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Original Paper

Influence of environmental variables on the floristics and structure of natural regeneration in a Mixed Ombrophilous Forest remnant

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Abstract

The present study explored the influence of edaphic variables and forest leaf cover on natural regeneration in a remnant of a Mixed Ombrophilous Forest (MOF) in southern Brazil. Principal component analysis (PCA) was used to elucidate the heterogeneity of edaphic and leaf cover variables among the sampling units, and the variables exhibiting the strongest correlations with the sampling units were selected. Subsequently, these variables were used to explain floristic patterns using canonical correspondence analysis (CCA). In PCA, the leaf area index explained only some variation in the data, and there was obvious heterogeneity in edaphic variables among the sample units. In the main canonical axis of the CCA, *Miconia cubatanensis*, *Myrcia multiflora*, *Casearia decandra*, and *Myrsine coriacea* showed greater correlation with variables associated with soil acidity. In contrast, *Allophylus guaraniticus* and *Cupania vernalis* showed a high correlation with variables related to bases. Overall, the analysis of soil physicochemical characteristics can allow for the more precise identification of indicator species for the restoration of remnant of MOF in southern Brazil.
Key words: araucaria forest, environmental analysis, physical-chemical attributes of the soil, phytosociology.

Resumo

O objetivo do estudo foi compreender a influência das variáveis edáficas e da cobertura foliar florestal no desenvolvimento da regeneração natural em um remanescente de Floresta Ombrófila Mista (MOF) no Sul do Brasil. A análise de componentes principais (PCA) foi utilizada para identificar a heterogeneidade das variáveis edáficas e de cobertura foliar entre as unidades amostrais, a partir da qual foram selecionadas as variáveis com maior correlação com as unidades amostrais. Posteriormente, essas variáveis foram utilizadas para explicar os padrões florísticos por meio da análise de correspondência canônica (CCA). A PCA mostrou que o índice de área foliar explica apenas parte da variação dos dados e que as variáveis de solo estudadas não são homogêneas entre as unidades amostrais. No eixo canônico principal da CCA, *Miconia cubatanensis*, *Myrcia multiflora*, *Casearia decandra* e *Myrsine coriacea* apresentaram maior correlação com variáveis associadas à acidez do solo. Em contraste, *Allophylus guaraniticus* e *Cupania vernalis* apresentaram alta correlação com variáveis relacionadas às bases. A análise das características físico-químicas do solo pode permitir a identificação mais precisa de espécies indicadoras para a restauração de remanescentes de MOF no Sul do Brasil.
Palavras-chave: floresta de araucária, análise ambiental, atributos físico-químicos do solo, fitossociologia.

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Introduction

In forest areas, diverse environmental conditions related to soil characteristics and canopy opening, among others, shape the mosaics of species associations, which further vary according to the microenvironment. Under specific conditions, species with varying edaphic and luminous demands coexist, thus increasing the local diversity (Teixeira & Assis 2009). The species geographic distributions in their natural habitats reflect complex interactions between several ecological factors, both biotic and abiotic, and both deterministic and stochastic (Aguiar *et al.* 2021). Environmental filtering, where the environment selects against certain species, is thought to be a major mechanism structuring communities (Cadotte & Tucker 2017).

Among the forest typologies occurring in the Atlantic Forest domain, the Mixed Ombrophilous Forest (MOF) is notable due to unique biological attributes including rare and endemic species (Oliveira-Filho *et al.* 2015). In this forest, the gymnosperms *Araucaria angustifolia* (Bertol.) Kuntze and *Podocarpus lambertii* Klotzsch *ex* Endl. coexist with angiosperms of the genera *Drimys*, *Ocotea*, and *Nectandra*, among others (Silva *et al.* 2017). However, natural vegetation has been replaced by areas with alternative land uses, such as urbanization and agricultural and silviculture activities. Therefore, these forests have become one of the most threatened forest types in Brazil (Negrini *et al.* 2014). In the state of Santa Catarina accelerated exploitation has transformed large areas of native vegetation into sparse and greatly altered remnants, leaving only 34% of the original coverage (Vibrans *et al.* 2021).

The MOF covers diverse environments with different geological, geomorphological, pedological, and climatic conditions, in which different types of soil can be found, ranging from shallow to deep and from dystrophic to eutrophic in relation to nutrient availability (Kersten *et al.* 2015). Considering the environmental heterogeneity of this phytoecological region, mainly associated with the climate and other environmental factors, and history of anthropogenic disturbances, it is expected that different forest fragments present great floristic variations (Higuchi *et al.* 2012a). In a previous study on the natural regeneration of a MOF at the same site as the present study, Ruggiero *et al.* (2021) found that approximately half of the species (51.67%) were found in only 5% of the sample units, demonstrating great species diversity in the regenerated MOF. The environmental heterogeneity associated with geographic location drives the diversity of forests, including the elements of different forest types (Teixeira & Assis 2009).

