Acta Botanica Brasilica 27(4): 751-760. 2013.

Relationships between structure of the tree component and environmental variables in a subtropical seasonal forest in the upper Uruguay River valley, Brazil[1]

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Received: 18 December, 2011. Accepted: 25 July, 2013

ABSTRACT

This study aimed to analyze relationships among the structure of the tree component, edaphic variables and canopy discontinuity along a toposequence in a seasonal upland (hillside) forest in southern Brazil. Soil and vegetation were sampled in 25 plots of 20 × 20 m each. We described the vegetation in terms of structure, richness and diversity, as well as by species distribution patterns. We evaluated canopy continuity, determined sloping and calculated spatial coordinates. We applied partial canonical correspondence analysis (pCCA) to determine whether species distribution correlated with environmental and spatial variables. We identified 1201 individuals belonging to 76 species within 30 families. The species with highest density and frequency were *Gymnanthes concolor* Spreng., *Calyptranthes tricona* D.Legrand, *Eugenia moraviana* O.Berg and *Trichilia claussenii* DC. The pCCAs indicated significant correlations with environmental and spatial variables. Sand content, boron content and soil density collectively explained 36.17% of the species matrix variation (total inertia), whereas the spatial variables x, y and xy^2 collectively explained 14.27%. The interaction between environmental and spatial variables explained nearly 4.5%. However, 45.05% remained unexplained, attributed to stochastic variation or unmeasured variables. Terrain morphology and canopy discontinuity had no apparent influence on richness, and changes in species distribution were correlated with sloping, which affects soil features and determines the directional distribution of some species.

Key words: sloping, soil drainage, spatial autocorrelation, toposequence

Introduction

Many studies in ecology aim to understand the rules of ecological assemblages of natural communities at different scales. For plant communities, the description of these patterns emphasizes the importance of spatial and temporal context in ecological processes that regulate coexistence or exclusion among species. Studies of the factors that promote environmental variation perceptible at the community level (local scale), such as physical and chemical variations in soil nutrient availability, humidity, light intensity, topography and intraspecific and interspecific competition (Huston 1994) may help to elucidate processes that generate or maintain the structure and diversity of a forest, allowing a better understanding of how certain patterns of spatial organization are able to influence the functioning of the community (Bell *et al*. 1993).

The landscape influences various environmental characteristics, such as light intensity, the distribution of nutrients and the water saturation of the soil (van den Berg & Santos 2003), and may act indirectly on the distribution of species (Budke *et al*. 2010), especially in areas with steep inclines. In this regard, several studies have demonstrated the importance of the topography and patterns that occur in areas with a sloping landscape—the flow of nutrients and water from the top to the base and its influence on the chemical and physical properties of the soil (Neary *et al*. 2009), as well as the interaction between vegetation and light incidence—which can lead to differences in the composition of tree communities and the distribution of many tree species (Clark *et al*. 1996).

Studies conducted in southern Brazil have shown the relationship between the distribution of tree species and

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factors associated with topography, such as riparian forests along flood gradients (Budke *et al.* 2010; Giehl & Jarenkow 2008) and hillside forests (Sühs & Budke 2011, Loregian *et al.* 2012). In general, studies have shown that most species have clustered spatial distribution, and that many generate dense clusters, decreasing the richness and abundance of other species in nearby areas. Sühs & Budke (2011) evaluated the distribution and association among tree species in a hillside forest, having observed greater association among species at more advanced successional stages and greater dissociation among species at distinct stages (for example, pioneer and shade-tolerant). These results highlight the role of biotic relationships, whereas relationships of facilitation and competition may often result in spatial patterns that are less dependent upon physical environment.

Although these factors are extremely important on the community scale, on a regional scale, climatic factors have been identified as determinants of the distribution of plant species (Giehl & Jarenkow 2012). From this perspective, deciduous forests have been described as being strongly associated with the seasonality of precipitation and temperature (Oliveira-Filho *et al.* 2009), which directly affect leaf fall throughout the year. The debate over the expansion of forested areas during the late Holocene in southern Brazil (Behling & Pillar 2007) has greatly encouraged a discussion on the floristic elements that compose these forests, especially due to the influx of species from different climates—especially humid tropical, Antarctic and tropical dry (deciduous) (Jarenkow & Budke 2009).

This study aims to investigate the relationship between the distribution of tree species and spatial-environmental variables in a hillside forest situated on a moderate slope gradient (average slope of 25%) and that, therefore, could offer different establishment conditions for tree species, suggesting a structural change along the gradient. Thus, the guiding hypothesis on the forest structure is that there is variation in the abundance of tree species throughout the toposequence, initially subject to soil variations and to the structure of the canopy itself. Based on these premises, we sought to answer the following questions: "What is the structure of the tree component of a seasonal hillside forest in the Uruguay River valley of southern Brazil?"; and "What are the main factors affecting the distribution of local abundance of such species?"

