



Connection between tree functional traits and environmental parameters in an archipelago of montane forests surrounded by rupestrian grasslands[☆]

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ABSTRACT

Forest islands are unique habitats standing out across mountains dominated by rupestrian grassland in southeastern Brazil. In this work we evaluated the relationship between the plant species functional traits (number of ecoregions in which a species occurs, potential height, mean height, mean basal area, mean leaf area) and ecological variables (leaf damage from chewing herbivores, the number of individuals) with environmental parameters (physical and chemical properties of the soil, canopy cover) of the tree communities in an archipelago of montane forest islands immersed in rupestrian grasslands. We found a strong connection between the traits of tree species and environmental parameters; habitats associated with high soil fertility and canopy cover (leaf area index) harbored species with high structural values (i.e., height and basal area), broad distribution among Brazilian ecoregions, high rates of leaf damage from chewing insects and fewer individuals. Habitats with low soil fertility and canopy cover values harbored species with low structural values, restricted geographic distribution and low rates of leaf damage by chewing insects. Although physical parameters play an important role in the establishment of forest islands, our results point to chemical indicators of soil fertility as a relevant environmental promoter, influencing the composition and structure of island tree communities. The impact of local habitat parameters on the tree species functional traits showed that habitat heterogeneity is essential in structuring tree communities in this natural archipelago of forest islands. We advocate that understanding the connection between habitat parameters and species functional traits can help to predict the ecological consequences of anthropogenic or natural impacts to those forests, supporting the development of effective conservation strategies.

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1. Introduction

Ecological relationships, whether antagonistic (e.g., predation, herbivory, competition) or mutualistic (e.g., pollination, seed dispersal), are important mechanisms for the maintenance of communities and can influence the distribution of species along environmental gradients (Gotelli and McCabe, 2002; Englund et al., 2009; Kraft et al., 2015). However, both regional (e.g., landscape

effects) and local environmental parameters may play a key role in the success of species establishment (Ackerly and Cornwell, 2007; Jamoneau et al., 2011), and therefore, environmental parameters could act as a filter or promoter, determining the establishment of some species (Southwood, 1988; Grime and Pierce, 2012).

Among local environmental parameters that are directly related to species distribution in tropical forests, soil properties, canopy cover, temperature, seasonality and rainfall stand out as filters or promoters to establishment (Lebrija-Trejos et al., 2010; Paine et al., 2011; Lasky et al., 2013). The response of each species to such environmental properties is dependent on their phenotypic characteristics expressed by genes under the influence of the environment. Functional traits can be defined as any measurable trait at the individual level that is directly or indirectly related to reproductive performance (fitness) (e.g., growth, fecundity, survival) (Violle et al., 2007). The relationship between plant functional traits and

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habitat properties can unveil drivers behind species distributions along environmental gradients. This might advance the understanding of ecosystem functions and represents a tool for predicting how changes in the properties of the habitat can influence species distribution and establishment (Lavorel and Garnier, 2002; de Bello et al., 2010).

The association between forest and grassland vegetation has fueled the interest of the scientific community, especially understanding how drivers control the natural boundaries between such very distinct ecosystems (Safford, 2007; Bond, 2008, 2010; Rehm and Feeley, 2015). There are many factors that can influence the expansion or contraction of forest edges on natural grasslands, among them climate (Harsh and Bader, 2011; Halladay et al., 2012; Halladay et al., 2012), seed dispersion and germination, and seedling establishment (Dullinger et al., 2004; Cierjacks et al., 2007; Körner, 2012; Rehm and Feeley, 2013), fire (Bond and Keeley, 2005; Veldman et al., 2015), soil patches (Coelho et al., 2016), as well as anthropogenic disturbances (Kolbek and Alves, 2008) stand out. Most studies on the subject have focused on high mountains, between 3000 and 4000 m a.s.l., where forests are replaced by grasslands with increasing altitude (Körner, 1998; Jobbágy and Jackson, 2000; Körner and Paulsen, 2004). However, tropical mountains of lower altitudes (between 1000 and 3000 m a.s.l.) or tropical snow-free mountains (Streher et al., 2017) exhibited naturally fragmented landscapes formed by forest islands immersed in a grassland matrix, characterizing true forest archipelagos. In such landscape, forests and grasslands coexist at the same altitudinal levels, indicating that additional factors such as soil physical and chemical parameters might be responsible for the distribution of tree species (Coelho et al., 2016). Thus, natural forest islands on mountaintops are excellent models for testing hypotheses involving the connection between local environmental properties and the functional traits of tree community. Understanding how environmental parameters of the habitat are related to the species composition of forest islands will improve knowledge regarding the genesis, maintenance and ecological connection between naturally fragmented forests and the grasslands in which they are immersed.

