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Patterns of diaspore functional diversity in *Araucaria* Forest successional stages in extreme southern Brazil

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Received: November 6 2013

Accepted: March 17 2014

Available online at <http://www.ufrgs.br/scerbio/ojs/index.php/rbb/article/view/2829>

ABSTRACT: (Patterns of diaspore functional diversity in *Araucaria* Forest successional stages in extreme southern Brazil). Dispersal is an essential process for community assembly, since it defines the species that have the potential to colonize a particular site. It is possible to infer the dispersal agent from the traits that constitute the plant dispersal syndrome, such as diaspore color and size. The vegetation of southern Brazil consists of forest-grassland mosaics, in which forest expansion is occurring where land management does not preclude the process. Here, we assessed: (1) if there is variation in the functional diversity of zoochorous diaspore traits of young trees along a canopy openness gradient in *Araucaria* and *Podocarpus* forest patches, and (2) what diaspore traits of tree species are associated with the canopy openness gradient. Additionally, we present a list of tree species occurring at the study site. Zoochory is the main dispersal syndrome in these forests, in both early and advanced stages of vegetation succession. Diaspore functional diversity decreased from large forest to small patches, likely due to habitat-use patterns of vertebrate seed dispersers. Our results suggest that the disperser fauna is essential to the forest-grassland dynamics throughout the process of forest expansion over the grassland.

Key words: diaspore trait, dispersal spectrum, forest expansion, *Pampa* biome, zoochory.

RESUMO: (Padrões de diversidade funcional de diásporos em manchas de floresta com Araucária no extremo sul do Brasil). A dispersão é um processo fundamental para a organização das comunidades, já que determina as espécies que colonizarão determinado sítio. A inferência do agente dispersor é possível através de atributos que compõem a síndrome de dispersão da planta, como tamanho e cor do diásporo. A vegetação do sul do Brasil é caracterizada por mosaicos formados por florestas e campos, sendo que a floresta está em expansão onde o manejo da terra não impede o processo. O objetivo desse trabalho foi avaliar: (1) se há variação na diversidade funcional de atributos de diásporos zoocóricos de árvores juvenis ao longo de um gradiente de abertura de dossel em manchas de floresta com *Araucaria* e *Podocarpus*, e (2) quais atributos de diásporo de espécies arbóreas estão relacionados ao gradiente de abertura de dossel. Além disso, apresentamos uma lista das espécies que ocorrem na área de estudo. A zoocoria é a síndrome de dispersão predominante nas florestas estudadas, tanto em estágios iniciais e avançados de sucessão vegetacional. A diversidade funcional dos diásporos decresce da floresta às manchas florestais pequenas sobre o campo provavelmente devido aos padrões de uso do habitat pelos vertebrados dispersores de sementes. Nossos resultados sugerem que a fauna de dispersores é essencial para a dinâmica do mosaico durante todo o processo de expansão da floresta sobre o campo.

Palavras-chave: atributo de diásporo, bioma *Pampa*, espectro de dispersão, expansão florestal, zoocoria.

INTRODUCTION

The structure and composition of a plant community can be influenced by several factors, including environmental heterogeneity, biotic interactions such as competition between species, and seed dispersal (Levin *et al.* 2003). Dispersal is an essential process for community assembly, as it may determine where the seed will be deposited. The particular site where a seed is deposited is critical for the success of seedling establishment (Janzen 1970, Willson 1992, Rondon Neto *et al.* 2001). One of the plant strategies to improve dispersion is to adapt their reproductive characters to different dispersal agents, constituting the dispersal syndromes (Ridley 1930). Thus, the characteristics that constitute the endozoochorous dispersal syndrome can be considered traits for disperser

attraction (Duarte *et al.* 2011). Then, it is possible to infer that a fruit or seed is dispersed by an animal from the diaspore attributes such as color, odor and size (Ridley 1930, Van der Pijl 1969, Howe & Smallwood 1982, Janson 1983). Anemochory and autochory can be inferred from traits such as the presence of winged structures or mechanisms of explosive dehiscence, respectively (Ridley 1930, Howe & Smallwood 1982). Considering that diaspore attributes influence plant fitness, we may consider them as functional traits.

The vegetation of southern Brazil consists of forest-grassland mosaics (Rambo 1956). The southern Brazilian grasslands (*Campos* grasslands) represent a vegetation remaining from a drier and colder climate than today, which is undergoing forest expansion due to the global

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climatic changes of the last millennia (Behling & Pillar 2007). The forest expansion over southern Brazilian grasslands is especially evident in sites with low intensity or absence of burning or grazing by domestic cattle (Overbeck *et al.* 2007). Forest expansion occurs both by edge dynamics (Oliveira & Pillar 2004) and by nucleation, in which the vegetation succession over grassland occurs with the establishment of pioneer tree species forming a small patch, which favors the establishment of late-succession tree species (Duarte *et al.* 2006a, b). Several studies have shown that zoochorous dispersal is essential for the occurrence of this process in the Brazilian *Araucaria* Forest, since most of the species involved in forest expansion are dispersed by the fauna, mainly vertebrates (Duarte *et al.* 2006a, b, 2007, 2011, Carlucci *et al.* 2011b). Despite the possible general importance of zoochory to the ecological dynamics of *Araucaria* Forest over its geographic distribution (Duarte *et al.* 2009), studies evaluating its role in forest-grassland ecotones were restricted to one geomorphological area, the South Brazilian Plateau (Duarte *et al.* 2006a, b, 2007, 2011, Carlucci *et al.* 2011b). There are few studies on the relative importance of dispersal syndromes in forest-grassland mosaics in other geomorphological regions, even in well-conserved areas such as the Serra do Sudeste, in extreme southern Brazil.

The Serra do Sudeste region is part of the Brazilian Pampa biome, the northeastern portion of the South American pampas grasslands; and is characterized by a mosaic formed by native grasslands managed for grazing, and by seasonal forests with a marked presence of *Araucaria angustifolia* and *Podocarpus lambertii* (Carlucci *et al.* 2011a). Few vegetation surveys have been performed in the region (Jurinitz & Jarenkow 2003, Giongo & Waechter 2007, Dadalt 2010), even though the Serra do Sudeste has been considered one of the best-conserved areas of extreme southern Brazil (Cordeiro & Hasenack 2009). In the region, the process of forest expansion is quite evident, even in grasslands used for cattle grazing (Carlucci *et al.* 2012), which is not the case for other regions in southern Brazil (Oliveira & Pillar 2004, Silva & Anand 2011).