Material and methods

Study site

The study area (central coordinates at 27°28'9"S; 51°54'5"W) is located in the municipality of Marcelino Ramos, in the northern micro-region of the Brazilian state of Rio Grande do Sul, with elevations ranging from 372 m to 594 m and an average slope of 28.7% (Fetter & Henke-Oliveira, 2010). The area comprises 469.7 hectares, with an original predominance of seasonal semideciduous subtropical broadleaf submontane forest (Oliveira-Filho 2009). In some difficult to access areas, especially slopes with steep inclines, some of the remaining vegetation has reached an advanced stage of ecological succession, suggesting the absence of selective cutting (timber extraction). The present study was carried out on one such slope with northern exposure.

According to the Köppen classification system, the climate of the region is type Cfa. The average monthly temperature ranges from approximately 12.5°C in the coldest month to approximately 22.0°C in the hottest month. Frost occurs frequently between May and August, especially at the higher elevations. There is no consistently dry period in the year, and the average annual rainfall is 1750 mm (Bernardi & Budke 2010). The predominant soil types in the study area are red latosols (typic hapludox), together with dystrophic entisols and dystrophic udorthents in the most elevated parts. The particle size analysis of the soil (at 0-20 cm in depth), performed at the Soil Analysis Laboratory of the *Universidade Federal do Rio Grande do Sul* (UFRGS, Federal University Rio Grande do Sul) School of Agronomy, revealed that it is clayey, especially at the lower elevations, and that the soil can hold a large volume of water and minerals, but has a deficient capacity for aeration and drainage.

For the collection of samples, 25 plots were established, 20 m apart (Mueller-Dombois & Ellenberg 1974), arranged in a toposequence with northern exposure. Each plot measured 20 × 20 m, the total area therefore being 400 m^2. We sampled all trees with a diameter at breast height (DBH) ≥ 15 cm. Individuals exhibiting branching below 1.3 m (i.e., below breast height) were included in the sample if one or more of the stems reached the minimum DBH. Any individual located on the boundary of a plot was recorded if more than half of its basal area was within the plot. For each individual sampled, we estimated the total height using a collecting rod of known length.

Specimens were identified down to the species level by consulting the specialized literature, by making comparisons with specimens in herbarium collections and by sending queries to specialists when necessary. The sample material was processed according to standard procedures and subsequently incorporated into the collection of the HPBR Herbarium at *Universidade Regional Integrada do Alto Uruguai e das Missões - URI*. The nomenclature follows Sobral *et al.* (2006), and species classification follows the Angiosperm Phylogeny Group III guidelines (APG III 2009). Structural parameters were estimated with the program FITOPAC 2 (Shepherd 2006), obtaining absolute values for density, frequency and dominance.

Within each plot, we collected five topsoil samples (0-20 cm) which were then mixed and homogenized to form a composite sample of approximately 500 g of soil. Samples for chemical and particle size analysis were sent to the Soil Analysis Laboratory of the UFRGS School of Agronomy.

Samples for the analysis of organic matter content, moisture and density of the soil were collected with the aid of a pitcher-type auger with a container 20 cm in height and 2 in. in diameter. We took care to remove the layer of leaf litter before collecting soil. For each plot, soil compaction was measured using a penetrometer with a dynamometer ring (Solotest, São Paulo, Brazil). Five measurements were made, and the arithmetic mean was obtained for each plot. Likewise, classes of rockiness were assigned (Santos *et al*. 2005), considering the proportion of the soil surface area and mass occupied by pebbles (2-20 cm in diameter) and stones (20-100 cm in diameter). The sampling was performed by visual analysis, in which 0 = not rocky to slightly rocky (pebbles or stones occupying < 1% of the area); 1 = moderately rocky (1-3%); 2 = rocky (3-15%); 3 = very rocky (15-50%); and 4 = extremely rocky (over 50%). For each plot, the sloping was evaluated according to the categories proposed by Santos *et al*. (2005), as follows: 0 = flat terrain (grade of < 3%); 1 = slightly inclined (3-8%); 2 = moderately inclined (8-20%); 3 = strongly inclined (20-45%); and 4 = steep (45-75%). The evaluation and quantification of the conformation of the ground surface by means of sloping categories allowed the plots to be arranged in order of increasing slope, starting from the highest part of the toposequence and considering the north-south geographical orientation based on the initial sampling design and the corresponding spatial variable y.

The discontinuity of the canopy was evaluated by means of hemispherical images obtained with the aid of a Canon EOS 300 camera equipped with a Raynox DCR 187 CF-PRO 185° circular lens converter, allowing a 180° image to be obtained. The images were taken during the spring, in the center of each plot and 1.5 m above ground level. The grayscale images were converted to black and white, the white corresponding to openings in the canopy and to black to areas closed off by the canopy. The edited photos were analyzed using the program Gap Light Analyzer 2.0 by calculating the proportion of canopy openness in 10 × 10 m sub-units, and generating, *a posteriori*, an average of discontinuity for each plot (Frazer *et al*. 1999).

