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ENVIRONMENTAL HETEROGENEITY AND NATURAL REGENERATION IN RIPARIAN VEGETATION OF THE BRAZILIAN SEMI-ARID REGION

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This study investigated the structure, diversity and composition of the regenerating shrub-tree species community along a stretch of riparian vegetation in relation to environmental heterogeneity. In the Environmental Protection Area of Pandeiros River, southeastern Brazil, the regenerating stratum on 70 plots (25 m^2) divided into four groups according to their soil characteristics and natural barriers was sampled. For each plot observations were made of variables related to several soil properties, canopy openness and flooding regime. In addition to the traditional calculation of phytosociological parameters and diversity, a canonical correspondence analysis (CCA) to examine the existing relationships between environmental variables and species distribution was performed. The families with the highest species richness were Fabaceae and Myrtaceae and the species with the highest importance value indices were *Zygia latifolia*, *Tapirira guianensis*, *Butia capitata*, *Bauhinia rufa* and *Hirtella gracilipes*. The CCA largely confirmed the groups that were originally proposed. The stretch of riparian vegetation studied was highly heterogeneous with regard to both the abiotic variables tested and floristic structure and composition.

Keywords. Canopy openness, diversity, ecotone, edaphic variables, flooding regime, phytosociology.

Introduction

The Brazilian semi-arid region occupies an area of approximately 1 million km^2 that is mainly characterised by an average annual rainfall of less than 800 mm, high potential evapotranspiration and an aridity index of 0.5 or a drought risk of more than 60% (Sampaio, 1995; Brasil, 2005). The northern region of Minas Gerais State

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is located within this environment and represents a transition area of difficult phytogeographical characterisation. The landscape observed is the result of the interaction between two major biomes: Caatinga and Cerrado (Brandão, 2000). Cerrado is a Brazilian savanna biome covering 23% of the country, and is one of the least-studied biomes in the world (Furley, 1999; Machado *et al.*, 2008). It has a significant number of endemic species and is considered a hotspot for the conservation of biodiversity in Brazil (Myers *et al.*, 2000). The situation for the Caatinga biome is very similar. Caatinga occupies 11% of the national territory and, despite being the only exclusively Brazilian biome, it is among the most degraded (Castelletti *et al.*, 2003). This biome, represented by scrub and dry forests (Sampaio, 1995), has a considerable number of endemic species, about which there is currently little zoological and botanical knowledge (Castelletti *et al.*, 2003).

In this ecotonal region, different phytophysiognomies are observed. The savanna formations are interrupted by dry tropical forests (Ribeiro & Walter, 1998) that are associated with interfluves, which are physiognomies that primarily occur in association with well-drained land, while riparian forest occurs in association with watercourses (Oliveira-Filho *et al.*, 1990; Ribeiro & Walter, 1998; Pinto *et al.*, 2005). These riparian forests are characterised by great environmental heterogeneity resulting from physical factors such as topographic and soil variations (Oliveira-Filho *et al.*, 2001; Budke *et al.*, 2006; Costa-Filho *et al.*, 2006) as well as biotic factors such as the influence of adjacent vegetation (Bertani *et al.*, 2001), resulting in a mosaic vegetation of high floristic diversity (Rodrigues & Leitão-Filho, 2000). The ecological and evolutionary importance of these biomes is great because they are considered important biodiversity repositories (Oliveira-Filho & Ratter, 1995). Similarly, the contribution of this vegetation to controlling water quality is paramount because it regulates nutrient levels (Martin *et al.*, 1984).

Although they are protected by Brazilian environmental legislation, the riparian forests have been altered by agricultural activities associated with the use of fires for farmland clearing and wood extraction. This has led to the degradation and fragmentation of these environments (Battilani *et al.*, 2005). Thus, detailed studies on the floristic composition and ecology of the remnant riparian forests are critical to support protection and recovery initiatives for such vegetation (Van den Berg & Oliveira-Filho, 2000). A knowledge of forest regeneration processes gives us an opportunity to understand how various species will eventually occupy the upper stratum through succession (Barreira *et al.*, 2002).

The early life stages of plants are determined by strong environmental influences, including both intra- and inter-specific competition and various environmental stresses (Ponge *et al.*, 1998). The abundance of species decreases towards the extremes of a gradient, with factors such as light and nutrients (Rodrigues *et al.*, 2007) determining the establishment of individuals in more favourable micro-sites (Oliveira-Filho *et al.*, 1990, 1994a). Differences in soil characteristics and variations in topography correspond to differences in floristic composition and plant community structure (Oliveira-Filho *et al.*, 1990, 1994a; Scarano *et al.*, 1997). Studies that seek to determine the preferred habitat of species generate knowledge that can be used for the restoration of degraded areas (Oliveira-Filho *et al.*, 1994a). Hence, our study aimed to answer the following questions: (i) what is the structure, diversity and composition of the regenerating shrub-tree community along a stretch of riparian vegetation in an ecotonal area in relation to environmental heterogeneity, and (ii) which environmental variables tested (soil, light and flooding regime) affect the distribution of regenerating species?

Materials and Methods

Study area

This study was conducted at Vida Silvestre Refuge in the Environmental Protection Area of Pandeiros River, municipality of Januária, north of Minas Gerais, Brazil. This environmental protection area covers 393,060 hectares representing the entire Pandeiros River basin, including the Januária, Bonito de Minas and Cônego Marinho municipalities; it is the largest sustainable conservation area in the state of Minas Gerais, preserving the only swampland in the state (Azevedo *et al.*, 2009). The Pandeiros River is part of the São Francisco basin (middle São Francisco), which is considered a major tributary of the left bank of this river (Azevedo *et al.*, 2009).

The vegetation bordering the Pandeiros River exhibits remarkable diversity of ecosystems due to the transitional effect between the Cerrado and Caatinga biomes, which generates a peculiar junction of riparian forest, dry forest, Cerrado (savanna) and Veredas (palm swamps) (Azevedo *et al.*, 2009), and it is a priority area for scientific research (Drummond *et al.*, 2005). Regarding geomorphology, the environmental protection area is embedded in the São Francisco Depression and São Francisco Plateau, where the soils are deep and generally sandy, unstructured and with high drainage arising from the transport and sedimentation of material carried by large water flows in past geological periods (IGA, 2006). These conditions cause the soil to be poor in nutrients, very acidic and lacking in organic matter (Naime, 1980).

The riparian forest area sampled lies between the coordinates 15°30′33.5″S and 44°45′12.7″W on the left bank and 15°30′27.9″S and 44°45′15.5″W on the right bank of the Pandeiros River. The reported altitude for the area varies between 459 and 488 m. According to the Köppen classification, the climate is tropical wet and dry or savanna climate (Aw), with a well-defined dry winter and rainy summers (Antunes, 1994). The average annual precipitation ranges from 900 mm to 1200 mm, and the average temperatures are between 21 and 24°C (INMet, 2008), with the highest levels of rainfall in December and January (Antunes, 1994).