Because of the great environmental and social importance of the MOF, the conservation and restoration of its remnants are essential (Higuchi *et al.* 2012a). For that it is necessary greater knowledge regarding the influence of environmental variables on the floristic and structural patterns of these forests (Higuchi *et al.* 2012b; Marcon *et al.* 2014; Negrini *et al.* 2014). Such studies are important because they provide information on the microsites of occurrence of tree species, which can facilitate the indication of species for restoration (Higuchi *et al.* 2012b). The presence of indicator species in specific environmental conditions may show that the maintenance of certain environmental conditions is essential for the conservation of biodiversity at the regional level. In addition, identifying species associated with different microenvironment allows the appropriate choice of taxa to be used in forest restoration programs, thus avoiding possible problems, such as the high mortality of seedlings or non-adapted seeds (Silva *et al.* 2017).

Given the above, considering the importance of environmental variables on the composition and floristic structure of vegetation, researches that propose an analysis of the influence of these variables on natural regeneration are relevant for understanding the spatial structure of communities. However, studies that evaluate the natural regeneration of MOF remnants with a focus on this aspect are still scarce in southern Brazil. To this end, the present study aimed to answer the following questions related to the natural regeneration of a remnant of MOF: (a) Which edaphic variables contribute to explaining the floristic patterns of natural regeneration in the forest under study? (b) Does the forest leaf area index influence the composition of naturally regenerated forests? (c) Is it possible to determine the indicator species of natural regeneration associated with edaphic variables?

Materials and Methods

Study area

This study was conducted in a forest remnant of the Private Reserve of Natural Heritage (PRNH) “Emílio Einsfeld Filho in the municipalities of Campo Belo do Sul and Capão Alto, Santa Catarina

(SC), Brazil. Sampling was conducted within a radius of up to 500 m from the coordinate point 28°02’55.00”S and 50°45’59.56”W. The remnant covers an area of 3,365 ha, with approximately 72% forest cover.

The PRNH is basically formed by the Mixed Ombrophilous Forest (IBGE 2012) that covers part of the reserve comprising forest in late successional stages. Much of the vegetation in the study area has suffered anthropogenic action through selective logging in the past. However, these interventions have ceased decades ago (Zeller 2010).

There are two dominant geomorphic units in the evaluated remnant forest: the Plateau of Campos Gerais and the Plateau Dissecado of the Iguaçu River/Uruguai River. The main soils identified at the remnant are the Neosols, the Cambisols and the Nitisols most present in the vicinity of the Pelotas and Canoas / Caveiras rivers (EMBRAPA 2006). The climate of the region, according to the Köppen climate classification, is characterized as humid subtropical mesothermal (Cfb). The average annual temperature is approximately 15.6 °C and the average annual precipitation reaches 1,735 mm (Alvares *et al.* 2013). The altitudinal gradient is between 650 to 900 m (ICMBio 2008).

Data collection

In 2016, 20 permanent circular sampling units were randomly set throughout the forest remnant of PRNH, with a 2.5 m radius, totaling a sampling area of 392.5 m² (Fig. 1). In each of these units, soil samples were collected, and the physical-chemical attributes were determined according to the methodology recommended by EMBRAPA (1997). To determine the density of the soil, in each sampling unit, two soil samples with the structures preserved were collected in metallic volumetric rings. Chemical variables were measured from soil collected from six sampling locations at a depth of 0–20 cm. The six soil samples with non-preserved structure were homogenized, and a composite sample comprising a sampling unit was obtained. The following parameters were determined: pH in water and the content of phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), aluminum