The Espinhaço Mountain Range (Cadeia do Espinhaço) is the largest mountain chain in Brazil and, especially in its southern portion, separates two biodiversity hotspots, the Cerrado and the Atlantic Forest (Silveira et al., 2016). The more humid eastern slopes of the mountains are covered by semi-deciduous forests associated with the Atlantic Forest domain, while the drier western slopes are covered by physiognomies associated with the Cerrado domain – predominantly *campo rupestre* (Silveira et al., 2016) – hereafter rupestrian grasslands. Part of the humidity of the eastern slope of the mountains reaches the transitional zones located near the mountaintops and advances over rupestrian grasslands located at higher altitudes (Coelho et al., 2016, 2018; Streher et al., 2017). When the moist conditions are associated with soil patches with chemical and physical parameters different from surrounding rupestrian grasslands soil, these areas of environmental suitability favor the establishment of tree-dominated physiognomies or forests islands, locally called *capões de mata* (Coelho et al., 2016 and references therein). Tree species are dispersed to these humid mountaintops predominantly by animals, via gallery forests from the eastern slope, forming archipelagos of forest islands (Coelho et al., 2018; Pereira et al., 2017). Since forest islands are not able to expand due to soil and micro environmental conditions, they increase the landscape complexity of the rupestrian grasslands (Coelho et al., 2016). However, understanding how these forest islands connect with local environmental conditions and what factors are determinant for their establishment and maintenance is a *sine qua non* requirement to unveil how forest islands integrate into the contrasting grassland matrix in which they are immersed. The soils of the rupestrian grasslands have acted as major environmen-

tal filter leading to a predominance of the stress-tolerant strategy in plant communities what points out to the existence of very specific conditions promoting the establishment of wet forest islands (Negreiros et al., 2014).

We investigate therefore the functional traits and associated environmental parameters of forest islands from Espinhaço range. We expect a strong connection between the functional traits and ecological variables of the tree community – number of ecoregions in which a species occurs, potential height, mean height, mean basal area, mean leaf area, foliar damage caused by chewing folivores, number of individuals – and the habitat parameters relevant to the establishment and maintenance of forest islands – physical and chemical soil properties, and canopy cover. Thus, the following hypotheses were tested: 1) leaf damage, leaf area, number of ecoregions, average height, potential height and average basal area respond positively to canopy cover and soil fertility, and 2) species abundance respond negatively to canopy cover and soil fertility.

2. Materials and methods

2.1. Study area

This study was carried out in Serra do Cipó in the southern portion of the Cadeia do Espinhaço, in the central region of the state of Minas Gerais, southeastern Brazil. According to the Köppen classification system, the climate of Serra do Cipó is type Cwb with well-marked seasonality of dry winters and humid summers (Alvares et al., 2013). The average rainfall in the region ranges from 1300 to 1600 mm and is concentrated between November and January (Madeira and Fernandes, 1999; Fernandes et al., 2016). The vegetation of Serra do Cipó is predominantly influenced by components of two important ecoregions in Brazil, the Cerrado domain to the west and the Atlantic Forest domain to the east. The soils associated with grasslands environments are generally acidic, with high levels of aluminum saturation and low levels of base saturation (Schaefer et al., 2016; Silveira et al., 2016). The Cerrado is represented predominantly by rupestrian grasslands located above 900 m, which covers more than half of the area of Serra do Cipó and hosts most of the diversity and endemism recorded for the region (Madeira et al., 2008).

The forest islands of the Espinhaço Range are forest formations of edaphic-climatic nature; that is, their maintenance is dependent on specific climate and soil parameters (see Coelho et al., 2016 for a review). They are immersed in a rupestrian grassland matrix and located above 1200 m a.s.l. (Fig. 1). Because they are close to the mountaintops, they are within the zone of influence of the tropical Atlantic mass arising from the eastern slope – more humid and within the Atlantic Forest domain – which loses strength on the western slope – drier and in the Cerrado domain (Coelho et al., 2016). Thus, these forest islands provide an important ecological service of protecting regions of springs and headwaters of the tributaries of important Brazilian rivers (Coelho et al., 2018). Seven forest islands were selected for this study (Fig. 2) based upon level of conservation, size and accessibility (Fig. 2).

2.2. Sampling design

A 20 × 50-m plot was placed in the center of each island and subdivided into 10 sub-plots of 10 × 10 m for a total of seven plots and 70 subplots for all the seven islands selected. All individual trees, with diameter at breast height (DBH) greater than 2.5 cm, in each plot were marked and numbered with aluminum tags. Information regarding the number of each individual, plot and subplot of their location were included with each tag. For each tagged tree, the height was measured with a Haglof Electronic Clinometer,



Fig. 1. Photos of forest islands immersed in rupestrian grasslands matrices at Serra do Cipó, southeastern Brazil. (a) internal detail of a forest island (capão de mata); (b) detail of an ecotone between rupestrian grasslands and forest islands, as well as the canopy with emergent individuals; (c) example of the insertion of forest islands in the rupestrian grasslands matrix.

since it provides more precise and accurate measurements, and the DBH (Diameter at Breast High) was measured with a tape measure (Mueller-Dombois and Elenberg, 1974).

