# Floristic composition and phytogeography of the tree component of Araucaria Forest fragments in southern Brazil

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**ABSTRACT** – (Floristic composition and phytogeography of the tree component of Araucaria Forest fragments in southern Brazil). The present study examined the floristic composition of three fragments of Araucaria Forest (AF) in the Planalto Catarinense region of southern Brazil as well as the floristic contextualization of these areas in relation to other remnant AF sites. Three AF fragments at different altitudes were analyzed in the municipalities of Campos Novos, Lages, and Painel. Fifty 200 m<sup>2</sup> plots were examined in each fragment and all of the trees with CBH (circumference at breast height)  $\geq$  15.7 cm were identified. In order to floristically contextualize the study fragments, comparisons were made with other remnant AF sites by way of dendrograms and NMDS (Non-metric multidimensional scaling). Environmental and spatial variables were plotted on the diagram produced by the NMDS to evaluate their influence on the floristic patterns encountered. The forest fragments studied demonstrated high floristic heterogeneity, indicating that AFs cannot be considered homogeneous formations and they could be classified into 3 phytogeographical categories: i) high altitude areas influenced by cloud cover/fog, including the Painel region; ii) areas of lesser altitude and greater mean annual temperatures situated in the Paraná River basin, and iii) areas situated in the Paraná and Upper-Uruguay river basins and the smaller basins draining directly into the southern Atlantic, near Campos Novos and Lages. The environmental variables most highly correlated with species substitutions among the sites were altitude, mean annual temperature of the most humid trimester.

Key words - Araucaria Forest, arboreal species, environmental variables

## **INTRODUCTION**

Mixed Ombrophilous Forests (MOF) (IBGE 1992), also known as Araucaria Forests (AF), represent one of the principal plant formations in southern Brazil. These forests predominate on the Brazilian Meridional Plateau, principally on the southern Catarinense Plateau, between 24° and 30° S latitude at altitudes that vary between 500 and 1400 m above sea level, with disjunct occupation of sites in elevated areas of the Serra do Mar and Mantiqueira Mountains in southeastern Brazil (Klein 1960). Their largest extensions cover the hydrographic basins of the rivers that drain into the Uruguay and Paraná rivers, following the altitudinal gradients from the higher lands of the Serra do Mar and Geral Mountains towards the interior (west). AFs, like most other Brazilian forests, are currently highly fragmented due to historical anthropogenic use and occupation of the land for agriculture, cattle raising, and (more recently) large-scale monoculture

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plantations of *Pinus* spp. These activities have reduced these once extensive and continuous forests to isolated fragments with sizes and levels of disturbance that vary from one locality to another (Klein 1978, Behling & Pillar 2007).

Araucaria angustifolia is the most characteristic species of the AF phytophysiognomy as it forms the upper canopy and has a dominant character in this vegetation. In spite of the fact that *A. angustifolia* predominates in the upper forest canopy (Leite & Klein 1990), the middle and lower strata demonstrate large diversities of species such as *Ocotea porosa* (Nees & Mart.) Barroso (*imbuia*), *Luehea divaricata* Mart. (*açoita-cavalo*), *Cedrela fissilis* Vell. (*cedro*), *Dicksonia sellowiana* (*xaxim*), and *Maytenus ilicifolia* Mart. ex Reissek (*espinheira-santa*) (Nascimento et al. 2001, Behling & Pillar 2007).

In light of the significant environmental heterogeneity in this region, associated principally with the climate, edaphic factors, and the history of anthropogenic disturbances, it would be expected that different AF fragments would show large floristic variations. According to Klein (1978), Santa Catarina State can be divided into four distinct phytophysiognomic areas: i) Araucaria Forests in the Iguaçu-Negro basin and in the upper regions of the river basins that drain into the Uruguay River; ii) Araucaria Forests of the Pelotas-Canoas basin; iii) Araucaria Forests of the extreme west; and iv) Araucaria Forest Nuclei of the Atlantic Rainforest. According to the classification system suggested by IBGE (1992), this phytophysiognomy may be subdivided according to its altitude and its proximity to water courses into Alluvial, Sub-Montane, Montane, and High-Montane formations.

The Catarinense Plateau is considered a strategic region for forest conservation as it contains numerous headwaters that form the hydrographic basin of the Uruguay River (Sgrott 2003) and is also part of the recharging area of the Guarani aquifer (Gomes et al. 2006). Little is currently known about the floristic and phytogeographical patterns of the arboreal components of AF forest fragments (Klein 1978, Formento et al. 2004) or their interactions with environmental and spatial variables. As such, the present study was designed to: i) describe the floristic composition of three AF fragments in the Catarinense Plateau region of southern Brazil; ii) determine the floristic similarities between these fragments in relation to other AF areas in southern Brazil; and iii) evaluate the influence of environmental and spatial variables on the phytogeographical patterns encountered.

## **MATERIAL AND METHODS**

#### Study areas

Three AF fragments located at different altitudes in the southern Catarinense Plateau were investigated. These fragments were located in the municipalities of Campos Novos (27°35'09.69" S and 51°09'15.07" W, altitude 712 m, area = 1,551.37 ha), Lages ( $27^{\circ}51'19.20''$  S and  $50^{\circ}10'33.39''$  W, altitude 993 m, area = 103.06 ha), and Painel (27°55'27.56" S and 49°56'30.14" W, altitude 1,196 m, area = 48.91 ha) (figure 1). According to the WORDCLIM databank (Hijmans et al. 2005), the mean annual precipitation levels in these fragment areas (from 1960-1990) were 1719, 1483, and 1569 mm in Campos Novos, Lages, and Painel respectively, with rainfall being well-distributed throughout the year. The mean annual temperatures (1960-1990) in these fragments were 17.1, 16.1, and 15 °C respectively. The climates in all three study areas were classified as Cfb, following the classification system of Köppen, being characterized by rainfall uniformly distributed throughout the year and without a dry season. The fragments studied were areas within the Canoas and Pelotas River hydrological basins, and their topography is, for the most part, slightly undulating to undulating. According to the vegetation classification system of IBGE (1992), the arboreal vegetation of the Catarinense Plateau region can be classified

