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Environmental conditions of the interior of the tropical forest and regeneration of tree species

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This study aimed to analyze the interactions between environmental variables and the occurrence of tree species in the understory of an Atlantic forest fragment in Southeastern Brazil. The vegetation data collection was carried out in ten locations, with trees having diameter at breast height (DBH) larger than 5 cm and with distinct physiographic characteristics, orientation and slope. The following variables were collected at each site: sum of the soil bases, soil moisture, leaf area index (LAI) and canopy transmissivity of photosynthetically active radiation (PAR). The interaction between environmental variables and vegetation was investigated employing the canonical correspondence analysis (CCA), using data from the natural regeneration (TNR) of forty-six species and the environmental variables of the locations studied. The Monte Carlo test showed that the correlation between TNR values for the species and environmental variables was statistically significant. The occurrence of four primary species groups was identified through this analysis. Considering the availability of solar radiation, one species group was observed to have occurred under the open canopy with high transmissivity of PAR, and another in locations with high LAI values and low PAR transmissivity. When soil variables were considered, we were able to distinguish two groups; a group of species showed preference for sites with fertile soil and high water content and another group that was more predominant in sites with drier soil, usually on steeper slopes.

Key words: Brazilian Atlantic forest, environmental heterogeneity, photosynthetically active radiation, leaf area index.

INTRODUCTION

Investigation of the behavior of forest species aiming to understand the ecology of these species is an important and current research issue, which have been studied by several researchers. Considering the current level of degradation of the forest ecosystems, a better understanding of, for example, the light or shade tolerances of a species, in high and low fertility soils could be very useful in the recuperation of degraded

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forest ecosystems. Studies seeking to indicate the best species for the recuperation of degraded environments are frequently performed; however, often the greatest challenge in these studies lies in the lack of information on the relationship between the species and the environment.

Considering these issues, phytosociology is one of the most important tools to study forest ecosystems. With this tool it is possible to describe the structure of the forest, and, therefore, make inferences about the relationships that exist among species. However, most phytosociology studies aiming to explain species' succession do not take environmental variables into consideration. Nevertheless, it is well known that these variables are essential to explain the presence or absence of certain species in different environments.

To better understand the process of succession in a forest, it is very important to establish a relationship between the environmental variables and the structural and floristic patterns of the vegetation (Higuchi et al., 2012; Wortley et al., 2013; Barthelemy et al., 2015). Previous studies have investigated mainly edaphic conditions, physiographic factors, and microclimatic characteristics of tropical rainforests.

The occurrence small-scale topographic variations leads to environmental differences among sites due to changes in the availability of solar radiation, hydrologic regime of the soil, and the availability of nutrients. Several studies have demonstrated that physiographic factors influence the distribution of species in tropical rainforests (Rodrigues et al., 2007; Higuchi et al., 2008; Silva et al., 2009; Gasper et al., 2015).

However, topography differences are not always enough to explain the distribution pattern of species in the rainforest. Some environmental variables are not entirely dependent on the topography, as for example the availability of solar radiation in the interior of the rainforest, which is also influenced by the transmissivity of solar radiation through the canopy, which is in turn controlled by the leaf area index. However, despite the fact that solar radiation is one of the most important environmental variables governing the rainforest species distribution pattern, studies on the ecology of tree species in tropical rainforests which take this environmental variable into consideration are practically nonexistent due to the difficulty of measuring this variable in field conditions.

The objective of this work was to study the relationship between the occurrence of tree species in the initial phase of their development and environmental variables measured at different sites in a fragment of the Atlantic Forest in Southeastern Brazil.

MATERIALS AND METHODS

Description of the area of study and database

This study was conducted at the Mata do Paraíso Research Station, located in the municipality of Viçosa, MG, Brazil (latitude = 20°45' South, longitude = 42°55' West and an average altitude of 690 m above sea level). The natural vegetation in the region of study is classified as semi-deciduous seasonal forest, and a portion of the tree species lose leaves in the winter. This type of vegetation is conditioned by the seasonal behavior of the climate, which is characterized by a hot summer with heavy rain, followed by a dry winter with a sharp drop in temperature. The percentage of deciduous trees, at Mata do Paraíso Research Station, varies between 20 and 50%.

According to Koppën classification, the regional climate is classified as *Cwb*, with poorly distributed rainfall throughout the year, with a rainy summer and a dry winter. The total annual precipitation average is 1,221 mm and the annual average temperature is 19.4°C. During the winter, the long-term average (from 1961 to 1990) monthly minimum temperature reaches10.1°C and, in the summer, the average monthly maximum temperature is 30°C in February, according to the Brazilian National Institute of Meteorology (INMET).

