Spatial distribution, association patterns and richness of tree species in a seasonal forest from the Serra Geral formation, southern Brazil

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RESUMO

(Distribuição, associação espacial e riqueza de espécies arbóreas em uma floresta decídua da formação Serra Geral, sul do Brasil). Este estudo objetivou determinar a distribuição espacial das espécies arbóreas mais abundantes num remanescente florestal e avaliar relações que possam ser responsáveis por estas distribuições, bem como comparar a riqueza específica esperada ao longo da formação Serra Geral no estado do Rio Grande do Sul, Brasil. Uma parcela de 1 hectare, subdividida em 100 unidades amostrais contíguas foi instalada e todos os indivíduos com pelo menos 4,8 cm de diâmetro à altura do peito foram medidos e identificados. Cada unidade amostral recebeu uma descrição de sua posição espacial por meio de coordenadas (x,y) para quantificar o padrão espacial e posteriormente aplicar um índice de associação para as espécies amostradas. A riqueza específica foi comparada a outros levantamentos realizados na região da encosta da Serra Geral do estado do Rio Grande do Sul por meio de rarefação. Foram amostrados 1.063 indivíduos distribuídos em 69 espécies e 33 famílias. A diversidade específica foi de 3,35 nats (equitatividade Pielou - J' = 0,79) e a maioria das espécies apresentou distribuição agregada. Padrões de associação e dissociação foram encontrados entre as espécies, demonstrando diferentes grupos florestais. Foi observado que existe um decréscimo de espécies Atlânticas no sentido leste para oeste na formação Serra Geral, sendo substituídas por espécies da floresta estacional.

Palavras-chave: Rarefação; métricas de diversidade; associação espacial; agregação

ABSTRACT

(Spatial distribution and association patterns of tree species in a seasonal forest from the Serra Geral formation, southern Brazil). This study aimed to determine the spatial distribution of the most abundant tree species, to look for relationships that may be responsible for their distribution and to compare the expected richness along the Serra Geral formation in the state of Rio Grande do Sul , Brazil. An one-hectare plot was divided in 100 contiguous 10 x 10 m sampling units and all individuals with at least 4.8 cm diameter at breast high were measured and identified. Each sampling unit received a description of the spatial position through metric coordinates (*x,y*) in order to quantify the spatial pattern. Later, an association index among species was applied. The observed richness was rarefied and compared to other surveys located on the slopes of Serra Geral in Rio Grande do Sul. We surveyed 1,063 individuals belonging to 69 species and 33 families, and the Shannon's diversity index showed a diversity of 3.35 nats (Pielou's species evenness - J' = 0.79). Most species showed an aggregated distribution. Both association and dissociation patterns occurred among species leading to distinct forest patches. The rarefaction results showed a decrease of Atlantic species, which were replaced by typical seasonal forest species, when analyzing floristic contingents towards the west.

Key words: Rarefaction; diversity metrics; spatial association; aggregation

Introduction

In nature, organisms frequently show an aggregated distribution, forming patches, gradients or other types of spatial patterns (Legendre & Fortin 1989; Dale *et al.* 2002). The analysis of such patterns is a relevant statistical tool in the area of forest dynamics (Pélissier 1998; Franklin & Rey 2007), which helps in understanding species ecology and providing information for its management and conservation (Perry *et al.* 2002; Bell *et al.* 2010). In Brazil, studies about spatial distribution of plants were scarce in the last decade (Nascimento *et al.* 2002) but have started to increase in recent years (*e.g.* Anjos *et al.* 2004; Lindenmaier & Budke 2006; Giehl *et al.* 2007; Paludo *et al.* 2009; Higuchi *et al.* 2010; Rode *et al.* 2010).

Due to advances in computational techniques in the past few decades (Perry *et al.* 2002; Hooten *et al.* 2003), several

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models have been created for the analysis of spatial patterns. In this sense, Dale *et al.* (2002) and Perry *et al.* (2002) described concepts and provided a broad framework for making decisions on analytical approaches and interpretations of spatial patterns. Among these methods, the Spatial Analysis by Distance Indices or SADIE, proposed by Perry (1995), has been successfully used in recent studies (Ferguson *et al.* 2000; Winder *et al.* 2001; Xu & Madden 2004; Lindenmaier & Budke 2006; Giehl *et al.* 2007; Rechenmacher *et al.* 2007), and has been useful in describing and quantifying spatial patterns (Xu 2003).

Based on the spatial pattern provided by SADIE, Perry & Dixon (2002) created a new method of association analysis. By identifying the spatial heterogeneity as a patch or a gap, this method is more efficient in detecting associations than a simple correlation co-efficient (Donovan *et al.* 2007; Bell *et al.* 2010). Through the analysis of spatial pattern and association, Donovan *et al.* (2007) emphasized the importance of termites in a tropical forest in Malaysia. Bell *et al.* (2010) built co-occurrence networks based on statistical analysis of the SADIE method, providing valuable information on the area of biological control in the United Kingdom. Gabriel *et al.* (2007), using SADIE's method, verified that the young individuals of *Cupania vernalis* Cambess. do not follow the distribution of adults in a forest remnant in southern Brazil.

The state of Rio Grande do Sul (southern Brazil) has, beyond areas of sandbanks and pioneer formations, humid and seasonal forests (Teixeira *et al.* 1986). Nowadays the best preserved areas are located on the slopes, along the Serra Geral and Serra do Sudeste formations, mainly in inaccessible areas (Jarenkow & Waechter 2001; Jurinitz & Jarenkow 2003).

The main entrance corridors of tropical species in this state occur in the east, through the Atlantic Corridor, and in the west, across the basins of the Paraná and Uruguay rivers (Rambo 1956; 1961). Species interpenetration occurs on the hillside areas of Serra Geral (Jarenkow & Waechter 2001). Rambo (1956; 1960) mentioned that as species move, from east to west, across the Serra Geral, there is a reduction trend in species richness, which is higher in Atlantic Forest *stricto sensu* and gradually becomes lower towards the seasonal forest. However, little has been discussed about this in recent years. Regardless of several structural studies about plant communities of the Serra Geral formation (Jarenkow 1994; Longhi *et al.* 1999; Longhi *et al.* 2000; Jarenkow & Waechter 2001; Lindenmaier & Budke 2006; Giehl *et al.* 2007; Sühs *et al.* 2010), the lack of standardized data, which occurs in most descriptive studies of terrestrial plant communities conducted in Brazil, makes it harder to compare their results (Sonego *et al.* 2007; Giehl & Budke 2011).

