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Interplays between Atta ants (Formicidae: Attini), soils and environmental properties in the Brazilian Neotropics: a preliminary assessment

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ABSTRACT: Leaf-cutting ants are the most important herbivore in the neotropics, represent active agents of pedobioturbation, and are regarded as ecosystem engineers. These ants have a wide variety of ecological functions, such as pollination, seed dispersal, and tree-growing control. Despite this importance, little is known on their distribution in relation to possible soil and environmental conditions that affect *Atta* ants occurrence. This study aimed to spatialize the main occurrences of Atta species in the Brazilian territory and evaluate the main environmental conditions driving ants species in the Brazilian tropical landscapes, at a preliminary basis. We compiled data of occurrence for 12 *Atta* species from Global Biodiversity Information Facility (GBIF) databases, and scientific literature (up to 2019) for each *Atta* species. To each point, we obtained the respective geoenvironmental data as soil properties, biome, geology, vegetation land use, and climate variables. From these data, possible zonalities of occurrence of 9/10 *Atta* species were discussed. We applied the principal components analysis (PCA) and Canonical Correspondence Analysis (CCA) to identify the environmental gradient and investigate the possible interplay between variables and species. Soil, vegetation, and land use attributes are the main drivers on the distribution of *Atta* at local scale where their evolutionary physiological and foraging adaptations allow them to nest and maintain the fungi culture. At broader scales, climatic attributes are key drivers of *Atta* distribution across Brazil, and also influence pedogenic processes. Our study demonstrates that species of *Atta* ants are not randomly dispersed in Brazil and are strongly associated with complex and diverse Brazilian landscapes. We remark that further studies on the distribution of leaf-cutting ants of the *Atta* genus in Brazil, as well as their evolutionary phylogenetics, are needed, based on larger database.

Keywords: saúva ants, geographical distribution, climate conditions, leaf-cutting ants.

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INTRODUCTION

Brazil is a continental country that presents a large variability of vegetation, soils and climate, with an economy based largely on agriculture and primary environmental resources. Widely distributed across the Brazilian territory, leaf-cutting ants of the genus *Atta* (Formicidae: Attini) have a complex ecological interplay and a significant economic impact on agriculture. Despite representing the largest populations of herbivores in the neotropics, the genus *Atta* sp. are also primarily responsible for soil turbation and nutrients cycling, along with termites, far surpassing other soil animals, such as worms (Whitford and Eldridge, 2013). Leaf-cutting ants represent active agents of pedobioturbation, and are considered ecosystems engineers (Lavelle et al., 2016).

Leaf-cutting ants have a wide variety of ecological functions such as pollination, seed dispersal and tree-growing control, contributing to the stability of many forest/savanna ecosystems, besides their active role in the flow of energy and matter, in soil aeration, and nutrients cycling (Moutinho et al., 2003; Peternelli et al., 2004; Leal et al., 2014). Despite representing benefits for the soils, leaf-cutting ants, in practically all phases of forest development and cultivation, are considered pests, as they directly affect productivity (Fowler et al., 1989; MAPA, 2016), so much that a greater effort to control agricultural pests in Brazil is focused on leaf-cutting ants (Fowler et al., 1989; Zanetti et al., 2002).

The Attine tribe, dates to 65 million years before present (BP), and stands out for having leaf-cutting ants (Schultz and Brady, 2008; Branstetter et al., 2017). The two genera of leaf-cutting ants within this tribe, the genus *Atta*, popularly known as *saúvas*, and the genus *Acromyrmex*, known as *quenquéns* ants (Fowler et al., 1989), are both neotropical. The *saúvas* showed a great irradiation between 15BP and 5BP, and are now widely distributed in the neotropics of South America, comprising 15 different species in Brazil alone (Fowler, 1995; Bacci et al., 2009). The key aspect related *Atta* ants is their position as a dominant herbivore in the neotropics, consuming hundreds of kilograms of plant material per year (Mikheyev et al., 2008). In foraging areas, a single colony can consume up to 50 % of the leaves available (Costa et al., 2018; Swanson et al., 2019). Despite being considered herbivores, they do not eat indigest plant material, but rather use it to maintain a mandatory symbiotic association with fungi. Ants provide food and protection to the fungus, while the fungus is the main food supply of the colony (Mueller et al., 2005; Mehdiabadi et al., 2012).

Plant material used for the fungi cultivation is chosen by a combination of high nutrition value and low toxicity (Nichols-Orians, 1991; Mundim et al., 2009). Therefore, leaf-cutting ants preferentially cut fresh, young leaves with high levels of nitrogen, zinc, calcium, and copper (Berish, 1986; Mundim et al., 2009) and low levels of tannins, saponins, and phenolic compounds (Nichols-Orians, 1991; Folgarait et al., 1996). When carried into the nests, all this material promotes a nutritional increase and accumulation of organic matter in the soil, which benefits the access of plant roots to these nutrients within the nests and even in the surrounding areas (Sternberg et al., 2007).

There are variations among ants both in the choice of the place to build their nests, as well in the way the soil is deposited (Pereira-Da-Silva, 1975; Moreira et al., 2004a). Due to the complexity of the nests, the ants choose the best locations, with adequate conditions of temperature and humidity to create the eggs, the young stages of the ant, and the symbiont fungus (Moreira et al., 2004b; Camargo and Forti, 2015). As ant colonies grow, tunnels and chambers expand radially (Alvarado et al., 1981; Moreira et al., 2004a; Jonkman, 2009) to maintain favorable conditions. Seasonal variations on microclimatic conditions in the colony can also alter the depth of the nest, although the spatial arrangement and design of the ant nests are generally species-specific (Moreira et al., 2004a,b).

Several factors and environmental conditions can influence the geographical distribution and richness of *Atta* ants, such as soil, vegetation, rainfall, temperature, and land-use history (Fowler et al., 1989; Swanson et al., 2019). The relationship with the climate, for example, is quite complex and not completely understood as well as the relationships between ants diversity and environmental aspects (Jenkins et al., 2011). Although temperate cool temperatures are a limiting factor, ants survive in a wide thermal and moisture spectrum due to an extensive and complex network of galleries, both horizontally and vertically depending on seasonal conditions, existing a continuous excavation process. Hence these networks can regulate the internal environment in terms of moisture, temperature, and gases concentration (CO_2, CH_4, N_2O, water vapor) (Swanson et al., 2019).

Few studies attempted to understand how the edaphoclimatic factors and land use, together, affect the distribution of *Atta* species. In this context, we aimed to spatialize the main occurrences of *Atta* species in the Brazilian territory and evaluate the main environmental conditions driving *Atta* ants in the Brazilian tropical landscapes. This preliminary study provides the first discussion on the interplay between the spatial distribution of *Atta* and key environmental variables.