In this study, we assessed: (1) if there is variation in the functional diversity of zoochorous diaspore traits of young trees along a canopy openness gradient in *Araucaria* and *Podocarpus* forest patches, and (2) what diaspore traits of tree species are associated with the canopy openness gradient. Additionally, we present a list of tree species occurring at the study site.

We hypothesized that diaspore functional diversity would be higher in communities with denser canopies, where we would find both small and large fruits. Lower functional diversity in small patches would be due to environmental filtering related to habitat use by dispersers and limiting conditions for sapling establishment in these habitats. We also expected lower fruit and seed sizes under sparser canopies, according to the pattern found for *Araucaria* Forest in another region of southern Brazil (Duarte *et al.* 2007).

MATERIAL AND METHODS

Study area

The study was conducted in a forest-grassland mosaic (ca. 30.8° S, 53.1° W), located in the Santana da Boa Vista municipality in the Serra do Sudeste, a geomorphologic complex characterized mainly by Precambrian granitic hills in Rio Grande do Sul, the southernmost state of Brazil. The study area is part of a landscape where the conifers *Araucaria angustifolia* (Bertol.) Kuntze and *Podocarpus lambertii* Klotzsch ex Endl. are the most prominent trees, dominating the canopies of most forest patches (Carlucci *et al.* 2012). This landscape (hereafter Santana da Boa Vista Formation) has a particular vegetation physiognomy and floristic composition within the context of the Camaquã River basin. The region includes the southern limit of distribution of the *Araucaria angustifolia* Forest (Carlucci *et al.* 2011a). The bedrock consists of gneiss (Dutra & Stranz 2003). The local climate between 1950 and 2000 was characterized by mean annual rainfall of 1473 mm, and mean annual temperature of 18.3 °C; during this period, the mean precipitation was 416 mm in the wettest quarter of the year and 332 mm in the driest quarter (Hijmans *et al.* 2005). Due to the variation in precipitation over the year, the forests of the region are seasonal. Locally, forests spread along streams and slopes, and also appear as isolated small patches across the grassland matrix. The grasslands are grazed by domestic cattle, but burning is not a common management practice in the region. The small forest patches, usually with an area of ca. 100 m², represent early forest successional stages, while large patches, covering dozens of hectares, represent late forest successional stages (Carlucci *et al.* 2012).

Vegetation sampling

We collected data on tree saplings in 40 circular plots (area = 4.5 ± 0.1 m²) (Carlucci *et al.* 2012). We placed half of the plots in 20 forest patches in the grassland matrix, and the other half within a large forest patch (area ca. 35 ha), in order to capture the widest variation of the environmental gradient. We considered that small forest patches spread through the grassland represent the initial stages of forest succession, while the forest interior represents more advanced stages of succession (Carlucci *et al.* 2012). In each plot, we recorded all tree saplings with heights of 15 to 100 cm. The data for species abundance by plot were arranged in a binary matrix (**W**).

Canopy openness

We measured the canopy openness as the environmental variable. We used this variable as a proxy of habitat for potential disperser animals, since we assumed that the plots in forest patches and in the forest interior belonged to different stages of forest succession (Carlucci *et al.* 2012). The data for the proportion of canopy openness in the plots were arranged in a univariate matrix **E**. For details of the canopy openness data see Carlucci *et al.* (2012).

Trait data

For all species recorded in the survey of tree saplings, we inferred the dispersal strategies through the diaspore traits, following the classification by Van der Pijl (1969). The fruit traits of size, type and color, and seed size and number of seeds per diaspore were compiled from the literature. Based on these traits, the species were classified in one of the following groups according to the dispersal syndrome: 1) endozoochory, diaspores with characteristics of attraction of frugivorous fauna, such as fleshy tissues and bright colors; 2) anemochory, presence of winged structures; 3) autochory, presence of mechanisms for explosive dehiscence.

In the data analysis of the survey of tree saplings, we used only the zoochorous species. We organized the diaspore traits (fruit size, type and color, and seed size and number of seeds per diaspore) in a matrix describing the species by traits (matrix **B**).

Data analysis

We used the method proposed by Pillar *et al.* (2009) for discriminating trait-convergence assembly patterns (TCAP), which basically consists of a Mantel correlation between a matrix of community-weighted trait means (**T**) (Garnier *et al.* 2004) and an environmental matrix (**E**). The correlation of matrix **T** with the matrix of environmental variable **E** ($\rho(\mathbf{TE})$) shows if functional similarities are related to environmental similarities, that is, shows trait-convergence patterns related to canopy openness. TCAP differs from a simple Mantel correlation in the way that iterations are made to produce null communities (see Pillar *et al.* 2009). To analyze diaspore TCAP associated with canopy openness, we used the package SYNCSA available in R (R Development Core Team 2012). To obtain the set of diaspore traits maximizing TCAP, we used the *max.tcap* function. Through the *syncsa* function, we obtained *P*-values. To assess how the diaspore traits are related to the canopy openness gradient, matrix **T** was submitted to a principal coordinates analysis (PCoA), using as the similarity measure the Euclidean distance between sampling units. The PCoA was performed in MULTIV v. 2.67 $\gamma\beta$ (V. Pillar, available at [<http://ecoqua.ecologia.ufrgs.br>]). In order to better explore the patterns of TCAP, we used linear regressions of mean values of each trait maximizing TCAP. The functional diversity for each community was measured by Rao's quadratic entropy and related to values of canopy openness through linear regression.

Tree species list

The list of tree species in the study area was compiled based on two sources: (1) survey of saplings of tree species (Carlucci *et al.* 2012), and (2) survey of tree species by walking across the area and recording every tree and tree sapling that was seen. Field excursions were conducted from January 2010 through March 2011. Individuals in the reproductive phase were collected and incorporated into the ICN Herbarium, at the Federal University of Rio

Grande do Sul (UFRGS). The collection numbers are provided in Table 1. Taxonomic classification of species follows the proposal of APG III (2009). The botanical names and their authors follow IPNI (2011).

