Revista Brasil. Bot., V.34, n.1, p.91-101, jan.-mar. 2011

Floristic relationships among inland swamp forests of Southeastern and Central-Western Brazil[1]

ALOYSIO DE PÁDUA TEIXEIRA[2,3] and MARCO ANTONIO ASSIS[2]

(received: June 03, 2009; accepted: January 27, 2011)

ABSTRACT – (Floristic relationships among inland swamp forests of Southeastern and Central-Western Brazil). We evaluated the floristic relationships among 20 swamp forests of Southeastern and Central-Western Brazil using multivariate analyses. Detrended correspondence analysis (DCA) and TWINSPAN (Two way indicator species analysis) indicated two distinct floristic groups among forests, according to the Phytogeographic Province (*Paranaense* or *Cerrado*) and their climate conditions, phytophysiognomies, and species composition. Within the same province, edaphic conditions and geographical distance, among other factors, may be responsible for similarities or dissimilarities among the forests floras. Our results indicated that, despite the low α diversity, γ diversity is high among the forests, as a result of the low floristic similarities among the remnants and the high number of unique species (55% of all species). Although floristically distinct, we concluded that the inland swamp forests of Southeastern Brazil and the gallery swamp forests of Central Brazil are part of the same forest formation. These forests have in common, in addition to the swampy environment, low plant species diversity and species that have high local densities, such as *Calophyllum brasiliense* Cambess.*, Cecropia pachystachya* Trécul*, Dendropanax cuneatus* Decne. & Planch.*, Guarea macrophylla* Vahl*, Magnolia ovata* (A. St.-Hil.) Spreng.*, Protium spruceanum* (Benth.) Engl. and *Tapirira guianensis* Aubl.

Key words - *Cerrado* province (Brazilian savannas), floristic similarity, gallery swamp forests, *Paranaense* province, γ diversity

RESUMO – (Relações florísticas entre florestas paludosas interioranas do Sudeste e Centro-Oeste do Brasil). As relações florísticas entre 20 florestas paludosas interioranas do Sudeste e Centro-oeste do Brasil foram avaliadas por meio de análises multivariadas. A DCA (Análise de correspondência destendenciada) e a TWINSPAN (*Two way indicator species analysis*) indicaram dois grupos floristicamente distintos, conforme a província fitogeográfica (Paranaense ou Cerrado) e suas condições de clima, fitofisionomias e composição de espécies. Dentro de uma mesma província, as condições edáficas e a distância geográfica, entre outros fatores, podem ser responsáveis por semelhanças ou dissimilaridades florísticas entre as florestas. Os resultados evidenciam que, apesar da baixa diversidade α, a diversidade γ é alta para essas formações, em função de baixas similaridades florísticas entre os remanescentes e do elevado número de espécies exclusivas (55% do total de espécies). Embora floristicamente distintas, conclui-se que as florestas paludosas interioranas do Sudeste do Brasil e as florestas de galeria inundáveis do Brasil Central são parte de uma mesma formação florestal. Estas florestas apresentam, em comum, além do ambiente paludoso, uma baixa diversidade vegetal e espécies com elevadas densidades locais, como C*alophyllum brasiliense* Cambess.*, Cecropia pachystachya* Trécul*, Dendropanax cuneatus* Decne. & Planch.*, Guarea macrophylla* Vahl*, Magnolia ovata* (A. St.-Hil.) Spreng.*, Protium spruceanum* (Benth.) Engl. e *Tapirira guianensis* Aubl.

Palavras-chave - diversidade γ, mata brejosa de galeria, Província do Cerrado, Província Paranaense, similaridade florística

Introduction

Swamp forests are unique riverside formations with regard to their floristic composition. Their occurrence is restricted to hydromorphic soils which are permanently saturated throughout most of the year (Leitão Filho 1982). Despite the specificity of the soil in which they occur, these forests are widely distributed in the Neotropics and present an interface with different neighboring forests or grasslands. In Southern and Southeastern Brazil, the swamp forests are linked mainly to different forests of *Paranaense* and Atlantic phytogeographic provinces, such as the seasonal semideciduous inland forests (Rocha *et al*. 2005, Teixeira & Assis 2005) and the rainforests of the coastal zone (Scarano 2002, 2006). In the central-northern portion of the state of São Paulo and in most of the state of Minas Gerais, as well as in Central Brazil, the swamp forests occur in swampy parts of gallery forests, which are associated with different phytophysiognomies of the *Cerrado* (Brazilian savannas), like the *cerradão* (woody *cerrado*) and *cerrado sensu stricto* (Oliveira Filho *et al*. 1990, Nogueira & Schiavini 2003, Gomes *et al*. 2004, Guarino & Walter 2005, Teixeira & Assis 2009). Within the same province, such as the coastal zone in Atlantic domain, the swamp forests may occur

1. Part of the thesis of first author, Programa de Pós Graduação em Ciências Biológicas (Biologia Vegetal), Universidade Estadual Paulista , Rio Claro, SP, Brazil.
2. Universidade Estadual Paulista, Instituto de Biociências, Departamento de Botânica, Caixa Postal 199, 13506-900 Rio Claro, SP, Brazil.
3. Corresponding author: teixeira.aloysio@gmail.br

in different edaphic conditions, such as on sandy, mainly Quaternary alluvium-derived substrates (Scarano 2002) or peat soils (Sztutman & Rodrigues 2002, Dorneles & Waechter 2004).

