

Influence of environmental variables on the shrub and tree species distribution in two Semideciduous Forest sites in Viçosa, Minas Gerais, Brazil

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Abstract: The floristic variations of shrub and tree components were studied in two sites of Semideciduous Forest, initial forest and mature forest, located in the Mata do Paraíso Forest Reserve, in Viçosa, State of Minas Gerais, Southeastern Brazil, in order to analyze the floristic similarity and the correlations between environmental variables and the distribution of tree species in these forests. Individual trees with a diameter at breast height (DBH) ≥ 4.8 cm were sampled in twenty 10 x 30 m plots (10 plots in each site). The plots were distributed systematically at 10 m intervals. The environmental variables analyzed were: the canopy openness and soil chemical and texture characteristics. The two forest sites showed clear differences in the levels of canopy openness and soil fertility, factors that reflect the floristic and successional differences of the shrub and tree component, revealed by the low similarity between these forests by cluster analysis. The canonical correspondence analysis (CCA) of environmental variables and species abundance indicated that the species in these forests studied are distributed under strong influence of canopy openness, moisture and soil fertility. *Rev. Biol. Trop.* 56 (3): 1557-1569. Epub 2008 September 30.

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The fragmentation process of the Atlantic Rain Forest has become accentuated in the last decades. This forest originally occupied 12% of the Brazilian territory. Currently it is reduced to only 5% of the territory, in the form of small fragments of varied sizes, shapes, degrees of isolation, neighborhood types and disturbance history. All these hinder conservation of its biological diversity (Viana and Tabanez 1996, SOS Mata Atlântica 1998).

The situation of the native vegetation of the Minas Gerais, part of the Atlantic Rain Forest, is similar to the situation to this biome. The drastic reduction of the plant cover was caused by expansion of the agricultural frontier, and formation of pasture land and urban agglomera-

tions. The originally predominant forest formation, the Semideciduous Forest, was severely modified by the coffee cycle, extensive livestock raising, and more recently, by sugarcane production. Thus the regional landscape is currently characterized as extremely fragmented, with Semideciduous Forest remnants at various stages of conservation. In this scenario, the presence of degraded and abandoned pasture is common, some of which are in the process of secondary succession (Silva Júnior *et al.* 2004).

The forest fragmentation today constitutes one of the greatest challenges for conservation as a result of human pressure exercised in various ways (Rodrigues *et al.* 2000). The

conservation of the last forest remnants and forest restoration in degraded areas depend on the knowledge of the composition and organization of the vegetation that still exists and its relationship with environmental factors.

The floristic composition of the Brazilian forest formations and their spatial heterogeneity have been related to climatic and altitude variations, within a regional escale (Oliveira Filho and Fontes 2000, Schudeller *et al.* 2001). At local level, topographic, edaphic and light variation also play important roles in the spatial organization of the shrub and tree vegetation, as reported in some studies (Torres *et al.* 1977, Rodrigues *et al.* 1989, Lieberman *et al.* 1995, Salis *et al.* 1995, Clark 2002, Martins *et al.* 2003).

This floristic heterogeneity associated to spatial environmental variations in the tropical forests constitutes an important factor that promotes the coexistence of tree species with different ecological requirements, enabling the high floristic diversity in these forests.

The present study was carried out in two Semideciduous Forest sites, at different successional stages, in the Mata do Paraíso Forest Reserve, Viçosa, Minas Gerais State, Southeastern Brazil, to ascertain the floristic similarity between the two forest sites and possible correlations among the shrub and tree distributions as well as the environmental variables related to soil and canopy.

MATERIALS AND METHODS

Study area description: The study was carried out in the Minas Gerais Atlantic Rain Forest region (20°48'07"S, 42°51'31"W) belonging to the Federal University of Viçosa, MG, area 195 hectares and altitude 690 to 800m, in the municipality of Viçosa, MG, Southeastern Brazil (Braz *et al.* 2002).

The climate in the region is of the Cwb type (Köppen) mesothermic with hot, rainy summers and cold, dry winters. The mean annual temperature is 21.8°C and the mean annual rainfall is 1314.2mm (Castro *et al.* 1983). The vegetation in the reserve consists

of areas of Semideciduous Forest sites (Velooso *et al.* 1991).