This study aimed to determine the spatial distribution of the most abundant tree species from a seasonal forest remnant in the central region of Rio Grande do Sul, Brazil, and to look for relationships that may be responsible for their distribution. Likewise, the horizontal structure, di-

versity and changes in species richness along the slopes of the Serra Geral region were also evaluated. In this sense, we tried to answer the following questions: i) how is the spatial pattern of the most abundant species sampled? ii) is there an association between the spatial distribution of these species? iii) is there reduction in the species richness, from east to west, along the Serra Geral formation?

Materials and methods

Study area

The study was conducted at Sinimbu, in the central region of Rio Grande do Sul State, Brazil, in a Private Reserve of Natural Heritage which belongs to the University of Santa Cruz do Sul. This reserve was officially created in 2009 (Brasil 2009) and has an area of 221.39 ha. Sühs *et al.* (2010) found 160 tree species in this area and observed that 12 are at risk of extinction. On the other hand, the same authors also found 11 exotic species and emphasized that these species must be controlled, especially the invasive ones.

According to Maluf (2000), the regional climate belongs to type STSBv, (subtropical, sub humid, with dry periods in summer). The average annual temperature is 19.3 °C and average annual rainfall is 1,547 mm, recorded in Santa Cruz do Sul, the nearest station (data supplied by the Laboratory of Meteorology, University of Santa Cruz do Sul). The local soils belong to an association of Ciríaco and Charrua mapping units (Streck *et al.* 2002).

Data collection

A plot of 1 hectare (100 x 100 m) was set in the reserve domain and divided in 100 contiguous 10 x 10 m sampling units (central point near coordinates 29º23'22"S – 52º32'00"W at 500 m.s.l. - map available in Sühs *et al.* (2010). The plot was set on a slope, because it had better forest, where we observed the presence of two non-rectilinear gullies along the sampling area. All individuals with diameter at breast height > 4.8 cm were measured and identified. Voucher specimens were deposited in the HCB Herbarium at the University of Santa Cruz do Sul. Specimens were identified through literature and by comparison with vouchers from the HCB Herbarium. The classification of families of angiosperms was defined according to the Angiosperm Phylogeny Group (APGIII 2009) while Smith *et al.* (2006) was used to classify tree-like ferns. The nomenclature of species was based on Forzza *et al.* (2010).

The species were classified according to their floristic contingents: western seasonal (basins of Paraná and Uruguay rivers), eastern wet (Atlantic contingent), wide geographical distribution, Araucaria forest and exotics (Jarenkow & Budke 2009, Jarenkow & Waechter 2001, Budke *et al.* 2004, Lindenmaier & Budke 2006, Sühs *et al.* 2010). We also grouped species by vertical distribution and in ecological groups of regeneration: "pioneer" for species that show an entirely heliophilous life cycle, "light-demanding"

and "shade tolerant" for those who tolerate some degree of shade (Budke *et al.* 2008). The species were divided into three height groups: small (average height < 8 m); medium (average height ≥ 8 m < 12 m) and tall (average height ≥ 12 m). Estimated height values were given in Sühs *et al.* (2010).

Twelve samples of topsoil (0-20 cm depth) were randomly collected in the area and formed a single composite sample that was taken for chemical and texture analysis. The results were interpreted according to Comissão de Química e Fertilidade do Solo – RS/SC (2004).

Data analysis

For each species, the phytosociological parameters of density, frequency and dominance (derived from tree basal area) (Mueller-Dombois & Ellenberg 1974) were calculated to describe the tree community structure. A histogram was constructed (class interval determined statistically at 4.8 cm) to express the diameter classes of individuals.

In order to answer the first question of our study, we applied the SADIE methodology to evaluate the spatial patterns of species (Perry 1995). Each sampling unit received a description of the spatial position through metric coordinates (x,y), mapped from an initial established point. Species showing more than 20 ind·ha^{-1} had their spatial distribution analyzed through the index of aggregation – I_a (Perry 1995). Values of $I_a > 1$ indicates aggregation (patches), $I_a < 1$ indicates regularity and $I_a = 1$ suggests randomness (Perry *et al.* 1996; Perry 1998). Negative values of aggregation indicates that a species-*i* does not occur in that position (gaps), providing further details on pattern analysis (Perry *et al.* 1999).

According to Perry (1998), the spatial pattern in a sampled population is quantified by SADIE by measuring the total effort (in terms of distance moved), which the individuals in the observed sample must expend to move to extreme arrangements, in order to keep individuals either at uniformly (regularly) or aggregated (patchy) intervals. By comparing counts of the observed spatial pattern with random needed rearrangements, the degree of non-randomness within a set of data can be quantified (Perry 1998). Once the sampling-unit counts are the same for each randomization, the original heterogeneity of the sampled data is preserved (Xu 2003). Finally, distribution maps were produced using the kriging technique from the index values generated for each cluster plot, in which the aggregation index of each species was interpolated along the sampling area. These analyses were performed with the SADIEshell program (Perry *et al.* 1996; Conrad *et al.* 2006).

We used SADIES's association index (Perry & Dixon 2002) to assess the spatial association of all sampled individuals, species richness and among most abundant species in order to answer the second question of this study. This spatial association refers to the similarity between the spatial patterns of two data sets, and it was equivalent to a spatially explicit correlation coefficient that tests the level of association between two populations (Bell *et al.* 2010). According

to Perry & Dixon (2002), a positive association is expected when the spatial distributions of two species join both in patches and gaps. In addition, if the spatial distribution of patches and gaps do not coincide, a spatial dissociation is expected. The spatial associations were undertaken with the SADIEshell program (Perry *et al.* 1996; Conrad *et al.* 2006).