Vegetation data and estimation of natural regeneration

To study natural regeneration, Higuchi et al. (2006) identified ten sites at the area Mata do Paraíso Research Station, based on physiographic characteristics, such as orientation and slope. Permanent plots were allocated in the selected sites, where phytosociological surveys of natural regeneration (individual trees with DBH < 5 cm) have been carried out since 1992. Following the methodology proposed by Garcia et al. (2011), an index of total natural regeneration (TNR) was calculated for each species.

Environmental measurements

The average slope values and sum of soil bases (between 0 - 10 cm of depth) of each location studied was determined by Pezzopane et al. (2002). The average values of transmissivity of photosynthetically active radiation and leaf area index were also obtained by Pezzopane et al. (2002), who carried out measurements in the four seasons of the year to conduct and characterize different conditions of radiation flux density, sun position and phonological stages of the vegetation. Soil samples were taken in 0 - 10 cm layer to determine soil moisture, using the gravimetric method, in the end of the dry season. Table 1 shows the summary of the environmental variables measured in this study.

Environmental and vegetation interaction

A multivariate analysis was used to investigate the relationship between environmental variables and the distribution of species within the forest. The canonical correspondence analysis (CCA) is a type of multivariate analysis that allows ordering species, characteristics of the location of occurrence and environmental variables concomitantly (Oliveira-Filho et al., 2007). The CCA identifies the higher correlation between variables and the distribution of the species for each ordination axis. This approach has the advantage in relation to the other methods of multivariate analysis to provide a significance test for the correlations between variables. Thus, the results of one canonical correspondence analysis can be used, for instance, to identify the preferred sites for a specific tree species, as shown by Oliveira-Filho et al. (1994, 2007), Meira-Neto et al. (2005), Carvalho et al. (2007), Ferreira-Junior et al. (2007), Geihl and Jerenknow (2008), Venturoli et al. (2010) and Marcuzzo et al. (2013).

In this study, the environmental and vegetation interaction were studied employing the canonical correspondence analysis (CCA), using data of total natural regeneration of the species (TNR) and

Table 1. Slope (SC), sum of bases (SB), soil moisture (SM), transmissivity of photosynthetically active radiation (t) and leaf area index (LAI) at the ten locations studied at theMata do Paraíso Research Station, in Viçosa, MG, Brazil.

Local	SC (%)	SB ($cmol_c.dm^{-3}$)	SM ($g.100 g^{-1}$)	t (%)	LAI
1	40	1.5	21.4	8.9	3.6
2	21	1.3	19.1	6.0	4.5
3	43	0.2	23.5	2.7	4.9
4	80	0.1	18.4	9.3	3.6
5	3	6.1	43.0	1.7	5.2
6	51	4.9	21.5	1.8	5.0
7	45	0.5	26.2	1.6	5.2
8	20	0.3	24.1	3.7	4.2
9	14	1.6	23.0	2.8	5.1
10	45	0.1	22.4	2.5	4.3

Source: Pezzopane et al. (2002).

Table 2. List of the species sampled in the natural regeneration stage at Mata do Paraíso Research Station, in Viçosa, MG, Brazil.

Species	Species
Allophylus edulis Radlk.	*Machaerium triste* Vogel
Anadenanthera peregrina (L.) Speg.	*Maprounea guianensis* Aubl.
*Annona sylvatica*A. St.-Hil.	*Matayba elaeagnoide s*Radlk.
*Apuleia leiocarpa*Vogel J. F. Macbr.	*Myrcia fallax* (Rich.) DC.
Bauhinia forticata Link	*Nectandra oppositifolia* Nees & Mart.
Brosimum guianensis (Aubl.) Huber	*Nectandra rígida* (Kurth) Nees
*Casearia aculeata*Jacq.	*Nectandra saligna* Nees
*Citharexylum myrianthum*Cham.	*Octeacorymbosa* (Meisn.) Mez
Copaifera langsdorffii Desf.	*Picramnia glazioviana* Engler
*Croton floribundus*Spreng.	*Piptadenia gonoacantha* (Mart.) J.F. Macbr
Cupania sp.	*Prunus sellowii* Koehne
Dalbergia nigra (Vell.) Allemao ex Benth.	*Pseudopiptadenia contorta* (DC.)
Erythroxylum pelleterianum A. St.-Hil.	*Psychotria conjungens* Müll. Arg.
Eugenia brasiliensis Lam.	*Psychotria sessilis* Vell.
Euterpe edulis Mart.	*Rheedia gardneriana* Plach. &Triana
Guapira opposite (Vell.) Reitz	*Siparuna guianensis*Aubl.
Guarea Guidonia (L.) Sleumer	*Sorocea bonplandii* (Baill.) Lanj. &Wess. Bôer
Inga edulis Mart.	*Sparattosperma leucanthum* (Vell.) K. Schum.
Jacaranda macrantha Cham.	*Swartzia myrtifolia* Sm.
Landenbergia hexandra (Pohl Klotzsch	*Vismia guianensis* (Aubl.) Pers.
Luehea grandiflora Mart. &Zucc.	*Vitex sellowiana* Cham.
Machaerium nyctitans(Vell.) Benth.	*Xylopia sericea*A St.-Hil.
Machaerium stipitatum (DC.) Vogel	*Zanthoxylum riedelianum* Engl.

