



Dispersion and aggregation patterns of tree species in *Araucaria* Forest, Southern Brazil

JOÃO PAULO DE MAÇANEIRO¹, ANDRÉ LUÍS DE GASPER²,
FRANKLIN GALVÃO³ and LAURI A. SCHORN⁴

¹Universidade Federal do Paraná/UFPR, Programa de Pós-Graduação em Engenharia Florestal, Departamento de Engenharia Florestal, Avenida Prefeito Lothário Meissner, 900, Jardim Botânico, 80210-170 Curitiba, PR, Brazil

²Fundação Universidade Regional de Blumenau/FURB, Centro de Ciências Exatas e Naturais, Departamento de Ciências Naturais, Rua Antônio da Veiga, 140, Victor Konder, 89012-900 Blumenau, SC, Brazil

³Universidade Federal do Paraná/UFPR, Setor de Ciências Agrárias, Departamento de Engenharia Florestal, Avenida Prefeito Lothário Meissner, 900, Jardim Botânico, 80210-170 Curitiba, PR, Brazil

⁴Fundação Universidade Regional de Blumenau/FURB, Centro de Ciências Tecnológicas, Departamento de Engenharia Florestal, Rua São Paulo, 3250, Itoupava Seca, 89010-971 Blumenau, SC, Brazil

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ABSTRACT

Studies about dispersal syndromes and spatial distribution can provide information about species ecology. However, few studies analyze these ecological patterns in different vegetation layers. In this work, we verified the relationship between the dispersion syndromes and the spatial distribution in different layers in *Araucaria* Forest. We sampled 180 plots with size and inclusion criteria that changed according to the vegetative layer. We sampled 15,545 individuals in 103 tree species. We found significant differences between the number of species in the dispersion syndromes ($\chi^2 = 11.52$; $P \leq 0.05$) and spatial distribution patterns ($\chi^2 = 10.94$; $P \leq 0.05$), being zoochoric and tends to clustering the most predominant. We also found a significant interaction between the dispersion syndromes and spatial distribution patterns in the analyzed layers ($F = 1,044$; $P < 0.0001$), with anemochoric species characterized by random distribution, autochoric in the cluster distribution and zoochoric in the tends to clustering. The results demonstrate that the tree species of the different layers are related to the type of dispersion and the aggregation pattern.

Key words: *Araucaria* forest, seed dispersal, spatial distribution, layers analysis.

INTRODUCTION

The Atlantic Forest hotspot covered ~1,300,000 km² of Brazilian territory and also a small portion of Argentina – 9,950 km² (Chebez and Hilgert 2003, De Angelo 2009) and Paraguay – 11,618

km² (Cartes and Yanosky 2003, Huang et al. 2007, 2009). It has high biodiversity (Stehmann et al. 2009), but, due to a historical process of 500 years of deforestation, it is currently highly fragmented, with only 11.7% of its original covering in Brazil (Ribeiro et al. 2011). Currently, the destruction of these forests for urban expansion and agricultural frontiers has resulted in high levels of fragmentation and threat to biodiversity (Tabarelli et al. 2010).

Correspondence to: João Paulo de Maçaneiro
E-mail: jpmacaneiro@gmail.com

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The fragmentation process in tropical and subtropical forests, change natural habitats, limit seed dispersal and provide aggregation of tree species, as well as promote a high loss of fauna and flora diversity due to the structural complexity of these forests (Nathan and Muller-Landau 2000, Padilha et al. 2015). Changes in habitats may, for example, reflect on the decline of populations of frugivorous animals (Cox and Kesler 2012), which are responsible for 80% of seed dispersion in forest canopy species (Beckman and Rogers 2013). Another consequence of the fragmentation is the strong tendency of aggregation of the tree species, because in the absence of disperser agents, the seeds tend to fall closer to its mother plant (Wilson et al. 2004, Nathan 2006), as well as their reproductive isolation and consequent reduction of genetic diversity (Reis et al. 2012).

For many tree species, the spatial distribution pattern is strongly correlated with seed morphology, since it differs in its ability to disperse seeds (Seidler and Plotkin 2006). In old growth tropical and subtropical forests, between 50 and 75% of tree species produce fleshy fruits, which facilitates the animal feeding (Beckman and Rogers 2013, Traveset et al. 2014). This dispersion by animals can lead to occasional accumulations of propagules, due to their behavior (Schupp et al. 2002). On the other hand, the diaspore of wind-dispersed species tends to travel long distances from its mother plant and the success of the dispersal is conditioned by the wind intensity and forest canopy pattern (Nathan and Katul 2005).

