MARCELO SILVA MADUREIRA

O PAPEL DE *Atta robusta* BORGMEIER, 1939 (HYMENOPTERA: FORMICIDAE) NA CICLAGEM DE NUTRIENTES E ESTRUTURA DA COMUNIDADE DE PLANTAS EM RESTINGA

Tese apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-graduação em Entomologia, para obtenção do título de *Doctor Scientiae*

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APROVADA: 30 de julho de 2012

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(Coorientadora)

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(Orientador)

“Há um menino, há um moleque, morando sempre no meu coração. Toda vez que
o adulto balança ele vem para me dar a mão...”
M. Nascimento e F. Brant

“Meu caminho é ida sem volta... Vou ver Cristina...”
C. Imperial e T. Maia

A conclusão deste trabalho é dedicada ao meu filho Pedro e à minha amada Cris.

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BIOGRAFIA

Marcelo Silva Madureira é biólogo e mestre em Entomologia pela Universidade Federal de Viçosa desde 2004. Em 2005 iniciou suas atividades como docente da Universidade do Estado da Bahia. Em 2008, iniciou seu doutorado em Entomologia pela UFV submetendo-se para defesa em julho de 2012.

RESUMO

MADUREIRA, Marcelo Silva, D.Sc., Universidade Federal de Viçosa, julho de 2012. **O papel de *Atta robusta* Borgmeier, 1939 (Hymenoptera: Formicidae) na ciclagem de nutrientes e estrutura da comunidade de plantas em Restinga.** Orientador: José Henrique Schoereder. Coorientadora: Tathiana Guerra Sobrinho.

Formigas cortadeiras aumentam a fertilidade do solo e o estado nutricional das plantas sobre seus ninhos. Estas formigas também podem alterar a comunidade de plantas devido à herbivoria e dispersão de sementes. *Atta robusta* é uma espécie de formiga cortadeira endêmica de restingas brasileiras onde atua como dispersora de sementes. Neste estudo foi investigado se *A. robusta* altera as propriedades químicas de espodossolos de restinga e o estado nutricional de plantas. Além disso, foram testadas as seguintes hipóteses: (i) *A. robusta* diminui a abundância e riqueza de espécies de plantas ao redor dos seus ninhos, (ii) a abundância e riqueza de espécies de plantas dispersadas por *A. robusta* são maiores nas proximidades dos seus ninhos e (iii) existe uma flora associada aos ninhos de *A. robusta*. As concentrações de P, K, Ca, Mg, matéria orgânica, valores de pH, saturação por alumínio e capacidade de troca catiônica foram obtidos a partir de sete sauveiros. As concentrações foliares de P, K, Ca e Mg foram obtidas de dez indivíduos de *Protium heptaphyllum* localizados sobre os ninhos. Para verificar o efeito dos sauveiros sobre a comunidade vegetal, a abundância e riqueza de espécies de plantas jovens foram determinadas em parcelas de 10x10 m localizadas sobre os ninhos e a 10, 20, 30, 40 e 50 m de distância. Solos influenciados por sauveiros apresentaram maiores teores de potássio e menor saturação por alumínio. As demais variáveis não foram significativamente afetadas. *A. robusta* não altera a comunidade de plantas. Dinâmica de potássio, teor de argila, nível do lençol freático e decomposição da matéria orgânica são discutidos como possíveis mecanismos causais dos efeitos dos sauveiros no solo e ausência de efeito na nutrição foliar de plantas. Forrageamento em plantas adultas distantes dos ninhos e predação de plântulas germinadas das sementes transportadas para o ninho pelas operárias são apontadas como principais explicações para ausência de efeitos dos sauveiros sobre a comunidade vegetal.

ABSTRACT

MADUREIRA, Marcelo Silva, D.Sc., Universidade Federal de Viçosa, July, 2012. **The role of *Atta robusta* Borgmeier, 1939 (Hymenoptera: Formicidae) in nutrient cycling and plant community structure at Restinga.** Adviser: José Henrique Schoereder. Co-adviser: Tathiana Guerra Sobrinho.

Leaf-cutting ants increase soil fertility and plant nutrient status on their nests. These ants can also alter the plant community due herbivory and seed dispersal. *Atta robusta* is an endemic leaf-cutting ant species from Brazilian Restinga where it is a seed disperser. In this study we verified if *A. robusta* alters chemical properties of Restinga spodosols and plant nutrient status. In addition, we tested the following hypotheses: (i) *A. robusta* decreases abundance and plant species richness around their nests, (ii) Abundance and species richness of plant dispersed by *A. robusta* are higher near to their nests and (iii) There is a typical flora associated to *A. robusta* nests. Organic matter, P, K, Ca, Mg concentrations and pH values, aluminum saturation and cation exchangeable capacity were obtained from seven *A. robusta* nests. We obtained P, K, Ca e Mg foliar content from ten *Protium heptaphyllum* plants located on nests. To verify the *A. robusta* nest effect on plant community, sapling abundance and species richness were sampled from 10x10 m plots delimited on nests and 10, 20, 30, 40 and 50 m from the nests. Soils under nest effects have more potassium content and lower aluminum saturation. The nests did not affect other variables significantly. *A. robusta* does not alter plant community. Potassium dynamic, clay content, groundwater level and decomposition of organic matter are suggested as causal mechanisms to nest effects on soil and null effects on plant nutrient status. Foraging on adult plants away from nests and seedling predation from seeds transported by workers to the nests are discussed as main explanations to nest null effects on plant community.

ÍNDICE

INTRODUÇÃO GERAL

Formigas cortadeiras do gênero *Atta* ocorrem desde o sul dos Estados Unidos até a região central da Argentina (Delabie *et* al. 2012), sendo consideradas como importantes modificadores do solo e de comunidades de plantas em ecossistemas tropicais. Estes insetos constroem seus ninhos no solo, ou sauveiros, e estes podem alcançar até 7m de profundidade e apresentar área de até 250m^2. Em geral, os sauveiros são formados por túneis que conectam câmaras subterrâneas onde a colônia cultiva o fungo simbionte que é usado principalmente como alimento para larvas, alojamento da rainha e de alados (Mariconi, 1970). Existem também câmaras que são usadas como local de descarte do lixo, que pode ser constituído por formigas mortas, folhas em decomposição e partes mais velhas do fungo (Forti *et al.* 2011). Por causa da constante decomposição de matéria orgânica, sauveiros são considerados como um importante local de ciclagem de nutrientes aumentando a concentração de vários elementos químicos no solo que podem ser disponibilizados para a vegetação (Moutinho *et al.* 2003; Sternberg *et al.* 2007; Sousa-Souto *et al.* 2007; Sousa-Souto *et al.* 2008).

Para alimentar o fungo simbionte, operárias utilizam flores, frutos e principalmente folhas frescas, apresentando um alto grau de polifagia. Em florestas tropicais, formigas cortadeiras podem consumir cerca de 2,5% da produção foliar (Wirth *et al.* 2003) e forragear em até 50% das espécies de plantas (Vasconcelos & Fowler 1990; Wirth *et al.* 2003). Por causa dessa intensa herbivoria, estas formigas são consideradas como modificadoras da estrutura da comunidade vegetal, reduzindo o número de espécies e a abundância de plantas nas proximidades de seus ninhos (Garretson *et al.* 1998; Vasconcelos & Cherrett 1997; Rao *et al.* 2001). Por outro lado, formigas cortadeiras podem atuar como dispersoras de sementes, afetando positivamente populações de plantas. Por exemplo, em ecossistemas de cerrado brasileiro, *Atta sexdens* e *A. laevigata* foram responsáveis pela dispersão de 66% das sementes produzidas por *Miconia rubiginosa*. Os ninhos dessas duas espécies foram considerados como locais de recrutamento para a *M. rubiginosa* por possuírem maior abundância de plântulas em relação à planta-mãe (Christianini & Oliveira 2009). Outros estudos descrevem como formigas cortadeiras aumentam a taxa de germinação e diminuem a predação de sementes (Peternelli *et al.* 2003; Teixeira 2007).