2.3. Collection of botanical material

Field campaigns took place from December 2012 to February 2013, the peak of the rainy season. Botanical material of each individual was collected with the help of a 9-stage pruning shears, each measuring 1.5 m. After identification, the specimens were deposited in the herbarium of the Departamento de Botânica-UFMG (BHCB). The classification of the species followed the system proposed by Angiosperm Phylogeny Group IV (APG IV, 2016).

Thirty mature and completely expanded leaves were collected from the apical third of each individual ($n=2008$ sampled). The leaves were pressed in the field and transported to the laboratory. After drying, all leaves were scanned using a desktop scanner at 300dpi resolution. Leaf damage caused by chewing insects was estimated for each leaf with the help of the program Image Tool (University of Texas Health Science Center at San Antonio, San Antonio, TX, USA). All images were calibrated to 0.1 mm before measurements and the program allowed no resolution errors greater than 1%. The average leaf damage of the 30 leaves of each individual was used as replicates.

2.4. Soil collection

A composite soil sample (of approximately 500 g) was collected in each subplot, which represented a valid estimate of the average of the nutritional levels of five simple samples of 100 g (modified

from Binkley and Vitousek, 1989), for a total of 10 composite samples per plot and 70 soil samples for the entire study. Sampling was done according to the procedures described by Dick et al. (1996). The pH in water was measured using the proportion of 1:2.5 (v/v) of soil:solution. The exchangeable cations Ca^{2+} , Mg^{2+} and Al^{3+} were extracted by a solution of 1 mol/L KCl and the contents of Ca^{2+} and Mg^{2+} were determined by titration with 0.01 mol/L EDTA and the contents of Al^{3+} by titration with 0.025 mol/L NaOH, according to EMBRAPA (1999). The elements P and K were extracted by Mehlich 1 solution. The potential acidity ($\text{H} + \text{Al}$) was extracted with a 0.5 mol/L calcium acetate solution at pH 7.0 and determined by alkalimetric titration of the extract (EMBRAPA, 1999). Aluminum saturation (m) and base saturation (V), were calculated with the equations $m = 100 \cdot \text{Al}^{3+} / (\text{K} + \text{Ca}^{2+} + \text{Mg}^{2+} + \text{Al}^{3+})$; and $V = 100 \cdot (\text{K} + \text{Ca}^{2+} + \text{Mg}^{2+}) / (\text{K} + \text{Ca}^{2+} + \text{Mg}^{2+} + \text{H} + \text{Al})$, respectively (Alvarez et al., 1999).

2.5. Canopy cover sampling by means of hemispheric photos

In January 2013 — at the peak of the wet season — a hemispheric photo was taken at the center of each subplot for a total of 10 hemispheric photos per plot and a total of 70 photos for the entire study. The photos were taken with the camera facing north and positioned 1.50 m above the ground with the aid of a tripod. The photos were taken early in the morning or late in the afternoon with a Nikon CoolPix 5400 digital camera with a FCE9 fisheye lens. The photos were evaluated using the software Gap light Analyzer 2.0, which was calibrated by altitude and coordinates (Frazer et al., 1999). Hemispherical images have a wide coverage (180°) with light openings between the angles of 0 to 75° , simultaneously. Using the Gap