environmental variables of the studied locations. The Monte Carlo Test was applied to evaluate correlation between the values of TNR and the environmental variables at 1% level of probability.

Among the sampled species found in the plot, we selected those that showed a number of individuals greater than or equal to eight. Thereafter, a new species selection was performed eliminating those that showed only one individual per sampling unit, following the criteria proposed by Higuchi et al. (2006). Among the 128 species sampled in the botanical survey, 46 were selected for the study of environmental interaction × species, corresponding to 36% of the total species (Table 2).

RESULTS AND DISCUSSION

The matrix of correlations between the environmental

Table 3. Correlation matrix of the first two ordination axes and the environmental variables (EV), obtained via canonical correspondence analysis, of the data collected in Mata do Paraíso Research Station, in Viçosa, MG.

Correlation	Species axis 1	Species axis 2	VA axis 1	VA axis 2	SB	SC	SM	LAI	T
Species axis 1	1.000								
Species axis 2		1.000							
EV axis1	0.974		1.000						
EV axis2		0.970		1.000					
SB	0.786	0.600	0.766	0.582	1.000				
SC	0.029	-0.720	0.028	-0.699	-0.411	1.000			
SM	0.590	0.432	0.575	0.419	0.658	-0.593	1.000		
LAI	0.595	-0.021	0.580	-0.021	0.471	-0.484	-0.522	1.000	
T	-0.584	0.144	0.656	0.139	-0.350	0.431	-0.499	-0.885	1.000

SB, SC, SM, LAI and t, correspond, respectively, to sum of bases ($cmol_c dm^{-3}$), terrain slope (%), soil moisture ($g100\ g^{-1}$), Leaf area index, and transmissivity of photosynthetically active radiation (%).

variables and the first two ordination axes generated by CCA is shown in Table 3. The correlations between environmental variables (EV) and species were high (0.974 and 0.970), showing that the environmental variables used in the study explained satisfactorily the first two ordination axes.

The eigenvalues measured from the body of one axis, for the first and second axes of ordination, were 0.395 and 0.302, respectively, which are considered low values. The first two axes were responsible for 43% of the total variance. According to Martins et al. (2008), in this type of study, low eigenvalues are expected to occur due to the complexity of the interaction among the factors that determine the floristic and structure of the vegetation. In this study, the Monte Carlo test, applied to both axes, showed that the correlation between the RNT values of the species and the environmental variables were statistically significant ($P<0.01$).

The soil moisture showed positive correlation with the sum of bases and the leaf area index, and was negatively correlated with the slope and transmissivity of PAR (Table 3). These results are expected and can be explained by the topography since gentle slopes tend to show elevated fertility and soil water content, which is in agreement with results presented by Botrel et al. (2001) and Machado et al. (2008). Moreover, the transmissivity of PAR and LAI govern the availability of energy for the evaporation of soil water; therefore, the lower the attenuation of solar radiation (lower LAI), the lower is the soil water content, as a consequence of greater evaporation on the soil surface.

A significant correlation between the leaf area index and transmissivity of PAR is also expected since the LAI determines the amount of solar radiation that penetrates the plant canopy, as shown in the work of Wirth et al. (2001), Marques-Filho et al. (2005), Keeling and Phillips (2007) and Russo et al. (2012).

The separation of the sampling units or of the species in the ordination space can be analyzed graphically, in which the environmental variables are represented as vectors with size proportional to the influence of each variable, with the location or the plotted species next to the vector that exerts the most influence upon them.