The sites chosen for the study have different disturbance and regeneration histories and were characterized by Silva Júnior *et al.* (2004). In one of the sites, called initial forest in this study, a process of forest regeneration has been detected in *Melinis minutiflora* pastures since 1963. The other forest site, called mature forest, has suffered from selective wood exploitation, forming a nucleus of well preserved forest, free from human actions in the last 40 years (Silva Júnior *et al.* 2004).

Currently, after more than 40 years of conservation, the Mata do Paraíso Forest Reserve presents an advanced process of regeneration forming one of the few areas with a substantial extension of preserved native forest in the region.

Vegetation survey: For the floristic and structural survey of the shrub and tree community, ten 10 x 30 m plots were allocated systematically, with 10m between plot spacing, in each forest site, totaling a 0.6 ha sample area. All the individuals with diameter ≥ 4.8 cm at 1.30m from the soil (DAP) were sampled, and the perimeter was measured at 1.30m above soil level (PAP). The height of the shrubs and trees in the plots was also estimated.

Botanical material was collected between January and May 2005. Identifications were made by consultations in the VIC Herbarium of the Plant Biology Department at the Federal University of Viçosa. The species were classified in families according to the Angiosperm Phylogeny Group II (APG II 2003) system.

Soil characterization: To characterize the initial and mature forest soil, eight simple soil samples were collected at a depth of 0-10 cm, forming a compound sample in each 10 x 30 m plot in the forests studied which was submitted to chemical and texture analysis in the Soil Department at the Federal University of Viçosa. The following variables were obtained: pH; P, K, Ca, Mg and Al contents, saturation by bases, organic matter (Defelipo and Ribeiro

1981), in addition to the sand, silt and clay contents and soil moisture. The edaphic variables obtained for the initial and mature forests were compared by the student t test for non-paired samples.

Canopy characterization: The initial and mature forest canopies were defined by hemispheric photographs taken in the center each plot using an 8 mm lens with 180 degree angle (fisheye lens) attached to a photographic camera with ASA 400 film turned towards the sky.

After developing, the photographs were digitized in a scanner and classified by the PHOTOSHOP 6.0 program and processed by the HEMIPLOT program (Steege 1993), and thus the percentage of canopy openness was estimated in each plot. The mean values of the canopy openness of the two forest sites were compared by the student t test for non-paired samples.

Floristic similarity between the two forest sites: FITOPAC program (Shepherd 1996) was used to analyze the floristic similarity among the plots set up in the two forest sites. A Jaccard Similarity Matrix (Mueller Dombois and Ellenberg 1974) was elaborated based on the presence or absence of species in the plots. Cluster analysis by the average linkage method (UPGMA) was used to interpret floristic similarity between the two forest sites.

Canonical correspondence analyses: The correlations between the environment and vegetation were analyzed by the canonical correspondence (CCA) (ter Braak 1987) using the PC-ORD program for Windows numeral 4.14 version (McCune and Mefford 1999). The species abundance matrix was formed from the number of individuals per plot of the species that presented five or more individuals in the total sample, in a total of 43 species used in canonical correspondence analysis. According to the recommendations by ter Braak (1995), the abundance values (a) were transformed by the expression $\ln(a+1)$ to compensate the deviations caused by a few very high values.

The environmental variable matrix included, in principle, all the soil chemical and texture variables, in addition to the percentage of canopy openness and soil moisture. Eleven environmental variables were eliminated after performing a preliminary CCA that were weakly correlated or highly redundant with other variables. The final CCA was processed with the eight most representative variables that were most strongly correlated with the classification axes: canopy openness percentage, sand, silt and soil moisture, pH, sum of the bases, saturation by aluminum and organic matter.

RESULTS

Soil characterization: Table 1 shows the soil characteristics (superficial 0-10 cm layer) of the initial and mature forests and the main differences in the soil chemical and texture properties.

The soils of the initial and mature forests were different in texture, presenting significant differences in sand and silt contents. The soil in the initial forest presented a larger percentage of sand (38.7%) while the mature forest soil presented a larger percentage of silt (21.4%) in addition to greater moisture.

The soil of the mature forest presented greater macro nutrient contents (P,K,CA and Mg) and lower aluminum contents compared to the soil of the initial forest that resulted in higher values of the sum of the bases (SB), saturation by bases (V), in addition to higher pH and greater organic matter content (MO).

