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Análise do componente regenerativo e atributos funcionais do sub bosque de plantios arbóreos antigos

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SUMÁRIO

Resumo

A fragmentação e a redução das Florestas naturais vem ocorrendo em muitas partes do mundo. Enquanto isso, as plantações de árvores para fins de silvicultura aumentam em extensão, muitas vezes substituindo áreas anteriormente cobertas pela vegetação natural. Considerando a situação florestal atual, as tentativas de aumentar a cobertura florestal natural são metas importantes no mundo todo. Este trabalho tem como principais objetivos: Avaliar a estrutura arbórea e regenerativa em monoculturas de espécies arbóreas (sem manejo) e áreas nativas. Avaliar a semelhança da regeneração nativa com as áreas de plantio. Estimar a influência de fatores ambientais sobre a regeneração de espécies nativas. Descrever a estrutura funcional do componente arbóreo adulto e regenerativo. Avaliar a diferenciação dos atributos funcionais entre as áreas e a influência dos fatores ambientais sobre esta variação. Este estudo foi realizado na Floresta Nacional de Passo Fundo, localizada no município de Mato Castelhano, Rio Grande do Sul, Brasil. Para tanto, foram selecionadas aleatoriamente cinco unidades amostrais para cada área. Dentro de cada uma das unidades amostrais foram demarcadas 10 subunidades para o levantamento do componente arbóreo adulto e regenerativo. O levantamento da vegetação mostrou que, além das áreas de Floresta Nativa, os plantios apresentaram um recrutamento de espécies tanto em fase regenerativa quanto adulta. No entanto, os plantios, no decorrer do tempo, causaram diferenças nas características do solo. Isto implicou em diferenças notáveis em termos de composição. Apesar destas diferenças, o estabelecimento de espécies nas áreas de plantio foi abundante, apresentando diversas famílias ocorrentes na Floresta Nativa. O componente adulto apresentou diferenças significativas para os traits entre as comunidades, enquanto o regenerativo apresentou apenas pequenas diferenças. A análise RLQ demonstrou a separação das áreas para ambos os componentes indicando diferenças na composição específica, funcional, edáfica e de incidência de luz. Nosso estudo mostra que devido ao componente regenerativo bem desenvolvido das áreas de plantios é possível a transformação dessas áreas em florestas naturais. Também podemos concluir que a ação das plantações como filtros ambientais influenciam diretamente o recrutamento e a riqueza de espécies assim como a diversidade funcional.

Palavras chave: regeneração; plantios antigos; atributos funcionais; filtros ambientais

1. INTRODUÇÃO GERAL

1.1 A Floresta com Araucária

A floresta com Araucária, também conhecida como Floresta Ombrófila Mista, é uma vegetação característica da Região Sul do Brasil. Seu estado de conservação é crítico e é representado por 1% de sua cobertura original (Medeiros et al. 2005). Originalmente este tipo florestal ocupava uma área de 919.565 ha, levando em conta todos os seus estádios de sucessão (Rio Grande do Sul, 2007).

A Floresta Ombrófila Mista tem a espécie *Araucaria angustifolia* como emergente e dominante do dossel, exibindo grande porcentagem de seus indivíduos no estrato superior (Leite e Klein, 1990). Muitas vezes esse tipo florestal apresenta uma característica continua de cobertura dando a impressão de se tratar de uma formação uniestratificada. Porém, nos estratos inferiores ao dossel formado pelas copas das *Araucarias* encontram-se uma infinidade de outras espécies que variam em termos de riqueza e abundância conforme o local onde está inserida e o estádio sussecional da comunidade florestal (Klein, 1960).

No Rio Grande do Sul a exploração dos recursos florestais em todas as formações, tem ocorrido, sem preocupações com a conservação e a sustentabilidade dos ecossistemas desde o início da colonização (Hueck, 1972). Os remanescentes da Floresta com *Araucaria* encontram-se, em muitos casos, muito alterados e estão em delicada situação de conservação (Rizzini, 1976). Os fragmentos atuais que possuem uma representatividade adequada são escassos, devido à alta fragmentação apresentada. Entre os fatores responsáveis pela fragmentação deste tipo florestal estão o extrativismo madeireiro, a ampliação das fronteiras e a colonização para fins agrícolas e pecuários (Sanqueta & Mattel, 2006). Jarenkow & Budke (2009), ressaltam que o estabelecimento de grandes empreendimentos energéticos e viários são fatores que ameaçam constantemente a integridade das florestas com araucária. Outro fator relevante para a mudança drástica da paisagem na Floresta Ombrófila Mista, são os plantios de espécies exóticas, como por exemplo, as do gênero *Pinus*. Em meados dos anos 70 estas espécies começaram a ser implantadas e gradativamente foram substituindo as espécies nativas, tornando as florestas nativas altamente degradadas e fragmentadas (Reis *et al*., 2007). Estes plantios ocupam extensas áreas, podendo até mesmo serem encontrados atualmente em Unidades de Conservação (UC). Nestas áreas os plantios estão abandonados, como é o caso da Floresta Nacional de Passo Fundo (FLONA de Passo Fundo), localizada em Mato Castelhano, RS. Nesta UC, 278 hectares (o que corresponde a cerca de 20% da área total da FLONA) são cobertos por plantios de *Pinus spp.* atualmente sem manejo e sujeitos a processos de sucessão natural. De modo semelhante, plantios com a própria *Araucaria angustifolia* ocupam consideráveis extensões desta área.

1.2 A Floresta Nacional de Passo Fundo

A Floresta Nacional de Passo Fundo teve seu início em 1946 com a compra de suas terras e então passou a ser vinculada ao extinto Instituto Nacional do Pinho. Esta Unidade de Conservação localiza-se ao norte do estado do Rio Grande do Sul no município de Mato Castelhano, entre as coordenadas 28°16'44'' e 28°20'40'' de latitude sul e 52°09'59'' e 52°12'35'' de longitude oeste. Esta UC foi criada em 25 de outubro de 1968, pela portaria 561 e atualmente é administrada pelo Instituto Chico Mendes de Conservação da Biodiversidade. Sua área é de 1358 ha, apresentando 365,4 ha de floresta nativa, 391,0 ha de plantio de *Araucaria angustifolia*, 278,0 ha de plantio de *Pinus* spp., 7,4 ha de plantio de *Eucalyptus* spp. e 323,6 ha ocupados por estradas, aceiros, capoeiras e açudes (IBAMA, 2008).

As Florestas Nacionais (FLONAS) apresentam como objetivo "o uso múltiplo sustentável dos recursos florestais e a pesquisa científica". Na medida em que venham a ocorrer articulações entre estas, as populações do entorno e as instituições de pesquisa e ensino, torna-se possível a geração de novos conhecimentos científicos e tecnológicos visando a construção gradativa de cadeias produtivas, por meio de arranjos locais que incluam os agricultores familiares que gerem renda e sejam capazes de contribuir para a melhoria da qualidade de vida das famílias ali existentes e da própria conservação dos recursos florestais (Brasil, 2000). As unidades de conservação assumem um papel fundamental na conservação dos ecossistemas, porém, no Brasil, a composição e a magnitude da biodiversidade nas áreas protegidas são pouco conhecidas (Hamilton, 2004). Na Floresta Nacional de Passo Fundo, as áreas de plantio (*Pinus spp.*, *Eucalyptus spp.* e *Araucaria angustifolia*) apresentam um alto potencial de regeneração de espécies nativas, tornando estudos que visem à conservação deste tipo florestal de extrema importância, uma vez que estas áreas podem tornar a se desenvolver em comunidades vegetais semelhantes às florestas nativas e auxiliando no manejo das UC's.

1.3 Monoculturas de espécies lenhosas

Os plantios, especialmente no caso de monoculturas de espécies exóticas, representam fisionomias florestais fortemente alteradas em comparação com a Floresta Nativa, isso significa perda de diversidade nativa e de habitat para a fauna. Devido a sua proximidade com fragmentos de floresta nativa, os plantios podem, por outro lado, apresentar um potencial importante para a regeneração e\ou restauração da FOM, principalmente em Unidades de Conservação, estas, de fundamental importância para a conservação de ecossistemas. Contudo, não se sabe ainda até que ponto é possível transformar plantios de espécies exóticas ou nativas em fisionomias naturais e quais técnicas e qual manejo seriam mais adequados para alcançar tal objetivo. Tem se observado em muitas plantações de *Pinus spp.* a formação de um sub-bosque nativo estabelecido a partir da regeneração natural. O estabelecimento de espécies nativas pode estar ligado à dispersão de espécies presentes em vegetação alóctone ou ao banco de sementes presente nas áreas plantadas (Aubert & Oliveira-Filho, 1994).

1.4 O componente regenerativo

A regeneração de espécies de uma área perturbada emana da interação de processos naturais de reestabelecimento de espécies em decorrência de suas características funcionais e ecológicas. O estudo desse componente nos permite a visualização de estratégias sobre o comportamento e desenvolvimento futuro da floresta, em decorrência das características específicas da área (Carvalho, 1982).

A avaliação do potencial regenerativo de um ecossistema deve inferir sobre processos que visem à manutenção da comunidade vegetal e descrever padrões de substituição de espécies ou de alterações estruturais (Guariguata & Ostertag, 2001). A regeneração de áreas naturais garante a manutenção de comunidades vegetais, pela manutenção do banco e da chuva de sementes, além da rebrota de indivíduos adultos (Harper, 1977). Os processos relacionados à dinâmica, sucessão ecológica e regeneração natural são de caráter imprescindível mediante as perturbações antrópicas (Pereira et al., 2001).

1.5 Atributos funcionais das espécies

A estrutura funcional de uma comunidade é representada pelo conjunto de atributos funcionais das espécies (Naeen & Bunker, 2009; Solbrig, 1994). Estas características de acordo com Cornelissen et al., 2003, podem ser morfológicas, fisiológicas ou estruturais. A avaliação dos padrões de uma comunidade pode ser avaliada tanto pela riqueza e abundância das espécies como pelos seus atributos funcionais (Weiher et al., 1998; Hooper et al., 2005). A avaliação de comunidades vegetais utilizando a composição específica pode nos conduzir a conclusões limitadas devido a ampla variação de espécies ao longo do gradiente fitogeográfico (Díaz et al. 2004).

As características funcionais da comunidade influenciam as propriedades e os processos ecossistêmicos (Petchey & Gaston 2006). Segundo Loreau et al., 2001 o aumento das características funcionais (diversidade funcional) dentro de uma comunidade está intimamente ligada com a estabilidade do ecossistema. A variação na estratégia ecológica das plantas determina quais os tipos de atributos funcionais apresentam vantagens em diferentes condições ambientais (Westoby & Wright, 2006). Quanto mais diversos forem os atributos presentes em uma comunidade, espera-se um aumento na eficiência da produtividade e na utilização de recursos (Díaz & Cabido, 2001).

As diferentes estratégias de crescimento das espécies estão relacionadas com um trade-off conhecido como espectro da economia da folha. Esta estratégia está ligada com o potencial de aquisição e conservação de recursos (Wright et al, 2004). Por exemplo, o aumento da massa foliar específica (SLA) e um baixo teor de matéria seca (LDMC) está relacionado com o crescimento rápido e o aumento da capacidade fotossintética. Por outro lado, um menor SLA e maior LDMC indicam a capacidade da planta lidar com poucos recursos ambientais, ocorrendo o crescimento mais lento e um aumento na vida útil da folha (Polley et al., 2013).

1.6 Objetivos deste trabalho

Neste contexto, o presente estudo buscou avaliar a estrutura do componente arbóreo adulto e regenerativo na floresta nativa e em plantios abandonados na Floresta Nacional de Passo Fundo, Rio Grande do Sul, Brasil, e, especificamente:

- Avaliar a composição taxonômica e funcional das três fisionomias estudadas;
- Avaliar o estabelecimento de espécies exóticas / invasoras nas áreas de estudo;
- Analisar quais fatores ambientais mais influenciam na regeneração das espécies nativas;
- Inferir se a estrutura funcional entre as áreas apresentam diferenças e se elas são explicadas pelos fatores ambientais.
- Avaliar se o recrutamento de indivíduos nos plantios fornece um potencial de transformação das plantações em áreas similares à floresta natural.

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Distinct tree regeneration patterns in *Araucaria* forest and old monoculture tree plantations.

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Abstract

Distinct tree regeneration patterns in *Araucaria* forest and old monoculture tree plantations. Throughout the world, plantations of tree species (native and exotic) for production purposes make up an important part of tree cover, often at the expense of natural forests. Monocultures of exotic and native species generally show a very distinct vegetation physiognomy when compared to natural forests. In the case of abandoned plantations, existing tree regeneration may provide a high potential for restoration of these areas. In this study, we evaluated composition and structure of the adult (upper layer) and regenerative (lower layer) tree component of natural *Araucaria* forest and of monoculture plantations of *Araucaria angustifolia* and *Pinus sp*., and their relationship with edaphic variables and sunshade discontinuity. We aimed to answer the following questions: To which extent do regeneration patterns of native species in the plantations resemble those in natural forests? Does natural regeneration provide a potential for transformation of plantations into natural forests? Does the exotic species regenerate in high abundances, and do other exotic/invasive species establish? Which environmental factors influence regeneration of native species? We expected to find differences in the species composition of the planted areas in relation to the native forest, and more pronounced in the regenerative component. Therefore, the soil parameters and the canopy discontinuity should also be distinct in the distinct vegetation formations. Density of species and tree individuals of the regenerative layer was significantly lower in the plantations, especially in the pine plantation, at the plot level. However, overall species richness was quite similar between vegetation types, with a total of 98 species distributed into 38 families. While light availability did not differ significantly, the soil parameters organic matter, pH, phosphorus and potassium showed significant differences among the vegetation types (in general, lower fertility in plantations). These variables were related to the specific

composition of areas, indicating influence of the vegetation on soil conditions and regeneration patterns. Overall, we conclude that restoration of plantations into natural forest based on the existing forest regeneration seems possible, but should be done with caution and under monitoring.

Keywords:

Araucaria angustifolia, Forest Dynamics, *Pinus sp*., Restoration, Succession

1 Introduction

While natural forests are being reduced and fragmented in many parts of the world, tree plantations increase in extent, many times replacing areas previously covered by natural vegetation. The main driver of the expansion of tree plantations is the high demand for wood, cellulose and other products. Planted forests differ considerably from natural forests, and this is especially true for plantations that are composed of a single species, in single-aged stands and under continuous management (Lee et al. 2005, Nations 2007, Reis et al. 2007). Although tree plantations provide vegetation cover and contribute to wood production, the diversity of species is generally reduced, even though there may be exceptions, often depending on the landscape context (Brockerhoff et al. 2008). However, little is known about the processes of natural regeneration of other tree species in plantation areas over time (Aubin, et al. 2008), for example in the case of abandonment.

Increased cover of natural forests is an important goal of environmental policy, both considering biodiversity and carbon stocks (Aide et al. 2012), including in Brazil. For the transformation of plantation areas into more natural forest, two main strategies exist: clear-cutting of plantation and subsequent restoration through plantation of native species, or gradual withdrawal of planted species via girdling or cutting. Often, clear-cutting even of stands of exotic species is not indicated as a first step of restoration of these areas, because, besides the severe impacts to the environment by clear-cutting itself, it demands great costs and delays the reestablishment of the forest (Ramula et al. 2008; Holmes et al. 2008, Dechoum 2010, Brown et al. 2015).

Natural regeneration of the tree species present in a given area is often a feasible way towards forest recovery (Lee et al. 2005). Identifying the best way of how to conduct the tree community towards natural or near-natural conditions will depend on our understanding of recruitment patterns and their dependence on the interaction of plants of a given species with their environment. Production and dispersal of seeds, light availability, edaphic conditions and subsequent establishment and survival of species are processes that contribute to the maintenance of the plant community and influence replacement patterns of species or structural changes in general (Harms et al. 2000, Denslow & Guzman 2000, Scariot 2000, Guariguata & Ostertag 2001).