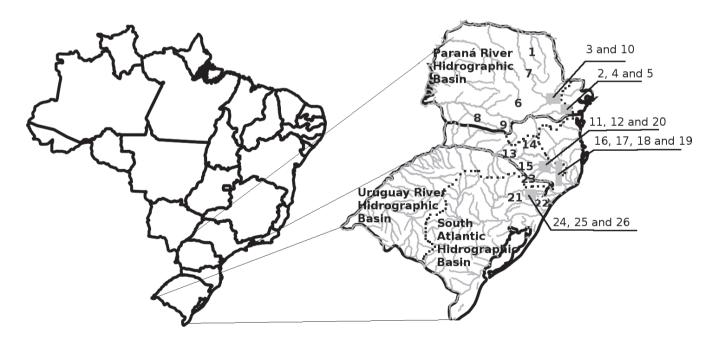


Figure 1. Location of the Araucaria Forest fragments in southern Brazil. 1. Arapoti, PR; 2. Pinhais, PR; 3. São João do Triunfo, PR; 4. Curitiba, PR; 5. Curitiba, PR; 6. Irati, PR; 7. Tibagi, PR; 8. Clevelândia, PR; 9. General Carneiro, PR; 10. Palmeira, PR; 11. Lages, SC; 12. Painel, SC; 13. Campos Novos, SC; 14. Caçador, SC; 15. Campo Belo do Sul, SC; 16. Bom Jardim da Serra, SC; 17. Urubici, SC; 18. Urubici, SC; 19. Bom Jardim da Serra, SC; 20. Lages, SC; 21. Nova Prata, RS; 22. São Francisco de Paula, RS; 23. Bom Jesus, RS; 24. Caxias do Sul, RS; 25. Vacaria, RS; 26. Criúva, RS; 27. São José dos Ausentes, RS.

as Montane and High-Montane Mixed Ombrophilous Forest. The fragments examined had different histories of use and disturbance, but like most of the AF remnants in the state, all of them had experienced intense harvesting of both lumber and non-lumber species during the 1960's.

The surveys of the floristic compositions of the arboreal components of the sites involved establishing 50 permanent plots ( $10 \times 20$  m = 200 m<sup>2</sup> each), totaling 1 ha, to sample each fragment area. The permanent plots were distributed (with 30 m spacing between them) along parallel transects through the forests. The spatial arrangements of these transects were designed to adequately sample the environmental variables present in the areas, such as edge × interior and other variations related to soil types and altitudinal and topographic gradients. As such, the numbers and lengths of the transects varied among the fragments as a function of the unique characteristics of each, taking into consideration their spatial parameters (e.g. shape and total area) and environmental heterogeneity (e.g., topography). All of the arboreal individuals in each plot with CBH (circumference at breast height, measured 1.30 m above soil level)  $\geq 15.7$  cm were identified and marked with

aluminum tags. Plant identifications were made by comparing them with herbarium samples and through consultations with specialist and the use of specialized literature. The angiosperm species were classified into families and genera according to the APG III system (2009). The botanical material collected was incorporated into the Santa Catarina State University herbarium (LUSC).

#### Phytogeographical contextualization

In order to phytogeographically contextualize the study localities, previous scientific publications of floristic lists and surveys of arboreal species of remnant Araucaria forests in southern Brazil were consulted (table 1). The information concerning each species was subject to a detailed revision with respect to habitat, nomenclature, and taxonomic synonyms (which were verified on the W3 Tropicos site) (Mobot 2010). The analyses did not include plants identified only to the family or genus level.

To analyze the relationships between the floristic compositions of the areas in terms of their environmental

Table 1. Floristic and phytosociological surveys of Araucaria Forest fragments in southern Brazil using cluster and ordination analyses. \* = Identification codes for the areas examined in the dendrogram and clustering analyses using NMDS analyses; s.m. = Sampling method; i.l. = Inclusion level; N<sup>o</sup> esp. = number of species; CBH = circumference at breast height; DBH = diameter at breast height; PCQ = point centered quarter.

*	Locality	Municipality	Source	s.m.	i.l.	Nº sp.	Climate
arapPR	Rio das Cinzas	Arapoti, PR	Blum et al. 2003	Plots	DBH≥ 10 cm	134	Cfa
pinPR	Condomínio Residencial Alphaville Graciosa	Pinhais, PR	Seger et al. 2005	Plots	$CBH \ge 15 \text{ cm}$	44	Cfb
sjtPR	Estação Experimental de São João do Triunfo	São João do Triunfo, PR	Sanquetta et al. 2000	Plots	$DBH \ge 10 \text{ cm}$	66	Cfb
cur1PR	Capão do Tigre	Curitiba, PR	Rondon Neto et al. 2002	Plots	$DBH \ge 5 \text{ cm}$	77	Cfb
cur2PR	Parque Municipal do Barigüi	Curitiba, PR	Kozera et al. 2006	PCQ	CBH ≥10 cm	97	Cfb
iraPR	Parque Ambiental Rubens Dalle Grave,	Irati, PR	Valério et al. 2008b	Plots	$DBH \ge 10 \text{ cm}$	39	Cfb
tibPR	Fazenda Batavo	Tibagi, PR	Dias et al. 1998	Plots	$DBH \ge 5 \text{ cm}$	127	Cfa
clePR	Clevelândia	Clevelândia, PR	Valério et al. 2008a	Plots	$DBH \ge 20 \text{ cm}$	26	Cfb
gcPR	Faz. Indústrias Pedro N. Pizzatto Ltda	General Carneiro, PR	Watzlawick et al. 2009	Plots	$DBH \ge 10 \text{ cm}$	39	Cfb
palPR	Três Morros	Palmeira, PR	Iurk 2008	Plots	All fertile phanerogams	134	Cfb
lagpbSC	Pedras Brancas	Lages, SC	This study	Plots	$DBH \ge 5 \text{ cm}$	92	Cfb
paiSC	Farofa	Painel, SC	This study	Plots	$DBH \ge 5 \text{ cm}$	49	Cfb
cnovSC	Ibicuí	Campos Novos, SC	This study	Plots	$DBH \ge 5 \text{ cm}$	87	Cfb
cacSC	Reserva Florestal Embrapa-Epagri	Caçador, SC	Negrelle & Silva 1992; Lingner et al. 2007	PCQ and plots	$DBH \ge 5 \text{ cm and } CBH \ge 60 \text{ cm},$	62	Cfb
cbsuSC	Capatazia Picassos	Campo Belo do Sul, SC	Formento et al. 2004	Plots	$DBH \ge 10 \text{ cm}$	60	Cfb