Rarefaction curves from the number of sampled individuals (Koellner *et al.* 2004) were created to compare species richness to other studies developed on the slopes of the Serra Geral region in Rio Grande do Sul, Brazil. By this methodology, the expected richness can be estimated in a random previously determined individual sample (Waite 2000). Following this, the results of other studies carried out in the slopes of the Serra Geral formation, in Rio Grande do Sul, were adapted for the construction of the rarefaction curves. In this way, a matrix of species abundance was built and, based on Forzza *et al.* (2010), the species names were updated and their synonymy was verified. The survey showing the lowest number of individuals was set as the basis for the comparison. Some studies were not included due to a low sampling effort or by omitting the names of species or grouping, which could weaken the comparison. Neophytes were excluded from this analysis but non-identified taxa or taxa identified at the level of family or genus were kept. Alpha (α) diversity was calculated through Shannon's diversity index with Pielou's evenness index (neophytes were excluded). Rarefaction and diversity analysis were performed within the PAST package (Hammer *et al.* 2001).

Spearman correlation coefficient (r_s) was used to verify whether there was a reduction of species richness from east to west along Serra Geral formation. In order to answer the third question of this study we further partitioned the amount of species from each floristic contingent (western seasonal and eastern wet). Correlation analyses were performed with JMP® software (Version 9. SAS Institute Inc., Cary, NC, 1989-2007).

Results

Soil

The soil samples showed high proportion of silt and low proportions of clay and sand, leading to a soil class "four", which group soils with medium content of organic matter, base saturation and pH. The cation exchange capacity (CEC) was considered high, in the same way as Calcium (Ca), Magnesium (Mg) and Sulfur (S). Zinc (Zn), Boron (B) and Manganese (Mn) levels were considered high, while copper (Cu) was considered medium. The Aluminum (Al) saturation was null and base saturation had a high rate (Tab. 1).

Structure

This study surveyed 1,024 living trees belonging to 69 species and 33 families. The species with highest absolute densities were *Casearia sylvestris*, with 127 individuals (12.4%),

Table 1. Physical and chemical parameters obtained with soil samples collected in a seasonal forest in central region of Rio Grande do Sul state, Brazil.

	Depth (cm)
Analysis	0-20
Sand (%)	21%
Silt (%)	59%
Clay (%)	20%
pH	5.6
P (mg/L)	7
K (mg/L)	296
O.M. (%)	4.9
Al (cmol$_c$/L)	0.0
Ca (cmol$_c$/L)	11.8
Mg (cmol$_c$/L)	2.9
H + Al (cmol$_c$/L)	4.9
CEC (cmol$_c$/L)	20.4
S (mg/L)	16.5
Zn (mg/L)	14.5
Cu (mg/L)	0.2
B (mg/L)	0.7
Mn (mg/L)	66
Fe (%)	0.13
Basis Saturation (%)	75.8
Al Saturation (%)	0.0

Nectandra megapotamica, with 106 (10.3%), *Sorocea bonplandii*, with 94 (9.2%), *Alchornea triplinervia*, with 72 (7.0%), *Cupania vernalis*, with 67 (6.5%) and *Allophylus edulis*, with 51 (5.0%). Together these species totaled 50.4% of surveyed individuals (Tab. 2). With respect to absolute frequency, a small number (13%) of the sampled species occupied higher values of frequency classes (between 20% and 60%), while 87% of sampled species had frequency classes between 0% and 20%. *Nectandra megapotamica* was the most frequent (AF = 59%). Regarding dominance, the overall basal area was 24.10 m²·ha⁻¹, where the highest values were recorded for *N. megapotamica*, which had 9.04 m²·ha⁻¹, *A. triplinervia* with 2.82 m²·ha⁻¹ and *Tetrorchidium rubrivenium* with 2.12 m²·ha⁻¹. Together these species account for 58% of the total value of dominance. *Nectandra megapotamica* held 37.5% of the total basal area, with several large sized individuals (height and diameter values above average). *Casearia sylvestris* and *Sorocea bonplandii* had high values of density and frequency and low values of dominance because they showed several well distributed small trees. On the other hand, *Tetrorchidium rubrivenium* and *Ocotea puberula* had higher values of dominance with lower values of frequency and density. Concerning the diameter, 50% of sampled individuals had diameters between 4.8 and 9.7 cm (Fig. 1).

Spatial distribution and association patterns

Twelve species showed absolute density higher than 20 individuals.ha⁻¹ and had their spatial pattern analyzed (Fig. 2 and 3). All of them were aggregated (I$_a$ > 1), except *Myrsine guianensis* and *Trichilia claussenii*. *Alchornea triplinervia*, *Cupania vernalis*, *Cabralea canjerana*, *Myrsine umbellata*, *Tetrorchidium rubrivenium* and *Diospyros inconstans* had significant aggregation values (Tab. 4).

The spatial distributions of *Alchornea triplinervia* and *Diospyros inconstans* were significantly associated to the spatial distribution of species richness per sampling unit or, as the case of *Cupania vernalis*, showed a dissociated pattern between overall species richness and plant species abundance (Tab. 4). The spatial distributions of *Casearia sylvestris*, *Alchornea triplinervia*, *Allophylus edulis*, *Myrsine umbellata* and *Tetrorchidium rubrivenium* were significantly associated with the overall number of individuals (Tab. 4). Furthermore, we verified that some species were significantly associated ($p < 0.025$) with each other. On this way, regardless of their abundance, the spatial patterns (distribution) are similar both in areas of patches (high abundance) and in areas of gaps (low abundance). At the same time, some species showed significant dissociation ($p > 0.975$) with each other, indicating that the spatial patterns in both areas (patches and gaps) did not match. According to this, Tab. 5 shows the significant dissociation between *Alchornea triplinervia* and *Cupania vernalis* and, as expected, their associations with other species, which were frequently dissimilar; *Diospyros inconstans* showed significant association with *A. triplinervia* and significant dissociation with *C. vernalis*, while *Myrsine guianensis* showed significant association with *A. triplinervia* and a dissociation trend with *C. vernalis*. The same occurred between *Sorocea bonplandii* and *Allophylus edulis*. Both of these species showed a tendency to be dissociated with each other but *S. bonplandii* showed a trend to be associated to *Cabralea canjerana*, which also showed a dissociation trend with *A. edulis*. Finally, we observed that *Casearia sylvestris* was significantly associated to *A. edulis* and showed a trend to be dissociated to *C. canjerana*. Only *C. vernalis* did not show associations with any other species.