Analyzing the ordination diagram of the locations studied (Figure 1), it is possible to see the formation of basically three groups. The first group, formed by locations 1, 2, 8 and 9, is under the influence of the transmissivity of PAR. These locations have the greatest transmissivity values of solar radiation and, consequently, the lowest LAI. Location 4 also showed high transmissivity of PAR, but it is not a part of the group, probably due to its steep slope. The second group, formed by locations 3, 4, 7 and 10 is affected by the terrain slope. Due to the steep slope at these locations, the soil water content and the sum of bases show low values.

The third group, formed by locations 5 and 6, is affected by the sum of bases, soil water content and LAI. Both locations showed elevated values for the sum of bases, soil water content, and LAI, but the slope of location 6 is relatively elevated, greater even than at locations 3, 7 and 10, which are affected by slope, as previously stated. However, location 6 has a slope in a terrain with a concave shape that could lead to greater water retention in the soil and better preservation of soil nutrients, which is in agreement with the results found by Ferreira-Junior et al. (2007) and Soares et al. (2015). In addition, the vegetation succession stage appears to be more advanced in location 6, resulting in a larger deposition of organic material in the soil, which may have interfered in the results from the soil sampling, carried out from 0 to 10 cm.

The ordination diagram to investigate the relationship between species and environmental variables is shown in Figure 2. The species that appear on the left side show a more consistent relationship with the transmissivity of PAR, which is associated with axis 1. The species located on the right side of the diagram are associated

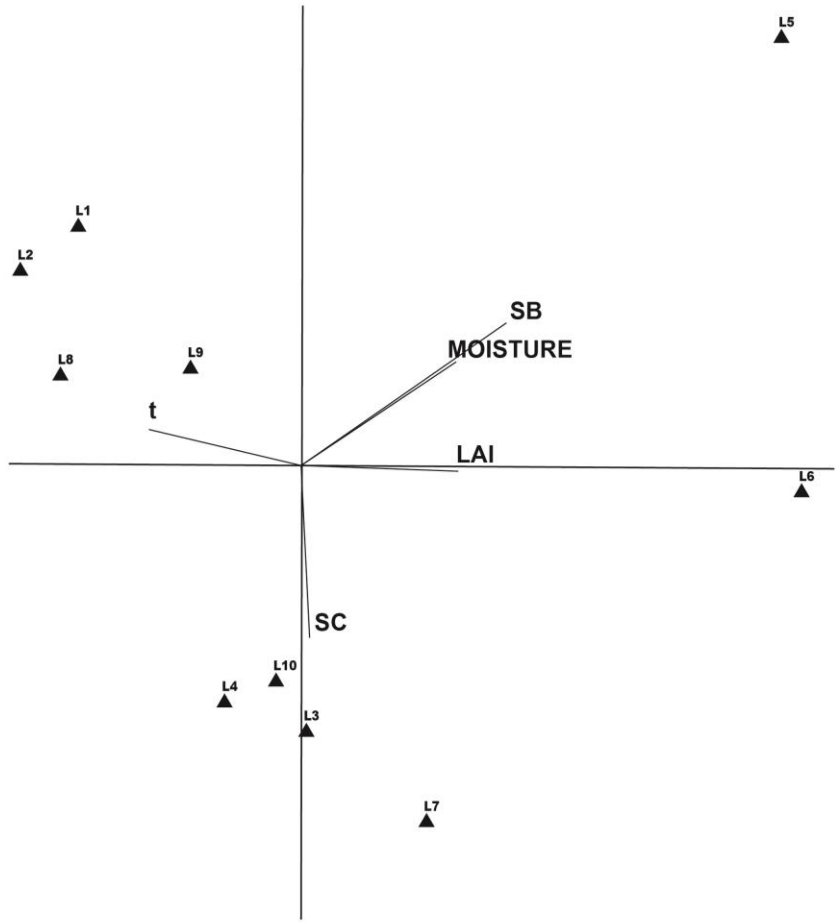

Figure 1. Ordination diagram produced using canonical correspondence analysis, showing the distribution of 10 locations and five environmental variables in Mata do Paraíso Research Station, in Viçosa-MG. Where SB, SC, MOISTURE, LAI and t, correspond, respectively, to sum of bases ($cmol_c$ dm^{-3}), terrain slope (%), soil moisture (g 100 g^{-1}), leaf area index, and transmissivity of photosynthetically active radiation (%).

with the sum of bases, soil water content and LAI. Another species group that appears on the bottom part of the diagram shows the most consistent relationship with average slope of the terrain, associated with axis 2. A noteworthy feature in this diagram is that the further away from the origin of the diagram a species is located, the stronger its relationship is with the environmental variables associated with the closest axis.