RESULTS

Overall, we recorded 73 tree species, belonging to 55 genera and 36 families (Table 1). Most species were zoochorous (84.93%); the proportions of anemochorous and autochorous species were much lower, 9.59% and 5.48%, respectively. In the vegetation survey we recorded 50 species; 23 of them occurred in both the small forest patches and the large forest patch, while 27 occurred only in the large patch (Table 2). The proportion of zoochory was similar among forest patches in both early and late stages of succession (Fig. 1).

The functional diversity was significantly associated with canopy openness ($R^2 = 0.53$; $P < 0.001$). We found that higher values of functional diversity were related to more-closed canopies (Fig. 2). We also found trait-convergence assembly patterns (TCAP) related to the canopy openness gradient. The traits responsible for maximization of TCAP [$\rho(\mathbf{TE})=0.51$] were: fruit size, fruit color (black, red) and number of seeds per diaspore. The PCoA revealed that larger fruit size, higher frequency of black and red fruits, and larger number of seeds per diaspore were related to more-closed (denser) canopies, in the forest interior (Fig. 3). The traits were highly and positively related to the first PCoA axis, which explained 61.5% of the variation in the data.

The regressions of each selected trait with canopy openness (Fig. 4) revealed that the fruit size, ratio of black and red fruits, and proportion of plants with one seed per diaspore were higher in communities inside the forest (R^2 values = 0.192, 0.259, 0.346 and 0.48, respectively).

DISCUSSION

The first remarkable result was that only approximately half of the species occurring in the large forest patch also occurred in the small forest patches scattered across the grassland. In a previous study, Carlucci *et al.* (2012) showed that there is a filtering of sapling individuals colonizing small patches, related to leaf traits. The authors argued that only saplings with low specific leaf area are able to resist the adverse conditions in the grassland, such as intense solar radiation and water stress. Nevertheless, there might be a filtering of individuals and ultimately species before establishment, i.e., during dispersal. Here, we showed that diaspores tended on average to be larger in the forest interior and smaller in the small patches. This pattern may be related to the use of habitat by dispersers. Vertebrates that disperse larger diaspores are likely to remain most of the time in the large forest patch, which seems to be the case for brown howler monkeys (*Alouatta guariba*), and birds such as toucans (*Ramphastos toco*), guans (*Penelope obscura*) and surucua trogons (*Trogon*

Table 1. Tree species recorded in *Araucaria* and *Podocarpus* forest patches in Santana da Boa Vista Municipality, Serra do Sudeste, Rio Grande do Sul, Brazil. The dispersal syndrome of each species is provided as follows: zoo, zoochory; anem, anemochory; auto, autochory. The species with collection number (M.B.Carlucci) were incorporated into the ICN Herbarium (UFRGS).