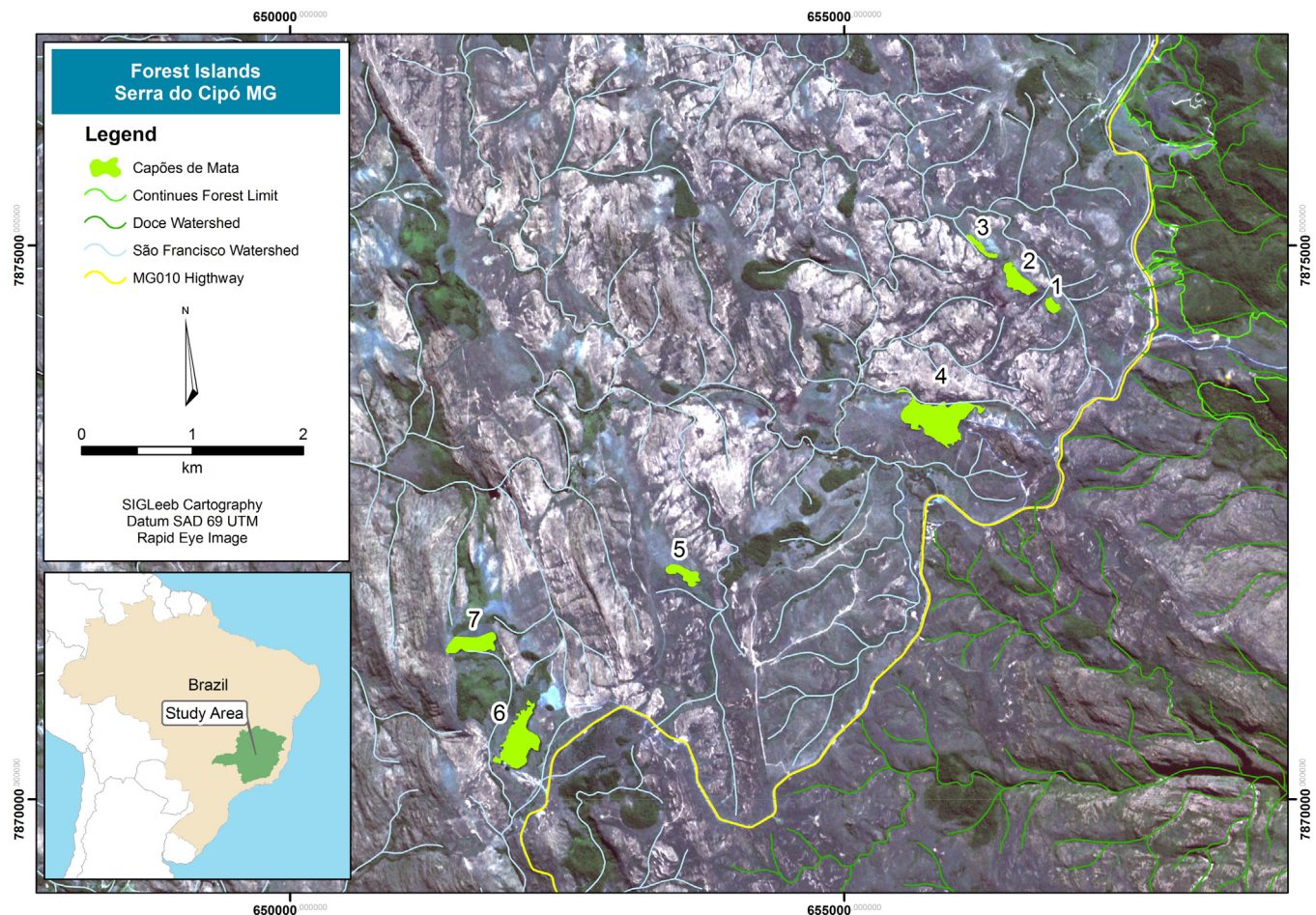


Fig. 2. Location of the seven Atlantic Forest islands at Serra do Cipó showing their association with the basins and sub-basins of the Rio São Francisco and Rio Doce rivers (source: Minas Gerais State Water Management Institute). The islands varied in size from 12,938 m² to 169,562 m², while their perimeters varied in length from 480 m to 2,836 m.

Light Analyzer software, we calculated the effective leaf area index (LAI) was calculated and integrated along the zenith angle from 0 a 75 ° (Welles and Norman, 1991).

2.6. Data analyses

A recent way of evaluating the response of functional traits of biological communities to habitat parameters was recently proposed by Dray et al. (2014), which combines two methods: the fourth-corner and RLQ (Dolédéc et al., 1996; Legendre et al., 1997). We used these two methods to test the hypothesis of connection between the functional traits of the tree species and the environmental parameters. The two methods are complementary as RLQ uses simultaneously three matrices: matrix “R” (habitat parameters), matrix “L” (occurrence or abundance of species) and matrix “Q” (functional traits of species). The two methods cross the functional traits of the species with the environmental parameters mediated by the occurrence of the species at the sites. The complementarity of the two methods is that while RLQ synthesizes multivariate structures, fourth-corner tests the pair-to-pair significance of functional traits and habitat parameters (Dray et al., 2014). Therefore, these two methods combined can point to those functional traits that are related to specific habitat parameters and how these act synergistically. In the floristic matrix “L”, rows corresponded to the areas (seventy 10 × 10 m subplots), while columns corresponded to the 142 species sampled, with each cell being filled with the values with presence and absence data. In the functional

matrix “Q”, rows corresponded to the 142 tree species and columns to the seven plant functional attributes.

For the functional matrix, the mean values of height, basal area, leaf area and leaf herbivory (leaf damage caused by chewing herbivores) were used in addition to the abundance of individuals. The potential height of each species, as well as the number of ecoregions in which they occur, were obtained from Oliveira-Filho (2014) and BFG (2015). In the environmental matrix “R”, rows corresponded to the 70 subplots, while columns corresponded to twelve environmental parameters. The environmental parameters were LAI and the following chemical and physical variables of the soil: pH, P, K, Ca²⁺ + Mg²⁺, K, Al³⁺, and H + Al, Al saturation, base saturation, total organic carbon, sand, and silt. Normality was achieved by means of logarithmic transformation, when necessary, to meet the assumptions of the tests. The fourth-corner analysis was first used to evaluate the significance of the correlation of species traits with each environmental parameter using the “combined” method of null models 2 and 4, as suggested by Dray and Legendre (2008). After this step, only biological traits that were significantly correlated with more than one environmental parameter were selected for the RLQ analysis. The best model to attend the goals of our study was not the most robust, but the more informative among those statistically significant. Only parameters which were not correlated with at least one trait were excluded of the model. The RLQ analysis aimed to find the combination of biological traits with maximum covariance with a given combination of habitat parameters (Dolédéc et al., 1996).