Atta robusta Borgmeier, 1939 é a única espécie do gênero *Atta* presente em restingas do Espírito Santo e Rio de Janeiro (Teixeira *et al.* 2003) e atualmente está incluída na lista oficial das espécies brasileiras ameaçadas de extinção (MMA, 2003). Ao contrário do que é descrito para outras espécies de formigas cortadeiras, o efeito dos sauveiros de *A. robusta* sobre as características químicas do solo bem como seu impacto sobre a vegetação ainda não é conhecido. Ninhos de *A. robusta* podem ser importantes locais de nutrientes para plantas de restinga uma vez que os solos destes ambientes são arenosos e de baixa fertilidade. Essas formigas também podem modificar a comunidade de plantas devido à herbivoria (Fowler 1995) e por transportar sementes de 36 espécies em direção aos seus ninhos (Teixeira 2008).

Dessa forma, o objetivo geral deste estudo foi investigar o efeito dos ninhos de *A. robusta* sobre as propriedades químicas dos solos e a estrutura de comunidade de plantas em torno de seus ninhos. Os resultados são apresentados em dois artigos que se encontram submetidos para os periódicos Soil Biology and Biochemistry e Acta Botanica Brasilica.

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The influence of *Atta robusta* (Formicidae) on chemical properties of Restinga spodosols

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ABSTRACT: Leaf-cutting ant nests are known to promote nutrient mineralization facilitating its access by plants. These nests may be an important nutrient source in oligotrophic environments if nutrient input prevails over natural loss. We hypothesized that *Atta robusta* nests modify chemical properties and increase foliar nutrient status of *Protium heptaphyllum* in oligotrophic Restinga soils. In this sense, we verified if the nests (i) increase mineral nutrients (P, K, Ca, and Mg) organic matter, cationic exchangeable capacity (CEC) and pH, (ii) diminish aluminum saturation and (iii) promote a higher nutrient foliar concentration in *P. heptaphyllum*. We sampled seven active *A. robusta* nests and seven control sites at three depths to collect soil variables. We compared the nutrient foliar status of *P. heptaphyllum* trees located on nests and control sites. From the four nutrients analyzed, only K content was higher in nests but the other parameters were not modified. The exception is aluminum saturation which was lower in sampled nests. In spite of this, a higher nutrient concentration in leaves from *P. heptaphyllum* did not occur on nests. Low clay content and proximity of groundwater are suggested as main explanations to null effects of nests. Furthermore, complexation of aluminum with organic acids from decomposition may explain its reduced saturation in nests.

Key words: Ant nests; clay content; plant nutrient status; groundwater; aluminum saturation; potassium.

1. INTRODUCTION:

In tropical ecosystems, leaf-cutting ant nests (genera *Atta* and *Acromyrmex*) form conspicuous structures, which can reach a surface area between 50 and 160m^2 (Farji-Brener and Silva, 1995). These nests promote environmental heterogeneity since excavation improves soil penetrability (Moutinho et al., 2003) and increase the surface of bare ground on nest area (Weber, 1972). In addition, leaf-cutting ant nests alter soil chemistry increasing cation exchangeable capacity (CEC), nutrient and organic matter concentration (Haines, 1978; Sousa-Souto et al., 2008). These chemical soil modifications are explained mainly by decomposition of plant material and nest refuse accumulated in underground chambers (Sternberg et al., 2007). Workers deposit plant material, mainly fresh leaves, to feed the fungus which in turn feeds the colony and releases nutrients from the organic matter to the soil. In addition, mineralization occurs when other microorganisms associated to nests decompose dead ants and plant detritus in refuse chambers (Farji-Brener, 2010). The effects of leaf-cutting ant nests on soil fertility are described to several habitats (Hudson et al., 2009; Moutinho et al., 2003; Sousa-Souto et al., 2008) and has been shown that plants access the nutrients available in nest-soil (Sousa-Souto et al., 2007; Sternberg et al., 2007).

Restinga vegetation occurs along the Brazilian coast on spodosols, being a typical component of Atlantic Forest complex. In Restinga soils, podzolization is the main pedogenic process summarized as following: elluviation of organic matter from surface H to illuvial B horizon which is characterized by aluminum accumulation (Gonzáles-Pérez et al., 2008). The downward migration of aluminum is explained by its complexation with organic acids derived from organic matter decomposition (Bardget, 2005). Restinga soils are quartzitic, sandy, characterized by leaching, high decomposition rates, high aluminum saturation and low nutrient availability (Lacerda et al., 1993). As in other sandy and oligotrophic ecosystems (Manlay et al., 2000), soil fertility in Restinga may be dependent of biotic activities.

In Restinga environments, functioning of leaf-cutting ant nests may be an important mechanism to nutrient cycling because soils around nests may have a higher organic matter and nutrient concentration, as verified in above cited studies. In this case, it is expected that nutrient input caused by nest functioning outweighs the natural loss of nutrient and organic matter described to Restingas. Additionally, organic acids released during the decomposition of plant material in the nests may enhance the formation of soluble organo-metal complexes and promote migration of aluminum deeper in the soil, decreasing aluminum saturation. An important effect of aluminum is its large ability to compete with base cations for exchange sites and thus to decrease the potential for absorption of nutrients (Lawrence et al., 1995). Therefore, a reduction of aluminum saturation may increase the cation exchangeable capacity, facilitating the nutrient uptake by plants on nest soils.

Atta robusta is an endemic leaf-cutting ant species being the only species of the *Atta* reported to Restingas of Rio de Janeiro and Espírito Santo states (Teixeira et al., 2004). Their nests are superficial (0.5 to 1.7m) and more spread relative to other *Atta* species nests. Externally the nests present several entrances surrounded by sand piles, which together may exceed 200m^2. This is a threatened species and studies about her ecological aspects are incipient. In this sense, current papers report its population status and geographic distribution (Fowler, 1995; Teixeira et al., 2004), the positive effect of plant cover on their nest density (Teixeira and Schoereder, 2003) and its importance as seed disperser (Teixeira *et al*. 2008). Contrary to other leaf-cutting ant species, there is a lack of knowledge about the effects of *A. robusta* nests on soil proprieties and plant nutrition. Therefore, understanding how *A. robusta* nests alter soil properties can be useful to explain pedological and plant community aspects in Restinga environments.

The aim of this study was to verify how *A. robusta* modify chemical proprieties of Restinga soils and plant nutrient status. We hypothesized that *Atta robusta* nests (i) increase soil nutrient concentration and (ii) facilitate the nutrient access by plants in Restingas. This may occurs due to (iii) increasing of CEC as consequence of cation releasing and (iv) decrease of aluminum saturation both caused by decomposition of organic matter.

2. METHODS:

2.1 Study area

We carried out the study in the Guriri Island (18°43’S, 39°45’W) near São Mateus, Espírito Santo state, Brazil. The Guriri Island harbors three different plant formations: Mangroves, Gallery forests and Restingas. The climate is warm and humid with an average annual temperature of 22°C and precipitation of 1200 mm. The wet season lasts from November to March and there is no pronounced dry period (Ururahy et al., 1983). We conducted the study in Restinga areas, which present a gradual complexity in their structure from beach, dunes, open restinga and Myrtaceae thicket. Specifically, we collected the data in Myrtaceae thicket areas, which have a higher plant cover, made up by trees up to 20 m high, most of them of the botanical family Myrtaceae (Araújo and Henriques, 1984). In this region *A. robusta* nest density was estimated as 1.63 per hectare (Teixeira and Schoereder, 2003).

