.47 meters, respectively.

To test the hypothesis that the ants act as primary dispersers at short distances of *S. lycocarpum* diaspores, direct observations of interaction behavioral of ants in naturally fallen fruits were carried out for 10 days, totaling 30 hours, divided into 15 hours of nighttime observations between 17h00 and 20h00, and 15 daytime observations between 5h00 and 8h00. During the nighttime observations, a white light flashlight was used to assist the ant behavioral assessments. Given the large number of workers interacting with the fruits, not all could be followed in its movement to the nests.

To determine the removal rate of seeds to the nests, 500 seeds were taken from five ripe fruits, washed in a sieve with running water to remove the pulp, and put to dry on filter paper. After drying, they were stained with white water-based ink and distributed at sundown. It was used 100 seeds per foraging trail, as a way of intensifying the sampling of interactions, in groups ranging from five to 50 seeds, every 1.0 meter, along their entire length depending on the length of each trail. To verify preference in the removal of seeds, another extracted seeds, were left with the pulp, and distributed in groups of about 30 seeds every 1.0 m along the foraging trail of each colony. Due to the bush-nest short distance in nest1 (0.96 m), which was under a *S. lycocarpum* individual, the 100 seeds were placed in two steps of 50 seeds each, with an hour interval.

The seed groups (with and without pulp) were observed simultaneously for three hours along the foraging trails, registering the interaction behavior with the seeds, the final destination of transported seeds and seeds lost in transport were collected again. Worker ants that were along the foraging trail to wards each of the five nests were collected, killed in a chamber containing ethyl acetate and classified into three distinct size classes, proposed in this study, regarding the individuals length, as follows: small, between 3 and 4.9 mm; medium between 5 and 8.9 mm and large between 9 and 12.9 mm. Some specimens were prepared with an entomological pin, identified by an expert and deposited at the Biodiversity Museum (MUBIO) of the Biological and Environmental Sciences College (FCBA), Grande Dourados Federal University (UFGD).

Results and Discussion

When the large worker ants found a fallen ripe fruit under the parent plant, they climbed and moved on the fruit, intensely moving their antennas, and other workers quickly approached and climbed the fruit as well. Once on the fruit, some individuals attached their mandibles in the pericarp and spun, making circular moves until remove portions of this layer. This behavior resulted in small openings used by other workers, which continued piercing the pericarp until transpose it fully.

As the larger ants pierced the exocarp, smaller workers entered the fruit through the opened passage and collected both the mesocarp and the seeds. Some of these workers removed the pulp from the seeds leaving them completely clean, while others transported it with parts of this material. Small workers, in most cases, carried only small pieces of pulp, taken directly from the fruit. This behavior occurred with workers from all studied colonies. Pulp removal can positively influence the seeds germination rate by decreasing fungal attack, as reported by Oliveira et al. (1995) and Leal & Oliveira (1998).

Pinto (1998) reported that soldier ants of *A. laevigata* cut the pericarp of *S. lycocarpum* fruits, and that different sizes of workers withdrew pulp while only the largest workers and soldiers carried the seeds to the nest. However, in this work, the presence of *A. laevigata* soldiers interacting with fruits and seeds was not observed, only workers from the different sizes proposed.

Regarding their behavior towards the seeds arranged along the trails, those closest to the nest entrance were perceived in a few seconds by workers, which became very agitated when examining them and carried immediately into the nest. However, sometimes small and medium workers gathered and carried a whole mass of seeds to the nest. These results are according to statements of Costa et al. (2007) and Zelikova & Breed (2008) that larger size ants have ease to carry seeds individually, while the smaller need help from others.

However, it was observed that the largest workers had some difficulty to collect the seeds due to the larger size of their mandibles compared to the seeds. Therefore, they grabbed in the middle region of the seeds with their mandibles, curved the body and pressing the seed against the sternum thorax to, apparently, put it in a better position, and only than carry it to the nest.