To perform RLQ, a correspondence analysis was employed for the floristic matrix, while principal component analysis (PCA) was used for the functional and environmental matrices. In the functional PCA, species received relative weight corresponding to the frequency in which they occurred in the areas, and in the environmental PCA the areas received relative weight corresponding to their species richness (Dolédec et al., 1996; Dray and Dufour, 2007; Pavoine et al., 2011). Both analyses were performed in the R environment (R Development Core Team, 2012) with the package “ade4” and some functions provided by Pavoine et al. (2011).

3. Results

There was a strong connection between the functional traits of the 142 tree species distributed among 2008 individuals and the environmental parameters in the forest islands. The seven functional traits of the species tested by the fourth-corner analysis were significantly correlated with more than one environmental parameter (Fig. 3). Leaf herbivory (leaf damage caused by chewing insects) was positively related to the leaf cover index (LAI) and to base saturation, and negatively correlated to Al saturation, Al and H + Al. Leaf area was also positively related to LAI and percentage of silt in the soil, and negatively correlated to Al concentration, and potential acidity (H + Al). The number of ecoregions and the mean height of the trees were positively related to some indicators of soil fertility (i.e., base saturation, Ca + Mg, K, and total organic carbon) and negatively correlated to Al saturation. On the other hand, potential height was positively related to the contents of K, P, percentage of organic carbon and percentage of organic sand, and negatively correlated to the percentage of silt. The mean basal area was negatively correlated to LAI, and positively correlated to indicators of soil fertility (i.e., Ca + Mg and K). The number of individuals was inversely correlated to mean tree height, negatively correlated to parameters associated with soil fertility (e.g., base saturation, pH and Ca + Mg) and positively correlated to Al saturation (Fig. 3).

The global association between species traits and habitat structure was strongly significant ($p=0.0001$), according to the test based on the total co-inertia of the RLQ analysis (Monte Carlo with 50,000 permutations). Axis 1 of the RLQ explained 75.2% of the total variation. The positive side of this axis represented areas with higher LAI, higher aluminum saturation, and lower soil fertility, represented by low cation content, low base saturation and low percentage of organic carbon (Fig. 4a). The most important species shared similar attributes, with lower number of ecoregions and lower potential height (Fig. 5b). The positive side of this axis was represented by, among others, the species *Geonoma schottiana* (Arecaceae), *Miconia paulensis* (Melastomataceae), *Tibouchina sellowiana* (Melastomataceae), *Solanum pseudoquina* (Solanaceae) and *Miconia brasiliensis* (Melastomataceae) (Fig. 5a). The negative side of RLQ axis 1 represented environments with higher soil fertility (higher Ca + Mg, K, organic carbon and base saturation contents) (Fig. 4a). The most important species here also shared similar attributes, such as a broader distribution among Brazilian ecoregions, and potential height (Fig. 4b), represented mainly by the species *Apuleia leiocarpa* (Fabaceae), *Pera glabrata* (Peraceae), *Hieronima alchorneoides* (Phyllanthaceae), *Nectandra membranacea* (Lauraceae) and *Richeria grandis* (Phyllanthaceae) (Fig. 5a).

Axis 2 of the RLQ analysis explained 22.4% of the total variation. The positive side of this axis represented sites environments with soils with more aluminum toxicity (e.g. Al, H + Al, and Al saturation), with higher concentrations of P and organic carbon, and lower base saturation, pH, LAI and Ca + Mg (Fig. 4c). The most important species in these areas share similar traits such as high potential height and abundance of individuals, and with low leaf area and

leaf herbivory (Fig. 4d). The positive side of the axis was represented by, among others, *Cabralea canjerana* (Meliaceae), *Casearia decandra* (Salicaceae), *Protium spruceanum* (Burseraceae), *Sapium glandulosum* (Euphorbiaceae) and *Leucochloron incuriale* (Fabaceae) (Fig. 5b). The negative side of axis 2 represented soil environments with high base saturation and pH, as well as high leaf cover values (LAI) (Fig. 4c). The most important species in these areas shared similar attributes, such as higher values of leaf area and leaf herbivory (Fig. 4d). The negative side of this axis was represented by, among others, the species *Cecropia pachystachya* (Cecropiaceae), *Piper gaudichaudianum* (Piperaceae), *Davilla elliptica* (Dilleniaceae), *Aegiphila verticillata* (Lamiaceae) and *Guatteria pogonopus* (Annonaceae) (Fig. 5b).