Structural survey of the regenerating community

Sampling of the regenerating stratum was conducted between October and November 2007 in 70 plots of 25 m^2 (5 m × 5 m) designated alongside the river course, 3 m from its bank, with an interval of 15 m between them. Plot distribution was systematic, with 35 plots on each river bank. However, due to the observed soil characteristics and the occurrence of disturbed stretches and some natural barriers (rock outcrops), the plots were divided into four groups with regard to location (Fig. 1):

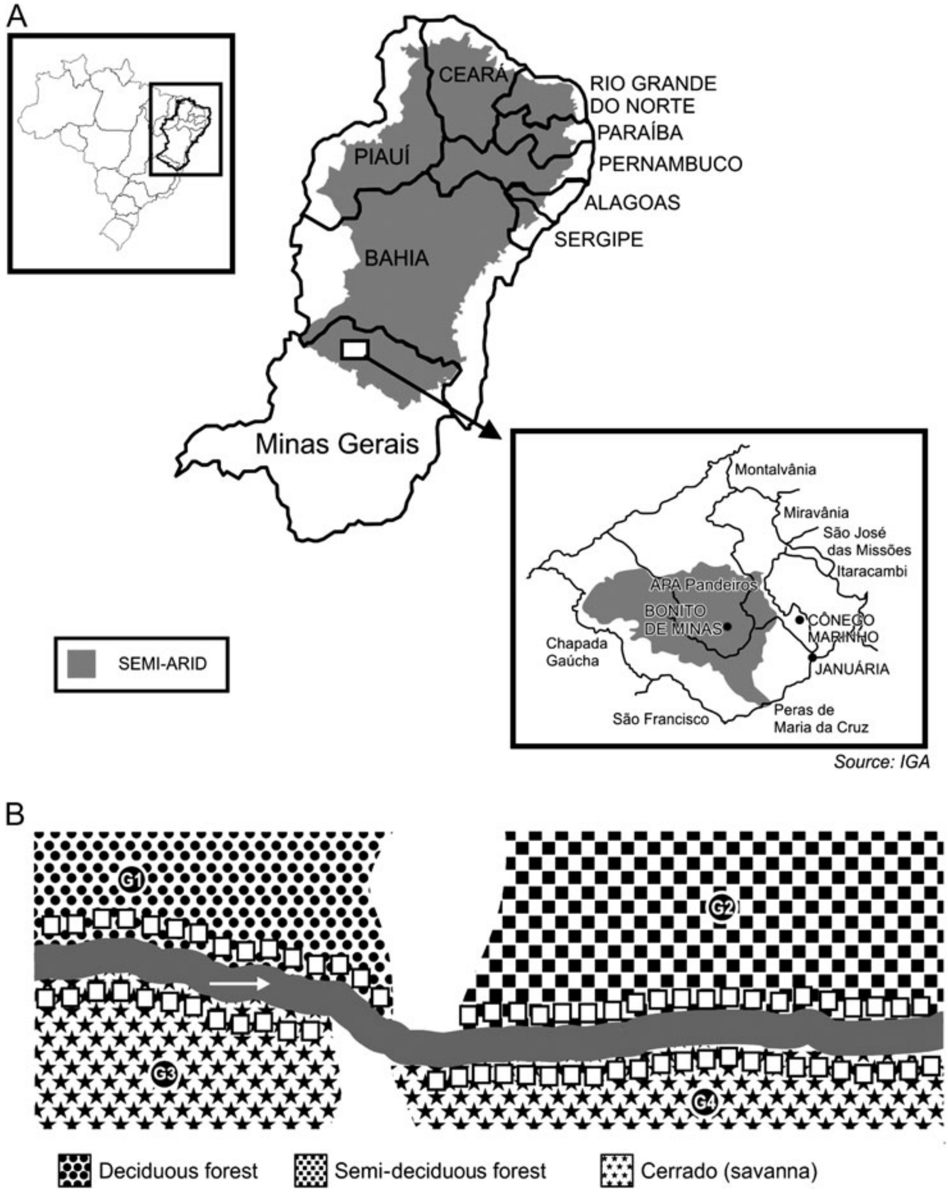

FIG. 1. (A) Location of the Brazilian semi-arid region and the Environmental Protection Area of Pandeiros River. (B) Distribution of the plots in the study area representing the different plot groups.

(1) plots close to limestone outcrops with lithic Neosol and haplic Cambisol soil types that are eutrophic, with low phosphorus availability, sandy texture and strongly undulating terrain resulting from sandstone alterations, with vegetation classified as deciduous seasonal forest (plots 1–15); (2) plots with cattle trampling, with soil characterised as red-yellow Oxisol that is dystrophic, with low phosphorus availability, sandy texture and gently undulating terrain, clothed with semi-deciduous seasonal forest (plots 16–35); (3) plots susceptible to flooding, with fluvic Neosol that is eutrophic, with low phosphorus availability, sandy texture and flat terrain, with Cerrado vegetation (plots 36–42); and (4) plots with dystrophic red-yellow Oxisol and haplic Entisols associated with low phosphorus availability, sandy texture and gently undulating terrain, also with Cerrado vegetation (plots 43–70). Due to the differing sizes of these areas, the number of plots was not equally distributed among them. We allocated 15, 20, 12 and 23 plots respectively to Groups 1, 2, 3 and 4. The soil classification follows EMBRAPA (1997) through field observation and physical and chemical analysis of soil properties.

All woody individuals of size class $\geq$ 1 cm dbs (diameter at the base of the stem) and $<$ 5 cm dbh (diameter at breast height; measured at a height of 1.3 m from the soil) were sampled and marked with numbered aluminium plates. Data on height, dbs and species name were recorded. Material from all of the species sampled was collected, identified *in loco* or sent to specialists. Voucher specimens were lodged at the Montes Claros Herbarium (HMC), Universidade Estadual de Montes Claros (UNIMONTES). Species were classified into families according to the Angiosperm Phylogeny Group II system (APG II, 2003).

Characterisation of environmental variables

To determine the influence of local environmental variables on the floristic composition and structure during natural regeneration processes, the following parameters were characterised: soil type (chemical and physical analysis), luminosity (canopy cover) and flooding regime (descriptive categories). The soil characterisation was performed in April 2008 on 10 m $\times$ 10 m areas (previously used for arboreal vegetation sampling; see Rodrigues *et al.*, 2009) inside which the plots of this study were set. For soil characterisation, a 500 g composite sample was collected from surface soil (0–20 cm). The textural and chemical analyses of samples were performed in the Soil Analysis Laboratory at the Instituto de Ciências Agrárias, Universidade Federal de Minas Gerais, following the EMBRAPA protocol (EMBRAPA, 1997). The soil variables measured were: pH, concentration of potassium, Mehlich phosphorus, remnant phosphorus, calcium, magnesium, aluminium and hydrogen+ aluminium, sum of bases, base saturation, organic matter, aluminium saturation, effective cation exchange capacity and capacity of soil to retain cations, and content of coarse and fine sand, silt and clay.