The *Araucaria* Forest comprises a large part of southern plateau (Klein 1960, IBGE 2012, Kersten et al. 2015), and it is the greatest phytogeographic unit in extension and the most fragmented in the Brazilian Atlantic Forest. *Araucaria* forests originally occupied 42,851 km² of the state of Santa Catarina (Klein 1978), but due to the intense fragmentation process it is currently reduced to only 24.4% of its original covering (Vibrans et

al. 2012). In addition, these remnants are largely represented by fragments of secondary forests in the intermediate and late stages of regeneration, with rare primary or initial forests (Sevegnani et al. 2012, Vibrans et al. 2013, Maçaneiro et al. 2015, Maçaneiro et al. 2016a).

Considering the current state of *Araucaria* Forest's fragmentation in Santa Catarina (see Vibrans et al. 2012), studies that analyze the correlation between dispersal syndromes and spatial distribution patterns are significant since they can provide information on the conservation status of the current remnants and on the autoecology of plant species (Cousens et al. 2008). In this sense, we analyzed the relationship between the dispersion syndromes and the spatial distribution patterns of *Araucaria* Forest in Southern Brazil, in order to contribute to the tree species' population ecology and answer the following questions: i) Does the strategy of seed dispersal in the *Araucaria* Forest reflect the pattern of spatial distribution of tree species? ii) Are there differences between the forest layers with the dispersion syndromes and the patterns of spatial distribution of tree species?

MATERIALS AND METHODS

STUDY AREA

The study area is located in RPPN Emilio Einsfeld Filho, Campo Belo do Sul, Santa Catarina, Southern Brazil with 6,328.60 ha and altitude ranging from 620 to 980 m, between 27°55' and 28°05'S and 50°55' and 50°44'W. The climate, according to Köppen's classification (Alvares et al. 2014), is Cfb - temperate oceanic climate, without dry season and with temperate summer. The average annual temperature varies between 16-17°C, with monthly averages between 11°C in the coldest month (July) and, 21°C in the hottest month (February). The annual relative moisture varies between 78-80% and, the total annual rainfall is well distributed

with 1,527 mm throughout the year (Pandolfo et al. 2002).

The study area vegetation is constituted by *Araucaria* Forest (also called as Mixed Ombrophilous Forest - IBGE 2012), mainly characterized by dense presence of Brazilian pine [*Araucaria angustifolia* (Bertol.) Kuntze]. The area was used for logging until 1985, and this exploration concentrated on the Brazilian pine and other species of economic interest (like *Ocotea porosa* (Nees & Mart.) Barroso, *Ocotea odorifera* (Vell.) Rohwer and *Cedrela fissilis* Vell.). Currently, the forest in the study area is characterized by degraded vegetation remnants due to selective use in the past. (Maçaneiro et al. 2016b) and characterized as a continuous fragment formed by corridors, especially through the river system.

DATA COLLECTION

We divided the vegetation in three layers: 1) upper tree layer (UTL); 2) lower tree layer (LTL) and, 3) natural regeneration (NR). In the first two layers, tree individuals have reached maturity and in the third layer, the plants are in the process of natural regeneration. We randomly assigned 180 plots of 10 x 50 m (500 m²) (including palms and tree ferns) with diameter at breast height (DBH) \geq 10 cm for UTL. In each part of the UTL we added a subplot of 10 x 25 m (250 m²), to access the LTL, characterized by individuals with 5 cm \leq DBH < 10 cm. For the NR survey, a circular plot with 2.5 m radius was inserted in the center of each UTL plot (19.6 m²), where we sampled all individuals with height \geq 50 cm and DBH < 5 cm. These plots were randomized and installed at a minimum distance of 20 m from the forest edge.

The botanical material was identified in the Laboratory of Dendrology and Dr. Roberto Miguel Klein Herbarium (FURB), from the Universidade Regional de Blumenau (FURB), as well as in available literature. We followed APG IV and PPG

I for species classification (APG IV 2016, PPG I 2016) and Brazilian Flora 2020 (2017) for scientific names.

DATA ANALYSIS

We classified the species as anemochoric, autochoric and zoochoric, following Pijl (1982), based on *Araucaria* Forest studies, such as Paise and Vieira (2005), Almeida et al. (2008), Liebsch and Mikich (2009), Liebsch et al. (2009), Klauberg et al. (2010), Negrini et al. (2012) and Ferreira et al. (2013).