Species	Dispersal Syndrome	Collection Number	Species	Dispersal Syndrome	Collection Number
ANACARDIACEAE			<i>Cedrela fissilis</i> Vell.	anem	-
<i>Lithraea brasiliensis</i> Marchand	zoo	7	<i>Trichilia clausenii</i> C.DC.	zoo	-
<i>Schinus lentiscifolius</i> Marchand	zoo	-	<i>Trichilia elegans</i> A.Juss.	zoo	-
<i>Schinus molle</i> L.	zoo	-	MORACEAE		
<i>Schinus polygamus</i> (Cav.) Cabrera	zoo	14	<i>Ficus luschnathiana</i> (Miq.) Miq.	zoo	-
ANNONACEAE			<i>Sorocea bonplandii</i> (Baill.) W.C.Burger, Lanjouw & Boer	zoo	-
<i>Annona neosalicifolia</i> H. Rainer	zoo	-	MYRTACEAE		
AQUIFOLIACEAE			<i>Acca sellowiana</i> (O.Berg) Burret	zoo	-
<i>Ilex brevicuspis</i> Reissek	zoo	-	<i>Blepharocalyx salicifolius</i> (Kunth) O.Berg	zoo	8
<i>Ilex dumosa</i> Reissek	zoo	17	<i>Eugenia uniflora</i> L.	zoo	-
ARAUCARIACEAE			<i>Eugenia uruguayensis</i> Cambess.	zoo	-
<i>Araucaria angustifolia</i> (Bertol.) Kuntze	zoo	-	<i>Myrcia palustris</i> DC.	zoo	5
ARECACEAE			<i>Myrcianthes pungens</i> (O.Berg) D.Legrand	zoo	-
<i>Syagrus romanzoffiana</i> (Cham.) Glassman	zoo	-	<i>Myrrhinium atropurpureum</i> Schott	zoo	-
ASTERACEAE			PODOCARPACEAE		
<i>Dasyphyllum spinescens</i> (Less.) Cabrera	anem	11	<i>Podocarpus lambertii</i> Klotzsch ex Endl.	zoo	10; 13
<i>Gochnatia polymorpha</i> (Less.) Cabrera	anem	6	PRIMULACEAE		
BERBERIDACEAE			<i>Myrsine coriacea</i> (Sw.) R.Br.	zoo	-
<i>Berberis laurina</i> Billb.	zoo	-	<i>Myrsine lorentziana</i> (Mez) Arechav.	zoo	-
BORAGINACEAE			QUILLAJACEAE		
<i>Cordia americana</i> (L.) Gottschling & J.S.Mill.	anem	-	<i>Quillaja brasiliensis</i> (A.St.-Hil. & Tul.) Mart.	anem	-
CANNABACEAE			RHAMNACEAE		
<i>Celtis iguanaea</i> (Jacq.) Sarg.	zoo	-	<i>Scutia buxifolia</i> Reissek	zoo	-
CARDIOPTERIDACEAE			RUBIACEAE		
<i>Citronella gongonha</i> (Mart.) R.A. Howard	zoo	-	<i>Guettarda uruguensis</i> Cham. & Schldt.	zoo	-
<i>Citronella paniculata</i> (Mart.) R.A. Howard	zoo	-	RUTACEAE		
CELASTRACEAE			<i>Zanthoxylum astrigerum</i> (R.S.Cowan) P.G. Waterman	zoo	-
<i>Maytenus muelleri</i> Schwacke	zoo	-	<i>Zanthoxylum fagara</i> (L.) Sarg.	zoo	-
EBENACEAE			<i>Zanthoxylum rhoifolium</i> Lam.	zoo	-
<i>Diospyros inconstans</i> Jacq.	zoo	-	SALICACEAE		
ERYTHROXYLACEAE			<i>Banara tomentosa</i> Clos	zoo	-
<i>Erythroxylum myrsinites</i> Mart.	zoo	-	<i>Casearia decandra</i> Jacq.	zoo	-
EUPHORBIACEAE			<i>Casearia sylvestris</i> Sw.	zoo	-
<i>Sapium glandulosum</i> (L.) Morong	zoo	-	<i>Salix humboldtiana</i> Willd.	anem	-
<i>Sebastiania brasiliensis</i> Spreng.	auto	-	<i>Xylosma pseudosalzmanii</i> Sleumer	zoo	-
<i>Sebastiania commersoniana</i> (Baill.) L.B.Sm. & Downs	auto	-	<i>Xylosma schroederi</i> Sleumer ex Herter	zoo	4
FABACEAE			<i>Xylosma tweediana</i> (Clos) Eichler	zoo	-
<i>Calliandra cf. brevipes</i> Benth.	auto	-	SAPINDACEAE		
<i>Erythrina crista-galli</i> L.	auto	-	<i>Allophylus edulis</i> (A.St.-Hil., Cambess. & A.Juss.) Radlk.	zoo	-
<i>Inga vera</i> Willd.	zoo	-	<i>Cupania vernalis</i> Cambess.	zoo	-
LAMIACEAE			<i>Matayba elaeagnoides</i> Radlk.	zoo	-
<i>Vitex megapotamica</i> (Spreng.) Moldenke	zoo	-	SAPOTACEAE		
LAURACEAE			<i>Chrysophyllum gonocarpum</i> (Mart. & Eichler ex Miq.) Engl.	zoo	-
<i>Cinnamomum amoenum</i> (Nees) Kosterm.	zoo	9	<i>Chrysophyllum marginatum</i> (Hook. & Arn.) Radlk.	zoo	-
<i>Nectandra megapotamica</i> (Spreng.) Mez	zoo	-	SOLANACEAE		
<i>Ocotea acutifolia</i> (Nees.) Mez	zoo	-	<i>Cestrum strigilatum</i> Ruiz & Pav.	zoo	-
<i>Ocotea puberula</i> (Rich.) Nees	zoo	-	STYRACACEAE		
<i>Ocotea pulchella</i> (Nees) Mez	zoo	18	<i>Styrax leprosus</i> Hook. & Arn.	zoo	-
MALVACEAE			SYMPLOCACEAE		
<i>Luehea divaricata</i> Mart. & Zucc.	anem	-	<i>Symplocos uniflora</i> (Pohl) Benth.	zoo	-
MELASTOMATAACEAE			THYMELAEACEAE		
<i>Miconia hyemalis</i> A.St.-Hil. & Naudin ex Naudin	zoo	12	<i>Daphnopsis racemosa</i> Griseb.	zoo	-
MELIACEAE			VERBENACEAE		
<i>Cabralea canjerana</i> (Vell.) Mart.	zoo	-	<i>Citharexylum montevidense</i> (Spreng.) Moldenke	zoo	19

Table 2. Occurrence of saplings of tree species in plots in the forest interior or small patches spread over grassland, in a forest-grassland mosaic with *Araucaria* in southern Brazil.

Species	Small patches	Forest interior	Species	Small patches	Forest interior
ANACARDIACEAE			<i>Trichilia elegans</i> A.Juss.		X
<i>Lithraea brasiliensis</i> Marchand	X	X	MORACEAE		
ANNONACEAE			<i>Sorocea bonplandii</i> (Baill.) W.C.Burger, Lanjouw & Boer		X
<i>Annona neosalicifolia</i> (Schltdl.) Ekman & R.E.Fr.		X	MYRTACEAE		
AQUIFOLIACEAE			<i>Blepharocalyx salicifolius</i> (Kunth) O.Berg	X	X
<i>Ilex brevicuspis</i>		X	<i>Eugenia uniflora</i> L.	X	X
ARAUCARIACEAE			<i>Eugenia uruguayensis</i> Cambess.	X	X
<i>Araucaria angustifolia</i> (Bertol.) Kuntze	X	X	<i>Myrcia palustris</i> DC.		X
ARECACEAE			<i>Myrcianthes pungens</i> (O.Berg) D.Legrand		X
<i>Syagrus romanzoffiana</i> (Cham.) Glassman		X	<i>Myrrhinium atropurpureum</i> Schott	X	X
ASTERACEAE			PODOCARPACEAE		
<i>Dasyphyllum spinescens</i> (Less.) Cabrera	X	X	<i>Podocarpus lambertii</i> Klotzsch ex Endl.	X	X
BORAGINACEAE			PRIMULACEAE		
<i>Cordia americana</i> (L.) Gottschling & J.S.Mill.		X	<i>Myrsine coriacea</i> (Sw.) R.Br.	X	X
CANNABACEAE			<i>Myrsine lorentziana</i> (Mez) Arechav.		X
<i>Celtis iguanaea</i> (Jacq.) Sarg.		X	RUBIACEAE		
CARDIOPTERIDACEAE			<i>Guettarda uruguensis</i> Cham. & Schltdl.		X
<i>Citronella paniculata</i> (Mart.) R.A.Howard		X	RUTACEAE		
CELASTRACEAE			<i>Zanthoxylum fagara</i> (L.) Sarg.	X	X
<i>Maytenus muelleri</i> Schwacke		X	SALICACEAE		
EBENACEAE			<i>Casearia decandra</i> Jacq.	X	X
<i>Diospyros inconstans</i> Jacq.		X	<i>Casearia silvestris</i> Sw.	X	X
ERYTHROXYLACEAE			<i>Xylosma pseudosalzmanii</i> Sleumer		X
<i>Erythroxylum myrsinites</i> Mart.	X	X	<i>Xylosma schroederi</i> Sleumer ex Herter	X	X
EUPHORBIACEAE			<i>Xylosma tweediana</i> (Clos) Eichler	X	X
<i>Sebastiania brasiliensis</i> Spreng.		X	SAPINDACEAE		
<i>Sebastiania commersoniana</i> (Baill.) L.B.Sm. & Downs		X	<i>Allophylus edulis</i> (A.St.-Hil., Cambess. & A.Juss.) Radlk	X	X
FABACEAE			<i>Cupania vernalis</i> Cambess.		X
<i>Calliandra cf. brevipes</i> Benth.		X	<i>Matayba elaeagnoides</i> Radlk.	X	X
LAURACEAE			SAPOTACEAE		
<i>Cinnamomum amoenum</i> (Nees) Kosterm.		X	<i>Chrysophyllum marginatum</i> (Hook. & Arn.) Radlk.	X	X
<i>Nectandra megapotamica</i> (Spreng.) Mez		X	SOLANACEAE		
<i>Ocotea puberula</i> (Rich.) Nees		X	<i>Cestrum strigilatum</i> Ruiz & Pav.	X	X
<i>Ocotea pulchella</i> (Nees) Mez	X	X	STYRACACEAE		
MALVACEAE			<i>Styrax leprosus</i> Hook. & Arn.	X	X
<i>Luehea divaricata</i> Mart. & Zucc.		X	SYMPLOCACEAE		
MELASTOMACEAE			<i>Symplocos uniflora</i> (Pohl) Benth.		X
<i>Miconia hiemalis</i> A.St.-Hil. & Naudin ex Naudin		X	THYMELAEACEAE		
MELIACEAE			<i>Daphnopsis racemosa</i> Griseb.	X	X
<i>Cedrela fissilis</i> Vell.		X	VERBENACEAE		
<i>Trichilia clausenii</i> C.DC.		X	<i>Citharexylum montevidense</i> (Spreng.) Moldenke	X	X