Swamp forests are restricted to hydromorphic soils that determine their natural fragmentation (Ivanauskas *et al*. 1997) and consequently expose their borders (Costa *et al*. 1997). This allows the occurrence of species that are prevalent in the surrounding formations, like the *cerrados* (Marques *et al*. 2003, Teixeira & Assis 2009), semideciduous seasonal forests (Toniato *et al*. 1998, Teixeira & Assis 2005) and rain forests (Lieberman *et al*. 1985, Scarano 2002) to occur in these forests. The typical species of well-drained soils usually have little influence on vegetation structure as they occur in low densities, but they are responsible for increasing the local richness of the swamp forests (Marques *et al*. 2003, Scarano 2006, Teixeira *et al*. 2008) and the floristic dissimilarity among the remnants (Costa *et al*. 1997, Ivanauskas *et al*. 1997, Teixeira & Assis 2005).

Although the floristic composition of swamp forests has been the subject of various studies, mainly in the state of São Paulo, very little is known about the floristic relationship among swamp forests in different regions of Brazil. This is a function of three factors: the lack of floristic surveys outside the state of São Paulo, the joint investigation of the flora of these forests together with that of other floristically diverse riverside forests (*e.g.* Rodrigues & Nave 2000, Silva *et al*. 2007, Martins *et al*. 2008) and the floristic evaluation of only a few samples in very restricted geographic portions (*e.g.* Costa *et al*. 1997, Teixeira & Assis 2005). For other Brazilian vegetation types, such as seasonal semideciduous forests, rainforests and *cerrados*, the climatic conditions represented by rainfall, humidity, temperature, existence and duration of a dry season or frost, have been cited as the main factors responsible for floristic and structural variations in regional scales of a few hundred kilometers (Salis *et al.* 1995, Torres *et al.* 1997, Oliveira Filho & Fontes 2000, Scudeller *et al.* 2001, Durigan *et al.* 2003).

A joint analysis of eight swamp forest remnants in the interior of the state of São Paulo showed that these forests have similar structural characteristics and that it is common to find, in several of the remnants, a concentration of many individuals from a few flood tolerant species. However, the low number of studies used for comparison and the spatial proximity among these samples did not enable the authors to evaluate the existence of phytogeographic patterns mainly related to climatic variables across different regions (Teixeira & Assis 2005), as seen in the other main vegetation types of Brazil. In the present study, a comparison was made of the floristic composition of swamp forests studied in the Southeastern and Central-Western regions of Brazil that present interface with seasonal semideciduous forests or *cerrados*. Our aim was to investigate the floristic similarities and differences among the swamp forests, considering not only the state of São Paulo, but also other states where studies have been performed. As the surrounding vegetation is considered an important factor that may contribute to the dissimilarity among the remnants, we predicted that the swamp forests that present interface with the *cerrados* would present greater floristic similarities, compared to the swamp forests present in the area of semideciduous seasonal forests, which in turn would form their own groups.

Material and methods

In order to compare the different swamp forests, we considered 20 studies on the inland of São Paulo (SP) and Minas Gerais (MG) States, as well as those in Central Brazil – Distrito Federal (DF), Mato Grosso (MT) and Mato Grosso do Sul (MS) – covering the *Paranaense* and *Cerrado* phytogeographic provinces, according to Cabrera & Willink (1973) (figure 1). In the *Cerrado* province, the swamp forests are called gallery swamp forests (*sensu* Ribeiro & Walter 2008). To determine whether a forest was to be included in the

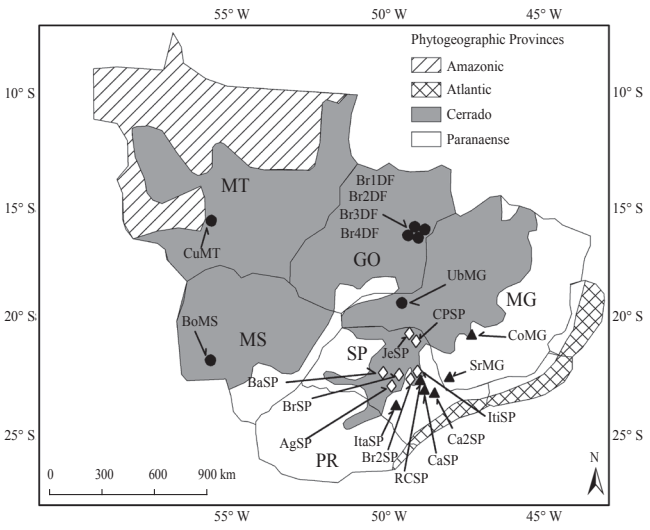

Figure 1. Brazilian phytogeographic provinces, based in Cabrera & Willink (1973), and the location of 20 studies used in the evaluation of floristic similarities among inland swamp forests of Southeastern and Central-Western Brazil. Codes in table 1 (▲ = seasonal semideciduous forest; ◇ = seasonal semideciduous forest/*cerrado* contact; ● = *cerrado*).

analyses, two characteristics had to be met: water saturated soil most of the year and water table near the surface in the dry season.

