SCIENTIA PLENA VOL. 19, NUM. 04 2023
www.scientiaplena.org.br doi: 10.14808/sci.plena.2023.042401

Relation between environmental factors and structure of Atlantic Forest fragments

Relação entre fatores ambientais e estrutura de fragmentos de Mata Atlântica

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(Recebido em 12 de julho de 2022; aceito em 24 de março de 2023)

Forest fragmentation affects the structure and interactions of plant communities on several levels and is considered one of the causes of the extinction of species. This study aimed to verify if size, isolation, altitude and soil attributes influence species richness, basal area, abundance and species composition in Atlantic Forest fragments. We sampled shrubby-arboreal individuals and soil of ten fragments, and measured area, altitude and isolation. To verify the effects of the environment on abundance, species richness and basal area, we utilized generalized linear mixed models; to detect patterns in species abundance distribution concerning altitude, we constructed ordination histograms; and to determine the associations between environment and species composition, we performed a canonical correspondence analysis. A group of species was related to soils with higher Base Saturation, Organic Matter, Phosphorus, Silt and pH; another group had more relationship to soil variables such as Aluminium, Iron, Clay and Altitude, and a third group was related to Sulfur, Zinc and Boron. Some species occurred only in smaller and less elevated fragments, and others were exclusive of larger and more elevated fragments. The size and isolation of fragments did not explain species richness. The interaction between soil texture and nutrients causes changes in the composition of the community. Species richness, abundance, basal area and density were higher in more fertile soils. The basal area of the species increases with fragment size, altitude and more fertile soils.
Keywords: habitat fragmentation, island biogeography, phytosociology.

Fragmentação florestal afeta a estrutura e as interações das comunidades de plantas em vários níveis, sendo considerado uma das principais causas da extinção de espécies. O objetivo deste estudo foi verificar se tamanho, isolamento, altitude e solo influenciam na riqueza de espécies, área basal, abundância e composição de espécies em fragmentos de Mata Atlântica. Nós amostramos indivíduos arbustivo-arbóreos, coletamos amostras de solo e mensuramos tamanho, altitude e isolamento de dez fragmentos. Para verificar efeitos do ambiente na abundância, riqueza de espécies e área basal nós utilizamos modelos lineares generalizados mistos; para detectar padrões nas distribuições de abundância de espécies em relação a altitude nós construímos histogramas de ordenação; e para determinar a associação entre ambiente e composição de espécies fizemos uma análise de correspondência canônica. Um grupo de espécies está relacionado mais com solos de maior Saturação de Bases, Matéria Orgânica, Fósforo, Silte e pH, outro grupo está relacionado com Alumínio, Ferro, Argila e Altitude, e um terceiro grupo está relacionado com Enxofre, Zinco e Boro. Algumas espécies ocorrem somente nos fragmentos menores e menos elevados e outras são exclusivas de fragmentos maiores e mais elevados. Tamanho e isolamento dos fragmentos não explicaram a riqueza de espécies. A interação entre textura do solo e nutrientes causa mudanças na composição da comunidade. Riqueza de espécies, abundância, área basal e densidade foram maiores em solos mais férteis. A área basal das espécies cresce com o aumento do tamanho do fragmento, altitude e solos mais férteis.
Palavras-chave: fragmentação de habitat, biogeografia de ilhas, fitossociologia.

1. INTRODUCTION

Forest fragmentation is considered one of the leading causes of extinction of species, interrupting plant succession and reducing its potential in ecosystem functions [1]. Fragmentation can affect the structure of plant populations on several levels, including changes in the interaction with pollinators, edge effects, less migration, and loss of genetic diversity resulting in endogamy and, consequently, declining local populations [2, 3]. Little is known about large-scale extinctions of forest species. The capacity to form persistent populations by prolonged clonal growth can be one of the characteristics responsible for their slow response to fragmentation [4]. As forest cover decreases, and community richness and abundance decrease, besides changes in functional traits, such as reducing shade-tolerant, animal-dispersed and small-seeded species [5, 6].

The populational reduction caused by fragmentation creates an effect of a genetic bottleneck, whereby the remaining individuals represent only a tiny sample of the original genic set. The genetic bottleneck results in populations incapable of adapting to new selective pressures, such as climatic changes or variations in available resources [7]. Besides, biological changes such as species extinction in the structure of communities are increasing in hyper-fragmented landscapes, reinforcing the concept of homogenization [8].

Thus, we shall increase knowledge of the effects of fragmentation and the importance of remnants for the plant community. Understanding the effects of altitude, size, shape, degree of isolation, characteristics of the surroundings and history of disturbances on the forest structure of the fragments is relevant for developing strategies for biodiversity conservation. Such knowledge can give us clues on the vulnerability of the fragments, gene flow and sustainability of natural populations [9]. Altitude is a relevant factor for having a leading influence mainly on temperature and humidity, which can favor or exclude some species due to the thermic variation [10, 11]. The species richness, mainly trees, decreases with increasing altitude [12].

According to the Theory of Island Biogeography, size and isolation can influence species richness [13], controlled by a stable species source, based on the balance between extinction and immigration [14]. The theory was adapted to predict the species richness in fragments [15] and explain the mechanisms responsible for the observed patterns. Several studies have applied that theory, mainly regarding isolation, which is also responsible for forming systems of species metapopulation once the dispersers occasionally cross the matrix [16-18]. The distance between fragments can influence dispersal and colonization, affecting fragment quality directly. Alteration of the species composition and favoring pioneer species, mainly on the edges, hinders the appearance and establishment of secondary species [3, 8], generally found further inside fragments [19].

The vegetation structure can also be influenced by water availability, acidity and superficial moisture [20], and concentration of soil nutrients [21, 22]. The interactions among moisture, texture and soil nutrients can increase basal area and contribute to plant growth. In the same way, they can determine habitat suitability, generating changes in species composition [23] and dominance among tree species [24].

The granulometric soil characteristics can also influence the vegetation establishment condition [25]. More clayey soils, for example, have higher water retention capacity. Water availability regulates the dynamics of soil nutrients and their plant absorption [26]. The soil granulometry determines the buildup of organic matter, calcium and phosphorus [27]. The accumulation of these elements results in high values of cation exchange capacity. Such conditions favor the supply to the plants for processes of biomass synthesis. Besides that, in neotropical forests, there is a direct and positive relationship between plant species richness and soil fertility and precipitation [12, 28].