According to Gorb & Gorb (1999), the ants shape and size determine the way they carry the seeds, reaffirming observations described in this work. Smaller workers (4.17±1,01mm) carried pulp or seeds separately, while the medium workers (6.79±1,12mm) carried seeds with pulp or cleaned them before carry to the nest. Medium workers were observed discarding intact seeds, without pulp, out of the nest. This behavior was observed in all colonies, suggesting that pulpe would be the reward for ant in this interaction. The largest workers (10.02±1.09 mm) constantly carried the seeds to the nest, but no discarding was observed. These observations allows to state that different sizes of A. laevigata individuals have different behaviors when interacting with the fruits and seeds of S. lycocarpum, and that the size of the collecting workers influence the behavior and the resource type collected directly from the fruit. In Atta sexdens L., 1758, Wilson (1980a, 1980b) also found the existence of division of labor, depending on body size and age, among workers.

One of the five nests studied, was under a *S. lycocarpum* individual and the workers of this colony concentrated their activities close to the bush, while other colonies foragedat greater distances from the nest entrance. In general, they collected

fruits parts, including dried fruit and leaves of *S. lycocarpum* in the litter fall, but they also collected leaves directly from small bushes of other plant species that were around the nests. The foraging activity of workers decreases as the sunlight increases at the dawn, when few workers were seen collecting resources. Hölldobler and Wilson (1990) report that leaf cutting ants prefer foraging during the night period when the temperature is cooler, which may explain this pattern of foraging.

Even with distance between bushes and nests varying between 0.96 and 19.47 meters, the ants were able to collect and carry the seeds through this interval, indicating the possibility of influencing the subpopulations maintenance of plant species, as reported by Schupp et al. (2010) regarding the role of dispersers at short distances. Dalling & Wirth (1998) found that individuals from the genus *Atta* are capable of carry seeds for over a hundred meters, but according to Andersen (1988), in environments of high density of ants acting as seed dispersers, they may rather move shorter distances for removing the seeds. Therefore, it was found that *A. laevigata* acts primarily in the removing and transport of *S. lycocarpum* seeds at short distances.

Although it is an experimental situation, all distributed seeds (100%) throughout the foraging trail were collected and carried to the nests. This high removal rate may be related to the lack of alternative resources, since the vegetation in the studied area had under gone significant damage by fire. Wenny (2001) suggests that plants have a better chance to succeed in recruiting new dispersers when a greater amount of seeds is directed to appropriate places. Some studies also report the relevance of propagules transport to the nests interior, which can provide safe places for seedlings development, since it is rich in nutrients (Heithaus, 1981; Culver & Beattie, 1983; Andersen, 1998).

Courtenay (1994) observed throughout a week, about 40% of seeds of S. lycocarpum discarded in the ants refuse, however, in the present study, it was found 1.6% of the marked seeds in the refuse material around the nest, excluding the seeds with pulp, which could not be identified in the refuse material. This fact, plus the observation that, some ants dropped the seeds along the trail, but then collected it again, indicates that the A. laevigata species behaved mainly as a predator of S. lycocarpum seeds. Also, despite the ants have carried the seeds away from the parent plant, what, according to Janzen (1970), would influence the dispersion process because they move away from the greatest competition areas during and after germination, they kept them inside their nests. Therefore, they might be using them as a substrate for fungi cultivation from which the ants feed, what would prevent them to germinate and originate a new individual of S. lycocarpum.

Another factor to consider is the lack of elaiosome in the *S. lycocarpum* seeds, an attractive structure for many ant species due its high content of lipids, proteins and sugars (Handel & Beattie, 1990). Seeds with this resource are collected and carried to the nests, where they are discarded after the removal of this structure (Passos & Oliveira, 2004).