MATERIALS AND METHODS

Study area

Brazil is a large territory in the neotropical zone of South America, with a complex geoenvironmental variability. According to Köppen-Geiger climate classification system (Peel et al., 2007), Brazil comprehends nine basic climate types: Tropical Rainforest (Af), Tropical Monsoon (Am), Tropical Savannah (Aw), Arid Steppe Hot (BSh), Arid Desert Hot (BWh), Temperature dry winter with warm summer (Cwb), Temperature dry winter with hot summer (Cwa), Temperature without a dry season and warm summer (Cfb) and Temperature dry summer with hot summer (Csa). In geological terms, Brazil has extensive exhumed Precambrian basement rocks, both igneous and metamorphic hate Precambrian to Paleozoic metasedimentary rocks, young Mesozoic to Cenozoic, sedimentary cover (Campos et al., 1974; Hasui et al., 2012) across the continental and coastal areas.

Brazilian soils encompass thirteen classes according to the Brazilian Soil Classification System (Santos et al., 2018) and eighteen according to Soil Survey Staff (2014), ranging from Acrisols, Cambisols, Chernozems, Podzols, Gleysols, Solonchaks, Ferrasols, Luvisols, Fluvisols, Lepptsols, Arenosols, Regosols, Nitisols, Histosols, Planosols, Solonetz, Plinthosols, and Vertisols. Brazil has six main biomes, represented by the Amazon Forest, Atlantic Forest, Dry *Caatinga*, Savanna (*Cerrado)*, *Pantanal,* and *Pampa* (IBGE, 2004a). Agricultural areas are a growing part of land-use types, since colonial times, with widespread deforestation of large areas of the Atlantic Forest biome (Dean, 1997), and fire remains a form of pasture to this day (Arroyo-Kalin, 2012). Alarming deforestation rates have been increasing in the last three decades, replacing rainforest and *Cerrado* by pasture land, agriculture, and urban areas (Rezende et al., 2018; Turubanova et al., 2018; Zaiatz et al., 2018).

Environmental data and spatial distribution

Registers of *Atta* in Brazil were obtained by the Global Biodiversity Information Facility (GBIF) databases, and scientific literature (Della-Lucia, 2011; GBIF, 2020). Twelve *Atta* species were identified, represented by *Atta cephalotes, A. laevigata, A. goiana, A. opaciceps, A. robusta, A. silvai, A. bisphaerica, A. capiguara, A. vollenweideri, A. sexdens piriventris, A. sexdens rubropilosa, and A. sexdens sexdens*. We chose not to use the very limited distribution of *A. goiana* and *A. silvai* due to scale compatibility and doubtful occurrence. For each *Atta* point in the territory, we extracted the respective geoenvironmental data. These data were biomes (IBGE, 2004a), climate (IBGE, 2002), and soils (Embrapa, 2011) on 1:5.000.000 spatial scale. Soil classes were adapted from the Brazilian Soil Classification System (Santos et al., 2018) to WRB (Soil Survey Staff, 2014). We also used the geology and vegetation land use map (IBGE, 2004b) at 1:1.000.000 scale (Campos et al., 1974). Soil properties, as total organic carbon (TOC), pH, sand, clay, Cation Exchange Capacity (CEC) were obtained by the inverse distance weighting (IDW) method from the soil database of Geoprocessing Laboratory (Labgeo) at Federal University of Viçosa. Climate attributes were annual average rainfall (AARainf), average rainfall wetter trimester (ARainWt), average rainfall driest trimester (ARainDt), annual amplitude temperature (AAmpT), annual average temperature (AATemp), average temperature wetter trimester (ATempWt) and average temperature driest trimester (ATempDt) obtained from the WorldClim (Hijmans et al., 2005). From these data, possible zonalities of occurrence of each *Atta* species were identified.

Statistical analyses

The *A. vollenweideri* data was considered in zone aspects as sufficient and excluded in all further statistical analysis. The selected 9 *Atta* species that present sufficient points and information about habitat and occurrence were submitted to statistical methods and zone mapping. The possible relations between *Atta* species occurrence with environmental variables were carried out using R Environment (R CoreTeam, 2020). Considering all 473 points that showed all the variables under study, obtained in the previous processing steps. To better describe the occurrence of the *Atta*'s species in relation to the different environmental features, we performed a relative proportion bar plotting. For all variables, we tested the normal distribution with the Shapiro-Wilk test, evaluated the Q-Q plot, and assessed homogeneity of variances by Lavene's test ($p<0.05$) using the "car" package (Fox and Weisberg, 2019). We used the Kruskal-Wallis' test followed by a post hoc Dunn's test ($p<0.05$) with the 'Dunn.test' package to compare the environmental properties (non-normally distributed data) represented by the CEC, TOC, pH, clay, sand, AATemp and AARainf, AAmpT, ATempWt and ATempDt, and ARainWt and ARainDt.

All variables were summarized with principal components analysis (PCA) to identify the environmental gradient (Qian et al., 2014; Villa et al., 2018). We also calculated Pearson correlations among all variables and the PCA ordination axes. The PCA was performed using the 'FactoMineR' package (Lê et al., 2008). To investigate a possible relationship between variables and species, a Canonical Correspondence Analysis (CCA) was used. For predictor selection, we assessed collinearity between selected predictor variables using Pearson correlation analysis; when two variables were strongly correlated ($r\geq0.7$) the most ecologically relevant predictors were selected (discarded variables were Average Annual Temperature and Average Annual Rainfall) for subsequent analyses for CCA. The environmental data were submitted to a multicollinearity test, to check the inflation factor of the variation (VIF <5). This analysis tests if the coefficients of variation are influenced by other explanatory variables, creating instability in the model (Borcard et al., 2011). Canonical Correspondence Analysis examines the similarity or dissimilarity in species composition (occurrence register point) along the environmental gradient. The significance of each variable in determining species compositional change was assessed by applying Monte Carlo randomizations (999 randomizations). The CCAs were performed using the ordiplot function of the "vegan" package (Oksanen et al., 2019).