The Atlantic Forest is a forest domain nowadays represented by small areas or fragments, mainly in the Brazilian South and Southeast regions [29]. It is reduced to 11.73% of its original extension, which covered circa 16,377,472 ha [30]. It is considered a “hotspot” for biodiversity conservation [31] and is one of the Brazilian ecosystems with the highest plant diversity index ever found in tropical forests. According to Castuera-Oliveira et al. (2020) [32], most areas with the highest tree and tree-like species richness were found in the Atlantic Forest and Amazon domains. Furthermore, Atlantic Forest contains a high level of endemism [33, 34].

Several studies have been made on this type of forest, including many floristic surveys [35-37], interactions with animals [38-40], litter production and nutrient cycling [41]. Others report the influence of soil and topography [42, 43]. In this context, there needs more knowledge on the relationships between vegetation structure and soil attributes, size and isolation, particularly of inland Atlantic Forest remnants. Once this type of forest is highly threatened, this information is necessary to subsidize the decision-makers in implementing public policies for its conservation.

Therefore, our objective was to asseess the phytosociological parameters and verify if the soil chemical and granulometric composition, in addition to size, altitude and distance between fragments, are related to variations in species richness, basal area, abundance and composition of shrubby-arboreal species of Seasonal Semideciduous Forest.

2. MATERIAL AND METHODS

2.1 Study area

Our study was carried out in ten fragments of Seasonal Semideciduous Forest in the west of the state of Paraná (Brazil), municipalities of Assis Chateaubriand and Toledo (Figure 1). The fragments are within 15 properties, some small farmland sections registered by the numbers Fragment 1 (24°33’56.1”S; 53°35’31.0”W), Fragment 2 (24°33’55.6”S; 53°35’50.6”W), Fragment 5 (24°31’25.5”S; 53°34’18.0”W), Fragment 6 (24°29’43.9”S; 53°37’29.3”W), Fragment 7 (24°38’59.3”S; 53°38’35.4”W), Fragment 8 (24°34’09.5”S; 53°35’11.9”W), Fragment 10 (24°27’46.2”S; 53°32’33.0”W) and Legal Reserves (at least 20% of the natural vegetation of a farm has to be permanently set aside and registered) belonging to the farms *Fazenda Alvorada* (Fragment 3) (24°33’10.2”S; 53°35’48.7”W), *Fazenda Primavera* (Fragment 4) (24°33’24.2”S; 53°36’19.8”W) and *Fazenda Sperafico* (Fragment 9) (24°41’01.5”S; 53°40’06.4”W).

The vegetation of Fragment 1 (Frag 1) is in a medium to advanced stage of succession, with large trees and the presence of lianas, interconnected with a permanent preservation area (APP), which allows a greater flow of fauna with other fragments. Fragment 2 (Frag 2) presents vegetation in a medium stage of ecological succession, has no connection with other fragments and is surrounded by annual crops; besides that, this fragment is next to a highway and has signs of degradation signs by agricultural residues. Fragment 3 (Frag 3) has vegetation in a medium stage of ecological succession, with the presence of lianas and occasional signs of timber extraction; it is part of a farm's legal reserve, without connection with other fragments. Fragment 4 (Frag 4) is also part of a farm's legal reserve, with an advanced stage of ecological succession, large trees and lianas and no signs of degradation; it has no connection with other fragments, but it is close to an APP. Fragment 5 (Frag 5) is a farm's legal reserve, with vegetation in medium to advanced stages of ecological succession, with signs of degradation on the edges; it is surrounded by agriculture. Fragment 6 (Frag 6) is in an advanced stage of ecological succession, with the presence of large trees and lianas, encompassing an APP area that connects with other fragments. Fragment 7 (Frag 7) has no connection with other fragments, it presents vegetation in a medium to advanced stage of ecological succession, with large trees and lianas. Fragment 8 (Frag 8) is in a medium stage of ecological succession, with large trees, surrounded by agriculture. Fragment 9 (Frag 9) has vegetation in a medium stage of ecological succession, with several signs of degradation, including garbage disposal and signs of timber extraction. Fragment 10 (Frag 10) has vegetation in a medium stage of ecological succession, few lianas and no signs of degradation.

All fragments are surrounded by crop and pastoral activities developed after clearing, mainly for soybean and corn. Six fragments are connected to the gallery forest of small creeks, and the other four are isolated, without connectivity. The elevation of the fragments varies between 378 and 600 m altitude.

The predominant forest formations in the studied region are Seasonal Semideciduous Forest and Mixed Ombrophilous Forest. The soil is Red Latosol [44], humid subtropical climate (Cfa) by the classification of Köppen [45], mean annual temperature of around 21.5°C and annual rainfall of approximately 1800 mm, with most frequent rains from October to March, the highest volumes occurring in December and January [46].

To construct the location map, we utilized the shapefiles of Brazil, states and municipalities provided by the Brazilian Institute of Geography and Statistics [47], of Atlantic Forest by the

Ministry for Environment [48], and Hydrographic Units by the Paraná Water Institute [49]. We created the map using the software QGis Version 3.4 [50].