2.2 Soil sample collection and chemical analyses

Seven active *A. robusta* nests were sampled in their central area defined as the largest sand piles (Teixeira et al., 2003). In each nest, we excavated manually a 1.5 x

1.5m pit and took soil samples at three depths (0-20, 50-70, 100-120cm) from each wall. We obtained soil control samples from sites located at least 100m from the nest edge following the same protocol applied to the nests. The four soil samples from the same depth were mixed and air-dried at 50°C for 48h. We determined P and K concentration with Melich I extractant. Ca and Mg were measured with 1M KCl. Organic matter content was determined according Walkey-Black method (OM= organic carbon X 1,724). Chemical properties included soil pH in water in a 1:2.5 soil mass: solution volume ratio and percentage of aluminum saturation. CEC was determined in 5g of soil with ammonium acetate at pH 7 (Embrapa, 1997).

2.3 Plant nutritional status

To evaluate if *A. robusta* nests increase the nutrient status of plants we compared the foliar nutrient concentration of *Protium heptaphyllum* (Aubl.) March (Burseraceae) individuals. This is a shade tolerant common species of Atlantic Forest biome and specimens used in this study were identified by a parataxonomist. We sampled ten adult plants with a trunk basal circumference of more than 40cm located on the nests and at a minimum distance of 100m from the nests (control plants). From each plant, we collected 30 apical leaves available in branches at two meters above soil surface. Plant material was digested using the micro-Kjeldahl method to determinate foliar concentrations of P, K, Ca and Mg (Silva 1999). P concentration was analyzed colourimetrically with a continuous flow analyzer and K, Ca, Mg concentrations were analyzed with Atomic Absorption Spectrophotometer (Silva, 1999).

2.4 Statistical analyses

To test if *A. robusta* nests modify Restinga soils, we compared chemical properties to each depth separately. We carried out One-way Analyses of Variance (ANOVA) using nests or control sites as explanatory variables. Response variables were: nutrient concentration (P, K, Ca and Mg), organic matter, aluminum saturation, pH and CEC. Likewise, to verify whether leaves of *P. heptaphyllum* located on *A. robusta* nests have more nutrients than leaves from plants far from the nests, we carried out an ANOVA in which the response variable was foliar nutrient concentration and explanatory variable was plant location (nest or control). We conducted all analyses under R environment (R Development Core Team, 2010), and were followed by residual analyses, to check for the suitability of the models and distributions adopted.

3. RESULTS:

In *A. robusta* nests, concentration of K was higher at 50-70cm depth ($F_{1,11}$=19.27;p=0.001; Fig.1) but there was no significant difference to other nutrients and depths (Table 1). In the same way, nests did not affect organic matter, pH and CEC (Table 1). On the other hand, *A. robusta* nests reduced aluminum saturation at three depths ($F_{1,11}$=15.9; p= 0.001; Fig. 2). In spite of this, there was no a higher nutrient content in leaves from *P. heptaphyllum* on nest soils (Table 2).

4. DISCUSSION:

From the four nutrients analyzed, only K content was higher in nests and this effect was significant only at 50-70cm depth. This may have occurred because the dynamics of K is faster relative to other elements, as consequence K become more available in soil (Domisch et al., 2008). In spodosols, the amount of organic matter and soil microbial activity decrease at deeper levels resulting in lower nutrient concentration (Bardget, 2005). Therefore, the higher K concentration at 50-70cm may be attributed to *A. robusta* nests because symbiotic fungus and microorganisms associated to subterranean chambers decompose the organic matter.

In contrast, *A. robusta* nests did not increase organic matter, P, Ca, Mg concentration, CEC and pH. These results indicate that natural loss of nutrient and organic matter described to spodosols (Bardget, 2005) prevails over the hypothesized action of *A. robusta* nests. Clay percentage in Restinga soils may be as low as 0% (Almeida Jr. et al., 2009) and we cannot exclude the possibility that low clay content may explain our results. Clay minerals have a high surface area to volume ratio determining the ability of the soil to retain nutrients after decomposition of organic matter. Thus, it seems that low clay content nullify the potential effects of *A. robusta* nests by connected process as following: the nest releases organic matter promoting its mineralization, but there is no enough clay to hold nutrients and organic matter, becoming the soil unable to retain cations and increase CEC.

Another explanation to the absence of effects of *A. robusta* nests on soil chemistry may be the groundwater proximity and its variation. In Restinga, groundwater may even reach the soil surface (Almeida Jr. et al., 2009; Magnago et al., 2010)**,** thus nutrients may be mineralized and rapidly leached if nest chambers are close to groundwater (Haines, 1983). As a consequence, low clay content and groundwater proximity may explain why nests did not increase the nutrient status of *P. heptaphyllum*.

Contrary to *A. robusta*, other leaf-cutting ant species have positive effects on soil nutrient content (Moutinho et al., 2003; Sousa-Souto et al., 2008) and plant nutrient status (Sousa-Souto et al., 2008; Sternberg et al., 2007). However, these studies were carried out in Brazilian Savanna and Tropical Forests soils, in which clay content may be more than 60% (Demattê and Demattê, 1993). Thus, the generalized wisdom about the positive effect of leaf-cutting ants on soil nutrient availability should be viewed with caution, because these effects should be dependent of soil class.

On the other hand, *A. robusta* nests decrease aluminum saturation in all depth sampled. In Restinga soils, aluminum is a main element occurring as insoluble and immobile hydroxides (Gonzáles-Pérez *et al.* 2008). However, its mobility can be enhanced when organic acids derived from vegetal decomposition promote the formation of soluble organo-metal complexes (Bardget, 2005). Probably, this process occurs in the *A. robusta* nest soil because the symbiotic fungus is constantly supplied with plant material (mainly fresh leaves), releasing organic acids which are able to associate to aluminum and dislocate it in water. In addition, other soil microorganisms associated to nests may release organic matter due to decomposition of plant detritus, old fungi and dead ants located in the refuse chambers (Pinto-Tomás et al., 2009; Farji-Brener, 2010).

If decreasing of aluminum saturation facilitates nutrient absorption, why *P. heptaphyllum* did not uptake more nutrients from the nests? According to Sternberg et al., (2007) there is an irregular pattern of nutrients access by plants in leaf-cutting ant nests. The latter authors verified that trees as far approximately 9-11m from the nest mound can uptake a higher amount of nutrient relative to trees from nest. Probably, this occurs because trees use nutrients available in refuse chambers located far from the nest center (Sternberg et al., 2007). Here, we suggest a similar mechanism to explain the non-significant differences between nutrient status of *P. heptaphyllum* surveyed. *A. robusta* nests are superficial and more spread than other *Atta* nests. Thus, its refuse chambers may be located away from nest center where plants surveyed were located.

Aluminum saturation is an important factor to determine the plant species composition by excluding plants with less tolerance to high aluminum concentration (Silva and Batalha, 2008; Andersen et al., 2010). Restinga soils are alics, i.e aluminum saturation is greater than 50%. Here, we found aluminum saturation less than 50% at all depth in the *A. robusta* nests. Thus, if aluminum saturation is determinant to plant establishment, a typical plant species composition around nests may be expected in Restingas. The majority of tropical environments have acidic soils containing high level of aluminum which is toxic to several plant species. However, in these ecosystems leaf-cutting ant nests are very common structures. For example, nest density can reach up six colonies per hectare in fragmented Neotropical rainforests (Rao et al., 2001). Thus, the depletion of aluminum saturation carried out by leaf-cutting ants may have an important implication to pedological mechanisms forming patches of soils with low aluminum content and promoting the plant establishment.