We calculated, for each population, the McGuinness index, to analyze the distribution pattern. This index is based on the relationship between the observed density and the expected density of individuals of a given species in the sample (McGuinness 1934). Thus, when the value is < 1 the distribution of the species is uniform; when it is equal to 1 the distribution is random; when it is > 1 and ≤ 2 the distribution tends to cluster and; when > 2 the distribution is clustered.

In order to verify if the dispersion syndromes and spatial distribution patterns differ in the analyzed layers, a partitioned chi-square test was applied using a level of significance $\alpha = 0.05$. Then, the existence of interaction between the dispersion syndromes and the spatial distribution patterns was tested through *two-way* ANOVA. In this analysis, the number of individuals of each species in the plots was considered, and a significance level of $\alpha = 0.05$ was applied. We tested the assumptions of normality, homoscedasticity and randomness (Zar 2010).

RESULTS

We sampled 15,545 individuals, belonging to 103 species, 76 genera and 44 families (Tables I and II). Myrtaceae had the highest richness (16 species), followed by Fabaceae and Lauraceae (7 species each); Euphorbiaceae, Rutaceae, Sapindaceae and Solanaceae (5 species each).

TABLE I
Analyzed parameters for the species in different layers of
***Araucaria* Forest in Southern Brazil.**

Parameters	Upper tree layer	Lower tree layer	Natural regeneration
Sample area (m ²)	90,000.00	45,000.00	3,534.30
Species number	98	85	89
Genus number	72	67	66
Families number	40	38	40
Individual number	8,362	3,105	4,078
Tree density (ind.ha ⁻¹)	929.1	690.0	11,538.4
Basal area (m ² .ha ⁻¹)	42.77	2.68	-

There were significant differences in the species dispersion syndromes and spatial distribution patterns in the analyzed layers (dispersion syndromes: $\chi^2 = 11.52$; $p \leq 0.05$; spatial distribution patterns: $\chi^2 = 10.94$; $p \leq 0.05$). Zoochoric is the most common syndrome (UTL = 69.4%, LTL = 70.6% and NR = 70.8%) with a tends to cluster the most common distribution pattern (UTL= 71.1%, LTL = 54.1% and NR= 58.4%) (Figure 1).

There are significant interaction (ANOVA, $F = 1,044$; $p < 0.0001$) between the dispersion syndromes and the patterns of spatial distribution in all layers, indicating that the species are influenced by these ecological characteristics (Figure 2). In the zoochoric species, more than 75% have tends to cluster spatial distribution.

DISCUSSION

Our results show that the dispersion syndromes and the patterns of spatial distribution of tree species vary according to the forest layer. In addition, the distribution of tree species is conditioned by the dispersion syndrome and the aggregation pattern. Regarding the dispersion syndromes, the prevalence of zoocoria is expected for the *Araucaria* Forest, occurring with greater intensity in the forest's lower layers where it can represent up to 80% of the tree species (Foster 1982, Beckman and Rogers 2013). In the present study, the high richness of zoochoric species may be an indication that the forest is in its late stage of regeneration, since the

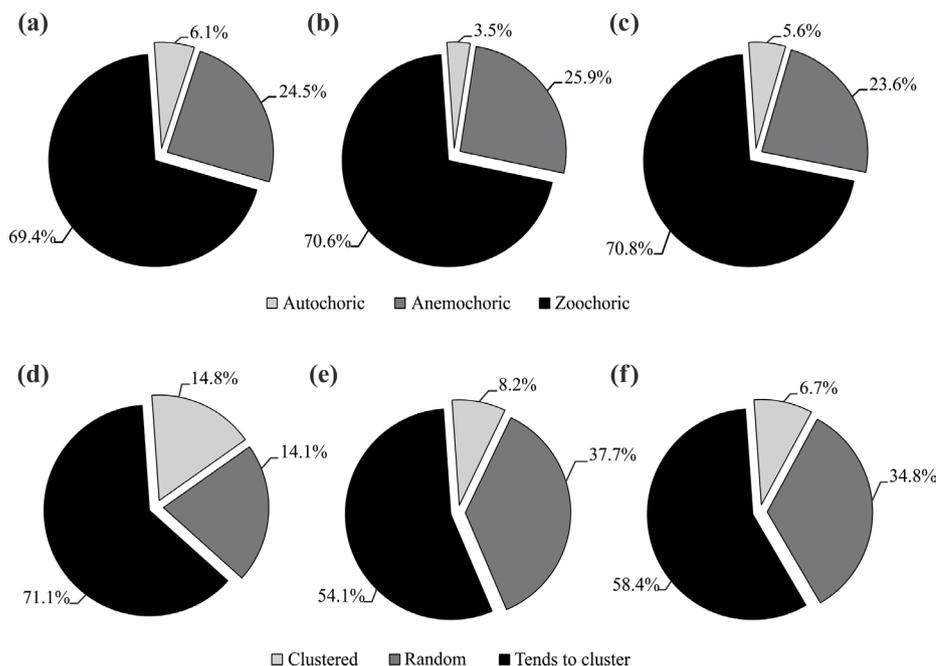


Figure 1 - Dispersion syndrome (%) and spatial distribution pattern (%) for upper tree layer (a, d); lower tree layer (b, e) and natural regeneration (c, f) of *Araucaria* Forest in Southern Brazil.