The percentage of canopy coverage was obtained by taking hemispherical photographs in each 5 m $\times$ 5 m plot using a Nikon® 8 mm fish-eye lens coupled to a Nikon® digital camera (D50 model) and attached to a monopod at 1.5 m above the ground. The camera was directed towards magnetic north and levelled with the aid of a spirit level. Photographs were taken during the early hours of the morning, avoiding the sun's reflection on the lens, in April and September of 2008, thereby accounting for coverage in the wet and dry seasons, respectively. The photographs were processed using Gap Light Analyzer software (Frazer *et al.*, 1999) after conversion of the images to black and white. White pixels in the photographs represent areas with no canopy and the proportion can be calculated.

Flooding regime characterisation was conducted in each plot by visual observation and grading of several variables including flooding (1 = absence; 2 = presence), sand deposition (1 = absence; 2 = presence), embankment height (1 = $\geq$ 4 m; 2 = $\geq$ 3 m and $<$ 4 m; 3 = $\geq$ 2 m and $<$ 3 m; 4 = $\geq$ 1 m and $<$ 2 m; 5 = flat), water speed (visual scale between a lentic environment and the occurrence of rapids, assigning scores from 1 to 5) and location on the river bend (1 = no curve; 2 = erosion; 3 = sedimentation). The product of the scores given to each variable was the flooding regime variable, and the higher the value, the greater the influence of flooding on the plot.

Data analysis

The structure of the regenerating community was described using the classical calculation of quantitative parameters: absolute and relative density, absolute and relative dominance (based on basal areas), absolute and relative frequency and importance value index (IVI) (Mueller-Dombois & Ellenberg, 1974), and the Shannon diversity index (H') and Pielou evenness (J') (Brower & Zar, 1984). For analysis of floristic similarity between groups, a Venn diagram was produced based on the presence or absence of species, allowing evaluation of the floristic composition (Oliveira-Filho & Ratter, 2004) and indicating the number of unique species common to the four plot groups. Furthermore, we calculated H' and J' for each group of plots. The H's were compared using the Hutcheson *t*-test (Zar, 1996). Comparisons were made in pairs because the Hutcheson *t*-test is the only test available for statistical comparisons between H' values (Nunes *et al.*, 2003).

To analyse the correlations between environmental and vegetation gradients, a canonical correspondence analysis (CCA) (Ter Braak, 1987) was performed using PC-ORD for Windows, version 4.14 (McCune & Mefford, 1999). The species matrix consisted of the cover value (relative density + relative dominance) of the individuals per plot relative to the total sample. In this analysis, only the 67 plots with identifiable individuals were used; three plots were excluded for not containing any individuals sampled. According to the recommendations of Ter Braak (1995), the cover values (a) were transformed by the expression $\ln(a + 1)$, to compensate for deviations caused by the very low and high values.

The environmental variables matrix initially included one categorical variable (groups) only to distinguish the four groups on the ordination diagram, 18 quantitative edaphic variables, two variables of the canopy opening percentage (dry and rainy seasons) and the flooding regime variable of each plot. However, after running a preliminary CCA, 17 of these quantitative variables were very weakly correlated or redundant and hence were excluded from the final analysis. The final CCA was processed with the categorical variable (which has no effect on the analysis itself) and the four variables that were most representative and strongly correlated with the ordination axes: the sum of bases, aluminium saturation, light during the rainy season and flooding regime. The Monte Carlo permutation test (Ter Braak, 1988) was performed to test the significance of the model. To verify the correlations among the 24 species that had at least 10 individuals and the four most representative environmental variables, Spearman's rank correlation coefficients were employed (Zar, 1996) for species relative dominance and variable values for each plot.

Results

Floristic composition, structure and diversity of the regenerating community

A total of 896 individuals were sampled in a 1750 m^2 area, resulting in an estimated 5120 individuals/ha. These individuals were distributed among 108 species belonging to 85 genera and 40 families (see Appendix, where authorship of species names is also given). The six families with the highest species richness were Fabaceae (28 species), followed by Myrtaceae (11 species), Rubiaceae (six species), Anacardiaceae, Bignoniaceae and Sapindaceae (five species each), which accounted for 73.9% of the total number of individuals.

The eight genera with the highest species richness were *Eugenia* L., with four species, and *Aspidosperma* Mart. & Zucc., *Bauhinia* L., *Copaifera* L., *Cordiera* A.Rich. & DC., *Hymenaea* L., *Machaerium* Pers. and *Psidium* L., with three species each. The genera that contributed the highest percentage of individuals were *Zygia* P.Browne (9.93%), *Tapirira* Aubl. (9.15%), *Bauhinia* (6.91%), *Myrcia* DC. (6.14%), *Cordiera* A.Rich. & DC. (4.80%), *Averrhoidium* Baill. (4.46%), *Hirtella* L. (4.02%), *Eugenia* (3.35%) and *Dilodendron* Radlk. (3.24%).

The 10 most abundant species represented 52.4% of the total number of individuals, and these were *Zygia latifolia*, with 89 individuals (9.93% of the total), *Tapirira guianensis*, with 82 (9.15%), *Bauhinia rufa*, with 60 (6.69%), *Myrcia guianensis*, with 53 (5.91%), *Averrhoidium gardnerianum*, with 40 (4.46%), *Hirtella gracilipes*, with 36 (4.01%), *Cordiera concolor*, with 30 (3.34%), *Dilodendron bipinnatum*, with 29 (3.23%), *Tocoyena formosa*, with 26 (2.90%), and *Astronium fraxinifolium*, with 25 (2.79%). The species with the highest importance values (IV) were *Zygia latifolia* (23.56), *Tapirira guianensis* (20.52), *Butia capitata* (19.91), *Bauhinia rufa* (14.76), *Hirtella gracilipes* (13.70), *Averrhoidium gardnerianum* (13.06), *Myrcia guianensis* (11.74), *Astronium fraxinifolium* (9.80), *Dilodendron bipinnatum* (9.34) and *Cordiera concolor* (9.21), which was related to high densities of *Z. latifolia*, *T. guianensis*, *M. guianensis* and *A. gardnerianum*, dominance by *B. capitata* and *A. fraxinifolium*, and a high frequency of *B. rufa*, *H. gracilipes*, *C. concolor* and *D. bipinnatum*.

The species diversity (H') in the total sample was 3.83, while the evenness (J') was 0.81. The diversity between the groups was significantly different ($P < 0.005$) except for between Groups 1 and 2 ($P > 0.05$). Plot Groups 1, 2, 3 and 4 presented 58, 60, 17 and 56 species, respectively, with H' of 3.58, 3.53, 1.96 and 3.28 and J' of 0.88, 0.86, 0.69 and 0.81.

Species–environment correlation analysis

The canonical correspondence analysis showed eigenvalues for the first two ordination axes of 0.60 (Axis 1) and 0.48 (Axis 2), respectively (Table 1, Figs 2 and 3). The first eigenvalue can be considered high (Ter Braak, 1995), meaning that the gradients are long; that is, there is high turnover of species along the gradient. The second eigenvalue indicates a short gradient where most of the species are distributed between the two extremes with variations only in their abundance. The first two axes explained 7.6% of the total variance. The small percentage of variance explained by the two axes indicates that part of the species variation is not explained by the measured variables. This result is normal in vegetation data and does not compromise the species–environment relationship analysis (Ter Braak, 1988; Rodrigues *et al.*, 2007) because the species–environment correlations were high on both axes: 0.896 (Axis 1) and 0.866 (Axis 2). Furthermore, the Monte Carlo permutation test indicated that the species coverage and environmental variables correlated significantly ($P < 0.05$).