Canopy characterization: The canopy openness ranged from 2.74% to 7.76% in the plots in the initial forest, presenting on average 5.85% canopy openness in this forest. The canopy openness ranged from 2.51% to 5.97% in the mature forest plots and the mean canopy openness of the forest was 3.69%. There were significant differences in the analysis of the canopy openness in the plots studied between the initial and mature forest ($p < 0.01$) (Table 2).

TABLE 1

Chemical and textural variables in 20 superficial soil samples (0-10 cm layer) collected in initial and mature forests in the Mata do Paraíso Forest Reserve in Viçosa, MG, Brazil

	Initial forest	Mature forest	<i>P</i> ^a
	Mean ± standard deviations	Mean ± standard deviations	
pH at H ₂ O	4.47 ± 0.09	5.38 ± 0.56	0.000**
P (mg dm ⁻³)	1.43 ± 0.45	2.55 ± 0.94	0.003**
K (mg dm ⁻³)	38.70 ± 3.02	66.70 ± 19.76	0.000**
Ca (cmol _c dm ⁻³)	0.814 ± 0.31	5.27 ± 1.78	0.000**
Mg (cmol _c dm ⁻³)	0.43 ± 0.16	1.45 ± 0.49	0.000**
Al (cmol _c dm ⁻³)	1.18 ± 0.34	0.17 ± 0.23	0.000**
H + Al (cmol _c dm ⁻³)	9.11 ± 0.95	4.96 ± 1.85	0.000**
SB (cmol _c dm ⁻³)	1.34 ± 0.42	6.89 ± 2.26	0.000**
t (cmol _c dm ⁻³)	2.52 ± 0.33	7.06 ± 2.07	0.000**
T (cmol _c dm ⁻³)	10.45 ± 0.87	11.85 ± 0.99	0.003**
V (%)	12.89 ± 4.12	57.66 ± 16.45	0.000**
m (%)	47.13 ± 12.40	3.52 ± 4.95	0.000**
MO (dag kg ⁻¹)	5.62 ± 0.42	7.04 ± 1.07	0.001**
Sand (%)	38.70 ± 3.23	23.50 ± 13.77	0.003**
Clay (%)	50.30 ± 5.12	55.10 ± 11.32	0.237 ^{NS}
Silt (%)	11.00 ± 5.03	21.40 ± 3.69	0.000**
Moisture (%)	27.11 ± 1.63	48.77 ± 8.94	0.000**

^a Comparisons were made by the non-paired t test (n=10), where: (** significance at the level of 1% probability; ^{NS} absence of significance). SB (sum of exchangeable bases); t (effective cationic exchange capacity); T (cationic exchange capacity at pH 7.0); V (saturation by bases index); m (saturation index by aluminum); MO (organic matter).

TABLE 2

Canopy openness values determined by hemispheric photographs in the plots in the initial and mature forests in the Mata do Paraíso Forest Reserve in Viçosa, MG, Brazil

Initial forest		Mature forest	
Plots	Canopy openness (%)	Plots	Canopy openness (%)
1	5.32	11	4.32
2	6.12	12	3.24
3	6.40	13	4.03
4	7.61	14	4.38
5	7.25	15	3.32
6	2.74	16	5.97
7	3.44	17	2.88
8	7.76	18	2.93
9	6.17	19	3.37
10	5.65	20	2.51
Mean ± standard deviations	5.846 ± 1.666*	Mean ± standard deviations	3.695 ± 1.014*

* Comparisons were made by the non-paired t test (P<0.01)

Floristic similarity between the two forest sites: Fig. 1 shows floristic relationships visualized by the dendrogram generated by the average linkage method (UPGMA), based on the Jaccard Similarity Matrix. The dendrogram shows graphically that two large plot clusters were formed. There was a 70% level similarity in the first group, established for the plots located in the initial forest (from 1 to 10), while the second group, at 23% similarity level, consisted of plots located in the mature forest (from 11 to 20).

The highest similarity indices were obtained between the plots belonging to the same forest site. Therefore the floristic composition is heterogeneous between the two sites resulting from the differences in the environmental variables studied.

Canonical correspondence analysis: The items and values of the analysis of canonical correspondence analysis (CCA) for the two first classification axes were 0.71 (axis 1) and 0.123 (axis 2), with the first axis explaining 36.0% and the second, 6.6% of the variance in the data.