Table II

Families and species sampled in different layers of *Araucaria* Forest in Southern Brazil. SD = dispersion syndrome; An = anemochoric; Au = autochoric; Zo = zoochoric; UTL = upper tree layer; LTL = lower tree layer; NR = natural regeneration; * = Species absent in the layer; C = clustered; R = random; Tc = tends to cluster.

Families	Species	SD	McGuinnes index			Spatial distribution		
			UTL	LTL	NR	UTL	LTL	NR
Adoxaceae	<i>Sambucus australis</i> Cham. & Schltldl.	Zo	1.49	*	*	Tc	*	*
Anacardiaceae	<i>Lithrea brasiliensis</i> Marchand	Zo	3.22	1.51	*	C	Tc	*
	<i>Schinus lentiscifolia</i> Marchand	Zo	1.18	1.00	*	Tc	R	*
	<i>Schinus terebinthifolia</i> Raddi	Zo	2.99	1.00	1.00	C	R	R
Annonaceae	<i>Annona emarginata</i> (Schltldl.) H.Rainer	Zo	1.21	1.42	1.39	Tc	Tc	Tc
Apocynaceae	<i>Aspidosperma tomentosum</i> Mart.	An	2.99	1.00	1.00	C	R	R
Aquifoliaceae	<i>Ilex dumosa</i> Reissek	Zo	1.65	*	*	Tc	*	*
	<i>Ilex theezans</i> Mart. ex Reissek	Zo	1.99	1.00	1.32	Tc	R	Tc
Araucariaceae	<i>Araucaria angustifolia</i> (Bertol.) Kuntze	Zo	1.94	1.41	1.40	Tc	Tc	Tc
Arecaceae	<i>Syagrus romanzoffiana</i> (Cham.) Glassman	Zo	1.51	1.00	1.47	Tc	R	Tc
Asteraceae	<i>Baccharis uncinella</i> DC.	An	*	1.00	*	*	R	*
	<i>Moquiniastrium polymorphum</i> (Less.) G. Sancho	An	1.85	1.00	1.00	Tc	R	R
	<i>Piptocarpha angustifolia</i> Dusén ex Malme	An	2.26	1.99	1.00	C	Tc	R
	<i>Vernonanthura discolor</i> (Spreng.) H.Rob.	An	1.99	1.00	1.00	Tc	R	R
Bignoniaceae	<i>Handroanthus catarinensis</i> (A.H.Gentry) S.Grose	An	1.00	1.00	1.00	R	R	R
	<i>Jacaranda micrantha</i> Cham.	An	1.70	1.38	1.00	Tc	Tc	R
Boraginaceae	<i>Cordia americana</i> (L.) Gottschling & J.S.Mill.	An	1.15	1.00	1.00	Tc	R	R
Canellaceae	<i>Cinnamodendron dinisii</i> Schwacke	Zo	2.34	1.42	1.53	C	Tc	Tc
Cardiopteridaceae	<i>Citronella gongonha</i> (Mart.) R.A.Howard	Zo	1.10	1.26	1.31	Tc	Tc	Tc
Celastraceae	<i>Maytenus aquifolia</i> Mart.	Zo	1.26	1.12	1.00	Tc	Tc	R
Clethraceae	<i>Clethra scabra</i> Pers.	Au	1.00	*	1.00	R	*	R
Cunoniaceae	<i>Lamanonia ternata</i> Vell.	An	1.84	1.32	1.00	Tc	Tc	R
	<i>Weinmannia humilis</i> Engl.	An	1.00	1.00	1.00	R	R	R
Cyatheaceae	<i>Alsophila setosa</i> Kaulf.	An	1.76	1.24	1.16	Tc	Tc	Tc
Dicksoniaceae	<i>Dicksonia sellowiana</i> Hook.	An	4.11	1.00	3.50	C	R	C
Erythroxylaceae	<i>Erythroxylum argentinum</i> O.E.Schulz	Zo	1.41	1.00	1.00	Tc	R	R
Escalloniaceae	<i>Escallonia bifida</i> Link & Otto	An	1.49	*	1.00	Tc	*	R
Euphorbiaceae	** <i>Aleurites moluccana</i> (L.) Willd.	Zo	1.49	1.24	1.00	Tc	Tc	R
	<i>Bernardia pulchella</i> (Baill.) Müll. Arg.	Zo	1.13	1.00	1.10	Tc	R	Tc
	<i>Sapium glandulosum</i> (L.) Morong	Au	3.12	1.77	2.17	C	Tc	C