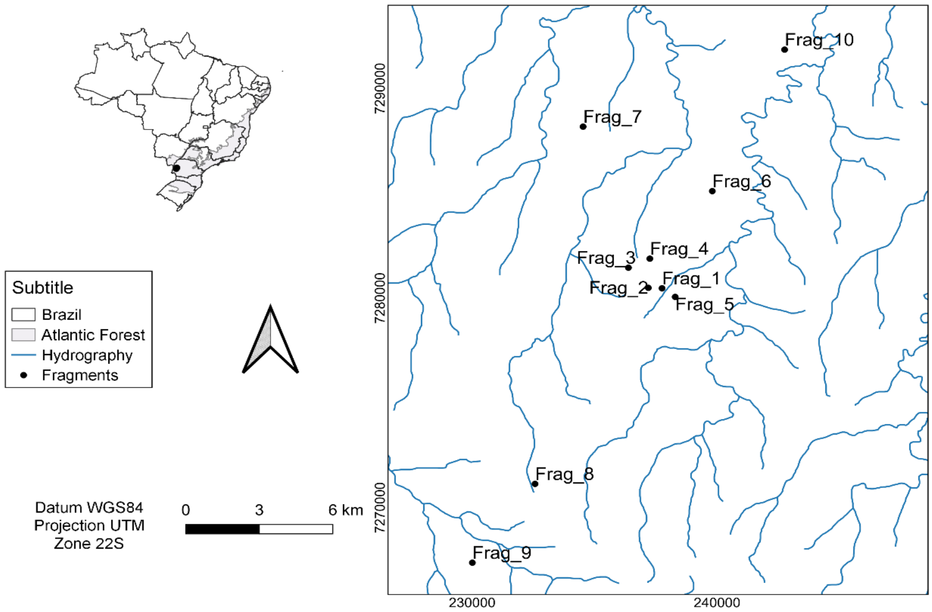

Figure 1: Distribution of ten remnant fragments of Atlantic Forest (Seasonal Semideciduous Forest) sampled in the municipalities of Assis Chateaubriand and Toledo, west of the state of Paraná, Brazil. Frag = Fragment.

2.2 Collection of data

We collected the data between April and September 2017, using the plot method according to Mueller-Dombois and Ellenberg (1974) [51], with some modifications. We marked ten sampling plots of 20x10 m in each fragment, with a minimum distance of 20 m between plots, totalling 100 plots. We measured the area of the fragments, the altitude and the distance between them, and all sampling areas were geo-referenced.

We sampled all shrubby-arboreal individuals with a circumference at breast height (CBH) ≥ 15 cm at 1.3 m aboveground. All sampled individuals were sequentially numbered with metal platelets. We collected vouchers of all individuals (fertile or not) for identification in the laboratory. We estimated the height of each individual by comparison with a dm-graduated rod. For individuals branched below 1.3 m, the basal areas of branches were calculated separately and then added. The collected material was dried and processed following standard botanic techniques and incorporated into the CGMS/UFMS herbarium. We used the bibliography of Lorenzi (2002) [52], Lorenzini (2002) [53], Lorenzini (2010) [54] and Ramos et al. (2008) [55] to help identify the species and consulted specialists. The conference of scientific names was carried out through the *Flora e Funga do Brasil* [56] website.

To establish the isolation degree, we calculated the average distances of each fragment from the other four closest fragments, utilizing satellite images from Google Earth. We adopted this method because five of the ten fragments are close to each other, and the other five are more separated at distances varying from 511 to 27,642 m (Appendix 1 – available at: <https://doi.org/10.6084/m9.figshare.22304131>. Therefore, seven distance classes between fragments were established (511, 963, 706, 4338, 4677, 7247 and 7396 m). We considered as zero isolation the fragments with connection with a gallery forest or other connected remnant fragments. This procedure was adopted because most semideciduous forest species are also found in riverine environments in the Atlantic Rain Forest domain [57, 58]. That was adopted because there was no big continuous area around our study sites. We used a GPS device to check the altitude and Google Earth to measure the fragment size variable [59].

2.3 Phytosociological analyses

The phytosociological attributes were calculated considering all plots together. The calculated attributes were relative density (RDe) which is the ratio of the number of individuals of a species (n) and the total number of individuals sampled (N); relative frequency (RF), which is the relationship between the absolute frequency (AF) of a particular species with the sum of the AFs of all sampled species; relative dominance (RDo) which is the ratio between the basal area (BA) of a species and the total (BA) of sampled species; importance value (IV) which provides an idea of the density, spatial dispersion and the dimension reached by a species, showing its ecological importance; and coverage value (CV) that provides information related to the number of individuals and the biomass of each species according to methods described by Mueller-Dombois and Ellenberg (1974) [51] and Martins (1991) [60], using FITOPAC software, version 2.1.2 [61].

2.4 Soil analyses

We collected 10 soil cores 0-20 cm deep in each plot using a 4 cm diameter corer. Then, we homogenized the 10 cores to obtain a compound sample per plot. The samples were placed in plastic bags identified with date, fragment number and plot number and sent to the Soils Laboratory of the Universidade Federal de São Carlos (UFSCar-Araras) for chemical and physical analyses. The chemical variables analyzed were Phosphorous (P), Organic Matter (O. M.), pH, Aluminium (Al), percentage of Base Saturation, representing the fertility (V), percentage of Aluminium Saturation (m), Sulfur (S), Boron (B), Copper (Cu), Iron (Fe), Manganese (Mn), Zinc (Zn), and the physical variables were: Clay, Total Sand (t. sand), and Silt.

2.5 Analyses of data

The data were analyzed utilizing R version 3.0.1 [62] (R Development Core Team, 2019). To verify the effects of the variables altitude, size, isolation and soil fertility and their interactions on abundance, species richness and basal area, we utilized generalized linear mixed models (GLMMs) with fragments as random factors. We selected the best set of predictor variables by using the backward stepwise selection method. We calculated a type III ANOVA table to verify the significance of each variable and the interactions in the model. We ran a PCA with the soil variables and used the first and second axes as predictor variables. The distribution of variables was verified using the package Fitdistrplus [63]. We utilized quasi-Poisson models to correct overdispersion for species richness and abundance (discrete ordinal variables) [64]. We utilized Gaussian distribution for the basal area (continuous variable with normal distribution). We utilized rarefaction to remove the species abundance effect in the analysis of species richness, using the package Vegan [65].

To detect the patterns in species abundance distribution concerning the altitude of the fragments, we constructed ordination histograms of species abundance distribution over these gradients.

To determine the possible associations between environmental variables and the composition of shrubby-arboreal species of the 100 plots, we performed a canonical correspondence analysis (CCA) using the package Vegan R [66]. CCA is a multivariate analysis that relates the composition of the community directly with the environmental variables [67]. We utilized two matrices, one of species abundance and one environmental containing variables of soil, size and altitude of fragments. We built a species matrix with the number of individuals per species/plot. We utilized the function 'envfit' of the package Vegan to identify variables and species that best explain the variation. The function 'envfit' uses data randomization define the significance of environmental variables. To determine the significance of the eigenvalue of the first canonical axis of the ordination, we performed the Monte Carlo test with 999 permutations [68].