In the studies, the sampling effort was quite varied, depending on different criteria for inclusion of individuals and the size of the samples (table 1). However, due to the low number of studies found, the sampling effort was not considered a restriction for including a study in the comparisons. For the study in the state of Mato Grosso (Oliveira Filho *et al*. 1990), held in different parts of a gallery forest, only the swampy portion was considered, described by the authors as "the *brejo* site lies in a more gently sloping part of the stream where the soils are very swampy". For this portion, we calculated the Shannon diversity index, based on the listing of the density of individuals per species provided in the article.

For the analyses we constructed a presence/absence matrix of the species in each remnant, considering the classification system of the Angiosperm Phylogeny Group (APG II 2003, Souza & Lorenzi 2005). We considered only those taxa identified at species level, which underwent a review of nomenclature to correct synonyms. The matrix was formed by 440 species of shrubs and trees, distributed in 203 genera and 77 families. The floristic similarity among the swamp forests was assessed by the Jaccard coefficient (S_J) and multivariate analyses of ordination and grouping. For the ordination analysis we used the DCA – Detrended Correspondence Analysis (Hill & Gauch 1980) and for the grouping analysis we used TWINSPAN – Two way indicator species analysis (Gauch & Whittaker 1981). The Jaccard coefficient was calculated for each pair of forests by the FITOPAC program (Shepherd 1994), considering the complete floristic list (440 species). For the multivariate analysis, the species occurring in only one remnant (241 or 55% of the total species) were excluded in order to better understand the possible groupings of the samples, according to their most frequent elements. Multivariate analyses were processed by the program PC-ORD version 4.0 (McCune & Mefford 1999).

Results

In the 20 comparative studies, the species most frequently found were *Calophyllum brasiliense* Cambess., *Dendropanax cuneatus* Decne. & Planch. and *Tapirira guianensis* Aubl. (19 studies or 95% of the total), *Magnolia ovata* (A. St.-Hil.) Spreng. (18 studies or 90%), *Cecropia pachystachya* Trécul and *Protium spruceanum* (Benth.) Engl. (17 studies or 85%) and *Guarea macrophylla* Vahl (14 studies or 70%). The richest genera were *Ocotea* and *Miconia* (20 species), *Ficus* (12), *Inga* (11) and *Myrcia* (10), while the families represented by a greater number of species were Fabaceae (48 species), Myrtaceae (39), Lauraceae (35), Melastomataceae (23), Rubiaceae (20), Moraceae (17), Euphorbiaceae (16), Annonaceae (15), Meliaceae (13), and Myrsinaceae (11).

The Jaccard coefficient (S_J) showed that, in general, the floristic similarity among the 20 areas was very low because, of the 380 floristic comparisons, only 15 had values greater than or equal to 0.25 (table 2). The highest similarity values, according to the coefficient, were observed between two forests studied in the Distrito Federal (Riacho Fundo and Acampamento streams, $S_J = 0.47$), between Jeriquara and Cristais Paulista, in state of São Paulo ($S_J = 0.39$) and between Acampamento stream and Mata da Onça, both in the Distrito Federal ($S_J = 0.39$). The forests studied in Mato Grosso, Mato Grosso do Sul and southern Minas Gerais (Coqueiral and Santa Rita de Caldas) showed low similarity coefficients between one another and with all other forests studied, indicating that they had the most unique floras in the samples.

The first division generated by TWINSPAN separated the forests studied mainly in the state of São Paulo from those studied in *Triângulo Mineiro* (a region in the state of Minas Gerais where Uberlândia is inserted) and Central Brazil (figure 2). As an indicator species, the analysis only pointed to *Richeria grandis* Vahl for the second group. The most important species in the first group were *Ardisia ambigua* Mart., *Aspidosperma cylindrocarpon* Müll. Arg., *Calyptranthes concinna* DC., *Citronella gongonha* (Mart.) R.A. Howard, *Cecropia glaziovi* Snethl., *Chionanthus trichotomus* (Vell.) P. S. Green, *Croton floribundus* Spreng., *Eugenia florida* DC., *Ficus obtusiuscula* (Miq.) Miq., *Geonoma brevispatha* Barb. Rodr., *Guapira opposita* (Vell.) Reitz, *Inga marginata* Willd., *Myrcia laruotteana* Cambess., *Nectandra nitidula* Nees, *Ocotea diospyrifolia* (Meisn.) Mez, *Pera obovata* (Klotzch) Baill., *Persea venosa* Nees & Mart. ex Nees, *Podocarpus sellowii* Klotzsch ex Endl., *Styrax pohlii* A. DC., *Syagrus romanzoffiana* (Cham.) Glassman, *Tabebuia umbellata* (Sond.) Sandwith, *Trichilia claussenii* C. DC. and *T. pallida* Sw., among others. In the second group, the preferential species were *Cybianthus glaber* A. DC., *Emmotum nitens* (Benth.) Miers, *Erythroxylum amplifolium* Baill., *Ferdinandusa speciosa* Pohl, *Gomidesia lindeniana* O. Berg, *Hirtella glandulosa* Spreng., *Ilex affinis* Gardner, *Lamanonia ternata* Vell., *Maprounea guianensis* Aubl., *Miconia cuspidata* Mart. ex Naudin, *Myrcia castrensis* (O. Berg) D. Legrand, *Protium heptaphyllum* (Aubl.) Marchand, *Pseudolmedia laevigata* Trécul, *Sclerolobium paniculatum* Vogel, *Styrax camporum* Pohl, *Tabebuia serratifolia* (Vahl) G. Nicholson, *Tococa formicaria* Mart., *Virola sebifera* Aubl.,

Table 1. Localities, codes, climatic (*sensu* Köppen 1948) and floristic data, sampling criteria and size of surveyed area of the 20 inland swamp forests of Southeastern and Central-Western Brazil. (Ne = number of identified species and used for floristic comparisons in this study; Te = total number of species in the original authors' list including morphospecies; H' = Shannon's diversity index. Criteria for inclusion: DBH = diameter at breast height; CBH = circumference at breast height; Th = trunk height; BD = basal diameter.