*	Locality	Municipality	Source	s.m.	i.l.	№ sp.	Climate
bjseSC	Estancias Ribeiro and Machado	Bom Jardim da Serra, SC	Eskuche 2007	-	_	28	Cfb
scobSC	Serra do Corvo Branco	Urubici, SC	Falkenberg 2003	Expeditions	All fertile phanerogams	83	Cfb
migrSC	Morro da Igreja	Urubici, SC	Falkenberg 2003	Expeditions	All fertile phanerogams	55	Cfb
srraSC	Serra do Rio do Rastro	Bom Jardim da Serra, SC	Falkenberg 2003	Expeditions	All fertile phanerogams	91	Cfb
lagSC	-	Lages, SC	Silva et al. (2012)	Plots	$DBH \ge 5 cm$	86	Cfb
npRS	Fazenda Tupi	Nova Prata, RS	Nascimento et al. 2001	Plots	DBH ≥ 9,6 cm	55	Cfb
sfpRS	Floresta Nacional de São Francisco de Paula	São Francisco de Paula, RS	Rosário 2001; Narvaes et al. 2005; Duarte et al. 2006	Plots	Height $\ge 2$ m; CBH $\ge 62.8$ cm; CBH $\ge 3$ cm; DBH $\ge 5$ cm	108	Cfb
bjRS	Rio Pelotas	Bom Jesus, RS	Brack et al. 2009	Walking	_	105	Cfb
cdsRS	Caxias do Sul	Caxias do Sul, RS	Ramos & Boldo 2007	Plots	_	125	Cfb
vacRS	Refugiados	Vacaria, RS	Mauhs 2002	Plots	Height $\geq 0.5$ m	57	Cfb
criRS	Criúva	Criúva, RS	Rondon Neto et al. 2002b	Plots	$DBH \ge 5 \text{ cm}$	37	Cfb
seroSC	Serra da Rocinha	São José dos Ausentes, RS	Falkenberg 2003	Expeditions	All fertile phanerogams	70	Cfb

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and spatial variables, we incorporated data concerning the altitude, climate (1960-1990), and geographical coordinates of each area. The geographic coordinates of the areas were based on the publications cited earlier. Altitudinal and climatic data were obtained from the WORLDCLIM databank (Hijmans et al. 2005), including: altitude (alt), Annual mean temperature (b1), Mean diurnal range (Mean of monthly (max temp - min temp)) (b2), Isothermality (b2/ b7) (x100) (b3), Temperature seasonality (standard deviation x100) (b4), Max temperature of warmest month (b5), Min temperature of coldest month (b6), Temperature annual range (b5-b6) (b7), Mean temperature of wettest quarter (b8), Mean temperature of driest quarter (b9), Mean temperature of warmest quarter (b10), Mean temperature of coldest quarter (b11), Annual precipitation (b12), Precipitation of wettest month (b13), Precipitation of driest month (b14), Precipitation seasonality (coefficient of variation) (b15), Precipitation of wettest quarter (b16), Precipitation of driest quarter (b17), Precipitation of warmest quarter (b18), and Precipitation of coldest quarter (b19).

#### Data analysis

Both the numbers of shared and exclusive species at the Campos Novos, Lages, and Painel sites were demonstrated using a Venn diagram. In order to evaluate the floristic relationships of these areas with other remnant AF sites in southern Brazil, a dendrogram displaying the hierarchical clustering of these areas was prepared utilizing the Sorensen coefficient as a measure of distance, and the UPGMA linking method as the cluster algorithm.

In order to determine the influence of environmental and spatial variables on the floristic patterns encountered, we employed NMDS (Non-metric multidimensional scaling) multivariate analysis with two dimensions (k = 2) (Minchin 1987), and utilized the Sorensen coefficient as a measure of similarity. Although a common practice, we did not exclude rare species from these analyses as they have little influence in NMDS (Muotka et al. 2002). The adequacy of the ordination for interpretation was evaluated using a "stress" value. The variations explained by the ordination axes were calculated from nonlinear adjustments between the distances of the area as defined in the ordination as well as the original dissimilarity in values between the areas (Oksanen 2011). The significance of the "stress" value encountered was evaluated according to the methodology proposed by McCune & Grace (2002) using the Monte Carlo test with 100 permutations. The environmental and spatial variables were adjusted a posteriori and inserted in the form of vectors into the ordination produced by NMDS, using 1000 permutations and excluding the redundant variables or those with low significance in the analysis (P < 0.001).