The CCA produced high species environment correlations on the two first axes: 0.973 (axis 1) and 0.979 (axis 2). The Monte Carlo permutation test indicated that the species abundance and environmental variables correlated significantly with the first and second classification axes ($p=0.01$). The variables that were most highly correlated with the first axes were, in decreasing order, saturation by aluminum, sum of the bases and soil moisture (Table 3).

The plot classification on the first axis (Fig. 2) showed clear differentiation for the edaphic and canopy openness characteristics from left to right, involving increased soil fertility, the silt fraction, pH, organic matter content, moisture and reduction in the aluminum content and canopy openness.

DISCUSSION

Soil characterization: The soil in the mature forest was eutrophic, with good saturation by bases (V), good effective cationic exchange capacity (t), and low aluminum values. The soil in the initial forest was dystrophic, with very low saturation by bases (V), low

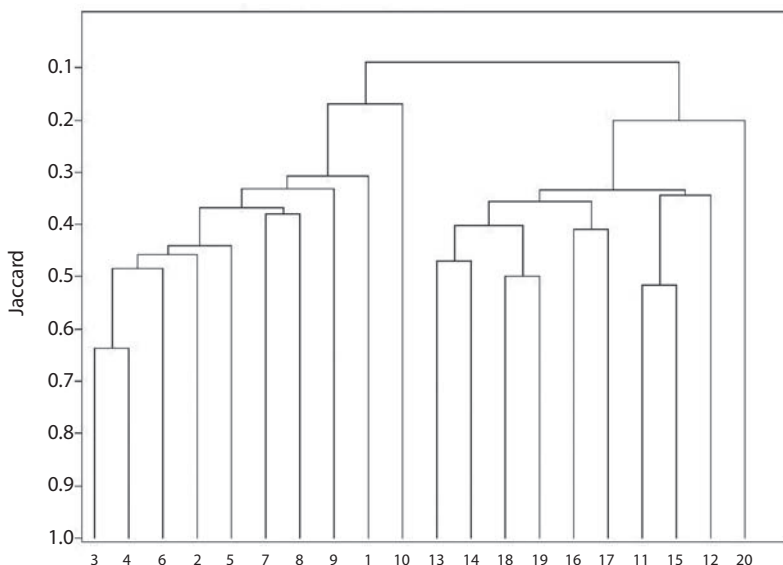


Fig. 1. Dendrogram obtained by the average linkage method (UPGMA) based on the Jaccard Similarity Matrix, for the presence and absence data of the species in the initial (plots 1 to 10) and mature forest (plots 11 to 20) in Viçosa, MG, Brazil.

TABLE 3

Canonical correspondence analysis (CCA): Canonical coefficients and internal correlations on the first two classification axes and weighted correlation matrix for the environmental variables used in the analysis. Correlations with absolute values superior to 0.5 are indicated in bold^a

IV	Correlation		CO	Sand	Silt	pH	SB	m	MO	Mt
	Axis 1	Axis 2								
AB ¹	-0.676	0.052	-							
Sand	-0.652	0.253	0.439	-						
Silt	0.815	-0.010	-0.427	-0.721	-					
pH	0.797	0.483	-0.461	-0.310	0.657	-				
SB ¹	0.911	0.364	-0.551	-0.462	0.740	0.964	-			
m ¹	-0.974	-0.060	0.663	0.514	-0.766	-0.815	-0.894	-		
MO ¹	0.714	0.016	-0.327	-0.840	0.700	0.503	0.640	-0.595	-	
Mt	0.899	-0.284	-0.636	-0.670	0.732	0.686	0.766	-0.784	0.599	-

^a CO (canopy openness); SB (sum of exchangeable bases); m (saturation index by aluminum); MO (organic matter); Mt: moisture.