Localities Municipality/State	Codes	Altitude (m)	Climate	Mean annual temperature (°C)	Mean annual precipitation (mm)	Ne	Te	Criteria for inclusion	Surveyed area (ha)	H'	References
Campinas (SP)	CaSP	660	Cwa	21.6	1,371	23	32	DBH ≥ 5 cm	0.87	2.45	Torres *et al.* 1994
Campinas (SP)	Ca2SP	600	Cwa	21.6	1,382	51	54	CBH ≥ 10 cm	0.20	2.80	Toniato *et al.* 1998
Itatinga (SP)	ItaSP	570	Cwa	19.7	1,373	36	39	CBH ≥ 15 cm	1.00	2.75	Ivanauskas *et al.* 1997
Brotas (SP)	BrSP	675	Cwa	22.0	1,428	44	49	CBH ≥ 15 cm	0.25	–	Costa 1996, Costa *et al.* 1997
Brotas (SP)	Br2SP	440	Cwa	22.0	1,428	42	51	DBH ≥ 5 cm	0.36	2.81	Marques *et al.* 2003
Agudos (SP)	AgSP	550	Cwa	21.8	1,464	36	38	CBH ≥ 15 cm	0.22	2.45	Paschoal & Cavassan 1999
Rio Claro (SP)	RCSP	640	Cwa	22.1	1,456	48	49	CBH ≥ 15 cm	0.45	2.10	Teixeira & Assis 2005, Teixeira *et al.* 2008
Bauru (SP)	BaSP	560	Cwa	20.6	883	32	33	CBH ≥ 15 cm	0.27	1.90	Carboni 2007
Itirapina (SP)	ItiSP	720	Cwa	20.8	1,523	36	37	CBH ≥ 10 cm	0.60	2.39	Teixeira *et al.* 2011
Cristais Paulista (SP)	CPSP	975	Cwb	20.4	1,591	84	88	CBH ≥ 10 cm	0.60	2.71	Teixeira & Assis 2009
Jeriquara (SP)	JeSP	840	Cwa	21.2	1,525	80	81	CBH ≥ 10 cm	0.60	2.81	Teixeira 2008
Uberlândia (MG)	UbMG	860	Aw	22.0	1,550	31	33	CBH ≥ 15 cm	0.62	2.27	Nogueira & Schiavini 2003
Coqueiral (MG)	CoMG	820	Cwb	19.3	1,493	99	99	DBH ≥ 5 cm	0.32	3.50	Rocha *et al.* 2005
Santa Rita de Caldas (MG)	SRMG	1,181	Cfb	–	1,695	110	110	DBH ≥ 5 cm	1.00	2.98	Loures *et al.* 2007
Bonito (MS)	BoMS	300	Aw	23.0	1,366	30	34	Th ≥ 1.3 m	0.32	2.35	Constantino 2002
Cuiabá (MT)	CuMT	360	Aw	25.6	1,421	52	53	BD ≥ 3 cm	0.048	3.25	Oliveira Filho *et al.* 1990
Brasília (DF)	Br1DF	1,100	Aw	22.3	1,481	63	64	DBH ≥ 15 cm	0.51	3.26	Souza 2003
Brasília (DF) – Riacho Fundo	Br2DF	1,100	Aw	22.3	1,481	46	53	DBH ≥ 3 cm	0.80	2.84	Guarino & Walter 2005
Brasília (DF) – Acampamento	Br3DF	1,100	Aw	22.3	1,481	51	58	DBH ≥ 3 cm	0.80	2.99	Guarino & Walter 2005
Brasília (DF) – Mata da Onça	Br4DF	1,100	Aw	22.3	1,481	88	93	DBH ≥ 3 cm	0.60	3.59	Walter 1995

Table 2. Matrix of Jaccard similarity coefficients among 20 inland swamp forests of Southeastern and Central-Western Brazil. Values above 0.25 indicate floristic similarity among forests and are highlighted in bold. Codes in table 1.