Alpha Diversity and Species Richness

The Shannon's diversity index (H') showed a diversity of 3.34 nats.ind with Pielou's evenness of J' = 0.79. According to the rarefaction procedure, the survey located in the farthest eastern region (municipality of Morrinhos do Sul) showed the highest species richness (92 species), followed by Montenegro, also located in the east (66) and this study, in central region (66 species), then Santa Maria in the west (55) and Vale do Sol in the central region (48) (Tab. 3). The latter, although located a bit westward, had more characteristics from the eastern contingent than the present one, probably due to its elevation, justifying its ordinance before our survey in Tab. 3. We did not find a reduction of species richness from east to west (r$_s$ = -0.61; p = 0.27). After partitioning the amount of species of eastern and western floristic contingents, we observed a trend of increasing

Table 2. Structural parameters of a seasonal forest in central region of Rio Grande do Sul state, Brazil, collected in 100 contiguous subplots of 10 x 10 m² each.

Family/species	ADo	AD	AF	EG	PC
SALICACEAE	1.321	175	71		
Banara parviflora (A.Gray) Benth.	0.167	18	18	LD-M	WDS
Banara tomentosa Clos	0.066	9	7	LD-S	PUB
Casearia decandra Jacq.	0.033	5	5	ST-M	PUB
Casearia sylvestris Sw.	0.979	127	57	LD-M	WDS
Xylosma pseudosalzmannii Sleumer	0.076	16	14	ST-S	PUB
LAURACEAE	10.236	127	70		
Aiouea saligna Meisn.	0.114	6	6	ST-M	ATL
Nectandra lanceolata Nees	0.051	2	2	LD-M	PUB
Nectandra megapotamica (Spreng.) Mez	9.036	106	59	LD-T	WDS
Ocotea puberula (Rich.) Nees	1.020	12	12	LD-T	WDS
Ocotea pulchella (Nees & Mart.) Mez	0.015	1	1	LD-T	WDS
EUPHORBIACEAE	5.050	126	60		
Actinostemon concolor (Spreng.) Müll.Arg.	0.018	8	7	ST-S	WDS
Alchornea triplinervia (Spreng.) Müll.Arg.	2.816	72	43	LD-T	WDS
Sapium glandulosum (L.) Morong	0.004	1	1	PI-M	WDS
Sebastiania brasiliensis Spreng.	0.003	1	1	LD-S	WDS
Sebastiania commersoniana (Baill.) L.B.Sm. & Downs	0.112	15	7	PI-M	WDS
Tetrorchidium rubrivenium Poepp.	2.115	29	21	LD-T	WDS
SAPINDACEAE	1.570	118	52		
Allophylus edulis (A.St.-Hil. *et al.*) Hieron. *ex* Niederl.	0.640	51	32	LD-M	WDS
Cupania vernalis Cambess.	0.930	67	35	LD-M	WDS
MORACEAE	0.562	104	59		
Ficus luschnathiana (Miq.) Miq.	0.295	10	9	LD-T	WDS
Sorocea bonplandii (Baill.) W.C.Burger *et al.*	0.267	94	54	ST-S	WDS
MELIACEAE	1.738	82	52		
Cabralea canjerana (Vell.) Mart.	0.873	40	34	LD-M	WDS
Cedrela fissilis Vell.	0.739	16	16	LD-T	WDS
Trichilia clausseni C.DC.	0.120	23	16	LD-S	PUB
Trichilia elegans A.Juss.	0.006	3	3	ST-S	PUB
PRIMULACEAE	1.060	80	45		
Myrsine coriacea (Sw.) R.Br. *ex* Roem. & Schult.	0.056	1	1	PI-T	WDS
Myrsine guianensis (Aubl.) Kuntze	0.511	46	34	LD-M	WDS
Myrsine umbellata Mart.	0.493	33	20	PI-M	WDS
FABACEAE	0.716	52	37		
Albizia edwallii (Hoehne) Barneby & J.W.Grimes	0.060	2	2	LD-T	PUB
Dalbergia frutescens (Vell.) Britton	0.011	3	3	LD-M	PUB
Enterolobium contortisiliquum (Vell.) Morong	0.027	1	1	LD-T	PUB
Inga marginata Willd.	0.010	1	1	LD-M	WDS
Inga vera Willd.	0.070	3	3	PI-T	PUB
Lonchocarpus nitidus (Vogel) Benth.	0.121	5	4	LD-M	PUB
Machaerium paraguariense Hassl.	0.235	19	13	LD-M	PUB
Myrocarpus frondosus Allemão	0.042	6	6	LD-M	PUB
Parapiptadenia rigida (Benth.) Brenan	0.141	12	10	LD-M	PUB

Table 2. Continuation.