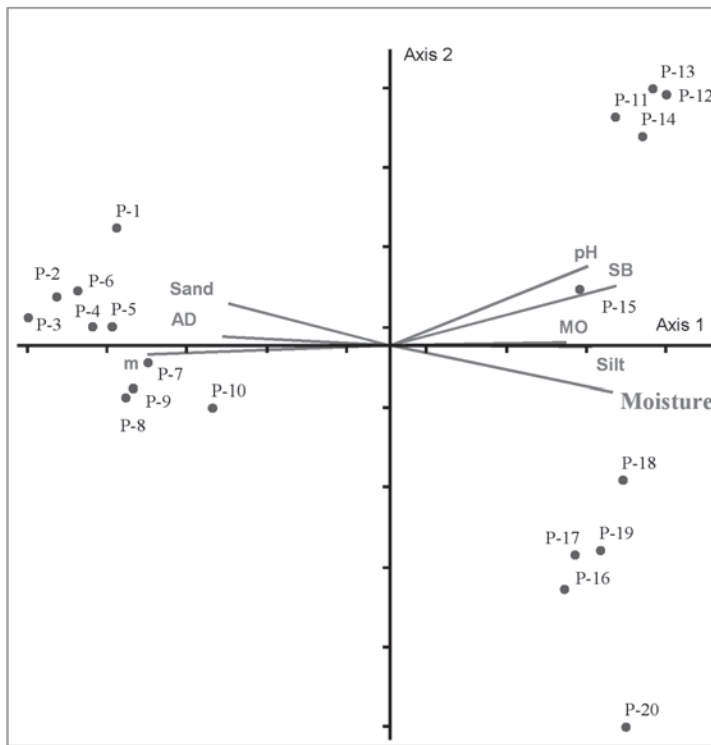


Fig. 2. Canonical correspondence analysis: ordering diagram of the plots in the initial forest (1 to 10) and mature forest (11 to 20) in the Forest Reserve Mata do Paraíso, Viçosa, MG, Brazil, based on the distribution of 43 shrub-tree species in 20 plots. The plots are represented by the corresponding numeration and the environmental variables by vectors (SB - sum of exchangeable bases; m - saturation index by aluminum; MO - organic matter; AD - canopy openness).

effective cationic exchange capacity (t) and high acidity (Alvarez *et al.* 1999). These differences in soil fertility in the two forest sites must be associated to the historic of soil use. The low fertility in the initial forest soil may be the result of its intensive use in the past as pasture. The techniques normally used in pasture renovation, such as burning plant remains, result in nutrient exportation and losses, mainly by volatilization and lixiviation (Kauffman *et al.* 1998, Ellingson *et al.* 2000).

The different edaphic characteristics presented by the initial and mature forest soils were important because they show the influence of soil quality on the succession process, accelerating this process in the more fertile environments, reaching more rapidly the stages of greater equilibrium and sustainability.

Canopy characterization: Compared to other studies that have also used hemispheric photographs, the canopy openness values in the mature forest were similar to those obtained in other well preserved tropical forests with closed canopy, while the values of the initial forest were similar to those reported in natural gaps (Brown 1993, Whitmore *et al.* 1993, Valverde and Silvertown 1997, Trichon *et al.* 1998, Martins and Rodrigues 2002).

As canopy openness is considered a good indicator of light conditions in the forest (Brown 1993, Whitmore *et al.* 1993, Trichon *et al.* 1998, Martins and Rodrigues 2002), these differences between the two forest sites must determine the division of this resource by species of the different ecological groups (Silva Júnior *et al.* 2004), contributing to the establishment of light requiring and shade tolerant species in the initial and mature forests, respectively.

Therefore the variations recorded for this parameter suggested a heterogeneous solar radiation penetration regimen in these environments that could thus generate different standards regarding the forest structure and ecology of the species present in these environments, forming an important source of spatial floristic heterogeneity in this forest fragment.

Floristic similarity between the two forest sites: The forest remnants can be considered floristically similar whenever they present at least 25% similarity (Müller Dumbois and Ellenberg 1974). Therefore, the initial and mature forests were not very similar. The heterogeneity between the two forest sites may result from variations in environmental conditions, the ecological preferences of the species and further from the diverse degrees of disturbance caused by man (Bertoni and Martins 1987).

The low floristic similarity between the initial and mature forests, with only 33 species common to the two areas, meant that all the plots in the initial forest formed a distinct group, differing from all the plots in the mature forest that formed another distinct group in the cluster analysis. These similarity groups thus established were related to the ecological conditions of these forest sites. Several different factors in association, such as disturbance history, successional stage, light quantity and quality, soil moisture and nutrient availability, influenced floristic heterogeneity between the two forest sites and accounted for the maintenance of the floristic diversity in this Semideciduous Forest.