On the other hand, the elaiosome is an attractive structure for ants from the genus Atta (Pizo & Oliveira, 2001), reinforcing the proposition of the interest of this ant species to the studied seed. This interest could be related to the chemical composition seed (e.g., high lipids composition) (Marshall et al., 1979; Skidmore e Heithaus, 1988; Brew et al., 1989). In addition, it was observed no other organism contributing to the removal and dispersal of seeds of S. lycocarpum during assessments. That may be a consequence of the fire in the studied area reducing the populations that would contribute to this function, or because they are missing in the area. Zelikova & Breed (2008) stated that, when mainly a small number of species in an environment perform the removal of seeds, the removal rate might decrease, by the loss of these species or their density reduction. According to Cordeiro et al. (2009), the loss of seed disperser organisms can endanger the plant species that depend on these for the dispersion process, or for the seeds germination, hence the establishment of new individuals and populations of this species. Thus the A. laevigata foraging becomes important for S. lycocarpum seed dispersal, even in small proportions and the short distances.

Ants from the genus *Atta*, on the other hand, build their nests deep and with an architecture that stabilizes the temperature and humidity fluctuations (Roces & Kleineidam, 2000; Farji-Brener, 2000), therefore, resistant to fire, enabling them to multiply and establish quickly in disturbed habitats (Rao, 2000; Santos et al., 2008). That could explain the permanency of these colonies in the area even after the fire, what increased the significance of the ants role as dispersers of *S. lycocarpum* seeds.

Although in this work had been demonstrated the A. laevigata as predators with few seeds discarded (1.6%), it is believed that the ant species activities in this studied area suggest an positive effect on the regeneration of the native vegetation.

Atta laevigata act in population control of S. lycocarpum, a pioneer plant species, by predation on their seeds, in addition to have a role in primary removing of S. lycocarpum seeds, favoring the dispersion at short distances. Thus, the ant A. laevigata would be acting as disperser of this plant species in natural regeneration areas.

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References

Almeida, S. P.; Proença, C. E. B.; Sano, S. M. & Ribeiro, J. F. (1998). Cerrado: Espécies vegetais úteis. 1 ed. Planaltina: EMBRAPA – CPAC. 464p.

Andersen, A. N. (1998). Dispersal distance as a benefit of myrmecochory. Oecologia, 75: 507-511.

Beattie, A. J. (1985). The Evolutionary Ecology of Ant-Plant Mutualisms. Cambridge University Press, Cambridge.

Bieber, A. G. D., M. A. Oliveira, M. A., Wirth, R.; Tabarelli, M. & Leal. I. R. (2011). Do abandoned nests of leaf-cutting ants enhance plant recruitment in the Atlantic Forest? Austral Ecology, 36: 220-232.

Brew, C.R, O'Dowd, D. J. & Rae, I.A. (1989). Seed dispersal by ants: behaviour-releasing compounds in elaiosomes. Oecologia, 80: 490-497.

Böhning-Gaese, K.; Gaese, B. H. & Rabemanantsoa, S. B. (1999). Importance of primary and secondary seed dispersal in the Malagasy tree *Commiphora guillaumini*. Ecology, 80: 821-832.

Castellani; E. D.; Damião Filho, C. F.; Aguiar, Paula; I. B. R. C. (2008). Morfologia de frutos e sementes de espécies arbóreas do gênero *Solanum* L. Revista Brasileira de Sementes, 30: 102-113.

Cordeiro, N. J. & H. F. Howe. (2003). Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. Proceedings of the National Academy of Sciences, 100: 14052-14056.

Cordeiro, N. J.; Ndangalasi, H. J.; Mcentee, J. P. & Howe, H. F. (2009). Disperser limitation and recruitment of an endemic African tree in a fragmented landscape. Ecology, 90: 1030-1041.

Costa, U. A. S.; Oliveira, M.; Tabarelli, M. & Leal, I. R. (2007). Dispersão de sementes por formigas em remanescentes de Floresta Atlântica nordestina. Revista Brasileira de Biociências, 5: 231-233.

Courtenay, O. (1994). Conservation of maned Wolf: fruitful relations in a changing environment. Canid News, 2: 41-43.