Functioning of leaf-cutting ant nests are regarded an important mechanism to nutrient cycling in tropical ecosystems. However, no current studies describe how these nests affect chemical properties in Restingas soils. Our findings show that *A. robusta* can increase K content and decrease aluminum saturation in these environments but other attributes, such as nutrients accumulation and its use by plants, should be more linked to pedological features of spodosols. Our study is the first to describe the effect of *A. robusta* on nutrient cycling in Restingas. In this sense, we suggest further studies to investigate if nutrients available in nests are lost to ground water. As *A. robusta* nests are superficial, further studies can verify if herbaceous plants uptake more nutrients on nests due to decreasing of aluminum saturation.

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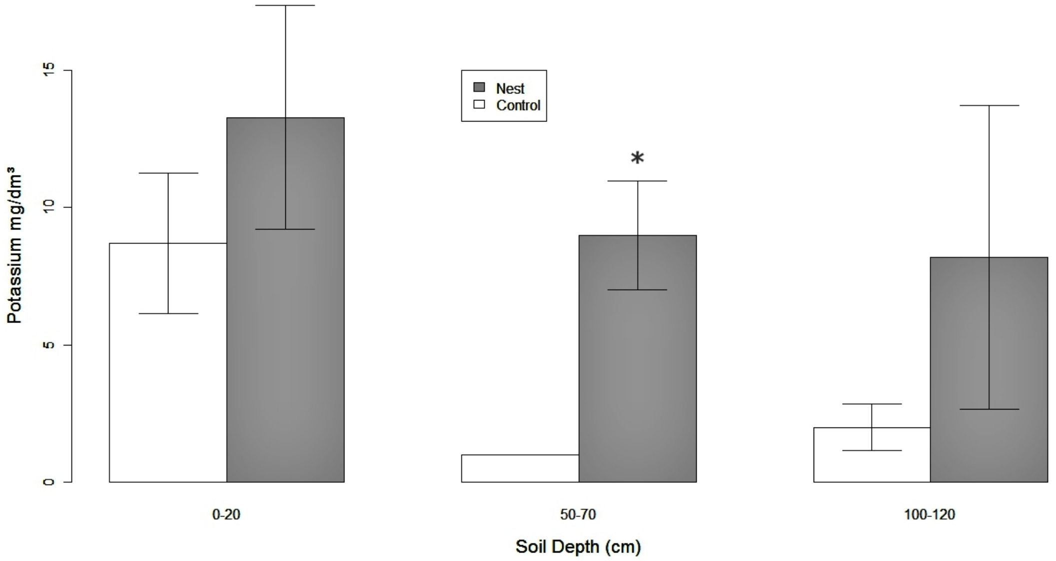

Fig. 1. Potassium concentration (mean ± SE) at three depths in *A. robusta* nests (gray bars) and control soils (white bars). Potassium content was higher only at 50-70cm depth only ($F_{1,11}$=19.27; p=0.001).

Table 1

Variables from Restinga soils (control) and *A. robusta* nests. The data represent means of seven replicates at three depths. Standard errors are shown in parentheses. There are no significant differences between sampled sites.

Variable		**Control**			**Nest**	
Depth (cm)	0-20	50-70	100-120	0-20	50-70	100-120
Ca	0.21 (0.1)	0.00 (0.0)	0.00 (0.0)	0.30 (0.2)	0.00 (0.0)	0.00 (0.0)
Mg	0.20 (0.1)	0.03 (0.0)	0.03 (0.0)	0.30 (0.1)	0.05 (0.1)	0.04 (0.1)
P	0.90 (0.1)	0.40 (0.1)	0.40 (0.1)	0.80 (0.2)	0.70 (0.1)	0.40 (0.1)
OM	1.10 (0.2)	0.10 (0.1)	0.10 (0.1)	1.30 (0.3)	0.20 (0.1)	0.20 (0.0)
pH	5.50 (0.1)	5.70 (0.1)	5.70 (0.1)	5.80 (0.1)	5.80 (0.1)	5.90 (0.1)
CEC	0.60 (0.2)	1.20 (0.2)	0.13 (0.1)	0.20 (0.1)	0.14 (0.4)	0.10 (0.4)

Ca and Mg (cmol$_c$/dm^3); P (mg/dm^3); OM= Organic matter (dag/kg); CEC= Cation exchangeable capacity (cmol$_c$/dm^3).

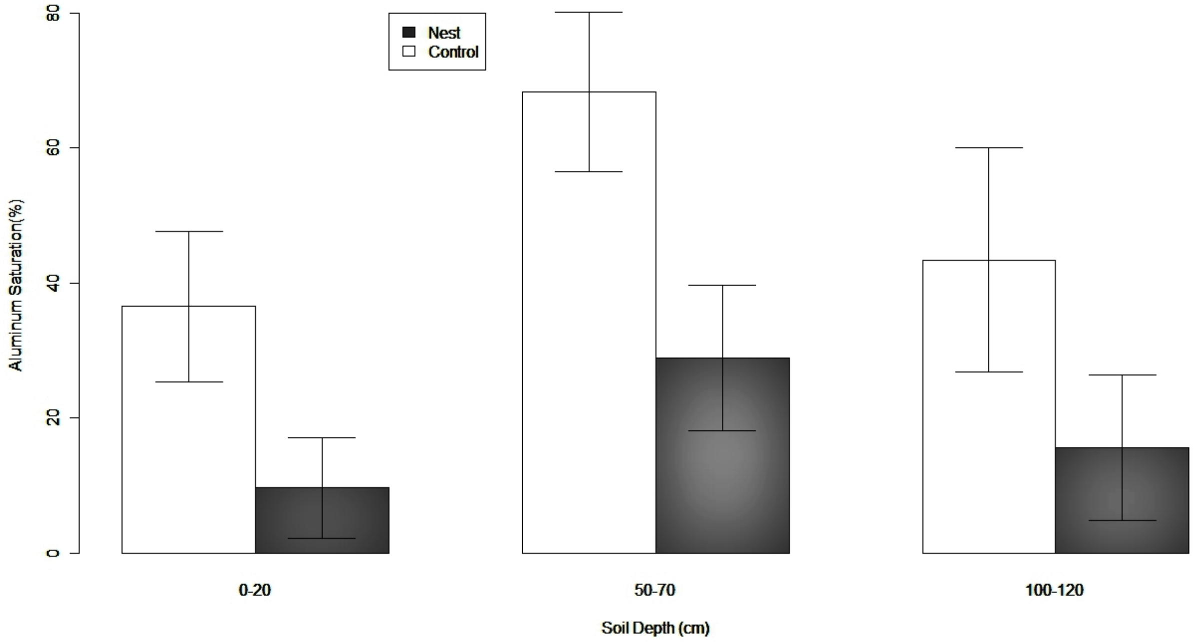

Fig. 2. Aluminum saturation (mean ± SE) in Restinga soils. There is a significant negative effect of *A. robusta* nests ($F_{1,11}$=15.9; p= 0.001). Gray bars represent soil samples from *A. robusta* nests and white bars represent non-nest soils.

Table 2

Nutrient content in leaves from *P. heptaphyllum* on restinga soils (control) and *A. robusta* nests. The data represent means from ten replicates. Standard errors are shown in parentheses. There are no significant differences between control and nests.

Nutrient (dag/kg)	Control	Nests
Ca	0.69 (0.10)	0.71 (0.15)
Mg	0.21 (0.01)	0.23 (0.02)
P	0.09 (0.00)	0.10 (0.01)

Leaf-cutting ants (*Atta robusta*, BORGMEIER 1939) do not alter plant community in Brazilian Restinga.