Araucaria forest is one of the forest formations of the southern part of the Atlantic Forest domain (Oliveira-Filho et al. 2013). This forest type occurs within a climatically clearly restricted region in the highlands of southern Brazil, with a small extension to southeastern Brazil. Anthropogenic activities, especially deforestation for expansion of agricultural purposes (Sanqueta & Mattel 2006), have reduced this formation to sparse fragments, where they often are altered in terms of structure and composition. Especially populations of *Araucaria angustifolia* (Bertol.) Kuntze itself, the conifer that determines the physiognomy of this mixed conifer-hardwood forest, have been reduced due to (past) selective logging and collection of seeds (Souza 2007). Studies that provide a basis for the conservation of this forest type are necessary (FUPEF-CNPQ 2001). Today, only 2,8 % of the area originally covered by *Araucaria* Forest remains (Fundação SOS Mata Atlântica/INPE 2001). In this situation, the transformation of tree plantations into natural forest is an opportunity to contribute to the conservation of this forest type. Brazil's

National Forests, a protected area category where sustainable use of forest resources as well as scientific research are expressed conservation aims, are appropriates sites to study how to achieve transformations of plantations into natural forests and then how to manage forests in a way that is compatible to conservation goals. In many National Forests, plantations of native and (mostly) exotic species had been established in the past, changing forest composition and many aspects of natural forest dynamics. Studies are needed to provide the scientific bases to be able to transform these areas into forests that are more similar to natural.

Here, we aimed to answer the following questions: To which extent do regeneration patterns of native species in the plantations resemble those in natural forests? Does natural regeneration provide a potential for transformation of plantations into natural forests? Does the planted exotic species regenerate in high abundances, and do other exotic/invasive species establish? Which environmental factors influence regeneration of native species? We answer these questions by help of an analysis of the composition and structure of the adult tree stratum and of the regenerative layer in monoculture plantations of a native (*Araucaria angustifolia*) and an exotic (*Pinus sp.*) tree species in a National Forest in Southern Brazil. We hypothesized that the plantations – especially the exotic tree plantation – would have less regeneration than natural forest, and that plantations may have led to changes of soil features that may negatively influence natural regeneration.

2 Material and methods

2.1 Study area

The Passo Fundo National Forest (FLONA), is located in the north of Rio Grande do Sul state in the Mato Castelhano municipality (28°16’44’’ to 28°20’40’’ S and

52°09’59’’ to 52°12’35’’ W). The FLONA’s total area is 1358 ha, with 365.4 ha of natural forest (*Araucaria* Forest), 391.0 ha of *Araucaria angustifolia* plantation (in monoculture), 278.0 ha of *Pinus* spp. plantation (in monoculture), 7.4 ha of *Eucalyptus* spp. plantation, and 323.6 ha occupied by scrublands, roads and infrastructure, firebreaks and ponds (ICMBio 2014). The predominant type of soil in the area is podzolic dark red soil (IBGE 2003). The different forest types are found in a mosaic of different patches, distributed throughout the area. The remaining fragments of *Araucaria* forest are in a good conservation state, with typical species composition and high species richness (Malysz 2010). Plantations had been established 60 years ago, and management was abandoned about 30 years ago, allowing for the spontaneous recovery that we analyze here.

2.2 Vegetation survey

We randomly selected five stands of natural Araucaria forest, monoculture plantations of *Araucaria angustifolia* and monoculture plantations of *Pinus* sp., distributed throughout the total area of the FLONA. In each forest stand, we sampled the adult tree component in five 10 x 10 m plots (sampling units, SUs), and the regenerative component (lower stratum) in subplots of 5 x 5 m, included in the SU. The selected stands were randomly arranged in the study areas, based on a numbered grid over the areas. Minimum distances between stands was 100 m, and we additionally considered an edge of 60 m where no plots were allocated. Minimum distance between plots per stand was 30 m. The total area sampled was 1.875 ha (1.5 ha for the upper stratum, 0.375 ha for the lower stratum).

For sampling of the adult component within each SU, all alive tree individuals with a perimeter at breast height (PBH = 1.3 m above ground) ≥ 15 cm were sampled in order to determine the phytosociological parameters (upper layer). Within each of the sub-plots, all living individuals with height ≥ 30 cm and PBH < 15 cm were sampled (lower layer). Individuals that presented bifurcation were included in the sample when the sum of the PBH of stems corresponded to the minimum PBH adopted. All individuals recorded were identified to the species level and measured for height.

2.3 Edaphic variables

Soil samples were taken in 75 plots (ie, 50% of the total number of plots). Each sample was composed by five sub-samples, four taken at the corner and one in the center of the plot that were subsequently homogenized and sent to the Soil Laboratory at the Universidade Federal do Rio Grande do Sul (UFRGS), in Porto Alegre, for analysis of the following variables: clay percentage, pH, SMP, phosphorus, potassium, percentage of organic matter, aluminum, calcium, magnesium, cation exchange capacity, percent saturation of CEC and the following ratios: Ca / Mg; Ca / K; Mg / K. Analysis followed the lab's standard procedures presented in Tedesco et al. (1995). For soil collection, all litter was removed. The soil depth considered was 20 cm.

2.4 Analysis of canopy discontinuity

Light incidence in each plot was estimated using hemispherical photos taken by a digital camera Canon EF-S 18-55 with a hemispheric fisheye lens Raynox DCR-CF 187 PRO 185º, allowing for a picture with an angle of 185º. Canopy opening of each SU was analyzed using Gap Light Analyzer (version 2.0) software, calculating the percentage of sunshade opening from the photographs obtained in the plots (Frazer et al. 1999).

2.5 Data analysis

For the description of the vegetation structure, we calculated the parameters proposed by Mueller-Dombois & Ellenberg (1974): absolute density (AD), absolute frequency (AF) and absolute dominance (ADo), as well as the Importance Value Index

(IVI). In order to evaluate the effect of tree density on species richness, we also performed rarefaction test based on minimum number of species (Gotelli & Colwell 2001).

Structural differences among the three vegetation types were explored using PCA (Principal Component Analysis), performed separately for each stratum. The three vegetation types were compared with respect to variables describing vegetation structure, total composition, density and richness, separately for the adult and regenerative stratum as well as environmental variables by randomization testing, using Chord distance (for multivariate data) and Euclidean distance (for univariate data) and 10,000 iterations. The relationships between species composition data and environmental variables (edaphic variables and sunshade discontinuity) were analyzed using canonical correspondence analysis (CCA).

All analysis were performed using the data obtained in the SUs pooled to the level of forest stand (i.e. n = five for each of the three forest types). PCA, rarefaction and regressions were performed in the R platform (R Development Core Team 2012), while randomization tests were performed in the software MULTIV (Pillar 2006).

3 Results

In the survey, a total of 5906 individuals were recorded in 1.875 ha total area. These individuals were distributed in 98 species and 38 families. The family with the highest number of species was Myrtaceae (15 species), followed by Fabaceae (seven), Lauraceae (six) and Euphorbiaceae (five). While the density of individuals in the tree layer did not vary significantly among forest types, the number of individuals in the regenerative stratum was significantly higher (p <0.001; F = 7.9908) in natural forest, compared to both plantation types (Table 1). In *Araucaria* plantations, the number of individuals per sample unit was almost twice that of the *Pinus* plantation ($p = 0.001$; F = 4.3776). In natural forest, there were significantly more tree species per sample unit. The same pattern was evident for the regenerative component, where again the *Araucaria* plantation showed higher values than *Pinus* plantation (Table 1). The rarefaction of data based on the plot with the smallest species number indicated that species number in both plantings was lower than that of natural forests independent of number of individuals, for both components.

Table 1. Number of individuals (NI), species (NS), Shannon index (H) and basal area (BA), species number after rarefaction (RA) for the entire data set, separately for stratum, as well as number of individuals and species per sample unit (data for the lower stratum extrapolated to 100 m²). Different letters indicate significant differences ($p < 0.01$), analyzed separately for each stratum.

Vegetation Type	**NI**	**NS**	**H'**	**BA**	**RA**	**NI ($100m^2$)**	**NS ($100m^2$)**
Upper Layer							
Natural forest	639	62	3.397	27.969	20.632	12.7	7.2 a
Araucaria plantation	703	50	2.511	27.490	14.931	13.0	5.8 b
Pine plantation	563	48	2.874	26.361	16.056	10.8	5.5 b
Lower Layer							
Natural forest	2322	76	3.507	0.400	24.176	51.0 a	14.9 a
Araucaria plantation	1042	69	3.579	0.327	23.963	19.1 b	10.9 b
Pinus plantation	637	61	3.484	0.504	21.721	10.4 c	5.1 c

As expected, the planted species showed the highest IVI values in their respective plantings (Table 2). *Araucaria angustifolia* appeared with high IVI values in the regenerative component in the pine plantation, but not in the planting of the species itself. In the pine plantation, the alien species *Hovenia dulcis*, considered an invasive species in RS (SEMA 2013), appeared with the second largest IVI in the lower stratum.

Table 2. Phytosociological parameters of the ten main species (based on IVI) of each stratum in the different forest types. AD = Absolute Density; AF = Absolute Frequency; ADo = Absolute Dominance and IVI = Importance Value Index. A: Upper Stratum, B: Lower (regeneration) stratum.

A: Tree layer (upper layer)

	Native Forest				***Araucaria* plantation**				**Pine plantation**			
Espécies	**AD**	**AF**	**ADo**	**IVI**	**AD**	**AF**	**ADo**	**IVI**	**AD**	**AF**	**ADo**	**IVI**
Araucaria angustifolia (Bertol.) Kuntze	106.0	64.0	29.2	68.8	572.0	100.0	48.2	144.3	48.0	30.0	1.3	11.6
Allophylus edulis Niederl.	184.0	60.0	1.5	25.0	100.0	54.0	0.4	16.5	28.0	18.0	0.3	6.0
Nectandra megapotamica Mez	84.0	44.0	2.2	16.2	-	-	-	-	-	-	-	-
Matayba elaeagnoides Radlk.	78.0	38.0	2.9	16.2	64.0	34.0	0.7	11.2	46.0	28.0	0.4	9.5
Casearia decandra Jacq.	88.0	44.0	0.7	13.9	92.0	48.0	0.6	15.2	40.0	28.0	0.3	8.7
Ilex brevicuspis Reissek	48.0	30.0	3.1	13.3	-	-	-	-	-	-	-	-
Prunus myrtifolia (L.) Urb.	46.0	30.0	2.1	11.3	56.0	32.0	0.6	10.1	-	-	-	-
Parapiptadenia rigida (Benth.) Brenan	40.0	24.0	1.7	9.3	-	-	-	-	26.0	18.0	0.1	5.6
Ocotea pulchella Mart.	30.0	22.0	1.9	8.7	-	-	-	-	-	-	-	-
Ocotea diospyrifolia (Meisn.) Mez	36.0	28.0	1.1	8.5	-	-	-	-	-	-	-	-
Casearia sylvestris Sw.	-	-	-	-	82.0	50.0	0.5	14.7	92.0	58.0	0.9	19.4

Ilex paraguariensis A.St.-Hil.	-	-	-	-	88.0	42.0	0.7	14.2	40.0	20.0	0.3	7.5
Cupania vernalis Cambess.	-	-	-	-	60.0	40.0	0.3	11.2	130.0	62.0	0.9	23.5
Dicksonia sellowiana (Pr.) Hook	-	-	-	-	26.0	16.0	0.6	5.6	-	-	-	-
Cinnamodendron dinisii Schwacke	-	-	-	-	26.0	16.0	0.1	4.6	-	-	-	-
Pinus sp	-	-	-	-	-	-	-	-	324.0	100.0	44.8	130.3
Campomanesia xanthocarpa O.Berg	-	-	-	-	-	-	-	-	46.0	26.0	0.3	9.0

B: Regeneration layer (lower layer)

	Native forest				*Araucaria* plantation				Pine plantation			
Cupania vernalis Cambess.	1504.0	80.0	0.3	22.4	752.0	66.0	0.3	24.3	680.0	50.0	1.4	55.4
Allophylus guaraniticus Radlk.	1224.0	64.0	0.3	19.8	-	-	-	-	-	-	-	-
Nectandra megapotamica Mez	1704.0	68.0	0.1	17.8	-	-	-	-	-	-	-	-
Trichilia elegans A.Juss.	1360.0	64.0	0.2	17.4	-	-	-	-	-	-	-	-
Maytenus dasyclada Mart.	1176.0	78.0	0.2	16.1	-	-	-	-	-	-	-	-
Parapiptadenia rigida (Benth.) Brenan	1176.0	58.0	0.2	15.1	-	-	-	-	200.0	20.0	0.1	9.3
Allophylus edulis Niederl.	712.0	68.0	0.2	14.1	328.0	54.0	0.2	16.24	160.0	24.0	0.08	8.81
Dalbergia frutescens (Vell.) Britton	920.0	76.0	0.1	11.9	-	-	-	-	-	-	-	-
Matayba elaeagnoides Radlk.	856.0	66.0	0.1	10.5	384.0	56.0	0.08	12.18	-	-	-	-
Ocotea diospirifolia (Meisn.) Mez	368.0	34.0	0.1	8.5	-	-	-	-	192.0	20.0	0.03	8.88
Casearia sylvestris Sw.	-	-	-	-	528.0	66.0	0.2	19.5	264.0	32.0	0.1	13.0
Dicksonia sellowiana (Pr.) Hook	-	-	-	-	72.0	8.0	0.4	16.9	-	-	-	-
Myrsine umbellata Mart.	-	-	-	-	504.0	54.0	0.1	15.4	-	-	-	-
Ilex paraguariensis A.St.-Hil.	-	-	-	-	384.0	48.0	0.2	14.3	-	-	-	-
Casearia decandra Jacq.	-	-	-	-	416.0	50.0	0.1	14.1	-	-	-	-

Myrciaria delicatula (DC.) O.Berg	-	-	-	-	448.0	48.0	0.05	11.3	-	-	-	-
Ilex brevicuspis Reissek	-	-	-	-	360.0	50.0	0.07	11.08	168.0	24.0	0.1	8.6
Hovenia dulcis Thunb.	-	-	-	-	-	-	-	-	56.0	4.0	0.7	19.3
Ocotea puberula Ness	-	-	-	-	-	-	-	-	504.0	48.0	0.01	17.74
Araucaria angustifolia (Bertol.) Kuntze	-	-	-	-	-	-	-	-	40.0	8.0	0.6	17.4
Eugenia pyriformis Cambess. in A.St.-Hil.	-	-	-	-	-	-	-	-	216.0	24.0	0.03	8.88

The ordination of forest stands using data of the adult component indicated a clear separation of the three forest types (Fig. 1a). The first two PCA axes (33.5% and 19.1%, respectively) indicate that this pattern was driven mostly by the abundance of *Araucaria angustifolia* and *Pinus sp*. For the regenerative component, pine plantations were separated from the other two forest types along the first axis (42,5% and 9,9% for the first two axes) (Fig. 1b).

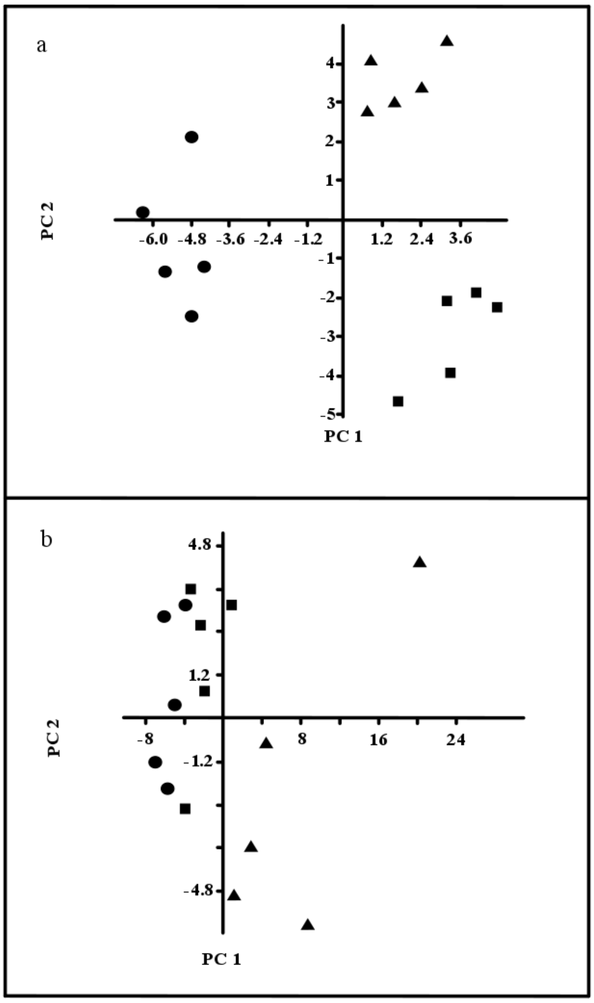

Figure 1 - Ordination diagram (PCA) of stands based on (a) the upper layer and (b) the lower layer. ■ = *Araucaria* plantation; ▲ = Natural Forest; ● = *Pinus* Plantation.