TABLE II (continuation)

Families	Species	SD	McGuinnes index			Spatial distribution		
			UTL	LTL	NR	UTL	LTL	NR
Fabaceae	<i>Sebastiania brasiliensis</i> Spreng.	Zo	1.48	2.22	4.70	Tc	C	C
	<i>Gymnanthes klotzschiana</i> Müll.Arg.	Au	1.77	3.97	1.98	Tc	C	Tc
	<i>Bauhinia forficata</i> Link	Au	2.99	*	1.00	C	*	R
	<i>Dalbergia frutescens</i> (Vell.) Britton	An	1.00	*	1.40	R	*	Tc
	<i>Inga virescens</i> Benth.	Zo	1.82	1.49	1.52	Tc	Tc	Tc
	<i>Muelleria campestris</i> (Mart. ex Benth.) M.J. Silva & A.M.G. Azevedo	An	1.99	1.56	1.36	Tc	Tc	Tc
	<i>Mimosa scabrella</i> Benth.	Au	2.47	1.00	1.00	C	R	R
	<i>Myrocarpus frondosus</i> Allemão	An	1.00	1.00	1.54	R	R	Tc
Lamiaceae	<i>Parapiptadenia rigida</i> (Benth.) Brenan	An	1.94	1.48	1.50	Tc	Tc	Tc
	<i>Vitex megapotamica</i> (Spreng.) Moldenke	Zo	*	1.00	*	*	R	*
Lauraceae	<i>Nectandra grandiflora</i> Nees	Zo	1.65	*	1.00	Tc	*	R
	<i>Nectandra lanceolata</i> Nees	Zo	1.66	1.24	1.32	Tc	Tc	Tc
	<i>Nectandra megapotamica</i> (Spreng.) Mez	Zo	3.04	1.53	2.07	C	Tc	C
	<i>Ocotea porosa</i> (Nees & Mart.) Barroso	Zo	2.99	1.00	*	C	R	-
	<i>Ocotea puberula</i> (Rich.) Nees	Zo	2.99	1.00	1.17	C	R	Tc
	<i>Ocotea pulchella</i> (Nees & Mart.) Mez	Zo	1.51	1.42	1.64	Tc	Tc	Tc
	<i>Persea willdenovii</i> Kosterm.	Zo	1.96	*	*	Tc	*	*
Lecythidaceae	<i>Cariniana estrellensis</i> (Raddi) Kuntze	An	1.00	1.48	*	R	Tc	*
Loganiaceae	<i>Strychnos brasiliensis</i> Mart.	Zo	1.83	1.36	1.04	Tc	Tc	Tc
Malvaceae	<i>Luehea divaricata</i> Mart. & Zucc.	An	2.37	2.10	1.06	C	C	Tc
Melastomataceae	<i>Miconia cinerascens</i> Miq.	Zo	1.00	1.00	1.15	R	R	Tc
Meliaceae	<i>Cedrela fissilis</i> Vell.	An	1.53	1.00	1.00	Tc	R	R
	<i>Trichilia claussenii</i> C.DC.	Zo	1.00	1.00	*	R	R	*
Myrtaceae	<i>Acca sellowiana</i> (O.Berg) Burret	Zo	1.65	1.00	*	Tc	R	*
	<i>Blepharocalyx salicifolius</i> (Kunth) O.Berg	Zo	1.09	1.12	1.28	Tc	Tc	Tc
	<i>Calyptanthes concinna</i> DC.	Zo	2.90	2.49	1.85	C	C	Tc
	<i>Campomanesia guaviroba</i> (DC.) Kiaersk.	Zo	1.57	1.39	1.27	Tc	Tc	Tc
	<i>Campomanesia guazumifolia</i> (Cambess.) O.Berg	Zo	1.00	*	1.00	R	*	R
	<i>Eugenia multicostata</i> D.Legrand	Zo	1.42	1.45	1.07	Tc	Tc	Tc
	<i>Eugenia pyriformis</i> Cambess.	Zo	1.27	1.01	1.08	Tc	Tc	Tc
	<i>Eugenia rostrifolia</i> D.Legrand	Zo	1.39	1.00	1.26	Tc	R	Tc
	<i>Eugenia</i> sp.	Zo	1.41	1.48	1.56	Tc	Tc	Tc
	<i>Eugenia uniflora</i> L.	Zo	1.99	1.34	1.33	Tc	Tc	Tc