RESULTS

Spatial distribution of the *Atta* species

The *A. laevigata* and *A. sexdens* are the two species with the largest distribution across the Brazilian territory. *A. laevigata* occupies 7.002.950 km², which represents 78.1 % of Brazil, while *A. sexdens* extends over 6.926.983 km² (77.2 %). Both *A. laevigata* and *A. sexdens* species occur throughout the Amazon, *Cerrado*, and Atlantic Forest biome domains (Figure 2e). The *A. sexdens* has three main subdivisions, the *A. sexdens sexdens* (4.621.580 km²; 51.5 %), in the Amazon and coastal Atlantic Forest biomes, whereas the *A. sexdens rubropilosa* (1.671.270 km²; 18.6 %) is located in central Brazil in *Cerrado* and parts of the highlands of Atlantic Forest; *A. sexdens piriventris* (634.133 km²; 7.1 %) is preferentially located along the borders of *Pampa* and southern Atlantic Forest. *A. vollenweideri* (263.401 km²; 2.9 %) partially share the same area with *A. sexdens piriventris,* at the extreme south of Brazil (Figure 1), under temperate/subtropical climate.

Atta cephalotes (3.916.930 km²; 43.7 %) shares an extensive forest area with *A. laevigata* and *A. sexdens sexdens*, covering the Amazon and the coastal Atlantic Forest biomes associated with tropical hot and wet conditions. On the other hand, *A. opaciceps* occupies 755.154 km² (8.4 %), with most occurrences in the Brazilian semi-arid zone (*Caatinga* biome). At the highlands of southern and southeastern regions *A. bisphaerica* (193.760 km²; 2.2 %) and *A. capiguara* (269.781 km²; 3.2 %), occur under special environmental conditions of the Atlantic Forest domain. Finally, *A. robusta* has the most restricted occurrence, representing 87.912 km² (1.0 %) of the coastal and sandy *Restinga* ranging from São Paulo to Pará (Figure 1).

All nine *Atta* species have registers in Ferrasols and Acrisols, which represent the most expressive soil classes in Brazilian territory. Cambisols are also common and only *A. cephalotes* and *A. opaciceps* have no records on this soil class (Figure 2a). Podzols are closely related to *A. robusta* along the coastline, followed by the *A. laevigata*, *A. sexdens sexdens*, and *A. cephalotes* in the Amazonian domain. Arenosols are also dominated by *A. robusta*, followed by *A. opaciceps* and *A. sexdens rubropilosa*. Nitisols have registers of *A. capiguara*, *A. sexdens piriventris*, *A. sexdens rubropilosa*, and *A. laevigata*. Planosols present a larger number of registers of *A. opaciceps*, with much less association with the following species: *A. robusta*, *A. laevigata*, *A. sexdens sexdens*, *A. sexdens piriventris*, and *A. bisphaerica* (Figure 2a). Most *Atta* ants are associated with low base saturation and dystrophy, except for *A. opaciceps* that occur mainly on eutrophic soils (Figure 2c).

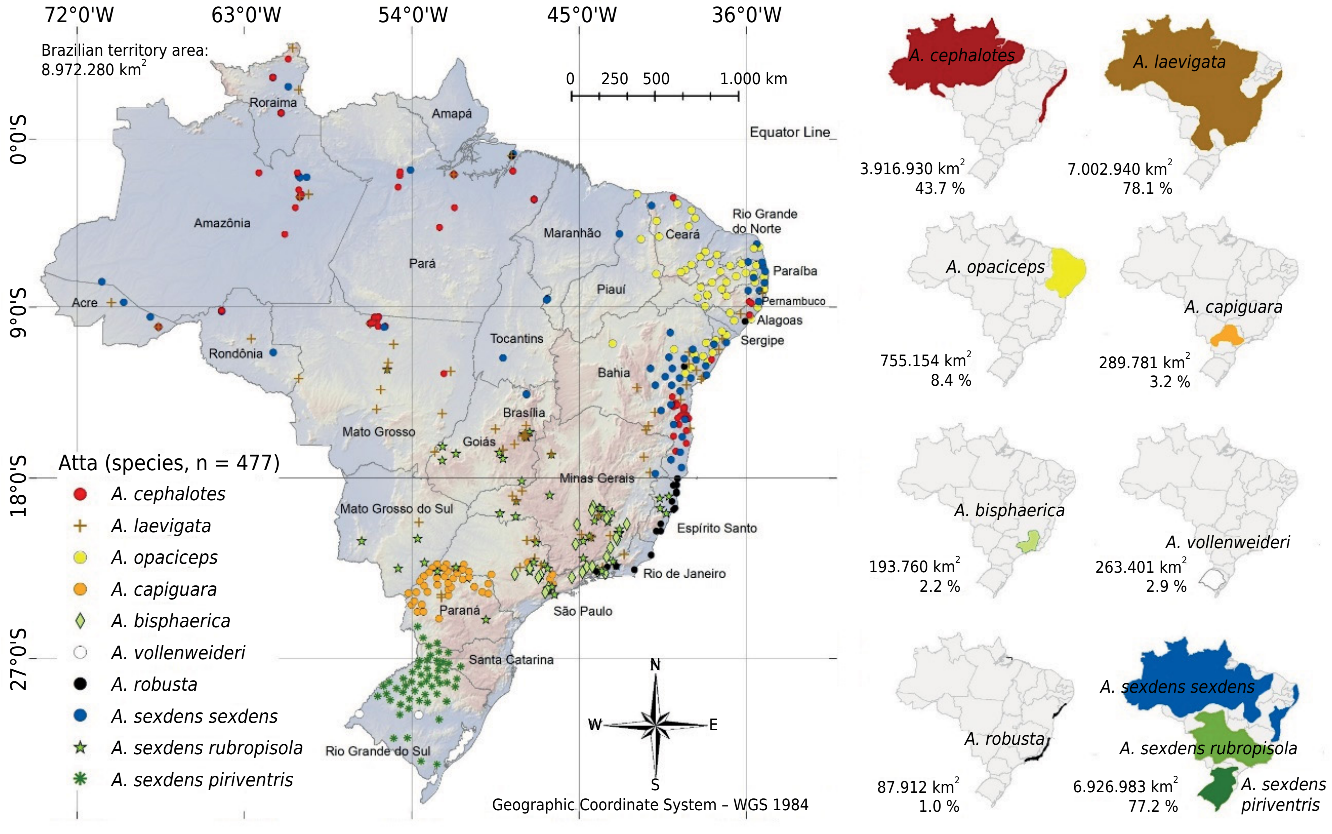

Figure 1. The genus *Atta* (Formicidae: Attini) spatial distribution at Brazilian territory.