Light availability and number of canopy (upper layer) trees did not differ between native forest and the plantings (Table 3). Clay content of soil showed no significant differences between the vegetation types. Potassium and Phosphorus were significant higher in the natural forest in comparison to the plantations, with significantly higher Phosphorus content in the *Araucaria* plantation than in the Pine plantation. Soil Organic Matter was significantly lower in the pine plantation. In the *Araucaria* planting, soil pH was slightly, but significantly, higher than in the other two vegetation types.

Table 3. Key environmental variables in three vegetation types. Different letters indicate significant differences between vegetation types (ANOVA with randomization test, Euclidean distance, 10,000 iterations).

Vegetation type	Clay (%)	pH	P mg/dm3	K mg/dm3	Soil Organic Matter (%)	Light availability (%)	Number of canopy trees
Native Forest	100.6	4.4 b	4.8 a	100.6 a	6.4 a	18.3	18.0
Araucaria plantation	72.4	4.6 a	4.0 a b	72.4 b	6.4 a	19.3	19.3
Pinus plantation	74.4	4.4 b	3.5 c	74.4 b	4.8 b	21.1	21.1

For variables that showed significant differences between treatments, canonical correlations analysis was performed to determine the influence of environmental factors on the composition of each component (upper and regenerative layer). Five variables had significant relationships when related to the adult tree component: Aluminum, clay percentage, potassium, base saturation and potassium calcium ratio. As for the regenerative tree component, the variables base saturation, potassium/calcium ratio and Aluminum were significantly related to the species composition.

The canonical correspondence analysis (CCA) using adult component data indicated different relations between the three types of forest. Native forest was related to a higher concentration of potassium in the soil, and *Araucaria* plantings to soils with a higher concentration of bases and a higher calcium / potassium ratio. Pine plantings, on the other hand showed a relation to more acid soils (Figure 2a). For data from the regenerative component, the areas of native forest were related to the concentration of potassium in the soil, with the most well conserved forest stand being an outlier and related to the other parameters (Figure 2b).

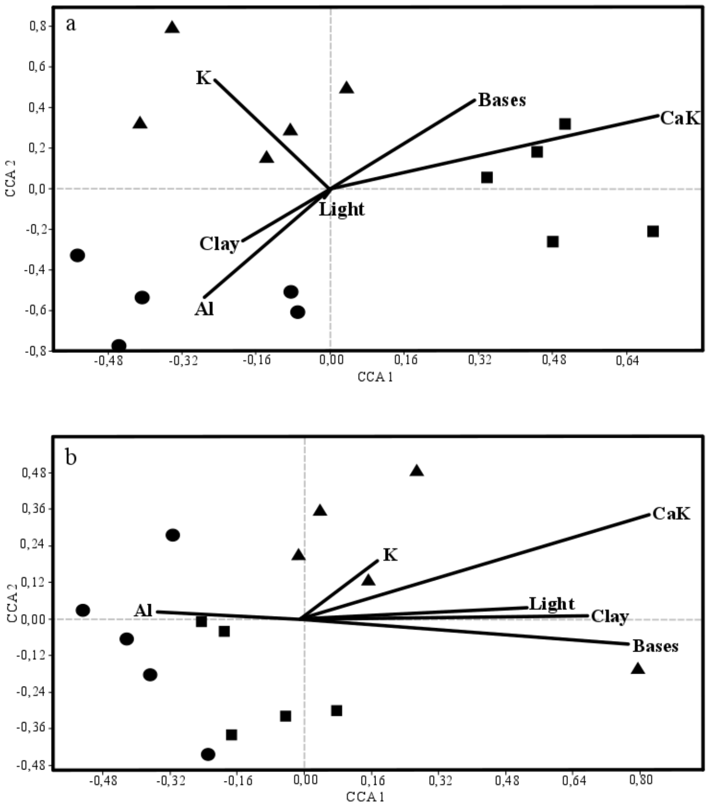

Figure 2 – CCA diagram of stands based on based on (a) the upper layer and (b) the lower layer. ■ = *Araucaria* plantation; ▲ = Natural Forest; ● = *Pinus* Plantation. Two plots (*Araucaria* Plantation).

4 Discussion

Even though the natural forests presented higher tree species richness, a number of native species could be found in the regenerative stratum of the two plantation areas

(Table 1). In both types of plantings, an understory layer of spontaneously recruiting species was formed, and they also included adult trees in reproductive stage. Monoculture plantations obviously differ from natural forest in physiognomic terms. Even so, the light availability in the understory layer did not differ significantly between the forests types analyzed in our study. However, pine plantation showed a trend towards a higher light input than in the other areas, in consequence of the cone-like shape of the tree crowns and the rare overlapping of their crows. Light incidence in the *Araucaria* plantation was slightly higher than in the natural forest, probably due to the fact that individuals of *A. angustifolia* in the plantation were smaller due to the high density of individuals and that thus less overlap between crowns existed than in a natural forest with species with different crown forms and height. Parrotta (1995), in a study on the natural regeneration in plantations, points light availability out as an important factor for on the establishment of the regenerative component. In our case, no severe limitation regarding this factor seems to exist.

However, the 60 years of plantation apparently have caused some strong differences in soil characteristics. The natural forest had higher potassium and phosphorus values than the plantations, and the organic matter content in the top-soil in the pine plantation was around 25% lower than in the other areas. Our result agrees with other studies that indicate differences both in physical end chemical soil parameters between pine plantations and natural forests (Kiehl 1979, Corrêa & Melo 1998, Rodrigues et al. 2006), and especially lower soil fertility under pine plantations (e.g. Scholes & Nowicki 1998).

After a period around 30 years without any management, both plantation types showed a well-developed natural undergrowth, despite the differences in edaphic factors found, and with a high total number of species in both cases, including *Araucaria* *angustifolia* and species of the Myrtaceae and Lauraceae, which are important families of *Araucaria* forests. On the stand level, however, values both for number of individuals and species were strikingly lower, even though species such as *Araucaria angustifolia* and *Campomanesia xanthocarpa*, both characteristic of forests in advanced successional stage, occurred. Pine individuals were rarely observed in the regenerative stage, both in the areas of *Pinus* plantation, as in other physiognomies studied, likely in consequence of the pioneer character of the species that makes its establishment in dense vegetation harder.

The plantations of *Araucaria angustifolia*, even with a high density of planted individuals (572 individuals/ha), showed an overall species richness similar to areas of natural forest, despite the lower numbers on the stand level, which indicates the natural regeneration potential of these areas. However, in *Pinus* plantation, *Hovenia dulcis*, indicative of degraded sites, was the second-most important species in terms of IVI. The presence of *Araucaria* itself, in both strata, likely is the result of the pioneer character of the species (Klein 1960, Rambo 1960, Backes 1988), which allowed for its establishment probably in the early stages of the plantation. Differences in terms of species density and number of individual trees on the plot level were highly significant for the lower stratum, with the largest contrast between natural forest and the pine plantation. Additionally, fewer species managed to reach the upper layer in the two types of plantings. Dominant species also clearly different among vegetation physiognomies, for both strata. The fact that number of species in the regeneration layer differed significantly and considerably (up to five-fold) between the three community types, but that basal area did not, indicates, nonetheless, clear differences in recruitment processes and community structure, as also indicated by the ordination analysis.

Despite these differences, the regenerative potential of the plantation was shown to be high in this study. In the studied case, the arrival and establishment of native species certainly has been facilitated by the relatively small size of the plantations (maximum size of the patches: ~60 ha) and the small distances to natural forest patches (maximum distance: ~600 m). These adjacent natural areas are important as seed sources. It has been shown that lack of seed dispersal in plantation can be a limiting factor for forest succession of degraded areas or of exotic plantations (Wijdeven et al. 2000). In case of larger distances to source areas, the natural succession of degraded areas can be delayed for many years. This specific landscape context (Powers et al. 1997) clearly must be considered when projecting our results to areas situated long away from natural forests that serve as propagule sources.

Overall, we conclude that there is potential for the transformation of the plantings into natural forest, as an understory layer that can grow into a tree layer was well established in the plantings, including some species that form the dossel of natural forest (Lee et al. 2005). Clear-cutting of the planted species, besides being much more expensive and devastating for the undergrowth, would likely bring more damage to the soil, such as erosion and soil compaction, impeding natural succession (Corlett 1999). Furthermore, a high recruitment of *Pinus* itself after clear-cutting is likely, given the fact that the species has a pioneer character and invasive behavior on open sites. For the study region, no management strategies aiming at transformation of plantings into natural forests exist so far. At any rate, management actions should have as principles not to harm the existing natural regeneration and not to compromise the soil layer (Ramula et al. 2008, Holmes et al. 2008, Falleiros et al. 2011). In the case of the Pine plantations, monitoring and control of the invasive *Hovenia dulcis* seems necessary. The concrete procedures, e.g. sizing of gaps in way that natural regeneration is facilitated and that negative effects are avoided, still need to be developed. In Brazil, National Forests have high potential as testing sites to establish the most promising management and restoration techniques, and the current debate on restoration presents a promising background for this. These sites are immediately available. Furthermore, conversion of plantings of exotic species is a necessary basis for the development of strategies of sustainable use of forest resources, a principal aim of National Forests.

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Appendix 1: Table of adult stratum sampled in the Native Forest. AD = Absolute Density; AF = Absolute Frequency; ADo = Absolute Dominance and IVI = Importance Value Index.

Espécies	AD	AF	Ado	IVI
Araucaria angustifolia	106,0	64,00	29,15	68,77
Allophylus edulis	184,0	60,00	1,53	24,98
Nectandra megapotamica	84,0	44,00	2,16	16,19
Matayba eleagnoides	78,0	38,00	2,85	16,17
Casearia decandra	88,0	44,00	0,69	13,87
Ilex brevicuspis	48,0	30,00	3,14	13,30
Prunus myrtifolia	46,0	30,00	2,14	11,34
Parapiptadenia rigida	40,0	24,00	1,69	9,29
Ocotea pulchella	30,0	22,00	1,92	8,66
Ocotea diospirifolia	36,0	28,00	1,10	8,45
Cupania vernalis	46,0	24,00	0,41	7,48
Cedrela fissilis	26,0	18,00	1,58	7,22
Nectandra lanceolata	18,0	16,00	1,79	6,70
Banara tomentosa	32,0	22,00	0,65	6,55
Cabralea canjerana	52,0	12,00	0,37	6,31
Casearia sylvestris	26,0	22,00	0,19	5,26
Sebastiania commersoniana	24,0	16,00	0,29	4,49
Myrsine umbellata	24,0	16,00	0,17	4,27
Myrciaria delicatula	28,0	14,00	0,12	4,24
Machaerium paraguariense	14,0	12,00	0,64	3,81
Cinnamodendron dinisii	12,0	12,00	0,69	3,73
Campomanesia guazumifolia	16,0	14,00	0,15	3,35
Sebastiania brasiliensis	20,0	12,00	0,08	3,28
Luehea divaricata	14,0	12,00	0,18	2,98
Sloanea monosperma	14,0	8,00	0,08	2,29
Campomanesia xanthocarpa	10,0	10,00	0,08	2,24
Myrciaria floribunda	12,0	8,00	0,09	2,14
Annona neosalicifolia	10,0	8,00	0,08	1,97
Eugenia pyriformis	8,0	8,00	0,14	1,92
Trichilia elegans	12,0	6,00	0,07	1,84
Allophylus guaraniticus	8,0	8,00	0,02	1,70
Vernonanthura discolor	6,0	4,00	0,31	1,55
Zanthoxylum rhoifolium	8,0	6,00	0,06	1,52
Eugenia uniflora	6,0	6,00	0,06	1,35
Annona rugulosa	6,0	6,00	0,05	1,35
Strychnos brasiliensis	6,0	6,00	0,02	1,30
Ocotea puberula	2,0	2,00	0,43	1,18
Inga virescens	4,0	4,00	0,14	1,09
Myrceugenia mesomischa	6,0	4,00	0,04	1,06
Dalbergia frutescens	6,0	4,00	0,02	1,03

Lamanonia ternata	4,0	4,00	0,07	0,96
Coussarea contracta	4,0	4,00	0,03	0,88
Citronella paniculata	4,0	4,00	0,02	0,88
Drimys brasiliensis	4,0	4,00	0,02	0,88
Syagrus romanzoffiana	4,0	4,00	0,02	0,87
Styrax leprosus	4,0	4,00	0,01	0,86
Cestrum intermedium	4,0	4,00	0,01	0,86
Zanthoxylum petiolare	4,0	4,00	0,01	0,85
Myrcianthes gigantea	4,0	2,00	0,04	0,64
Lithaea brasiliensis	2,0	2,00	0,09	0,57
Eugenia involucrata	2,0	2,00	0,08	0,56
Cordia americana	2,0	2,00	0,05	0,51
Calyptranthes concinna	2,0	2,00	0,03	0,48
Cedrela odorata	2,0	2,00	0,02	0,46
Ilex paraguariensis	2,0	2,00	0,02	0,45
Ilex theezans	2,0	2,00	0,02	0,45
Vitex megapotamica	2,0	2,00	0,02	0,45
Eugenia ramboi	2,0	2,00	0,01	0,43
Rudgea jasminoides	2,0	2,00	0,01	0,43
Citrus sp	2,0	2,00	0,01	0,43
Sorocea bonplandii	2,0	2,00	0,01	0,43
Celtis brasiliensis	2,0	2,00	0,01	0,43

Appendix 2: Table of regenerative stratum sampled in the Native Forest. AD = Absolute Density; AF = Absolute Frequency; ADo = Absolute Dominance and IVI = Importance Value Index.

Espécies	AD	AF	Ado	IVI
Cupania vernalis	1504,0	80,00	0,29	22,39
Allophylus guaraniticus	1224,0	64,00	0,29	19,81
Nectandra megapotamica	1704,0	68,00	0,14	17,83
Trichilia elegans	1360,0	64,00	0,19	17,40
Maytenus dasyclada	1176,0	78,00	0,15	16,13
Parapiptadenia rigida	1176,0	58,00	0,16	15,06
Allophylus edulis	712,0	68,00	0,19	14,06
Dalbergia frutescens	920,0	76,00	0,07	11,93
Matayba eleagnoides	856,0	66,00	0,05	10,46
Ocotea diospirifolia	368,0	34,00	0,14	8,46
Casearia decandra	368,0	46,00	0,11	8,32
Myrciaria delicatula	304,0	32,00	0,14	8,15
Rudgea parquioides	680,0	40,00	0,03	7,18
Myrceugenia mesomischa	448,0	26,00	0,07	6,14
Myrsine umbellata	312,0	36,00	0,07	6,04
Annona rugulosa	168,0	14,00	0,11	5,11
Coussarea contracta	360,0	30,00	0,03	4,93
Banara tomentosa	168,0	16,00	0,10	4,93
Sebastiania brasiliensis	208,0	16,00	0,08	4,50
Bernardia pulchella	424,0	22,00	0,02	4,32
Ilex brevicuspis	200,0	36,00	0,03	4,25
Casearia sylvestris	152,0	22,00	0,06	4,07
Campomanesia xanthocarpa	192,0	28,00	0,03	3,66
Araucaria angustifolia	240,0	28,00	0,01	3,44
Sebastiania commersoniana	136,0	16,00	0,04	3,12
Myrciaria floribunda	240,0	12,00	0,03	3,00
Campomanesia guazumifolia	176,0	20,00	0,02	2,98
Ocotea puberula	168,0	30,00	0,00	2,91
Strychnos brasiliensis	160,0	26,00	0,01	2,88
Styrax leprosus	144,0	24,00	0,02	2,88
Cinnamodendron dinisii	160,0	22,00	0,02	2,79
Cestrum intermedium	104,0	12,00	0,05	2,76
Sloanea monosperma	96,0	18,00	0,03	2,74
Eugenia uniflora	104,0	18,00	0,03	2,69
Luehea divaricata	24,0	6,00	0,07	2,59
Celtis brasiliensis	152,0	26,00	0,00	2,57
Brunfelsia cuneifolia	112,0	18,00	0,02	2,45
Schaefferia argentinensis	128,0	8,00	0,03	2,14
Machaerium paraguariense	88,0	18,00	0,02	2,14
Ocotea pulchella	112,0	20,00	0,01	2,12

Ilex paraguariensis	96,0	14,00	0,02	2,09
Cedrela fissilis	48,0	12,00	0,03	1,88
Cabralea canjerana	56,0	10,00	0,02	1,66
Symplocos tetrandra	72,0	16,00	0,00	1,54
Calyptranthes concinna	104,0	8,00	0,01	1,50
Gymnanthes concolor	48,0	2,00	0,03	1,41
Zanthoxylum rhoifolium	56,0	14,00	0,00	1,31
Eugenia pyriformis	64,0	12,00	0,01	1,28
Prunus myrtifolia	72,0	12,00	0,00	1,22
Blepharocalyx salicifolius	64,0	10,00	0,01	1,17
Nectandra lanceolata	64,0	10,00	0,00	1,09
Zanthoxylum petiolare	40,0	8,00	0,01	0,99
Syagrus romanzoffiana	40,0	10,00	0,00	0,92
Citronella paniculata	24,0	4,00	0,01	0,85
Rudgea jasminoides	40,0	6,00	0,01	0,83
Xylosma pseudosalzmanii	48,0	6,00	0,01	0,82
Citrus sp	24,0	6,00	0,01	0,78
Cordia americana	16,0	4,00	0,01	0,73
Drimys brasiliensis	40,0	4,00	0,01	0,67
Eriobotrya japonica	24,0	4,00	0,01	0,64
Myrsine coriacea	32,0	6,00	0,00	0,60
Dasyphyllum spinescens	24,0	6,00	0,00	0,55
Picrasma crenata	16,0	2,00	0,01	0,49
Ilex dumosa	8,0	2,00	0,01	0,49
Annona neosalicifolia	16,0	4,00	0,00	0,42
Cinnamomum amoenum	24,0	4,00	0,00	0,40
Solanum sanctaecatharinae	8,0	2,00	0,01	0,40
Jacaranda micrantha	8,0	2,00	0,00	0,31
Myrcia palustres	16,0	2,00	0,00	0,27
Ilex theezans	8,0	2,00	0,00	0,24
Myrrhinium atropurpureum	8,0	2,00	0,00	0,20
Myrcianthes gigantea	8,0	2,00	0,00	0,19
Sorocea bonplandii	8,0	2,00	0,00	0,19
Eugenia involucrata	8,0	2,00	0,00	0,19
Sapium glandulosum	8,0	2,00	0,00	0,17

Appendix 3: Table of adult stratum sampled in the *Araucaria angustifolia* plantation. AD = Absolute Density; AF = Absolute Frequency; ADo = Absolute Dominance and IVI = Importance Value Index.

