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SUCESSÃO ECOLÓGICA APÓS ABANDONO, EM ÁREA DE ECÓTONO CAMPO-FLORESTA, NO BIOMA PAMPA

Trabalho de Conclusão de Curso para obtenção do título de Bacharel em Ciências Biológicas, apresentado conforme as normas técnicas da Revista Iheringia.

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Ecological Succession after land abandonment in a forest-grassland ecotone in the Pampa biome[1]

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ABSTRACT – We investigated the succession in a forest-grassland mosaic area kept free from management and disturbance for more than 10 years. We analyzed establishment of shrub and tree species on grassland sites, aiming at quantifying forest advancement over grassland. Further, we evaluated the effects of trees planted in a restoration project as facilitators of the spontaneous establishment of woody species. We sampled and compared both superior and inferior strata of forest, restoration planting and grassland sites regarding height, basal area, abundance and richness of woody species. We found that the restoration project with the introduction of trees was effective in accelerating establishment of forest species, since the lower stratum was very similar to the one of the forest, and both were very different from the grassland. The grassland sites showed significantly less individuals and species in the upper layer. Most of these belonged to pioneer zoochoric species which might act as nurse plants, attracting dispersing animals and possibly altering light, soil and other resources availability, thus facilitating colonization by light intolerant species and favoring further forest expansion. Altogether, successional processes in the grassland after ten years are still rather weak.

Keywords: colonization, forest-grassland mosaic, forest expansion, forest nucleation, regeneration, shrub encroachment.

RESUMO – Sucessão ecológica após abandono, em área de ecótono campo-floresta, no bioma Pampa. Nós investigamos a sucessão ecológica em área de mosaico campo-floresta mantida livre de manejo e distúrbios há mais de dez anos. Foi avaliado o estabelecimento de espécies arbustivas e arbóreas nas áreas de campo, com o intuito de quantificar o avanço florestal sobre o campo. Além disso, foi avaliado o efeito de indivíduos arbóreos, plantado em um projeto de restauração, como facilitadores do estabelecimento espontâneo de espécies lenhosas. Para tanto, foram amostrados e comparados os estratos inferior e superior de áreas floresta nativa, de plantio para restauração e campestres, quanto à altura, área basal, abundância e riqueza de espécies lenhosas. O projeto de restauração através do plantio de espécies nativas mostrou-se efetivo em acelerar o processo de avanço florestal sobre o campo, uma vez que o estrato regenerante dos ambientes de plantio e da matriz florestal são bastante semelhantes entre si e ainda bastante diferentes do estrato regenerante campestre. As áreas de campo apresentaram um número significativamente menor de indivíduos e espécies lenhosas no estrato inferior. A maioria destes indivíduos pertenciam a espécies pioneiras zoocóricas, que podem atuar como plantas-berçário, alterando a disponibilidade de luz, umidade e outros recursos e facilitando, assim, a colonização por espécies menos tolerantes e favorecendo ainda mais o avanço florestal. De forma geral, o processo de sucessão nas áreas campestre, passados dez anos, é ainda incipiente.

Palavras-chave: colonização, mosaico campo-floresta, expansão florestal, nucleação, regeneração, avanço de arbustos.

INTRODUCTION

Rio Grande do Sul's landscape is formed by two dominating vegetation physiognomies: grasslands and forests. Originally covering 40 and 60% of the State's area, respectively, these two vegetation types commonly occur in mosaics, as in the Campos de Cima da Serra region, the granitic hills of Porto Alegre and in Serra do Sudeste (Cordeiro & Hasenack 2009).

The question of how this mosaic originated has been a matter of discussion since the first European naturalists began to study our fauna and flora by the end of the 19th century. Rambo (1956) – through his own observations and knowledge of natural history – concluded that Rio Grande do Sul exhibits, in principle, climatic conditions suitable for forest development. Recent palynological studies confirmed that grasslands are a relict vegetation formation that established and prevailed under a colder and drier climate scenario, which started to shift towards moister and warmer conditions approximately 5,000 years ago. Considering climate alone, we would expect to see today a generalized and still ongoing natural process of forest advancement over grasslands. However, anthropogenic influence is a decisive factor in the shaping of our landscape, and grasslands have been historically maintained by livestock grazing and/or fires which limit forest advancement (Behling 2002, 2004, 2009, Pillar 2003).

In abandoned areas – such as former rangelands – it has been observed that the process of succession quickly unfolds, with the formation of forest patches in the grassland matrix, as well as forest encroachment from the edge of the forest into the grassland. Grassland shrub and pioneer tree species play an important role in this process, which remains, however, poorly studied in general, and especially in the Pampa biome. The available studies – Duarte *et al.* 2006a, b; Hermann, 2009; Oliveira & Pillar 2004, among others – have all been conducted in the Campos de Cima da Serra region, in the Atlantic forest biome. Furthermore, with the exception of the observational study by Oliveira & Pillar (2004), long term studies are missing – even though these are important to investigate succession processes (Müller *et al.* 2012).

Ecological succession can be defined as the whole set of biotic and abiotic changes that succeed in time and space in an interconnected way as a community develops (Walker & Chapin 2003). As vegetation structure assumes new features, physical and chemical characteristics of the environment – such as soil, light and humidity – are also altered, and these new changes influence vegetation structure in return, by affecting plant-plant as well as plant-animals interactions such as competition and facilitation. When the previously established community of a given area is partially or completely removed by a disturbance event, it is followed – if conditions allow – by new colonization and establishment, i.e., secondary succession takes place (Walker & Chapin 1987, Pillar 1994, Walker 2005).

Soil and seed bank characteristics and dispersion ability of the surrounding vegetation are determinant factors in succession processes. However, these processes can be accelerated or altered by ecological restoration. Ecological restoration aims at recovering structural and functional aspects of a degraded community, by reestablishing ecological processes responsible for resilience and stability (SER 2004, Nery et al. 2013). A general pathway of succession, under climatic and soil conditions that allow for forest establishment, goes from vegetation dominated by ruderal species able to occupy disturbed areas to the formation of a forb-graminoid matrix and later establishment of shrubs and trees (Walker & Chapin 2003, Pillar 1994). If conservation strategies aim at development of forest restoration, the simplest restoration strategy is to abandon the area and allow secondary succession to unfold without human intervention. An option to accelerate this process is to plant woody species that might act as perches for birds and accelerate the creation of the conditions required by less tolerant/specialist species (Pillar 1994, Tres *et al.* 2007). This technique has been successfully applied in many types of ecosystems around the world, including in different forest types in Brasil (*e.g*. Rodrigues *et al*. 2009).

Forest species responsible for colonizing grassland areas must be able to tolerate stressful conditions which are quite different from the ones in forest understory, such as high oscillations in temperature and soil humidity, high transpiration rates and competition with grasses and herbs. Isolated trees and shrubs which establish in the grassland matrix may facilitate germination and growth of less tolerant species under their canopies. This phenomenon is known as the nurse plant effect (Duarte, 2006a). Nurse plants act changing resources availability and thus favoring establishment of less tolerant species. Forest-grassland ecotone areas are considered to exhibit such extreme conditions in which nurse plants play a major role for the development of forest communities beyond their original boundaries. They also attract birds which act as seed dispersers. Several studies have pointed out the importance of nurse plants in forest advancement over open areas (Hermann 2009, Duarte 2006a).