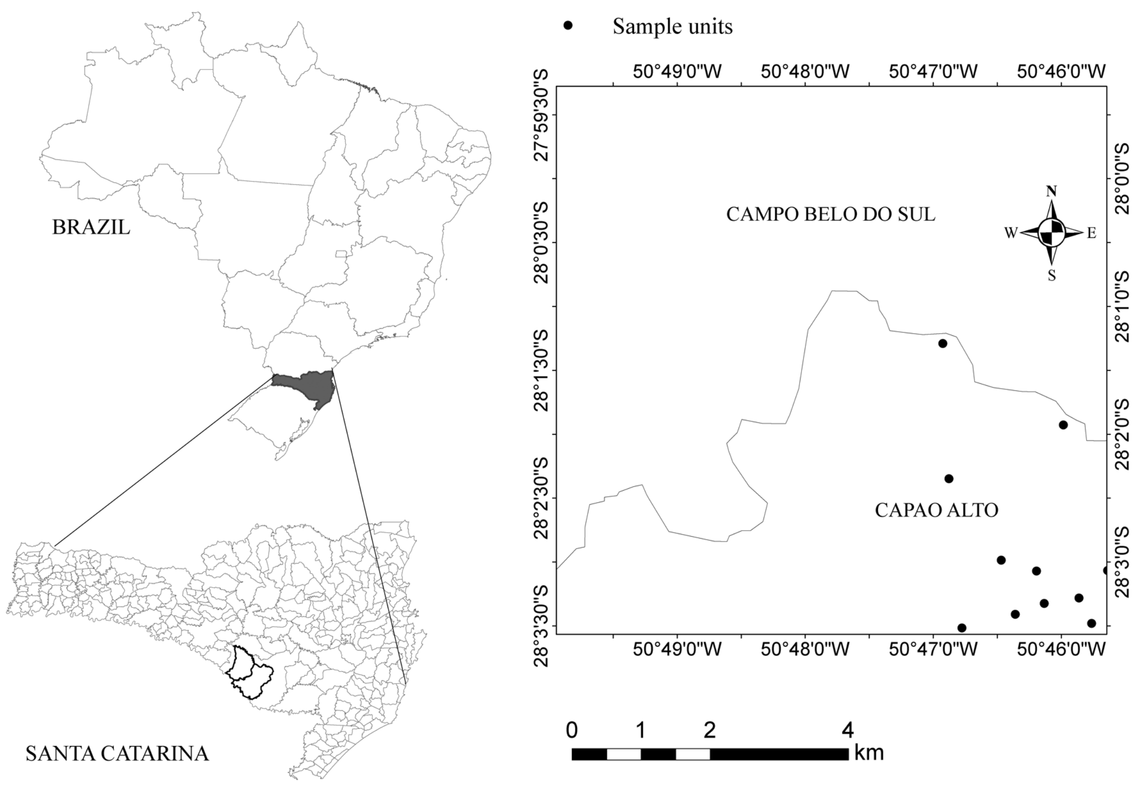

Figure 1 – Geographic location of the sample units in a remnant of the Mixed Ombrophilous Forest in Santa Catarina, Brazil.

(Al), organic matter (OM), the capacity to exchange cations at pH 7 (CTC), Al saturation (m), and base saturation (V).

Sampling of the regenerating community was conducted by surveying the number and height of the regenerating trees, by species, and by sample. All tree individuals with a minimum height of 0.50 m and circumference at breast height of less than 15 cm were measured.

The parameters used to estimate the structure of regeneration were density and frequency (Mueller-Dombois & Ellenberg 1974; Souza & Soares 2013) and the category of size and value of regeneration (Finol 1971; Souza & Soares 2013). The absolute and relative values were calculated for each parameter. The parameter regeneration size category (SC) (absolute and relative) refers to the distribution of individuals in height classes. This parameter was calculated for each species which were divided into three size classes: class I (0.5–1.1 m); class II (1.1–3.0 m); and class III (> 3.0 m).

The category of absolute size by species is obtained by determining the phytosociological values (PV) for each class of natural regeneration, according to expression 1, 2 and 3. The phytosociological value represents the proportion of individuals observed in each size class in relation to the total number of individuals obtained in the sample (Finol 1971).

$$PV_{ij} = PV_J . n_{ij}; PV_j = \left(\frac{N_j}{N}\right) \quad (1)$$

$$SC_i = \sum_{j=1}^{J} n_{ij} . \left(\frac{N_j}{N}\right) \quad (2)$$

where: PV_{ij} = phytosociological value of species i-th in the j-th size class: PV_j = phytosociological value of the j-th size class; n_{ij} = number of individuals of the species i-th in the j-th size class; N_j = total number of individuals in the j-th size class; N = total number of naturally regenerating individuals in all size classes; SC_i = absolute size class of the species i-th.

The category of relative size, by species, is obtained according to expression 3:

$$RSC_i = \frac{SC_i}{\sum_{i=1}^{s} SC_i} * 100 \quad (3)$$

where: RSC_i = relative size class of regeneration of the species i; SC_i = absolute size class of the species i.

The regeneration value (RV), in turn, expresses the importance of each species in the community and is obtained by adding the density, frequency, and regeneration size category in absolute and relative terms (Souza & Soares 2013).

The leaf area index (LAI) was determined using LAI-22000 (Li-Cor®) in each sampling unit. We calculated LAI by collecting light levels that penetrate the canopy, using two sensor units. The first unit was placed in an open area and under ambient lighting conditions, where diffuse lighting measurements were obtained every 15 s, whereas the other was placed inside the forest, with measurements noted manually. The sensor is divided into five angular bands of view with respect to the zenith (7, 23, 38, 53 and 68°), measuring the interception of light by the cover above and below the canopy, in five different angles (Li-Cor 2010). In this way, the fraction of light that crosses the vegetative canopy (transmittance) at different angles is recorded and used in the calculation of LAI.

Species identification

Identification at the genus and species level was carried out through expert consultation and specialized literature. The individuals were classified at family level according to the APG IV system (APG IV 2016). For the classification of species in regeneration guilds, the following classes were used: pioneer (Pi), climax demanding light (CL), and climax tolerant to shadow (CS) (classifications are based on those described by Oliveira-Filho 1994).

Data analysis

Phytosociological calculations included all arboreal species in the area. For multivariate analysis, only species with more than 10 individuals were considered. First, the normality of the data was tested using the Shapiro-Wilk test, which demonstrated that the number of climax species demanding light and pioneers did not present a normal distribution.

Therefore, to obtain normality, the data for these groups were logarithmically transformed (base 10 log). Sample sufficiency was tested using the rarefaction method based on the number of individuals (Gotelli & Colwell 2001), with 95% confidence interval, calculated using the Biodiversity package in R.