Espécies	AD	AF	Ado	IVI
Araucaria angustifolia	572,0	100,00	48,23	144,29
Allophylus edulis	100,0	54,00	0,42	16,45
Casearia decandra	92,0	48,00	0,55	15,16
Casearia sylvestris	82,0	50,00	0,53	14,73
Ilex paraguariensis	88,0	42,00	0,67	14,15
Cupania vernalis	60,0	40,00	0,32	11,20
Matayba eleagnoides	64,0	34,00	0,66	11,15
Prunus myrtifolia	56,0	32,00	0,57	10,09
Dicksonia sellowiana	26,0	16,00	0,64	5,55
Cinnamodendron dinisii	26,0	16,00	0,12	4,61
Myrsine umbellata	14,0	14,00	0,10	3,40
Luehea divaricata	14,0	12,00	0,06	3,02
Ilex brevicuspis	14,0	10,00	0,07	2,71
Nectandra megapotamica	12,0	10,00	0,14	2,70
Sapium glandulosum	8,0	8,00	0,33	2,45
Parapiptadenia rigida	10,0	10,00	0,05	2,39
Zanthoxylum rhoifolium	10,0	10,00	0,04	2,37
Campomanesia xanthocarpa	10,0	10,00	0,03	2,36
Cabralea canjerana	10,0	8,00	0,09	2,15
Alsophila setosa	18,0	2,00	0,21	1,98
Machaerium paraguariense	12,0	6,00	0,06	1,92
Symplocos tetrandra	8,0	8,00	0,03	1,90
Cedrela fissilis	6,0	6,00	0,28	1,89
Ocotea diospirifolia	10,0	6,00	0,05	1,76
Styrax leprosus	6,0	6,00	0,10	1,57
Annona rugulosa	6,0	6,00	0,06	1,48
Sebastiania commersoniana	6,0	6,00	0,05	1,47
Nectandra lanceolata	8,0	4,00	0,06	1,32
Ocotea pulchella	6,0	4,00	0,03	1,11
Vernonanthura discolor	4,0	4,00	0,03	0,97
Cestrum intermedium	4,0	4,00	0,02	0,96
Citrus sp	4,0	4,00	0,02	0,95
Vitex megapotamica	4,0	4,00	0,02	0,95
Allophylus guaraniticus	4,0	4,00	0,01	0,94
Annona neosalicifolia	2,0	2,00	0,09	0,62
Sloanea monosperma	2,0	2,00	0,07	0,59
Banara tomentosa	2,0	2,00	0,04	0,53
Hovenia dulcis	2,0	2,00	0,02	0,49
Ateleia glazioviana	2,0	2,00	0,02	0,49
Ficus luschnathiana	2,0	2,00	0,01	0,48

Lamanonia ternata	2,0	2,00	0,01	0,48
Calyptranthes concinna	2,0	2,00	0,01	0,47
Solanum sanctaecatharinae	2,0	2,00	0,01	0,47
Maytenus aquifolia	2,0	2,00	0,01	0,47
Xylosma pseudosalzmanii	2,0	2,00	0,01	0,47
Myrciaria delicatula	2,0	2,00	0,01	0,47
Rudgea jasminoides	2,0	2,00	0,00	0,47
Eugenia uniflora	2,0	2,00	0,00	0,47
Zanthoxylum petiolare	2,0	2,00	0,00	0,47
Dalbergia frutescens	2,0	2,00	0,00	0,47

Appendix 4: Table of regenerative stratum sampled in the *Araucaria angustifolia* plantation. AD = Absolute Density; AF = Absolute Frequency; ADo = Absolute Dominance and IVI = Importance Value Index.

Espécies	AD	AF	Ado	IVI
Cupania vernalis	752,0	66,00	0,26	24,33
Casearia sylvestris	528,0	66,00	0,20	19,49
Dicksonia sellowiana	72,0	8,00	0,40	16,90
Allophylus edulis	328,0	54,00	0,20	16,24
Myrsine umbellata	504,0	54,00	0,13	15,42
Ilex paraguariensis	384,0	48,00	0,15	14,34
Casearia decandra	416,0	50,00	0,13	14,14
Matayba eleagnoides	384,0	56,00	0,08	12,18
Myrciaria delicatula	448,0	48,00	0,05	11,30
Ilex brevicuspis	360,0	50,00	0,07	11,08
Araucaria angustifolia	296,0	36,00	0,08	9,72
Dalbergia frutescens	264,0	46,00	0,03	8,20
Ocotea pulchella	208,0	38,00	0,05	7,48
Ocotea puberula	256,0	48,00	0,00	7,26
Cinnamodendron dinisii	176,0	26,00	0,07	6,90
Maytenus dasyclada	232,0	34,00	0,03	6,62
Allophylus guaraniticus	176,0	26,00	0,05	6,19
Nectandra megapotamica	184,0	28,00	0,03	5,87
Parapiptadenia rigida	160,0	26,00	0,03	5,43
Symplocos tetrandra	184,0	30,00	0,01	5,06
Ocotea diospirifolia	136,0	22,00	0,04	4,97
Eugenia pyriformis	144,0	16,00	0,04	4,54
Styrax leprosus	144,0	20,00	0,02	4,26
Calyptranthes concinna	104,0	16,00	0,03	3,74
Myrsine coriacea	136,0	22,00	0,01	3,71
Dasyphyllum spinescens	112,0	20,00	0,01	3,34
Machaerium paraguariense	56,0	12,00	0,04	3,32
Coussarea contracta	96,0	14,00	0,02	3,12
Zanthoxylum rhoifolium	72,0	12,00	0,03	3,01
Syagrus romanzoffiana	40,0	8,00	0,04	2,67
Campomanesia xanthocarpa	80,0	14,00	0,01	2,42
Bernardia pulchella	120,0	8,00	0,01	2,39
Sebastiania commersoniana	40,0	8,00	0,03	2,33
Eugenia uniflora	48,0	10,00	0,01	1,96
Annona neosalicifolia	40,0	6,00	0,03	1,96
Myrceugenia mesomischa	32,0	8,00	0,02	1,65
Myrciaria floribunda	32,0	6,00	0,02	1,61
Vitex megapotamica	16,0	4,00	0,03	1,61
Xylosma pseudosalzmanii	56,0	8,00	0,00	1,49
Cedrela fissilis	40,0	10,00	0,00	1,42

Eugenia ramboi	32,0	6,00	0,01	1,34
Nectandra lanceolata	32,0	8,00	0,01	1,30
Rudgea parquioides	40,0	8,00	0,00	1,29
Maytenus aquifolia	16,0	4,00	0,02	1,26
Sloanea monosperma	24,0	6,00	0,01	1,23
Strychnos brasiliensis	24,0	6,00	0,01	1,18
Blepharocalyx salicifolius	32,0	8,00	0,00	1,12
Sapium glandulosum	16,0	4,00	0,01	1,02
Prunus myrtifolia	24,0	6,00	0,00	0,97
Luehea divaricata	8,0	2,00	0,02	0,91
Annona rugulosa	24,0	6,00	0,00	0,86
Inga virescens	8,0	2,00	0,01	0,71
Banara tomentosa	16,0	4,00	0,00	0,69
Trichilia elegans	24,0	4,00	0,00	0,66
Piptocarpha angustifolia	16,0	4,00	0,00	0,59
Maytenus muelleri	16,0	4,00	0,00	0,55
Eugenia pluriflora	16,0	4,00	0,00	0,54
Campomanesia guazumifolia	8,0	2,00	0,01	0,49
Brunfelsia cuneifolia	8,0	2,00	0,01	0,49
Cestrum intermedium	16,0	2,00	0,00	0,39
Rudgea jasminoides	16,0	2,00	0,00	0,38
Eriobotrya japonica	8,0	2,00	0,00	0,37
Zanthoxylum petiolare	8,0	2,00	0,00	0,31
Cordia ecalyculata	8,0	2,00	0,00	0,30
Inga vera	8,0	2,00	0,00	0,30
Ilex theezans	8,0	2,00	0,00	0,28
Citrus sp	8,0	2,00	0,00	0,28
Myrsine loefgrenii	8,0	2,00	0,00	0,27
Celtis brasiliensis	8,0	2,00	0,00	0,27

Appendix 5: Table of adult stratum sampled in the *Pinus* plantation. AD = Absolute Density; AF = Absolute Frequency; ADo = Absolute Dominance and IVI = Importance Value Index.

Espécies	AD	AF	Ado	IVI
Pinus sp	324,0	100,00	44,75	130,26
Cupania vernalis	130,0	62,00	0,85	23,46
Casearia sylvestris	92,0	58,00	0,85	19,42
Araucaria angustifolia	48,0	30,00	1,26	11,63
Matayba eleagnoides	46,0	28,00	0,40	9,49
Campomanesia xanthocarpa	46,0	26,00	0,31	9,00
Casearia decandra	40,0	28,00	0,28	8,74
Ilex paraguariensis	40,0	20,00	0,32	7,49
Allophylus edulis	28,0	18,00	0,26	5,97
Parapiptadenia rigida	26,0	18,00	0,13	5,55
Vernonanthura discolor	26,0	14,00	0,22	5,06
Prunus myrtifolia	16,0	12,00	0,59	4,54
Nectandra megapotamica	18,0	16,00	0,15	4,53
Annona neosalicifolia	26,0	10,00	0,12	4,21
Sebastiania commersoniana	20,0	12,00	0,11	3,98
Annona rugulosa	18,0	12,00	0,07	3,72
Cabralea canjerana	16,0	10,00	0,17	3,40
Luehea divaricata	14,0	10,00	0,16	3,21
Nectandra lanceolata	14,0	10,00	0,09	3,08
Zanthoxylum rhoifolium	12,0	10,00	0,17	3,04
Cedrela fissilis	10,0	10,00	0,23	2,98
Machaerium paraguariense	12,0	10,00	0,05	2,81
Ilex brevicuspis	10,0	6,00	0,47	2,77
Ocotea diospirifolia	8,0	8,00	0,09	2,22
Sapium glandulosum	10,0	4,00	0,05	1,64
Sebastiania brasiliensis	8,0	4,00	0,03	1,44
Hovenia dulcis	6,0	4,00	0,04	1,27
Calyptranthes concinna	6,0	4,00	0,04	1,26
Myrsine umbellata	4,0	4,00	0,06	1,13
Solanum sanctaecatharinae	4,0	4,00	0,04	1,10
Styrax leprosus	4,0	4,00	0,01	1,04
Celtis brasiliensis	4,0	4,00	0,01	1,04
Campomanesia guazumifolia	6,0	2,00	0,04	0,94
Cestrum intermedium	6,0	2,00	0,02	0,90
Trema micranta	2,0	2,00	0,08	0,67
Myrciaria delicatula	2,0	2,00	0,06	0,62
Inga virescens	2,0	2,00	0,03	0,57
Cinnamodendron dinisii	2,0	2,00	0,03	0,57
Banara tomentosa	2,0	2,00	0,03	0,56
Trichilia elegans	2,0	2,00	0,01	0,54

Eugenia uniflora	2,0	2,00	0,01	0,53
Ateleia glazioviana	2,0	2,00	0,01	0,53
Citrus sp	2,0	2,00	0,01	0,53
Symplocos tetrandra	2,0	2,00	0,01	0,52
Syagrus romanzoffiana	2,0	2,00	0,01	0,52
Cinnamomum amoenum	2,0	2,00	0,00	0,52
Strychnos brasiliensis	2,0	2,00	0,00	0,51
Bernardia pulchella	2,0	2,00	0,00	0,51

Appendix 6: Table of regenerative stratum sampled in the *Pinus* plantation. AD = Absolute Density; AF = Absolute Frequency; ADo = Absolute Dominance and IVI = Importance Value Index.

Espécies	AD	AF	Ado	IVI
Cupania vernalis	680,0	50,00	1,38	55,41
Hovenia dulcis	56,0	4,00	0,71	19,26
Ocotea puberula	504,0	48,00	0,01	17,74
Araucaria angustifolia	40,0	8,00	0,62	17,40
Casearia sylvestris	264,0	32,00	0,11	13,03
Parapiptadenia rigida	200,0	20,00	0,09	9,29
Ocotea diospirifolia	192,0	20,00	0,09	9,22
Eugenia pyriformis	216,0	24,00	0,03	8,88
Allophylus edulis	160,0	24,00	0,08	8,81
Ilex brevicuspis	168,0	24,00	0,06	8,58
Ocotea pulchella	184,0	22,00	0,05	8,23
Nectandra megapotamica	136,0	24,00	0,07	8,09
Dalbergia frutescens	160,0	22,00	0,04	7,52
Zanthoxylum rhoifolium	120,0	16,00	0,07	6,61
Matayba eleagnoides	128,0	20,00	0,03	6,48
Myrciaria delicatula	208,0	10,00	0,03	6,29
Campomanesia xanthocarpa	104,0	16,00	0,07	6,28
Nectandra lanceolata	160,0	14,00	0,01	5,70
Cinnamomum amoenum	96,0	16,00	0,02	5,00
Myrsine umbellata	120,0	12,00	0,02	4,65
Annona neosalicifolia	80,0	10,00	0,06	4,61
Cabralea canjerana	88,0	14,00	0,02	4,33
Sebastiania commersoniana	64,0	12,00	0,03	3,82
Annona rugulosa	64,0	12,00	0,02	3,73
Eugenia uniflora	64,0	10,00	0,02	3,39
Cedrela fissilis	56,0	12,00	0,01	3,24
Machaerium paraguariense	64,0	6,00	0,03	2,92
Pinus sp	40,0	8,00	0,02	2,66
Cestrum intermedium	64,0	6,00	0,02	2,60
Gymnanthes concolor	56,0	2,00	0,04	2,38
Myrsine coriacea	40,0	8,00	0,00	2,12
Prunus myrtifolia	24,0	6,00	0,03	2,10
Ilex paraguariensis	24,0	6,00	0,02	1,89
Maytenus aquifolia	32,0	4,00	0,02	1,84
Styrax leprosus	32,0	6,00	0,00	1,70
Trichilia elegans	40,0	4,00	0,01	1,67
Calyptranthes concinna	24,0	6,00	0,01	1,58
Luehea divaricata	24,0	6,00	0,00	1,50
Syagrus romanzoffiana	24,0	6,00	0,00	1,48
Cinnamodendron dinisii	32,0	4,00	0,01	1,44