surrucura). These dispersers would hardly carry large diaspores far from the forest to the small forest patches scattered across the grassland matrix. Likewise, a study in a montane Atlantic Forest of southeastern Brazil showed that fleshy fruits of Myrtaceae and Lauraceae trees are usually consumed by medium- to large-bodied arboreal frugivores, such as howler monkeys, woolly spider monkeys, cotingas, toucans, aracarís and cracids (Tabarelli & Peres 2002).

In addition, we found higher functional diversity of diaspores in the forest interior. In addition to the above-mentioned dispersers, many other bird and mammal seed dispersers use the forest-grassland mosaic. While some of these animals are essentially restricted to the large forest, most dispersers use the entire landscape, both

forest and grassland. For example, Hartz *et al.* (2012) evaluated the role of migratory birds acting as seed dispersers, and suggested that some species participate in the process of *Araucaria* Forest expansion by dispersing plant species from the forest interior to the forest patches across grasslands. It is unlikely to find a disperser that is restricted to the grassland matrix and that would use only small patches, at least in our study area. We would therefore expect to observe a higher diversity of dispersers using the large forest rather than the small patches. A higher diversity of dispersers may in part explain the higher functional diversity of diaspores in the forest interior. Large and structurally diverse forest patches may be refuge areas that provide more-stable resources, and this stability may be reflected in high richness and

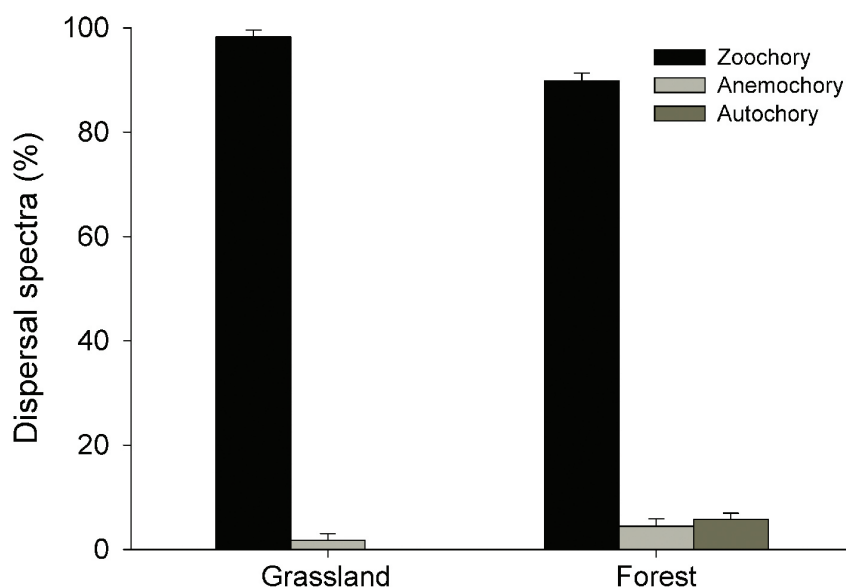


Figure 1. Dispersal spectrum of tree-sapling communities established in small forest patches in native grassland (Grassland) and in the interior of a large forest patch (Forest) in Santana da Boa Vista Municipality, Serra do Sudeste, Rio Grande do Sul, Brazil. Large vertical bars represent mean proportions; small lines above bars represent standard errors. For dispersal syndromes of species, see Table 1.

abundance of mammal species (Friend & Taylor 1985). On the other hand, the few dispersers exploiting the small patches would transport diaspores with a smaller range of traits in these locations.