The dataset of species abundance matrix per plot, soil parameters per plot and fragment coordinates are available at: <https://doi.org/10.6084/m9.figshare.22304131>.

3. RESULTS

3.1 Floristics and phytosociology

We recorded 2237 shrubby-arboreal individuals of 145 species distributed in 99 genera and 43 families (Appendix 2 and Appendix 3 – available at: <https://doi.org/10.6084/m9.figshare.22304131>). The species richest families were Fabaceae (24 species), followed by Myrtaceae (11 spp.), Euphorbiaceae, and Meliaceae (10 spp.) (Figure 2a).

Cabralea canjerana was the most abundant species (Figure 2b), followed by *Alchornea glandulosa*, *Nectandra megapotamica* and *Ocotea silvestris*. The species *A. glandulosa* and *A. triplinervia* showed the highest values of importance (6.87 and 6.27, respectively) since they present high density, frequency and dominance (Figure 2c) (Appendix 3). We found the species *Cabralea canjerana* (IV = 4.68) with high density and frequency, and mean values of dominance and the species *Astronium graveolens* (IV = 3.92) with high density and median values of frequency and dominance (Figure 2c) (Appendix 3). The ten species with the highest IV values represent 39% of all IV sampled (Figure 2c) (Appendix 3).

Among the ten species with the highest IV and most abundant, seven occur in all fragments (absolute frequency = 100%); they are *A. glandulosa*, *A. triplinervia*, *A. graveolens*, *Balfourodendron riedelianum*, *C. canjerana*, *Nectandra megapotamica*, and *Ocotea silvestris* (Figure 2c) (Appendix 3). Another eight species occurred in all fragments: *Allophylus edulis*, *Aspidosperma polyneuron*, *Chrysophyllum gonocarpum*, *Chrysophyllum marginatum*, *Dalbergia frutescens*, *Jacaratia spinosa*, *Prunus myrtifolia*, and *Trichilia catigua*. Of the 145 species, 30 were very frequent, occurring in at least eight fragments (Appendix 3).

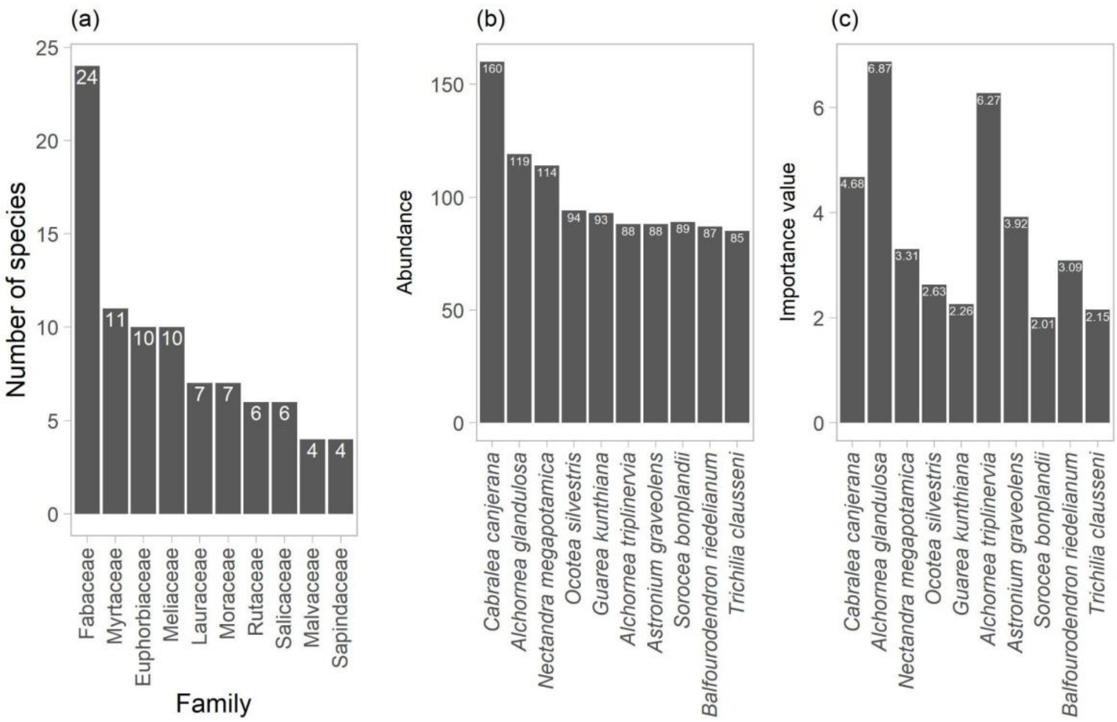

Figure 2. Number of species of the ten richest families (a); abundance (b) and importance value (c) for the ten most abundant species in fragments of Atlantic Forest, Paraná, Brazil.

3.2 Association between plant community and environmental factors

Silt, pH, V, Fe, Al, Clay and organic matter were the variables that most contributed to the variation in the first PCA axis. The variables with more contribution in the second axis were Cu, Mn and Sand (Figures 3a and 3b). Those soil variables in the first axis (PC1) and their interaction with Altitude influenced the species richness and abundance. Basal area was influenced only by soil, without interaction with Altitude (Table 1). We did not detect relationships between our response variables with the second axis of the soil PCA (PC2). In higher altitudes, species richness had negative correlation with soil (PC1), while in lower altitudes, the correlation was positive (Table 1). That means, in higher altitudes, the relative enhancement in Silt, V and pH concentrations (concerning decrease in Al, m, Fe and Clay concentrations) provide higher species richness (Figures 3 and 4a). The abundance had a positive correlation with soil at higher altitudes and a negative correlation at lower altitudes (Table 1). In other words, in higher altitudes, the relative enhancement in Silt, V and pH concentrations (concerning decrease in Al, m, Fe and Clay concentrations) provide lower abundance (Figures 3 and 4b). The basal area had a negative correlation with soil PC1 (Table 1), indicating that the relative enhancement in Silt, V and pH concentrations (concerning decrease in Al, m, Fe and Clay concentrations) provide a higher basal area (Figures 3 and 4c).