Symplocos uniflora	24,0	4,00	0,01	1,32
Xylosma pseudosalzmanii	16,0	4,00	0,01	1,31
Banara tomentosa	8,0	2,00	0,02	1,00
Sloanea monosperma	16,0	4,00	0,00	0,99
Dasyphyllum spinescens	16,0	4,00	0,00	0,98
Symplocos tetrandra	16,0	4,00	0,00	0,98
Coussarea contracta	16,0	4,00	0,00	0,97
Allophylus guaraniticus	16,0	4,00	0,00	0,96
Celtis brasiliensis	16,0	4,00	0,00	0,96
Maytenus dasyclada	24,0	2,00	0,01	0,92
Sebastiania brasiliensis	8,0	2,00	0,02	0,90
Cordia americana	16,0	2,00	0,00	0,65
Blepharocalyx salicifolius	8,0	2,00	0,00	0,57
Lonchocarpus campestres	8,0	2,00	0,00	0,56
Casearia decandra	8,0	2,00	0,00	0,54
Inga virescens	8,0	2,00	0,00	0,53
Bernardia pulchella	8,0	2,00	0,00	0,49
Vernonanthura discolor	8,0	2,00	0,00	0,48
Maytenus muelleri	8,0	2,00	0,00	0,48
Myrciaria floribunda	8,0	2,00	0,00	0,47

Functional patterns of trees communities in *Araucaria* forest and old monoculture plantations of trees

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Abstract

A functional perspective on a tree community is helpful for understanding forest dynamics, especially to understand vegetation recovery after other land uses. Knowledge about ecological filters and survival strategies trees are also important for the restoration of degraded areas. This study, conducted in subtropical southern Brazil, aims to evaluate the functional composition and structure of adult and regenerative components in natural *Araucaria* forest, *Araucaria* plantations and plantations of exotic *Pinus*. Plantations had been established 60 years ago and were abandoned around 30 years ago. Per forest type, we studied five patches, each with 10 sample units of 10 x 10 m. We analyzed differences in functional diversity, functional richness and in community weighted mean trait values, including leaf traits and reproductive traits. RQL analysis was used to indicate the association of community structure with environmental variables and biotic factors We found clear differences for most traits and for functional richness for the regenerative component, while the adult component was more similar among forest types. A clear separation in RQL ordination, associated to the trait variation, for the adult component but not the regenerative trees also indicates that with time, communities are becoming

functionally more similar. In our study, plantations were shown to be environmental filters directly influencing the recruitment and species richness and functional diversity. We conclude that for restoration of *Araucaria* forest, passive restoration may be the best strategy.

Keywords: *Araucaria angustifolia*, Atlantic Forest, Forest Dynamics, Functional diversity, *Pinus sp*., Succession

Introduction

Functional characteristics are important to understand the relationship between plant species and the environmental factors that influence their performance and dynamics (e.g. Díaz & Cabido, 2001; Díaz et al., 2016). The functional characteristics of a forest community can help to explain the coexistence of species in space and time, and the range of plant functional traits indicates the ecological advantages of different plant strategies to different environmental conditions (Wright, 2002; Westoby & Wright, 2006). Changes in land use, such as conversion of natural vegetation into plantations, result in clear changes of composition, dynamics and processes of ecosystems in response to changed or new environmental filters, at both the site and the landscape scale (e.g. Garnier et al., 2007, Laliberté et al., 2009). These changes can alter abundances of certain species or modify considerably the functional structure of the entire community (Raevel et al., 2012). They may have long lasting effects, affecting natural regeneration of such communities for decades. Information on community functional composition thus can improve our ability to understand and forecast the dynamics of succession, and from an applied perspective, help to select appropriate strategies to manage these changes.

To evaluate the recovery potential of degraded areas from a functional perspective on the community level, plant traits related to dispersal and establishment (Cramer et al., 2008) and traits related to growth under stressful environmental conditions (e.g. Funk et al., 2008) are especially relevant. They can indicate factors that limit or promote the recovery of vegetation by succession, or the restoration of the affected plant communities (Weiher et al. 1998; Asanok et al., 2013), for example, when evaluating regeneration patterns. In addition to analysis of specific traits, synthetic measures, as functional indices and functional composition (i.e. community weighted mean of traits – CWM), are helpful to indicate overall patterns of the community and ecosystem level functioning (Diáz et al.

2007). Functional diversity, among other indices (Mason et al. 2007), is used to quantify the distribution of a set of traits within the community (Mouillot et al., 2005). Functional diversity can help to understand species coexistence, as species are subjected to the action of environmental filters that narrow the establishment of functional characteristics in space and time within a community (Zobel, 1997; Mason et al., 2007).

The invasion or introduction of alien species can lead to communities and ecosystems that differ considerably from their natural counterparts, not only in species composition, but also concerning their functionality (Foley et al., 2005; Parton et al., 2007; Cornwell et al., 2008). Tree plantations with exotic species are an example of this, especially when in form of monocultures. In southeastern South America, tree plantations, mostly pine and eucalypt, have increased considerably in the past two decades, which turns the evaluation of their effects on plant and animal communities inside the plantations and in their surroundings an important issue (e.g. Zurita et al. 2006, Fischer et al. 2014). Moreover, transformation of monocultures into natural forests can be an important conservation and restoration strategy (Mendonça-Lima et al., 2014). However, only few studies evaluate the potential for this (e.g. Mendonça-Lima et al., 2014; Podadera et al., 2015) and the successional processes that may ultimately lead to the establishment of near-natural forests are not well understood.

Brazil's Araucaria Forest, with the conspicuous conifer tree *Araucaria angustifolia* in the upper layer of a subtropical broadleave forest, is part of Brazil's Atlantic Forest biome and that is restricted to the highland region of southern and small parts of southeastern Brazil, today presents only about 1% of its original area (Medeiros et al., 2005). The main factor responsible for this reduction is extensive clearcutting in the past, to get land for agriculture and livestock (Sanqueta & Mattel, 2006). As pointed out by Jarenkow & Budke (2009), the establishment of large energy projects and roads are factors that today continue to threaten the integrity of the remaining patches of Araucaria Forest. Therefore, studies aimed at the conservation and restoration of this forest are of high importance.

This study aims to evaluate the functional composition and structure of the regenerative and adult component of three different forest types: Araucaria Forest, abandoned plantations of *Araucaria angustifolia* and abandoned pine plantations. We wish to elucidate successional processes from a functional perspective. In the plantations, established some 60 years ago, spontaneous establishment processes have been taking place during the past 30 years, and a previous study (Malysz & Overbeck submitted) showed much lower recruitment of tree individuals in the plantations than in the natural forest, as well as lower soil fertility in plantations. More specifically, we aimed to answer the following questions: How does the functional structure (diversity and composition) of the tree community differ between natural forest and both types of plantation? Which environmental factors better explain the variation? We hypothesized: (1) Lower soil organic matter and lower soil nutrient content in pine plantations should act as a filter for regeneration, reducing functional diversity and richness; (2) Regeneration within the pine plantation should depend on pioneer species with light and easily dispersed seeds; (3) No or lower differences in regeneration patterns should exist between *Araucaria* plantations and the native forest, due to high contribution of *Araucaria angustifolia* itself in both types of communities to regeneration, predominating species with heavy, animal-dispersed seeds. Altogether, we expected that differences should be stronger for the adult component when compared to the regenerative component, as tree recruitment in the plantations and other successional processes after abandonment of management should slowly contribute to higher similarity among forest types.

Methods

Study area

Our study was conducted in the Passo Fundo National Forest (FLONA Passo Fundo), located in the north of Rio Grande do Sul state, Brazil, in the Mato Castelhano municipality (28 ° 16'44 " to 28 ° 20'40 " S and 52 ° 09'59 " to 52 ° 12'35 " W). This protected area has a total area of 1358 ha, of which 365.4 ha are native forest (Araucaria forest, characterized by the dominant species *Araucaria angustifolia* and the co-occurrence of many broadleaf species), 391 ha are abandoned plantings of *Araucaria angustifolia* in monoculture, 278 ha are abandoned plantings of *Pinus* spp. in monoculture, and 331 ha with other occupations (ICMBio, 2014). Plantings were made in 1947 and managed for 35 years, since then they are subjected to natural succession without any management interventions. In the following, we refer to the three communities as three distinct forest types: native forest and the respective plantings. The three types form an irregular mosaic of forest stands, with stand size ranging from 10 to 60 ha. Soils in the region are loamy, well-drained and deep. In a previous study (Malysz

& Overbeck submitted) we described principal differences among the forest types regarding soil features (Tab. 1).

Table 1. Soil features and habitat characteristics of the three studied forest types (native forest, Araucaria plantation, pine plantation). Different letters indicate significant differences ($p<0.05$). Canopy trees refer to individuals with diameter at breast high ≥5 cm. Mean of canopy openness was measured through hemispheric photographs and analyzed with 'Gap light analyzer' program. From Malysz & Overbeck (submitted).

Forest type	Clay (%)	pH	P (mg/dm^3)	K (mg/dm^3)	Soil organic matter (%)	Light availability (%)	Canopy trees (#)
Native Forest	100.6	4.4 b	4.8 a	100.6 a	6.4 a	18.3	18.0
Araucaria plantation	72.4	4.6 a	4.a b	72.4 b	6.4 a	19.3	19.3
Pinus plantation	74.4	4.4 b	3.5 c	74.4 b	4.8 b	21.1	21.1

Study design and vegetation sampling

Five stands were randomly chosen for each forest type, distributed throughout the entire area. In each of these forest stands, we established 10 sampling units (SU) of 10 by 10 m, situated at least 20 m from the edge of the forest stand. A detailed presentation of the structural characteristics of the tree communities and of the principal species can be found in Malysz & Overbeck (submitted). For the adult component, all living tree individuals with a perimeter at breast height (PBH = 1.3 m above ground) ≥ 15 cm within each SU were sampled. The survey of the regenerative tree component was performed in sub-plots of 5 x 5 m with this SU. In each sub-plot, all living tree individuals with height ≥ 30 cm and PBH <15 cm were sampled. Individuals that presented bifurcation were included in the sample when the sum of the basal areas of stems corresponded to the minimum PBH adopted. All sampled individuals were identified to the species level.

We selected 10 traits (Table 2) that represent key processes of the plant strategies in relation to competitive ability, dispersal, resource exploration and response to disturbances (Cornelissen et al., 2003). Leaf traits were obtained from our field measurements or from the database of Plant Ecology Lab of the Federal University of Rio Grande do Sul. In both cases, data collection and measures were performed according to standardized protocols (Cornelissen et al., 2003, Pérez-Harguindeguy et al. 2013). In general, we sampled 10 leaves or leaflets in the case of compounded leaves (including petioles) of at least five adult individuals per species. These leaves were weighed fresh and dried (60°C for 72 h), scanned and analyzed with the software ImageJ to obtain the leaf area (Schneider et al., 2012). With these measurements we calculated the SLA and LDMC. When possible, were collected at least 10 mature seeds, which were oven-dried for 48 h at 80° C and then weighted in order to calculate seed mass. For species that were not seeding, seed mass data, as well as data on all others traits, was taken from the literature.

Table 2: List of traits considered to each species and to further compare the functional structure of communities according to the three forest types.

Trait (labels)	**Measurements**	**Relation with plant performance ***
Leaf area (LA)	Individual area of leaf or leaflets in compound leaves (mm^2)	Competitive ability
Specific leaf area (SLA)	Area of a fresh leaf divided by its oven-dry mass ($m^2\ kg^{-1}$)	Competitive ability / Potential growth rate
Leaf dry matter content (LDMC)	Oven-dry mass divided by its fresh mass ($mg\ g^{-1}$)	Resource-use strategies
Leaf thickness (LT)	Thickness of a laminar leaf (mm) calculated by 1/SLA*LDMC	Resource-use strategies
Leaf nitrogen content (LNC)	Total amount of N per unit of dry leaf mass ($mg\ g^{-1}$)	Growth and productivity
Leaf phosphorus content (LPC)	Total amount of P per unit of dry leaf mass ($mg\ g^{-1}$)	Growth and productivity
Potential plant height (He)	Maximum height that plant may attain according to the literature information (m)	Competitive ability (competition for light)
Wood density (WD)	Oven-dry mass of a stem section divided by the volume of the same section fresh (g/cm^3)	Growth and resistance
Seed mass (SM)	Oven-dry mass of an average seed of a species (g)	Dispersal ability and establishment
Zoochory (Zo)	Main mode of dispersal of the propagule. Categories: zoochory (1), without zoochory (0)	Dispersal ability

* according to Cornelissen et al. (2003) and Perez-Harguindeguy et al. (2013).

Data analyses

Based on the species trait matrix and on the species density matrix, we calculated two functional diversity indices: Rao's quadratic entropy (Rao, 1982) and the functional richness (Fric). Rao's quadratic entropy expresses the community trait diversity as the sum of the dissimilarities among all possible pairs of species in the trait space weighted by the product of species relative abundances. The functional richness (Fric) is a complementary component of trait diversity, which represents the amount of trait space filled by a community (Villéger et al. 2008). It is expressed as the smallest convex set (or minimum convex hull) enclosing the volume of the n-dimensional trait space occupied by the species in a community (Cornwell et al. 2006). We compared values of functional diversity (Rao) and richness (Fric) between forest types (native forest and the two types of plantation) by ANOVA (one way) and Tukey post-hoc tests to detect differences between treatments.

CWM trait values indicate the mean of each trait weighted by the relative abundance of the species in the community and thus can inform dominant traits in the community (Lavorel et al. 2008), which can be related to the mass ratio hypothesis (Grime, 1998). Each sampling unit is here considered the operational community. We compared the three forest types regarding CWM of each trait, by using ANOVA and post-hoc test (Tukey).

To understand the association of community structure with environmental variables and biotic factors we applied the RLQ analysis, which is a fourth corner method that uses ordination analyses to relate environmental characteristics and species traits (Doledec et al. 1996; Dray et al. 2002; Dray & Legendre, 2008; ter Braak et al. 2012). Here, additionally to the species trait matrix (matrix **Q**) and the species abundance per community (matrix **L**), we consider an environmental matrix (matrix **R**). In our case the matrix **R** consisted of soil variables (percentage of clay and organic matter, pH, phosphorus, potassium, aluminum, calcium and magnesium content) and a measure of light availability (canopy openness). These analyzes were performed using R software (R Development Core Team, 2016), using packages *FD* and *ade4*.

Results

Functional richness showed significant differences between the native forest and the two plantation forests (*Pinus* and *Araucaria*) for the adult component. Native *Araucaria* forest showed the highest values, while the plantations did not differ between each other (Fig. 1). In relation to functional diversity, forest types differed significantly from each other only for the regenerative component.