Among the species, having occurrences that are strongly correlated to transmissivity of PAR, are: *Croton floribundus, Sparattosperma leucanthum, Machaerium nyctitans, Xylopia sericea, Dalbergia nigra*, *Anadenanthera peregrina* and *Piptadenia gonoacantha.* These species occur more readily in the locations with an open canopy, as shown in the phytosociological study conducted by Garcia et al. (2011) in the same plots. The occurrence of the following species: *Citharexylum myrianthum*, *Vitex sellowiana, Jacaranda macrantha, Casearia aculeata, Erythroxylum pelleterianum, Machaerium stipitatum, Bauhinia forticata* and *Annona sylvatica* also showed relationship with the transmissivity of PAR, but less consistently, as shown by their closer proximity to the origin of the diagram. The grouping observed in the diagram appears to be consistent, since these species are considered primary and secondary succession species in the works of Higuchi et al. (2006), Garcia et al. (2011) and Martins et al. (2008).

On the opposite side of the vector of transmissivity of solar radiation, that is, species affected by LAI, the following species: *Picramnia glazioviana, Swartzia myrtifolia, Sorocea bonplandii, Psychotria conjungens, Nectandra oppositifolia*, *Cupania* sp. and *Inga edulis* can be found. These species occur in locations with low transmissivity of PAR (high LAI), and are amongst those with the highest RNT in locations 5 and 6, which showed a closed canopy with high LAI values. The species that compose this group require shady conditions; at least in the initial life stage, the majority of them was classified as