Family/species	ADo	AD	AF	EG	PC
EBENACEAE	0.148	21	16		
Diospyros inconstans Jacq.	0.148	21	16	LD-S	PUB
MONIMIACEAE	0.099	20	17		
Hennecartia omphalandra J.Poiss.	0.056	5	5	ST-S	PUB
Mollinedia schottiana (Spreng.) Perkins	0.043	15	12	ST-S	ATL
CUNONIACEAE	0.431	14	11		
Lamanonia ternata Vell.	0.431	14	11	LD-M	WDS
MELASTOMATACEAE	0.110	14	13		
Miconia pusilliflora (DC.) Naudin	0.110	14	13	LD-M	WDS
SAPOTACEAE	0.111	13	10		
Chrysophyllum gonocarpum (Mart. & Eichler *ex* Miq.) Engl.	0.040	3	3	ST-M	PUB
Chrysophyllum marginatum (Hook. & Arn.) Radlk.	0.071	10	8	LD-M	PUB
RUTACEAE	0.069	11	10		
Citrus X limon (L.) Osbeck	0.003	1	1	U-S	EXT
Zanthoxylum caribaeum Lam.	0.067	10	10	LD-S	WDS
BORAGINACEAE	0.080	11	9		
Cordia americana (L.) Gottschling & J.S.Mill.	0.003	1	1	LD-S	PUB
Cordia ecalyculata Vell.	0.011	3	3	ST-S	PUB
Cordia trichotoma (Vell.) Arráb. *ex* Steud.	0.066	7	7	LD-M	WDS
MALVACEAE	0.102	9	8		
Luehea divaricata Mart. & Zucc.	0.102	9	8	PI-M	WDS
MYRTACEAE	0.032	6	6		
Eugenia involucrata DC.	0.006	2	2	ST-S	PUB
Eugenia rostrifolia D.Legrand	0.021	2	2	ST-S	PUB
Eugenia uniflora L.	0.005	2	2	LD-S	WDS
CYATHEACEAE	0.027	6	1		
Alsophila setosa Kaulf.	0.027	6	1	ST-S	WDS
ANNONACEAE	0.025	5	5		
Annona sylvatica A.St.-Hil.	0.025	5	5	LD-S	WDS
NYCTAGINACEAE	0.085	5	5		
Pisonia ambigua Heimerl	0.085	5	5	LD-M	WDS
SIMAROUBACEAE	0.084	5	3		
Picrasma crenata (Vell.) Engl.	0.084	5	3	LD-M	PUB
LAMIACEAE	0.023	3	2		
Vitex megapotamica (Spreng.) Moldenke	0.023	3	2	LD-M	WDS
RUBIACEAE	0.012	3	3		
Coutarea hexandra (Jacq.) K.Schum.	0.009	2	2	ST-M	PUB
Randia armata (Sw.) DC.	0.002	1	1	ST-S	WDS
ANACARDIACEAE	0.079	2	2		
Lithrea brasiliensis Marchand	0.079	2	2	LD-M	PUB
PROTEACEAE	0.013	2	2		
Roupala montana var. *brasiliensis* (Klotzsch) K.S.Edwards	0.013	2	2	ST-M	ARA
RHAMNACEAE	0.074	2	2		
Hovenia dulcis Thunb.	0.074	2	2	PI-M	EXT

Continues.

Table 2. Continuation.

Family/species	ADo	AD	AF	EG	PC
URTICACEAE	0.011	2	1		
Urera baccifera (L.) Gaudich. *ex* Wedd.	0.011	2	1	LD-S	PUB
ARALIACEAE	0.068	1	1		
Schefflera morototoni (Aubl.) Maguire *et al.*	0.068	1	1	LD-T	PUB
BIGNONIACEAE	0.022	1	1		
Tecoma stans (L.) Juss. *ex* Kunth	0.022	1	1	PI-M	EXT
CANNABACEAE	0.006	1	1		
Trema micrantha (L.) Blume	0.006	1	1	PI-S	WDS
CARICACEAE	0.028	1	1		
Vasconcellea quercifolia A.St.-Hil.	0.028	1	1	LD-M	WDS
ROSACEAE	0.070	1	1		
Prunus myrtifolia (L.) Urb.	0.070	1	1	LD-T	WDS
SOLANACEAE	0.017	1	1		
Cestrum intermedium Sendtn.	0.017	1	1	LD-M	PUB

ADo = absolute dominance (m².ha⁻¹); AD = absolute density (ind.ha⁻¹); AF = absolute frequency (%); EG = ecological groups; T = tall; M = medium; S = small; LD = light-demanding; ST = shade-tolerant; PI = pioneer; U = undetermined; PC = phytogeographic characteristics; WDS = widely distributed species; PUB = species from basins of Paraná and Uruguay rivers; ATL = Atlantic contingent species; EXT = exotic species; ARA = species from Araucária forest; Table ranked in absolute density per family.
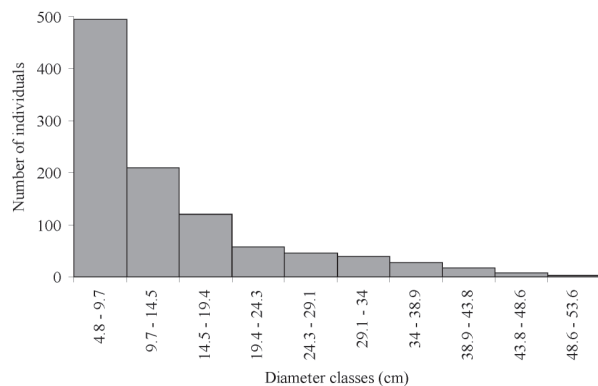

Figure 1. Distribution of tree individuals by diameter class (class interval of 4.8 cm), obtained in a survey in a seasonal forest in the central region of Rio Grande do Sul State, Brazil.

species for the western seasonal species (r_s = 0.80; p = 0.10) from east to west and a trend of decreasing for the eastern wet species (r_s = -0.90; p = 0.03) in the same direction. There was no correlation between eastern wet and western seasonal (r_s = -0.60; p = 0.28).

Discussion

50% of the sampled individuals had a diameter between 4.8 and 9.7 cm (Fig. 1). This result highlights the importance of the understory and regenerating individuals in the community, while, if we had adopted a higher inclusion criterion

(*e.g.* 10 cm DBH, as used in some studies in tropical and subtropical forests), we would have found only middle and upper layers and half of the surveyed individuals.

Spatial distribution and association patterns – Three species that showed aggregation in the present study also had aggregation in the study of Lindenmaier & Budke (2006), located in Cachoeira do Sul, Rio Grande do Sul, in a riverine forest. Although they used a higher inclusion criterion, *Casearia sylvestris*, *Sorocea bonplandii* and *Cabralea canjerana* showed significant values of aggregation in their survey, the latter had a significant value of aggregation in our study. This could indicate that these species present aggregation not only due to local factors but also as a natural behavior.

Most species showed significant or relatively high values of association or dissociation with other ones. In other words, all of them had some degree of association or dissociation, not occurring regularly in the horizontal space. The causes of such patterns are not well understood or studied, although credit has mainly focused on biotic and abiotic interactions. Nevertheless, some considerations can be made to understand part of these processes; if there is association between species, it indicates that they occupied the same areas (patches and gaps) in the survey. So we can infer that I) one of them is being (or has been) favored by the other (Levine, 1999; Brooker *et al.* 2008), which may indicate habitat changing in the way one or both species had been successfully established (facilitation); II) both are (or could have) benefiting from a third biotic or abiotic factor(s); III)

Table 3. Data of surveys realized in the slope of Serra Geral formation, in Rio Grande do Sul state, Brazil, after the adaptation procedure (revision of synonyms, exclusion of neophytes), ordered from east to west.