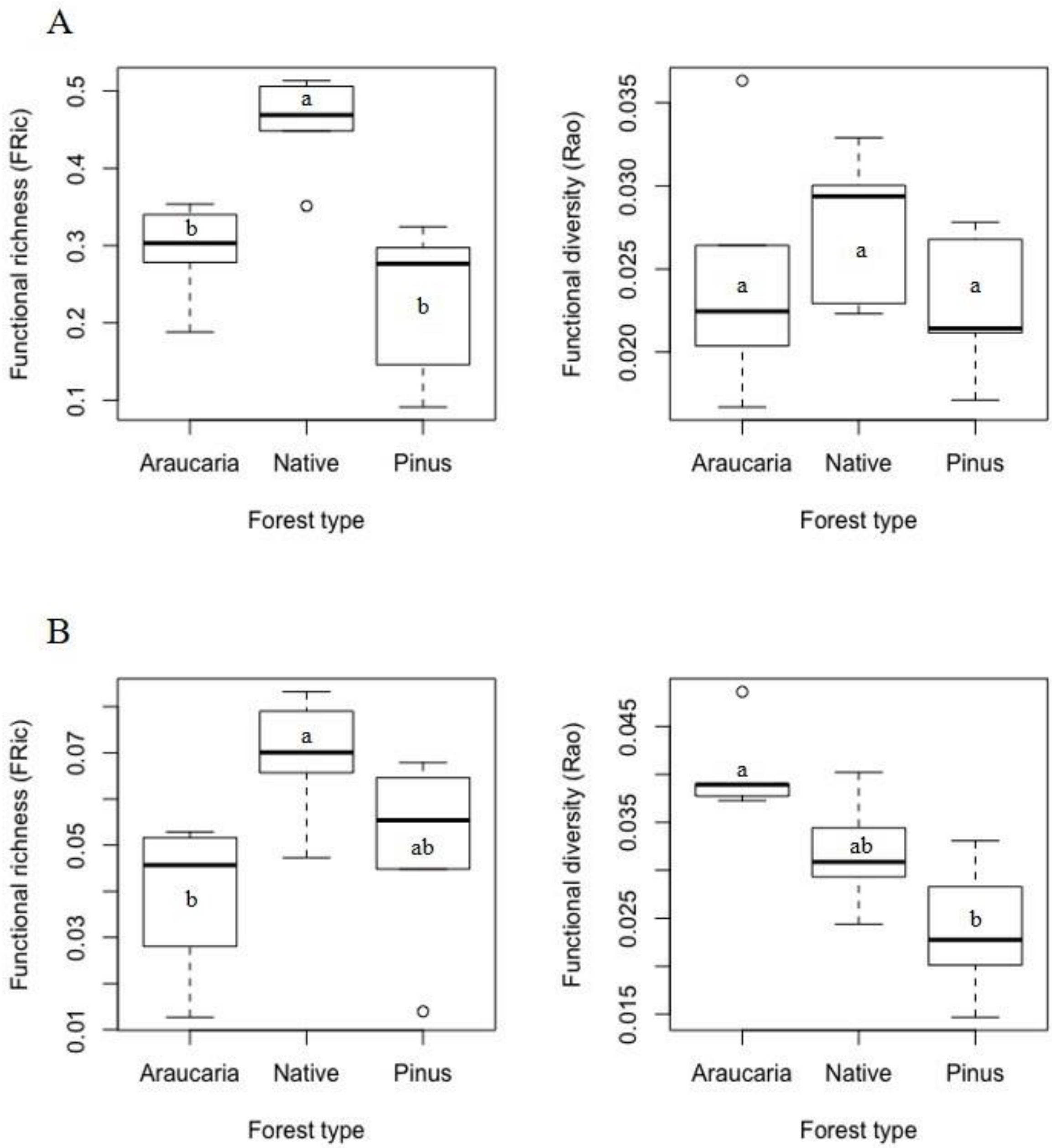

Figure 1. Boxplots showing the diversity and functional richness of regenerative component (A) and adult component (B) for different forest type (native forest, *Araucaria* plantation and *Pinus* plantation). Thick lines in the center of the box indicate the median, the boxes indicate the first and third quartiles, and the whiskers represent the lowest datum within 1.5 IQR of the lower quartile, and the highest datum within 1.5 IQR of the upper quartile. Dots are outliers; Different letters indicated significant differences between forest types.

Comparing CWM values for individual traits of the three forest types, we found significant differences between the communities, particularly in respect to the adult component (Table 3 and Appendix 1). Differences concerned leaf traits (SLA, LT, LNC, LPC), reproductive trait (seed mass) and traits related to competitive ability and growth (WD and potential height) (Table 1 and Appendix 1).

Table 3. Mean values of each community-weighted mean traits (CWM) of native forest and abandoned forest plantations (Pine and Araucaria) for regenerative (R) and adult (A) components. Different letters indicate significant differences between forest types.

Trait	Component	Native Forest	Pine Plantation	Araucaria Plantation	f	p
LA	R	14.04 a	18.51 a	15.88 a	1.74	0.217
	A	**16.11 a**	**18.08 a**	**9.93 b**	**11.57**	**0.001**
SLA	R	**16.25 a**	**13.75 b**	**13.34 b**	**8.77**	**0.004**
	A	**14.61 a**	**13.61 a**	**10.04 b**	**26.2**	**<0.001**
LDMC	R	384.10 a	401.43 a	398.16 a	3.35	0.069
	A	399.64 a	398.41 a	398.67 a	0.01	0.984
LT	R	**0.23 b**	**0.24 b**	**0.27 a**	**7.19**	**0.008**
	A	**0.24 b**	**0.26 b**	**0.38 a**	**42.86**	**<0.001**
LNC	R	**1.97 ab**	**2.15 a**	**1.86 b**	**7.01**	**0.009**

	A	**1.82 a**	**1.92 a**	**1.42 b**	**23.71**	**<0.001**
LPC	R	**0.15 a**	**0.15 a**	**0.14 b**	**5.25**	**0.022**
	A	**0.14 a**	**0.15 a**	**0.12 b**	**13.21**	**<0.001**
He	R	21.81 a	23.22 a	22.14 a	1.78	0.21
	A	**24.45 b**	**24.17 b**	**30.92 a**	**41.17**	**<0.001**
WD	R	0.68 a	0.64 a	0.66 a	2.82	0.098
	A	**0.65 a**	**0.65 a**	**0.58 b**	**26.23**	**<0.001**
Sm	R	0.45 a	0.34 a	0.46 a	0.63	0.549
	A	**0.79 b**	**0.54 b**	**2.70 a**	**55.89**	**<0.001**
Zo	R	0.83 a	0.87 a	0.91 a	1.72	0.22
	A	0.91 a	0.92 a	0.96 a	2.29	0.144

The RLQ of the regenerative component indicates the separation of the different forest types, but with some overlap of native forest and *Araucaria* plantation (Fig. 2a). In this stratum, differentiation of areas in terms of species composition was not strong, but differences in terms of trait values, soil parameters and incidence of light were clear (Fig. 2 – A-C-E).

The RLQ of the adult component indicates a clear separation of forest types, explained almost completely by the first two axes (Eigenvalues 0.73 and 0.06). The native forest is characterized by secondary and late-successional species, with higher SLA and WD values, and soils with higher phosphorus and potassium content. *Araucaria* plantations are characterized by abundant amount of *Araucaria* itself – quite obvious – as well as other species with larger seeds dispersed by animals, and by soils with higher organic matter. *Pinus* plantations are characterized by the increased presence of pioneer species with large leaves, higher LNC and LPC content, with autochoric and anemocoric dispersal (including pine itself), and more clayey soils with higher aluminum content (Fig. 2 – A-B-C).

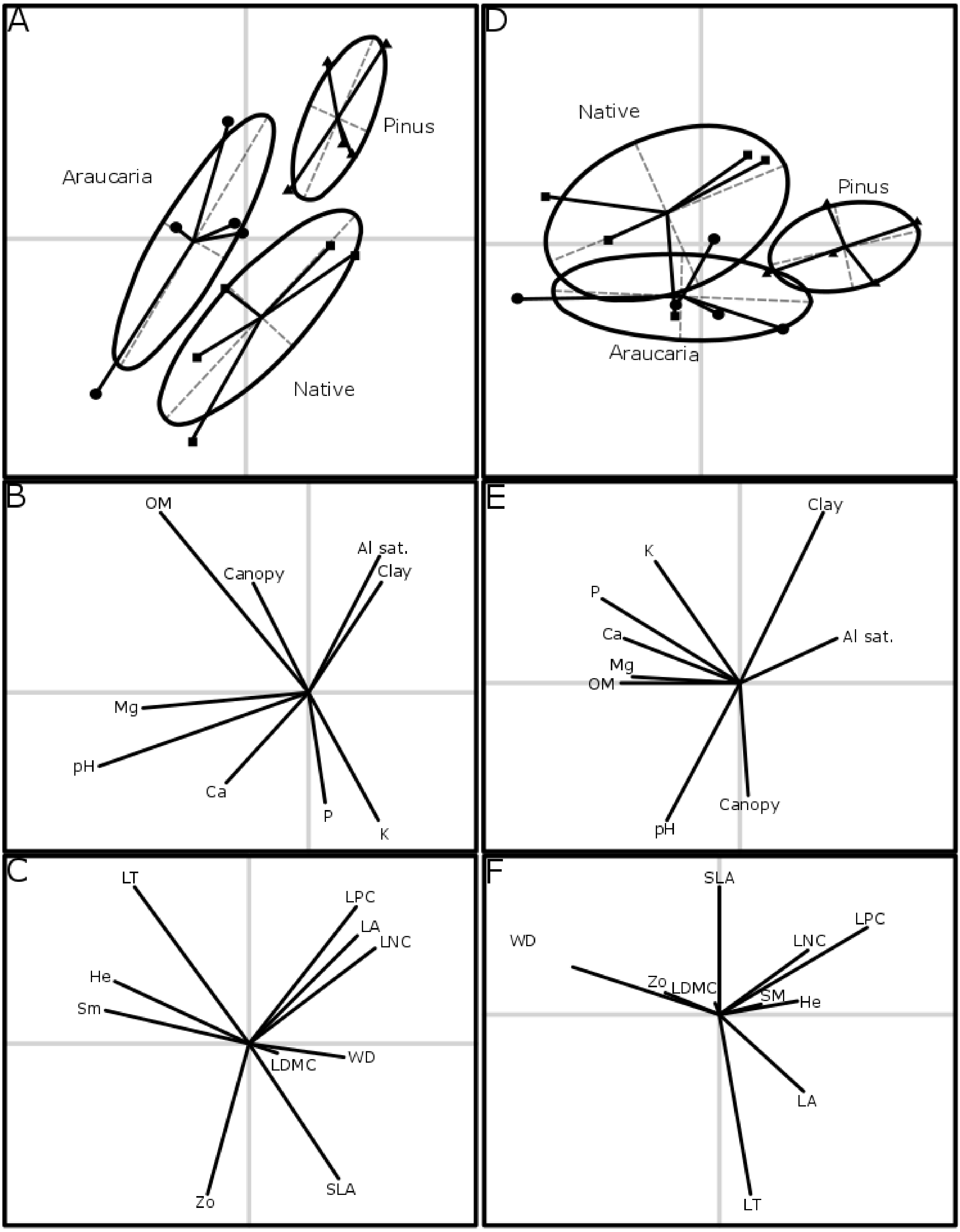

Figure 2. RLQ of the adult (A-B-C) and regenerative (D-E-F) components. In the analysis, R comprises environmental variables, L species abundance distribution matrix and Q comprises the functional attributes of the species. A, D - mean position of species in the RLQ plan. B, E - environmental variables. C, F - functional traits. ■ (square) = Native forest; ● (ball) = *Araucaria* plantation; ▲ (triangle) = *Pinus* plantation.

Discussion

The general aim of this study was to elucidate functional patterns of natural forest and abandoned tree plantations in subtropical southern Brazil. In our study area, spontaneous succession in *Araucaria* and *Pinus* monocultures could take place for a period of almost 35 years since abandonment of management. The analysis of functional traits in succession research has repeatedly been pointed out as useful to assess the impacts of community changes on ecosystem properties (Garnier et al. 2004; Lavorel et al. 1999). Here, we consider the use of traits to be useful as they help to understand dispersal (Kraft et al. 2008) and recruitment patterns related to plant strategies (Reich et al. 2003). The separate analysis for the adult and regenerative components allowed us to consider temporal aspects of succession, even though admittedly in a rather coarse way. Regarding the design and conditions of our study (all three forest types were situated in mosaics of stands with areas between 10 and 60 ha), we can expect that other factors that have been shown to influence tree recruitment in plantations, such as distance from source area (Martin-Queller et al. 2013), plantation age (Brockerhoff et al. 2003) and strong soil differences prior to planting (Wang et al. 2012) should not be of high importance and we can thus evaluate effects of the plantings as such. Our results contribute to a better understanding of community and successional dynamics. They are also relevant for the development of restoration and management strategies that envision the transformation of tree plantations into more natural forest communities.

Although the functional diversity did not present significant differences between the forest types in both strata, functional richness was significantly higher in the native forest. It has been shown before that differences in functional composition are not always accompanied by changes in functional diversity (Mandle & Ticktin, 2015): Functional richness and functional diversity indicate different aspects of the functional composition of plant communities (Mason et al. 2005). Functional diversity is the sum of similarities between the features of the species present in the community and considers species abundance. In contrast, functional richness concerns the number and the volume of traits in a community, being strongly associated to species richness (Villéger et al. 2008; Cornwell et al. 2006). The stronger differences in functional richness found for the adult component in our study indicate that environmental filtering within the plantings was stronger in the past than today. The regenerative component in the former plantation areas may already be result of more suitable environmental conditions, e.g. in consequence of the presence of a developing upper stratum. Consequences are less light and higher humidity, but also higher heterogeneity, which certainly contribute to increase the variability in traits of species that can colonize. Thus, considering the functional diversity, the regenerative stratum of native forests and Araucaria plantings did not differ anymore. However, differences in functional richness between them are still observed, which should be more related to species richness.

In our study, specifically the traits related to the leaf economic spectrum were useful to contrast the different tree communities of the adult component, reinforcing the importance of these traits in comparative plant ecology (Cornelissen et al. 2003; Díaz et al. 2016). When analyzing community weighted means of traits, we found considerable differences among adult tree communities, but not for the regenerative component. Adult communities in the *Araucaria* plantations showed differences in most of traits analyzed, when compared to the native forest and *Pinus* plantations. This indicates clearly that the different tree communities exerted different filtering roles in early successional stages, regarding both dispersal processes and plant strategies, with pioneer species – characterized by high LA, high SLA, low LDMC, high concentrations of nitrogen and phosphorus (Cornelissen et al. 2003) – becoming established in higher abundances. However, for the regenerative component, i.e. individuals with a DBH below 15 cm, *Araucaria* plantation presents difference between the other forest types, namely LT, SLA, LPC and LNC. This can be explained by the less canopy openness of *Araucaria* plantation communities due to the intense densification of planted trees. Apparently, in our case, plantations served as environmental filters for tree recruitment in early phases of abandonment, while this effect became lower in later stages. The higher amount of leaf nitrogen found in the regenerative component of *Pinus* plantation indicates a greater growth capacity and productivity of the species present. This rate is directly and proportionally influenced by the incidence of light at the respective site, and leaf traits related to the fitness of the species (Cornelissen et al., 2003). The density of the wood also tended to show higher values in the areas of natural forest. This attribute indicates the allocation of individual biomass, increased strength and increased survival rate.

In contrast to the adult component, an overlap between the native forest and *Araucaria* plantations was found for the regenerative component, indicating the higher similarity of younger communities than old ones. Further, the analysis revealed relations between abiotic factors and functional attributes for the regenerative component, as hypothesized. The native forest showed a higher organic matter content than the plantations: this corresponds to previous findings on differences of soil properties between native forest and Pine plantations in other regions where lower C content of soil was found in plantations (Kasel & Benett, 2007). Our analyses revealed a direct relation of this factor to mean values of wood density, but indirect with P and N leaf content regarding the species of the regenerative component, which thus indicates a preference of slow growing species and high strength. Light incidence has been shown to be an important factor influencing tree recruitment (Parrota, 1995). In our case, though, no significant differences were found among vegetation types. However, in earlier phases of the plantings, higher light incidence may have favored establishment of pioneer species since we can see some relation between higher canopy cover and higher leaf thickness for both community components. Aluminum concentration and percentage of clay in the soils were correlated to *Pinus* plantation and with high P and N content in the leaves of present species. The aluminum concentration here observed seems not be affecting the presence of fast growth species in the Pinus plantation sites, but other studies observed an association of this element to low SLA and high LDMC indicating less investment in growing individuals (Scholes & Nowicki, 1998, Májeková et al. 2014).

As *Araucaria* is a native species of the region, and indeed a species that physiognomically dominates the forests, we had expected that *Araucaria* plantations would present higher overall similarity with the native forest than with the plantings of the exotic species, which was in fact observed. In the latter, the presence of the exotic species *Hovenia dulcis*, a species included in the official list of invasive plants in Rio Grande do Sul (SEMA, 2013), that has shown to have negative impacts on tree species composition (Lazzarin et al. 2015) and which does not occur in the native forest, is a clear sign of degradation. Apart from the direct effects of these plants in the community, in this case the regeneration in the Pine plantations, these sites are problematic as they serve as propagule sources for close-by communities (Zanchetta & Diniz 2006). This species generates great impact in natural areas, changing not only the dominance but the physiognomy of the communities, generating loss of natural diversity, as invasive species in general.

Nonetheless, just as found by Mendonça-Lima et al. (2014) and indicated in our own analysis of the floristic composition and vegetation structure, both types of plantations showed considerable recruitment of native species, and we can expect that the communities get more similar over time. In the case of our study systems, we still may not be able to call them 'catalysts' for recovery of degraded areas (Mendonca-Lima et al. 2014), as they likely will not be helpful for the recovery of near-by sites – at least in the case of Pine. For this species, good dispersal of seeds to nearby area should indeed remain a problem for long periods: as long as fruiting pine trees are present, non-forested areas in the vicinity will suffer from *Pinus* invasion. Seed rain from *Araucaria*, on the other hand, can be considered positive: *Araucaria* trees have been found to have an important role as perching structures for birds, and thus their establishment in degraded areas may in fact contribute to regeneration processes (Streit et al. 2014).