Environment and plant data classification: The eigenvalues of the canonical correspondence analysis (CCA) for the two first axes were considered high compared with other studies on Semideciduous Forests in southeastern Brazil (Martins *et al.* 2003, Souza *et al.* 2003, Camagos 2004, Martins and Rodrigues 2005), which indicated the occurrence of species restricted to the environment of certain plots in each forest site.

Similarly to the cluster analysis, CCA also presented a clear distinction between the plots in the initial forest (1 to 10) and those in the mature forest (11 to 20), regarding the edaphic and canopy openness characteristics. The initial forest environment presented acid soil, with low fertility, and greater canopy openness that helped light penetration. The mature forest was situated on soil with greater chemical fertility

and lower acidity, the canopy was closed and the understory very shaded.

Species classification by CCA (Fig. 3) indicated that *Vernonanthura diffusa*, *Sparattosperma leucanthum*, *Xylopia sericea*, *Senna macranthera*, *Siparuna guianensis*, *Psychotria vellosiana*, *Piptocarpha macropoda*, *Miconia cinnamomifolia*, *Erythroxylum pelleterianum*, *Luehea grandiflora* and *Vismia guianensis* were more abundant in areas with greater luminosity, sandy soils, low fertility, moisture and acid.

The distribution of this group of species corroborated their successional classification as pioneers or initial secondary individuals, associated to open environments and poor soils. *Senna macranthera* and *Luehea grandiflora* were also strongly related to better drained, acid and low nutrient soils in a study carried

out in a Semideciduous forest fragment in Minas Gerais, Brazil (Souza *et al.* 2003).

In a cloud forest in southeastern Brazil, *Psychotria vellosiana* distribution presented strong correlation with greater canopy openness, which was justified by its greater light requirement because it is short and does not reach the forest canopy, and it depends on locations with more open canopy (Carvalho *et al.* 2000). *Xylopia sericea* and *Miconia cinnamomifolia* were more abundant on poor soils, with greater aluminum contents and more clay in another forest fragment in Viçosa, Minas Gerais, Brazil (Martins *et al.* 2003), and were associated with well-drained soils (Lorenzi 1992).

Siparuna guianensis is considered a generalist for habitat, and can be found in open environments with low fertility soils of the

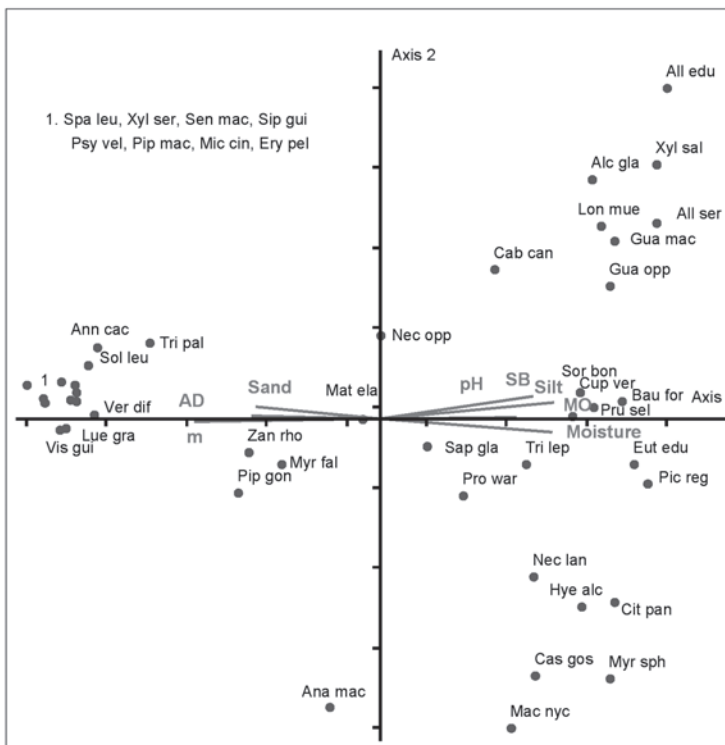


Fig. 3. Canonical correspondence analysis: ordering diagram of the species based on the distribution of shrub and tree species in 20 plots in the initial and mature forests in the Forest Reserve Mata do Paraíso, Viçosa, MG, Brazil. The species are represented by their abbreviated names (Table 4) and the environmental variables by vectors (SB - sum of exchangeable bases; m - saturation index by aluminum; MO - organic matter; AD - canopy openness).