The internal correlations between environmental variables and the first two ordination axes (Table 1) showed that the variables that most strongly correlated with Axis 1 were aluminium saturation and canopy openness during the rainy season (April light). For Axis 2, the sum of bases and flooding regime were the variables that showed significant correlations. In contrast, in the weighted correlations between variables, positive interrelationships were detected for the variables

TABLE 1. Canonical correspondence analysis (CCA) of 70 plots used to sample the regenerating community, soil, canopy openness and flooding regime in the riparian vegetation of the Pandeiros River (Minas Gerais State, Brazil). The values are intraset correlations in the first two ordination axes, and correlations of environmental variables used in this analysis

	Intraset correlations		Environmental variables		
Environmental variables	Axis 1	Axis 2	Sum of bases	Aluminium saturation	Flooding regime
Sum of bases	0.382	**–0.683**			
Aluminium saturation	**–0.837**	0.013	–0.328		
Flooding regime	–0.387	–0.464	0.098	0.137	
April light	**–0.609**	0.438	–0.489	**0.640**	0.062

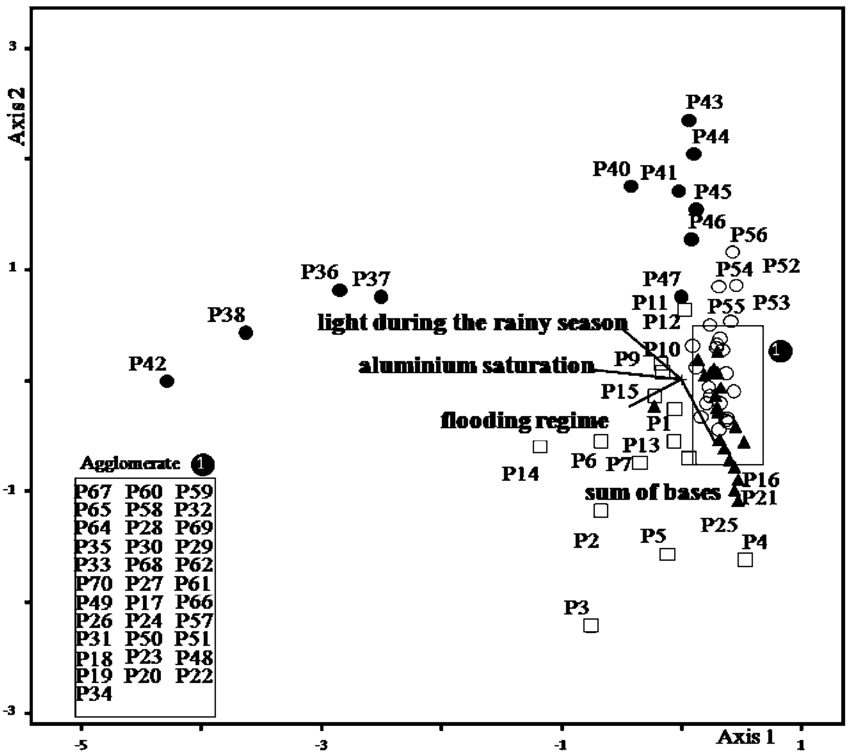

FIG. 2. Ordination diagram of the 67 sample plots in the riparian vegetation of the Pandeiros River (Minas Gerais State, Brazil) by canonical correspondence analysis (CCA) of species cover, and correlation with four environmental variables (vectors). □ = lithic Neosol and haplic Cambisol; ▲ = red-yellow Oxisol; ● = fluvic Neosol; ○ = red-yellow Oxisol and haplic Entisols.

aluminium saturation and light in the wet season (0.640), and negative interrelationships were found between the light in the rainy season and the sum of bases (–0.489), indicating that plots with more open canopies had higher aluminium levels and lower levels of the sum of bases.

The ordination of plots according to the environmental variables (Fig. 2) showed that three groups were formed along Axis 1. The first group is composed of Groups 2 and 4, followed by a group comprised of Group 1 and some plots of Group 3, and a third group was formed by the remaining plots of Group 3. The second axis separated the second grouping according to soil fertility because the first group showed the highest sum of bases. Groups 2 and 4 are not clearly separated, with the second axis showing a small separation in relation to the sum of bases content. The formation of these clusters indicates the heterogeneity of the environment studied, showing that other factors (besides the soil criteria characteristics initially used), such as light and flooding, are also responsible for this differentiation, which allows for