TABLE II (continuation)

Families	Species	SD	McGuinness index			Spatial distribution		
			UTL	LTL	NR	UTL	LTL	NR
	<i>Myrceugenia</i> sp.	Zo	1.59	1.02	1.35	Tc	Tc	Tc
	<i>Myrcia hatschbachii</i> D.Legrand	Zo	1.00	*	1.00	R	*	R
	<i>Myrcia palustris</i> DC.	Zo	1.24	1.10	1.29	Tc	Tc	Tc
	<i>Myrcia selloi</i> (Spreng.) N.Silveira	Zo	1.00	*	1.00	R	*	R
	<i>Myrcia</i> sp.	Zo	1.17	1.01	1.49	Tc	Tc	Tc
	<i>Myrcianthes pungens</i> (O.Berg) D.Legrand	Zo	1.11	1.21	1.45	Tc	Tc	Tc
Peraceae	<i>Pera glabrata</i> (Schott) Poepp. ex Baill.	Zo	2.54	1.07	1.00	C	Tc	R
Phytolaccaceae	<i>Seguiera aculeata</i> Jacq.	An	1.74	1.36	1.38	Tc	Tc	Tc
	<i>Seguiera langsdorffii</i> Moq.	An	1.00	*	*	R	*	*
Podocarpaceae	<i>Podocarpus lambertii</i> Klotzsch ex Endl.	Zo	1.64	1.31	1.50	Tc	Tc	Tc
Primulaceae	<i>Myrsine coriacea</i> (Sw.) R.Br. ex Roem. & Schult.	Zo	1.96	1.90	1.68	Tc	Tc	Tc
	<i>Myrsine lancifolia</i> Mart.	Zo	*	*	1.99	*	*	Tc
	<i>Myrsine umbellata</i> Mart.	Zo	3.22	1.31	1.00	C	Tc	R
Proteaceae	<i>Roupala montana</i> var. <i>brasiliensis</i> (Klotzsch) K.S.Edwards	An	1.52	1.00	1.47	Tc	R	Tc
Quillajaceae	<i>Quillaja brasiliensis</i> (A.St.-Hil. & Tul.) Mart.	An	1.23	1.00	*	Tc	R	*
Rosaceae	<i>Prunus brasiliensis</i> (Cham. & Schltdl.) D.Dietr.	Zo	1.80	*	1.99	Tc	*	Tc
	<i>Prunus myrtifolia</i> (L.) Urb.	Zo	1.24	1.15	1.07	Tc	Tc	Tc
Rubiaceae	<i>Rudgea parquioides</i> (Cham.) Müll. Arg.	Zo	*	*	1.28	*	*	Tc
Rutaceae	<i>Helietta apiculata</i> Benth.	An	1.86	1.13	1.67	Tc	Tc	Tc
	<i>Pilocarpus pennatifolius</i> Lem.	Au	1.00	*	*	R	*	*
	<i>Zanthoxylum kleinii</i> (R.S.Cowan) P.G.Waterman	Zo	1.62	1.00	1.00	Tc	R	R
	<i>Zanthoxylum petiolare</i> A.St.-Hil. & Tul.	Zo	1.00	1.00	1.00	R	R	R
	<i>Zanthoxylum rhoifolium</i> Lam.	Zo	1.30	1.41	1.00	Tc	Tc	R
Salicaceae	<i>Casearia decandra</i> Jacq.	Zo	1.58	1.55	1.54	Tc	Tc	Tc
	<i>Casearia obliqua</i> Spreng.	Zo	1.45	1.37	1.11	Tc	Tc	Tc
	<i>Casearia sylvestris</i> Sw.	Zo	1.00	3.99	1.00	R	C	R
	<i>Xylosma ciliatifolia</i> (Clos) Eichler	Zo	1.71	1.72	1.25	Tc	Tc	Tc
Sapindaceae	<i>Allophylus edulis</i> (A.St.-Hil. et al.) Hieron. ex Niederl.	Zo	1.32	1.46	1.70	Tc	Tc	Tc
	<i>Allophylus guaraniticus</i> (A.St.-Hil.) Radlk.	Zo	1.99	*	3.64	Tc	*	C
	<i>Allophylus puberulus</i> (Cambess.) Radlk.	Zo	1.49	1.17	2.30	Tc	Tc	C
	<i>Cupania vernalis</i> Cambess.	Zo	2.85	2.57	1.55	C	C	Tc