In order to identify the environmental heterogeneity between the sampling units, a principal component analysis (PCA) was used, from which the environmental variables with the highest correlation with the sampling units were selected and eliminated redundant variables. Next, these variables were used to explain the floristic patterns through canonical correspondence analysis (CCA), which aimed to order the sampling units according to the environmental and floristic characteristics. The environmental variables were standardized using the "normalize" method from the Vegan library's decostand function (Oksanen *et al.* 2018). The analyses were performed using the PAST® 2013 version 2.17c (Hammer *et al.* 2001) and R (version 3.5.0) (R Development Core Team 2008).

The significance of CCA and soil variables was examined using permutation tests, with a maximum number of 999 permutations, using the anova.cca function of the Vegan package (Oksanen *et al.* 2018). The Monte Carlo permutation test was performed to determine the level of significance of the main axis of canonical ordering (Ter Braak & Prentice 1988).

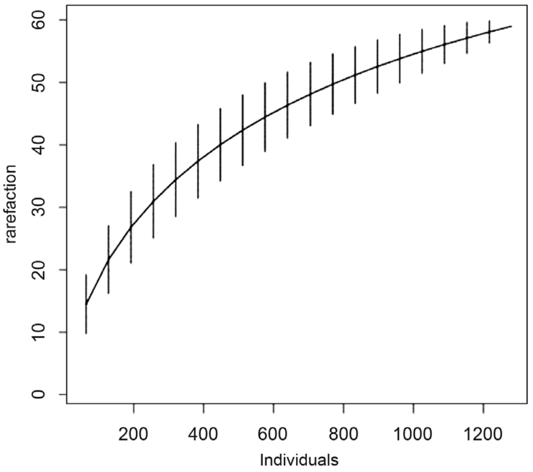

Figure 2 – Rarefaction curve estimating the expected richness according to the number of individuals of a remnant of the Mixed Ombrophilous Forest. Middle line = represents the average values of richness; vertical lines = standard deviation.

Results and Discussion

Floristic structure

Overall, 11,185 ind ha^{-1} were found. The surveyed individuals belonged to 66 species, 39 genera, and 27 botanical families. Among these, seven species were not identified, two were identified only at the family level, and four at the genus level. The unidentified species showed values below 1% in relation to the relative natural regeneration (RNR%) in the community. The number of individuals, species, genera, and families present in the Mixed Ombrophilous Forest (MOF) can be quite variable, which may be due to different environmental conditions, succession stages, and other factors (Figueiredo-Filho *et al.* 2010).

Through the rarefaction curve it was possible to observe that the minimum number of individuals estimated was 64 (± 2.38), with a richness of 14 species. And the maximum number of individuals estimated was 1,281 (± 0.92), with a richness of 59 species (Fig. 2). This result indicates that sampling included a large part of the species in the area.

The number of species belonging to the Myrtaceae family was the highest; however, the density of individuals in the family was the second-highest. The Sapindaceae family had the highest number of individuals per hectare owing to the presence of *Allophylus guaraniticus* and *Matayba elaeagnoides*, both of which are representative at density and on relative natural regeneration of forest community.

The species *Allophylus guaraniticus* (9.9%), *Myrcia multiflora* (9.9%), *Casearia decandra* (9.4%), *Myrsine coriacea* (8.1%) and *Matayba elaeagnoides* (5.5%), were found to have the highest density and relative natural regeneration values (Tab. 1). Together, they accounted for 47% of the total density and 42% of the relative natural regeneration. The other species showed low density, being present in less than 40% of the sample units and having less than 4% representativeness in natural regeneration. Our results corroborates with other study that found in the lower strata of MOF many representatives of the Myrtaceae family, with emphasis on the genera *Myrcia* and *Eugenia*, along with Salicaceae (*Casearia* and *Xylosma*), Sapindaceae (*Allophylus* and *Cupania*), Rutaceae, Symplocaceae, and Aquifoliaceae (*e.g.*, Roderjan *et al.* 2002).

Allophylus guaraniticus, most important species found in the community, has also been observed in other studies conducted in the MOF. It was considered as one of the species with the greatest potential for regeneration in the studied community by Callegaro *et al.* (2015). The species *M. multiflora* was considered the second most important in the community. This results corroborates with the study of Dorneles & Warcheter (2004). The species was characterized by Kunz *et al.* (2008) as a typical understory species, whereas Seger *et al.* (2005) described *M. multiflora* as an intermediate or sub-canopy species.

Table 1 – Phytosociological parameters of species organized in the descending order of their relative natural regeneration value in a Mixed Ombrophilous Forest remnant in Santa Catarina, Brazil.