All of the analyses were made using the R statistical program (R Development Core Team 2010). The Limma package (Gentleman et al. 2004) was used to create the Venn diagram and the Vegan (Oksanen et al. 2009) and Cluster (Maechler et al. 2011) packages were used for multivariate analyses.

## RESULTS

## Species composition and richness

A total of 147 species, 93 genera and 53 plant families were encountered in the three study fragments (table 2). Eight species were identified only to the family level (four species in Campos Novos, three species in Lages, and one species in Painel) and four only to the genus level (one species each in Campos Novos and Lages and two species in Painel); eight taxa were not identified at all due to the impossibility of making collections (two in Campos Novos, three in Lages, and three in Painel).

The families that most contributed to species richness in the three remnant areas evaluated were Myrtaceae (26 species), Fabaceae (12), Asteraceae (8), Lauraceae (8), Salicaceae (7), Solanaceae (7), and Aquifoliaceae (6). Together, these families comprised 50.68% of the total number of species identified. The richest genera were *Solanum* (7 species), *Myrcia* (7), *Ilex* (6), *Eugenia* (5), *Myrceugenia* (5), *Maytenus* (4), and *Ocotea* (4). Myrtaceae stood out as the family with the greatest species richness in all the three areas

Table 2. Floristic list of the tree species sampled in Araucaria Forest fragments located in the municipalities of Campos Novos (1), Lages (2), and Painel (3) on the Santa Catarina Plateau in southern Brazil. M/N = municipalities where the specimens were collected (1, 2 and 3) followed by their identification numbers at the LUSC Herbarium; specimens without identification numbers were not incorporated into the herbarium.