4. Discussion

Our results demonstrated that species established on less fertile soils experienced lower rates of leaf damage, than species established on more fertile soils, which suffered higher rates of leaf damage. That is, leaf damage caused by chewing insects was significantly related to the canopy cover index and parameters associated with fertility (i.e. base saturation, Al saturation, Al and H + Al). Species such as *Cecropia pachystachya*, *Piper gaudichaudianum*, *Davilla elliptica*, *Aegiphila verticillata* and *Guatteria pogonopus* were associated with more fertile soils and were experienced higher herbivory, while species such as *Cabralea canjerana*, *Casearia decandra*, *Protium spruceanum* and *Sapium glandulosum* were associated with less fertile soils with higher concentrations of aluminum, and experienced less foliar damage from herbivorous insects. Several studies have shown that resource concentration is positively related to the activity of herbivorous insects (Coley et al., 1985; Endara and Coley 2011). For instance, in an experiment conducted in the Peruvian Amazon, Fine et al. (2004) demonstrated that when herbivores were excluded from areas with infertile soils, species possessing costly defenses against natural enemies were than in competitive disadvantages. Finally, there may also exist a relationship between the preference of some species we studied for soils with high Al concentration, Al-accumulating and reduced herbivory (Souza et al., 2014 and references therein). The existence of Al accumulating species on forest islands is an important characteristic to be investigated and that may explain in part the species composition of forest islands.

The results have also showed that leaf area was negatively related to the concentration of aluminum and potential acidity, which are strong indicators of soil fertility. In addition, leaf area was also positively related to the canopy coverage index. The most frequent species in areas with higher canopy cover (e.g. *Cecropia pachystachya*, *Piper gaudichaudianum*, *Davilla elliptica*, *Aegiphila verticillata* and *Guatteria pogonopus*) have the larger leaf areas, a strategy associated with maximizing light interception (Falster and Westoby, 2003). The leaf area of tree species plays an important evolutionary role in convergent adaptations, photosynthetic activity, carbon assimilation and water and energy balance, as well as light capture and ecological relationships, such as herbivory and organic matter decomposition (Freschet et al., 2011). The current literature points out to a decline in tree leaf area with a decrease in soil moisture and fertility (Dwyer et al., 2014), corroborating our findings. In infertile soils, species and individuals with smaller leaves are favored because of the slow vegetative growth under these conditions (McDonald et al., 2003). The increase in leaf area is directly associated with survival, nutrient retention and protection against desiccation (Fonseca et al., 2000). Small leaves are favored in environments with high solar incidence and low water availability, as the habitats holding forest islands in the present study, thereby

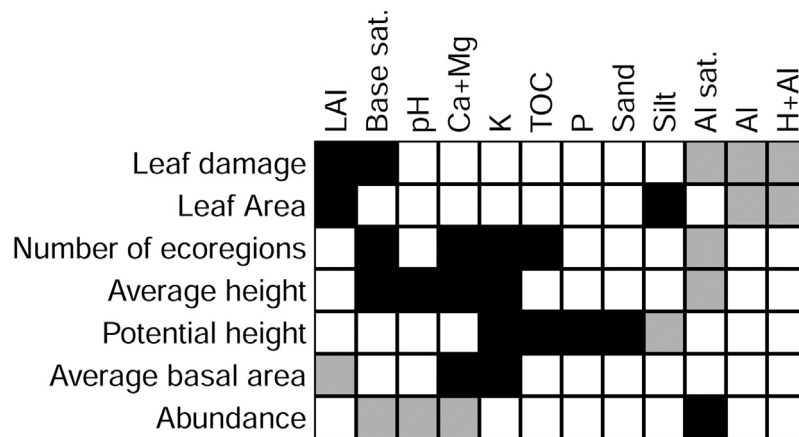


Fig. 3. Results of the fourth-corner analysis representing the relationship between ecological variables and environmental parameters of the vegetation of forest islands at Serra do Cipó, southeastern Brazil. Non-significant correlations are denoted in white, significant positive correlations in black and significant negative correlations in grey. The level of significance was $\alpha=0.05$.