TABLE 4

Tree-shrub species sampled (number of individuals ≥ 5) in the initial and mature forests in the Forest Reserve Mata do Paraíso, in Viçosa, MG, and respective abbreviated names

Abbreviated Names	Species	Family
Alc gla	<i>Alchornea glandulosa</i>	Euphorbiaceae
All edu	<i>Allophylus edulis</i>	Sapindaceae
All ser	<i>Allophylus sericeus</i>	Sapindaceae
Ana mac	<i>Anadenanthera macrocarpa</i>	Fabaceae
Ann cac	<i>Annona cacans</i>	Annonaceae
Bau for	<i>Bauhinia forficata</i>	Fabaceae
Cab can	<i>Cabralea canjerana</i>	Meliaceae
Cas gos	<i>Casearia gossypiosperma</i>	Salicaceae
Cit pan	<i>Citronella paniculata</i>	Icacinaceae
Cup ver	<i>Cupania vernalis</i>	Sapindaceae
Ery pel	<i>Erythroxylum pelleterianum</i>	Erythroxylaceae
Eut edu	<i>Euterpe edulis</i>	Arecaceae
Gua mac	<i>Guarea macrophylla</i>	Meliaceae
Gua opp	<i>Guapira opposita</i>	Nyctaginaceae
Hye alc	<i>Hyeronima alchorneoides</i>	Euphorbiaceae
Lon mue	<i>Lonchocarpus muehlbergianus</i>	Fabaceae
Lue gra	<i>Luehea grandiflora</i>	Malvaceae
Mac nyc	<i>Machearium nyctitans</i>	Fabaceae
Mat ela	<i>Matayba elaeagnoides</i>	Sapindaceae
Mic cin	<i>Miconia cinnamomifolia</i>	Melastomataceae
Myr fal	<i>Myrcia fallax</i>	Myrtaceae
Myr sph	<i>Myrcia sphaerocarpa</i>	Myrtaceae
Nec lan	<i>Nectandra lanceolata</i>	Lauraceae
Nec opp	<i>Nectandra oppositifolia</i>	Lauraceae
Pic reg	<i>Picramnia regnelli</i>	Picramnaceae
Pip gon	<i>Piptadenia gonoacantha</i>	Fabaceae
Pip mac	<i>Piptocarpha macropoda</i>	Asteraceae
Pro war	<i>Protium warmingiana</i>	Burseraceae
Pru sel	<i>Prunus sellowii</i>	Rosaceae
Psy vel	<i>Psychotria vellosiana</i>	Rubiaceae
Sap gla	<i>Sapium glandulatum</i>	Euphorbiaceae
Sen mac	<i>Senna macranthera</i>	Fabaceae
Sip gui	<i>Siparuna guianensis</i>	Siparunaceae
Sol leu	<i>Solanum leucodendron</i>	Solanaceae
Sor bon	<i>Sorocea bonplandii</i>	Moraceae
Spa leu	<i>Sparattosperma leucanthum</i>	Bignoniaceae
Tri lep	<i>Trichilia lepidota</i>	Meliaceae
Tri pal	<i>Trichilia pallida</i>	Meliaceae
Ver dif	<i>Vernonanthura diffusa</i>	Asteraceae
Vis gui	<i>Vismia guianensis</i>	Clusiaceae
Xyl sal	<i>Xylosma salzmannii</i>	Salicaceae
Xyl ser	<i>Xylopia sericea</i>	Annonaceae
Zan rho	<i>Zanthoxylum rhoifolium</i>	Rutaceae

Cerrado (Oliveira Filho and Ratter 1995), in the Semideciduous forest understory (Martins *et al.* 2003), and on fragment borders with greater light incidence (Souza *et al.* 2003).

This group of species adapted to more selective edaphic conditions, such as high acidity, low moisture and fertility as well as greater luminosity, present potential for use in forest restoration projects in degraded areas, such as degraded pastures.