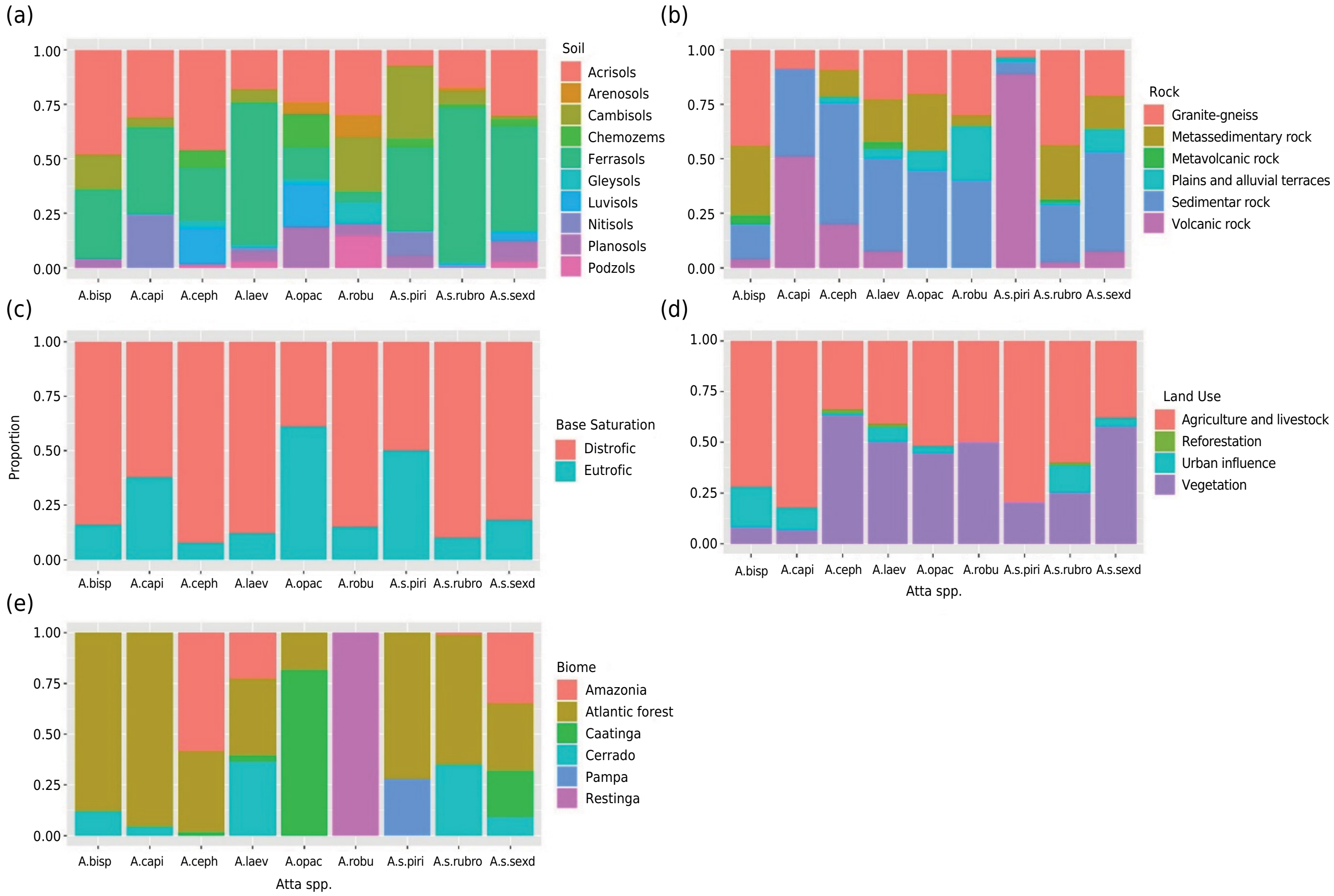

Figure 2. The proportion of *Atta* points occurrence and respective variables of the soils (a), rocks (b), land-use (d), base saturation (c) and biome (e).

All the nine *Atta* species have registers on ancient granite-gneiss basement rocks and sedimentary covers. Igneous rock of volcanic type revealed the presence of *A. sexdens piriventris* and *A. capiguara* preferably, and these two species appear to be absent from metamorphic or sedimentary rocks. The Quaternary sedimentary sequences are concentrated at the coastline with a close relationship with the presence of *A. robusta*, *A. sexdens sexdens*, *A. opaciceps*, *A. laevigata*, and *A. cephalotes* (Figure 2b).

Nine of ten *Atta* species are found on the Atlantic Forest, with *A. robusta* exclusively related to coastal *Restinga* vegetation. Five species are found in *Cerrado* (*A. bisphaerica*, *A. capiguara*, *A. laevigata*, *A. sexdens rubropilosa*, and *A. sexdens sexdens*), three in the Amazonian region (*A. cephalotes*, *A. laevigata*, and the *A. sexdens sexdens*), two in grassy *Pampa* (*A. sexdens piriventris* and *A. vollenweideri*) and only one specie in *Caatinga* - *A. opaciceps* - with a small extension in the ecotonal zone with the Atlantic Forest (Figures 1 and 2e).

Most *Atta* species are found in lands under agricultural and livestock land use (*A. capiguara*, *A. sexdens piriventris,* and *A. bisphaerica)* or natural vegetation (*A. cephalotes*, A. *laevigata*, and *A. sexdens sexdens*). *A. robusta* and *A. sexdens piriventris* have not been recorded in urban areas (Figure 2d).

Atta - environment interplays

To unveil the main relationships between leaf-cutting and *Atta* ants and environmental variables, we discuss the PCA results. Firstly, the PCA of soil properties explained 71.5 % of the variance in the edaphic aspects (Figure 3). The PCA1 explained 48.5 %, with a positive correlation with clay (R = 0.88, p<0.001), TOC (R = 0.71, p<0.001) and CEC (R = 0.40, p<0.001), and inversely, negative with sand (R = - 0.90, p<0.001) and pH (R = - 0.42, p<0.001). The PCA2 explained 23 % and was positively correlated with CEC (R = 0.71, p<0.001) and pH (R = 0.70, p<0.001), and negatively correlated with sand (R = - 0.22, p<0.001) and TOC (R = - 0.32, p<0.001).

The PCA of climate attributes explained 73.2 % of the variance and the temperature regime attributes were more important than rainfall attributes (Figure 4). The PCA1 explained 47.4 % and was positively correlated with AATemp (R = 0.87, p<0.001), ATempDt (R = 0.90, p<0.001), ATempWt (R = 0.86, p<0.001), ARainWt (R = 0.41, p<0.001), and negatively with AAmpT (R = - 0.71, p<0.001). The PCA2 explained 25.8 % and was positively correlated with AARainf (R = 0.97, p<0.001), ARainWt (R = 0.78, p<0.001), ARainDt (R = 0.36, p<0.001) and AAmpT (R = 0.33, p<0.001).