Table 1: Results of generalized linear mixed models. R2m = R squared for fixed effect (marginal effect). R2c = R squared for both fixed and random effect (conditional effect). Significant results ($p < 0.05$) in bold.

	R^2m	R^2c		F	Pr(>F)
Richness	0.150	0.198	Size	0.385	0.574
			Altitude	0.004	0.951
			Distance	0.061	0.815
			Soil (PC1)	0.227	0.636
			Soil (PC2)	1.234	0.295
			Altitude: Soil (PC1)	**5.171**	**0.026**
			Size: Distance	2.615	0.190
Basal Area	0.096	0.096	Tamanho	0.001	0.978
			Altitude	1.975	0.181
			Soil (PC1)	**5.397**	**0.027**
			Size: Soil (PC1)	1.863	0.183
Abundance	0.116	0.116	Altitude	0.802	0.386
			Distance	2.826	0.137
			Soil (PC1)	2.514	0.118
			Altitude: Soil (PC1)	**5.716**	**0.019**

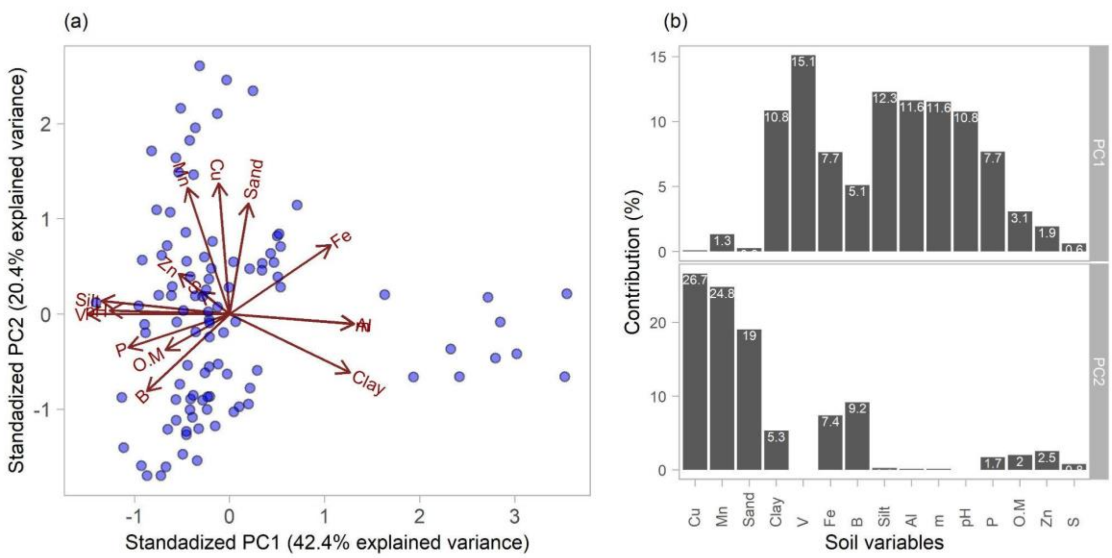

Figure 3: Principal Components Analysis from soil variables (a) and the contribution of the soil variables to the first and second axis (b) in fragments of Atlantic Forest, Paraná, Brazil.

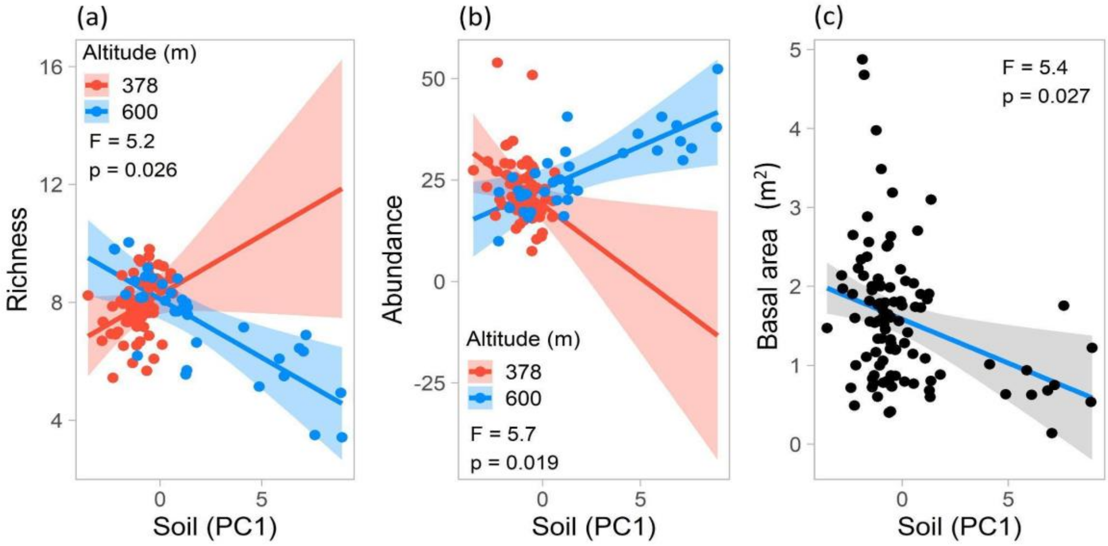

Figure 4: Relationship of environmental variables (soil fertility, Altitude, size and distance between fragments) with species richness (a) abundance (b), and basal area (c) of shrubby-arboreal species in fragments of Atlantic Forest, Paraná, Brazil.

There was a homogeneous distribution of species over the gradient in the ordination performed with the species abundance concerning the fragment altitude. Some species occurred only in fragments at higher altitudes (538 to 600 m); a typical example is *Araucaria angustifolia*; in contrast, other species were exclusive to less elevated fragments (378 to 439 m), e.g. *Talisia esculenta*, *Piper gaudichaudianum, Euterpe edulis* and *Campomanesia guazumifolia* (Appendix 4). That factor did not affect the variation in species richness of the vegetation.