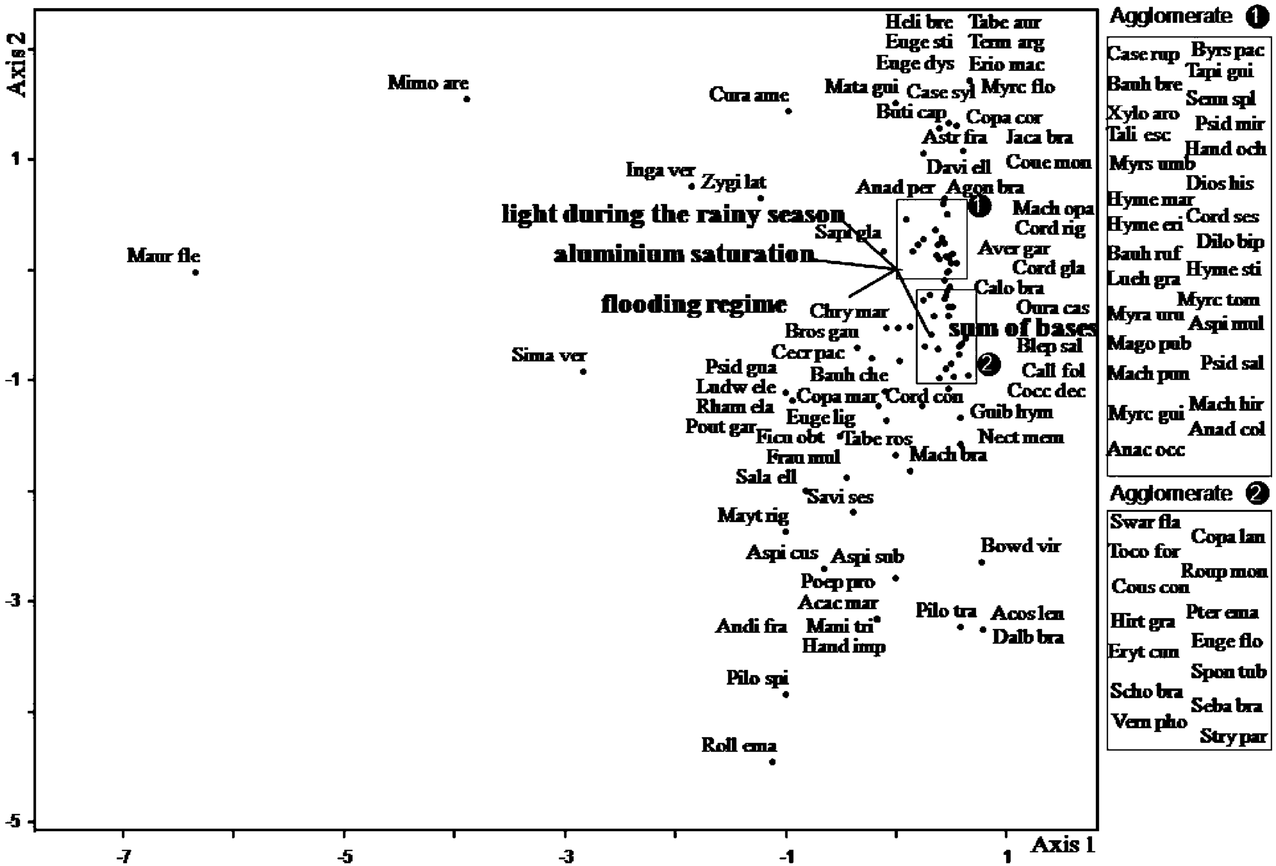

FIG. 3. Ordination diagram of a 110-species sample in the riparian vegetation of the Pandeiros River (Minas Gerais State, Brazil) by canonical correspondence analysis (CCA) of species cover. The species are indicated by their abbreviated names (full names are given in the Appendix).

environments that are close together to become floristically and structurally differentiated.

The species ordination diagram (Fig. 3) indicated that species such as *Acacia martii*, *Acosmium lentiscifolium*, *Andira fraxinifolia*, *Aspidosperma cuspa*, *A. subincanum*, *Bowdichia virgilioides*, *Dalbergia brasiliensis*, *Fraunhofera multiflora*, *Handroanthus impetiginosus*, *Machaonia brasiliensis*, *Manilkara triflora*, *Maytenus rigida*, *Pilocarpus spicatus*, *P. trachylophus*, *Poeppigia procera*, *Rollinia emarginata*, *Salacia elliptica*, *Savia sessiliflora* and *Tabebuia roseoalba* are related to more fertile soils that are associated with limestone outcrops. However, species such as *Cordiera concolor*, *Hirtella gracilipes*, *Myrcia guianensis*, *Ouratea castaneifolia*, *Tapirira guianensis*, *Zygia latifolia* and *Tabebuia roseoalba* mentioned above correlated significantly with base saturation (Table 2). At the other extreme, there are species such as *Brosimum gaudichaudii*, *Cecropia pachystachya*, *Copaifera martii*, *Ficus obtusifolia*, *Ludwigia elegans*, *Mauritia*

TABLE 2. Spearman's rank correlation coefficients, with respective significance, between species cover and the environmental variables used in the CCA for the species with 10 or more individuals in the riparian vegetation of the Pandeiros River (Minas Gerais State, Brazil)

Species	Sum of bases	Aluminium saturation	Flooding regime	Canopy openness (rainy season)
Anadenanthera colubrina	0.052 NS	0.067 NS	–0.171 NS	0.055 NS
Astronium fraxinifolium	–0.043 NS	–0.138 NS	–0.029 NS	0.294*
Averrhoidium gardnerianum	0.167 NS	–0.157 NS	–0.381**	–0.014 NS
Bauhinia rufa	0.014 NS	–0.217 NS	–0.394***	0.113 NS
Byrsonima pachyphylla	–0.154 NS	–0.097 NS	–0.097 NS	0.023 NS
Copaifera langsdorffii	0.098 NS	–0.097 NS	–0.008 NS	–0.095 NS
Cordiera concolor	0.442***	–0.151 NS	–0.075 NS	–0.210 NS
Cordiera rigida	0.149 NS	–0.080 NS	–0.272*	0.013 NS
Dilodendron bipinnatum	0.073 NS	–0.145 NS	–0.423***	0.064 NS
Diospyros hispida	0.074 NS	–0.138 NS	–0.416***	0.104 NS
Eugenia florida	0.147 NS	–0.118 NS	–0.063 NS	–0.258*
Hirtella gracilipes	0.367**	–0.169 NS	–0.125 NS	–0.241*
Hymenaea eriogyne	0.094 NS	–0.097 NS	–0.174 NS	–0.050 NS
Inga vera	–0.187 NS	0.217 NS	0.221 NS	0.241*
Machaerium opacum	0.080 NS	–0.097 NS	–0.149 NS	0.198 NS
Myracrodruon urundeuva	0.141 NS	–0.104 NS	–0.034 NS	0.048 NS
Myrcia guianensis	0.257*	–0.046 NS	–0.376**	0.008 NS
Ouratea castaneifolia	0.259*	–0.089 NS	–0.169 NS	–0.031 NS
Roupala montana	0.219 NS	–0.118 NS	–0.145 NS	–0.014 NS
Tabebuia roseoalba	0.272*	–0.104 NS	–0.052 NS	–0.259*
Tapirira guianensis	–0.250*	–0.138 NS	0.033 NS	–0.114 NS
Tocoyena formosa	0.228 NS	–0.145 NS	–0.177 NS	–0.012 NS
Xylopia aromatica	–0.016 NS	–0.125 NS	–0.174 NS	0.173 NS
Zygia latifolia	–0.408***	0.213 NS	0.292*	0.158 NS

$^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$; NS, not significant.

flexuosa, *Pouteria gardneri*, *Psidium guajava*, *Rhamnidium elaeocarpum* and *Simarouba versicolor* that are associated with flooding. *Averrhoidium gardnerianum*, *Bauhinia rufa*, *Cordiera rigida*, *Dilodendron bipinnatum*, *Diospyros hispida*, *Myrcia guianensis* and the aforementioned *Zygia latifolia* also correlated with the flooding regime. Finally, the species *Curatella americana*, *Inga vera*, *Mimosa arenosa* and *Zygia latifolia* are associated with the flooded areas with high light intensity. Other species that correlated with light in the rainy season were *Astronium fraxinifolium*, *Eugenia florida*, *Hirtella gracilipes*, *Tabebuia roseoalba* and the aforementioned *Inga vera*.

The differentiation between the groups can be seen when comparing the number of species that are shared between and unique to groups. Only nine species (8.33%) were common to the four groups of plots: *Astronium fraxinifolium*, *Bauhinia rufa*, *Byrsonima pachyphylla*, *Curatella americana*, *Dilodendron bipinnatum*, *Tapirira guianensis*, *Tocoyena formosa*, *Xylopia aromatica* and *Zygia latifolia*, and 55.55% of species occurred only in a single group, with 20, 17, 3 and 20 species being unique to Groups 1, 2, 3 and 4, respectively (Fig. 4), showing that there are large changes in the species present between plot groups.

Discussion

The floristic composition of the regenerating stratum of the riparian vegetation of the Pandeiros River showed some similarities to other Brazilian riparian forests and to the tree stratum sampled in the same area. The families Fabaceae, Rubiaceae, Sapindaceae and Myrtaceae were also important in a survey of natural forest regeneration in the Tamanduá Forest Reserve in the Federal District (Silva *et al.*, 2004), and the families Fabaceae, Anacardiaceae and Bignoniaceae were also the most representative of the tree stratum in that study area (Rodrigues *et al.*, 2009).