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RESUMO: (Formigas cortadeiras (*Atta robusta*, BORGMEIER 1939) não alteram a comunidade de plantas em restinga brasileira). *Atta robusta* é uma espécie de formiga cortadeira que atua como dispersora de sementes em restingas brasileiras. Nós verificamos se estas formigas alteram a comunidade de plantas analisando o efeito da distância dos seus ninhos sobre a comunidade de plantas jovens. Testamos se próximo aos ninhos (i): Existem menores abundância e riqueza de espécies, (ii): Existem maiores abundância e riqueza de espécies de plantas dispersadas por *A. robusta* e (iii) Existe uma composição típica de espécies sobre os ninhos. Abundância e riqueza de espécies de plantas foram obtidas de parcelas de 10x10m situadas a 0, 10, 20, 30, 40 e 50m distantes dos ninhos. Análises de regressão linear foram usadas para verificar o efeito da distância dos ninhos sobre a abundância e riqueza de espécies de plantas. Índices de dissimilaridade de Bray-Curtis foram usados para detectar diferenças na composição de plantas jovens entre ninhos (0m) e outras parcelas (10-50m). Nenhuma hipótese foi corroborada. Sugerimos que o forrageamento preferencial em plantas adultas localizadas em locais ensolarados para explicar a ausência de efeitos negativos na comunidade de plantas jovens. Predação de plântulas foi proposta como principal mecanismo para explicar a falta de associação entre plantas dispersadas por *A. robusta* e seus ninhos. Ao contrário de outras formigas cortadeiras, *A. robusta* não afeta o recrutamento de plantas e de acordo com o conceito de eficiência da dispersão de sementes, esta espécie não é um dispersor eficiente.

Palavras-chave: Comunidade de plantas jovens, dispersão de sementes, recrutamento de plantas, sauveiros.

ABSTRACT: *Atta robusta* is a leaf-cutting ant species that acts as seed disperser in Brazilian Restingas. We verified if these ants alters plant community analyzing the effect of distance from their nests on sapling communities. We hypothesized that near to nest (i): there is a lower abundance and species richness to sapling species, (ii) there is a higher abundance and species richness of plant species dispersed by *A. robusta* and (iii) there is a typical sapling species composition on nests. We obtained sapling species richness and abundance from 10 x 10 m plots disposed at 0, 10, 20, 30, 40 and 50 m away from the *A*. *robusta* nests. We performed linear regression analyses to verify the effect of nest distance on sapling abundance and species richness. Bray-Curtis dissimilarity index were used to detect differences in sapling species composition among nests (0m) and other plots (10-50m). None of the hypotheses postulated were accepted. We suggest a preferential foraging on adult plants located at sunny sites to explain the absence of negative effects on saplings communities. Seedling predation was proposed as main mechanism to explain the no-association among plants dispersed by *A*. *robusta* and ant nests. Contrary to other leaf-cutting ants, *A. robusta* does not exert a negative effect on plant recruitment and according to seed dispersal effectiveness concept this species is not an efficient disperser.

Key words: Ant nests, plant recruitment, sapling community, seed dispersal.

Introduction:

Leaf-cutting ants (*Atta* spp. and *Acromyrmex* spp.) are regarded as main primary consumers in the Neotropical region and modifiers of the structure of the plant community (Garretson *et al.* 1998; Correa *et al.* 2010). Unlike many herbivores, they present a high level of polyphagy cutting up to 2,5% of the total foliage in tropical ecosystems (Wirth *et al*. 2003) and up 50% of plant species around their nests (Vasconcelos & Fowler 1990). In tropical ecosystems, leaf-cutting ants have a negative effect on plant recruitment by pruning the surround sapling or seedling community. For example, in Costa Rican rain forest, active nests of *Atta cephalotes* decrease small plant abundance and diversity relative to adjacent vegetation (Garretson *et al.* 1998). Similarly, the effect of *Atta laevigata* herbivory diminishes seedling survival, affecting forest regeneration in Central Amazonia (Vasconcelos & Cherrett 1997). In addition, the herbivory of *Atta sexdens* and *A*. *cephalotes* is an important cause of reduced plant recruitment in Venezuelan land-bridge islands because their negative effects are more significant in small remnants (Rao *et al.* 2001).

On the other hand, leaf-cutting ants may collect seeds and fruits on the floor and carry them to the nests (Leal & Oliveira, 1998; Peternelli *et al.* 2003; Valentim *et al.* 2007) or sometimes leave them on the foraging trail (Teixeira 2007). In the nest, the workers remove the pulp or elaiosome and deposit the cleaned seeds in the subterranean chambers (Farji-Brener & Illes, 2000) or put away in above-ground refuse piles (Dalling & Wirth, 1998; Teixeira, 2007). Seed dispersal by leaf-cutting ants provides benefits to the plants such as: decreasing of seed predation (Teixeira 2007) and/or increasing of seed germination and seedling survival (Peternelli *et al.* 2003; Teixeira 2007). However, in other cases no positive effect on seed germination has been founded (Leal & Oliveira 1998; Varela & Perera 2003).

In addition, leaf-cutting ants are considered effective seed dispersers due to benefic effects on plant abundance. The seed dispersal effectiveness regards two factors linked to disperser: quantity of seeds dispersed and quality of seeds dispersal: fate of dispersed seeds and their chance of reaching maturity (Schupp *et al.* 2010). The quantitative contribution of leaf-cutting ants to seeds dispersal has been studied for *Miconia rubiginosa* in Brazilian Savanna. In this sense, *Atta sexdens* and *A. laevigata* were responsible for 66% of the seeds removal and their nests were considered hotspots of *M. rubiginosa* recruitment having more seedlings and saplings than beneath the parent plants (Christianini & Oliveira 2009).

Due to the possible antagonist effects of herbivory and seed dispersal, leaf-cutting ants can alter the structure of the plant community at least by two processes. Firstly, leaf-cutting ant nests may have lower plant abundance and species richness than beyond their influence, due to direct attack to the nearest plants or make cleaning areas (Farji-Brener & Illes, 2000). Secondly, plants dispersed by leaf-cutting ants may be more abundant and representative around nest area than in other areas, because in such sites plants may have high rates of germination and escape from predation. Therefore, plant communities under the influence of leaf-cutting ants may have more individuals from seeds carried by workers and those survivors to attack of colony. In this case, a typical composition of flora is expected around nests (Farji-Brener & Illes, 2000). Changes on plant composition due to *Atta* herbivory have been reported (Rao *et al.* 2001). However, the effects of seed dispersal by leaf-cutting ants on plant community are unknown and should be further investigated (but see Farji-Brener & Illes, 2000).

In the Brazilian restinga, a habitat that occurs along the coastline, a particular species of leaf-cutting ant, *A. robusta*, can be an interesting model to study the effects of leaf-cutting ants on plant community. This endemic leaf-cutting ant species is the only

Atta species reported to restingas of Rio de Janeiro and Espírito Santo states (Teixeira *et al.* 2003). Although *A. robusta* cut leaves (Fowler 1995), no study describes its effect on vegetation. Probably such a lack in the studies occurs because this is not a species reported as a pest, and therefore its herbivory effect has been largely ignored (Teixeira *et al.* 2003). In contrast, the role of *A. robusta* as seed disperser is better-known. *A. robusta* carries seeds of 36 plant species from 17 families and the distances of seed transport can reach up to 100 m (Valentim *et al.* 2007). Of these, 20 species have their seeds deposited on refuse dumps outside the nests after pulp fruit removal by workers. In addition, *A. robusta* increases the seedling density of four plant species on their nests (Teixeira 2007). *Eugenia rotundifolia* seed germination rates, for instance, increased after manipulation by workers and seed predation was lower on nest areas. Despite the higher mortality rates followed by seed dispersal, seedlings of *Protium heptaphyllum* were more abundant in the nest areas than beneath the parent plants. Moreover, seedlings of two additional plant species were more abundant on *A. robusta* nests than below adult plants (Teixeira 2007).