Of the 145 recorded species, 15 occurred in all studied fragments. Four species occurred only in the largest fragment (894,863 m^2) (*Vitex megapotamica*, *Myroxylon peruiferum*, *Machaerium hirtum* and *Casearia decandra*). Another 11 species were exclusive to the smallest fragment (46,394 m^2); however, none is a pioneer (*Trichilia elegans*, *Symplocos revoluta*, *Solanum mauritianum*, *Siparuna guianensis*, *Bunchosia pallescens*, *Rudgea parquioides*, *Myrcia splendens*, *Miconia lepidota*, *Machaerium paraguariense*, *Colubrina glandulosa* and *Cariniana estrellensis*).

The canonical correspondence analysis (CCA) (Figure 5) shows the position of the 13 environmental variables and 17 significant species for the ordination. The eigenvalues for the first two axes were 0.21 (axis 1) and 0.18 (axis 2), explaining 20% of the total accumulated variation concerning the environmental variables. The first canonical axis was significant ($p>0.01$), indicating a relation between the species and the environmental variables.

The chemical (S; Zn; B; M.O.; P; V; Al; Fe; pH) and physical (Silt and Clay) soil components and Altitude were significant for the CCA (Table 2). The components with the strongest correlation with axis 1 were Altitude, Clay, Fe (negative correlation), P, O. M. and Silt (positive correlation). *Trichilia claussenii, Trichilia pallida* and *Guarea kunthiana* showed a positive relationship with Phosphorous, Silt, soils with high fertility, high pH and more organic matter. *Ocotea silvestris, Alchornea triplinervia, Terminalia glabrescens, Jacaranda micrantha, Guarea macrophylla, Prunus myrtifolia* and *Casearia sylvestris* seem to be related to soils with higher concentrations of iron, Aluminium and clay. *Lonchocarpus cultratus, Casearia sylvestris, Schizolobium parahyba, Centrolobium tomentosum, Parapiptadenia rigida, Cedrela fissilis* and *Pseudolmedia laevigata* seem to be related to higher levels of Sulfur, Zinc and Boron.

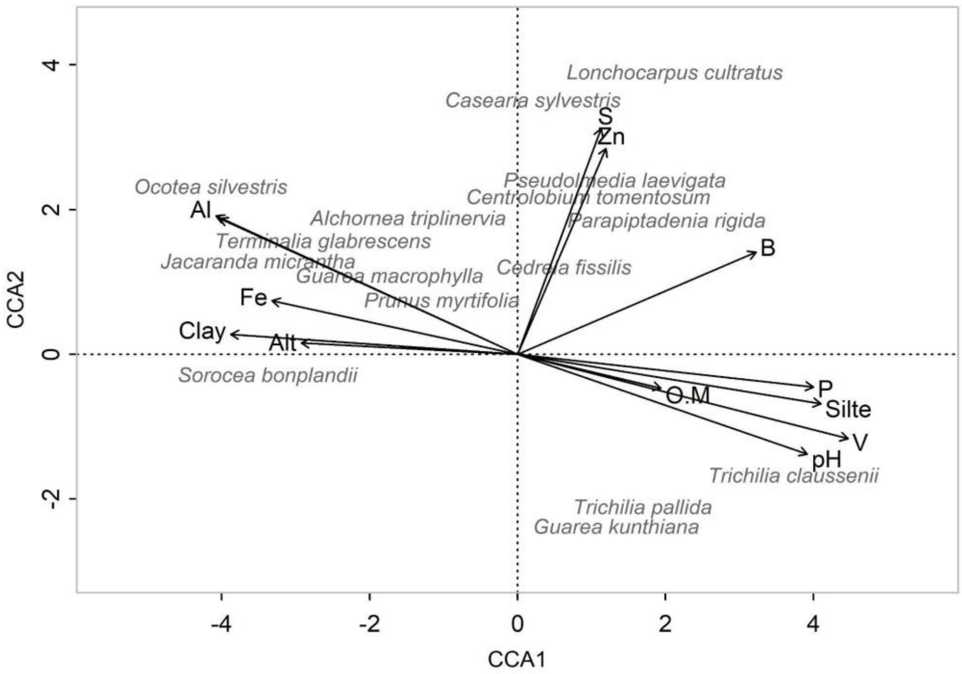

Figure 5. Canonical Correspondence Analysis between environmental variables (soil components and altitude of the fragments) and abundance of the shrubby-arboreal species per plot in ten fragments of Atlantic Forest sampled in the west of the state Paraná, Brazil. Representing the variables and significant species for explanation of the variation: Phosphorous (P), Iron (Fe), Organic Matter (O. M.), Aluminium (Al), Percentage of Base Saturation, that represent the soil fertility (V), Percentage of saturation by Aluminium (m), Sulfur (S), Boron (B), Zinc (Zn), pH, Silt, Clay and Altitude (Alt).

Table 2: Means (± standard deviation) of environmental variables for each fragment of Seasonal Semideciduous Forest in west of the Paraná state, Brazil, and the significance values for the CCA (= p< 0.05). Fragments 1 to 10 (F), soil variables: Phosphorous (P); organic matter (O.M.); pH; Aluminium (Al); Percentage of Base Saturation, representing soil fertility (V); Percentage of Aluminium saturation (m); Sulfur (S); Boron (B); Copper (Cu); Iron (Fe); Manganese (Mn); Zinc (Zn); Clay; Total sand (T. sand); Silt, Altitude and Size.*