In conclusion, our study indicates that plantations act as environmental filters for tree recruitment when compared to native forest, causing stronger recruitment of pioneer species with certain functional characteristics and differences in functional diversity and richness. However, their effects become weaker over time as regenerative communities are already more similar to native forests. Considering the propensity of Pine to establish easily in gaps with higher light availability, passive restoration, even though it will lead decades, may be more successful, and of course much more low-cost, than felling and removal of Pine trees. Effects of the individual removal of *Pinus* trees, including on recruitment of Pine itself in gaps, or of alternative strategies, such as girdling, should be analyzed in experimental plots. Altogether, the functional approach used here was important in allowing for a deeper understanding of the filtering effect of the plantations as well as the successional processes under way.

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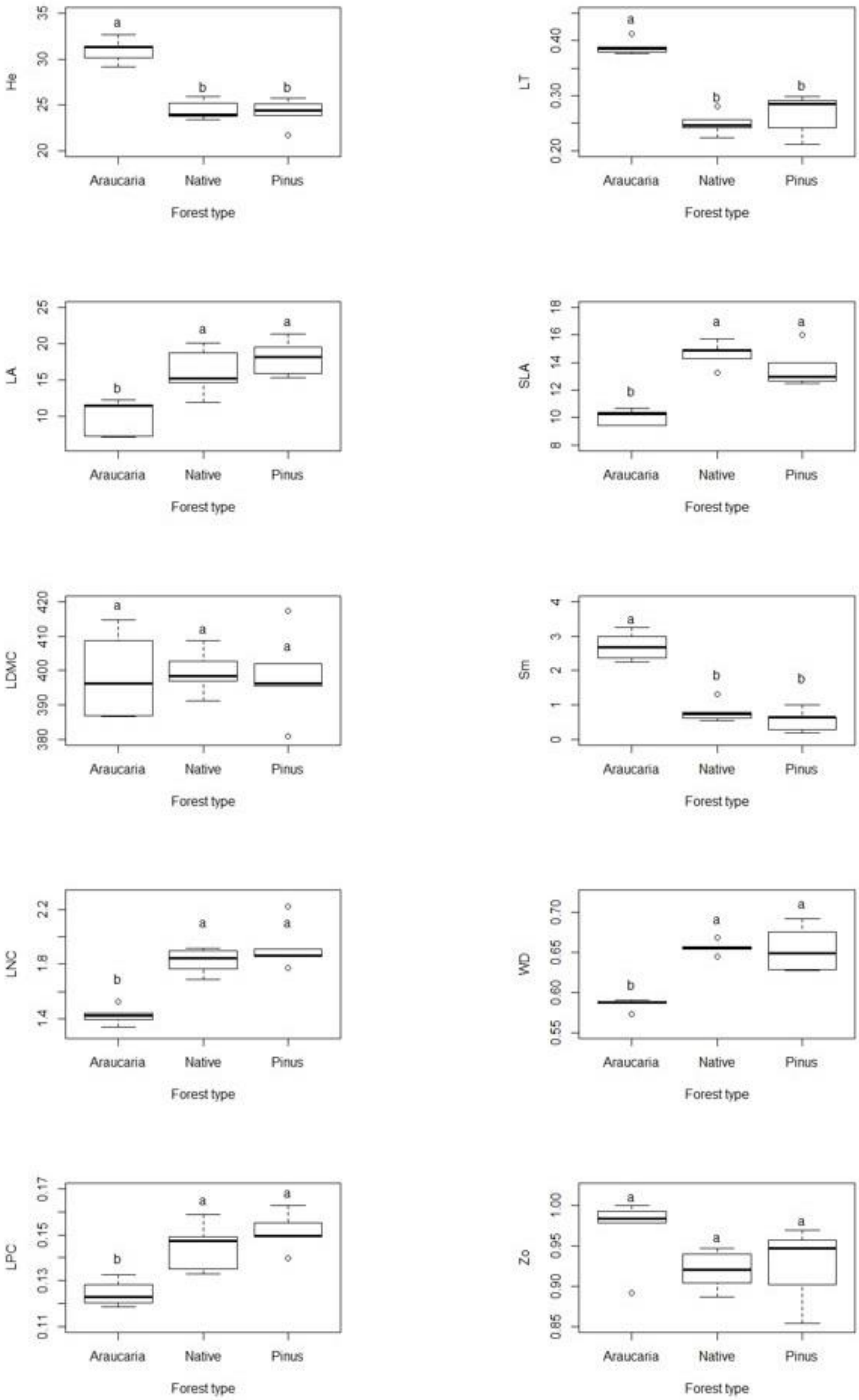
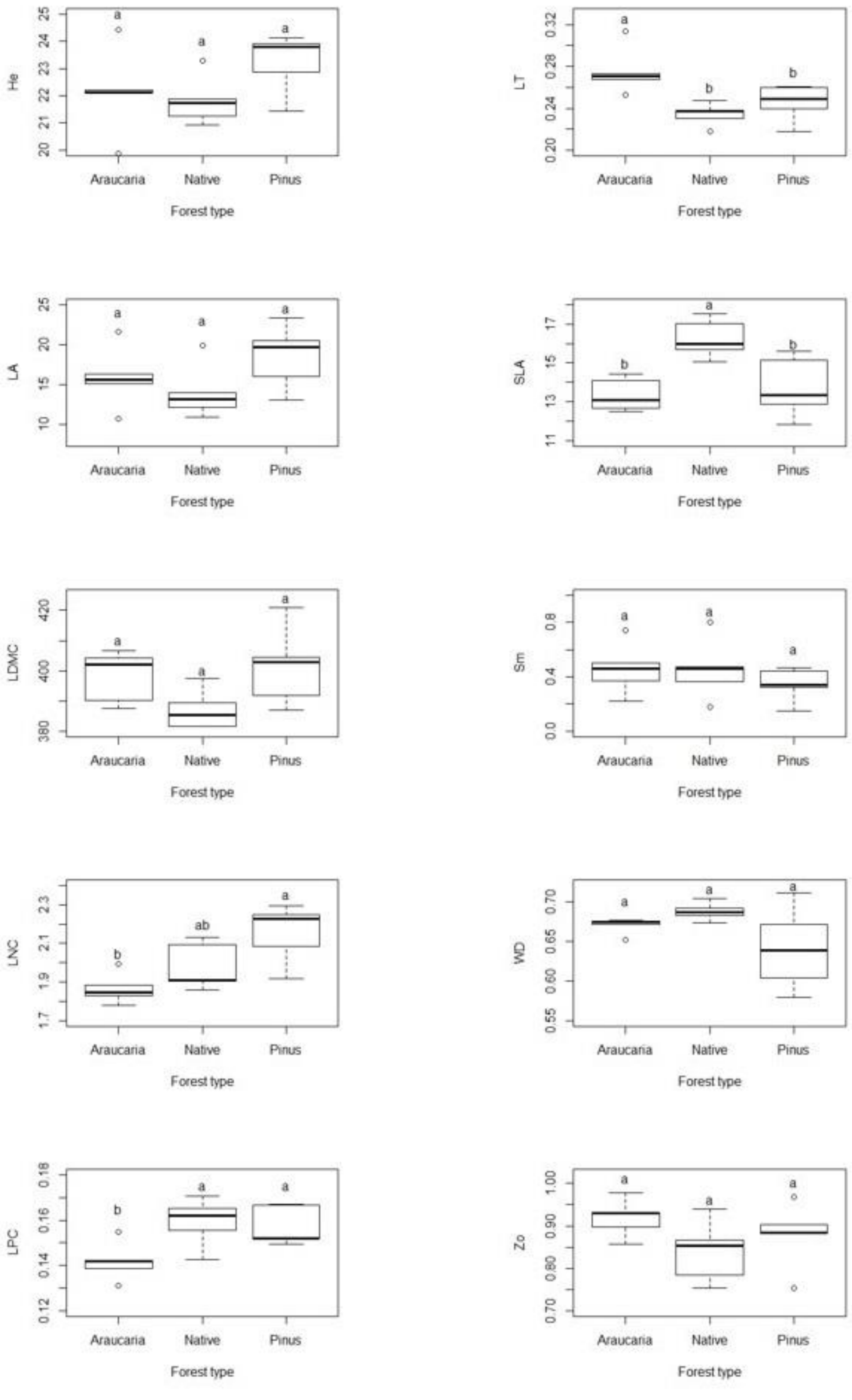
Appendix 1

Boxplots of CWM of traits values considering the adult component of the communities, according to the forest type: Araucaria = *Araucaria* Plantation; Native = Native forest and Pinus = *Pinus* plantation. Different letters mean statistically differences between forest types. See trait labels in the Table 2.



Appendix 2

Boxplots of CWM of traits values considering the regenerative component of the communities, according to the forest type: Araucaria = *Araucaria* Plantation; Native = Native forest and *Pinus* = *Pinus* plantation. Different letters mean statistically differences between forest types. See trait labels in the Table 2.



Appendix 3

Functional traits of adult component species used for CWM analysis. LA = Leaf area; SLA = Specific leaf área; LDMC = Leaf dry matter content; LT = Leaf thickness; LNC = Leaf nitrogen content; LPC = Leaf phosphorus content; He = Potential plant height; WD = Wood density; Sm = Seed mass and Zo = Zoochory.

	LA	SLA	LDMC	LT	LNC	LPC	He	WD	Sm	Zo
Allophylus edulis	11.846	18.598	373.082	0.175	1.39	0.13	19	0.65	0.0182	1
Annona neosalicifolia	19.270	20.569	341.931	0.144	2.8	0.17	19	0.61	0.6250	1
Annona rugulosa	23.372	21.993	290.727	0.161	2.45	0.12	14	0.46	0.3509	1
Araucaria angustifolia	1.292	5.593	374.251	0.553	0.91	0.1	42	0.48	5.4878	1
Banara tomentosa	15.777	21.197	305.683	0.159	2.5	0.17	16	0.60	0.0008	1
Cabralea canjerana	33.965	16.638	313.777	0.203	2.11	0.15	25	0.54	0.8333	1
Campomanesia guazumifolia	73.633	35.830	397.495	0.083	2	0.18	15	0.61	0.0377	1
Campomanesia xanthocarpa	22.529	13.135	403.886	0.209	1.2875	0.13	28	0.86	0.0585	1
Casearia decandra	6.265	17.314	551.752	0.176	2	0.13	25	0.66	0.0213	1
Casearia sylvestris	15.159	12.206	414.219	0.250	2.275	0.133	22	0.71	0.0119	1
Cedrela fissilis	26.099	19.680	330.075	0.221	3.02	0.3	30	0.49	0.0280	0
Cestrum intermedium	22.401	22.050	234.403	0.203	4	0.23	15	NA	NA	1
Cinnamodendron dinisii	14.017	8.101	462.853	0.277	NA	NA	20	0.57	0.3571	1
Cupania vernalis	24.460	11.560	404.028	0.302	1.72	0.19	25	0.66	NA	1
Ilex brevicuspis	9.266	17.255	328.469	0.199	1.73	0.08	21	0.54	0.0031	1
Ilex paraguariensis	13.641	6.191	435.027	0.470	1.35	0.12	19	0.60	0.0075	1
Luehea divaricata	25.666	12.817	386.493	0.225	1.68	0.23	26	0.56	0.0040	0
Machaerium paraguariense	16.960	35.050	345.333	0.116	3.9	0.24	25	0.50	0.3517	0
Matayba elaeagnoides	13.961	12.460	332.273	0.276	1.98	0.18	23	0.81	NA	1
Myrciaria delicatula	1.915	10.521	436.202	0.225	NA	0.14	12	0.85	NA	1
Myrciaria floribunda	8.258	10.412	482.135	0.201	1.6	0.07	23	0.79	0.0606	1
Myrsine umbellata	64.173	6.650	372.585	0.488	1.09	0.06	20	0.86	0.0667	1
Nectandra lanceolata	83.824	18.475	484.646	0.112	2.2	0.15	26	0.70	0.7194	1
Nectandra megapotamica	9.585	10.208	430.390	0.260	2.06	0.12	27	0.75	0.4082	1
Ocotea diospyrifolia	43.278	24.688	477.430	0.086	2.9	0.27	25	0.53	0.5556	1
Ocotea pulchella	7.755	8.374	486.812	0.260	1.7	0.14	25	0.65	0.3333	1
Parapiptadenia rigida	0.185	12.305	484.213	0.172	NA	0.16	35	0.85	0.0299	0
Prunus myrtifolia	18.976	11.304	417.538	0.273	1.88	0.14	23	0.74	0.1327	1

Sebastiania brasiliensis	8.713	13.526	323.624	0.258	1.8	0.2	18	0.67	NA	1
Sebastiania commersoniana	7.640	11.382	422.940	0.219	1.9	0.12	19	0.64	0.0174	1
Sloanea monosperma	21.347	22.716	474.523	0.192	1.4	0.08	20	0.88	NA	1
Styrax leprosus	10.198	9.707	440.023	0.237	1.4	0.08	20	0.41	0.1250	1
Vernonanthura discolor	24.033	6.887	346.527	0.466	1.645	0.13	24	0.54	0.0006	1
Zanthoxylum rhoifolium	6.584	9.985	374.631	0.323	1.683	0.09	23	0.57	0.0137	1

Appendix 4

Functional traits of regenerate component species used for CWM analysis. LA = Leaf area; SLA = Specific leaf área; LDMC = Leaf dry matter content; LT = Leaf thickness; LNC = Leaf nitrogen content; LPC = Leaf phosphorus content; He = Potential plant height; WD = Wood density; Sm = Seed mass and Zo = Zoochory.

	LA	SLA	LDMC	LT	LNC	LPC	He	WD	Sm	Zo
Allophylus edulis	11.846	18.598	373.082	0.175	1.390	0.130	19	0.651	0.018	1
Allophylus guaraniticus	3.943	22.279	305.892	0.148	1.470	0.160	15	0.580	NA	1
Annona neosalicifolia	19.270	20.569	341.931	0.144	2.800	0.170	19	0.610	0.625	1
Annona rugulosa	23.372	21.993	290.727	0.161	2.450	0.120	14	0.460	0.351	1
Araucaria angustifolia	1.292	5.593	374.251	0.553	0.910	0.100	42	0.480	5.488	1
Banara tomentosa	15.777	21.197	305.683	0.159	2.500	0.170	16	0.600	0.001	1
Bernardia pulchella	18.575	17.994	322.156	NA	NA	NA	NA	NA	NA	NA
Blepharocalyx salicifolius	4.984	10.827	426.428	0.226	1.600	0.090	20	0.708	0.015	1
Brunfelsia cuneifolia	16.448	17.418	312.085	NA	NA	NA	NA	NA	NA	NA
Cabralea canjerana	33.965	16.638	313.777	0.203	2.110	0.150	25	0.540	0.833	1
Calyptranthes concinna	10.781	9.432	467.638	0.241	1.600	0.080	17	0.770	0.056	1
Campomanesia guazumifolia	73.633	35.830	397.495	0.083	2.000	0.180	15	0.610	0.038	1
Campomanesia xanthocarpa	22.529	13.135	403.886	0.209	1.288	0.130	28	0.860	0.058	1
Casearia decandra	6.265	17.314	551.752	0.176	2.000	0.130	25	0.664	0.021	1
Casearia sylvestris	15.159	12.206	414.219	0.250	2.275	0.133	22	0.710	0.012	1
Cedrela fissilis	26.099	19.680	330.075	0.221	3.020	0.300	30	0.490	0.028	0
Celtis iguanaea	21.558	14.354	326.784	0.213	2.600	0.110	12	0.655	0.106	1
Cestrum intermedium	22.401	22.050	234.403	0.203	4.000	0.230	15	NA	NA	1
Cinnamomum amoenum	8.118	7.617	441.879	0.298	1.600	0.090	21	0.510	NA	1
Cinnamodendron dinisii	14.017	8.101	462.853	0.277	NA	NA	20	0.570	0.357	1