	CaSP	ItaSP	BrSP	Ca2SP	AgSP	Br2SP	RCSP	UbMG	CoMG	ItiSP	SRMG	Br2DF	Br3DF	BaSP	BoMS	CuMT	Br1DF	JeSP	Br4DF
CaSP	1.00																		
ItaSP	0.16	1.00																	
BrSP	0.22	0.21	1.00																
Ca2SP	0.21	0.23	**0.30**	1.00															
AgSP	0.23	0.18	0.21	0.23	1.00														
Br2SP	0.18	0.16	0.18	0.15	0.16	1.00													
RCSP	0.22	0.22	**0.31**	**0.36**	0.24	0.14	1.00												
UbMG	0.15	0.14	0.12	0.14	0.18	0.12	0.13	1.00											
CoMG	0.05	0.11	0.12	0.14	0.07	0.07	0.14	0.07	1.00										
ItiSP	0.16	0.22	0.18	0.19	**0.26**	0.15	0.20	0.22	0.07	1.00									
SRMG	0.05	0.10	0.09	0.13	0.07	0.06	0.09	0.04	0.12	0.07	1.00								
Br2DF	0.13	0.11	0.08	0.10	0.14	0.11	0.12	0.24	0.08	0.17	0.04	1.00							
Br3DF	0.16	0.12	0.16	0.13	0.19	0.09	0.15	0.21	0.08	0.23	0.07	**0.47**	1.00						
BaSP	**0.28**	**0.28**	0.17	**0.26**	0.21	0.16	**0.27**	**0.26**	0.07	**0.28**	0.07	0.16	0.22	1.00					
BoMS	0.10	0.12	0.14	0.14	0.12	0.09	0.15	0.09	0.04	0.06	0.02	0.07	0.09	0.11	1.00				
CuMT	0.04	0.05	0.05	0.06	0.06	0.08	0.04	0.12	0.04	0.06	0.03	0.08	0.08	0.09	0.04	1.00			
Br1DF	0.09	0.11	0.08	0.09	0.08	0.12	0.07	0.16	0.08	0.13	0.07	0.21	0.20	0.17	0.07	0.11	1.00		
JeSP	0.13	0.17	0.19	0.21	0.21	0.18	0.22	0.21	0.10	**0.27**	0.14	0.15	0.20	0.23	0.08	0.10	0.13	1.00	
Br4DF	0.10	0.12	0.11	0.12	0.14	0.10	0.11	0.20	0.08	0.15	0.08	**0.38**	**0.39**	0.17	0.04	0.10	0.24	0.20	1.00
CPSP	0.10	0.17	0.14	0.18	0.15	0.16	0.17	0.15	0.14	0.24	0.13	0.17	0.17	0.18	0.04	0.08	0.19	**0.39**	0.24

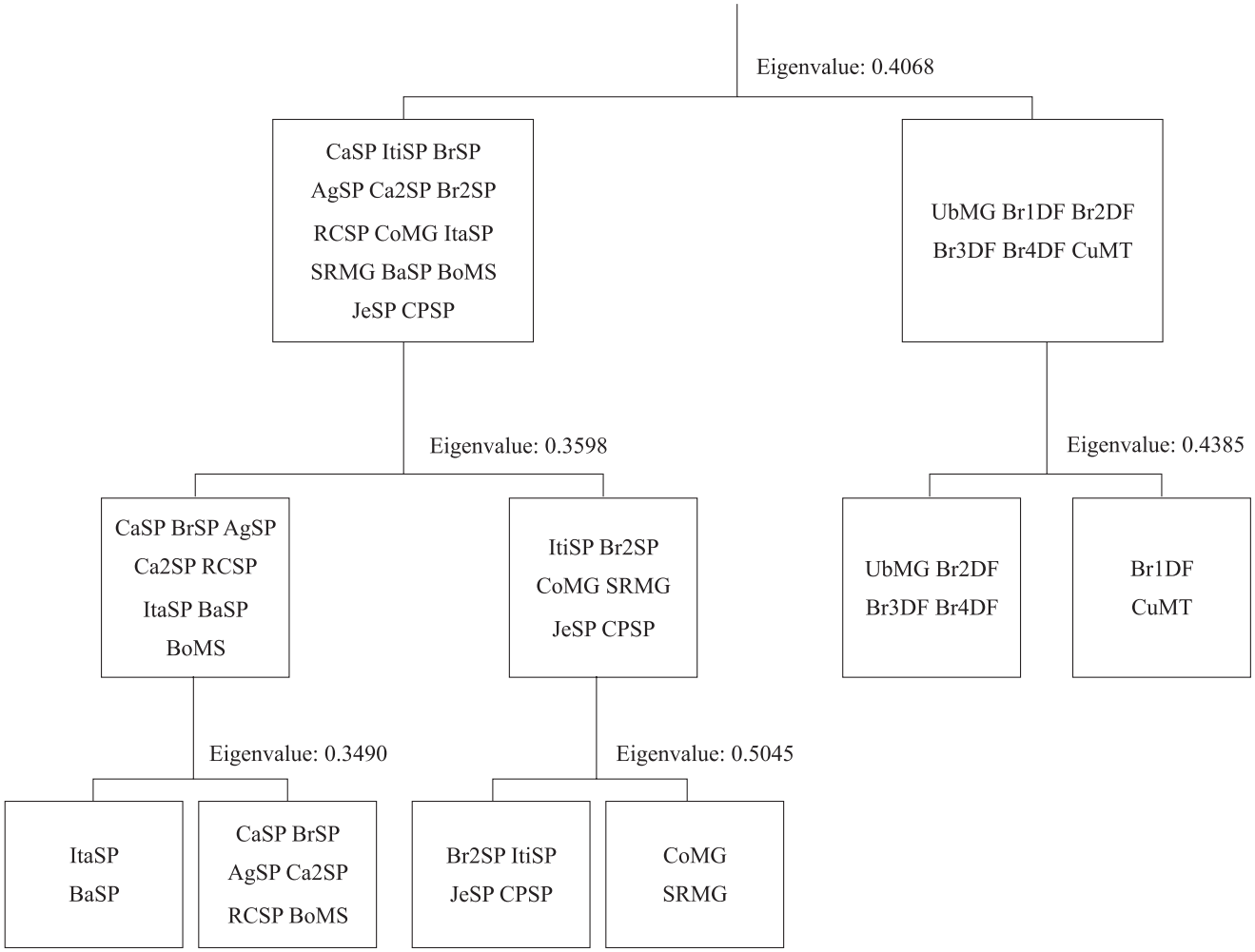

Figure 2. Cladogram, based on TWINSPAN, with groups of 20 inland swamp forests of Southeastern and Central-Western Brazil. Codes in table 1.