Data analysis

The soil variables, rockiness levels, sloping levels, average soil compaction levels and average canopy openness levels were the set of environmental variables used in the analyses. The spatial variables consisted of the coordinates of the geometric center of the plot, x and y, plus seven variables derived from them—x^2, x^3, y^2, y^3, xy, x^2y and xy^2—following the polynomial model proposed by Borcard *et al*. (1992). For these variables, it is worth noting that x is the variation on the east-west axis, and y in the north-south axis in regard to the arrangement of the plots.

In order to determine whether quantitative variations in tree species correlated with environmental and spatial variables, we adopted partial canonical correspondence analysis (pCCA), performed following the interactive procedure described by Borcard *et al*. (1992), which requires the preparation of three matrices. The first matrix represents species density and consists of the number of individuals per plot; in the present study, only species with more than five sampled individuals were included. As recommended by ter Braak & Smilauer (1998), the density values underwent logarithmic transformation prior to the analysis process because the distributions showed very low frequencies for the higher values. The other two are the spatial and environmental matrices described above. The variables evaluated in percentage values were transformed by arc sine function of the square root.

Subsequently, there were four pCCAs related to the species matrix: with environmental variables (pCCA$_1$); with spatial variables (pCCA$_2$); with environmental variables and spatial covariates (pCCA$_3$); and with spatial variables and environmental covariates (pCCA$_4$). For this, we used the program CANOCO 4.5 (Braak & Smilauer 1998). In pCCA$_1$ and pCCA$_2$, we used the progressive selection of environmental variables together with Monte Carlo tests to determine the significance of relationships and to eliminate variables that presented strong correlations with others already included in the model. Monte Carlo tests (Braak & Smilauer 1998) were applied to all four pCCAs, and the results were used in order to estimate the amount of variation in species abundance that was distinctly explained by environmental and spatial variables (pCCA$_1$ and pCCA$_2$), the proportion indistinctly explained by the two sets of variables (pCCA$_3$ and pCCA$_4$) and the proportion of variation that was unexplained (Borcard *et al*. 1992).

Results

We sampled 1201 individuals across 76 species in 30 families (Tab. 1). Myrtaceae was the family with the greatest richness, with 12 species, followed by Fabaceae, with nine; Lauraceae, with five; Meliaceae, Rutaceae, Salicaceae and Sapindaceae, with four each; and Boraginaceae and Rubiaceae, with three each. Of the 30 families, four accounted for 74% of the individuals, Myrtaceae occupying the first position (28.4%), followed by Euphorbiaceae (28.3%), Meliaceae (10.9%) and Lauraceae (6.2%). Each of the other families accounted for ≤ 5%. *Gymnanthes concolor*, *Calyptranthes tricona*, *Eugenia moraviana* and *Trichilia claussenii* were the species with the highest density and frequency, collectively accounting for 57% of the individuals sampled (Tab. 1).

The analysis of the distribution of individuals by height (Fig. 1) revealed that the majority (49.7%) were in the 7-11 m height class and that the numbers of individuals decreased progressively across the subsequent classes. Among the species whose individuals included medium-sized trees *Eugenia Moraviana, Trichilia claussenii* and *Ocotea odorifera* stand out. Emergent trees with a height ≥ 17 m included individu-

Table 1. Species and their botanical families, together with the structural parameters absolute density, absolute dominance and absolute frequency, for tree species sampled in a remnant of subtropical seasonal forest in the upper Uruguay River Valley, southern Brazil.