Families	Species	M/N
Adoxaceae	Sambucus australis Cham. & Schltdl.	1 (D2494)
Anacardiaceae	Lithraea brasiliensis Marchand	1 (D2495), 2 (D2594)
	Schinus lentiscifolius Marchand	2
	Schinus polygamus (Cav.) Cabrera	2 (D2596), 3 (D2554)
	Schinus terebinthifolius Raddi	2 (D2595)
Annonaceae	Annona rugulosa (Schltdl.) H.Rainer	1 (D2496), 2 (D2597)
	Annona sylvatica A.StHil.	1
Apocynaceae	Aspidosperma australe Müll.Arg.	1
Aquifoliaceae	Ilex brevicuspis Reissek	2
-	Ilex dumosa Reissek	1 (D2497), 2 (D2598)
	Ilex microdonta Reissek	2 (D2599), 3 (D2555)
	Ilex paraguariensis A.StHil.	2 (D2600), 3 (D2556)
	Ilex taubertiana Loes.	3 (D2557)
	Ilex theezans Mart. ex Reissek	2 (D2601), 3 (D2558)
Araliaceae	Oreopanax fulvus Marchal	1, 2 (D2602)
Araucariaceae	Araucaria angustifolia (Bertol.) Kuntze	1, 2, 3 (D2559)
Arecaceae	Syagrus romanzoffiana (Cham.) Glassman	1
Asparagaceae	Cordyline spectabilis Kunth & Bouché	1 (D2498)
Asteraceae	Baccharis caprariifolia DC.	3
	Baccharis dentata (Vell.) G.Barroso	3
	Dasyphyllum spinescens (Less.) Cabrera	2,3
	Dasyphyllum tomentosum (Spreng.) Cabrera	2 (D2603)
	Gochnatia polymorpha (Less.) Cabrera	2 (D2604)
	Piptocarpha angustifolia Dusén	1, 3
	Symphyopappus itatiayensis (Hieron.) R.M.King & H.Rob.	3
	Vernonanthura discolor (Spreng.) H.Rob.	1 (D2499), 2 (D2605), 3 (D2560)
Berberidaceae	Berberis laurina Billb.	2 (D2606), 3 (D2561)
Bignoniaceae	Handroanthus albus (Cham.) Mattos	2 (D2607)
-	Jacaranda puberula Cham.	1 (D2500), 2 (D2608)
Canellaceae	Cinnamodendron dinisii Schwacke	1 (D2501), 2 (D2609)
Cannabaceae	Celtis iguanaea (Jacq.) Sarg.	2 (D2610)
	Trema micrantha (L.) Blume	1
Cardiopteridaceae	Citronella paniculata (Mart.) R.A.Howard	1 (D2502), 2 (D2611)
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Families	Species	M/N
Celastraceae	Maytenus aquifolia Mart.	1 (D2503)
	Maytenus boaria Molina	2 (D2612)
	Maytenus dasyclada Mart.	2 (D2613)
	Maytenus ilicifolia Mart. ex Reissek	3 (D2562)
	Schaefferia argentinensis Speg.	1 (D2504)
Clethraceae	Clethra scabra Pers.	1 (D2505), 2 (D2614), 3 (D2563)
Cordiaceae	Cordia americana (L.) Gottschling & J.J.Mill.	1 (D2506)
Cunoniaceae	Lamanonia ternata Vell.	1 (D2507), 2 (D2615)
Cyatheaceae	Cyathea delgadii Sternb.	1 (D2508)
Dicksoniaceae	Dicksonia sellowiana Hook.	1 (D2509), 2, 3 (D2564)
Elaeocarpaceae	Sloanea monosperma Vell.	1 (D2510)
Erythroxylaceae	Erythroxylum deciduum A.StHil.	2 (D2616)
Escalloniaceae	Escallonia bifida Link & Otto	2 (D2617)
Euphorbiaceae	Gymnanthes concolor (Spreng.) Müll.Arg.	1 (D2511)
	Sapium glandulosum (L.) Morong	1, 2
	Sebastiania brasiliensis Spreng.	1 (D2512), 2 (D2618)
	Sebastiania commersoniana (Baill.) L.B.Sm. & Downs	1, 2 (D2619)
Fabaceae Faboideae	Dalbergia frutescens (Vell.) Britton	1 (D2513), 2 (D2620)
	Erythrina falcata Benth.	1
	Lonchocarpus campestris Mart. ex Benth.	1
	Machaerium paraguariense Hassl.	2 (D2621)
	Machaerium stipitatum (DC.) Vogel	2 (D2622)
	Myrocarpus frondosus Allemão	1
Fabaceae Mimosoideae	Albizia niopoides (Spruce ex Benth.) Burkart	1
	Inga lentiscifolia Benth.	3 (D2565)
	Inga sessilis (Vell.) Mart.	2 (D2623)
	Inga striata Benth.	1 (D2514)
	Mimosa scabrella Benth.	1, 2, 3 (D2566)
	Parapiptadenia rigida (Benth.) Brenan	1 (D2515)
Lamiaceae	Vitex megapotamica (Spreng.) Moldenke	1 (D2516)
Lauraceae	Cinnamomum amoenum (Nees & Mart.) Kosterm.	2 (D2624), 3 (D2567)
	Nectandra lanceolata Nees	2
	Nectandra megapotamica (Spreng.) Mez	1 (D2517), 2
	Ocotea diospyrifolia (Meisn.) Mez	2
	Ocotea porosa (Nees & Mart.) Barroso	1 (D2518)
	Ocotea puberula (Rich.) Nees	2
	Ocotea pulchella Mart.	1 (D2519), 2 (D2625), 3 (D2568)
	Persea willdenowii Kosterm.	1 (D2520), 3 (D2569)
Malvaceae	Luehea divaricata Mart.	1 (D2521)
Melastomataceae	Miconia hiemalis A.StHil. & Naudin ex Naudin	2 (D2626)
	<i>Miconia cinerascens</i> Miq.	1 (D2522)
Meliaceae	Cabralea canjerana (Vell.) Mart.	1, 2
	Cedrela fissilis Vell.	1, 2 (D2627)
	Trichilia claussenii C.DC.	1 (D2523)
	Trichilia elegans A.Juss.	1 (D2524)
Myrtaceae	Acca sellowiana (O.Berg) Burret	2 (D2628), 3 (D2570)
	Blepharocalyx salicifolius (Kunth) O.Berg	2 (D2629), 3 (D2571)
	Calyptranthes concinna DC.	2 (D2630), 3 (D2572)
	Campomanesia guazumifolia (Cambess.) O.Berg	1
	Campomanesia xanthocarpa O.Berg	1, 2 (D2631), 3
	Eugenia pluriflora DC.	2 (D2632)
	Eugenia pyriformis Cambess.	2 (D2633)
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Families	Species	M/N
	Eugenia ramboi D.Legrand	1
	Eugenia uniflora L.	1 (D2525), 2 (D2634)
	Eugenia uruguayensis Cambess.	2 (D2635)
	Myrceugenia euosma (O.Berg) D.Legrand	2 (D2636), 3 (D2573)
	Myrceugenia glaucescens (Cambess.) D.Legrand & Kausel	3
	Myrceugenia myrcioides (Cambess.) O.Berg	2 (D2637), 3 (D2574)
	Myrceugenia ovata (Hook. & Arn.) O.Berg	2 (D2638), 3 (D2575)
	Myrceugenia oxysepala (Burret) D.Legrand & Kausel	3 (D2576)
	Myrcia bombycina (O.Berg) Nied.	1
	Myrcia guianensis (Aubl.) DC.	1 (D2640), 2
	Myrcia hartwegiana (O.Berg) Kiaersk.	3
	Myrcia hatschbachii D.Legrand	2
	Myrcia laruotteana Cambess.	- 2 (D2641)
	<i>Myrcia multiflora</i> (Lam.) DC.	2
	Myrcia palustris DC.	2 (D2642)
	Myrcianthes gigantea (D.Legrand) D.Legrand	1, 2 (D2643)
	Myrcianthes pungens (O.Berg) D.Legrand	1
	Myrrhinium atropurpureum Schott	2 (D2644), 3 (D2577)
	Plinia trunciflora (O.Berg) Kausel	1
Phytolaccaceae	Seguieria americana L.	1
Picramniaceae	Picramnia parvifolia Engl.	1 (D2526)
Podocarpaceae	Podocarpus lambertii Klotzsch ex Endl.	2 (D2645)
Polygonaceae	Ruprechtia laxiflora Meisn.	1 (D2527)
Primulaceae	Myrsine coriacea (Sw.) Roem. & Schult.	1 (D2527) 1 (D2528), 2 (D2646), 3 (D2578)
1 Innulaceae	Myrsine guianensis (Aubl.) Kuntze	1 (D2529), 2 (D2040), 3 (D2578) 1 (D2529)
	Myrsine umbellata Mart.	1 (D2529) 1 (D2530), 2 (D2647)
Proteaceae	Roupala montana Aubl.	1 (D2531), 2 (D2648), 3 (D2579)
Quillajaceae	Quillaja brasiliensis (A.StHil. & Tul.) Mart.	2 (D2649)
Rhamnaceae	Rhamnus sphaerosperma Sw.	2 (D2650), 3 (D2580)
Rhannaceae	Scutia buxifolia Reissek	2 (D2650), 5 (D2580) 2 (D2651)
Rosaceae	Prunus myrtifolia (L.) Urb.	1 (D2532), 2 (D2652), 3 (D2581)
Rubiaceae	<i>Chomelia obtusa</i> Cham. & Schltdl.	1 (D2532), 2 (D2052), 5 (D2561) 1 (D2533)
Rublaceae	Cordiera concolor (Cham.) Kuntze	1 (D2533) 1 (D2534)
	Coutarea hexandra (Jacq.) K.Schum.	1 (D2535), 2 (D2653)
Rutaceae	Helietta apiculata Benth.	1 (D2536), 2 (D2655) 1 (D2536)
Kulaceae	Zanthoxylum fagara (L.) Sarg.	1 (D2537)
	Zanthoxylum Jugara (E.) Sarg. Zanthoxylum kleinii (R.S.Cowan) P.G.Waterman	1 (D2538), 2 (D2654), 3 (D2582)
	Zanthoxylum kheimi (K.S.Cowall) 1.G. waterinan Zanthoxylum rhoifolium Lam.	1 (D2558), 2 (D2654), 5 (D2582) 1, 2 (D2655), 3 (D2583)
Salicaceae	Banara parviflora (A.Gray) Benth.	1, 2 (D2033), 3 (D2383) 1 (D2539)
Sancaccac	Banara tomentosa Clos	1 (D2540), 2 (D2656)
	Casearia decandra Jacq.	1 (D2540), 2 (D2657) 1 (D2541), 2 (D2657)
	*	
	<i>Casearia obliqua</i> Spreng.	2 (D2658) 1 (D2542)
	<i>Casearia sylvestris</i> Sw.	1 (D2542)
	<i>Xylosma ciliatifolia</i> (Clos) Eichler	1, 2 (D2659), 3
Samindaaaaa	<i>Xylosma tweediana</i> (Clos) Eichler	1 (D2543), 2 (D2660) 1 (D2544), 2 (D2661)
Sapindaceae	Allophylus edulis (A.StHil. et al.) Radlk.	1 (D2544), 2 (D2661) 1 (D2545), 2 (D2662), 2 (D2584)
	Allophylus guaraniticus (A.StHil.) Radlk.	1 (D2545), 2 (D2662), 3 (D2584)
	Cupania vernalis Cambess.	1 (D2546), 2 (D2663) 1 (D2547), 2 (D2664)
Sanataaaac	Matayba elaeagnoides Radlk.	1 (D2547), 2 (D2664)
Sapotaceae	<i>Chrysophyllum marginatum</i> (Hook. & Arn.) Radlk. <i>Solanum mauritianum</i> Scop.	1 (D2548) 3 (D2585)
	NOUMUM MAUFUMUM NCOD	1 (17/292)
Solanaceae	Solanum pabstii L.B.Sm. & Downs	2 (D2665), 3 (D2586)