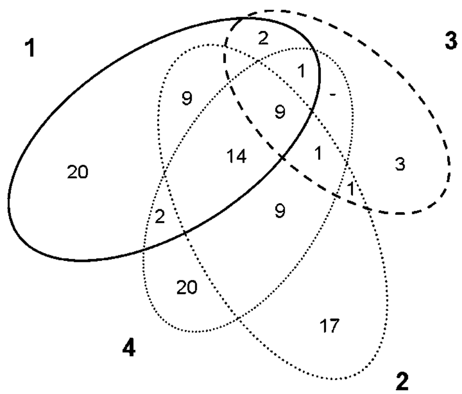

FIG. 4. Venn diagram produced from the shared and unique species between Groups 1, 2, 3 and 4 in the riparian vegetation of the Pandeiros River (Minas Gerais State, Brazil).

The species *Zygia latifolia* and *Butia capitata*, which have the first and third positions in order of importance (IVI) respectively, are normally found in very wet areas in Brazil (Lorenzi *et al.*, 2004; Nunes *et al.*, 2007), and *Tapirira guianensis* (second position) is considered a generalist (Oliveira-Filho & Ratter, 2004).

The Shannon diversity index, both for the total sample and for each individual plot except for Group 3, may be considered high compared with other studies on regenerating strata, such as those of Silva *et al.* (2004) and Oliveira & Felfili (2005) who respectively found diversity indices of 2.89 and 3.02 in central Brazil. The distribution of individuals among species as described by Pielou's evenness calculation ($J' = 0.81$) indicated that, in all probability, there is no concentration of the abundance of any species, which indicates the absence of ecological dominance (Dalanesi *et al.*, 2004). This diversity is further shown by the fact that only nine species were common to the four groups of plots, affirming the presence of strong environmental heterogeneity.

The riparian vegetation studied presents a great diversity of species, which may be due to the influence of other types of vegetation (Oliveira-Filho & Ratter, 2004). This type of contact is very evident from the occurrence of typical species of the Cerrado flora, including *Astronium fraxinifolium*, *Curatella americana*, *Davilla elliptica*, *Eugenia dysenterica*, *Handroanthus ochraceus*, *Hymenaea stigonocarpa*, *Jacaranda brasiliana*, *Machaerium opacum*, *Magonia pubescens*, *Pterodon emarginatus*, *Tocoyena formosa* and *Xylopia aromatica* (Mendonça *et al.*, 1998), and other species commonly found in seasonal forests, such as *Anadenanthera colubrina*, *Casearia rupestris* and *Myracrodruon urundeuva* (Prado & Gibbs, 1993). In addition to the contribution exerted by the adjacent physiognomies, we observed the occurrence of species common to riparian areas, such as *Casearia sylvestris*, *Cecropia pachystachya*, *Copaifera langsdorffii*, *Inga vera* and *Zygia latifolia* (Oliveira-Filho & Ratter, 2004), showing the transitional character of the studied area.

Many studies have observed the occurrence of vegetation mosaics associated with riparian communities (Metzger *et al.*, 1997; Laurance *et al.*, 2010). The confirmation of a floristic identity shared between the predetermined groups indicates the plant recruitment response to the high level of environmental heterogeneity in riparian zones. The grouping of the plots within Group 1 is due to soil colour, which is indicative of distinct fertility properties, which are of great importance in the spatial distribution and structure of tropical forests (Oliveira-Filho *et al.*, 1990, 1994a; Scarano *et al.*, 1997; Carvalho *et al.*, 2005). The plots in Groups 2 and 4 do not differ markedly in relation to species composition and structure, probably due to the presence of the same type of soil. However, the separation of certain plots of these groups with regard to soil fertility may be due to the forest composition of each group, where Group 2 represents a composition closer to the semi-deciduous forest and Group 4 one closer to the Cerrado.

In some cases, light can affect species differentiation more than soil variables (Oliveira-Filho *et al.*, 1998); this can be seen in the plots of Group 3, where there was a clear direct relationship with canopy openness. Light availability has an important role in natural regeneration because the quality and quantity of light determines the survival of species, particularly affecting germination and seedling growth (Beckage & Clark, 2003; Gómez *et al.*, 2004; Madeira *et al.*, 2009). The incidence of light during the growing season (rainy season) is a variable that influences the establishment of different species because canopy gaps are especially favourable sites for seedling recruitment and establishment (Denslow, 1980; Brokan, 1985). This fact may explain the significant effect of light during the rainy season on the richness and abundance of species observed during the natural regeneration process that, despite occurring within this riparian zone, is probably disrupted during the drought due to the hydric deficit in the upper layers of soil where most young plant roots are located. Thus, the recruitment and establishment of individuals are influenced by the amount of canopy cover at the time of the year that is most favourable for growth and establishment of recruits. However, separation of certain plots was also observed. This is probably due to the aluminium saturation level because plots 36, 37, 38 and 42 showed a higher concentration of aluminium and higher values of canopy openness and species that occurred exclusively in them, such as *Mimosa arenosa* and *Mauritia flexuosa*. *Mimosa arenosa* is one of the typical Caatinga species that occurs in areas where vegetation cover suffers continuing deforestation (Soares, 2004), while *Mauritia flexuosa* usually occurs in poorly drained, slightly sandy and soaked soils (Lorenzi *et al.*, 2004).

Another important factor leading to great environmental heterogeneity is the fact that periodic floods vary in their extent (Oliveira-Filho *et al.*, 1994b; Bertani *et al.*, 2001; Sieben *et al.*, 2009). This can be observed in the influence of the flooding regime in the Group 3 plots and in some Group 1 plots. The most marked effects of the flooding regime were in plots 2, 3, 5, 6 and 7 from Group 1 and all Group 3 plots. Species such as *Inga vera*, *Matayba guianensis*, *Psidium guajava*, *Rhamnidium elaeocarpum*, *Rollinia emarginata*, *Salacia elliptica* and *Savia sessiliflora* were restricted to those plots. Some studies have reported that some of these species are typical of humid environments, including Nunes *et al.* (2007) and Silva *et al.* (2007) who found *Inga vera* and *Rollinia emarginata* respectively in these environments. Therefore, the selectivity caused by frequent flooding may lead to differences in floristic composition (Giehl & Jarenkow, 2008) because these variations in flood intensity have an important role in regeneration dynamics (Oliveira-Filho *et al.*, 1998) as soil moisture is a key factor that controls seed germination and seedling establishment (Battaglia *et al.*, 2000).