Considering the qualitative component of seed dispersal effectiveness, i.e. probability of seeds reaching maturity (Schupp *et al.* 2010), *A. robusta* may be an effective seed disperser since it increases germination of seeds and improves seedling survival around their nests. However, the analysis of effectiveness dispersal by *A. robusta* can be more complete by studying the response of sapling community. Sapling abundance and diversity represent the net result of seedlings emergence and mortality indicating trends of the adult plant community (Duarte *et al.* 2006). Thus, sapling communities around *A. robusta* nests can indicate if this species is an effective seed disperser.

Although *A. robusta* cut leaves and transport seeds to their nests, no earlier study has investigated how it could modify the plant community such as evidenced to other leaf-cutting ant species. In this study, we investigated if *A. robusta* alters sapling community in a Brazilian restinga. The questions were (i): does *A. robusta* diminish abundance and species richness of all plant species near to their nests? (ii): Are plants dispersed by *A. robusta* more represented and abundant on nest vicinity? Finally we verified if (iii): there is a different plant species composition on the *A. robusta* nests.

Material and methods:

Study area - We carried out this study at three Restinga sites of Espírito Santo State, southeastern Brazil. We carried out samplings mainly at Comboios Biological Reserve (19°38'-19º45'S; 39°45'-39º55'W) with ca. 833 ha and in an adjacent privately owned area both located in Linhares. The third study site is an Environmental Protection Area of Aracruz (19°50'05''S 40°03'00''W) with ca. 3,925 ha.

Restinga is a type of vegetation occurring along the Brazilian coastline that presents a gradual complexity in structure from beach inwards, with dunes, open restinga and Myrtaceae thicket (Araújo & Henriques, 1984). We collect the data in Myrtaceae thicket areas, which have a higher plant cover, made up by trees up to 20 m high, most of them of the family Myrtaceae (Araújo & Henriques 1984). The climate is warm and humid with an average annual temperature of 22°C and precipitation of 1200 mm. The wet season lasts from November to March and there is no pronounced dry period (Ururahy *et al.* 1983).

Sapling communities around *Atta robusta* nests - We considered saplings those no woody plants with basal circumference sizing 1.5-5.0 cm and up to 50 cm high. This range of size minimizes the chance of including plants that have been recruited before colony foundation. We obtained sapling species richness and abundance from 10 x 10 m plots disposed at 0, 10, 20, 30, 40 and 50 m far away from the *Atta robusta* (Borgmeier) nests. We used the nest itself as 0 m distance and the largest sandy piles as its central area. Other plots (10 to 50 m) were delimited from the nest edge following the foraging trail. We used this range of distance because average of dispersal is ca. 33m and seeds are dropped on the way to the nest forming seedling clusters (Teixeira 2007). In this sense, we believe that by using this range of distance we can know the influence of seed dispersal by *A. robusta* on sapling community. To avoid pseudoreplication, only one plot was sampled for each nest. So, we obtained five replications for each measure of distance. Saplings and adults plants were identified at species level by a parataxonomist. Plant species were assigned to two plant group, "Dispersed by *A. robusta"* or *"*Other" when their seeds are not known to be used by the ants. Plants dispersed by *A. robusta* were identified according to checklist available in Teixeira (2007) which reports data from extensive study about seed dispersion by this ant species in Brazilian Restinga.

Data analysis - To verify if presence of *A. robusta* nests decreases sapling abundance and species richness, we performed two linear regression analyses. In each analysis we used sapling individuals and species identified as "Other" as response variable. The explanatory variable was nest distance. We expected positive relationships between response variables and nest distance. Plant species belonging to "Dispersed by *A. robusta*" group were not used in these analyses to avoid a possible addition of individuals and species richness.

A. robusta transport seeds to their nests where seedling emergence is favored. Therefore, the ants may increase sapling abundance and species richness of "Dispersed by *A. robusta"* plants around their nests. We verified if vicinity of *A. robusta* nests harbor more sapling abundance of four species. The species are: *Eugenia rotundifolia* (Myrtaceae), *Protium heptaphyllum* (Burseraceae), *Pera parvifolia* (Euphorbiaceae) and *Tapirira guianensis* (Anacardiaceae). We used these species because their seedling abundance was higher on *A. robusta* nests according to previous study (Teixeira 2007). Additionally, we tested if species richness of all plant species dispersed by *A. robusta* is higher near to the nests. We performed linear regression analyses in which response variables were sapling abundance of each four species separately and species richness of all species dispersed by *A. robusta*. Nest distance was the explanatory variable. In this case, we expected negative relationships between response variables and nest distance. To avoid include saplings primarily dispersed by parent plants, sapling individuals were excluded from the analyses when their respective adult plants were present in the plot sampled.

Models tested followed Poisson distribution, corrected for overdispersion whenever needed, followed by residual analyses to check for the suitability of models and distributions employed. We carried out above analyses under R environment (R Development Core Team 2010).

Finally, we verified if *A. robusta* alters plant composition around their nests. The difference between sapling communities on nests and each other plots (10 to 50 m) was calculated using the Bray-Curtis dissimilarity index from containing matrix species abundance values. In addition, a non metric multidimensional scaling (NMDS) was plotted to explain the spatial differences in sapling communities. Then, a one way analysis of similarity (ANOSIM) was performed by 10,000 permutations to generate an "R" statistic and associated *p* value. The "R" represents a dissimilarity measure. Values equal to 1 indicate total dissimilarity and 0 if perfect similarity occurs. The similarities percentage routine (SIMPER) were used to calculate the individual species contributing to the separation between two sapling communities (Clarke 1993). The SIMPER routine decomposes average Bray–Curtis dissimilarities between all pairs of samples, into percentage contributions from each species, listing the species in decreasing order of contribution. These analyses were carried out using PAST program (Hammer *et al.* 2001).

Results:

We collected 180 plant species from 60 families, fifteen of which are dispersed by *A. robusta* (table 1). *A. robusta* nests did not exert effects on sapling community. To "Other" plant species group, neither abundance ($F_{1,28}$= 1.96; p=0.17) nor species richness of saplings were influenced by nest distance ($F_{1,28}$= 0.97; p=0.33). There are no significant relationships between sapling abundance and nest distance to the four species analyzed separately (*Protium heptaphyllum*: $F_{1,28}$= 3.910; p=0.6; *Eugenia rotundifolia*: $F_{1,28}$= 0.057; p=0.8; *Pera parvifolia*: $F_{1,28}$= 0.002; p=1; *Tapirira guianensis*: $F_{1,28}$= 0.280; p=0.6). Similarly, species richness of plant dispersed by *A. robusta* was not higher around nests when analyzed together ($F_{1,28}$= 0.710; p=0.5). Finally, sapling communities did not differ between nests and other plots (R=0.022; p=0.34).

Discussion:

A. robusta does not reduce sapling abundance and species richness around their nests. We suggest that *A. robusta* preferentially cut leaves from adult plants instead of foraging on sapling community around their nests. It is expected that leaf-cutting ants maximize the intake energy and at the same time minimize their costs to foraging (Kost *et al.* 2011). They usually do it foraging on young leaves which have more nutrient content (Mundim *et al.* 2009). Thus, adult plants may be more harvested by *A. robusta* workers because they may have more young leaves relative to saplings. An additional argument to this idea is the preference by leaf-cutting ants to forage on plants located at sunny sites (Nichols-Orians, 1991) and/or pioneer species due to higher nutrient concentration, so-called palatable forage hypothesis (Farji-Brener 2001). Contrary to other leaf-cutting ant species, nests of *A. robusta* are more abundant in the shaded habitats and there is a positive relationship between their nest abundance and arboreal plant cover (Teixeira & Schoereder, 2003). However, the same fungus species is cultivated by all leaf-cutting ants (Silva-Pinhati *et al.* 2004), therefore it is reasonable to suggest that *A. robusta* also prefers forage on sunny or pioneer plant to supply nutritional fungi requirements. In summary, we propose that *A. robusta* did not alter sapling communities because it forages preferentially on adult and/or pioneer plants which may have more palatable leaves.