Species	AD	AF	RSC	RNR
	(ind ha^{-1})	(%)	(%)	(%)
Allophylus guaraniticus (A. St.-Hil.) Radlk.	1324.8	60	11.7	9.9
Myrcia multiflora (Lam.) DC.	1222.9	75	10.9	9.9
Casearia decandra Jacq.	1121.0	80	10.0	9.4
Myrsine coriacea (Sw.) R.Br. *ex* Roem. & Schult.	1044.6	50	9.6	8.1
Matayba elaeagnoides Radlk.	611.5	45	6.2	5.5
Eugenia sp.	509.6	30	4.3	4.0
Miconia cubatanensis Hoehne	509.6	10	5.0	3.5
Allophylus sp.	280.3	45	2.2	3.1
Cupania vernalis Cambess.	305.7	30	3.0	3.0
Allophylus edulis (A.St.-Hil. *et al.*) Hieron. *ex* Niederl.	280.3	35	2.5	2.9
Dalbergia frutescens (Vell.) Britton	331.2	20	3.0	2.7
Annona emarginata (Schltdl.) H.Rainer	203.8	30	1.9	2.3
Nectandra megapotamica (Spreng.) Mez	229.3	25	2.0	2.2
Styrax leprosus Hook. & Arn.	152.9	30	1.5	2.0
Araucaria angustifolia (Bertol.) Kuntze	203.8	20	1.9	1.9
Cinnamodendron dinisii Schwacke	178.3	20	1.2	1.6
Sebastiania brasiliensis Spreng.	203.8	5	1.8	1.4
Symplocos sp.	101.9	20	1.0	1.3
Podocarpus lambertii Klotzsch *ex* Endl.	101.9	20	0.8	1.3
Rudgea parquioides (Cham.) Müll.Arg	101.9	15	1.0	1.1
Eugenia uniflora L.	76.4	15	0.7	1.0
Miconia cinerascens Miq.	76.4	10	0.8	0.8
US-8	101.9	5	1.1	0.8
Bernardia pulchella (Baill.) Müll.Arg	76.4	10	0.7	0.8
Myrcia hartwegiana (O.Berg) Kiaersk.	76.4	10	0.7	0.8
Critoniopsis cf. *quinqueflor*a (Less.) H.Rob.	101.9	5	1.0	0.8
Symplocos tetrandra Mart. Miq.	127.4	5	0.7	0.8
Casearia obliqua Spreng.	101.9	5	0.9	0.8
Gymnanthes klotzschiana Müll.Arg.	76.4	10	0.5	0.7
Ocotea pulchella (Nees & Mart.) Mez	76.4	10	0.5	0.7
Cabralea canjerana (Vell.) Mart. subsp.	76.4	10	0.3	0.7
Solanum mauritianum Scop.	76.4	5	0.5	0.6
Ocotea sp.	51.0	10	0.5	0.7

Species	AD	AF	RSC	RNR
	(ind ha^{-1})	(%)	(%)	(%)
Sorocea bonplandii (Baill.) W.C. Burger, Lanjouw & Boer	51.0	10	0.4	0.6
Luehea divaricata Mart. & Zucc.	51.0	10	0.3	0.6
Solanum sanctae-catharinae Dunal	51.0	10	0.3	0.6
Machaerium stipitatum (DC.) Vogel	51.0	5	0.5	0.5
Vernonanthura discolor (Spreng.) H.Rob.	51.0	5	0.5	0.5
Calyptranthes concinna DC.	51.0	5	0.5	0.5
Ilex brevicuspis Reissek	51.0	5	0.4	0.5
Machaerium paraguariense Hassl.	51.0	5	0.4	0.5
Celtis iguanaea (Jacq.) Sarg.	25.5	5	0.3	0.3
Clethra scabra Pers.	25.5	5	0.3	0.3
Daphnopsis racemosa Griseb.	25.5	5	0.3	0.3
Erythroxylum deciduum A.St.-Hil.	25.5	5	0.3	0.3
Ilex paraguariensis A.St.-Hil.	25.5	5	0.3	0.3
Myrcia brasiliensis Kiaersk.	25.5	5	0.3	0.3
Myrcia oblongata DC.	25.5	5	0.3	0.3
Myrsine umbellata Mart.	25.5	5	0.3	0.3
Ocotea puberula (Rich.) Nees.	25.5	5	0.3	0.3
US-3	25.5	5	0.3	0.3
US-4	25.5	5	0.3	0.3
US-5	25.5	5	0.3	0.3
US-6	25.5	5	0.3	0.3
US-7	25.5	5	0.3	0.3
Roupala montana Aubl.	25.5	5	0.3	0.3
Brunfelsia cuneifolia J.A.Schmidt	25.5	5	0.2	0.3
Brunfelsia pilosa Plowman	25.5	5	0.2	0.3
Campomanesia guaviroba (DC.) Kiaersk.	25.5	5	0.2	0.3
Ilex sp.	25.5	5	0.2	0.3
Muellera campestris (Mart. *ex* Benth.) M.J. Silva & A.M.G. Azevedo	25.5	5	0.2	0.3
US-2	25.5	5	0.2	0.3
US-9	25.5	5	0.2	0.3
Schaefferia argentinensis Speg.	25.5	5	0.2	0.3
Solanum pabstii L.B.Sm. & Downs	25.5	5	0.2	0.3
Solanum sp.	25.5	5	0.2	0.3
US-1	25.5	5	0.0	0.3

AD = absolute density; AF = absolute frequency; RSC = Relative Size Category; RNR = relative natural regeneration.