Variables	**F01**	**F02**	**F03**	**F04**	**F05**	**F06**	**F07**	**F08**	**F09**	**F10**	**Pr (<r)**
Altitude (m)	455	460	473	484	480	429	428	563	542	429	0.0001*
Size (m^2)	95.7	78.4	90.3	200.4	46.4	894.9	819.5	215.9	88.8	64.9	0.0659
P (mg/dm^3)	16.1 (2.4)	17.9 (3.9)	17.5 (3.5)	16.3 (3.2)	15.5 (4.5)	12.4 (3.6)	13.2 (2.1)	12.2 (1)	7 (1.1)	15.5 (3.9)	0.0001*
O.M. (g/dm^3)	32.3 (11.7)	32.7 (7.2)	34.7 (6.1)	33.3 (4.7)	31 (4.3)	28.2 (7.1)	29.6 (4.4)	28.8 (4.4)	24.6 (1.8)	31.4 (5.5)	0.0172*
pH ($CaCl_2$)	5.65 (0.1)	5.43 (0.3)	5.6 (0.2)	5.51 (0.2)	5.67 (0.3)	5.89 (0.2)	5.91 (0.2)	5.5 (0.3)	4.12 (0.3)	5.39 (0.3)	0.0001*
Al (mmol/dm^3)	0.11 (0)	0.24 (0.4)	0.1 (0)	0.33 (0.4)	0.26 (0.2)	0.23 (0.2)	0.25 (0.3)	0.39 (0.2)	19.29 (12.2)	0.52 (0.5)	0.0001*
V (%)	90.36 (4)	85.54 (5.1)	88.87 (2.6)	87.56 (3.6)	90.44 (3)	85.77 (3.5)	82.59 (4.6)	71.16 (6.9)	28.3 (14.8)	87.87 (4.9)	0.0001*
m (%)	0.09 (0.1)	0.2 (0.3)	0.1 (0)	0.26 (0.3)	0.18 (0.1)	0.23 (0.2)	0.31 (0.4)	0.7 (0.3)	35.97 (23.3)	0.43 (0.5)	0.0001*
S (mg/dm^3)	19.4 (12.7)	8.6 (10.8)	11.9 (5.5)	8.3 (5.8)	13.1 (5.5)	3.3 (2)	3.7 (1.9)	8.3 (6.7)	9.1 (5.3)	14 (2.8)	0.0001*

B (mg/dm^3)	0.446 (0.2)	0.402 (0.2)	0.538 (0.2)	0.44 (0.1)	0.434 (0.1)	0.321 (0.1)	0.332 (0.1)	0.21 (0)	0.182 (0.1)	0.227 (0.1)	0.0001*
Cu (mg/dm^3)	11.93 (2.6)	6.23 (1.3)	4.2 (0.5)	4.58 (0.8)	9.14 (2.1)	10.73 (1.9)	8.64 (1.3)	9.36 (1.3)	8.02 (2)	16.39 (3.4)	0.6867
Fe (mg/dm^3)	16.4 (5.8)	12.3 (2.8)	12 (3.2)	11.5 (2.5)	12.4 (4.2)	15.5 (2.8)	14.6 (2.8)	19.8 (3)	25.8 (5.4)	17.8 (4.4)	0.0001*
Mn (mg/dm^3)	86.65 (24.6)	49.71 (7.9)	46.43 (9.1)	51.77 (12.9)	65.57 (12.5)	94.84 (10.5)	84.65 (12)	84.74 (11.5)	40.01 (12.1)	117.58 (12.4)	0.0775
Zn (mg/dm^3)	10.68 (4.7)	5.37 (2)	5.52 (1.3)	5.48 (1.4)	7.38 (1.8)	7.02 (1.2)	7.2 (2.6)	5.12 (0.9)	4.01 (4.4)	5.21 (1.2)	0.0003*
Clay (g/Kg)	442 (0)	536 (0)	498 (0)	515 (0)	463 (0)	500 (0)	527 (0)	541 (0)	626 (0)	439 (0)	0.0001*
Sand (g/Kg)	153 (0)	120 (0)	106 (0)	97 (0)	116 (0)	101 (0)	127 (0)	152 (0)	130 (0)	160 (0)	0.1652
Silt (g/Kg)	405 (0)	344 (0)	396 (0)	388 (0)	421 (0)	399 (0)	346 (0)	307 (0)	244 (0)	401 (0)	0.0001*

4. DISCUSSION

4.1 Floristics and phytosociology

The richest families (Figure 2) show resemblances with the reports by Rosseto and Vieira (2013) [69], which analyzed a forest remnant of Seasonal Semideciduous Forest and found Fabaceae and Myrtaceae being the families with the highest species richness within Angiosperms. Gris et al. (2014) [70] analyzed fragments of Seasonal Semideciduous Forest under varying levels of disturbance and observed the predominance of Fabaceae, Meliaceae, Lauraceae, Myrtaceae and Moraceae. Likewise, Bald et al. (2021) [71], in a forest remnant of Seasonal Semideciduous Forest, found Fabaceae, Meliaceae, Rutaceae, Lauraceae and Myrtaceae as the richest families. Souza et al. (2019) [72] and Adenesky-Filho et al. (2017) [73] found as predominant families Fabaceae, Myrtaceae, Lauraceae, Euphorbiaceae and Meliaceae, and Estevan et al. (2016) [74] found Fabaceae, Meliaceae, Myrtaceae and Lauraceae. Fabaceae was also the family with the highest species richness and stood out in most surveys done in Seasonal Semideciduous Forests [36, 75-78] due to the capacity of nitrogen fixation of many species, which favors the regeneration in soils with nutrient deficiency, or that underwent some disturbance [79, 80].

Many resemblances in species composition exist when compared with other studies in nearby areas of Seasonal Semideciduous Forest [70, 71, 74] and transitional areas between Semideciduous and Mixed Forests [72, 73, 78] (Appendix 2); however, there are differences in the structure of the communities, mainly in the species that present the highest abundances and IV, probably due to the different conditions of each area, whether related to the environment or anthropic activities.

Among the species with the highest IV, some resemblances can be observed between our study and Gris et al. (2014) [70], e.g., *Cabralea canjerana, Balfourodendron riedelianum, Alchornea triplinervia, Guarea kunthiana* and *Sorocea bonplandii* stand out in both studies, the same for the study carried out by Bald et al. (2021) [71] where the species with the highest IV include *G. kunthiana, B. riedelianum* and *C. canjerana.* These resemblances are attributed to the proximity of the areas (western Paraná), similar conditions for developing these species and the same type of phytophysiognomy, Seasonal Semideciduous Forest. The study by Estevan et al. [74] in fragments of Seasonal Semideciduous Forest in northern Paraná also showed resemblances with the present study, the most important species were the same: *Trichilia clausseni, C. canjerana; Nectandra megapotamica; S. bonplandii* and *G. kunthiana.* When considering the density, resemblances are also observed with the study by Souza et al. (2019) [72], with an abundance of *S. bonplandii, N. megapotamica, C. canjerana* and *B. riedelianum.*

The species that were very frequent, occurring in all fragments, are common and important species in this type of phytophysiognomy, some of them are classified as endangered, such as *B. riedelianum* and *Aspidosperma polyneuron* [81], which highlights the importance of the conservation of these fragments.