Species	Family	AD	ADo	AF
Gymnanthes concolor Spreng. – SWD	Euphorbiaceae	309	1.4729	100
Calyptranthes tricona D. Legrand – PUB	Myrtaceae	205	2.8443	100
Eugenia moraviana O.Berg – PUB	Myrtaceae	85	2.3561	96
Trichilia claussenii C.DC. – SWD	Meliaceae	84	0.7457	96
Pilocarpus pennatifolius Lem. – PUB	Rutaceae	44	0.2791	40
Ocotea odorifera (Vell.) Rohwer – ATL	Lauraceae	36	1.3228	76
Sebastiania brasiliensis Spreng. – SWD	Euphorbiaceae	31	0.5298	44
Chrysophyllum marginatum (Hook. & Arn.) Radlk. – PUB	Sapotaceae	26	0.6576	60
Nectandra megapotamica (Spreng.) Mez – SWD	Lauraceae	22	2.1193	60
Calyptranthes grandifolia O. Berg – ATL	Myrtaceae	20	0.6548	56
Cabralea canjerana (Vell.) Mart – SWD	Meliaceae	19	1.7787	40
Trichilia elegans A. Juss. – PUB	Meliaceae	18	0.1059	44
Myrsine umbellata Mart. – SWD	Primulaceae	17	0.4069	36
Casearia silvestris Sw. – SWD	Salicacaceae	15	0.4486	48
Calliandra foliolosa Benth. – PUB	Fabaceae	15	0.0964	48
Prunus myrtifolia (L.) Urb. – SWD	Rosaceae	14	1.3883	44
Calyptranthes lucida Mart. ex DC. – ATL	Myrtaceae	13	0.4909	36
Ilex dumosa Reissek – SWD	Aquifoliaceae	13	0.2540	36
Chrysophyllum gonocarpum (Mart. & Eichler) Engl. – PUB	Sapotaceae	12	0.1442	44
Lonchocarpus campestris Mart. ex Benth. – PUB	Fabaceae	11	0.4042	36
Cedrela fissilis Vell. – SWD	Meliaceae	10	0.6927	32
Allophylus edulis (A. St.-Hil., Cambess. & A. Juss.) Radlk. – SWD	Sapindaceae	10	0.3019	24
Ocotea diospyrifolia (Meisn.) Mez – PUB	Lauraceae	9	0.8320	24
Cordia trichotoma (Vell.) Arráb. ex Steud. – SWD	Boraginaceae	8	0.3824	28
Inga marginata Willd. – SWD	Fabaceae	8	0.0513	32
Cupania vernalis Cambess. – SWD	Sapindaceae	8	0.0800	16
Nectandra lanceolata Nees – SWD	Lauraceae	7	0.8166	20
Eugenia schuechiana O.Berg – PUB	Myrtaceae	7	0.0463	28
Luehea divaricata Mart. & Zucc. – SWD	Malvaceae	6	0.5480	20
Casearia decandra Jacq. – PUB	Salicaceae	6	0.1087	20
Syagrus romanzoffiana (Cham.) Glassman – SWD	Arecaceae	6	0.2164	12
Sloanea monosperma Vell. – PUB	Elaeocarpaceae	5	1.6220	20
Parapiptadenia rigida (Benth.) Brenan – PUB	Fabaceae	5	0.9110	20
Cordia americana (L.) Gottschling & J.E.Mill. – PUB	Boraginaceae	5	0.4411	16
Zanthoxylum caribaeum Lam. – ATL	Rutaceae	5	0.1945	20
Coussarea contracta (Walp.) Müll.Arg. – PUB	Rubiaceae	5	0.0491	20
Apuleia leiocarpa (Vogel) J.F. Macbr. – PUB	Fabaceae	5	0.0535	16
Campomanesia xanthocarpa O.Berg – SWD	Myrtaceae	4	0.5802	16
Balfourodendron riedelianum (Engl.) Engl. – PUB	Rutaceae	4	0.1247	16
Aspidosperma australe Müll.Arg. – PUB	Apocynaceae	4	0.1080	16
Ficus luschnathiana (Miq.) Miq. – SWD	Moraceae	4	0.0722	12
Cordia ecalyculata Vell. – PBU	Boraginaceae	4	0.0549	12
Celtis iguanaea (Jacq.) Sarg. – SWD	Cannabaceae	4	0.0315	12
Coutarea hexandra (Jacq.) K. Schum – PUB	Rubiaceae	4	0.0771	8
Styrax leprosus Hook. & Arn. – PUB	Styracaceae	3	0.2532	12
Allophylus puberulus (Cambess.) Radlk. – PUB	Sapindaceae	3	0.0829	12

Continues

Table 1. Continuation.

Species	Family	AD	ADo	AF
Annona neosalicifolia H.Rainer – SWD	Annonaceae	3	0.0637	12
Banara tomentosa Clos – PUB	Salicaceae	3	0.0469	12
Jacaranda micrantha Cham. – PUB	Bignoniaceae	2	0.0705	8
Lonchocarpus nitidus (Vogel) Benth. – PUB	Fabaceae	2	0.0611	8
Pisonia ambigua Heimerl . – PUB	Nyctaginaceae	2	0.0526	8
Urera baccifera (L.) Gaudich. ex Wedd. – PUB	Urticaceae	2	0.0241	8
Trema micrantha (L.) Blume – SWD	Cannabaceae	2	0.0212	8
Myrciaria floribunda (West ex Willd.) O.Berg – ATL	Myrtaceae	2	0.0166	8
Zanthoxylum petiolare A. St.-Hil. & Tul. – PUB	Rutaceae	2	0.0124	8
Eugenia ramboi D. Legrand – PUB	Myrtaceae	2	0.0070	8
Citronella paniculata (Mart.) R.A.Howard – SWD	Cardiopteridaceae	2	0.0561	4
Phytolacca dioica L. – SWD	Phylolaccaceae	1	0.2166	4
Lonchocarpus muehlbergianus Hassl. – PUB	Fabaceae	1	0.1767	4
Erythroxylum deciduum A. St.-Hil. – PUB	Erythroxylaceae	1	0.1053	4
Enterolobium contortisiliquum (Vell.) Morong – PUB	Fabaceae	1	0.0998	4
Solanum mauritianum Scop. – SWD	Solanaceae	1	0.0484	4
Ocotea puberula (Rich.) Ness – SWD	Lauraceae	1	0.0436	4
Ceiba speciosa (A.St.-Hill.) Ravenna – PUB	Malvaceae	1	0.0418	4
Myrcia sp.	Myrtaceae	1	0.0241	4
Erythroxylum myrsinites Mart. – SWD	Erythroxylaceae	1	0.0127	4
Inga vera Willd. – PUB	Fabaceae	1	0.0109	4
Campomanesia guazumifolia (Cambess.) O.Berg – PUB	Myrtaceae	1	0.0097	4
Xylosma pseudosalzmannii Sleumer – PUB	Salicaceae	1	0.0095	4
Seguieria guaranitica Speg. – SWD	Phytolaccaceae	1	0.0095	4
Myrsine loefgrenii (Mez) Imkhan – SWD	Primulaceae	1	0.0072	4
Eugenia uniflora L. – SWD	Myrtaceae	1	0.0037	4
Allophylus guaraniticus (A. St.-Hil.) Radlk. – PUB	Sapindaceae	1	0.0032	4
Symplocos lanceolata DC. – PUB	Symplocaceae	1	0.0029	4
Cordiera concolor (Cham.) Kuntze – PUB	Rubiaceae	1	0.0018	4
Eugenia rostrifolia D. Legrand – PUB	Myrtaceae	1	0.0018	4