In this study, we aim at analyzing succession processes in a forest-grassland ecotone. The study was developed in an area of interface between riparian forest and grasslands which has been kept free of any management or disturbance regime – such as grazing and fire – for thirteen years prior to our study. We compared shrub and tree species recruitment on three kinds of sites: abandoned grassland, riparian forest and at a planting of native species conducted to accelerate forest restoration site (hitherto referred to as planting site). Specifically, we aimed at 1) characterizing succession processes in grassland areas abandoned more than a decade ago and 2) evaluating the effects of the restoration project on native species recruitment. Furthermore, our objective is to contribute to knowledge on formation and dynamics of south Brazilian forest-grassland ecotones, which have not received much attention, especially in the Pampa biome. As far as we know, no study of succession processes in abandoned grassland is available for southern RS.

We expected to find a 1) higher recruitment by woody species in the lower stratum of grassland areas, regarding both abundance, due to the presence of grasslands shrub species with high recruitment rates (e.g., from Asteraceae), and richness, since grassland sites can be colonized by both grassland species and forest pioneers; 2) different composition patterns between vegetation types, as typical taxa differ in grasslands and forest, with composition of recruiting species in plantings closer to that in forests.

MATERIAL AND METHODS

Study site

The city of Cachoeirinha is located in the physiographical region Central Depression (Depressão Central) in eastern RS. The floodplains of the Gravataí river are formed by alfisols (planossols according to the Brazilian soil terminology), formed by a coarse mixture of sand, clay and gravel from alluvial deposits. Climate is Cfa, according to the Köppen classification, with no water deficit, average annual temperature of 19.7º C and average annual precipitation of 1528 mm. The original vegetation cover is formed by pioneer formations (floodplains), Semideciduos Seasonal Forest (sites with a slightly hilly topography), wetlands and grasslands (Teixeira 2007).

Most of the natural vegetation in the region has been modified to some extent by anthropogenic action, and the original vegetation cover has been substituted by secondary formations. The least urbanized areas of the municipality are located north and west of the urbanized area, and they are covered mainly by shrub and forest formations – often occurring as small forest patches locally called “capões” – and riparian forests inserted in a grassland matrix (Teixeira 2007).

Situated at coordinates 20º52’41.53” S and 51º05’50.22” W, the Cachoeirinha Environmental Park was created by the tobacco company Souza Cruz. It occupies 90% of the 208 ha of their industrial site. Its main purpose is the conservation of local biodiversity and water resources, the restoration of riparian forests along the Nazario creek and the restoration of areas previously occupied by human activities. Environmental education activities are developed with school children.

Previous to its acquisition by Souza Cruz, the area was used for livestock raising and private cottages. Since 2000, grassland vegetation has not been under management or suffered any kind of disturbance (such as grazing, mowing or fire). In 2001, aiming at accelerating natural forest regeneration and widening of the remaining riparian forest, plants of several native species were planted in lines close to the edge of the existing riparian forest remnants (Fonseca 2013).

In the former grassland areas, despite the visually predominant cover of herbaceous and grassy species, the process of ecological succession can be observed, with the development of grassland shrubs and the recruitment of a few woody shrub and tree species (Appendix 1). The riparian forest that had previously suffered from selective logging of commercially important species is going through intense regeneration since disturbances ceased.

Vegetation sampling

Sampling of the woody vegetation was conducted between September 2013 and February 2014. The upper stratum was sampled in 60 plots of 5 m x 20 m (sampling units - SUs), evenly distributed in riparian forest (F1 to F20), forest restoration plantings (R1 to R20) and grassland (G1 to G20) sites, amounting to a total of 6000 m^2 sampled. The minimum distance between plots was 20 m. Restoration plots were always set parallel to forest ones, but this was not possible with grassland plots which thus were randomly distributed in the grassland patches. In each SU, individuals of woody species with diameter at breast height (DBH) equal or superior to 5 cm were identified, and height and DBH were recorded. These individuals were considered as the upper stratum of our sites.

In order to characterize the lower stratum, consisting of shrubs and/or regenerating trees, five 2 m x 2 m subplots were established in each SU (1200 m^2 total). Besides species identification and recording of height of all woody individuals that were higher than 30 cm and had a DBH smaller than 5 cm (including those with a lignified stem base), vegetation height at five spots, depth and cover of the litter layer, total cover of the herbaceous stratum, percentage of bare soil and cover of standing dead biomass were recorded. Data from subplots were grouped together for analysis and extrapolated to the total area of the larger SUs. When species identification was not possible in the field, plant material was collected and identified with the aid of literature and experts from the UFRGS Department of Botany. For classification of species into families, we used APG-III

(Angiosperm Phylogeny Group 2009) and for checking of scientific names, the Tropicos database (Tropicos 2013).

Data analysis

For each species-stratum-site combination (lower or upper stratum of grassland, forest or planting site), we determined the absolute and relative density (AD and RD), frequency (AF and RF) and basal area (ABA and RBA – only for higher stratum individuals) and the IVI. For the upper stratum, the IVI was calculated as the arithmetic mean of RD, RF and RBA; for the lower stratum, the IVI was obtained by the average of RD and RF (Müller-Dombois & Ellenberg, 1974). Shannon-Wienner Diversity Index (H') and Pielou's Evenness Index (J') were also determined in order to characterize community structures of the three different kinds of sites sampled in this study (grasslands, riparian forest and planting).

Differences in species richness, abundance, H' and J' values among sites were evaluated, for each stratum, by randomization testing, using Euclidean distance and 10,000 iterations. Total abundance values of typical grassland, edge and forest habitat species and of different growth forms (subshrubs, shrubs, treelets and trees) in each stratum (based on Matzenbacher 2011) were compared among sites in the same way.

In order to explore relations between woody species diversity in the lower and upper strata grassland areas, as well as their respective abundances, linear regression models were calculated. The distance between grassland and forest plots was also compared to lower stratum species density in grassland.

An ordination analysis (Principal Coordinates Analyses, based on Chord distance) was performed for the total data set (both strata) with the aim of identifying compositional and structural differences in regeneration and recruitment patterns among sites. Absolute density of each plot (with subplots values extrapolated to the plot area) was used as descriptor of sampling units.

Software Multiv (Pillar 2004) was used for all data analyses.

RESULTS

Community composition

Regarding all three sets of plots, 6,652 woody individuals were sampled, belonging to 128 species and 39 botanical families (Appendix 2). The richest family was Asteraceae (18), followed by Myrtaceae (15), Fabaceae (8) and Rubiaceae (6). In the lower stratum, 5,897 individuals, belonging to 122 species and 38 families, were sampled. Of these, 1,915 were registered in grassland plots (479 per 100 m^2; 50 species and 24 families), 2,231 in forest plots (558 per 100 m^2; 71 species, 28 families), and 1,751 in restoration plots (438 per 100 m^2; 78 species, 30 families). In the upper stratum, 755 individuals, belonging to 62 species and 29 families were registered; 73 of which in the grassland (4 per 100 m^2; 9 species and 8 families), 450 in the forest (23 per 100 m^2; 51 species and 26 families) and 232 in the restoration plantings (12 per 100 m^2; 28 species and 18 families).

In the lower stratum, the most important species in grassland plots were *Eupatorium laevigatum*, *Cordia monosperma*, *Myrsine coriacea* and *Eupatorium sp*., which together amounted for 42% of the total IVI. *Myrsine coriacea*, *Mimosa bimucronata* and *Schinus terebinthifolius* were responsible for 61% of the total IVI of the upper stratum. The most species rich families in the grassland were Asteraceae, Melastomataceae and Fabaceae (Tables 1 and 2).

In the lower stratum of the forest, the most important species were *Faramea montevidensis, Mollinedia elegans, Psychotria leiocarpa* and *Sebastiania serrata*, while the forest canopy (upper stratum) was characterized by *S. serrata, Allophylus edulis, Casearia sylvestris* and *Luehea divaricata*, representing 47% of total IVI. Myrtaceae was the richest family for both strata. Several forest understory Rubiaceae shrubs were present.