In contrast to our hypothesis, we did not find significant variation in seed size related to canopy openness. Seed size is usually related to a plant strategy for establishment, as larger seeds are expected to have higher survivorship due to their energy stocks (Duarte *et al.* 2007). Thus, this

stage of establishment appears not to be determinant for the sapling community assembly in our system. Further, the statistical approach that we used (TCAP trait set maximization) might be too strict, as the set containing seed size had $\rho(TE) = 0.46$, which is also high. On the other hand, we found that seed number matters. Diaspores with one seed were associated with small forest patches. Duarte *et al.* (2007) found that an apparent association between seed number and forest successional stage was

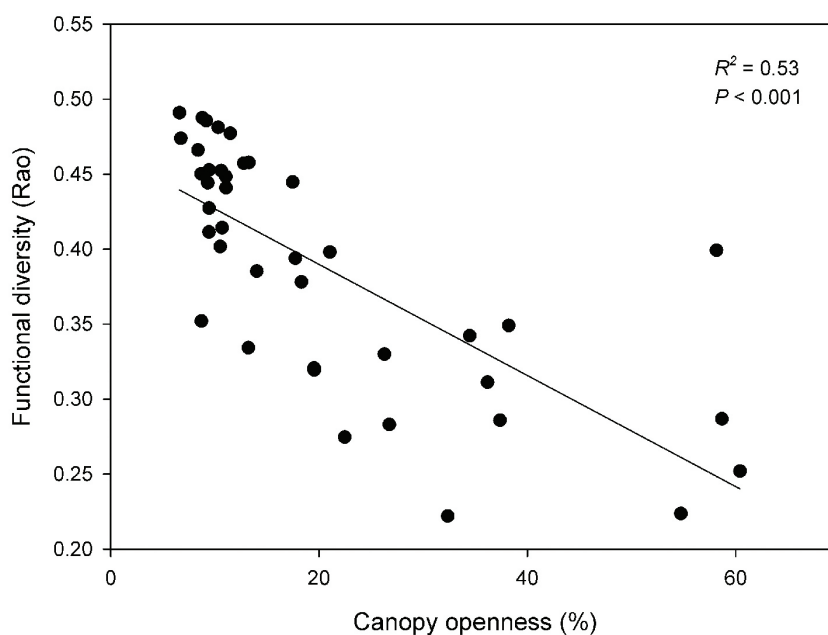


Figure 2. Linear regression of functional diversity values of diaspore traits on canopy openness gradient. Each point represents a community (n=40).

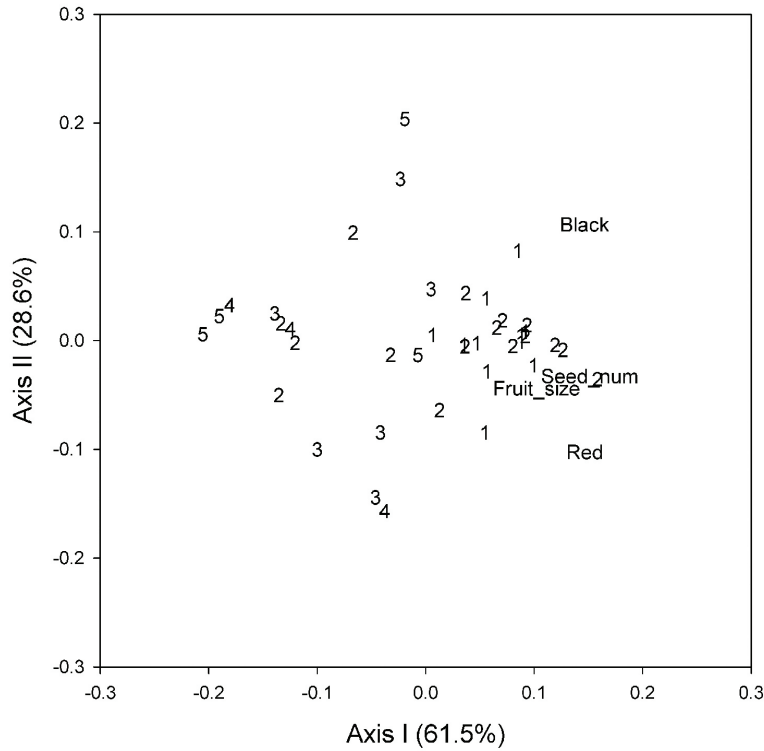


Figure 3. Diagram of Principal Coordinates Analysis (PCoA) of juvenile tree species communities described by the mean values of their diaspore traits. Communities are represented by canopy openness classes: class 1, 0 to 10%, class 2, 10 to 20%, class 3, 20 to 35%, class 4, 35 to 50%, class 5, higher than 50%. Diaspore traits: Fruit_size, fruit size; Seed_num, number of seeds per diaspore; Black, black-colored fruits; Red, red-colored fruits.