Culver, D. C. & Beattie, A. J. (1983). Effects of ant mounds on soil chemistry and vegetation patterns in a Colorado Montane Meadow. Ecology, 64: 485-492.

Dalling, J. W. & Hubbell, S. P. (2002). Seed size growth rate and gap microsite conditions as determinants of recruitment successes for pioneer species. Journal of Ecology, 90: 557-568.

Dalling, J. W. & Wirth, R. (1998). Dispersal of *Miconia argentea* seeds by the leaf-cutting ant *Atta colombica*. Journal of Tropical Ecology, 14: 705-710.

Edwards, G. R. & Crawley, M. J. (1999). Rodent seed predation and seedling recruitment in mesic grassland. Oecologia, 118: 288-296.

Endringer, F. B. (2011). Comportamento de forrageamento da formiga *Atta robusta* Borgmeier 1939 (Hymenoptera: Formicidae) – Dissertação de Mestrado (Produção Vegetal), Universidade Estadual do Norte Fluminense Darcy Ribeiro, Rio de Janeiro. 66f.

Farji-Brener, A. G. (2000). Leaf-cutting ant nest in temperate environments: mounds, mound damage and nest mortality rate in *Acromyrmex lombicornis*. Studies on Neotropical Fauna and Environment, 35: 131-138.

- Farji-Brener, A. G. & Silva, J. F. (1996). Leaf-cutter ants (*Atta laevigata*) aid to the establishment success of *Tapirira velutinifolia* (Anacardiaceae) seedlings in a parkland savanna. Journal of Tropical Ecology, 12: 163-168.
- Farnese, F. S., Campos, R. B. F. & Fonseca, G. A. (2011). Dispersão de diásporos não mirmecocóricos por formigas: influência do tipo e abundância do diásporo. Revista Árvore, 35: 125-130.
- Gorb, S. N. & Gorb, E. V. (1999). Dropping rates of elaiosome-bearing seeds during transport by ants (*Formica polyctena* Foerst): Implications for distance dispersal. Acta Oecologica, 20: 509-518.
- Handel, S. N. & Beattie, A. J. (1990). Seed dispersal by ants. Scientific American, 263: 76-83.
- Harper, J. L. Lovell, P. H. & Moore, K. G. (1970). The shapes and sizes of seeds. Annual Review of Ecology and Systematics, 1: 327-356.
- Heithaus, E. R. (1981). Seed predation by rodents on three ant-dispersed plants. Ecology, 62: 136-145.
- Hölldobler, B. & Wilson, E. O. (1990). The ants. Cambridge: Harvard University Press, 732p
- Howe, H. F. & Miriti, M. N. (2004). When seed dispersal matters. Bio Science, 54:651-660.
- Howe, H. F. & Smallwood, J. (1982). Ecology of seed dispersal. Annual Review of Ecology and Systematics, 13: 201-228.
- Janzen, D. H. (1970). Herbivores and the number of tree species in tropical forests. American Naturalist, 104: 501-529.
- Kaspari, M. (1993). Removal of seeds from neotropical frugivore droppings: ants responses to seed number. Oecologia, 95: 81-88.
- Leal, I. R. & Oliveira, P. S. (1998). Interactions between fungus-growing ants (Attini), fruits and seeds in Cerrado vegetation in southeast Brazil. Biotropica, 30: 170-178.
- Marshall, D. L.; Beattie, A. J. & Bollenbacher, W. E (1979). Evidence for diglycerides as attractants in an ant-seed interaction. Journal of Chemical Ecology, 5: 335-344.
- Moutinho, P. D.; Nepstad, D. C. & Davisson. E. A (2003). Influence of leaf-cutting ant nest on secondary forest growth and soil properties in amazona. Ecology, 84: 1265-1276.
- Oliveira Filho A.T & Oliveira, L.C. (1988). A Biologia floral de uma população de Solanum lycocarpum St. Hill. (Solanaceae) em Lavras MG. Revista Brasileira de Botânica, 11: 23-32.
- Oliveira, P. S.; Galetti, M.; Pedroni, F. & Morellato, L. P. C. (1995). Seed cleaning by *Mycocepurus goeldii* ants (Attini) facilitates germination in *Hymenaea courbaril* (Caesalpiniaceae). Biotropica, 27: 518-522.