Local	n	area	S	R1020	s	A sp	B sp	E sp	H'	J'
Morrinhos do Sul, RS [1]	2822	1.00	112	92	3.14	22.04	5.06	11.5	3.66	0.77
Montenegro, RS [2]	3514	1.83	78	66	2.36	4.93	3.77	13.0	3.06	0.70
Vale do Sol, RS [3]	1855	1.00	55	48	2.15	5.49	13.7	10.9	2.24	0.56
Sinimbu, RS [4]	1020	1.00	66	66	0.00	2.0	28.0	35.0	3.34	0.79
Santa Maria, RS [5]	1427	1.00	58	55	1.45	0.79	18.5	22.1	3.07	0.75

n = number of individuals; area = survey area (hectare); S = species richness; A sp = number of species from Atlantic contingent; B sp = number of species from basins of Paraná and Uruguay rivers; E sp = number of widely distributed species; R1020 = species richness acquired with rarefaction curves for 1020 individuals (with standard deviation = s); H' = Shannon's diversity index; J' = Pielou's evenness index; [1] Jarenkow (1994); [2] Longhi *et al.* (2008); [3] Jarenkow & Waechter (2001); [4] This study; [5] Giehl *et al.* (2007).

Table 4. Values obtained with index of aggregation and association for species with at least 20 individuals surveyed in a seasonal forest in central region of Rio Grande do Sul state, Brazil.

Espécie	N	I a	Mvj	Mvi	Spi x Spp	Spi x Nind
Casearia sylvestris	127	1.028	-1.036	1.051	0.0315	<0.0001 +
Nectandra megapotamica	106	1.050	-1.039	1.049	0.7736	0.1228
Sorocea bonplandii	94	1.109	-1.109	1.030	0.0497	0.1722
Alchornea triplinervia	72	1.676 ***	-1.669 ***	1.373 **	<0.0001 +	<0.0001 +
Cupania vernalis	67	1.490 ***	-1.491 ***	1.251 *	0.9979 -	0.8083
Allophylus edulis	51	1.055	-1.055	0.983	0.0532	0.0032 +
Myrsine guianensis	46	0.952	-0.954	0.925	0.0886	0.0697
Cabralea canjerana	40	1.322 **	-1.322 **	1.183	0.4245	0.5212
Myrsine umbellata	33	1.358 **	-1.355 **	1.431 **	0.0624	0.0176 +
Tetrorchidium rubrivenium	29	1.202 *	-1.209	1.129	0.0701	0.0071 +
Trichilia claussenii	23	0.957	-0.954	0.992	0.0524	0.3865
Diospyros inconstans	21	1.404 **	-1.401 **	1.258 *	0.0047 +	0.1076

*$P<0.1$; ** $P<0.05$; *** $P<0.01$; (+) = significant association; (-) = significant dissociation ; N = density (ind.ha^{-1}); I_a = index of aggregation; Mvj = average value of I_a for gaps; Mvi = average value of I_a for patches. Spi x Spp = P values obtained with association index between spatial distribution of species "i" (Spi) and spatial distribution of number of species for each sampling unit (Spp); Spi x Nind = P values obtained with association index between spatial distribution of species "i" and spatial distribution of number of individuals for each sampling unit (Nind).

Table 5. Probability values (*p)* obtained with association analysis between trees species with at least 20 individual surveyed in a seasonal forest in central region of Rio Grande do Sul, Brazil. Significant association (+) occurs when $p < 0.025$ and significant dissociation (-) when $p > 0.975$.