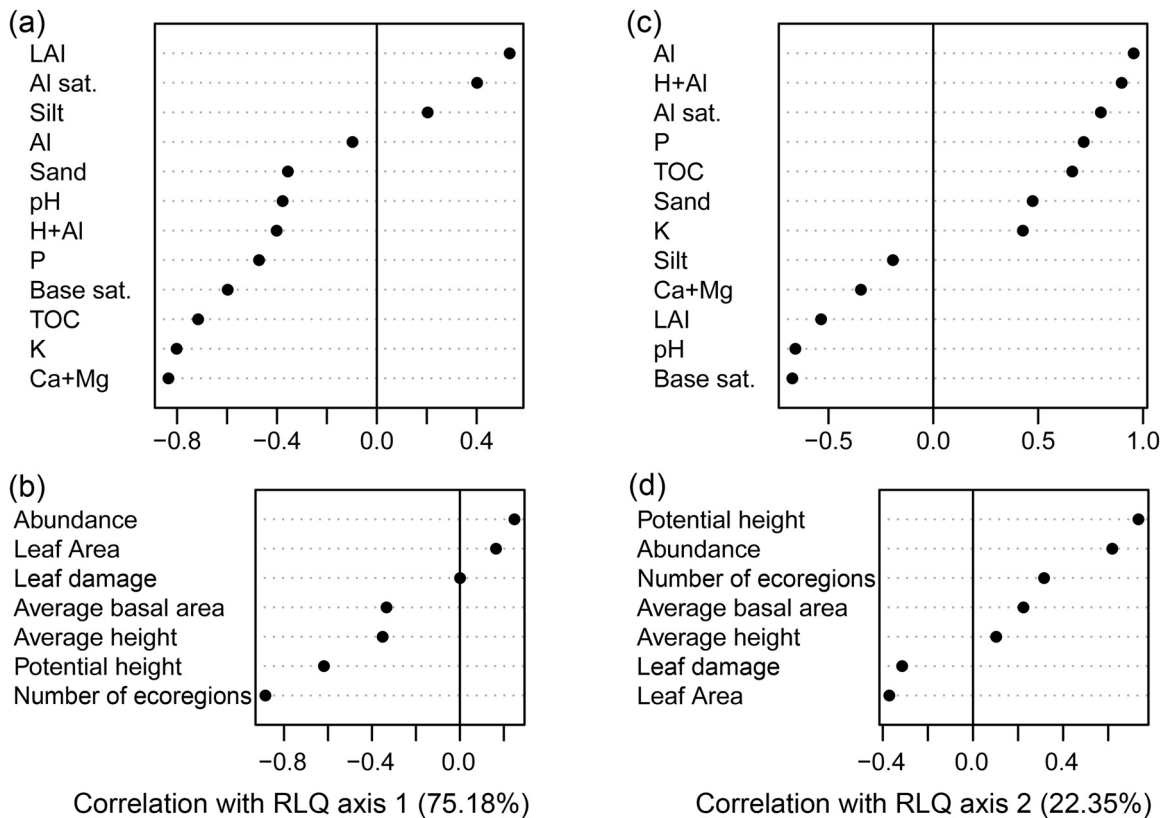


Fig. 4. Relationship between biological variables and environmental parameters of the vegetation of forest islands at Serra do Cipó, southeastern Brazil. (a) Pearson correlation between environmental parameters and the coordinates of the areas on axis 1 of the RLQ analysis. (b) Pearson correlation between the biological variables and the coordinates of the species on axis 1 of the RLQ analysis. (c) Pearson correlation between the environmental parameters and the coordinates on axis 2 of the RLQ analysis. (d) Pearson correlation between the biological variables and the coordinates on axis 2 of the RLQ.

maximizing the efficiency of photosynthetic activity (Wright et al., 2004; Poorter and Rozendaal 2008; Ordoñez et al., 2009).

We have also demonstrated that the more widely distributed species – those occurring in a greater number of Brazilian ecoregions – were sampled preferentially in more fertile soils, and with lower acidity and aluminum concentration. Areas with less fertile soils preferentially harbored species with more restricted distributions. In an extensive review, Coelho et al. (2016) demonstrated that the establishment and development of forest islands are strongly related to soil parameters, both chemical and physi-

cal, which was corroborated by the results reported here. Species such as *Apuleia leiocarpa*, *Pera glabrata*, *Hieronyma alchorneoides* and *Nectandra membranacea*, which are distributed widely among different Brazilian ecoregions, are connected to the parameters of soil fertility, while *Cabralea canjerana*, *Casearia decandra*, *Protium spruceanum* and *Sapium glandulosum* are more closely associated with the Atlantic Forest and comparatively less fertile soils – with lower nutrient levels, and with higher acidity and aluminum concentrations. Additional evidence suggest that soil parameters are directly related to species composition within the same plant for-