V. urbaniana Warb., *Xylopia aromatica* (Lam.) Mart. and *X. emarginata* Mart., among others. The following more frequent species stood out as non-preferential: *Calophyllum brasiliense, Cecropia pachystachya, Guarea kunthiana* A. Juss., *G. macrophylla, Magnolia ovata, Hyeronima alchorneoides* Allemão, *Protium spruceanum* and *Tapirira guianensis,* among others.

In the DCA, the eigenvalues for the first two axes were 0.456 (axis 1) and 0.238 (axis 2). These two ordination axes were responsible for explaining 65% of the variance of the data. Axis 1 separated the forests mainly according to the phytogeographic province in which they are inserted (figure 3A). On the left of the diagram prevailed swamp forests that present interface with seasonal semideciduous forests in the states of São Paulo and Minas Gerais. At the other extreme, on the right side, are the swamp forests that occur in the *Cerrado* province: Uberlândia (state of Minas Gerais), Distrito Federal and state of Mato Grosso. Between the two situations, but closer to the first group, we found the forests studied in the state of São Paulo, located in municipalities with a contact zone between forests and *cerrado* such as Bauru, Agudos, Itirapina, Cristais Paulista and Jeriquara. The distribution of some species in the remnants can be seen in figure 3 (B-I). The two analyses (TWINSPAN and DCA) were consistent, showing similar groups.

Discussion

The recent increase in the number of studies in swamp forests and the insertion of new locations within the state of São Paulo and outside the state has enabled the evaluation of the floristic differences among the forests. The high number of unique species (55% of a total of 20 studies) suggests that the floristic composition of swamp