Araucaria angustifolia, despite dominating the studied forest typology, was the 15th most important species in relation to the others. The low participation of *A. angustifolia* in the regenerative stratum has been reported by authors who studied MOF (*e.g.*, Lingner *et al.* 2007; Higuchi *et al.* 2015). *Araucaria* was one of the most important species in the occupying forest canopy in a study by Lingner *et al.* (2007); however, it was absent in the lower stratum. This condition indicates that this species has low regenerative potential in the understory of such forests (Higuchi *et al.* 2015). *Araucaria* spp. require particular soil conditions (Longhi *et al.* 2010). The species has a limited number of regenerating individuals in the understory of the MOF; this limitation is even more extreme at high altitudes (> 1,500 m) (Dalla Rosa *et al.* 2016).

Environmental variables

In the present study, the LAI varied from 1.05 to 5.17 $m^2 m^{-2}$, with an average of 3.08 $m^2 m^{-2}$ (Tab. 2). The percentage of clay in the soil varied from 22% to 54%, which, according to the Comissão de Química e Fertilidade do Solo (2004) indicates that the soil of the studied remnant have a medium to clayey texture. The values of soil density ranged from 0.28 to 1.00 g cm^{-3}. These results are less than those considered critical for clayey soils (1.4 to 1.6 g cm^{-3}) (Reichert *et al.* 2003). In the study area, saturation by basis (V) indicated that the soil had low nutrient availability (31.13%), being classified as dystrophic soil, according to EMBRAPA (2018). A low percentage of V indicates that the quantities of cations are reduced. In these situations, the soil is likely to be acidic and contain aluminum at levels that are toxic to most plants (Sobral *et al*. 2015). The saturation by aluminum (m) was 37.40%, which was higher than the limit tolerated by plants (20.10%) (Osaki 1991). The pH in H_2O (4.37) was also characteristic of soils with high acidity, according to Sobral *et al.* (2015).

The results of the PCA showed that the first two axes explained 68.8% of the total data variation (axis 1 = 47.6%; axis 2 = 17%) (Fig. 3). The leaf area index (LAI) had a weak correlation with the PCA axes, suggesting that, in fact, they explain the variation in the data only to a small extent. The correlations were not statistically significant ($p < 0.05$).

Through PCA, we found that the values of the soil variables did not occur homogeneously in the sample units. The vectors related to soil acidity

Table 2 – Average values of leaf area index and soil physical-chemical attributes in a Mixed Ombrophilous Forest remnant in Santa Catarina, Brazil.

Environmental variables	Minimum	Maximum	Average	Standard deviation
LAI ($m^2 m^{-2}$)	1.05	5.17	3.08	1.06
Sd (g cm^{-3})	0.28	1.00	0.74	0.16
Clay (%)	22.00	54.00	36.95	9.00
pH	3.60	5.60	4.37	0.66
OM (%)	7.20	11.50	8.82	1.15
V (%)	4.87	28.65	31.13	30.69
m (%)	0.00	91.40	37.40	27.95
CEC ($cmol_c$ dm^{-3})	15.77	28.60	28.06	7.74
Al ($cmol_c$ dm^{-3})	0.90	5.50	2.64	1.93
Ca ($cmol_c$ dm^{-3})	0.10	23.60	6.01	6.45
Mg ($cmol_c$ dm^{-3})	0.10	7.50	1.50	1.76
P (mg dm^{-3})	2.50	10.20	6.42	2.31
K (mg dm^{-3})	62.00	286.00	151.00	56.94

LAI = leaf area index; Sd = soil density; pH = pH in H_2O (1:1); OM = organic matter; V = saturation by basis; m = saturation by aluminum; CEC = pH7 cation exchange capacity; Al = aluminium; Ca = calcium; Mg = magnesium; P = phosphorus; K = potassium.

point to the right side of the quadrant. The vectors belonging to the basic variables point to the left side. Thus, the sampling units can be broken down into two groups: sampling units where the soils are less acidic and more fertile represented by the left side of the ordering diagram and sampling units in which the soils are more acidic, with a higher aluminum content (Al), occurring on the right side of the diagram.

However, most of the sample units were located on the right side of the quadrant. The variables that indicate higher acidity content in the soil had a strong positive correlation with axis 1 together with the ecological group of pioneer (Pi), climax tolerant to shadow (CS), and regeneration density (Dreg) and were negatively correlated with variables associated with saturation by basis (V), pH, leaf area index (LAI), and climax demanding of light (CL). In axis 2, the main components of variation were related to the variables phosphorus (P), organic matter (OM) and cation exchange capacity (CEC). In this axis, LAI and CS are positively and negatively correlated to Dreg, CL, P, and clay. These variables explain most of the data variation and determine the environmental patterns found in the sample units.

In the CCA, the results show that 43% (0.3273) of the total inertia (0.7528) are explained by the axes of the CCA, where axis one explains 20.7% (0.1561) and axis two 11.4% (0.08384) (Fig. 4). Using the Monte Carlo permutation test, the model was statistically significant (0.019 $p < 0.05$) at the level of 5% probability, as well as the first ordering axis (0.023 $p < 0.05$). Among the soil variables, only OM (0.014 $p < 0.05$) and V (0.016 $p < 0.05$) explained the data variation significantly. The percentage not explained by the ordering axes can be related to other variables that were not analyzed or could be of a stochastic nature (Balduíno 2001).