In the upper stratum of planting plots, S*chinus terebinthifolius, Psidium cattleyanum, Inga marginata* and *Erythroxylum deciduum* stood out with the highest IVIs, and Fabaceae was the richest family. *Myrsine coriacea, Lantana camara, Prunus myrtifolia* and *Psychotria carthagenensis* were the most important regenerating species (lower stratum). Myrtaceae and Lauraceae contributed with the highest proportion of total richness.

Overall frequency was the most distinguishing parameter for the upper stratum and density for the lower stratum (Appendix 2).

Table 1. Phytosociological parameters for the ten most important species in the lower stratum of each type of site (Grassland = G, Forest = F and Planting = P), sampled in the Cachoeirinha Environmental Park. Parameters shown: extrapolated abundance (EA, extrapolated to the total area sampled in the upper stratum = 6000 m^2), absolute and relative density (AD and RD), frequency (AF and RF) and importance value index (IVI).

Species	Site	EA	D (ni/ha)	AF	RD (%)	RF (%)	IVI (%)
Eupatorium laevigatum	G	2170	10850	0.85	22.7	7.5	15.1
Cordia monosperma	G	1775	8875	0.65	18.5	5.7	12.1
Myrsine coriacea	G	1020	5100	0.75	10.7	6.6	8.6
Eupatorium sp.	G	775	3875	0.45	8.1	4.0	6.0
Baccharis dracunculifolia	G	335	1675	0.6	3.5	5.3	4.4
Eupatorium inulifolium	G	415	2075	0.5	4.3	4.4	4.4
Leandra australis	G	380	1900	0.45	4.0	4.0	4.0
Schinus terebintifolius	G	175	875	0.65	1.8	5.7	3.8
Baccharis trimera	G	250	1250	0.55	2.6	4.8	3.7
Eupatorium pedunculosum	G	280	1400	0.4	2.9	3.5	3.2
Faramea montevidensis	F	1625	8125	0.9	14.6	4.3	9.5
Mollinedia elegans	F	1600	8000	0.9	14.4	4.3	9.3
Psychotria leiocarpa	F	1050	5250	0.85	9.4	4.1	6.7
Psychotria carthagenensis	F	695	3475	0.9	6.2	4.3	5.3
Sebastiania serrata	F	690	3450	0.85	6.2	4.1	5.1
Piper aduncum	F	880	4400	0.45	7.9	2.1	5.0
Eugenia hiemalis	F	555	2775	0.95	5.0	4.5	4.8
Nectandra grandiflora	F	665	3325	0.45	6.0	2.1	4.1
Myrcia glabra	F	310	1550	0.9	2.8	4.3	3.5
Myrcia multiflora	F	285	1425	0.8	2.6	3.8	3.2
Myrsine coriacea	P	1415	7075	0.95	16.2	5.1	10.6
Leandra australis	P	975	4875	0.8	11.1	4.3	7.7
Prunus myrtifolia	P	690	3450	0.65	7.9	3.5	5.7
Psychotria carthagenensis	P	585	2925	0.5	6.7	2.7	4.7
Schinus terebinthifolius	P	260	1300	0.85	3.0	4.5	3.8
Psidium cattleianum	P	260	1300	0.6	3.0	3.2	3.1
Psychotria leiocarpa	P	300	1500	0.45	3.4	2.4	2.9
Myrcia multiflora	P	250	1250	0.55	2.9	2.9	2.9
Cestrum strigillatum	P	335	1675	0.35	3.8	1.9	2.8
Mimosa bimucronata	P	235	1175	0.5	2.7	2.7	2.7

Table 2. Phytosociological parameters for the five most important species in the upper stratum of each type of site (Grassland = G, Forest = F and Planting = P), sampled at the Cachoeirinha Environmental Park. Parameters shown: abundance (A) on total sampled area (6000 m^2), absolute

and relative density (D and RD), frequency (AF and RF) and basal area (ABA and RBA), and importance value index (IVI).

Species	Site	A	BA (m2)	D (ni/ha)	AF	RD (%)	RF (%)	RBA (%)	IVI (%)
Myrsine coriacea	G	21	13059.3	105	0.25	28.8	26.3	32.1	28.7
Mimosa bimucronata	G	16	9142.1	80	0.1	21.9	10.5	22.4	17.8
Schinus terebinthifolius	G	13	5229.7	65	0.15	17.8	15.8	12.8	15.8
Zanthoxylum rhoifolium	G	5	3424.2	25	0.15	6.8	15.8	8.4	10.6
Sapium glandulosum	G	4	5608.0	20	0.1	5.5	10.5	13.8	9.4
Sebastiania serrata	F	208	26781.8	1040	0.8	46.2	9.1	34.2	29.3
Allophylus edulis	F	34	4062.0	170	0.65	7.6	7.4	5.2	6.9
Casearia silvestris	F	26	5164.3	130	0.65	5.8	7.4	6.6	6.6
Luehea divaricata	F	16	4364.9	80	0.35	3.6	4.0	5.6	4.2
Prunus myrtifolia	F	15	2269.2	75	0.3	3.3	3.4	2.9	3.3
Schinus terebinthifolius	P	60	10401.2	300	0.7	25.9	13.6	33.6	23.2
Psidium cattleianum	P	56	8427.0	280	0.6	24.1	11.7	27.2	20.2
Inga marginata	P	13	2347.6	65	0.35	5.6	6.8	7.6	6.5
Erythroxylum deciduum	P	15	712.4	75	0.4	6.5	7.8	2.3	5.9
Mimosa bimucronata	P	10	955.2	50	0.35	4.3	6.8	3.1	4.9

Structural aspects

For several structural parameters, significant differences were found among the three categories of sites. Richness of the lower stratum, but not density, differed significantly between grassland and the other two sites (P = 0.0001), with lower values in grassland (Table 3).

Table 3. Mean abundance and species richness per sampling unit (100 m^2) for each type of site and stratum, sampled at the Souza Cruz Environmental Park, Cachoeirinha, RS. Different letters after species richness indicate statistically significant differences (P < 0,05).

	Stratum	Grassland	Forest	Planting
Abundance	Lower	97.5 a	111.55 a	87.55 a
	Upper	3.65 a	22.5 b	11.6 c
Species Richness	Lower	11.35 a	20.95 b	18.75 b
	Upper	0.95 a	8.75 b	5.15 c

Grassland sites revealed a significantly higher density of shrub individuals than the two other sites, while tree species density was lower. Forest plots had higher density of treelet individuals and subshrubs densities were not significantly different in any comparison (Figure 3).

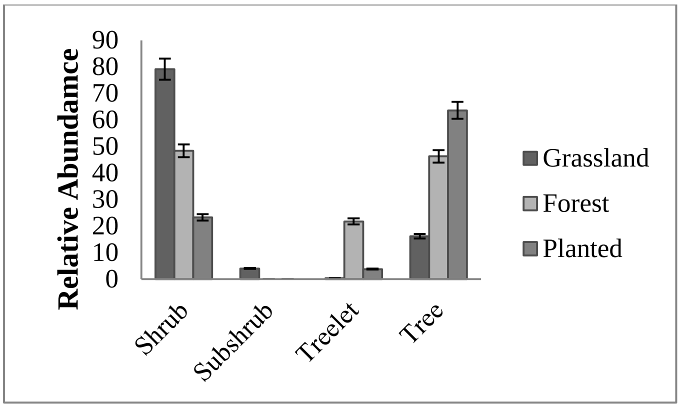

Figure 3. Relative abundance of shrubs, subshrubs, subtrees and trees, in the lower stratum of grassland, forest and planted sites, at the Souza Cruz Environmental Park, Cachoeirinha, RS.