The CCA of soil properties explained 76.7 % (CCA1, 53.3 %; CCA2, 23.4 %) of *Atta* species variances according to pedology (Figure 5a). The CCA separated *Atta* species along pedological gradients, on which *A. opaciceps*, *A. sexdens sexdens*, and *A. capiguara* were positively associated with high pH and sand content, while *A. sexdens piriventris*, *A. sexdens rubropilosa*, and *A. bisphaerica* were linked to clay and organic carbon contents. *A. cephalotes* has positively associated with CEC whereas *A. robusta* was inversely correlated with this variable.

The CCA of climate attributes explained 77 % (CCA1, 46.4 %; CCA2, 30.6 %) of *Atta* species variances according to climatology (Figure 5b). The CCA divided *Atta* species with temperature and rainfall regimes. *A. opaciceps*, *A. sexdens sexdens*, *A. cephalotes*, *A. robusta*, and *A. laevigata* were positively associated with higher temperatures; while *A. capiguara*, *A. sexdens rubropilosa*, and *A. bisphaerica* were linked to high rainfall and thermal amplitude, and *A. sexdens piriventris* associated with high pluviosity in the driest trimester and thermal amplitude, and *A. opaciceps* with hot, dry climates.

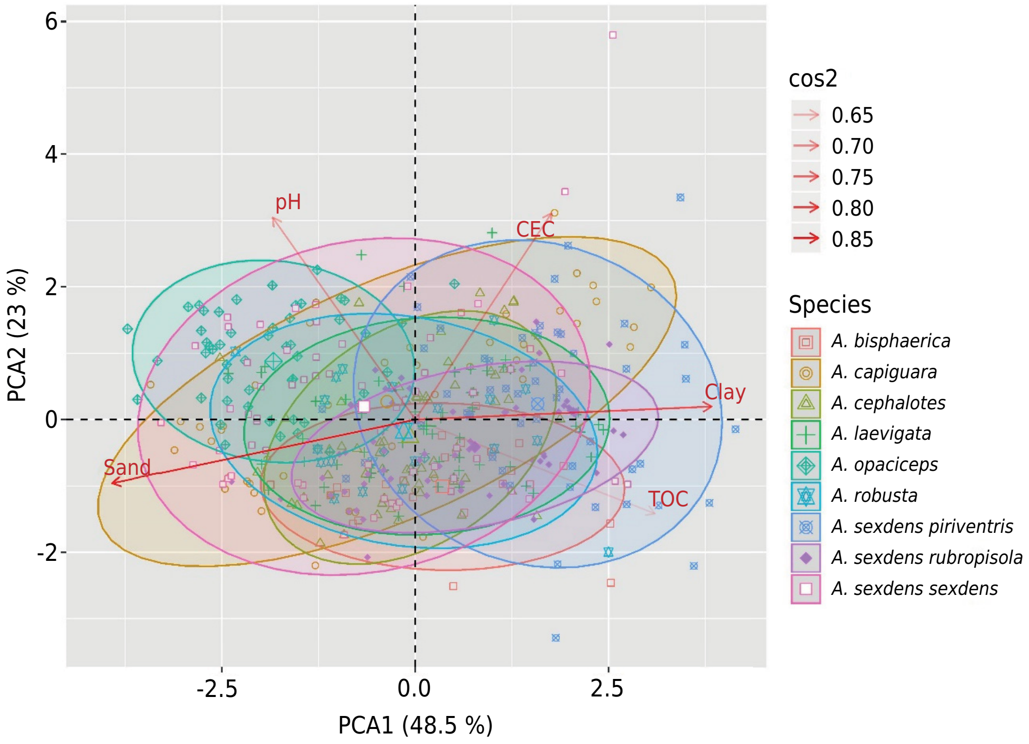

Figure 3. Principal Component Analysis (PCA) of relations between the *Atta* species points and soil properties. The soil variables are Total Organic Carbon (TOC), cation exchangeable capacity (CEC), pH, sand, and clay. Pearson correlation of each vector is indicated in cos2.

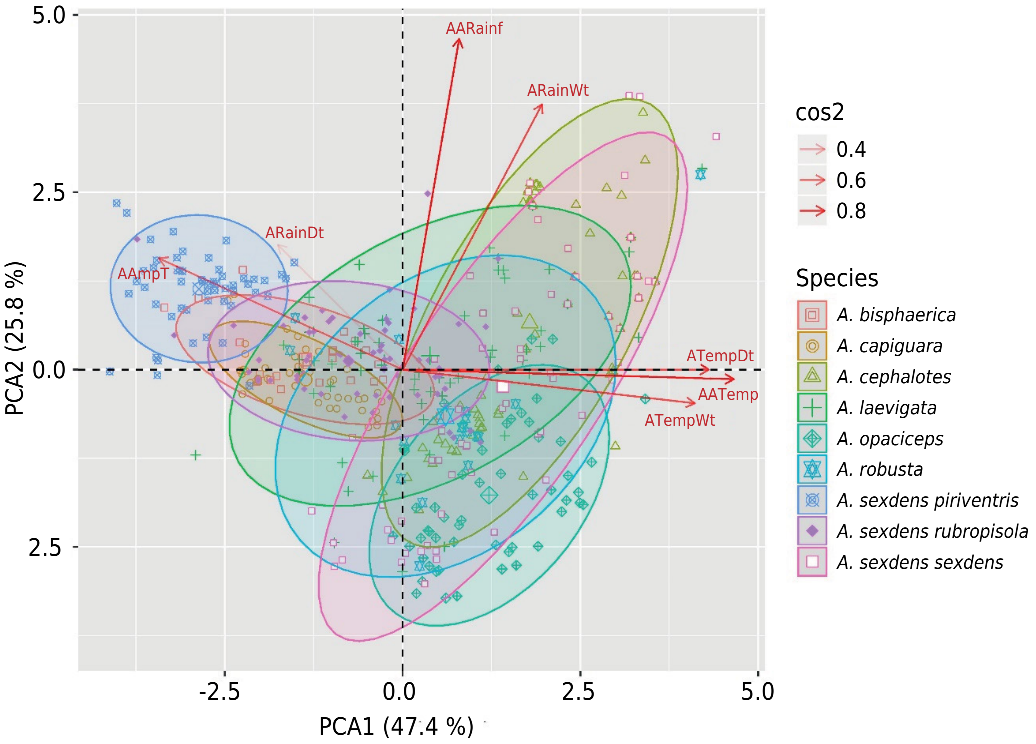

Figure 4. Principal Component Analysis (PCA) of relations between the *Atta* species points and climatic aspects. The variables are annual average rainfall (AARainf), average rainfall wetter trimester (ARainWt), average rainfall driest trimester (ARainDt), annual amplitude temperature (AAmpT), annual average temperature (AATemp), average temperature wetter trimester (ATempWt), and average temperature driest trimester (ATempDt). Pearson correlation of each vector is indicated in cos2.