Pioneer species (Pi) and climax tolerant to shadow (CS) were organized in both ordering axes and correlated with variables related to soil acidity. In contrast, the climax demanding light (CL) were correlated with basic variables. It is important to note that the groupings formed by the species according to environmental conditions have arbitrary limits, i.e., even with subjectively established limits, the grouped species have different ecological requirements with greater overlap between them, in relation to the evaluated soil variables (Meira-Neto *et al.* 2005). The species have heterogeneous environmental adaptations in the context of recovery of degraded areas, resulting in the fact that, for each environmental situation, there is a set of species more suitable for use in recovery (Higuchi *et al.* 2016). Therefore, it is necessary to consider the variations of

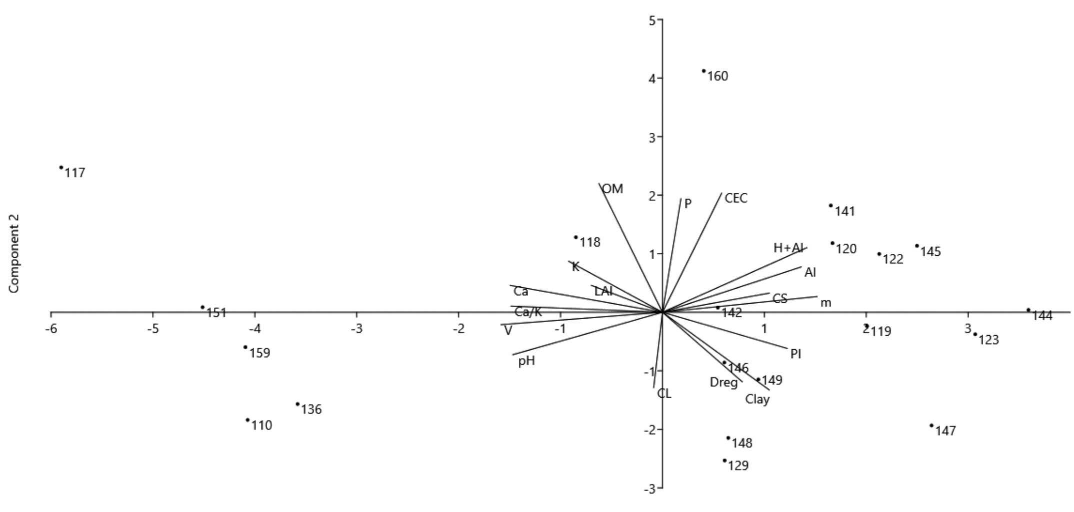

Figure 3 – Principal component analysis applied to environmental variable matrix and sample units in a Mixed Ombrophilous Forest remnant in Santa Catarina, Brazil. m = saturation by aluminum; CEC = pH7 cation exchange capacity; OM = organic matter; V = saturation by basis; pH = pH in H_2O; H+Al = potential acidity; Ca/K = calcium / potassium ratio; Ca = calcium; K = potassium; Al = aluminium; P = phosphorus; LAI = leaf area index; Dreg = regeneration density; Pi = pioneer; CL = climax demanding light; CS = climax tolerant to shadow.

vegetation associated with the environment in the definition of conservation and recovery of degraded areas (Higuchi *et al.* 2012b; Marcon *et al.* 2014).

The first axis of canonical ordering showed that the species that obtained the highest positive scores were *M. cubatanensis* (Mcub), *D. frutescens* (Dfru) *e M. coriacea* (Mcor) (Fig. 4). In contrast, the highest negative scores were attributed to *A. guaraniticus* (Agua), *Allophylus edulis* (Aedu) and *Cupania vernalis* (Cver). The environmental variables, on the same axis, that obtained the highest positive scores were clay and m. The highest negative scores were attributed to pH and V. In the second axis of canonical ordering, the species with the highest positive scores were *Allophylus edulis* (Aedu) and *C. decandra* (Cdec), whereas the highest negative scores were *M. cubatanensis* (Mcub), *D. frutescens* (Dfru) and *A. guaraniticus* (Agua). For the soil variables, the highest positive scores were attributed to CEC, and m; and negative for V and pH. This demonstrates that species can behave