Families	Species	M/N		
	Solanum paranense Dusén	3 (D2587)		
	Solanum pseudoquina A.StHil.	1 (D2549), 3 (D2588)		
	Solanum ramulosum Sendtn.	3 (D2589)		
	Solanum sanctaecatharinae Dunal	1 (D2550), 2 (D2666), 3 (D259		
Solanum variabile Mart.		3 (D2591)		
Styracaceae	Styrax leprosus Hook. & Arn.	1 (D2551), 2 (D2667)		
Symplocaceae	Symplocos uniflora (Pohl) Benth.	1 (D2552), 2 (D2668)		
Thymelaeaceae	Daphnopsis racemosa Griseb.	2 (D2669), 3 (D2592)		
Verbenaceae	Duranta vestita Cham.	2 (D2670)		
Winteraceae	Drimys brasiliensis Miers	1 (D2553), 2 (D2671), 3 (D2593)		

continuation

studied. The families that most contributed to arboreal floristic richness in Campos Novos were Myrtaceae (9 species), Fabaceae (8), Salicaceae (6), Euphorbiaceae (4), Lauraceae (4), Meliaceae (4), Rutaceae (4), and Sapindaceae (4); the species distributions among these different genera were quite homogeneous, although Myrsine stood out with three species. The families that most contributed to species richness in Lages were Myrtaceae (18 species), Lauraceae (6), Aquifoliaceae (5), Salicaceae (5), Anacardiaceae (4), Asteraceae (4), and Sapindaceae (4); the most important genera were Myrcia (5 species), Ilex (5), Eugenia (4), Myrceugenia (3), Ocotea (3), and Schinus (3). The families that most contributed to species richness in Painel were Myrtaceae (11 species), Solanaceae (7), Asteraceae (6), Aquifoliaceae (4), and Lauraceae (3); the richest genera were Solanum (7 species), Myrceugenia (5), and Ilex(4).

The species richnesses values in the remnant forest areas at Campos Novos, Lages, and Painel were 87, 91 and 49 respectively (figure 2). Only a low percentage of species were shared among all three sample areas (10.88%). The site with the greatest proportion of exclusive species was Campos Novos (45.98%), while Painel had the lowest (26.53%); the latter site shared 67.35% of its species with Lages. Of the total number species encountered in Lages, 48.35% were shared with Campos Novos, 36.26% with Painel, while 32.97% were exclusive.

## Phytogeography

Examinations of the AF fragments in southern Brazil indicated the existence of three large floristic groups (figure 3). Group 1 was composed of high-montane areas in the states of Santa Catarina and Rio Grande do Sul; Group 2 was formed by forest remnants in Paraná State in the Paraná River basin (Arapoti, Tibagi, and Irati); and

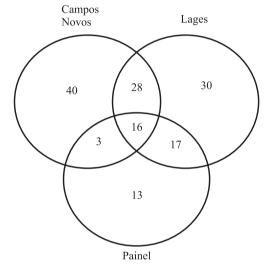


Figure 2. Venn diagram with species distributions in Araucaria Forest fragments located in the municipalities of Campos Novos, Lages, and Painel in Santa Catarina State, Brazil.

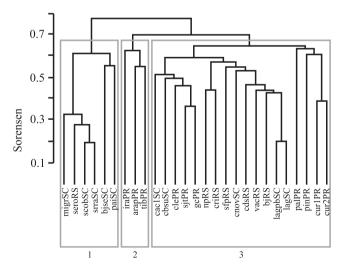


Figure 3. Dendrogram produced by cluster analysis of the Araucaria Forest remnants examined in southern Brazil, using the Sorensen coefficient is a measure of distance and UPGMA as the clustering algorithm. See table 1 for the locality names.