Subplots in grassland areas were almost exclusively composed by individuals from typical grassland species and a few species typical for forest edges. Grassland shrubs and subshrubs (e.g. *Eupatorium spp*. and *Baccharis spp*.) were among the most important. Forest and planting communities were mainly formed by forest interior and edge species, but also by a few grassland species individuals. All differences were highly significant (Fig 2).

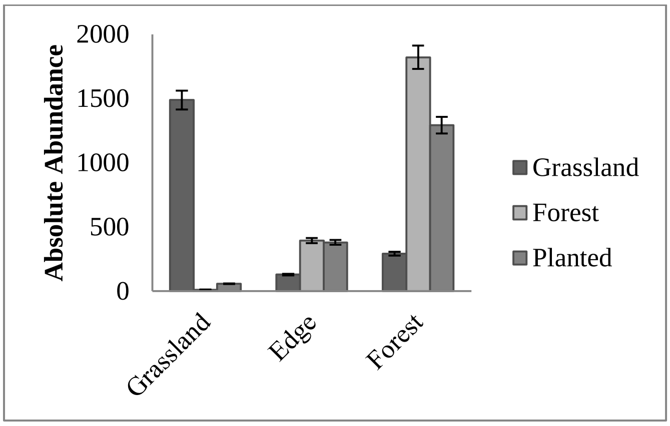

Figure 2. Absolute abundance of typical grassland, edge and forest species (following Matzenbacher 2011), recorded in the regenerating stratum of grassland, forest and planted sites, at the Souza Cruz Environmental Park, Cachoeirinha, RS.

Values of the Shannon-Wienner Diversity Index and Pielou's Evenness Index were very similar among all three sites (*ca.* 2.8 and 0.6 respectively), and may be considered intermediate. No significant correlations were found between the different parameters, except for total richness of grassland plots and shrub density (r = 0.803).

Floristic similarity between vegetation types, based on Jaccard's similarity coefficient, between lower and upper strata of grassland plots was low. The lower stratum in the areas with the restoration planting, formed by spontaneous regenerating understory shrubs and tree species seedlings, was more similar to the riparian forest understory than to any other vegetation type/stratum. Second highest similarity value was between lower and upper forest strata (Table 4).

Table 4. Similarity matrix based on Jaccard coefficient. Grassland Lower Stratum = GL, Grassland Upper Stratum = GU, Forest Lower Stratum = FL, Forest Upper Stratum = FU, Planted Lower Stratum = PL, Planted Upper Stratum = PU. The lowest and highest matrix values are preceded by *.

	Grassland		**Forest**		**Planted**	
	Lower Stratum	**Upper Stratum**	**Lower Stratum**	**Upper Stratum**	**Lower Stratum**	**Upper Stratum**
GL	1					
GU	0.1569	1				
FL	0.1959	*0.0714	1			
FU	0.2169	0.1321	0.5195	1		
PL	0.2427	0.1013	*0.5434	0.4176	1	
PU	0.1642	0.1935	0.2208	0.3167	0.3086	1

The dispersion graph based on the ordination analysis shows a very clear grouping of SUs according to type of site, revealing differences in species composition patterns of sampled areas. *M. elegans*, *P. cattleyanum* and *E. laevigatum*, were the most correlated species to forest, planting and grassland plots, respectively (Fig. 3).

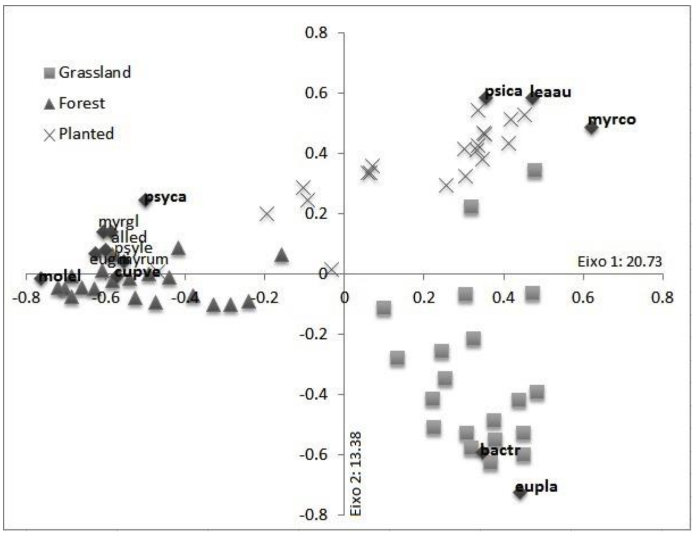

Figure 3. Dispersion diagram of the two first PCoA axes, based on Chord distance matrix among SUs (data of both strata were grouped together for each SU). Species with highest correlation to

axes (>0.4) are indicated as follows: molel = *Mollinedia elegans*; cupve = *Cupania vernalis*; myrum = *Myrsine umbellata*; eughi = *Eugenia hiemalis*; psyle = *Psychotria leiocarpa*; alled = *Allophilus edulis*, mygl = *Myrcia glabra*; psyca = *Psychotria carthagenensis*; psica = *Psidium cattleyanum*; pscat = *Psidium cattleyanum*; leaau = *Leandra australis*; myrco = *Myrsine coriacea*; bactr = *Baccharis trimera*; eupla = *Eupatorium laevigatum*.

DISCUSSION

The phenomenon of forest species establishment over abandoned grasslands has been investigated by several studies conducted in Rio Grande do Sul Araucaria forest-grasslands mosaic as well as in the granitic hills of Porto Alegre. General results point to two main mechanisms by which forest species colonize undisturbed grassland areas: nucleation process triggered by nurse plants and encroachment from the forest edge (Oliveira & Pillar 2004, Müller *et al.* 2012, Duarte *et al.* 2006b, Hermann 2009). Restrictions to establishment of forest species in grassland might include litter accumulation and competition by forbs and grasses in the herbaceous layer (Facelli & Pickett 1991, Boldrini & Eggers 1996, Dos Santos 2011).

Contrarily to our suggested hypotheses, grassland areas sampled in this study did not show a statistically significant difference in abundance of regenerating woody species when compared to forest and forest under restoration. Even more strikingly, values for species richness were significantly lower in grassland plots. On the other hand, diversity and evenness coefficient values (H’ and P’) – which take into account both richness and species abundances – were similar for grassland, forest and forest restoration plantings. Individuals found in grassland sites were mainly typical grassland shrubs from the Asteraceae family, such as *Eupatorium* and *Baccharis* spp. The few adult individuals from forest species forming a widely scattered upper stratum/canopy in grassland areas belonged to pioneer zoochoric species, such as *Myrsine coriacea* and *Schinus terebinthifolius*.

The dispersion diagram revealed a clear separation of the regenerative stratum in forest from that of grassland and of areas with the forest restoration planting along the horizontal axis. The low explanation power obtained for the ordination axes likely is due to high internal variation among plots from the same sites. In fact, plots from the same type of habitat were very heterogeneous and had different dominance patterns. Nonetheless, variance analyses revealed highly significant differences in total richness values for each site.

Our data did not reveal a strong advancement of forest species over grassland, as few adult woody individuals were found (73) in the 20 grassland plots. Richness and density of woody regenerating and adult individuals was not related to distance from forest edge, nor to total vegetation, litter or bare soil cover. However, considering that the abundant grassland shrubs lead to changes in vegetation structure and may serve as facilitators for establishment of other woody species, we can assume that they initate a process of forest expansion, helping tree species individuals to overcome forb-graminoid dominance. As they are grassland species that do not occur in the forest, this is not evidenced in the ordination analysis. Mechanisms of community change in consequence of increased shrub abundance in grassland still need to be investigated in more detail. These species do not seem to serve as perches, but there might be other effects, such as competition to the herbaceous layer, thus increasing establishment chances for pioneer forest species (Dos Santos *et al*. 2011).