The diversity of interactions between environmental factors such as soil type and species responses results in environmental heterogeneity that determines the formation of habitat mosaics (Hutchings *et al.*, 2003). According to Levin (1992), all biological systems exhibit a high level of heterogeneity and patchiness, which are fundamental factors in the dynamics of populations and communities. Thus, despite the search for patterns to make ecological studies more quantitative, increased evidence of the importance of heterogeneity leads to a dilemma between practical and theoretical ecology (Sparrow, 1999). The data obtained here show the impossibility of implementing a single model of riparian vegetation recovery throughout the São Francisco basin. This is because, even in short tracts within a single river basin, there is great differentiation in the structure and diversity of the flora during natural regeneration caused by environmental factors such as soil type, light conditions and flooding regime. As a consequence, our knowledge of the patterns of natural regeneration in tropical vegetation is still in its infancy and research to increase our understanding of these processes should be a priority for conservation of biodiversity.

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Appendix

Family and species recorded in the riparian vegetation of the Pandeiros River (Minas Gerais State, Brazil) with respective structure parameters. Abb = abbreviated species name; VN = voucher number; N = number of individuals; AD = absolute density (individuals/ha); AF = absolute frequency (%); AD_o = absolute dominance (m^2/ha); and IV = importance value (%).

	Abb	VN	N	AD	AF	AD_o	IV
Anacardiaceae							
Anacardium occidentale L.	Anac occi	159	3	17.143	4.286	1.679	1.383
Astronium fraxinifolium Schott ex Spreng.	Astr frax	130	25	142.857	18.571	18.746	9.790
Myracrodruon urundeuva Allemão	Myra urun	158	11	62.857	11.429	1.450	3.373
Spondias tuberosa Arruda	Spon tube	221	1	5.714	1.429	0.086	0.359
Tapirira guianensis Aubl.	Tapi guia	150	82	468.571	18.571	39.075	20.510
Annonaceae							
Rollinia emarginata Schltdl.	Roll emar	165	1	5.714	1.429	0.149	0.373
Xylopia aromatica (Lam.) Mart.	Xylo arom	156	16	91.429	15.714	10.123	6.479
Apocynaceae							
Aspidosperma cuspa (Kunth) S.F.Blake ex Pittier	Aspi cusp	217	2	11.429	2.857	1.696	1.045
Aspidosperma multiflorum A.DC.	Aspi mult	243	5	28.571	4.286	2.962	1.881
Aspidosperma subincanum Mart. ex A.DC.	Aspi subi	189	4	22.857	4.286	0.309	1.201
Arecaceae							
Butia capitata (Mart.) Becc.	Buti capi	89	2	11.429	2.857	89.438	19.855
Mauritia flexuosa L.f.	Maur flex	389	4	22.857	1.429	11.644	3.172
Asteraceae							
Vernonanthura phosphorica (Vell.) H.Rob.	Vern phos	70	1	5.714	1.429	1.155	0.588
Bignoniaceae							
Handroanthus impetiginosus (Mart. ex DC.) Mattos	Hand impe	123	3	17.143	1.429	0.329	0.635
Handroanthus ochraceus (Cham.) Mattos	Hand ochr	141	1	5.714	1.429	0.113	0.365
Jacaranda brasiliana (Lam.) Pers.	Jaca bras	117	1	5.714	1.429	0.085	0.359
Tabebuia aurea (Silva Manso) Benth. & Hook.f. ex S.Moore	Tabe aure	153	1	5.714	1.429	0.751	0.502
Tabebuia roseoalba (Ridl.) Sandwith	Tabe rose	222	10	57.143	11.429	3.425	3.685
Boraginaceae							
Cordia glabrata (Mart.) A.DC.	Cord glab	182	2	11.429	2.857	1.034	0.903
Celastraceae							
Fraunhofera multiflora Mart.	Frau mult	161	3	17.143	2.857	0.170	0.830
Maytenus rigida Mart.	Mayt rigi	149	2	11.429	1.429	0.578	0.577
Salacia elliptica (Mart. ex Schult.) G.Don	Sala elli	124	3	17.143	2.857	1.389	1.091
Chrysobalanaceae							
Couepia monteclarensis Prance	Coue mont	172	2	11.429	1.429	2.666	1.024
Hirtella gracilipes (Hook.f.) Prance	Hirt grac	225	36	205.714	25.714	27.130	13.962

Clusiaceae							
Calophyllum brasiliense Cambess.	Calo bras	199	4	22.857	4.286	0.383	1.217
Combretaceae							
Terminalia argentea (Cambess.) Mart.	Term arge	174	1	5.714	1.429	0.325	0.411
Dilleniaceae							
Curatella americana L.	Cura amer	132	8	45.714	8.571	4.125	3.153
Davilla elliptica A.St.-Hil.	Davi elli	176	1	5.714	1.429	0.424	0.432
Ebenaceae							
Diospyros hispida A.DC.	Dios hisp	57	17	97.143	18.571	5.301	6.015
Erythroxylaceae							
Erythroxylum cuneifolium (Mart.) O.E.Schulz	Eryt cune	90	1	5.714	1.429	0.410	0.429
Euphorbiaceae							
Sapium glandulosum (L.) Morong	Sapi glan	155	2	11.429	2.857	3.037	1.333
Sebastiania brasiliensis Spreng.	Seba bras	218	2	11.429	2.857	0.494	0.788
Fabaceae–Caesalpinioideae							
Bauhinia brevipes Vogel	Bauh brev	406	1	5.714	1.429	0.197	0.383
Bauhinia cheilantha (Bong.) Steud.	Bauh chei	77	1	5.714	1.429	0.080	0.358
Bauhinia rufa (Bong.) Steud.	Bauh rufa	105	60	342.857	37.143	9.785	14.757
Copaifera coriacea Mart.	Copa cori	370	5	28.571	5.714	4.772	2.498
Copaifera langsdorffii Desf.	Copa lang	125	12	68.571	10.000	1.909	3.354
Copaifera martii Hayne	Copa mart	80	6	34.286	4.286	1.041	1.581
Guibourtia hymenaefolia (Moric.) J.Léonard	Guib hyme	118	2	11.429	2.857	0.999	0.896
Hymenaea eriogyne Benth.	Hyme erio	191	12	68.571	10.000	8.516	4.770
Hymenaea martiana Hayne	Hyme mart	115	5	28.571	5.714	1.688	1.837
Hymenaea stigonocarpa Mart. ex Hayne	Hyme stig	114	1	5.714	1.429	0.095	0.361
Poeppigia procera C.Presl	Poep proc	91	1	5.714	1.429	0.597	0.469
Senna splendida (Vogel) H.S.Irwin & Barneby	Senn sple	246	3	17.143	4.286	0.335	1.095
Fabaceae–Faboideae							
Acosmium lentiscifolium Schott	Acos lent	142	1	5.714	1.429	0.062	0.354
Andira fraxinifolia Benth.	Andi frax	160	6	34.286	1.429	1.941	1.315
Bowdichia virgilioides Kunth	Bowd virg	223	2	11.429	2.857	0.933	0.882
Dalbergia brasiliensis Vogel	Dalb bras	126	3	17.143	1.429	0.735	0.722
Machaerium hirtum (Vell.) Stellfeld	Mach hirt	64	6	34.286	5.714	0.619	1.720
Machaerium opacum Vogel	Mach opac	184	11	62.857	10.000	4.160	3.725
Machaerium punctatum (Poir.) Pers.	Mach punc	101	2	11.429	2.857	0.155	0.715
Pterodon emarginatus Vogel	Pter emar	67	5	28.571	4.286	2.058	1.687
Swartzia flaemingii Raddi	Swar flae	92	7	40.000	7.143	2.036	2.364
Fabaceae–Mimosoideae							
Acacia martii Benth.	Acac mart	149	1	5.714	1.429	1.229	0.383
Anadenanthera colubrina (Vell.) Brenan	Anad colu	69	10	57.143	10.000	1.239	2.987
Anadenanthera peregrina (L.) Speg.	Anad pere	63	1	5.714	1.429	0.917	0.537
Calliandra foliolosa Benth.	Call foli	102	7	40.000	2.857	1.808	1.628