The other extreme of the environmental gradient represented by axis 1 included *Sorocea bonplandii*, *Cupania vernalis*, *Prunus sellowii*, *Euterpe edulis*, *Picramnia regnelli*, *Citronella paniculata*, *Guarea macrophylla*, *Guapira opposita*, *Trichilia lepidota* and *Hyeronima alchorneoides*, that occurred in more shady environments with more fertile soil, moisture and greater organic matter content. This plant group was characterized mainly by late secondary species that regenerated in the shade, such as *Euterpe edulis*, *Picramnia regnelli*, *Guarea macrophylla* and *Trichilia lepidota* that were found in this forest site with more closed canopy, in addition to the greater soil moisture and fertility, suitable conditions for regeneration. *Picramnia regnelli* is a low tree that does not naturally reach the forest canopy, and completes its reproductive cycle in the shaded understory.

The number of shade tolerant species in this forest site resulted in a negative relationship between the openness level of the canopy and light incidence on the lowest stratas that hindered regeneration of the heliophyte species of the initial successional stages (Durigan *et al.* 2000). Under closed canopy, late secondary species can still tolerate shade by means of low growth rates for long periods (Souza and Válio 2003).

The set of greater shading, greater soil moisture contents and greater fertility of the soil in the mature forest may favor regeneration of more demanding late species. These ecological conditions may be particularly important for *E. edulis*, a shade tolerant Palm that prefers soils with higher fertility and moisture (Souza and Válio 2003).

Some species in this group have been indicated and used in riparian forest restoration, including *Citronella paniculata*, *Hyeronima alchorneoides* and *Euterpe edulis* (Martins 2007), but all have potential for this purpose and for enriching plantations in burnt clearings and secondary forests.

The set of results attained corroborated studies that report the spatial floristic heterogeneity of Brazilian Semideciduous Forests, determined by the complexity of the relationship between environmental and distribution variables of the tree and shrub species in these forests (Pagano and Leitão Filho 1987, Rodrigues *et al.* 1989, Martins and Rodrigues 2002, Martins *et al.* 2003, 2004, Souza *et al.* 2003, Silva Júnior *et al.* 2004).

The canonical correspondence analysis (CCA) of the environmental variables and tree and shrub species abundance indicated that these were distributed in the studied forest sites, which were strongly influenced by the canopy openness, soil moisture and chemical fertility.

The initial forest environment presented acid soils, with poor fertility and greater canopy openness, helping in light penetration that favored the establishment of pioneer and initial secondary species such as *Vernonanthura diffusa*, *Sparattosperma leucanthum*, *Xylopia sericea*, *Senna macranthera*, *Siparuna guianensis*, *Psychotria vellosiana*, *Piptocarpha macropoda*, *Miconia cinnamomifolia*, *Erythroxylum pelleterianum*, *Luehea grandiflora* and *Vismia guianensis*.

The mature forest occurred on more fertile soils, the canopy was more closed which reduced light penetration and favored the establishment mainly of late secondary species such as *Sorocea bonplandii*, *Prunus sellowii*, *Euterpe edulis*, *Picramnia regnelli*, *Citronella paniculata*, *Guarea macrophylla*, *Guapira opposita*, *Trichilia lepidota* and *Hyeronima alchorneoides*.

RESUMEN

Estudiamos las variaciones florísticas de arbustos y árboles en dos sitios de un bosque semicaducifolio, bosque

primario y bosque maduro, en la Reserva Forestal Mata do Paraíso, en Viçosa, Estado de Minas Gerais, Sudeste de Brasil, para analizar la similitud florística y las correlaciones entre las variables ambientales y la distribución de tres especies en estos bosques. Árboles individuales con diámetro a la altura del pecho (DAP) \geq 4.8 cm. fueron muestreados en veinte parcelas de 10 x 30 m (10 parcelas en cada sitio). Las parcelas se distribuyeron sistemáticamente a intervalos de 10 m. Las variables ambientales fueron analizadas así: la abertura del dosel y características químicas y de textura del suelo. Los dos sitios de bosque mostraron diferencias evidentes en la abertura del dosel y fertilidad del suelo, factores que reflejan las diferencias florísticas y sucesionales de arbustos y árboles, revelado por la baja similitud entre estos bosques por medio de análisis de conglomerados. El análisis de correspondencia canónica (CCA) de variables ambientales y abundancia de especies indican que las especies en los bosques estudiados están distribuidas bajo una fuerte influencia de la abertura del dosel, humedad y fertilidad del suelo.

Palabras clave: bosque semicaducifolio, análisis de correspondencia canónica, relación suelo-vegetación, fotografías hemisféricas, Brasil.

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