Sapling communities are good predictors of the structure of woody plant community (Duarte *et al.* 2006). Some studies report a negative effect on sapling communities by other leaf-cutting ant species and describe their role on the plant recruitment (Vasconcelos & Cherret, 1997; Garretson *et al.* 1998; Rao *et al.* 2001). Contrary to these studies, we did not find a negative effect of *A. robusta* on sapling communities. Therefore, we suggest that this species do not influences the natural mechanism of plant recruitment in restinga areas.

Plants dispersed by *A. robusta* are not more abundant or representative around their nests. In this sense, seed dispersal to the nests is not sufficient to modify the sapling community structure. *A. robusta* workers promote a clumped disposal of seedlings increasing their abundance (Teixeira 2007). However, this does not result in a higher sapling abundance or diversity on nests. We suggest that density-dependent mortality of seedlings may explain this result because competition among siblings should reduce the initial seedlings aggregates, thus no influencing sapling abundance and species richness. Seedlings aggregates also could disappear due to natural expansion of nests. *A. robusta* heap excavated soil around their nests and sand piles could cause seedling mortality on nests by burial (Culver & Beattie, 1983).

Nevertheless, ant seedling-predation may be more appropriate to explain the lack of association between nests and "Dispersed by *Atta robusta"* plant group. Workers may cut seedlings or saplings from seeds transported to their nests. After pulp consumption, workers deposit the cleaned seeds on sand mounds near to nest entrances, thus it is possible to suggest that in the sand mounds the seedlings have high probability to be killed by workers (Farji-Brener & Sasal 2003). This happens to seedlings of *Protium heptaphyllum* consumed by *Atta sexdens* nullifying the seedlings clumps formed on nest entrances after seed dispersal (Silva *et al.* 2007). *Atta robusta* also promotes seedlings aggregates of *P. heptaphyllum* on their nest (Teixeira 2007).Therefore, seedling mortality by herbivory should explain the non-significant relationship between *P. heptaphyllum* abundance and nest distance. By generalization, seedling predation by workers around nests should explain non significant relationship between sapling abundance and species richness of "Dispersed by *A. robusta"* plants and nest distance.

Some studies report how ants modify the plants distribution by seed dispersal showing a positive association between ant nests and seedlings (Passos & Oliveira, 2003; Christianini & Oliveira 2009). Here, we used saplings to verify the effect of seed dispersal by *Atta robusta* on plant communities. We believe that saplings are more suitable than seedlings to evaluate the qualitative component of seed effectiveness dispersal because they can indicate chance of seeds reach maturity. Therefore, by using a better indicator, we suggest that *Atta robusta* is not an efficient disperser since abundance and species richness of plant dispersed on their nest are the same relative to surrounding vegetation.

In conclusion, we did not found a typical sapling species composition around nests. This indicates that potential herbivory on saplings and seed dispersal are insufficient to exclude or add different species around nests. Although *Atta robusta* is a leaf-cutting ant species and acts as a seed disperser, it not alters sapling community and probably does not affect the natural process of plant regeneration in restingas. Further studies may explain the reasons for this. Thus, we suggest research which verify if *Atta robusta* preferentially forage on adult and pioneer plants located in sunny sites. Long term studies are necessary to investigate if normal activities of colony as pruning of seedlings on sand piles and soil excavation explain the absence of association between nests and "Dispersed by *A. robusta"* plant group.

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Table1.: Plant species sampled in plots located around *A. robusta* nests (0-50m). Plant species names highlighted in bold have seeds dispersed by *A. robusta*.

FAMILY	SPECIES
AMARANTHACEAE	*Amaranthus* sp.
ANACARDIACEAE	***Anacardium occidentale*** L.
	Astronium graveolens Jacq.
	Schinus terebenthifolius Raddi
	Tapirira guianensis Aubl.
ANNONACEAE	*Annona acutiflora* Mart.
	Guatteria sellowiana Schldtl.
	Duguetia flagellaris Huber
	Oxandra sp.
	Xylopia sericeae A. St. Hil
APOCYNACEAE	*Aspidosperma cylindrocarpon* Müll Arg
	Condylocarpon intermedium Müll Arg
	Himatanhtus bracteatus Woodson
	Rauwolfia sp.
	Tabernaemontana salzmanni A. DC.
ARACEAE	*Anthurium raimundii* Mayo, High & Nadruz
	Philodendron pedatum (Hooker) Kunth
	Philodendron fragantissimum(Hooker) Kunth
ARALIACEAE	*Dendropanax cuneatus* Decne & Planch
ASCLEPIDACEAE	*Blepharodon nitidum* (Vell.) J.F. Macbr
ASTERACEAE	*Mikania diversifolia* DC.
ARECACEAE	***Allagoptera arenaria*** (Gomes) Kuntze
	Bactris bahiensis Noblick ex A.J Henderson
	Bactris vulgaris Barb. Rodr.
	Desmoncus orthacanthos Mart.
BIGNONIACEAE	*Lundia virginalis* DC.
	Mansoa difficilis (Cham.) Bureau & K. Schum
	Tabebuia obtusifolia (Cham.) Bureau
BOMBACACEAE	*Eriotheca macrophylla* (K. Schum) A. Robyns
	Pseudobombax grandiflorum (Cav.) A. Robyns
BORAGINACEAE	*Cordia taguahyensis* Vell.
	Tournefortia bicolor Sw.
BROMELIACEAE	*Aechmea* sp.
	Bromelia antiacantha Bertol.
	Quesnelia quesneliana (Brongan) L.B. Smith
BROMELIACEAE	*Pseudananas sagenarius* (Arruda) Camargo
BURSERACEAE	***Protium heptaphyllum*** (Aubl.) Marchand
CAESALPONNIACEAE	*Senna affinis* (Benth.) H.S. Irwin & Barneby
CAPPARACEAE	*Capparis flexuosa* (L.) L.
CLUSIACEAE	*Kielmeyera albopunctata* Saddi
	Kielmeyera membranacea Casar.

	Rheedia brasiliensis (Mart.) Planch. & Triana
CACTACEAE	*Cereus fernambucensis* Lem.
	Opuntia brasiliensis (Wild.) Haw.
CELASTRACEAE	*Maytenus obtusifolia* Mart.
	Maytenus cestrifolia Reiss.
COMMELINACEAE	*Dichorisandra penduliflora* Kunth
CHRYSOBALANACEAE	***Couepia schottii*** Fritsch
	Hirtella burchellii Britton
	Hirtella hebeclada Moric ex A.P. DC.
	Licania Kunthiana Hook
	Parinari excelsa Sabine
CONVOLVULACEAE	*Ipomoea phyllomega* (Vell.) House
CYPERACEAE	*Eleocharis interstincta* (Vahl.) Rhoem & Schult
DILLENACEAE	*Tetracera lasiocarpa* Eich in Marp
	Davilla rugosa Poir.
EUPHORBIACEAE	***Pera parvifolia*** Mul l. Arg.
	Pogonophora schomburgkiana Miers
	Sebastiania brasiliensis Spreng.
ERYTROXYLACEAE	*Erythroxylum subsessile* (Mart.) O.E. Schulz
	Erythroxylum sp.
FABACEAE	*Andira fraxinifolia* Benth
	Exostyles venusta Schott ex Spreng
	Machaerium aculeatum Raddi
	Ormosia arbórea (Vell.) Harnu
	Swartzia apétala (Vogel) R.S Cowan
	Swartzia simplex Urban
	Zollernia glabra (Spreng.) Yakovlev
	Zollernia modesta A.M. de Carvalho & Barneby
FLACOURTIACEAE	*Casearia commersoniana* Cambess
	Casearia sp.
HIPPOCRATEACEAE	*Tontelea miersii* (Peyr.) A.C. Sm.
ICACINACEAE	*Discophora guianensis* Miers
IRIDACEAE	*Neomarica sabini* (Lindl.) Chuckr
LAURACEAE	*Licaria guianensis* Aubl.
	Ocotea argentea Mez
	Ocotea confertiflora (Meisn) Mez
	Ocotea divaricata (Nees) Mez
	Ocotea neesiana (Miq.) Kosterm
	Ocotea notata (Nees) Mez
	Ocotea elegans Mez
LECYTHIDACEAE	*Eschweilera ovata* (Cambess.) Miers
MALPIGHIACEAE	***Byrsonima sericea*** DC.
	Heteropterys chrysophylla Kunth
	Stigmaphyllon blanchetii C.E Anderson
MARANTACEAE	*Stromanthe porteana* Griseb.