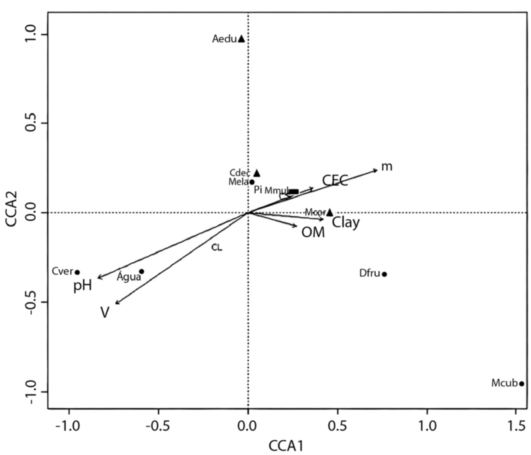

Figure 4 – Canonical correspondence analysis, applied to the matrices of environmental variables and the most abundant regenerating species in a Mixed Ombrophilous Forest remnant in Santa Catarina, Brazil. m = saturation by aluminum; CEC = pH7 cation exchange capacity; OM = organic matter; V = saturation by basis; pH = pH in H_2O; Pi and ▲ = pioneer; CL and ● = climax demanding light; CS and ▬ = climax tolerant to shadow; Aedu = *Allophylus edulis*; Agua: *Allophylus guaraniticus*; Cdec: *Casearia decandra*; Cver: *Cupania vernalis*; Dfru: *Dalbergia frutescens*; Mela: *Matayba elaeagnoides*; Mcub: *Miconia cubatanensis*; Mmul: *Myrcia multiflora*; Mcor: *Myrsine coriacea*.

differentiated in each environment, due to the different environmental variables and associations (Marcon *et al.* 2014).

It was possible to identify some groups of species in the dispersion of the points generated by the orthogonal arrangement of the two main axes of canonical ordering. Group 1 comprised the species *A. guaraniticus* (Agua) and *C. vernalis* (Cver), which were associated with soils with medium to high values of V and pH, and low values of Al. Therefore, these species seems to be adapted to more fertile soils with low level of acidity. Similar results were found by Higuchi *et al.* (2012b), in which *A. guaraniticus* represented the group corresponding to the highest pH values (> 5.6), indicating that this species has a preference for less acids soils.

The second group comprised the species *D. frutescens* (Dfru), *M. cubatanensis* (Mcub), and *M. coriacea* (Mcor). These species are associated with plots whose soil characteristics include soils with medium to high levels of clay and Al, in addition to low levels of bases. So, the conditions of the physical environment, associated with the soil characteristics condition community organization (Marcon *et al.* 2014). As a pioneer species (Vibrans *et al.* 2013), the presence of *M. coriacea* can be justified in units with moderate acidity and low soil fertility. This is a characteristic of r-strategist plants adapted to highly unstable environments (Magnano *et al.* 2013).

Matayba elaeagnoides (Mela), *C. decandra* (Cdec) and *M. multiflora* (Mmul) were found in the near the center of the ordering diagram, showing a low correlation with the soil variables, which may indicate that the main variation of this species may be associated with other environmental factors not addressed in this study. *Casearia decandra* (Cdec) has been described as a generalist species, owing to its easy adaptation to different habitats. This characteristic may be linked to their pioneering habit, as this ecological group comprises individuals with greater resistance to abiotic factors and less nutritional requirements (Narvaes *et al.* 2008). Likewise, the non-pioneer species *M. elaeagnoides* and *M. multiflora* showed similar associations with soil variables, suggesting that species responses to the tested variables are not limited to ecological groups.

Miconia cubatanensis (Mcub), *Dalbergia frutescens* (Dfru), and *A. edulis* (Aedu) occurred in both acidic soils and soils with low acidity, suggesting that these species can more easily adapt to the environment. However, the greatest correlation occurred with variables related to soil acidity. Therefore, we suggest that these species may be preferred for restoration of degraded areas in the MOF region, owing to apparently good adaptation to both soil environments.

Presumably, the functional characteristics of species explain the variability in the probability of establishment and growth in a given environment. In addition, different functional characteristics can vary within species, between populations, or even within the same population. Such interspecific variations may reflect the genetic diversity among individuals, which is typically conferred by phenotypic plasticity in response to variations in environmental factors (Larson *et al.* 2015; Jager *et al.* 2015; Galetti 2021). Thus, the different responses of regenerating species to soil variables observed in the present study may also be related to the functional characteristics of species present in naturally regenerated MOFs. Additionally, the functional attributes of species may reflect their ecological strategies, resulting from the balance between the benefits of resource allocation (trade-offs) at the expense of energy (Moreno 2019; Mazon 2021).

Our findings can be considered a preliminary reference for the association of plant community composition with pedological characteristics at a certain site. However, these results must be interpreted with caution and validated through additional complementary studies, given that the interactions of species with the environment go far beyond specific information (Ferreira Junior *et al.* 2009). In addition to edaphic factors, other environmental variables, such as light and temperature as well as species autecology, are pivotal in shaping the spatial distribution of species within a community.

In the present study in a remnant Mixed Ombrophilous Forest (MOF), environmental heterogeneity explained part of the tree species composition during regeneration. Associations of regenerating species with two groups of soil variables were identified: (a) moderate-to-high values of V and low values of aluminum and (b) with moderate-to-high content of clay and aluminum.

Miconia cubatanensis, *Dalbergia frutescens* and *Myrsine coriacea* were strongly associated with variables related to soil acidity, while *Allophylus guaraniticus* and *Cupania vernalis* were highly associated with variables related to the presence of bases in the soil. Thus, these species can be considered the indicators of the respective soil characteristics in the study area. Overall, the analysis of soil physicochemical characteristics in areas to be restored can allow for the more precise identification of species in the MOFs of southern Brazil. In the present study, the leaf area index did not affect the floristic composition of the regenerating stratum.

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