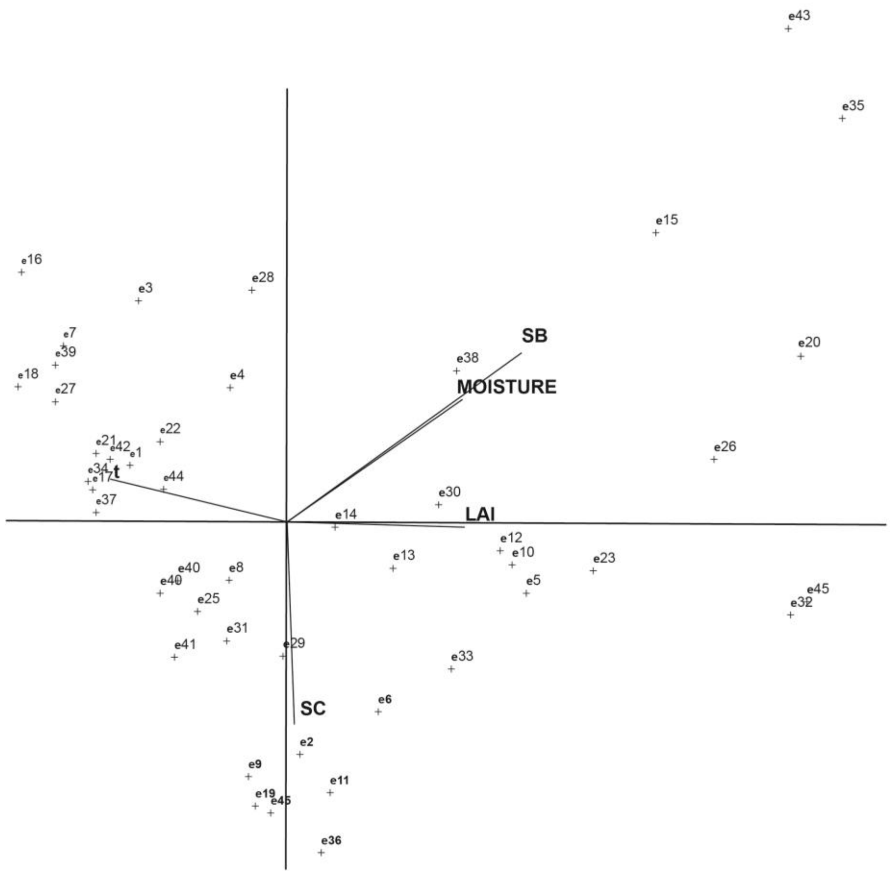

Figure 2. Ordination diagram produced using canonical correspondence analysis, showing the distribution of 46 species and five environmental variables sampled in Mata do Paraíso Research Station, in Viçosa-MG. Where SB, SC, MOISTURE, LAI and t, correspond, respectively, to sum of bases ($cmol_c.dm^{-3}$), terrain slope (%), soil moisture ($g.100g^{-1}$), leaf area index, and transmissivity of photosynthetically active radiation(%). e1-*Luehea grandiflora,* e2-*Pseudopiptadenia contorta,* e3-*Anadenanthera peregrina,* e4-*Annona sylvatica,* e5-*Psychotria conjungens,* e6-*Rheedia gardneriana,* e7-*Machaerium nyctitans,* e8-*Psychotria sessilis,* e9-*Zanthoxylum riedelianum,* e10-*Cupania sp,* e11-*Matayba elaeagnoides,* e12-*Nectandra oppositifolia,* e13-*Nectandra rígida,* e14-*Octea corymbosa,* e15-*Nectandra saligna,* e16-*Croton floribundus,* e17-*Jacaranda macrantha,* e18-*Sparattosperma leucanthum,*e19-*Copaifera langsdorffii,* e20- *Guarea Guidonia,* e21-*Casearia aculeata,* e22-*Machaerium stipitatum,* e23-*Sorocea bonplandii,* e24-*Siparuna guianensis,* e25-*Apuleia leiocarpa,* e26-*Inga edulis,* e27-*Dalbergia nigra,* e28-*Piptadenia gonoacantha,* e29-*Eugenia brasiliensis,* e30-*Maprounea guianensis,* e31-*Myrcia fallax,* e32-*Swartzia myrtifolia,* e33-*Guapira opposita,* e34-*Vitex sellowiana,* e35-*Euterpe edulis,* e36-*Landenbergia hexandra,* e37-*Citharexylum myrianthum,* e38-*Prunus sellowii,* e39-*Xylopia sericea,* e40-*Vismia guianensis,* e41-*Machaerium triste,* e42-*Erythroxylum pelleterianum,* e43-*Allophylus edulis,* e44-*Bauhinia forticata,* e45-*Picramnia glazioviana,* e46-*Brosimum guianensis.*

late secondary by Higuchi et al. (2006), Garcia et al. (2011) and Martins et al. (2008).

The species group formed by *Allophylus edulis, Euterpe edulis, Nectandra saligna, Guarea guidonia* and *Prunu ssellowii* was strongly affected by the sum of bases and soil moisture. The extension of the vectors in the opposite direction shows the group of species formed by *Machaerium triste, Myrcia fallax*, *Apuleia leiocarpa, Vismia guianensis, Siparuna guianensis* and *Psychotria sessilis,* which develop in areas with low soil water content. To the following species: *Landenbergia hexandra, Brosimum guianensis, Copaifera langsdorffii, Zanthoxylum riedelianum, Pseudopiptadenia contorta, Rheedia gardneriana* and *Eugenia brasiliensis,* can be added to this group, since they show a more consistent relationship with the terrain slope, which is negatively correlated to soil moisture.

The results of species environment interaction obtained through the use of this methodology are in agreement with previous results found in literature. For example, the strong positive relationship with the moisture content of the soil in the case of *Euterpe edulis* and *Allophylus edulis* is in agreement with results found by Rondon-Neto et al. (2002) that considers these species to be selective hygrophytes. On the other hand, the preference of *Apuleia leiocarpa* for drier soil is in agreement with Garcia et al. (2011), which consider this to be a species from high ground, and usually shows lower water content in the soil.

Ecophysiological studies performed by Pezzopane et al. (2002) demonstrated that the species *C. floribundus* shows high photosynthetic potential, behavior typical of full sun plants, and that the species *S. bonplandii,* under the same incidence values of solar radiation, showed lower photosynthetic rate values, showing typical behavior of shade plants. In this work, *C. floribundus* is classified as a species that occurs beneath a more open canopy and the opposite was observed for *S. bonplandii.*

The results obtained in this study indicate the environmental preferences for the species with the greatest natural regeneration index in the studied forest fragment, which can enhance the understanding of the ecology of the species of the Atlantic Forest. This knowledge could be of great use in the elaboration of projects, for example, of forest management or even in the definition of species and design of degraded area regeneration projects and establishment of ecological corridors.

Conclusions

Results of the study showed that it was possible to identify the occurrence of four primary species groups. Considering the availability of solar radiation, two species groups were observed; one species group that occurs under the open canopy with high transmissivity of solar radiation and another that occurs in locations with high LAI, that is, under closed canopy. Two species groups were observed considering soil characteristics; one species group showed preference for environments with fertile soil and high water content while another group showed preference for environments with drier soil, predominantly on steeper slopes.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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