AD – absolute density; ADo – absolute dominance; AF – absolute frequency; SWD – species of wide distribution; PUB – Paraná and Uruguay River Basin migration corridor (primary distribution); ATL – Atlantic corridor (primary distribution).

als from the species *Cabralea canjerana* and *Cedrela fissilis*, both reaching up to 25 m. Among tree species characteristic of humid tropical climates, *O. odorifera*, *Calyptranthes grandifolia*, *Calyptranthes lucida*, *Cordiera concolor* and *Coussarea contracta* predominated.

Considering the relationships that species showed with the environmental and spatial variables, the eigenvalues of the four pCCAs were very low (< 0.15) for the first two axes (Tab. 2). Of the total variation in species, pCCA$_1$ and pCCA$_2$ explained 36.17% and 14.27%, respectively, indicating that the most important relationship is purely environmental and therefore depends little on spatial aspects (pCCA$_3$).

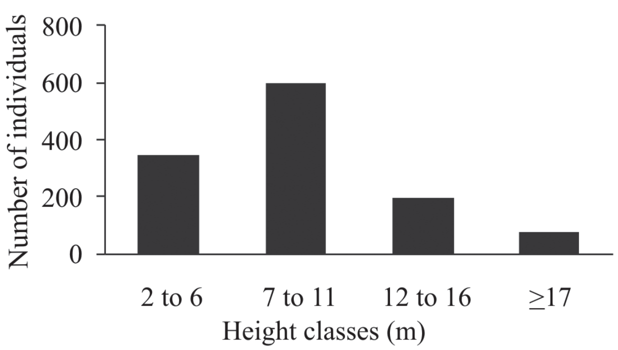

Figure 1. Distribution of individual trees in height classes in a subtropical seasonal forest in the upper Uruguay River Valley, southern Brazil.

Table 2. Summary of partial canonical correspondence analysis of the abundance of 76 tree species sampled in a remnant of subtropical seasonal forest in the upper Uruguay River Valley, southern Brazil, showing interactions with environmental and spatial variables, as well as the results of the corresponding Monte Carlo permutation tests.

		pCCAs							
		Total inertia (sum of the eigenvalues): 1.219							
Parameters		pCCA$_1$		pCCA$_2$		pCCA$_3$		pCCA$_4$	
		Environment		Space		Environment-Space		Space-Environment	
		Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalues		0.126	0.105	0.115	0.077	0.115	0.089	0.076	0.063
Species vs. environment or space		0.864	0.870	0.816	0.842	0.928	0.914	0.847	0.922
Cumulative variation (%)									
Species data		10.3	19	9.5	15.8	11.6	20.6	9.8	17.9
Species vs. environment or space		28.5	52.4	50.1	83.6	29.7	52.7	43.5	80
Sum of canonical eigenvalues (trace)		0.441		0.230		0.386		0.174	
Monte Carlo permutation tests									
First canonical axis	F	2.071		2.194		1.966		1.622	
	p	0.0595		0.0037		0.1051		0.2232	
All canonical axes	F	1.703		1.629		1.598		1.444	
	p	0.0002		0.0015		0.0025		0.0352	
Internal correlations with axes (r)									
Boron		−0.24	−0.20			0.07	0.65		
Soil density		0.39	0.03			0.45	0.04		
Sand		−0.55	0.60			0.13	0.18		
Organic material		−0.21	0.07			0.10	0.42		
Spatial variable *x*				−0.39	0.68			0.71	−0.25
Spatial variable *y*				0.40	0.72			0.35	−0.83
Spatial variable xy^2				−0.17	0.75			0.76	−0.34

pCCA – partial canonical correspondence analysis.