TABLE II (continuation)

Families	Species	SD	McGuinnes index			Spatial distribution		
			UTL	LTL	NR	UTL	LTL	NR
Solanaceae	<i>Matayba elaeagnoides</i> Radlk.	Zo	2.43	1.98	1.37	C	Tc	Tc
	<i>Brunfelsia pilosa</i> Plowman	Zo	1.00	1.00	1.26	R	R	Tc
	<i>Capsicum flexuosum</i> Sendtn.	Zo	1.06	1.00	1.54	Tc	R	Tc
	<i>Solanum mauritianum</i> Scop.	Zo	1.00	1.00	1.00	R	R	R
	<i>Solanum sanctaecatharinae</i> Dunal	Zo	1.97	2.54	1.18	Tc	C	Tc
	<i>Solanum</i> sp.	Zo	1.00	1.00	1.00	R	R	R
Styracaceae	<i>Styrax leprosus</i> Hook. & Arn.	Zo	2.38	1.45	1.60	C	Tc	Tc
Thymelaeaceae	<i>Daphnopsis racemosa</i> Griseb.	Zo	*	*	1.00	*	*	R
Winteraceae	<i>Drimys brasiliensis</i> Miers	Zo	1.48	1.24	1.32	Tc	Tc	Tc

** Alien species.

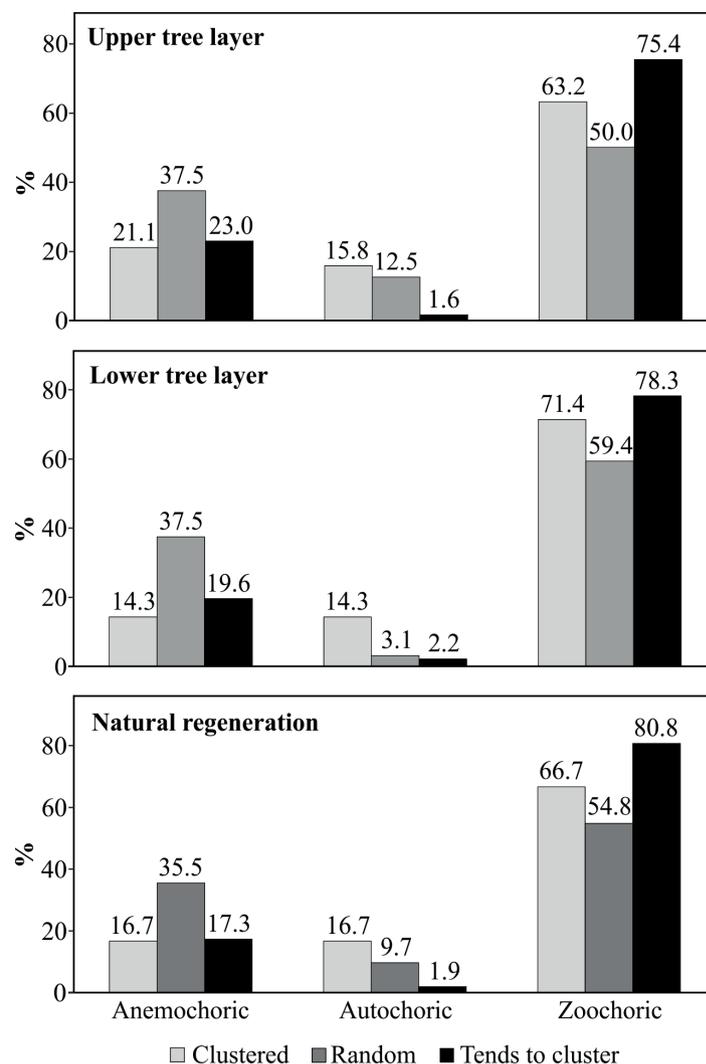


Figure 2 - Species spatial distribution pattern by dispersion syndrome in different layers of an *Araucaria* Forest in Southern Brazil.

proportion of zoochoric species tends to increase according to the progression in the successional process (Liebsch et al. 2008). The Myrtaceae, Lauraceae and Sapindaceae families are generally identified as the most important of the *Araucaria* Forest in Santa Catarina (Klein 1978, Gasper et al. 2013), mainly because it represents a great part of the species with zoochoric dispersion (Liebsch and Mikich 2009, Klauberg et al. 2010, Negrini et al. 2012). These families are also typical of well-conserved forests and exhibit the characteristic of high abundance of individuals under the *Araucaria* Forest canopy, which are an important source of resources for the frugivorous animals (Klein 1960, Reitz and Klein 1966, Paise and Vieira 2005).