Group 3 was formed by a large number of remnant areas distributed among three states located in the hydrographic basins of the Paraná and Uruguay rivers and those rivers that drain directly into the southern Atlantic. The forest remnant located in the municipality of Painel was placed in Group 1 and was the most floristically distinct but showed greater floristic similarity with Bom Jardim da Serra, SC. The fragment area in Lages (Group 3) demonstrated greater floristic similarity with another fragment from the same municipality, and both of them demonstrated high similarity with Bom Jesus, Vacaria, Caxias do Sul, Campos Novos, and São Francisco de Paula – all of which are situated in the Upper-Uruguay region.

The "stress" value in the NMDS ordination analysis (figure 4) was 15.78% (P < 0.01), which corresponds to an explained variance of 97.51% – indicating that the diagram was adequate for our interpretations. The floristic groups defined in the dendrogram are indicated in the NMDS diagram by continuous lines. The variables that demonstrated elevated significance (P < 0.001) (table 3) within the ordination are represented by vectors. It can be seen that the variables that best explained the separation of the three groups were altitude (alt), Annual mean

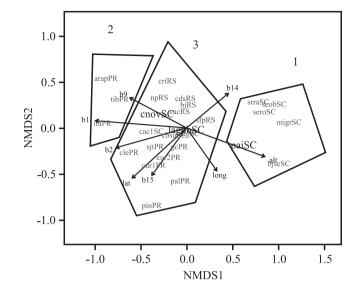


Figure 4. Ordination diagram produced by NMDS (Nonmetric multidimensional scaling) analysis of Araucaria Forest remnants located in southern Brazil. (Alt = altitude; b1 = Annual mean temperature; b2 = Mean diurnal temperature range; b9 = Mean temperature of driest quarter; b14 = Precipitation of driest month; b15 = Precipitation seasonality; lat = latitude; long = longitude). See table 1 for the locality names.

Table 3. Environmental and spatial variables (P < 0.001) fitted to the ordination produced by NMDS of the Araucaria Forest fragments in southern Brazil. \* = Identification codes for the areas; long = longitude (°); lat = latitude (°); alt = altitude (m); b1 = Mean annual temperature (°C); b2 = Mean daily thermal amplitude (°C); b9 = Mean temperature during the most humid trimester (°C); b14 = Precipitation during the driest month (mm); b15 = Precipitation seasonality (variation coefficient). Acronyms for the Brazilian states: RS = Rio Grande do Sul; PR = Paraná; SC = Santa Catarina.

Area*	Municipality	Geographical and climatic variables							
Alta	Municipality	long. (W)	lat. (S)	alt.	b1	b2	b9	b14	b15
arapPR	Arapoti, PR	49.9605	23.8525	613	19.8	12.1	17.4	48	3.82
pinPR	Pinhais, PR	49.1305	25.4069	920	17.1	10.0	13.9	77	3.12
sjtPR	São João do Triunfo, PR	50.0988	25.5717	891	17.1	11.7	13.3	78	2.92
Cur1PR	Curitiba, PR	49.2424	25.4592	907	17.2	10.2	14.3	75	2.97
Cur2PR	Curitiba, PR	49.2424	25.4592	907	17.2	10.2	14.3	75	2.97
iraPR	Irati, PR	50.6307	25.4656	859	17.3	11.7	13.5	74	2.66
tibPR	Tibagi, PR	50.4166	24.516	764	18.5	12.7	14.9	54	2.88
clePR	Clevelândia, PR	52.2275	26.3317	939	16.5	13.3	16.4	130	1.9
gcPR	General Carneiro, PR	51.4247	26.4369	1162	15.3	12.3	11.4	112	1.39
palPR	Palmeira, PR	50.0260	25.6033	808	17.4	11.7	13.5	74	2.96
lagpbSC	Lages, SC	50.1882	27.9162	993	16.1	10.5	12.4	99	1.61
paiSC	Painel, SC	50.1049	27.9289	1196	15.0	10.2	12.5	105	1.55
cnovSC	Campos Novos, SC	51.1808	27.6021	711	17.0	11.1	17	112	1.31
cacSC	Caçador, SC	51.0166	26.7833	934	16.3	12.1	12.1	117	1.19
cbsuSC	Campo Belo do Sul, SC	50.8166	28.0001	956	16.0	10.5	15.9	120	1.11
bjseSC	Bom Jardim da Serra, SC	49.6249	28.3370	1319	13.9	9.5	11.3	112	1.62
scobSC	Urubici, SC	49.3663	28.0575	1491	12.9	9.4	10.6	115	1.75
migrSC	Urubici, SC	49.4832	28.1333	1501	12.9	9.4	10.5	115	1.66
-									continue

A	Maniainalita	Geographical and climatic variables							
Area*	Municipality	long. (W)	lat. (S)	alt.	b1	b2	b9	b14	b15
srraSC	Bom Jardim da Serra, SC	49.5499	28.4001	1329	13.7	9.4	11.2	113	1.60
lagSC	Lages, SC	50.3211	27.8534	916	16.5	10.6	12.8	95	1.61
npRS	Nova Prata, RS	51.8839	28.9324	395	18.4	10	14.5	112	1.07
sfpRS	São Francisco de Paula, RS	50.3833	29.4501	814	15.5	9.5	16.7	137	0.90
bjRS	Bom Jesus, RS	50.6132	28.4128	866	16.4	10	13.8	114	1.25
cdsRS	Caxias do Sul, RS	51.2500	28.7500	786	16.9	10.4	18.7	125	1.25
vacRS	Vacaria, RS	50.9333	28.6668	843	16.5	9.9	13.9	127	1.11
criRS	Criúva, RS	50.9303	29.0047	856	16.3	9.6	13.7	133	1.14
seroRS	São José dos Ausentes, RS	49.9499	28.7834	1187	14.3	9.5	11.8	122	1.31

continuation

temperature (b1), and Mean temperature of driest quarter (b9). The extremes of this gradient are represented by the areas in Group 1 (with the highest and coldest sites) and by the areas of Group 2 (with the lowest altitude and warmest sites). Internally within Group 3 (which had the largest area), the greatest species substitution occurred along an environmental gradient associated with latitude (lat), Precipitation seasonality (coefficient of variation) (b15), and Precipitation of driest month (b14).