Coussarea contracta	23.621	15.280	260.048	NA	NA	NA	NA	NA	NA	NA
Cupania vernalis	24.460	11.560	404.028	0.302	1.720	0.190	25	0.660	NA	1
Dalbergia frutescens	17.098	26.599	332.811	0.128	3.310	0.250	18	0.690	NA	0
Dasyphyllum spinescens	10.439	16.326	265.357	0.272	NA	NA	18	0.830	0.001	0
Drimys brasiliensis	25.217	8.693	333.330	0.352	1.000	0.130	17	0.400	0.005	1
Eugenia pyriformis	9.629	8.358	495.758	0.249	2.200	0.130	20	NA	0.855	1
Eugenia uniflora	6.795	17.207	378.162	0.154	1.600	0.100	18	0.828	NA	1
Actinostemon concolor	29.378	8.774	366.125	0.353	1.135	0.070	20	0.660	0.380	0
Ilex brevicuspis	9.266	17.255	328.469	0.199	1.730	0.080	21	0.540	0.003	1
Ilex paraguariensis	13.641	6.191	435.027	0.470	1.350	0.120	19	0.600	0.008	1
Machaerium paraguariense	16.960	35.050	345.333	0.116	3.900	0.240	25	0.500	0.352	0
Matayba elaeagnoides	13.961	12.460	332.273	0.276	1.980	0.180	23	0.810	NA	1
Maytenus aquifolia	28.906	7.902	396.871	0.319	1.900	0.130	15	0.700	0.150	1
Maytenus dasyclada	2.016	22.810	341.735	NA	NA	NA	NA	NA	NA	NA
Myrsine coriacea	11.971	14.038	316.913	0.232	1.820	0.110	19	0.594	0.020	1
Myrciaria delicatula	1.915	10.521	436.202	0.225	NA	0.140	12	0.850	NA	1
Myrciaria floribunda	8.258	10.412	482.135	0.201	1.600	0.070	23	0.785	0.061	1
Myrceugenia mesomischa	5.969	11.603	410.544	0.214	1.600	0.080	5	NA	NA	1
Myrsine umbellata	64.173	6.650	372.585	0.488	1.090	0.060	20	0.860	0.067	1
Nectandra lanceolata	83.824	18.475	484.646	0.112	2.200	0.150	26	0.700	0.719	1
Nectandra megapotamica	9.585	10.208	430.390	0.260	2.060	0.120	27	0.750	0.408	1
Ocotea diospyrifolia	43.278	24.688	477.430	0.086	2.900	0.270	25	0.530	0.556	1
Ocotea puberula	15.102	8.923	415.167	0.322	3.040	0.200	30	0.433	0.165	1
Ocotea pulchella	7.755	8.374	486.812	0.260	1.700	0.140	25	0.650	0.333	1
Parapiptadenia rigida	0.185	12.305	484.213	0.172	NA	0.160	35	0.850	0.030	0
Prunus myrtifolia	18.976	11.304	417.538	0.273	1.880	0.140	23	0.741	0.133	1
Rudgea jasminoides	25.619	9.890	291.515	0.391	2.120	0.110	12	NA	NA	1
Rudgea parquioides	2.922	5.606	303.250	0.590	1.530	NA	NA	NA	NA	1
Schaefferia argentinensis	6.066	20.846	355.746	NA	NA	NA	NA	NA	NA	NA
Sebastiania brasiliensis	8.713	13.526	323.624	0.258	1.800	0.200	18	0.670	NA	1
Sebastiania commersoniana	7.640	11.382	422.940	0.219	1.900	0.120	19	0.637	0.017	1
Sloanea monosperma	21.347	22.716	474.523	0.192	1.400	0.080	20	0.880	NA	1

Strychnos brasiliensis	21.858	62.829	209.578	0.076	NA	NA	NA	NA	NA	NA
Styrax leprosus	10.198	9.707	440.023	0.237	1.400	0.080	20	0.413	0.125	1
Syagrus romanzoffiana	34.534	7.928	477.070	0.264	2.000	0.150	26	0.812	3.528	1
Symplocos tetrandra	6.805	10.408	308.673	0.359	1.740	NA	18	0.490	NA	1
Trichilia elegans	4.103	17.673	430.424	0.136	NA	NA	13	NA	NA	1
Xylosma pseudosalzmanii	9.326	10.914	393.440	0.241	1.320	0.120	18	0.650	NA	1
Zanthoxylum rhoifolium	6.584	9.985	374.631	0.323	1.683	0.090	23	0.569	0.014	1

Appendix 5

Functional traits of adult component species used for RLQ analysis. LA = Leaf area; SLA = Specific leaf área; LDMC = Leaf dry matter content; LT = Leaf thickness; LNC = Leaf nitrogen content; LPC = Leaf phosphorus content; He = Potential plant height; WD = Wood density; Sm = Seed mass and Zo = Zoochory.

	LA	SLA	LDMC	LT	LNC	LPC	He	WD	Sm	Zo
Allophylus edulis	11.846	18.598	373.082	0.175	1.39	0.13	19	0.65	0.0182	1
Annona neosalicifolia	19.270	20.569	341.931	0.144	2.8	0.17	19	0.61	0.6250	1
Annona rugulosa	23.372	21.993	290.727	0.161	2.45	0.12	14	0.46	0.3509	1
Araucaria angustifolia	1.292	5.593	374.251	0.553	0.91	0.1	42	0.48	5.4878	1
Banara tomentosa	15.777	21.197	305.683	0.159	2.5	0.17	16	0.60	0.0008	1
Cabralea canjerana	33.965	16.638	313.777	0.203	2.11	0.15	25	0.54	0.8333	1
Campomanesia guazumifolia	73.633	35.830	397.495	0.083	2	0.18	15	0.61	0.0377	1
Campomanesia xanthocarpa	22.529	13.135	403.886	0.209	1.2875	0.13	28	0.86	0.0585	1
Casearia decandra	6.265	17.314	551.752	0.176	2	0.13	25	0.66	0.0213	1
Casearia sylvestris	15.159	12.206	414.219	0.250	2.275	0.133	22	0.71	0.0119	1
Cedrela fissilis	26.099	19.680	330.075	0.221	3.02	0.3	30	0.49	0.0280	0
Ilex brevicuspis	9.266	17.255	328.469	0.199	1.73	0.08	21	0.54	0.0031	1
Ilex paraguariensis	13.641	6.191	435.027	0.470	1.35	0.12	19	0.60	0.0075	1
Luehea divaricata	25.666	12.817	386.493	0.225	1.68	0.23	26	0.56	0.0040	0
Machaerium paraguariense	16.960	35.050	345.333	0.116	3.9	0.24	25	0.50	0.3517	0
Myrciaria floribunda	8.258	10.412	482.135	0.201	1.6	0.07	23	0.79	0.0606	1
Myrsine umbellata	64.173	6.650	372.585	0.488	1.09	0.06	20	0.86	0.0667	1
Nectandra lanceolata	83.824	18.475	484.646	0.112	2.2	0.15	26	0.70	0.7194	1
Nectandra megapotamica	9.585	10.208	430.390	0.260	2.06	0.12	27	0.75	0.4082	1

Ocotea diospyrifolia	43.278	24.688	477.430	0.086	2.9	0.27	25	0.53	0.5556	1
Ocotea pulchella	7.755	8.374	486.812	0.260	1.7	0.14	25	0.65	0.3333	1
Prunus myrtifolia	18.976	11.304	417.538	0.273	1.88	0.14	23	0.74	0.1327	1
Sebastiania commersoniana	7.640	11.382	422.940	0.219	1.9	0.12	19	0.64	0.0174	1
Styrax leprosus	10.198	9.707	440.023	0.237	1.4	0.08	20	0.41	0.1250	1
Vernonanthura discolor	24.033	6.887	346.527	0.466	1.645	0.13	24	0.54	0.0006	1
Zanthoxylum rhoifolium	6.584	9.985	374.631	0.323	1.6833333	0.09	23	0.57	0.0137	1

Appendix 6

Functional traits of regeneration component species used for RLQ analysis. LA = Leaf area; SLA = Specific leaf área; LDMC = Leaf dry matter content; LT = Leaf thickness; LNC = Leaf nitrogen content; LPC = Leaf phosphorus content; He = Potential plant height; WD = Wood density; Sm = Seed mass and Zo = Zoochory.

	LA	SLA	LDMC	LT	LNC	LPC	He	WD	Sm	Zo
Allophylus edulis	11.846	18.598	373.082	0.175	1.390	0.130	19	0.651	0.018	1
Annona neosalicifolia	19.270	20.569	341.931	0.144	2.800	0.170	19	0.610	0.625	1
Annona rugulosa	23.372	21.993	290.727	0.161	2.450	0.120	14	0.460	0.351	1
Araucaria angustifolia	1.292	5.593	374.251	0.553	0.910	0.100	42	0.480	5.488	1
Banara tomentosa	15.777	21.197	305.683	0.159	2.500	0.170	16	0.600	0.001	1
Blepharocalyx salicifolius	4.984	10.827	426.428	0.226	1.600	0.090	20	0.708	0.015	1
Cabralea canjerana	33.965	16.638	313.777	0.203	2.110	0.150	25	0.540	0.833	1
Calyptranthes concinna	10.781	9.432	467.638	0.241	1.600	0.080	17	0.770	0.056	1
Campomanesia guazumifolia	73.633	35.830	397.495	0.083	2.000	0.180	15	0.610	0.038	1
Campomanesia xanthocarpa	22.529	13.135	403.886	0.209	1.288	0.130	28	0.860	0.058	1
Casearia decandra	6.265	17.314	551.752	0.176	2.000	0.130	25	0.664	0.021	1
Casearia sylvestris	15.159	12.206	414.219	0.250	2.275	0.133	22	0.710	0.012	1
Cedrela fissilis	26.099	19.680	330.075	0.221	3.020	0.300	30	0.490	0.028	0
Celtis iguanaea	21.558	14.354	326.784	0.213	2.600	0.110	12	0.655	0.106	1
Drimys brasiliensis	25.217	8.693	333.330	0.352	1.000	0.130	17	0.400	0.005	1
Actinostemon concolor	29.378	8.774	366.125	0.353	1.135	0.070	20	0.660	0.380	0
Ilex brevicuspis	9.266	17.255	328.469	0.199	1.730	0.080	21	0.540	0.003	1
Ilex paraguariensis	13.641	6.191	435.027	0.470	1.350	0.120	19	0.600	0.008	1
Machaerium paraguariense	16.960	35.050	345.333	0.116	3.900	0.240	25	0.500	0.352	0
Maytenus aquifolia	28.906	7.902	396.871	0.319	1.900	0.130	15	0.700	0.150	1

Myrsine coriacea	11.971	14.038	316.913	0.232	1.820	0.110	19	0.594	0.020	1
Myrciaria floribunda	8.258	10.412	482.135	0.201	1.600	0.070	23	0.785	0.061	1
Myrsine umbellata	64.173	6.650	372.585	0.488	1.090	0.060	20	0.860	0.067	1
Nectandra lanceolata	83.824	18.475	484.646	0.112	2.200	0.150	26	0.700	0.719	1
Nectandra megapotamica	9.585	10.208	430.390	0.260	2.060	0.120	27	0.750	0.408	1
Ocotea diospyrifolia	43.278	24.688	477.430	0.086	2.900	0.270	25	0.530	0.556	1
Ocotea puberula	15.102	8.923	415.167	0.322	3.040	0.200	30	0.433	0.165	1
Ocotea pulchella	7.755	8.374	486.812	0.260	1.700	0.140	25	0.650	0.333	1
Prunus myrtifolia	18.976	11.304	417.538	0.273	1.880	0.140	23	0.741	0.133	1
Sebastiania commersoniana	7.640	11.382	422.940	0.219	1.900	0.120	19	0.637	0.017	1
Styrax leprosus	10.198	9.707	440.023	0.237	1.400	0.080	20	0.413	0.125	1
Syagrus romanzoffiana	34.534	7.928	477.070	0.264	2.000	0.150	26	0.812	3.528	1
Zanthoxylum rhoifolium	6.584	9.985	374.631	0.323	1.683	0.090	23	0.569	0.014	1

Conclusão

Esta tese teve como base o objetivo de avaliar a recuperação florestal em antigos plantios arbóreos abandonados na Floresta Nacional de Passo Fundo, Rio Grande do Sul, Brasil, e comparar estes dados com dados obtidos em floresta nativa. Em geral, nosso estudo mostra que existe regeneração por espécies nativas nas áreas de plantio e, com isso, um potencial de transformação nas áreas de plantio em floresta natural. Uma vez as áreas plantadas apresentadas o recrutamento de espécies com diferenças em suas características funcionais, riqueza e abundancia, a tendência ao longo do tempo é se tornarem mais semelhantes às áreas naturais. Acredito que este trabalho possa ser de grande utilidade para o entendimento das dinâmicas da comunidade florestal local e ser utilizado para possíveis ações de manejo, visando o reestabelecimento da vegetação nativa dentro da Floresta Nacional de Paso Fundo. Um próximo passo seria instalar experimentos para avaliar o efeito de diferentes maneiras de reduzir o número de indivíduos de *Pinus* no plantio.

Appendix: Lista das espécies arbóreas ocorrentes nos três tipos de vegetação na FLONA Passo Fundo, RS, separadamente para os dois componentes estudados (1 = presença, 0 = ausência).

Espécies	**Adultas**			**Regeneração**		
	Nativa	**Plantio *Araucaria***	**Plantio *Pinus***	**Nativa**	**Plantio *Araucaria***	**Plantio *Pinus***
Casearia decandra	1	1	1	1	1	1
Araucaria angustifolia	1	1	1	1	1	1
Banara tomentosa	1	1	1	1	1	1
Nectandra megapotamica	1	1	1	1	1	1
Allophylus edulis	1	1	1	1	1	1
Prunus myrtifolia	1	1	1	1	1	1
Ocotea pulchella	1	1	0	1	1	1
Sebastiania commersoniana	1	1	1	1	1	1
Casearia sylvestris	1	1	1	1	1	1
Nectandra lanceolata	1	1	1	1	1	1
Cedrela fissilis	1	1	1	1	1	1
Campomanesia xanthocarpa	1	1	1	1	1	1
Sebastiania brasiliensis	1	0	1	1	0	1
Machaerium paraguariense	1	1	1	1	1	1
Myrsine umbellata	1	1	1	1	1	1
Matayba elaeagnoides	1	1	1	1	1	1
Campomanesia guazumifolia	1	0	1	1	1	0
Luehea divaricata	1	1	1	0	0	0
Cupania vernalis	1	1	1	1	1	1
Annona neosalicifolia	1	1	1	1	1	1
Ilex brevicuspis	1	1	1	1	1	1
Ocotea diospyrifolia	1	1	1	1	1	1
Parapiptadenia rigida	1	1	1	1	1	1
Zanthoxylum rhoifolium	1	1	1	1	1	1
Ilex paraguariensis	1	1	1	1	1	1
Cestrum intermedium	1	1	1	1	1	1
Myrciaria delicatula	1	1	1	1	1	1
Cinnamodendron dinisii	1	1	1	1	1	1
Annona rugulosa	1	1	1	1	1	1
Sloanea monosperma	1	1	0	1	1	1
Cabralea canjerana	1	1	1	1	0	1
Vernonanthura discolor	1	1	1	0	0	0
Myrciaria floribunda	1	0	0	1	1	1
Styrax leprosus	1	1	1	0	0	0
Eugenia pyriformis	0	0	0	1	1	1
Celtis iguanaea	0	0	0	1	1	1
Dalbergia frutescens	0	0	0	1	1	1
Trichilia elegans	0	0	0	1	1	1
Allophylus guaraniticus	0	0	0	1	1	1
Maytenus dasyclada	0	0	0	1	1	1
Bernardia pulchella	0	0	0	1	1	1

Coussarea contracta	0	0	0	1	1	1
Blepharocalyx salicifolius	0	0	0	1	1	1
Cinnamomum amoenum	0	0	0	1	0	1
Syagrus romanzoffiana	0	0	0	1	1	1
Rudgea parquioides	0	0	0	1	1	0
Eugenia uniflora	0	0	0	1	1	1
Gymnanthes concolor	0	0	0	1	0	1
Xylosma pseudosalzmanii	0	0	0	1	1	1
Ocotea puberula	0	0	0	1	1	1
Myrsine coriacea	0	0	0	1	1	1
Symplocos tetrandra	0	0	0	1	1	1
Myrceugenia mesomischa	0	0	0	1	1	0
Dasyphyllum spinescens	0	0	0	1	1	1
Calyptranthes concinna	0	0	0	1	1	1
Schaefferia argentinensis	0	0	0	1	0	0
Strychnos brasiliensis	0	0	0	1	1	0
Maytenus aquifolia	0	0	0	0	1	1
Brunfelsia cuneifolia	0	0	0	1	0	0
Drimys brasiliensis	0	0	0	1	0	0
Rudgea jasminoides	0	0	0	1	0	0