- Passos, L. & Oliveira, P. S. (2002). Ants affect the distribution and performance of *Clusia criuva* seedlings, a primarily bird-dispersed rainforest tree. Journal of Ecology, 90: 517-528.
- Passos, L. & Oliveira, P.S. (2004). Interactions between ants and fruits of *Guapira opposita* (Nyctaginaceae) in a Brazilian sand plain rain forest: ant effects on seeds and seedling. Oecologia, 139: 376-382.
- Pinto, F. S. (1998). Efeitos da dispersão de sementes por animais e dos fatores edáficos sobre a germinação, crescimento e sobrevivência das plântulas de lobeira *Solanum lycocarpum*. 68f. Dissertação (Mestrado em Ecologia). Universidade de Brasília, Brasília.
- Pizo, M. A. & Oliveira, P. S. (2001). Size and lipid contend of non myrmecochorus diaspores: effects on the interaction with litter-foraging ants in Atlantic Rain Forest of Brazil. Plant Ecology, 157: 37-52.
- Rao, M. (2000). Variation in leaf-cutter ant (*Atta* sp.) densities in forest isolates: the potential role of predation. Journal of Tropical Ecology, 16: 209-225.
- Reader, R. J. (1993). Contral of seedling emergence by ground cover and seedling in relation to seed size for some old-field species. Journal of Ecology, 81: 169-175.
- Roberts, J. T. & E. R. Heithaus. (1986). Ants rearrange the vertebrate-generated seed shadow of a neotropical fig tree. Ecology, 67: 1046-1051.
- Roces, F. & Kleineidam, C. (2000). Humidity preference for fungus culturing by workers of the leaf-cutting ant *Atta* sexdens rubropilosa. Insects Sociaux, 47: 348-350.
- Santos, B. A., Peres, C. A.; Oliveira, M. A.; Grillo, A.; Alves-Costa, C. P. & Tabarelli, M. (2008). Drastic erosion in functional attributes of tree assemblages in Atlantic Forest fragments of northeastern Brazil. Biological Conservation, 141: 249-260.
- Skidmore, B. A. & Heithaus, E. R. (1988). Lipid cues for seed-carrying by ants in *Hepatica americana*. Journal of Chemical Ecology, 14: 2185-2196.
- Santos, M. M. E. (2007). Secondary seed dispersal of *Ricinus communis* Linnaeus (Euphorbiaceae) by ants in secondary growth vegetation in Minas Gerais. Revista Árvore, 31: 1013-1018.
- Schupp, E. W., Jordano, P., & Gómez, J. M. (2010). Seed dispersal effectiveness revisited: a conceptual review. New Phytology, 188: 333-353.
- Stiles, E. W. (1980). Patterns of fruit presentation and seed dispersal in bird-disseminated woody plants in the earsten deciduous forest. American Naturalist, 116: 670-688.
- Wenny, D. G. (2001). Advantages of seed dispersal: A reevaluation of directed dispersal. Evolutionary and Ecological Research, 3: 51-74.

Wilson, E. O. (1980a). Caste and division of labor in leafcutter ants (Hymenoptera-Formicidae: *Atta*). I. The overall pattern in *Atta sexdens*. Behavioral Ecology and Sociobiology, 7:143-156.

Wilson, E. O. (1980b). Caste and division of labour in leafcutter ants (Hymenoptera: Formicidae: *Atta*). II. The ergonomic optimization of leaf cutting. Behavioral Ecology and Sociobiology, 7: 157-165. Zelikova, T. J. & Breed, M. D. (2008). Effects of habitat disturbance on ant community composition and seed dispersal by ants in a tropical dry forest in Costa Rica. Journal of Tropical Ecology, 24: 309-316.