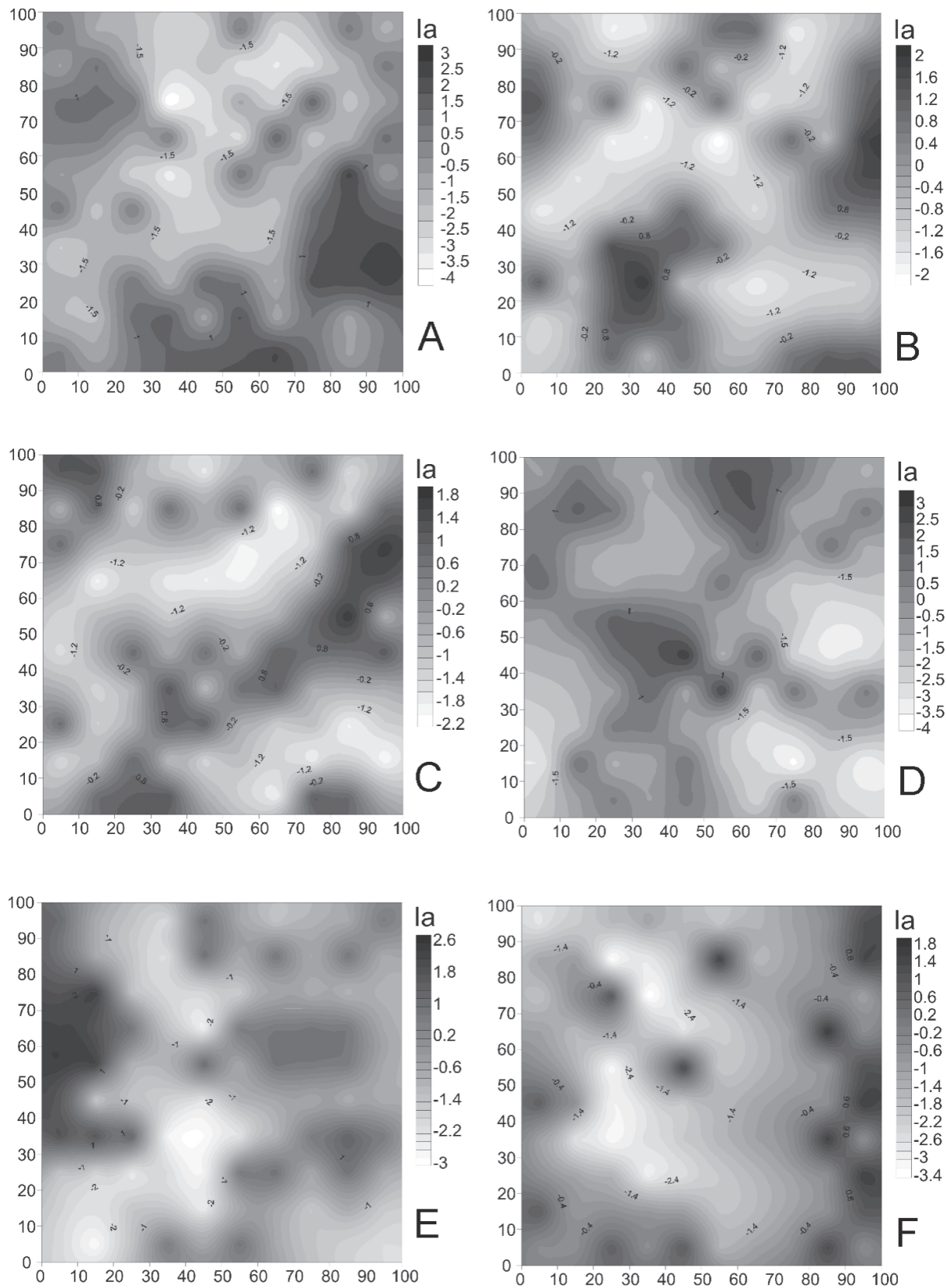|	Dio_inc	Tri_cla	Tet_rub	Myr_umb	Cab_can	Myr_gui	All_edu	Cup_ver	Alc_tri	Sor_bon	Nec_meg
Cas_syl	0.1185	0.5497	0.6473	0.0901	0.9165	0.7495	0.0008+	0.3421	0.0591	0.7008	0.8071
Nec_meg	0.9390	0.6773	0.1045	0.0311	0.8453	0.8749	0.4803	0.4358	0.0591	0.4521	
Sor_bon	0.8582	0.1916	0.2284	0.8225	0.0507	0.0758	0.8808	0.4069	0.0331		
Alc_tri	0.0014+	0.4462	0.2294	0.1397	0.0606	0.0098+	0.2379	0.9970-			
Cup_ver	0.9964-	0.7664	0.5698	0.5916	0.6232	0.8779	0.1982				
All_edu	0.1758	0.7570	0.1435	0.0504	0.9402	0.6372					
Myr_gui	0.1750	0.4053	0.0478	0.0937	0.0016+						
Cab_can	0.1499	0.0415	0.4258	0.9534							
Myr_umb	0.1720	0.9608	0.1891								
Tet_rub	0.9274	0.9233									
Tri_cla	0.6757										

Figure 2. Spatial distribution of *Alchornea triplinervia* (Spreng.) Müll.Arg. (A), *Casearia sylvestris* Sw. (B), *Allophylus edulis* (A.St.-Hil. *et al.*) Hieron. *ex* Niederl. (C), *Cupania vernalis* Cambess. (D), *Cabralea canjerana* (Vell.) Mart. (E) and *Diospyros inconstans* Jacq. (F). Ia = aggregation index.
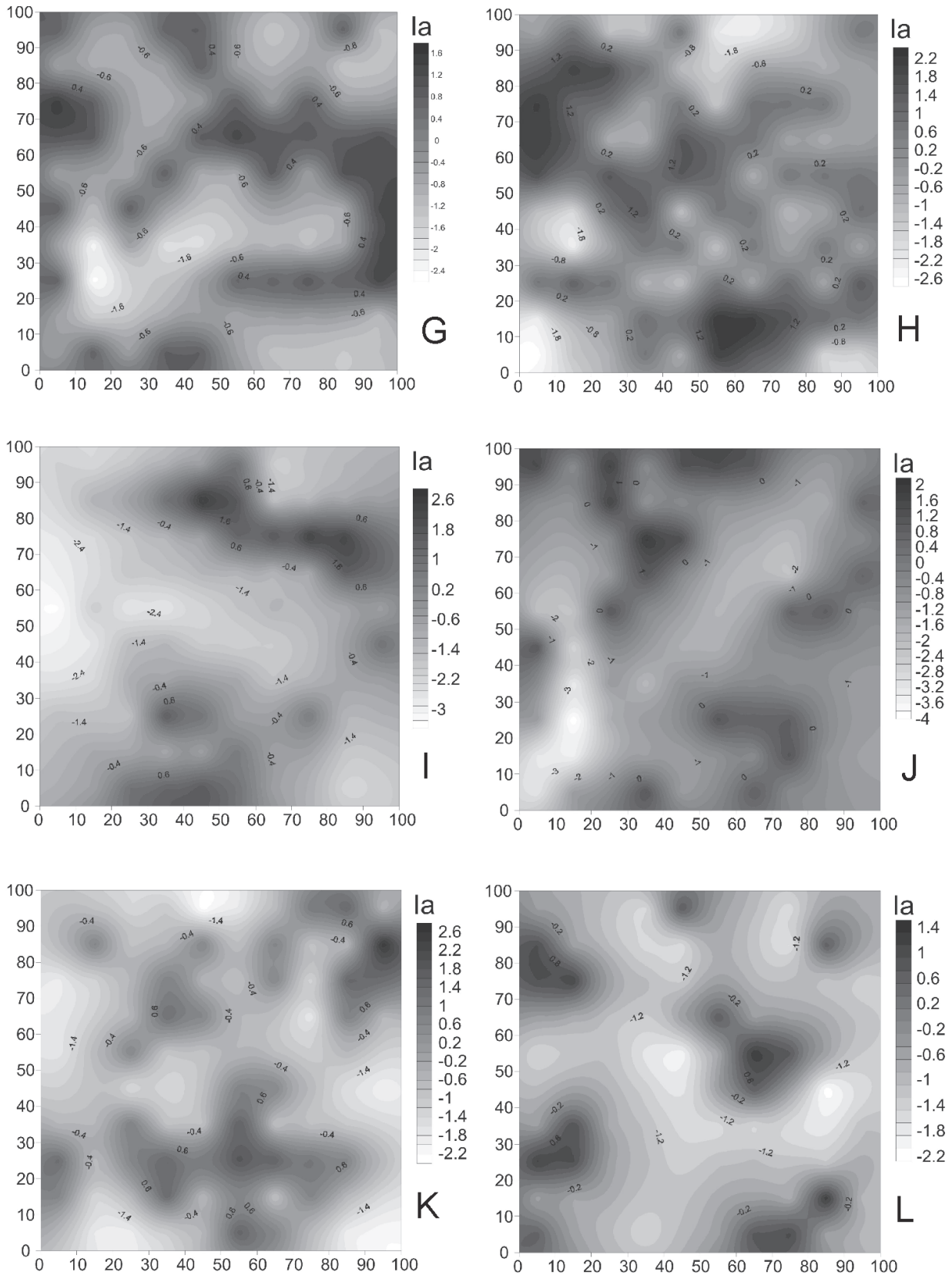
Figure 3. Spatial distribution of *Myrsine guianensis* (Aubl.) Kuntze (G), *Sorocea bonplandii* (Baill.) W.C.Burger *et al.* (H), *Myrsine umbellata* Mart. (I), *Tetrorchidium rubrivenium* Poepp. (J), *Nectandra megapotamica* (Spreng.) Mez (K) and *Trichilia claussenii* C.DC. (L). Ia = aggregation index.