However, pCCA$_3$ and pCCA$_4$ together explained 4.51% of the variation, indicating that the spatial structure of the environment itself plays a role. Therefore, more than half of the total variation (55%) was explained by the environmental aspects, by the spatial aspects, or by the interaction between the two. However, 45.06% of species variation is stochastic or not explainable by the variables evaluated (Fig. 2). The Pearson's correlation coefficient (r) for species in relation to environmental variables and spatial variables showed higher values for the environmental variables in the first two axes, ranging from 0.86 to 0.87, while those for the spatial variables ranged from 0.81 to 0.84 (Tab. 2). For all four pCCAs, Monte Carlo permutation tests indicated highly significant differences between the correlations found and those generated by chance, both for the first canonical axis and for the set of all canonical axes (Tab. 2).

Among the environmental variables, sand showed stronger correlations with pCCA$_1$. Boron correlated weakly with the first axis of pCCA$_1$ but was retained because of its strong correlation with the second axis of pCCA$_3$. Soil density showed a weak correlation with the first axis of pCCA$_1$ but correlated more strongly with in the first axis of pCCA$_3$. Organic matter was correlated with the second axis of pCCA$_3$. The observed values for canopy openness ranged from 2.5% to 18% (mean, 8.5%) and showed no influence on the distribution of species along the toposequence.

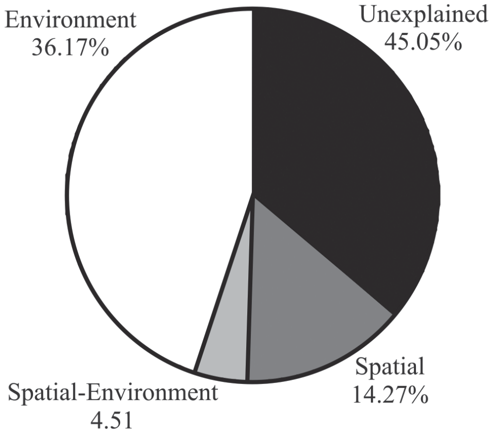

Figure 2. Proportional distribution of the factors explaining the variation in the matrix of species with a density of ^{3} 5 individuals in a stretch of subtropical seasonal forest in the upper Uruguay River Valley, southern Brazil.

The spatial variables, *x*, *y* and xy^2 produced strong correlations ($r = 0.68$-0.83). The variable *x* correlated strongly with the first axis of $pCCA_4$. The variable *y*, which corresponds to the change in relief conformity (sloping) from the bottom to the top of the toposequence, presented significant correlations in the second axis of $pCCA_2$, increasing to approximately 0.83 in the second axis of $pCCA_4$. The spatial variable xy^2 showed correlations between approximately 0.75 and approximately 0.76, in the second axis of $pCCA_2$ and the first axis of $pCCA_4$, respectively.

For the graphical representation of the analysis, we chose $pCCA_3$ to explore only the effects of environmental variables (Fig. 3). The ordination separated the plots according to environmental variables, and soil density was negatively correlated with sand, boron and organic matter (Fig. 4).

The species ordination by pCCA (Fig. 4 and 5) suggested that the distribution of species such as *Sloanea monosperma, Eugenia schuechiana, Cordia trichotoma* and *Casearia decandra* was related to soils that had higher proportions of sand (those in the plots located at the base of the toposequence). At the other extreme of this gradient we observed species such as *Apuleia leiocarpa*, *Parapiptadenia rigida*, *Nectandra lanceolata* and *Cupania vernalis*. In intermediate conditions or conditions indifferent to environmental variables are species such as *Gymnanthes concolor*, *Chrysophylum marginatum*, *Ocotea diospyrifolia* and *Trichilia claussenii*.

As for the geographical distribution of species, we found that the vast majority of them occur along the migration corridor formed by the basins of the Paraná and Uruguay rivers, followed by species of wide distribution and finally by a small group of species characteristic of coastal areas (Atlantic corridor). Prominent in the latter group are *Calyptranthes lucida*, *Calyptranthes grandifolia*, *Myrciaria floribunda*, *Ocotea odorifera* and *Zanthoxylum caribaeum* (Tab. 1).