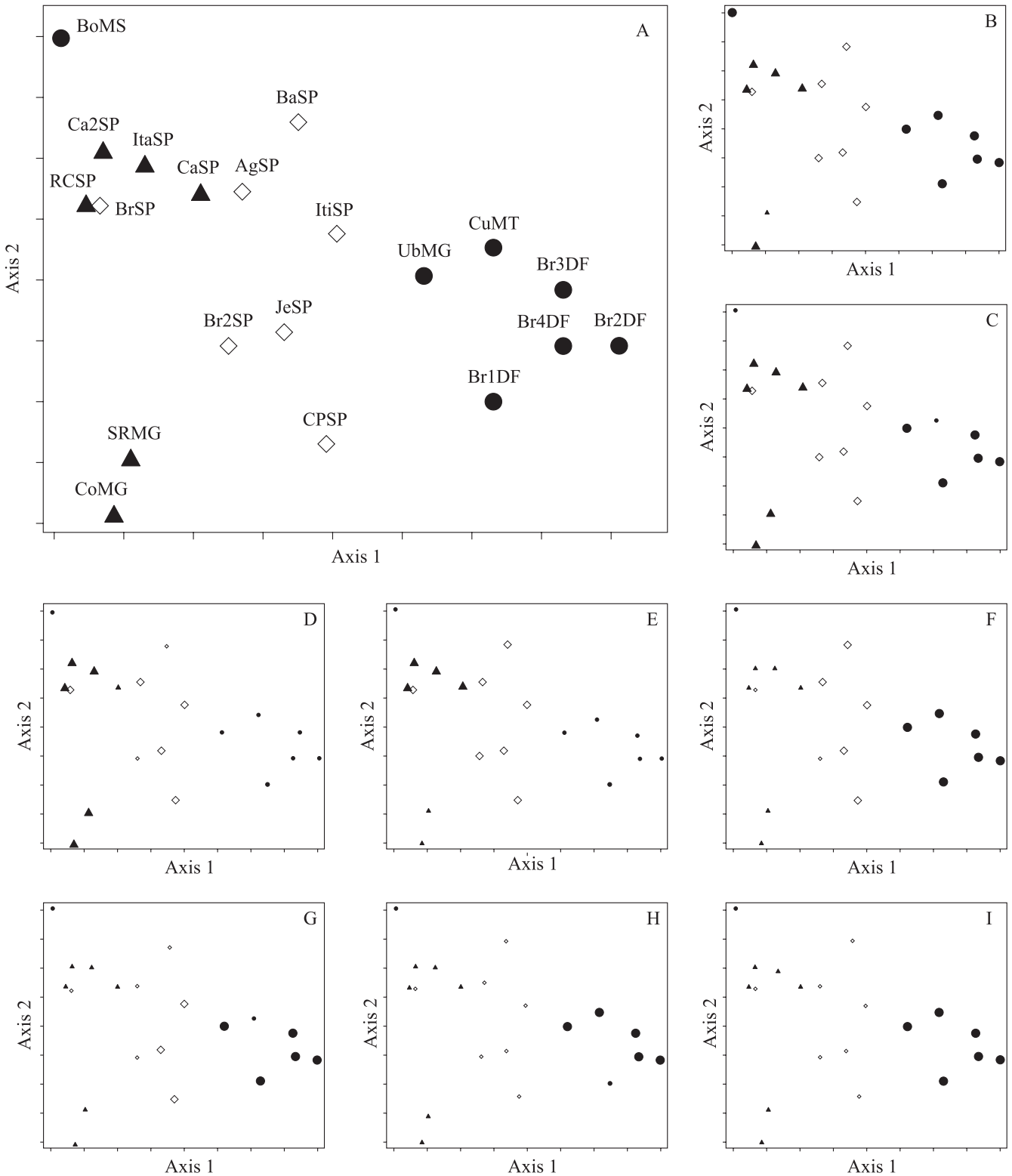

Figure 3. DCA – Ordination diagrams for 20 inland swamp forests of Southeastern and Central-west Brazil, according to the presence or absence of the 199 shrubs and trees species (A) and the occurrence of eight species for the forests (expressed by the largest symbols) – *Calophyllum brasiliense* (B); *Magnolia ovata* (C); *Tabebuia umbellata* (D); *Styrax pohlii* (E); *Xylopia emarginata* (F); *Pseudolmedia laevigata* (G); *Ferdinandusa speciosa* (H); *Richeria grandis* (I). The forest codes are found in the table 1 and the symbols indicate the predominant vegetation type in the municipality where each forest was studied (▲ = seasonal semideciduous forest; ◇ = seasonal semideciduous forest/*cerrado* contact; ● = *cerrado*).

forests is quite heterogeneous and that each remnant has floristic peculiarities that are defined by a set of factors that vary between and within each phytogeographical province. Confirming the initial expectation, the forests were grouped according to the phytogeographical province in which they are located, indicating the importance of the surrounding matrix (semideciduous forest, *cerrado* or contact between the semideciduous forest and the *cerrado*) in the definition of the floristic groupings observed. The main factor that varies between the provinces is the climate, with a predominance of Köppen's Cw in the *Paranaense* province and Aw in the *Cerrado*. Among the major climatic differences are the lower average temperatures in the former and increased seasonality in the rainfall of the latter (Oliveira Filho & Ratter 1995).

Although some populations are widely distributed and have high local densities in swamp forests, like *Calophyllum brasiliense, Cecropia pachystachya, Guarea macrophylla, Dendropanax cuneatus, Hyeronima alchorneoides, Protium spruceanum* and *Tapirira guianensis,* other species, tolerant to water saturation of the soil, were associated to forests of a given province. For example, *Podocarpus sellowii*, *Styrax pohlii* and *Tabebuia umbellata* were important only in the swamp forests of the *Paranaense* province and *Ferdinandusa speciosa* and *Richeria grandis* were only important in the *Cerrado* province. Moreover, some species typical of swamp forests of Central Brazil, such as *Mauritia flexuosa* L. f.*, Pseudolmedia laevigata* and *Xylopia emarginata* (Oliveira Filho *et al.* 1990, Guarino & Walter 2005), were also found in the state of São Paulo, but restricted to swamp forests established in the municipalities with a greater or lesser degree of *cerrado* cover.

Complimentary species, in turn, may also have wide distribution in swamp forests, regardless of the phytogeographical province, or they may be associated with forests from a certain province. Species like *Casearia sylvestris* Sw.*, Copaifera langsdorffii* Desf.*, Lacistema hasslerianum* Chodat*, Myrcia splendens* (Sw.) DC.*, Ocotea corymbosa* (Meisn.) Mez*, O. pulchella* Mart.*, Pera glabrata* (Schott) Poepp. ex Baill.*, Platypodium elegans* Vogel*, Rapanea umbellata* (Mart.) Mez and *Siparuna guianenses* Aubl., eventually found in swamp forests, occur in *cerrados* as well as in seasonal semideciduous and riverside forests (*e.g.* Costa & Araújo 2001, Nunes *et al.* 2003, Teixeira *et al.* 2004, Teixeira & Rodrigues 2006). On the other hand, species like *Ardisia ambigua, Aspidosperma cylindrocarpon, Citronella gongonha, Cecropia glaziovi, Croton floribundus, Ficus obtusiuscula, Guapira opposita, Inga marginata, Syagrus romanzoffiana* and *Trichilia claussenii,* preferentially found in the group from swamp forests in the state of São Paulo, are commonly found in forests of the *Paranaense* province (*e.g.* Pagano *et al.* 1987, Oliveira Filho *et al.* 1994, 2001, Carvalho *et al.* 1996, Santos & Kinoshita 2003). Species like *Emmotum nitens, Hirtella glandulosa, Maprounea guianensis, Sclerolobium paniculatum, Styrax camporum, Virola sebifera* and *Xylopia aromatica,* and other important species from the swamp forests of the *Triângulo Mineiro* and Central Brazil, are common species in the *Cerrado* phytophysiognomies, especially the *cerradão* (*e.g.* Oliveira Filho & Ratter 1995, 2002). With regard to *S. paniculatum*, it should be emphasized that this species is currently treated as three different taxa that occur in different habitats in the *Cerrado* (gallery forests, *cerrado sensu lato* and transition forests of the Amazon) (Oliveira Filho 2006, Silva & Lima 2007). Although they have low local densities mainly in better drained soils or on the edges of swamp forests, the complementary species can contribute greatly to an increase in the γ diversity (regional) of these forests. Moreover, the preferential species in a given province were probably the most responsible for the low similarity values found among the forests here investigated, as well as the floristic groupings observed.