4.2 Association between plant community and environmental factors

As expected, species richness increased in fragments with higher Silt, pH and base saturation (soil fertility) at higher altitudes. The high nutrient availability favored the co-occurrence of a higher number of species, as observed by Ding et al. (2012) [82], with possible low levels of competition among them. The trend of a decreased abundance of individuals in less fertile and less elevated fragments can be explained by the easy access to these areas that favored logging, mainly of taller trees, leaving gaps inside the fragments. That allowed the establishment of pioneer species with high levels of germination and growth [8], thus increasing the number of individuals.

However, in more elevated fragments (538 to 600 m), there was an increase in the abundance of individuals despite low soil fertility, Silt and pH. That might have occurred due to less anthropic pressure since the areas were inadequate for agriculture by the declivity, allowing the maintenance of secondary species until the present.

Regarding basal area, we observed a reduction trend with a relative decrease in soil fertility, Silt and pH. That pattern can be related more to human activity, as in these areas, we observed a high number of stumps of cut trees and only a few tall trees left, which probably caused the decline of the basal area. Thus, increased density and reduced basal area are also related to anthropic pressures, mainly selective logging for wood, though forbidden in areas registered as Legal Reserves.

A high soil base saturation in some fragments favored the development of a higher number of trees for abundant resources, thus increasing the basal area in these remnants. That pattern was also reported by Ding et al. (2012) [82], that the highest concentrations of nutrients, besides a high base saturation, allowed the highest species richness, and increased basal area.

Size and isolation of the fragments were not representative factors for variation in species richness in our study, not presenting a pattern as expected by the Theory of Island Biogeography [14]. The species richness of each fragment varied independently of isolation and size. Isolated fragments had a species richness comparable to closer fragments, whereas smaller fragments presented the same number of species as larger fragments, occurring only with slight changes in their composition. The lack of relationship with isolation is probably associated with the fragmentation time, which occurred mainly in the last 50 years [83], which may have to be longer for this effect to appear.

That can also explain the occurrence of exclusive species in fragments with different sizes that, before deforestation, maintained seed flow all over the original area. After suppression and fragmentation of the vegetation, the remaining protected areas sheltered the same composition, i.e. some trees were already there even before logging started, persisting until the present. That explains why some species occurred only in the tiniest remnant (46,394 m^2); in counterpart, other species were recorded in the largest fragment (894,863 m^2), as in the case of *Vitex megapotamica*, *Myroxylon peruiferum*, *Machaerium hirtum* and *Casearia decandra*. However, that might be only a random effect of sampling.

Therefore, all fragments, independently of size, are of high importance for conservation in the region since they can be one of the last remnants where a species still occurs, thus, increasing the need to conserve small fragments. Small fragments reduce the isolation between larger fragments, maintaining the mosaics functionally connected [84-86]. If fully protected, these small forest fragments can play an essential role in maintaining ecosystem services, such as carbon absorption and shelter for biodiversity [87]. Forest remnants, even tiny, support the movement of carnivores in man-dominated landscapes in the Atlantic Forest [88]. Likewise, for birds, it is suggested that small fragments increase connectivity, mainly in landscapes with a higher percentage of permeable matrix [89]. For reptiles, the fragment area was the main predictor for species richness, which decreases with reduced fragment area; even so, those authors point out that the importance of these small fragments can not be neglected for conservation [90].

High soil acidity in some fragments conditioned high levels of Aluminium and Iron, which can inhibit the development of a group of plants and benefit others physiologically more adapted. Such conditions select tolerant species that are best adapted to lower fertility. A similar pattern was observed by Cestaro and Soares (2004) [91], that soil fertility and Aluminium levels were the main drivers for differences in vegetation structure.

Some fragments had high soil concentrations of Sulfur, Zinc and Boron, with most associated species belonging to the family Fabaceae (*Lonchocarpus cultratus, Schizolobium parahyba, Centrolobium tomentosum, Parapiptadenia rigida*), as shown in the CCA graph. When available in high concentrations, these micronutrients, especially S, enhance plant productivity and quality [92]. Despite low base saturation and little organic matter [93], Sulfur stimulates plant vegetative development. Sulfur is an essential nutrient in the plant protein synthesis, besides helping in Nitrogen fixation, primarily by legumes. Zinc is responsible for maintaining the structural integrity of the cell membrane. Zinc deficiency hinders the activity of enzymes involved in carbon fixation, thus, reducing net photosynthesis [94]. Boron is a fundamental micronutrient for the growth of meristematic tissues, besides helping the functioning of the cell membrane, transport of auxins and carbohydrate metabolism [95].

Some species were associated with or occurred exclusively at higher elevation fragments. *Araucaria angustifolia,* a species with distribution in altitudes varying from 500 to 1500 m [96], was only found in the most elevated fragment. Altitude exerts a known relation with temperature and moisture, causing considerable changes in climate, soil and natural vegetation upward the altitudinal gradient, favoring species more adapted to such conditions, e.g. *A. angustifolia* [10].

5. CONCLUSION

Therefore, soils with higher base saturation (fertility) show higher species richness, and the interaction between soil texture and nutrients causes changes in the composition of the shrubby-arboreal community. Higher soil fertility also favors higher density, without much difference between species richness regarding size and isolation of fragments. The basal area of the species increases with fragment size and altitude, as well as in more fertile soils, whereas in fragments at lower altitudes, the basal area of the species is lower. Altitude plus high soil fertility favors the basal area of some species, allowing their occurrence exclusively in more elevated fragments. We highlight the relevance of forest fragments in the conservation of the species.

6. ACKNOWLEDGMENTS

This study was financed in part by the Fundação Universidade Federal de Mato Grosso do Sul – UFMS/MEC – Brazil. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001, scholarship to DJGM, DG, EBS and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for research grant GAD-J and AP. We are grateful to the Programa de Pós-Graduação em Biologia Vegetal - PPGBV / UFMS and to the botanists of the Instituto de Biociências (INBIO, UFMS) for their assistance in identifying the species; Ismari, Fernando, Hellen, Elaine and Jair for their assistance in the fieldwork.

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