Discussion

Composition and structure of the tree component

The great species richness of Myrtaceae and Fabaceae has been considered a common pattern in forests in Brazil (Gandolfi *et al.* 1995; Ivanauskas *et al.* 1999; Durigan *et al.* 2000; Budke *et al.* 2004; Oliveira-Filho *et al.* 2006). Myrtaceae is considered a family with high richness in all forests in southern Brazil (Jurinitz & Jarenkow 2003; Budke *et al.* 2004; Giehl & Jarenkow 2008). For the family Fabaceae, in the seasonal forest along the upper Uruguay River, the richness and abundance of individuals are attributed mainly to the geographical location, which coincides with the entrance corridor of seasonal (tropical dry) species in Rio Grande do Sul, as opposed to the Atlantic corridor species, which occur in the rain forest (tropical humid) region to the east (Rambo 1961; Jarenkow & Waechter 2001). This intermediate position on the gradient of east-west continentality in South America (Oliveira-Filho *et al.* 2006), with some climatic and geographic variables that resemble those of more humid forests, allowed the occurrence of species from tropical moist environments, such as *Ocotea odorifera*, *Calyptranthes grandifolia*, *Cordiera concolor*, *Myrciaria floribunda* and *Zanthoxylum caribaeum* between subtropical

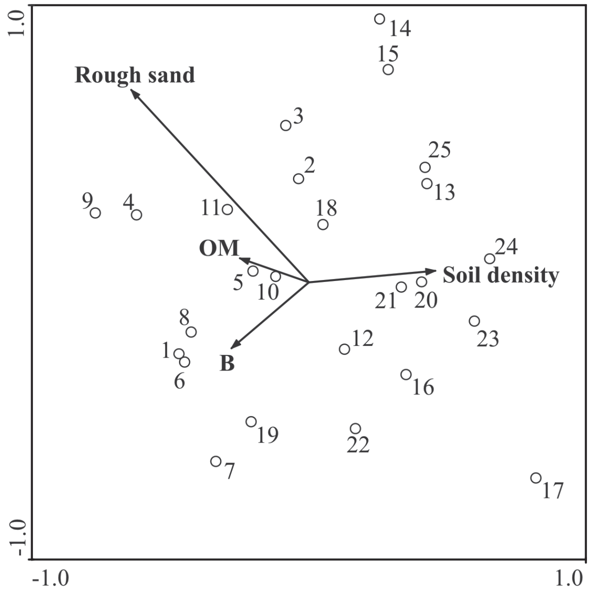

Figure 3. Ordination diagram of plots (species abundance) and environmental variables with significant association, representing the first two axes generated by partial canonical correspondence analysis, for the arboreal component in a subtropical seasonal forest in the upper Uruguay River Valley, southern Brazil. OM = organic matter, B = boron.

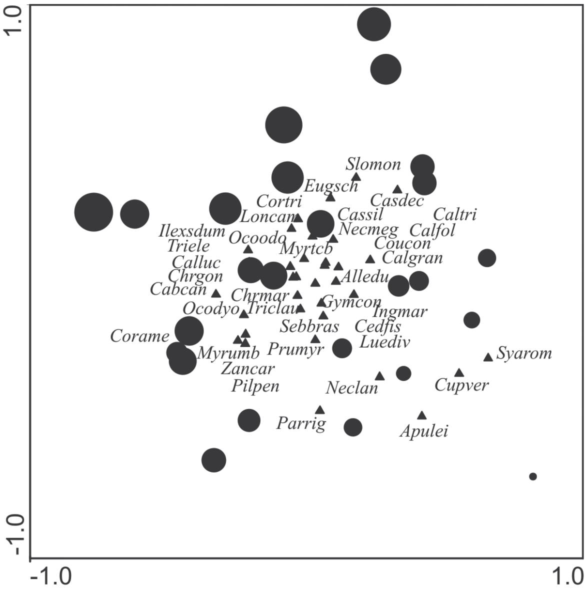

Figure 4. Ordination diagram of plots (species abundance) and the environmental variable "sand",* representing the first two axes generated by partial canonical correspondence analysis for the arboreal component in a subtropical seasonal forest in the upper Uruguay River Valley, southern Brazil.
*The size of each circle represents the proportion of sand in each plot.

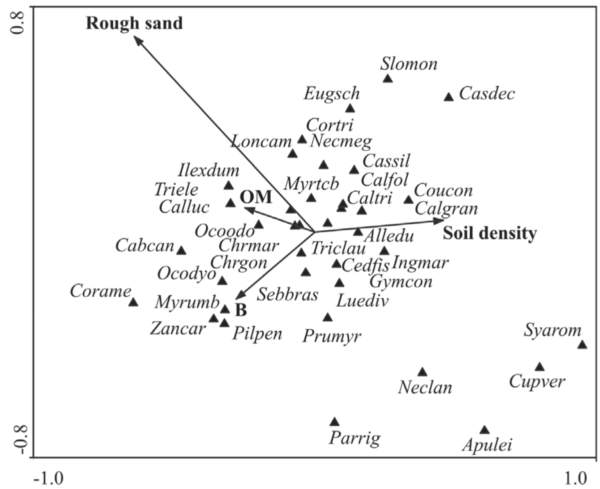

Figure 5. Ordination diagram for species* with abundance – 5 individuals and environmental variables with significant association, representing the first two axes generated by partial canonical correspondence analysis for the arboreal component in a subtropical seasonal forest in the upper Uruguay River Valley, southern Brazil.
B – boron, OM – organic matter.
*Species names have been abbreviated as shown in Table 1.

seasonal forests in the region of the upper Uruguay River. Likewise, the present study was the first recorded occurrence of *Calyptranthes lucida* in a non-coastal region of southern Brazil, indicating the possibility of dispersal of species from humid tropical areas over a larger geographical area, with subsequent retraction and current occurrence restricted to areas of lower elevation, along the upper Uruguay River. As a result, the forest remnants in areas that border the confluence of the Pelotas and Paraná rivers form an extremely important corridor for structural and phytogeographic studies, because they are home to a great diversity of species from other areas.