MELASTOMATACEAE	*Miconia cinnamomifolia* (Mart. & DC) Naudin
	Miconia prasina (Sw) DC.
	Miconia sp.
	Mouriri Doriana Saldanha ex Cogn.
MELIACEAE	*Trichilia casaretti* C. DC.
	Trichilia pallens C. DC.
	Trichilia tetrapetala C. DC.
MENISPERMACEAE	*Abuta selloana* Eicher
MORACEAE	*Ficus arpazusa* Casar.
MIMOSACEAE	*Inga capitata* Desv.
	Inga flagelliformis (Vell.) Mart.
	Inga laurina (Sw.) Wild
	Inga subnuda Salzm. ex Benth.
	Piptadenia adiantoides (Spreng.) Macbr.
	Pseudopiptadenia contorta (DC.) GP Lewis & M.P.M de Lima
MYRSINACEAE	*Myrsine guianensis* (Aubl.) Kuntze
MYRTACEAE	*Campomanesia guazumifolia* Cambess. O. Berg
	Eugenia cf. *badia*
	Eugenia brasiliensis Lam.
	Eugenia fusca O.Berg
	Eugenia ligustrina O.Berg
MYRTACEAE	*Eugenia* cf. *melanogyna* (D. Legrand) Sobral
	Eugenia menandroana Barroso et Peixoto
	Eugenia platyphylla O. Berg
	Eugenia cf. *tyguyensis*
	Eugenia punicifolia (Kunth) DC.
	Eugenia rotundifolia Casar.
	Eugenia uniflora Lin.
	Eugenia subterminalis DC.
	Gomidesia martiana O. Berg
	Marlierea excoriata Mart.
	Marlierea grandifolia O. Berg
	Marlierea obversa Legrand
	Myrcia bergiana O. Berg
	Myrcia fallax (Rich) DC.
	Myrcia riodocensis G.M Barroso et Peixoto
	Myrciaria floribunda (West ex Wild) O. Berg
	Plinia involucrata (Berg) Mc Vaugh
	Plinia renatiana Barroso et Peixoto
	Psidium sp.
NYCTAGINACEAE	*Guapira opposita* (Vell.) Reitz
	Guapira pernambucensis (Casar.) Lundl
	Guapira subferruginosa (Mart ex Schum) Lundell
	Neea floribunda Poepp & Endl
OCHNACEAE	*Ouratea* aff. *multiflora* (DC.) Eugl.
	Ouratea cuspidata Engl.
ORCHIDACEAE	*Epidendrum densiflorum* Hook
	Vanilla chamissonis Klotzsch
OLACACEAE	*Schoepfia obliquifolia* Turcz

PASSIFLORACEAE	*Passiflora ovalis* (Vell.) Killip
POACEAE	*Lasiacis ligulata* A. Hitchc. & Chase
	Merostachys sp.
POLYGONACEAE	***Coccoloba alnifolia*** Casar.
	Coccoloba arborescens (Vell.) R.A Howard
PIPERACEAE	*Piper arboreum* (Trel.) Yunck.
	Piper corcovadensis (Miq.) . DC.
RHAMNACEAE	*Ziziphus platyphylla* Reissek
RUBIACEAE	*Coutarea hexandra* (Jacq.) K. Schum.
	Faramea bahiensis Müll. Arg.
RUBIACEAE	*Melanopsidium nigrum* Colla
	Psychotria carthagenensis Jacq
	Psychotria gracilenta Müll. Arg.
RUBIACEAE	*Randia armata* Sw. DC.
	Rudgea sp.
RUTACEAE	*Esenbeckia grandiflora* Mart.
	Pilocarpus grandiflora Engl.
RUTACEAE	Pilocarpus microphyllus Stapf ex Wardl.
	Rauia sp.
SAPOTACEAE	*Ecclinusa ramiflora* Mart.
	Manilkara triflora Monach
	Manilkara salzmanni i (A. DC.) Lam.
	Pouteria caimito (Ruiz & Pav.) Radlk
	Pouteria coelomatica Rizzini
	Pouteria sp.
	Pouteria peduncularis (Mart & Eichler) Baehni
SAPINDACEAE	*Allophylus petiolulatus* Radlk
	Cupania emarginata Cambess
	Cupania rugosa Radlk
	Cupania sp.
	Paullinia riodocensis Somner
	Paullinia rubiginosa Cambess
	Paullinia ternata Radlk
	Serjania dentata (Vell.) Radlk
SCROPHULARIACEAE	*Otacanthus platychilus* Radlk
SIMAROUBACEAE	*Simaba subcymosa* A. St-Hil & Tul
	Simarouba amara Aubl.
	Picramnia bahiensis Turcz.
	Picramnia sellowii Planch.
SMILACACEAE	*Smilax brasiliensis* Spreng.
	Smilax spicata Vell.
SOLANACEAE	*Solanum melissarum* L. Bohs
	Solanum polytrichum Moric
TILIACEAE	*Luehea mediterrânea* (Vell.) Angely

4. Conclusões gerais:

Atta robusta modifica parcialmente as propriedades químicas dos solos de restinga. Neste sentido foram verificados um aumento do teor de potássio em profundidades de 50 a 70 cm e uma redução da saturação por alumínio em todas as profundidades analisadas. Apesar disso, indivíduos de *Protium heptaphyllum* localizados sobre os sauveiros não apresentaram maiores concentrações de nutrientes em suas folhas. Estes resultados indicam que a perda natural de nutrientes descrita para espodossolos prevalece sobre o possível acréscimo de nutrientes realizado por sauveiros.

Ao contrário de outras espécies de formigas cortadeiras, *A. robusta* não altera a abundância, composição e riqueza de espécies de plantas jovens (saplings) ao redor dos seus ninhos. Provavelmente, a herbivoria sobre plantas jovens não afeta negativamente a comunidade de plantas. Por outro lado, os ninhos não apresentaram maiores abundância e diversidade de do grupo de plantas que tem suas sementes transportadas por *A. robusta*. Uma vez que plantas jovens podem indicar as possíveis tendências da estrutura da comunidade de plantas adultas, pode-se concluir que *A. robusta* não interfere no processo natural de recrutamento de plantas em restinga.

O papel das formigas cortadeiras na ciclagem de nutrientes do solo e na modificação de comunidades de plantas é bem descrito para outras espécies do gênero *Atta* em outros ecossistemas. No entanto, esses aspectos eram desconhecidos para ambientes de restinga. Este trabalho é o primeiro a investigar como *A. robusta* modifica propriedades químicas dos solos e a comunidade de plantas. Estudos posteriores podem investigar se a redução da saturação por alumínio facilita uma maior absorção de nutrientes em plantas de porte herbáceo e explicar porque *A. robusta* não altera a comunidade de plantas ao redor dos seus ninhos. Sugere-se que esta espécie forrageie principalmente em plantas adultas e distantes dos ninhos e que a predação sobre plântulas dos montes de terra solta explique a ausência de associação entre os ninhos e aquelas plantas que têm suas sementes dispersadas por *A. robusta*.