DISCUSSION

All nine *Atta* species showed records nutrients-poor dystrophic soils and ancient weathered granite-gneiss and sedimentary terrains, which represent most of the Brazilian geology, with Precambrian shields and Paleozoic platform covers (Hasui et al., 2012). *A. opaciceps* and *A. sexdens piriventris* are the two species with a high occurrence in nutrient-rich eutrophic soils, whereas *A. capiguara* has a close occurrence in eutric Nitisols associated with basalts rocks of the Paraná Basin (Hasui et al., 2012).

The close association between Atta and dystrophic soils may be attributed to the acid conditions required for fungus culture, where more fertile soils can increase the competition of soil microbiota (Bento et al., 1991; Moutinho et al., 2003; Siciliano et al., 2014), leading to lower fungi richness (Sun et al., 2016). There are differences between *Atta* species in their ability to control invasive microorganisms that can damage the colony's fungal culture (Vieira et al., 2015) and acid, weathered soils may promote lesser invasion risk. In addition, nutrient-poor dystrophic soils, such as Ferrasols (*Latossolos*), have a friable microaggregate structure that favors the establishment of new colonies (Ker, 1997; Schoereder and Silva, 2008), resulting in a positive feedback.

Soil structure is considered very important in driving spatial distribution and nesting of leaf-cutters ants (Costa-Milanez et al., 2017). In soils with high clay content, ants roll or "pelletize" soil particles into 1- to 3-mm-sized aggregates used building blocks in the construction of wind turrets over vent openings in nests of *A. vollenweideri*, for instance (Swanson et al., 2019). *A. cephalotes* also uses pellets in their nests and *A. sexdens* sub-species create a drier, less dense, more porous mound with pelletized soils that enhance evaporation in nests depths ranging from 0.50 to 2.00 m (Swanson et al., 2019) (Figure 6). Note that the deeper chamber of *A. sexdens* sub-species, at 1.90 m

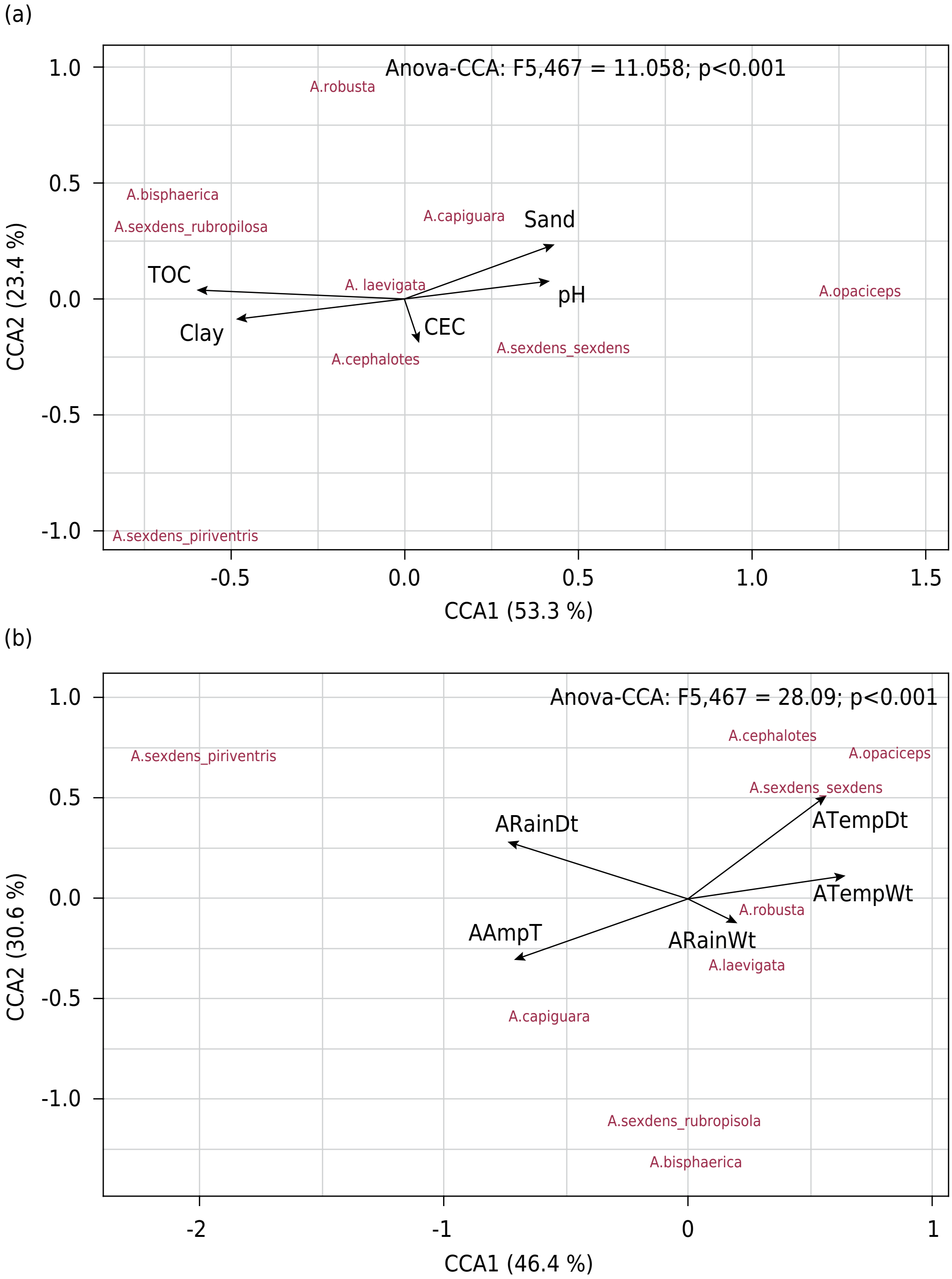

Figure 5. Canonical correspondence analysis (CCA) of soil and climate properties associated with different *Atta* species occurrence. In A, the soil aspects of Total Organic Carbon (TOC), cation exchangeable capacity (CEC), pH, sand, and clay. In B, the climate attributes of annual average rainfall (AARainf), average rainfall wetter trimester (ARainWt), average rainfall driest trimester (ARainDt), annual amplitude temperature (AAmpT), annual average temperature (AATemp), average temperature wetter trimester (ATempWt), and average temperature driest trimester (ATempDt).

depth, (Figure 6c) display cominuted fragments of plastic brought to the nest by the indiscrimate cutting behaviour of *Atta sexdens* sub-species. The microaggreegates are clearly visible in the old, abandoned chambers (Figures 6a and 6b.) Poor soils raises their importance in ecosystem functions.