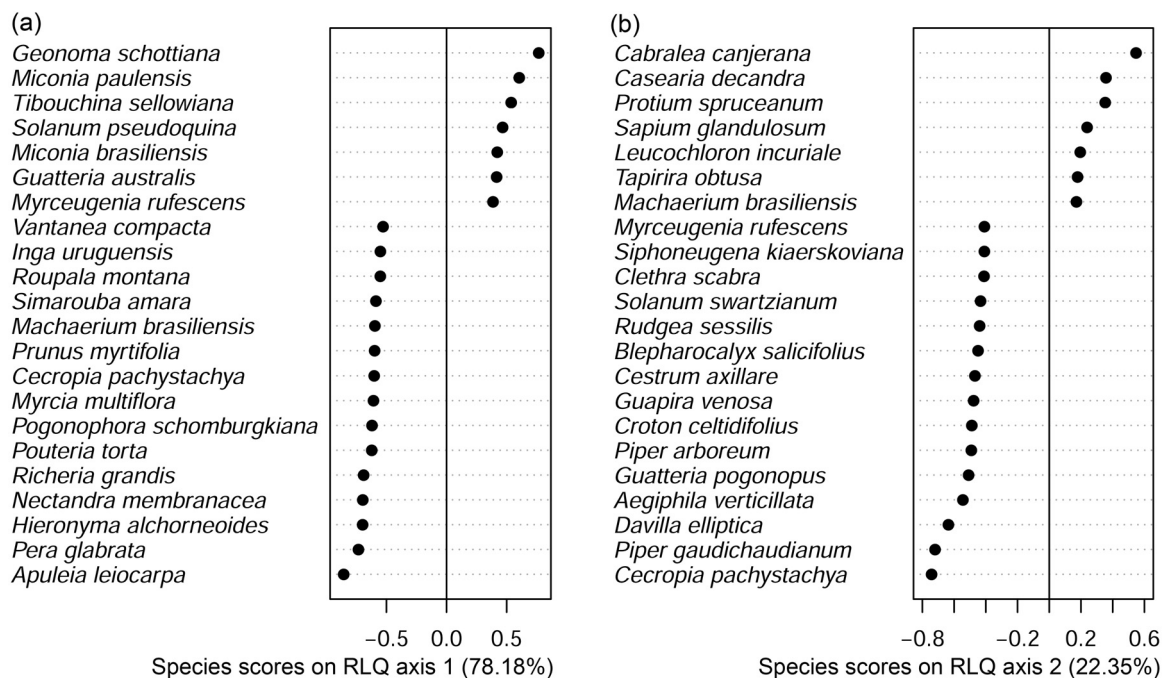


Fig. 5. Position of tree species more connected to the ecological gradient revealed of the forest islands at Serra do Cipó, southeastern Brazil, by RLQ analysis. Circles indicate the values of the coordinates of each tree species on axis 1 (a) and axis 2 (b) of the RLQ analysis. See supplementary material for all species.

mation, with species responding to pH and Al^{3+} as well as other fertility indicators, revealing different competitive capacities under different soil conditions (Oliveira-Filho et al., 2001; Pinto et al., 2005; Sanchez et al., 2013). The influence of soil parameters is also associated with the occurrence of species among different physiognomies of the Atlantic Forest, some of which are classified as rare, while others are more generalist or common (Caiafa and Martins, 2010).

The mean height and basal area were related to soil fertility parameters (e.g., high concentration of base saturation, low aluminum concentration and lower acidity) of forest islands. There was a strong connection between soil parameters and the establishment of certain species. Potential height connected with the same environmental parameters (K, TOC, P, sand), showing that not only individuals but also largest species (e.g. *Apuleia leiocarpa*, *Pera glabrata*, *hieronyma alchorneoides* and *Nectandra membranacea*) were established in more fertile soils. Studies have already demonstrated the strong influence of soil on vegetation structure associated with the Atlantic Forest (Budke et al., 2007; Pereira et al., 2007). Species with higher values of height and basal area are associated with greatest resource availability due to high metabolic demands and biomass accumulation (Van den Berg and Oliveira-Filho, 1999; Oliveira-Filho et al., 2001).

Species abundance across the islands was positively related to acidic, aluminum rich and less fertile soils. Soils of low fertility limit growth and the accumulation of biomass by trees, which can lead to low values of functional traits as mean height, basal area and an increase in density, that is, greater abundance of trees with lower values of height and basal area (Guariguata and Ostertag, 2001; Higuchi et al., 2008). In addition, forest islands are located on mountaintops and are exposed to strong gusts of wind, which causes frequent tree falls (Coelho et al., 2016). In a small forest, such as the islands studied here, tree falls alter the successional stage of the vegetation (Connell, 1978; Budke et al., 2010). Succession is likely a strong driver for the patterns of connection between species and the environmental parameters, since it affects the composition and structure of the tree community as well as the formation and con-

dition of the soil, leading to similar early successional conditions (Freschet et al., 2011).

The present study showed the strong connection between species traits and environmental parameters. Islands with more fertile, less acidic soils with higher canopy cover exhibited species with higher structural values (i.e., height and basal area), wider distribution among Brazilian ecoregions, higher rates of leaf herbivory and fewer individuals. On the other hand, islands with less fertile, more acidic soils, with high levels of aluminum and lower canopy cover presented species with lower structural values, more restricted distributions among Brazilian ecoregions and lower rates of leaf damage from chewing insects. Although the physical parameters of the soil played a more important role than the chemical properties for the establishment of forest islands, the results reported here point out to chemical indicators of soil fertility as a relevant environmental promoter for tree species, allowing not only the establishment but also the development, and thus as key factors determining vegetation composition.

The understanding of how naturally isolated communities are structured, based on functional traits and environmental parameters can be applied to understand human-derived fragmented landscapes (Laurance, 2008). The present study has shown the role of local environmental parameters strongly influencing the functional trait composition in tree communities also indicating that habitat heterogeneity is essential in structuring tree communities in this archipelago of natural islands of Atlantic rainforest (Cadotte and Tucker, 2017). The connection of local environmental parameters with the species functional traits can help predict the effects of anthropogenic and natural impacts, such as fire (see Coelho et al., 2018), and support the development of effective conservation strategies.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.flora.2017.04.003>.

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