Regarding species richness and abundance, recruitment of adult woody forest species was significantly higher in forest restoration areas when compared to grasslands. While only nine species were found established in the upper stratum of grassland plots, the planted area adjacent to the forest exhibited 44 different species, and 23 of these were not in the list of planted species, so that they must have been dispersed from the forest. The set of woody species found colonizing grasslands and planting areas are subsets of the ones found in the forest matrix, including those which were successful in dispersing and establishing themselves to outside the forest understory. Thus it is natural to expect that – due to characteristics of the dispersal process and the microenvironmental conditions promoted by the planting – restored areas closer to the forest source will show an increased colonization regarding both number of species and individuals as areas of grassland further from the forest edge and without any restoration intervention. This pattern is evidenced by the high similarity coefficient observed between the lower stratum of planting and forest areas, even though it does not reflect in a higher number of adult non-planted individuals: here, grasslands showed higher numbers (73 vs. 54, for 73 and 232, respectively).

Duarte *et al.* (2007) has observed that most woody species found colonizing grassland areas had small red to dark diaspores, indicating the importance of frugivorous birds as seed carriers from the forest to the grassland matrix. The same was found at the present study. The two most abundant and frequent forest species found established as adult individuals in the grassland matrix, namely *Myrsine coriacea* and *Schinus terebinthifolius*, are dispersed by birds. Zoochoric dispersion syndrome has been shown to be very important to forest expansion by several studies of seedlings distribution patterns in grasslands (Duarte *et al*. 2006a, Duarte *et al*. 2006b, Fontoura *et al*. 2006; Zanini *et al*. 2006; Dos Santos & Pillar 2007). These species are important in attracting forest seeds dispersers and in further colonization. The absence/lack of a nurse-plant species as effective as *Araucaria* might account for the low number of woody forest tree seedlings observed in comparison to the study by Duarte *et al.* (2007).

In our study, we observed that many individuals of typical grassland shrub species, commonly denominated "vassouras" in Portuguese ("brooms"), such as *Baccharis dracunculifolia*, were at the end of their life cycle (of *ca*. ten years) and had not apparently favored the development of other woody species, nor did they manage to renew their own populations. Dos Santos *et al.* (2011) found that the most important factor increasing seed rain and recruitment of forest species were dense shrub associations and isolated araucarias that served as perches as discussed above, while isolated shrubs did not favor seed rain and further forest species establishment any more than open grassland areas.

Overall, it seems that secondary succession in the Souza Cruz Environmental Park's grassland areas – after more than a decade of ceasing of all disturbances – is still in a rather incipient stage, even though the distance between our grassland plots and the riparian forest is very short (*ca*. 50 m, on average). As for now, only a rather weak trend of formation of shrub associations near forest edges and small forest nuclei developing under isolated trees could be observed, however, indicating a more definitive forest expansion phenomenon in the future. The planting of forest pioneer species did contribute to acceleration of forest regeneration and secondary succession in grassland areas.

As future perspectives this study has the investigation of functional traits, especially those related to dispersion, colonization and establishment abilities. These might help in reaching a better understanding of the mechanisms responsible for successful colonization of woody species in grasslands. Long term studies with permanent plots would be the ideal approach for a more conclusive evaluation of vegetation development and to access succession trends.

Our study raises yet another question. The current conservation approach in the Environmental Park is focused on riparian forests, including the attempt to accelerate natural recovery of forest by help of the forest plantings. If not only riparian forest but also grassland diversity conservation were objects of conservation, it must be taken into account that this vegetation has evolved under disturbance regimes and had been subjected to fire and grazing for the last thousands of years; therefore, management– through fire and grazing – can be considered as adequate, if not necessary, for conservation (Pillar & Velez 2010). High biodiversity and endemism levels of grassland vegetation in Rio Grande do Sul, especially in the Pampa Biome, on the one hand, the lack of consideration in conservation policy on the other hand, has only recently been thoroughly discussed, and the need of management for conservation and restoration has been proposed (Overbeck *et al*. 2007, 2013). It has been pointed out recently that tropical and subtropical grasslands around the world are not adequately considered from a conservation perspective (Parr *et al*. 2014). The inclusion of grassland conservation into the management objectives of the Souza Cruz Environmental Park seems an interesting option regarding the potential to increase awareness for grassland conservation in the environmental education programs conducted in the park.

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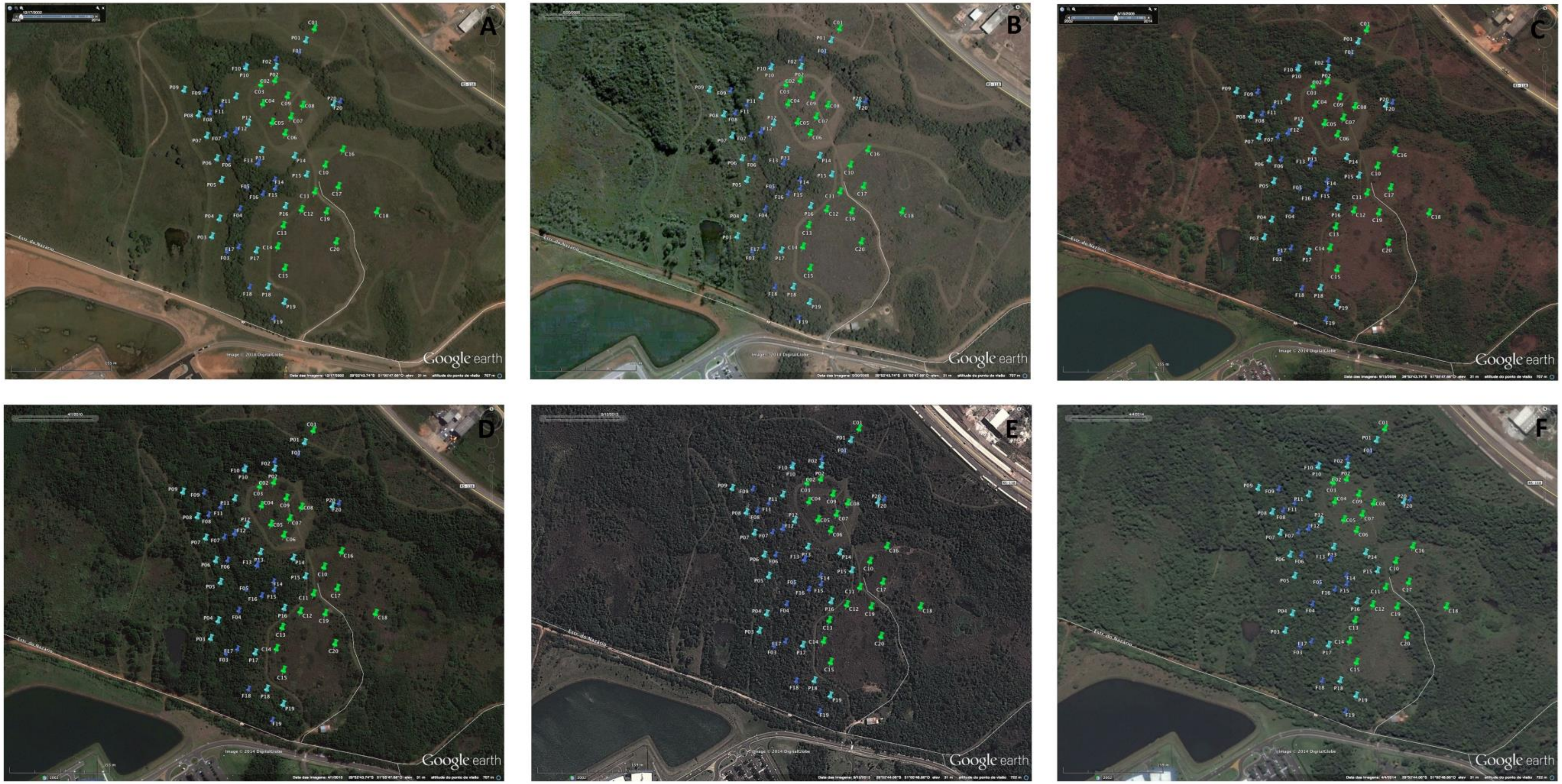
APPENDIX

Appendix 1. Satelite images of the Cachoeirinha Environmental Park area over the years of 2002 and 2014. A = 2002, B = 2005, C = 2009, D = 2010, E = 2013, F = 2014. Source: Google Earth.