## DISCUSSION

The numbers of species encountered in each fragment in the present study were indicative of low richness (in the case of Painel) as well as elevated richness (in the case of Lages and Campos Novos) in comparison with other studies undertaken in AF fragments in southern Brazil with values that varied between 134 in Arapoti and Palmeira (PR) to 26 in Clevelândia (PR) (see table 1). Myrtaceae, the plant family that most contributed to species richness in the three study fragments, had already been cited by Mori et al. (1983) as the richest family in different Atlantic Forest formations. Additionally, a number of studies undertaken in southern Brazil have confirmed important contributions of Myrtaceae to species richness (e.g. Jurinitz & Jarenkow 2003).

The low percentages of species shared among the three fragments studied indicated that AFs are not floristically homogeneous formations. The ordination of the study areas and their relationships with the spatial and environmental variables examined demonstrated that the remnant AF areas have floristic variations that are associated with their distributions from West to East and North and South, reflecting the overall environmental heterogeneity of the region. It is worth noting that aspects related to historical perturbations in these areas also influence tree species distributions (even though this factor was not evaluated the present study) (Silva et al. 2009).

To the east, near the coast, there are important mountain chains formed by the Serra do Mar and Serra Geral mountains that constitute the highest elevations in southern Brazil. Heavy fogs frequently occur in these localities as well as snap freezes and frequent snowfalls, principally in the Serra Catarinense and Serra Gaúcha regions. This is where the areas forming floristic Group 1 are found, including the present study fragment in the municipality of Painel. A number of species encountered in this fragment were exclusive to Lages and Campos Novos, principally those belonging to the genera *Ilex*, Baccharis, Symphyopappus, Myrceugenia, and Solanum that contain high-altitude indicator species. The genera Drimys and Clethra which Webster (1995) identified as typical of Neotropical cloud-forest areas also occur in this fragment. The low richness observed in Painel might be a result of the high rigor and selectivity of the climatic conditions in that area.

Land elevation gradually diminishes westward as the principal watercourses in the region drain towards the Paraná and Uruguay rivers. The AF accompany the principle hydrographic basins forming these rivers, from the highest elevations to altitudes near 500 m (where the climate becomes warmer and there are stronger influences of typical components of seasonal forests). The area near Campos Novos, along the Canoas River (which together with the Pelotas River forms the Uruguay River), is an example of this situation, with a significant proportion of its species being exclusive in relation to those seen at Lages and Painel, including: *Schaefferia argentinensis, Cordia americana, Myrocarpus frondosus,* and *Parapiptadenia rigida* – all typical of Seasonal Deciduous Forests of the Upper-Uruguay river basin.

The influence of altitudinal gradients on the floristic patterns of neotropical forests has been demonstrated

by a number of authors (e.g. Oliveira Filho et al. 1994, 2005, Oliveira Filho & Fontes 2000, Scudeller et al. 2001) and was shown to be (together with temperature) one of the principal variables that influenced species distributions in the three area studied here. As was noted by Oliveira Filho & Fontes (2000), various environmental changes occur along this gradient - such as temperature variations and the occurrence of freezing events - which can explain the strong changes observed in species distributions. Considering the three areas evaluated in the present study, Campos Novos is positioned at one of the extremes of this gradient at an altitude of 700 m and Painel at the other (1196 m). Both of these areas share large numbers of species with the Lages site (993 m), which is geographically situated between the two extremes and can be considered a transition area.

Passing through states of Santa Catarina to Rio Grande do Sul from north to south, there are two large hydrographic basins that together form the Platina Basin (the Paraná and Uruguay river basins). Even though this region does not experience a well-defined dry season, our results demonstrated an environmental gradient between these two basins associated principally with the precipitation regime (b14 and b15) (see figure 3). These results corroborate observations made by Klein (1978), who classified the AFs in Santa Catarina State in terms of their hydrographic basins. Authors such as Silva et al. (2006) likewise observed the tendency of areas that occur in the same hydrological basin to cluster in terms of their species compositions. One of the factors that could help explain the observed floristic compartmentalization in terms of hydrological basins would be the influence of riparian forests that function as dispersal corridors for arboreal species. This concept of tree species migration has been examined by a number of authors using different methodologies (e.g. Rambo 1951, Budke et al. 2004).

The Araucaria forests analyzed here could be classified into three distinct phytogeographical units: i) high altitude areas with lower mean annual temperatures and influences of cloud/fog cover (where the Painel site was established); ii) lower altitude areas with greater mean annual temperatures, situated in the Paraná River basin; iii) areas situated in the Paraná and Upper-Uruguay river basins as well as the smaller river basins that drain directly into the southern Atlantic (the Campos Novos and Lages sites). The environmental variables most closely correlated with the high levels of species substitutions among three sites were altitude, mean annual temperature, and mean temperature of driest quarter. Acknowledgments – The authors thank CNPq for financial support through Edital MCT/CNPq 15/2007, which allowed us to undertake this study; the Brochmann Polis – Industrial and Florestal S/A company for allowing us access to their property at Campos Novos; and Tio Deja and Sr. Jorge Gamborgi for graciously allowing us access to their properties in Painel and Lages respectively.

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