Leaf-cutter ants remove 1-2 tons of fresh plant material annually that is rapidly decomposed in the nest by symbiotic fungi, promoting changes in physical, chemical and biological conditions, and also affecting the availability of nutritional resources and habitats for other organisms such as plants (Swanson et al., 2019). The fine root biomass is higher within leaf-cutting ant nests, with higher densities around and within external and internal

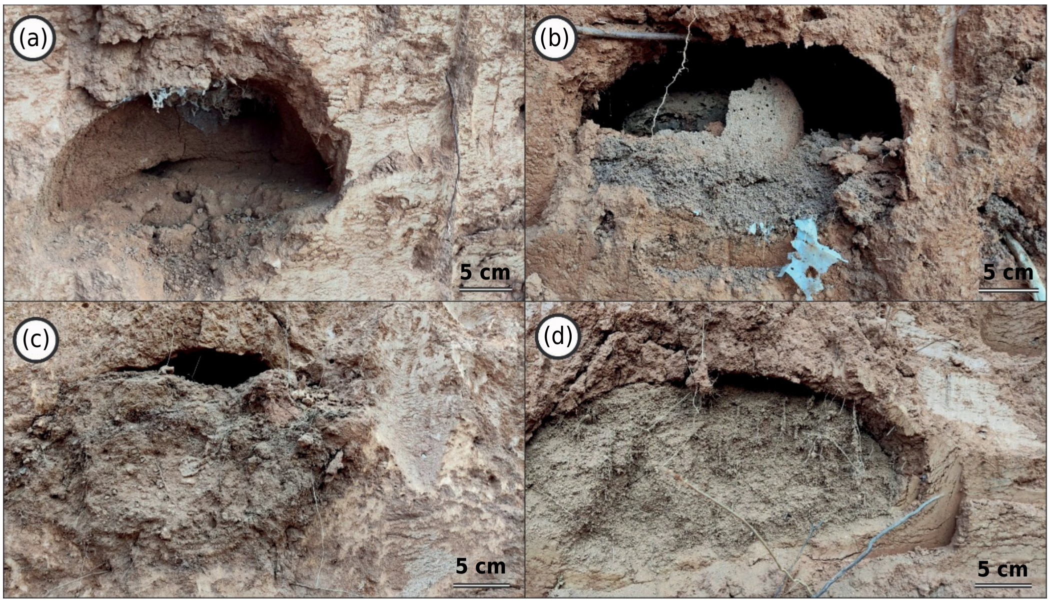

Figure 6. The progressive infilling of a nest chamber with microaggregates (100-300 micrometers in diameter) of Oxisol (*Latossolo*) within a gneiss saprolite from Viçosa, MG.

litter chambers, evidencing its important role as an enhancer of nutritional quality in poor soils (Swanson et al., 2019).

Results showed the overlapping of three different species in Amazon, but with different correlations with soil attributes. *A. laevigata* do not have any preference, whereas *A. cephalotes* is correlated with soils with high TOC, CEC, and *A. sexdens sexdens* is more positively correlated with sand contents and pH. *A. cephalotes* is closely related to old, mature native forest environments, being an indicator of their conservation status. *A. laevigata* prefers disturbed habitats, in secondary regenerating process, and *A. sexdens sexdens*, the most flexible of all species, can be found in both environments (Fowler et al., 1989; Vasconcelos and Cherrett, 1995; Forti et al., 2020).

Overlapping of *A. sexdens rubropilosa*, *A. capiguara*, and *A. bisphaerica* does not imply competition. *A. sexdens rubropilosa* and *A. bisphaerica* have a positive correlation with TOC and clay content in soils, while *A. capiguara* have an opposite correlation, also reported by Forti et al. (2020). *A. s. rubropilosa* prefers dicots, while *A. capiguara* and *A. bisphaerica* prefer monocots (Fowler et al., 1989; Cabral, 2015; Pereira et al., 2016), and these species are more associated, respectively, with pasture and sugarcane areas. This can indicate that replacing natural vegetation and large monoculture monocotyledonous plantations may be an important factor in disseminating and increasing population density of these species (Forti et al., 2020).

Atta sexdens rubropilosa predominates in Ferrasols, generally of clayey texture, with organic-rich and microbiota-rich surface horizons (Vieira et al., 2015). The nests of this species are built up to approximately 0.15 m depth (Vieira et al., 2015). These shallow nests afford greater production of antibiotic compounds inside metapleural glands, which help control the invading microbiota (Vieira et al., 2015). These physiological traits favored during the evolution allowed the of *A. sexdens rubropilosa* nesting in the Brazilian highlands, with widespread distribution in southeastern Brazil (Cabral, 2015; Vieira et al., 2015).

In southern Brazil, just two species occur *A. sexdens piriventris* and *A. vollenweideri*. Although both species can be found in the same region, *A. sexdens piriventris* occur in *Araucária* Forest and *Pampa*. This species is associated with clayey soils, and can be found in Grasslands below 1000 m, and associated or not with *Araucária* (Giesel et al., 2013, 2020). The *A. vollenweideri* occurs mainly in the southern grasslands of lowland *Pampa*, preference foraging monocots, whereas *A. sexdens piriventris* prefers dicots (Fowler et al., 1989; Cosarinsky and Roces, 2007). *A. vollenweideri* have a low density of secretory cells, build their nests at greater depths – down to 0.368 m - in deeper clayey horizons, and with less microbial biomass due to the need to protect their colonies during flooding periods (Vieira et al., 2015). These physiological characteristics evolved to nesting in open, grassy, soil environments (Cabral, 2015; Vieira et al., 2015).

Atta robusta is restricted to coastal sandy areas with incipient pedological development, on the Quaternary fluvio-marine sediments where *Restinga* vegetation grows (Fowler, 1995; Cabral, 2015). It also has a strong association with sandy *Restinga* soils, being replaced by *A. sexdens rubropilosa* in places of clayey soils or disturbed by anthropic action (Fowler, 1995). The Restinga soils are commonly nutrient-poor (Scarano, 2002). The predominant soils in this pedoenvironments are Spodosols and Quartzarenic Neosols (Rossi and Mattos, 2002; Gomes et al., 2007). The occurrence of this species is related to greater temperature/rainfalls variations and low altitudes (Dáttilo et al., 2012).