there is stand-specific competition between them (Goldberg & Barton 1992; Devictor *et al.* 2010) or it had existed at some moment; and IV) both species developed mechanisms to coexist among each other (*e.g.*, creating microsites favorable for coexistence) or among other unknown factors (Christie & Armesto 2003; Silvertown 2004).

Alchornea triplinervia was associated with seven species (two significant associations and 4 tendencies) and had only one dissociation (significant). Thus, this species also had an association tendency with the spatial distribution of species richness per sampling unit, suggesting that this species occurs in areas with high heterogeneity. The question is why these interactions occur and whether this species itself is the cause of such heterogeneity. The association trends of *Alchornea triplinervia* with *Myrsine umbellata* and with *Sorocea bonplandii* can be emphasized. We can infer that after the last disturbance (*e.g.* canopy opening by the fall of a large tree), *M. umbellata* was one of the first tree species which became established, due to its pioneer characteristic (Oliveira *et al.* 2005). *Alchornea triplinervia*, which is light-demanding (Rôças *et al.* 1997) and occupied the highest layer in the present survey, was probably benefited (I) and could establish itself. Finally, *S. bonplandii*, which is shade tolerant (Budke *et al.* 2008), could establish itself (I) in the shade provided by *A. triplinervia* and occupy the lowest layer. At the same time and corroborating this hypothesis, there was a dissociation trend between *Myrsine umbellata* and *Sorocea bonplandii*, since their preferences (*e.g.* regarding luminosity requirements) are different.

Nectandra megapotamica tends to be associated with *Alchornea triplinervia* and *Tetrorchidium rubrivenium*. This three species are light-demanding (Vaccaro *et al.* 1999; Budke *et al.* 2008) and were large trees in the survey (so they occupied the same stratum). It is still not known if there is some type of facilitation between them (I) or if there is another factor that could benefit them (II), but we can infer that maybe there was (or still there is) competition between them (III) or these species have developed co-existing mechanisms (IV). The same can be inferred to the significant associations that occurred between *Casearia sylvestris* with *Allophylus edulis* and *Myrsine guianensis* with *Cabralea canjerana*, for example. All of them are light-demanding species (Budke *et al.* 2008) and had an average size in the survey, occupying the same stratum.

Cupania vernalis had significant dissociation with the spatial distribution of species richness per sampling unit and tends to be dissociated with the spatial distribution of the number of individuals per sampling unit. Nevertheless, *C. vernalis* was the only species that did not have an association with other species. In a recent study, Gabriel *et al.* (2007) showed that the young individuals of *C. vernalis* did not follow the distribution of adults in a forest in southern Brazil. This may be an important strategy of this species and reinforces the hypothesis that it forms dense and dominant groups.

Alpha Diversity and Species Richness – The value of species diversity obtained through the Shannon Index (H') of 3.35 nats.ind can be considered high when compared to other surveys made on the slopes of the Serra Geral formation. We attribute this elevated value to natural disturbances in the location: I) due to the terrain's inclination and soil characteristics, the two gullies in the studied area probably interfered in the dominance of one species, and II) these gullies provide a permanent canopy gap, which favored the establishment of widely distributed pioneer or light-demanding species with low density values. The influence and functioning of these disturbances in the richness of tropical and subtropical forests, has been demonstrated in current studies (Schintzer & Carson 2001; Sheil & Burslem 2003; Smith *et al.* 2005). These disturbances play an important role in the structure of plant communities, leading to environmental heterogeneity in time and space at different scales (Budke *et al.* 2010).

A reduction of species richness can be seen from east to west when comparing the farthest east survey, located in the tropical rain forest domain, with our survey and with the farthest west survey, both located in the seasonal forest domain. The latter had 40% less species than the farthest east one. However, the correlation analysis done with the total amount of species of each survey showed that there is not a clear reduction of species richness from east to west because some of the compared surveys showed an oscillation in their richness values, so that the reduction line from east to west was not rectilinear. This fact can be related to local factors and not regional, because canopy gaps, big tree falls, or other local disturbances may create microsites which influence species richness and forest structure (Christie & Armesto 2003; Smith *et al.* 2005; Budke *et al.* 2010). It is also worth noting that two surveys, despite being in relatively close longitudes (e.g., our survey and the survey done in Vale do Sol), may have differences in their richness due to the elevation factor (Budke *et al.* 2004). From this premise, the present survey (done at 500 m.s.l.) had less species from the east contingent and also more species from the west contingent than the survey located in Vale do Sol (done at 100-140 m.s.l.), which is located a few kilometers to the west. So we considered that the survey of Vale do Sol had more characteristics from the east contingent than the present one.

After partitioning the amount of species of each floristic contingent (western seasonal, eastern wet and wide geographical distribution) for each survey, a pattern became clear with the correlation analysis: at the same time that a reduction of the eastern wet species from east to west occurs, there is an increase of western seasonal species in the same direction. From this, we can infer that beyond a species reduction process there is a replacing process of the Atlantic species to seasonal tree species towards the west.

Acknowledgements

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