Most species in the analyzed layers tend to cluster in the forest. This characteristic has already been reported for 65% of the species by Kanieski et al. (2012). However, regenerating species may have a tendency to cluster and, adult trees to occur in groups (see Nascimento et al. 2001). This may occur due to the interactions with the dispersing agents or because of a density-dependent competition increase, where population fluctuations of plants depend directly on the size of the previous population, which in turn is determined by intrinsic ecological processes (see Berryman 1999, Knape and Valpine 2012). For example, Beckman and Rogers (2013) mention that some animals can deposit seeds in favorable environments for their germination (clearings, tree trunks, forest edges), or even in the same place, as in the case of tapirs (Giombini et al. 2009), where they generate an aggregate pattern of palm *Syagrus romanzoffiana* (Cham.) Glassman. Boyer et al. (2006) point out that some primates follow mental maps and choose their path according to a criterion of maximum efficiency to find scarce resources (fruits and seeds) in a heterogeneous environment, such as tropical forests. These animals may deposit seeds in aggregate at some sites, however, the foraging patterns are generalized and seed dispersal in the forest may be random (Boyer et al. 2006).

Furthermore, the aggregation pattern of many tree species will depend on the secondary dispersion event, promoted by insects or rodents on the soil (Forget et al. 2005, Vander Wall et al. 2005, Silva et al. 2012). For example, the aggregation of seeds dispersed by animals at specific sites depends on the number of seeds per defecation, the aggregation of defecations and the persistence of seed entering the deposition sites over time, among others (Beckman and Rogers, 2013). In altered secondary forests, the tendency of aggregation of zoochoric species may occur due to habitat fragmentation, for absence of dispersant animals the seeds of the trees tend to be dispersed near the mother plant (Wilson et al. 2004, Nathan 2006). However, in well-conserved secondary forests where dispersal animals are present, seed aggregation may occur in greater proportion under nests or along paths used by animals that travel small and long distances (Schupp et al. 2002, Boyer et al. 2006) and in environments similar to the mother plant (Cavallero et al. 2012). In the present study, several ecological factors may be contributing to the aggregation of zoochoric species (see Boyer et al. 2006, Beckman and Rogers 2013). However, detailed studies on the interactions between dispersing agents and tree species should be performed to confirm this hypothesis.

The anemochoric dispersion was characterized by the predominance of species with random distribution. In forest ecosystems, this result is usually expected, since the seeds of anemochoric species have winged structures that favor transport by the wind (Barbosa et al. 2012). Moreover, these seeds can reach long distances from their point of origin according to the intensity of the wind and the distribution of treetops (Nathan et al. 2001, Beckman and Rogers 2013). The higher proportion of anemochoric species with a random distribution suggests that these species, once dispersed by the wind and not having a specific place for their deposit, are randomly distributed in all forest layers.

The clustered distribution was the most representative in autochoric species. These species have explosive mechanisms of dispersion or are dispersed by gravity (Barbosa et al. 2012), in addition to having small dispersion distance in relation to other means, which results in a high density of seeds and seedlings near the mother plant (Narbona et al. 2005, Nathan 2006). Due to these ecological traits, generally autochoric species tend to present a clustered distribution pattern (Ricklefs 2010, Barbosa et al. 2012). However, although autochoric is uncommon in Neotropical forests (see Howe and Smallwood 1982, Talora and Morellato 2000, Barbosa et al. 2012), these species are important for forest fragments regeneration. For example, Lopes et al. (2012) verified that, in the absence of anemochoric and zoochoric species, the succession of fragmented forests is driven by the dynamics of some autochoric species, which gradually move to more distant places. The results show that the species of different layers of forest are related to the type of dispersion and the aggregation pattern, since the existence of a significant interaction between the dispersion syndromes and the spatial distribution patterns was verified. The distribution of the dispersion syndromes and the spatial distribution patterns of the species presented significant differences in the analyzed layers and most of the species showed a zoochoric distribution and a tends to cluster distribution. The anemochoric species characterized the pattern of random distribution, followed by the autochoric species with clustered distribution pattern. We conclude that further studies on the dispersion and aggregation of tree species in neotropical forests take into account the interaction between these ecological traits.

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