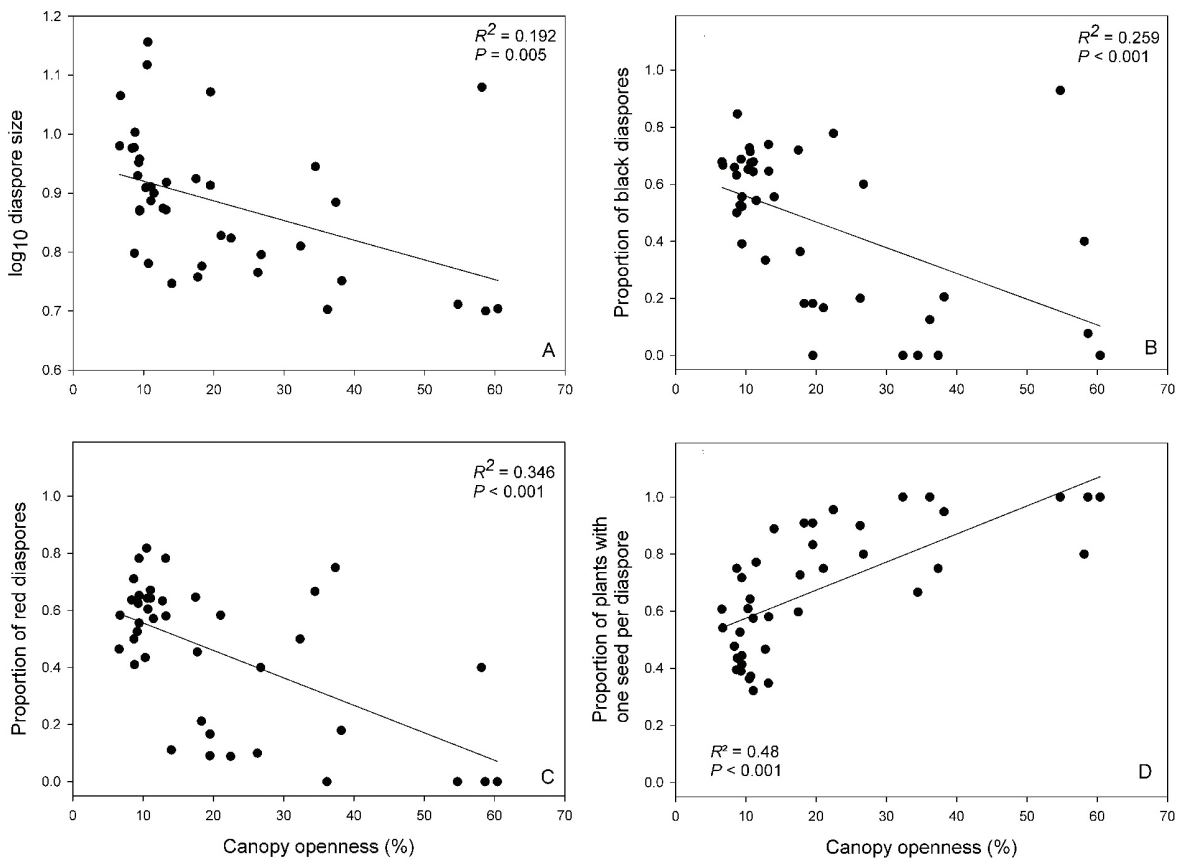


Figure 4. Regressions of selected traits and canopy openness. A. Community-weighted means for diaspore size.; B. Proportion of black-colored diaspores. C. Proportion of red-colored diaspores. D. Proportion of plants with one seed per diaspore. Each point represents a community (n=40).

mediated by phylogeny; accordingly, one-seeded species colonizing small patches may be phylogenetically closer to each other.

Our study confirms the general pattern of dominance of the zoochorous dispersal syndrome in the forests of southern Brazil. Other studies conducted in different forest formations of Rio Grande do Sul have found the same pattern of predominance of zoochory (Rondon Neto *et al.* 2001, Jurinitz & Jarenkow 2003, Budke *et al.* 2004, Bergamin & Mondin 2006). The prevalence of zoochory in the forests of southern Brazil is strong evidence of the importance of this syndrome in the dynamics of forest communities (Duarte *et al.* 2009). The present study showed that the disperser fauna indeed mediates the forest expansion from the earlier stages of succession, in the small forest patches, to the later stages, in the forest interior. In other words, we could say that the fauna is driving succession.

In conclusion, zoochory is the main dispersal syndrome in these forests, in both early and advanced stages of vegetation succession. The reason that diaspore functional diversity decreases from large forest to small patches is likely to be the patterns of habitat use by vertebrate seed dispersers. Our results suggest that the disperser fauna is essential to the forest-grassland dynamics throughout the process of forest expansion over the grassland. Therefore, the decline of animal seed-dispersal populations, for example because of anthropogenic pressure, can undermine the process of ecological succession and ultimately affect the resulting vegetation structure. Thus, efforts to conserve forest-grassland mosaics should consider protecting areas that allow the maintenance of viable populations of both the flora and the disperser fauna (Duarte *et al.* 2006b).

ACKNOWLEDGEMENTS

Field excursions were funded with resources from CNPq (479083/2008-8) and CAPES (PROF). H.S. was supported by an undergraduate scholarship from FA- PERGS (BIC and PROBIC-UFRGS); M.B.C. was supported by a MSc scholarship from CAPES (2009-2011) and a PhD scholarship from CNPq (141451/2011-4); V.D.P. was supported by a PQ fellowship from CNPq (306573/2009-1).

REFERENCES

APG III 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society*, 161: 105-121.

BEHLING, H. & PILLAR, V.D. 2007. Late Quaternary vegetation, biodiversity and fire dynamics on the southern Brazilian highland and their implication for conservation and management of modern *Araucaria* forest and grassland ecosystems. *Philosophical Transactions of the Royal Society of London B*, 362: 243-251.

BERGAMIN, R.S. & MONDIN, C.A. 2006. Composição florística e relações fitogeográficas do componente arbóreo de um fragmento florestal no município de Barra do Ribeiro, Rio Grande do Sul, Brasil. *Pesquisas Botânica*, 57: 217-230.

BUDKE, J.C., GIEHL, E.L.H., ATHAYDE, E.A., EISINGER, S.M. &

ZÁCHIA, R.A. 2004. Florística e fitossociologia do componente arbóreo de uma floresta ribeirinha, arroio Passo das Tropas, Santa Maria, RS, Brasil. *Acta Botanica Brasilica*, 18: 581-589.

CARLUCCI, M.B., JARENKOW, J.A., DUARTE, L.D.S. & PILLAR, V.D. 2011a. Conservação da Floresta com Araucária no Extremo Sul do Brasil. *Natureza & Conservação*, 9: 111-114.

CARLUCCI, M.B., DUARTE, L.D.S. & PILLAR, V.D. 2011b. Nurse rocks influence forest expansion over native grassland in southern Brazil. *Journal of Vegetation Science*, 22: 111-119.

CARLUCCI, M.B., STREIT, H., DUARTE, L.D.S. & PILLAR, V.D. 2012. Individual-based trait analyses reveal assembly patterns in tree sapling communities. *Journal of Vegetation Science*, 23: 176-186.

CORDEIRO, J. & HASENACK, H. 2009. Cobertura vegetal atual do Rio Grande do Sul. In: PILLAR, V.D., MÜLLER, S.C., CASTILHOS, Z.M.S. & JACQUES, A.V.A. (eds.). *Campos Sulinos: conservação e uso sustentável da biodiversidade*. MMA. p. 285-299.

DADALT, L.P. 2010. *Padrões de diversidade da vegetação lenhosa da região do Alto Camaquã, Rio Grande do Sul, Brasil*. 61 p. Dissertação (Mestrado em Ecologia). Universidade Federal do Rio Grande do Sul, Porto Alegre, 2010.

DUARTE, L.D.S., MACHADO, R.E., HARTZ, S.M. & PILLAR, V.D. 2006a. What saplings can tell us about forest expansion over natural grasslands. *Journal of Vegetation Science*, 17: 799-808.