Appendix 2. Complete list of species sampled in the lower and upper strata of each type of site, at the Cachoeirinha Environmental Park. Parameters shown: density per ha (D), basal area (BA, for upper stratum only) and importance value index (IVI). Letters (G, F and P) preceding parameters stand for grassland, forest and planted sites, respectively. Values shown with commas for decimal places.

Family/Species	**Growth form**	**Habitat**	**Lower Stratum**						**Upper Stratum**								
			GD	**FD**	**PD**	**G IVI**	**F IVI**	**P IVI**	**GD**	**FD**	**PD**	**GBA**	**FBA**	**PBA**	**G IVI**	**F IVI**	**P IVI**
Acanthaceae																	
Justicia brasiliana Roth	shrub	forest	-	375	-	-	0,005	-	-	-	-	-	-	-	-	-	-
Anacardiaceae																	
Lithraea brasiliensis Marchand	tree	forest	-	-	25	-	-	0,002	-	20	-	-	1014,3	-	-	0,02	-
Schinus terebinthifolius Raddi	tree	forest	875	-	1300	0,038	-	0,038	65	5	300	5229,7	211,1	8427,0	0,16	0,00	0,23
Annonaceae																	
Annona sp. L.	tree		-	-	50	-	-	0,002	-	5	10	-	79,6	100,7	-	0,00	0,01
Annona sylvatica A. St.-Hil.	tree	forest	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Apocynaceae																	
*Aspidosperma austral*e Müll. Arg.	tree	forest	-	-	25	-	-	0,002	-	-	5	-	-	20,4	-	-	0,01
Aquifoliaceae																	
Ilex dumosa Reissek	tree	edge	-	-	25	-	-	0,002	-	-	-	-	-	-	-	-	-
Arecaceae																	
Syagrus romanzoffiana (Cham.) Glassman	tree	forest	-	750	450	-	0,021	0,011	-	10	-	-	403,1	-	-	0,01	-
Asteraceae																	
Baccharis articulata (Lam.) Pers.	subshrub	grassland	125	-	-	0,010	-	-	-	-	-	-	-	-	-	-	-
Baccharis dracunculifolia DC.	shrub	grassland	1675	-	-	0,044	-	-	-	-	-	-	-	-	-	-	-
Baccharis trimera (Less.) DC.	shrub	grassland	1250	-	-	0,037	-	-	-	-	-	-	-	-	-	-	-
Eupatorium sp. 1 L.		grassland	-	-	25	-	-	0,002	-	-	-	-	-	-	-	-	-
Eupatorium sp. 2 L.			3875	-	-	0,060	-	-	-	-	-	-	-	-	-	-	-
Eupatorium bupleurifolium DC.	shrub	grassland	50	-	-	0,005	-	-	-	-	-	-	-	-	-	-	-

Appendix 2 continued

Family/Species	Growth form	Habitat	Lower Stratum						Upper Stratum								
			GD	**FD**	**PD**	**G IVI**	**F IVI**	**P IVI**	**GD**	**FD**	**PD**	**GBA**	**FBA**	**PBA**	**G IVI**	**F IVI**	**P IVI**
Eupatorium intermedium DC.	shrub	grassland	150	-	-	0,006	-	-	-	-	-	-	-	-	-	-	-
Eupatorium inulifolium Kunth	shrub	grassland	2075	-	-	0,044	-	-	-	-	-	-	-	-	-	-	-
Eupatorium ivifolium L.	shrub	grassland	175	-	-	0,008	-	-	-	-	-	-	-	-	-	-	-
Eupatorium laevigatum Lam.	shrub	grassland	10850	-	-	0,151	-	-	-	-	-	-	-	-	-	-	-
Eupatorium pauciflorum Kunth	shrub	grassland	150	-	-	0,006	-	-	-	-	-	-	-	-	-	-	-
Eupatorium pedunculosum Hook. & Arn.	shrub	grassland	1400	-	-	0,032	-	-	-	-	-	-	-	-	-	-	-
Eupatorium subhastatum Hook. & Arn.	subshrub	grassland	775	-	-	0,024	-	-	-	-	-	-	-	-	-	-	-
Gochnatia polymorpha (Less.) Cabrera	tree	forest	-	-	50	-	-	0,003	-	-	-	-	-	-	-	-	-
Senecio heterotrichius DC.	subshrub	grassland	325	-	-	0,008	-	-	-	-	-	-	-	-	-	-	-
Vernonanthura nudiflora (Less.) H. Rob.	subshrub	grassland	925	-	-	0,014	-	-	-	-	-	-	-	-	-	-	-
Vernonanthura tweedieana (Baker) H. Rob.	shrub	grassland	1125	-	50	0,025	-	0,003	-	-	-	-	-	-	-	-	-
Bignoniaceae																	
Handroanthus heptaphyllus (Vell.) Mattos	tree	forest	-	75	-	-	0,004	-	-	-	-	-	-	-	-	-	-
Handroanthus umbellatus (Sond.) Mattos	tree	forest	-	-	-	-	-	-	-	10	-	-	158,7	-	-	0,01	-
Jacaranda micrantha Cham.	tree	forest	-	-	-	-	-	-	-	-	15	-	-	164,7	-	-	0,02
Boraginaceae																	
Cordia americana (L.) Gottschling & J.S. Mill.	tree	forest	75	50	-	0,005	0,003	-	-	15	5	-	2320,6	24,4	-	0,02	0,01
Cordia monosperma (Jacq.) Roem. & Schult.	shrub	grassland	8875	-	-	0,121	-	-	-	-	-	-	-	-	-	-	-

Appendix 2 continued

Family/Species	Growth form	Habitat	Lower Stratum						Upper Stratum								
			GD	FD	PD	G IVI	F IVI	P IVI	GD	FD	PD	GBA	FBA	PBA	G IVI	F IVI	P IVI
Cactaceae																	
Cereus hildmannianus K. Schum.	shrub	edge, grassland	-	-	-	-	-	-	-	5	-	-	456,5	-	-	0,00	-
Cannabaceae																	
Celtis iguanaea (Jacq.) Sarg.	treelet	forest	-	150	125	-	0,005	0,003	-	5	10	-	63,2	79,3	-	0,00	0,01
Trema micrantha (L.) Blume	tree	forest	-	-	-	-	-	-	-	5	-	-	86,7	-	-	0,00	-
Celastraceae																	
Maytenus dasyclados Mart.	shrub	forest	-	475	50	-	0,015	0,003	-	5	-	-	57,7	-	-	0,00	-
Erythroxylaceae																	
Erythroxylum argentinum O. E. Schulz	tree	forest	-	125	325	-	0,006	0,015	-	30	5	-	3503,3	41,5	-	0,02	0,01
Erythroxylum deciduum A. St. Hil.	tree	forest	25	-	100	0,002	-	0,005	-	15	75	-	175,5	955,2	-	0,01	0,06
Euphorbiaceae																	
Sapium glandulosum (L.) Morong	tree	forest	125	25	350	0,010	0,001	0,015	20	5	25	5608,0	655,2	103,7	0,09	0,01	0,02
Sebastiania brasiliensis Spreng.	tree	forest	-	75	-	-	0,004	-	-	20	-	-	291,7	-	-	0,01	-
Sebastiania commersoniana (Baill.) L.B. Sm. & Downs	tree	forest	-	-	150	-	-	0,006	-	-	-	-	-	-	-	-	-
Sebastiania serrata (Baill. ex Müll. Arg.) Müll. Arg.	tree	forest	-	3500	425	-	0,053	0,006	-	1040	5	-	26781,8	76,5	-	0,29	0,01
Fabaceae																	
Apuleia leiocarpa (Vogel) J.F. Macbr.	tree	forest	-	175	25	-	0,005	0,002	-	-	40	-	-	455,2	-	-	0,03
Collaea stenophylla (Hook. & Arn.) Benth.	subshrub	edge, grassland	200	-	-	0,011	-	-	-	-	-	-	-	-	-	-	-
Erythrina cristagalli L.	tree	forest	-	-	-	-	-	-	5	-	-	1194,0	-	-	0,03	-	-
Inga marginata Willd.	tree	forest	-	-	375	-	-	0,011	-	-	65	-	-	712,4	-	-	0,07
Inga vera Willd.	tree	forest	-	-	325	-	-	0,011	-	-	35	-	-	380,7	-	-	0,03