A. robusta is found preferentially associated with native vegetation of *Restinga* thickets foraging *Clusia fluminensis* Planch. & Triana, a dominant species in *Restingas* (Fowler, 1995). The varying foraging habits of *A. robusta*, from the exotic species *Terminalia catappa* L. to the mangrove species (*Rhizophora mangle* L.), indicate that soils are more important for their presence than the plant species used for the cultivation of fungi. The widespread urbanization of coastal environments, including *Restingas*, poses a risk of extinction to *A. robusta* given its small geographical distribution and threats to its natural habitat (Fowler, 1995).

In the semi-arid *Caatinga*, an environment of severe conditions for many species, generalist species, such as *A. laevigata*, *A. sexdens sexdens*, and *A. sexdens rubropilosa* occur, but with a greater importance of the only "endemic" species of the genus, *A. opaciceps* (Fowler et al., 1989; Ulysséa and Brandão, 2013; Siqueira et al., 2017). Our results illustrate a greater association of *A. opaciceps* with the core semiarid area, with hotter and drier climates (Figure 5b) (Siqueira et al., 2018), whereas the other species are present in the transitional ecotones with the adjacent biomes. In addition to this occurrence in central *Caatinga*, *A. opaciceps* is well-adapted to anthropogenic landscapes (Knoechelmann et al., 2020), with a preference for open, shrubby vegetation, where *Atta* may contribute to maintaining this spatial pattern of vegetation, as postulated by Knoechelmann et al. (2020).

Atta ants are a key component of the biopedological system responsible for numerous nutritional, chemical, and structural changes in soils. Soils affected by nests tend to have greater microbial activity and production of hyphae and roots (Leite et al., 2018; Fernandez-Bou et al., 2019). The organic matter inputs in deep horizons and the disposal of residues, both in the garbage chambers of the colonies and at the surface outside the nests, enhances soil nutrition as well as nutrient cycling (Farji-Brener and Silva, 1995; Leite et al., 2018; Santos et al., 2019).

In addition to nutritional improvement, they increase soil aeration and infiltration by creating macropores, breaking seed dormancy, and consequently improving local physical conditions for subsequent colonization by plants during ecological succession (Sternberg et al., 2007; Giesel et al., 2013; Leite et al., 2018). In semiarid regions, *A. opaciceps* pedological activities may be even more important for the ecosystem's resilience, since in the mounds nests act as collectors of the water flow in the short rainy season, directing nutrients and humidity to local points that can be instrumental in recruiting and maintaining new plants (Leite et al., 2018).

As our results indicate, *Atta* species are well adapted to disturbed landscapes revealing that *Atta* is a genus resilient to environmental disturbances (Diehl et al., 2017; Segat et al., 2017). These species were associated with young forests (Vasconcelos and Cherrett, 1995; Segat et al., 2017), forest edges (Silva et al., 2018), road edges (Forti et al., 2020), grazing sites (Leite et al., 2018) and open habitats (Dalle Laste et al., 2019; Swanson et al., 2019). This indicates that the wide dispersion of the *Atta* genus may have been favored by increased degradation of biomes (Siqueira et al., 2017).

The wide range of *A. laevigata* in open areas and disturbed habitats (Vasconcelos and Cherrett, 1995; Leite et al., 2018; Forti et al., 2020) may be related to the high abundance of pioneer species with high-nutrient contents in leaves, combined with a lower concentration of secondary chemical compounds that inhibit predation (Vasconcelos and Cherrett, 1995). Also, *A. laevigata* forages in both monocotyledons and dicots and this may explain its wide distribution in Brazil (Fowler et al., 1989; Vasconcelos and Cherrett, 1995; Vieira-Neto and Vasconcelos, 2010; Siqueira et al., 2017).

Given their ecological characteristics, some species may have an important role as a pedological agent counteracting the anthropogenic impacts. Agricultural activities cause soil compaction, lower infiltration, and greater runoff, consequences that are compensated or buffered by *Atta*'s pedobioturbation activity (Lavelle et al., 2016; Leite et al., 2018). The bioturbation performed by *Atta* ants acts in the structural arrangement of soils from construction to the maintenance of nests, galleries, chambers, and tunnels, bringing material from the deepest horizons to the surface, mixing organo-mineral aggregates, and creating new layers (Lavelle et al., 2016; Leite et al., 2018). Hence, *A. robusta* in *Restinga* can be an agent that affects podzolization processes, contributing to the formation of the spodic Bh horizon, for example.

This study supports further studies focused on the evolution of the genus *Atta*. This genus appeared approximately 8 to 13 million years ago, suggesting that irradiations, mainly across neotropical South America, are rather recent (Schultz and Brady, 2008; Bacci et al., 2009). It should be the case of the subgenus *Neoatta*, composed of the species *A. sexdens sexdens*, *A. sexdens piriventris*, *A. sexdens rubropilosa* and *A. robusta*, the most derived compared with the basal subgroups of the genus (Schultz and Brady, 2008; Bacci et al., 2009). Even these more differentiated species have different preferences regarding the clade of fungus used as food (Mueller et al., 2018). This adaptive irradiation is supposedly linked to the different environments/soils that *Atta* experienced during the successful advance throughout the Brazilian land surface, resulting in most species closely related to certain environmental conditions, as previously showed and discussed.

Also, further studies on the occurrence of the genus *Atta* and its environmental interplays, mainly in inland areas, such as the western Amazon and the *Pantanal* biome, are urgently needed to enhance our understanding of the role of *Atta* in anthropogenic, agropastoral landscapes.

CONCLUSIONS

Key species of *Atta* leaf-cutting ants in the neotropics are not randomly dispersed in the Brazilian landscape but have a close relationship with the complex environmental heterogeneity of the Brazilian neotropical zone. Latitudinal altitudinal climate gradients, soils, vegetation, geology, and anthropic landscapes - urbanization, agriculture, and livestock - are all interwoven with the spatial land distribution of the leafcutter *Atta* ants.

At a large scale, the spatial distribution of *Atta* was most correlated with a climatic gradient. At local scales, soil properties appear to be more determinant. The *Atta* species that occurs on most of the Brazilian land surface are the generalists *A. sexdens* and *A. laevigata*, while other species are most restricted to special environmental conditions, such as *A. robusta* at the sandy coastal plains, and *A. opaciceps*, concentrated in the semiarid Northeastern region.

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SUPPLEMENTARY DATA

Supplementary data to this article can be found online at https://www.rbcsjournal.org/wp-content/uploads/articles_xml/1806-9657-rbcs-45-e0210073/1806-9657-rbcs-45-e0210073-suppl01.pdf

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