Inga vera Willd.	Inga vera	356	18	102.857	4.286	5.195	3.811
Mimosa arenosa (Willd.) Poir.	Mimo aren	195	3	17.143	2.857	0.343	0.867
Zygia latifolia (L.) Fawc. & Rendle	Zygi lati	192	89	508.571	25.714	44.158	23.528
Lauraceae							
Nectandra cuspidata Nees	Nect memb	140	2	11.429	2.857	0.234	0.732
Loganiaceae							
Strychnos parvifolia A.DC.	Stry parv	204	4	22.857	5.714	1.140	1.608
Malpighiaceae							
Byrsonima pachyphylla A.Juss.	Byrs pach	66	20	114.286	10.000	9.548	5.884
Malvaceae							
Eriotheca macrophylla (K.Schum.) A.Robyns	Erio macr	361	1	5.714	1.429	0.423	0.432
Helicteres brevispira A.St.-Hil.	Heli brev	152	1	5.714	1.429	0.483	0.445
Luehea grandiflora Mart. & Zucc.	Lueh gran	68	1	5.714	1.429	1.176	0.593
Moraceae							
Brosimum gaudichaudii Trécul	Bros gaud	147	3	17.143	4.286	1.521	1.349
Ficus obtusifolia Kunth	Ficu obtu	109	1	5.714	1.429	0.226	0.389
Myrsinaceae							
Myrsine umbellata Mart.	Myrs umbe	62	1	5.714	1.429	0.918	0.538
Myrtaceae							
Blepharocalyx salicifolius (Kunth) O.Berg	Blep sali	58	1	5.714	1.429	0.292	0.404
Eugenia dysenterica DC.	Euge dyse	154	3	17.143	1.429	1.848	0.960
Eugenia florida DC.	Euge flor	170	17	97.143	14.286	5.328	5.333
Eugenia ligustrina (Sw.) Willd.	Euge ligu	129	9	51.429	7.143	4.589	3.135
Eugenia stictopetala DC.	Euge stic	216	1	5.714	1.429	0.278	0.400
Myrcia guianensis (Aubl.) DC.	Myrc guia	65	53	302.857	24.286	8.935	11.730
Myrcia tomentosa (Aubl.) DC.	Myrc tome	193	2	11.429	2.857	0.604	0.811
Myrciaria floribunda (H.West ex Willd.) O.Berg	Myrc flor	203	5	28.571	1.429	0.523	0.900
Psidium guajava L.	Psid guaj	148	1	5.714	1.429	0.238	0.392
Psidium myrtoides O.Berg	Psid mirs	144	3	17.143	2.857	1.229	1.057
Psidium salutare (Kunth) O.Berg	Psid salu	108	1	5.714	1.429	1.044	0.565
Ochnaceae							
Ouratea castaneifolia (DC.) Engl.	Oura cast	71	10	57.143	8.571	4.108	3.373
Olacaceae							
Schoepfia brasiliensis A.DC.	Scho bras	353	4	22.857	5.714	0.959	1.569
Onagraceae							
Ludwigia elegans (Cambess.) H.Hara	Ludw eleg	52	3	17.143	4.286	3.147	1.697
Opiliaceae							
Agonandra brasiliensis Miers ex Benth. & Hook.	Agon bras	54	1	5.714	1.429	1.864	0.740
Phyllanthaceae							
Savia sessiliflora (Sw.) Willd.	Savi sess	162	7	40.000	4.286	0.897	1.662

Polygonaceae							
Coccoloba declinata (Vell.) Mart.	Cocc decl	183	7	40.000	7.143	1.314	2.210
Proteaceae							
Roupala montana Aubl.	Roup mont	157	15	85.714	14.286	8.935	5.883
Rhamnaceae							
Rhamnidium elaeocarpum Reissek	Rham elae	175	1	5.714	1.429	0.270	0.399
Rubiaceae							
Cordiera concolor (Cham.) Kuntze	Cord conc	165	30	171.429	21.429	11.282	9.207
Cordiera rigida (K.Schum.) Kuntze	Cord rigi	187	10	57.143	7.143	1.580	2.601
Cordiera sessilis (Vell.) Kuntze	Cord sess	143	3	17.143	2.857	0.670	0.937
Coussarea contracta (Walp.) Benth. & Hook.f. ex Müll.Arg.	Cous cont	122	2	11.429	2.857	0.730	0.838
Machaonia brasiliensis (Hoffmanns. ex Humb.) Cham. & Schltdl.	Mach bras	127	2	11.429	2.857	0.259	0.738
Tocoyena formosa (Cham. & Schltdl.) K.Schum.	Toco form	63	26	148.571	20.000	10.121	8.283
Rutaceae							
Pilocarpus spicatus A.St.-Hil.	Pilo spic	164	6	34.286	2.857	3.091	1.791
Pilocarpus trachylophus Holmes	Pilo trac	107	4	22.857	2.857	1.305	1.185
Salicaceae							
Casearia rupestris Eichler	Case rupe	182	2	11.429	1.429	0.353	0.528
Casearia sylvestris Sw.	Case sylv	88	2	11.429	2.857	1.126	0.923
Sapindaceae							
Averrhoidium gardnerianum Baill.	Aver gard	212	40	228.571	22.857	19.657	13.049
Dilodendron bipinnatum Radlk.	Dilo bipi	151	29	165.714	20.000	13.439	9.329
Magonia pubescens A.St.-Hil.	Mago pube	178	1	5.714	1.429	0.175	0.378
Matayba guianensis Aubl.	Mata guia	72	1	5.714	1.429	0.088	0.360
Talisia esculenta (A.St.-Hil.) Radlk.	Tali escu	224	4	22.857	4.286	3.080	1.795
Sapotaceae							
Chrysophyllum marginatum (Hook. & Arn.) Radlk.	Chry marg	190	4	22.857	1.429	0.623	0.809
Manilkara triflora (Allemão) Monach.	Mani trif	173	1	5.714	1.429	2.721	0.924
Pouteria gardneri (Mart. & Miq.) Baehni	Pout gard	215	5	28.571	1.429	1.554	1.120
Simaroubaceae							
Simarouba versicolor A.St.-Hil.	Sima vers	145	2	11.429	0.459	0.021	0.702
Urticaceae							
Cecropia pachystachya Trécul	Cecr pach	84	6	22.857	0.917	0.416	2.003