Appendix 2 continued

Family/Species	Growth form	Habitat	Lower Stratum						Upper Stratum								
			GD	FD	PD	G IVI	F IVI	P IVI	GD	FD	PD	GBA	FBA	PBA	G IVI	F IVI	P IVI
Mimosa bimucronata (DC.) Kuntze	tree	forest	300	-	1200	0,016	-	0,027	80	40	50	9142,1	1382,2	1581,4	0,18	0,02	0,05
Parapiptadenia rigida (Benth.) Brenan	tree	forest	-	25	125	-	0,001	0,006	-	5	30	-	548,2	221,5	-	0,00	0,03
Peltophorum dubium (Spreng.) Taub.	tree	forest	-	-	-	-	-	-	-	10	5	-	137,8	47,4	-	0,01	0,01
Hypericaceae																	
Hypericum brasiliense Choisy	shrub	grassland	375	-	-	0,011	-	-	-	-	-	-	-	-	-	-	-
Lamiaceae																	
Aegiphila integrifolia (Jacq.) B.D. Jacks.	treelet	forest	75	50	50	0,005	0,003	0,003	-	25	-	-	1203,8	-	-	0,02	-
Vitex megapotamica (Spreng.) Moldenke	tree	forest	125	-	25	0,006	-	0,002	-	15	35	-	1757,0	532,3	-	0,01	0,03
Lauraceae																	
Cinnamomum verum J. Presl	tree	forest	-	-	75	-	-	0,005	-	-	-	-	-	-	-	-	-
Endlicheria paniculata (Spreng.) J.F. Macbr.	tree	forest	-	175	25	-	0,009	0,002	-	-	-	-	-	-	-	-	-
Nectandra grandiflora Nees & Mart. ex Nees	tree	forest	-	3325	1500	-	0,041	0,027	-	30	-	-	2008,9	-	-	0,02	-
Ocotea puberula (Rich.) Nees	tree	forest	-	25	150	-	0,001	0,009	-	45	10	-	3082,6	90,5	-	0,03	0,01
Ocotea pulchella (Nees & Mart.) Mez	tree	forest	50	225	25	0,005	0,009	0,002	-	10	-	-	66,7	-	-	0,01	-
Loganiaceae																	
Strychnos brasiliensis (Spreng.) Mart.	tree	forest	-	225	125	-	0,006	0,004	-	-	-	-	-	-	-	-	-
Malvaceae																	
Luehea divaricata Mart.	tree	forest	50	50	1025	0,005	0,003	0,023	30	80	40	1415,4	4364,9	1441,3	0,06	0,04	0,04
Malvaceae sp. 1 Juss		forest	-	25	275	-	0,001	0,006	-	-	-	-	-	-	-	-	-
Malvaceae sp. 2 Juss			-	-	50	-	-	0,002	-	-	-	-	-	-	-	-	-
Malvaceae sp. 3 Juss		grassland	25	-	-	0,002	-	-	-	-	-	-	-	-	-	-	-

Appendix 2 continued

Family/Species	Growth form	Habitat	Lower Stratum						Upper Stratum								
			GD	FD	PD	G IVI	F IVI	P IVI	GD	FD	PD	GBA	FBA	PBA	G IVI	F IVI	P IVI
Triumfetta semitriloba Jacq.	shrub	edge	-	750	275	-	0,013	0,006	-	-	-	-	-	-	-	-	-
Melastomataceae																	
Leandra australis (Cham.) Cogn.	shrub	edge	1900	100	4875	0,040	0,004	0,077	-	-	-	-	-	-	-	-	-
Miconia cinerascens Miq.	shrub	forest, edge	50	100	450	0,005	0,003	0,017	-	-	-	-	-	-	-	-	-
Miconia hiemalis A.St.-Hil. & Naudin ex Naudin	treelet	edge	50	-	-	0,005	-	-	-	-	-	-	-	-	-	-	-
Miconia sellowiana Naudin	treelet	edge	25	625	250	0,002	0,019	0,014	-	10	-	-	68,7	-	-	0,00	-
Tibouchina asperior (Cham.) Cogn.	shrub	grassland	725	-	-	0,010	-	-	-	-	-	-	-	-	-	-	-
Meliaceae																	
Cedrela fissilis Vell.	tree	forest	-	-	25	-	-	0,002	-	15	-	-	1186,4	-	-	0,01	-
Guarea macrophylla Vahl	tree	forest	-	25	50	-	0,001	0,003	-	-	-	-	-	-	-	-	-
Trichilia elegans A. Juss.	tree	forest	-	50	50	-	0,003	0,003	-	-	-	-	-	-	-	-	-
Monimiaceae																	
Mollinedia elegans Tul.	shrub	forest	-	8000	475	-	0,093	0,014	-	5	-	-	31,8	-	-	0,00	-
Moraceae																	
Ficus luschnathiana (Miq.) Miq.	tree	forest	-	50	-	-	0,003	-	-	10	-	-	3897,4	-	-	0,02	-
Sorocea bonplandii (Baill.) W.C. Burger, Lanj. & Wess. Boer	tree	forest	-	1050	-	-	0,021	-	-	5	-	-	62,9	-	-	0,00	-
Myrtaceae																	
Blepharocalyx salicifolius (Kunth) O. Berg	tree	edge	-	75	325	-	0,003	0,015	-	20	-	-	347,4	-	-	0,01	-
Calyptranthes concinna DC.	tree	forest	-	250	75	-	0,009	0,005	-	-	-	-	-	-	-	-	-
Campomanesia rhombea O. Berg	tree	forest	-	400	100	-	0,012	0,005	-	5	-	-	346,6	-	-	0,00	-