DUARTE, L.D.S., DOS SANTOS, M.M.G., HARTZ, S.M. & PILLAR, V.D. 2006b. Role of nurse plants in *Araucaria* Forest expansion over grassland in south Brazil. *Austral Ecology*, 31: 520-528.

DUARTE, L.D.S., CARLUCCI, M.B., HARTZ, S.M. & PILLAR, V.D. 2007. Plant dispersal strategies and the colonization of *Araucaria* forest patches in a grassland-forest mosaic. *Journal of Vegetation Science*, 18: 847-858.

DUARTE, L.D.S., CARLUCCI, M.B. & PILLAR, V.D. 2009. Macroecological analyses reveal historical factors influencing seed dispersal strategies in Brazilian *Araucaria* forests. *Global Ecology and Biogeography*, 18: 314-326.

DUARTE, L.D.S., CARLUCCI, M.B., FONTANA, C.S., HARTZ, S.M. & PILLAR, V.D. 2011. Plant diaspore traits as indicators of mutualistic interactions in woody vegetation patches developing into a grassland-forest mosaic. *Community Ecology*, 12: 126-134.

DUTRA, T. & STRANZ, A. 2003. História das Araucariaceae: a contribuição dos fósseis para o entendimento das adaptações modernas da família no Hemisfério Sul, com vistas a seu manejo e conservação. In: RONCHI, L. & COELHO, O. (Eds.). *Tecnologia, diagnóstico e planejamento ambiental*. São Leopoldo: UNISINOS. p. 293-351.

FRIEND, G.R. & TAYLOR, J.A. 1985. Habitat preferences of small mammals in tropical open-forest of the Northern Territory. *Australian Journal of Ecology*, 10: 173-185.

GARNIER, E., CORTEZ, J., BILLÈS, G., NAVAS, M.-L., ROUMET, C., DEBUSSCHE, M., LAURENT, G., BLANCHARD, A., AUBRY, D., BELLMANN, A., NEILL, C. & TOUSSAINT, J.-P. 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, 85: 2630-2637.

GIONGO, C. & WAECHTER, J.L. 2007. Composição florística e espectro de dispersão das espécies arbóreas de uma floresta mista com *Podocarpus*, Rio Grande do Sul. *Revista Brasileira de Biociências*, 5(s2): 333-335.

HARTZ, S.M., PINHEIRO, G.C., MENDONÇA-LIMA, A. & DUARTE, L.D.S. 2012. The potential role of migratory birds in the expansion of *Araucaria* Forest. *Natureza & Conservação*, 10: 52-56.

HIJMANS, R.J., CAMERON, S.E., PARRA, J.L., JONES, P.G. & JARVIS, A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25: 1965-1978.

HOWE, H. F. & SMALLWOOD, J. 1982. Ecology of seed dispersal. *Annual Review of Ecology, Evolution, and Systematics*, 13: 201-228.

IPNI 2011. The International Plant Names Index. Available at: <http://www.ipni.org> Accessed in 2011.

JANSON, C.H. 1983. Adaptation of fruit morphology to dispersal agents in a Neotropical forest. *Science*, 219: 187-189.

- JANZEN, D.H. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist*, 104: 501-528.
- JURINITZ, C.F. & JARENKOW, J.A. 2003. Estrutura do componente arbóreo de uma floresta estacional na Serra do Sudeste, Rio Grande do Sul, Brasil. *Revista Brasileira de Botânica*, 26: 475-487.
- LEVIN, S.A., MULLER-LANDAU, H.C., NATHAN, R. & CHAVE, J. 2003. The ecology and evolution of seed dispersal: a theoretical perspective. *Annual Review of Ecology, Evolution, and Systematics*, 34: 575-604.
- OLIVEIRA, J.M. & PILLAR, V.D. 2004. Vegetation dynamics on mosaics of Campos and *Araucaria* forest between 1974 and 1999 in Southern Brazil. *Community Ecology*, 5: 197-202.
- OVERBECK, G.E., MÜLLER, S.C., FIDELIS, A., PFADENHAUER, J., PILLAR, V.D., BLANCO, C.C., BOLDRINI, I.I., BOTH, R. & FORNECK, E.D. 2007. Brazil's neglected biome: The South Brazilian Campos. *Perspectives in Plant Ecology, Evolution and Systematics*, 9: 101-116.
- PILLAR, V.D., DUARTE, L.D.S., SOSINSKI J.R., E.E. & JONER, F. 2009. Discriminating trait-convergence and trait-divergence assembly patterns in ecological community gradients. *Journal of Vegetation Science*, 20: 334-348.
- R DEVELOPMENT CORE TEAM. 2012. R: A language and environment for statistical computing. In: *R Foundation for Statistical Computing*. Vienna. Available at <<http://R-project.org/>>
- RAMBO, B. 1956. *A Fisionomia do Rio Grande do Sul*. Porto Alegre: Selbach. 417 p.
- RIDLEY, H. 1930. *The Dispersal of Plants Throughout the World*. Kent: L. Reeve & Co. 744 p.
- RONDON-NETO, R.M., WATZLAWICK, L.F. & CALDEIRA, M.V.W. 2001. Diversidade florística e síndromes de dispersão de diásporos das espécies arbóreas de um fragmento de Floresta Ombrófila Mista. *Revista Ciências Exatas e Naturais*, 3: 209-2016.
- SILVA, L.C.R. & ANAND, M. 2011. Mechanisms of *Araucaria* (Atlantic) Forest Expansion into Southern Brazilian Grasslands. *Ecosystems*, 14: 1354-1371.
- TABARELLI, M. & PERES, C.A. 2002. Abiotic and vertebrate seed dispersal in the Brazilian Atlantic forest: implications for forest regeneration. *Biological Conservation*, 106: 165-176.
- VAN DER PIJL, L. 1969. *Principles of Dispersal in Higher Plants*. New York: Springer-Verlag. 154 p.
- WILLSON, M. 1992. The Ecology of Seed Dispersal. In: FENNER, M. (ed). *Seeds: The Ecology of Regeneration in Plant Communities*. Wallingford: CABI Publishing. p. 61-85.