The species with the highest density in our study are also extremely abundant in other studies conducted in southern Brazil (Jarenkow & Waechter 2001; Budke *et al.* 2004; Lindenmaier & Budke 2006; Sühs & Budke 2011). However, one aspect that stands out is the clear presence of individuals emerging from a dense canopy of moderate height. This pattern was also observed by Jarenkow & Waechter (2001) for the central region of Rio Grande do Sul, where the deciduous element participates with a relatively low density and particularly with individuals reaching a large size. Nevertheless, species from the Atlantic corridor eventually generate a dense canopy and understory, especially with small trees.

Relationships between species and spatial-environmental variables

The eigenvalues of the first two ordination axes were low due to the high similarity between plots, which generated a short gradient with little species replacement. Much of the species distribution was found to be environmentally structured and less associated with the spatial variables, while the spatial variable *y*, corresponding to the pitch axis of the area in the north-south direction, was significant. A small portion of the fraction of the variation existing in the data itself is derived from the spatial autocorrelation between the distribution of the species and spatially structured variables, suggesting that the purely spatial effects play a minor role than do the environmental effects in explaining the variation in the species matrix. Notably, spatially explicit phenomena must be considered in terms of scale and experimental design, so as not to overestimate the influence of horizontal space in a community. Similarly, the proportion of the variation in the species matrix that could not be explained by the available environmental variables does not affect the significance of the species-environment relationships (Brack & Smilauer 1998), and such "noise" is common in vegetation data, due in part to the fact that not all favorable sites are occupied by their respective species (Titeux *et al.* 2004).

The species distribution in the present study area was strongly correlated with soil texture. As expected, the plots located in the lower toposequence showed a higher proportion of sand, which allows inferences to be made regarding drainage, indicating that these area have high permeability and low water retention capacity. Through soil density, it is possible to evaluate the mass of material contained in a known volume; density allows us to evaluate the porosity and other textural characteristics of each sample. The fact that this variable was important in the distribution of some important species reveals a direct relationship with sand content, as sandy soils exhibit lower porosity than do clayey soils (Azevedo & Dalmolin 2006).

The results we obtained for canopy discontinuity are considered intermediate in relation to the 9.0-26.0% reported for other semideciduous forests or even the 0.2-6.0% reported for evergreen forests (Martins & Rodrigues 2002; Montgomery & Chazdon 2002; van den Berg & Santos 2003; Meira Neto *et al.* 2005). Although canopy discontinuity showed no correlation with individuals already established, it must certainly contribute to the distribution of regenerating individuals, as must other factors, such as the availability of water and nutrients. However, in the present study, canopy discontinuity was observed at a specific time of year (in the spring) and should also be measured during different seasons. If the discontinuity values are very low during other seasons, the remnants in question would not be classified as deciduous, as in other studies (Veloso *et al.* 1991), but would instead be classified as being in an intermediate position between seasonal broadleaf forests and evergreen forests.

The occurrence of species from tropical moist environments associated with the coastal rainforests of Brazil, indicates a likely retraction in the current geographical distribution of these species, making the upper Uruguay River an area of maintenance of forest species with disjunct distribution. The results also revealed that the distribution of many species is environmentally structured, reflecting the topographical conditions of the land, particularly those related to soil drainage, with less involvement of spatial variables in the explanation of the species distribution (low spatial autocorrelation). Although variation in species abundance occurs along the toposequence, the absence of catastrophic disturbances or even limiting factors or stress generated low species substitution throughout this topographical gradient.

Acknowledgements

The authors would like to thank Dr. Elisabete Maria Zanin, for her critical reading of the initial draft of the manuscript; the City of Marcelino Ramos, for providing access to the facilities within the protected area, as well as for granting permission to collect and work in the *Parque Natural Municipal Mata do Rio Uruguai Teixeira Soares*; the *Laboratório de Sistemática e Ecologia Vegetal* (ECOSSIS, Plant Systematics and Ecology Laboratory) of the *Universidade Regional Integrada do Alto Uruguai e das Missões* - URI, Campus de Erechim, for providing logistical support; and the anonymous reviewers, for their helpful suggestions and recommendations. This study received financial support from the URI Graduate Program in Ecology and from the Brazilian *Conselho Nacional de Desenvolvimento Científico e Tecnológico* (CNPq, National Council for Scientific and Technological Development; Grant no. 483775/2007).

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