Appendix 2 continued

Family/Species	Growth form	Habitat	Lower Stratum						Upper Stratum								
			GD	FD	PD	G IVI	F IVI	P IVI	GD	FD	PD	GBA	FBA	PBA	G IVI	F IVI	P IVI
Campomanesia xanthocarpa Mart. ex O. Berg	tree	forest	-	-	50	-	-	0,003	-	-	-	-	-	-	-	-	-
Eugenia hiemalis Cambess.	tree	edge	50	2800	450	0,003	0,049	0,017	-	20	-	-	140,4	-	-	0,01	-
Eugenia pyriformis Cambess.	tree	forest	-	-	25	-	-	0,002	-	-	-	-	-	-	-	-	-
Eugenia uniflora L.	tree	forest, grassland	-	125	1025	-	0,006	0,021	-	-	10	-	-	63,7	-	-	0,01
Eugenia verticillata (Velloso) Angely	treelet	edge	-	650	-	-	0,017	-	-	10	-	-	159,2	-	-	0,01	-
Myrcia glabra (O. Berg) D. Legrand	tree	edge	-	1575	650	-	0,036	0,020	-	25	-	-	1126,0	-	-	0,02	-
Myrcia multiflora (Lam.) DC.	tree	edge	400	1425	1250	0,013	0,032	0,029	-	10	-	-	386,0	-	-	0,01	-
Myrcia oblongata DC.	tree	forest	-	-	1700	-	-	0,025	-	-	-	-	-	-	-	-	-
Myrcia palustris DC.	tree	edge, grassland	175	175	125	0,008	0,008	0,007	30	15	-	1443,6	141,0	-	0,06	0,01	-
Myrcianthes gigantea (D. Legrand) D. Legrand	tree	forest	-	200	50	-	0,005	0,003	-	15	-	-	1241,9	-	-	0,01	-
Myrcianthes pungens (O. Berg) D. Legrand	tree	forest	-	-	200	-	-	0,010	-	-	-	-	-	-	-	-	-
Psidium cattleyanum Sabine	tree	forest	-	100	1300	-	0,002	0,031	-	-	280	-	-	2347,6	-	-	0,20
Psidium salutare (Kunth) O. Berg	subshrub	grassland	300	-	-	0,008	-	-	-	-	-	-	-	-	-	-	-
Onagraceae																	
Ludwigia elegans (Cambess.) H. Hara	subshrub	grassland	550	-	-	0,008	-	-	-	-	-	-	-	-	-	-	-
Piperaceae																	
Piper aduncum L.	shrub	forest	-	4400	-	-	0,050	-	-	-	-	-	-	-	-	-	-
Primulaceae																	
Myrsine coriacea (Sw.) R. Br. ex Roem. & Schult.	tree	forest	5100	450	7075	0,086	0,015	0,107	105	35	30	13059,3	675,8	680,4	0,29	0,02	0,03
Myrsine lorentziana (Mez) Arechav.	tree	forest	-	-	-	-	-	-	-	15	-	-	298,7	-	-	0,01	-
Myrsine umbellata Mart.	tree	edge	-	500	125	-	0,018	0,006	-	15	-	-	920,2	-	-	0,01	-
Rosaceae																	
Eriobotrya japonica (Thunb.) Lindl.	tree	forest	-	-	25	-	-	0,002	-	-	-	-	-	-	-	-	-

Appendix 2 continued

Family/Species	Growth form	Habitat	Lower Stratum						Upper Stratum								
			GD	FD	PD	G IVI	F IVI	P IVI	GD	FD	PD	GBA	FBA	PBA	G IVI	F IVI	P IVI
Prunus myrtifolia (L.) Urb.	tree	forest	75	250	3450	0,005	0,011	0,057	-	75	30	-	2269,2	1513,4	-	0,03	0,04
Rubiaceae																	
Faramea montevidensis (Cham. & Schltdl.) DC.	treelet	forest	-	8125	425	-	0,095	0,009	-	15	-	-	65,1	-	-	0,01	-
Guettarda uruguensis Cham. & Schltdl.	tree	forest	25	50	-	0,002	0,003	-	-	-	-	-	-	-	-	-	-
Psychotria carthagenensis Jacq.	shrub	forest	-	3525	2925	-	0,055	0,047	-	-	-	-	-	-	-	-	-
Psychotria leiocarpa Cham. & Schltdl.	shrub	forest	-	5250	1500	-	0,067	0,029	-	-	-	-	-	-	-	-	-
Psychotria suterella Müll. Arg.	treelet	forest	-	175	-	-	0,006	-	-	-	-	-	-	-	-	-	-
Rudgea parquioides suspb. parquioides Müll. Arg.	shrub	forest	-	175	-	-	0,007	-	-	-	-	-	-	-	-	-	-
Rutaceae																	
Zanthoxylum fagara (L.) Sarg.	tree	edge	-	50	25	-	0,002	0,002	-	45	5	-	1339,6	53,8	-	0,02	0,01
Zanthoxylum rhoifolium Lam.	tree	forest	175	150	500	0,015	0,007	0,022	25	55	15	3424,2	1479,9	173,2	0,11	0,03	0,01
Salicaceae																	
Banara parviflora (A. Gray) Benth.	tree	forest	-	50	-	-	0,002	-	-	5	-	-	71,6	-	-	0,00	-
Casearia decandra Jacq.	tree	forest	-	175	-	-	0,008	-	-	10	-	-	135,3	-	-	0,01	-
Casearia sylvestris Sw.	tree	forest	50	225	400	0,003	0,009	0,015	-	130	-	-	5164,3	-	-	0,07	-
Xylosma tweediana (Clos) Eichler	tree	forest	-	25	-	-	0,001	-	-	-	-	-	-	-	-	-	-
Sapindaceae																	
Allophylus edulis (A. St.-Hil., A. Juss. & Cambess.) Hieron. ex Niederl.	tree	edge	-	1175	900	-	0,027	0,021	-	170	15	-	4062,0	259,1	-	0,07	0,02
Cupania vernalis Cambess.	tree	forest	-	1000	25	-	0,027	0,002	-	15	-	-	500,7	-	-	0,01	-
Matayba elaeagnoides Radlk.	tree	forest	25	375	50	0,002	0,015	0,002	-	10	5	-	252,7	21,7	-	0,00	0,01

Appendix 2 continued

Family/Species	Growth form	Habitat	Lower Stratum						Upper Stratum								
			GD	FD	PD	G IVI	F IVI	P IVI	GD	FD	PD	GBA	FBA	PBA	G IVI	F IVI	P IVI
Matayba guianensis	tree	forest	-	-	25	-	-	0,002	-	-	-	-	-	-	-	-	-
Sapotaceae																	
Chrysophyllum marginatum (Hook. & Arn.) Radlk.	tree	forest	-	150	125	-	0,007	0,007	-	35	-	-	1221,4	-	-	0,02	-
Scrophulariaceae																	
cf. *Buddleja thyrsoides* Lam.	shrub	grassland	275	-	-	0,005	-	-	-	-	-	-	-	-	-	-	-
Solanaceae																	
Cestrum intermedium Sendtn.	tree	forest	-	125	50	-	0,004	0,003	-	-	-	-	-	-	-	-	-
Cestrum strigillatum Ruiz & Pav.	tree	forest	-	25	1675	-	0,001	0,029	-	-	-	-	-	-	-	-	-
Solanum mauritianum Scop.	tree	edge	75	-	25	0,005	-	0,002	5	-	-	226,9	-	-	0,03	-	-
Solanum pseudocapsicum L.	subshrub	grassland	725	-	150	0,021	-	0,007	-	-	-	-	-	-	-	-	-
Styracaceae																	
Styrax leprosus Hook. & Arn.	tree	forest	50	100	250	0,005	0,004	0,011	-	-	-	-	-	-	-	-	-
Symplocaceae																	
Symplocos uniflora (Pohl) Benth.	tree	grassland	-	-	25	-	-	0,002	-	-	5	-	-	0,0	-	-	0,01
Thymelaeaceae																	
Daphnopsis racemosa Griseb.	treelet	forest	50	650	975	0,003	0,020	0,023	-	-	-	-	-	-	-	-	-
Verbenaceae																	
Lantana camara L.	shrub	edge	825	-	350	0,028	-	0,008	-	-	-	-	-	-	-	-	-
NI 1			-	-	25	-	-	0,002	-	-	-	-	-	-	-	-	-
NI 2			-	25	-	-	0,001	-	-	-	-	-	-	-	-	-	-