Within the same province, the spatial proximity, soil and climatic conditions, history of human interventions and stochastic events may be influencing the floristic similarities or differences among the swamp forests. The influence of spatial proximity can be determined by observing the highest rates of similarity found between the forests studied in the same municipality (like Brasília, Distrito Federal) or in adjacent municipalities, such as Jeriquara and Cristais Paulista. However, the floristic similarity between nearby areas is not a rule, as other studies located within the same municipality, such as Campinas or Brotas (state of São Paulo), did not show great floristic similarity amongst one another. Additionally, the influence of altitude can be seen, for example, in the floristic composition of the forest studied in Santa Rita de Caldas (state of Minas Gerais), which is situated about 1,180 m above sea level and is therefore subjected to low temperatures and frost occurrence. This forest contains species typical of Southern Brazil, such as *Araucaria angustifolia* (Bertol.) Kuntze*, Ilex paraguariensis* A. St.-Hil. and *Dicksonia sellowiana* Hook. (Loures *et al.* 2007).

The forest studied in Bonito (state of Mato Grosso do Sul) had the most distinct soil conditions, since these soils are influenced by carbonate rocks, resulting in the deposition of limestone, high calcium content and alkaline pH. These conditions foster the occurrence

of species found in seasonal deciduous forests on calciferous or basalt formations and in the *Caatinga* province (Constantino 2002). These factors may have influenced the low floristic similarity between this forest and the other forests analyzed.

Considering the floristic comparison among eight swamp forest remnants studied in the interior of São Paulo, Teixeira & Assis (2005) listed 149 species, of which 70% occurred in only one of the remnants. By increasing the analysis by 12 more studies, including those carried out in other states, the number of species increased to 440 in total, 55% of which were restricted to only one remnant. While there may be a tendency towards a decrease in the number of unique species with the increase in the number of studies and while the α diversity is low in most of the remnants, the γ diversity of these forests can be considered high, due to the high number of species, most of them unique, and low floristic similarity among forests. The main factor responsible for increasing the γ diversity is the inclusion of studies from the *Cerrado* province, with distinct phytophysiognomies, flora and climatic conditions from the *Paranaense* province. These conditions foster the establishment of different complementary species in swamp forests, supporting the hypothesis that the surrounding vegetation exerts an important contribution to the flora of these forests.

Although distinct floristic composition exist among the swamp forests, with low similarity values and complementary species originating mainly from the predominant matrix in the region, we can conclude that the inland swamp forests of Southeastern Brazil and the swamp forests of Central Brazil, called swamp gallery forests, should be treated as part of the same forest type. Besides the swampy environment, these forests share low plant diversity and species with high local densities, such as *Calophyllum brasiliense, Cecropia pachystachya, Dendropanax cuneatus, Guarea macrophylla, Magnolia ovata, Protium spruceanum* and *Tapirira guianensis*. These species should inevitably be used in these formations for forest restoration projects, together with exclusive or preferential species from the phytogeographical province in which the swamp forests are located.

Acknowledgments – We thank Capes for the doctoral scholarship provided to the first author; Fapesp for the research grant (Process 07/52613-5); Bruno MT Walter, Jeanine M. Felfili (*in memoriam*) and Maria T.Z. Toniato, for sending floristic checklists to add to our database; Leandro J. Fonseca for designing the map; Bruno M.T. Walter and the anonymous referees for their constructive comments on the manuscript.

References

APG II. 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. Botanical Journal of the Linnean Society 141:399-436.

CABRERA, A.L. & WILLINK, A. 1973. Biogeografia da América Latina. Secretaria General de la Organización de los Estados Americanos, Washington.

CARBONI, M. 2007. Composição, estrutura e diversidade vegetal de uma floresta estacional semidecídua ribeirinha com influência fluvial permanente (mata de brejo) em Bauru – SP. Dissertação de mestrado, Universidade Estadual Paulista, Botucatu.

CARVALHO, D.A., OLIVEIRA FILHO, A.T. & VILELA, E.A. 1996. Flora arbustivo-arbórea de mata ripária do médio Rio Grande (Conquista, Estado de Minas Gerais). Cerne 2:48-68.

CONSTANTINO, R. 2002. Estudo florístico e estrutural de um trecho de floresta ribeirinha entre os rios Formoso e Formosinho, em Bonito/MS. Dissertação de mestrado, Universidade Estadual Paulista, Rio Claro.

COSTA, A.A. & ARAÚJO, G.M. 2001. Comparação da vegetação arbórea de cerradão e de cerrado na Reserva do Panga, Uberlândia, Minas Gerais. Acta Botanica Brasilica 15:63-72.

COSTA, F.R.C. 1996. Aspectos florísticos, estruturais e ecológicos de um remanescente de mata ciliar do ribeirão da Onça, Brotas, SP. Dissertação de mestrado, Universidade de São Paulo, São Carlos.

COSTA, F.R.C., SCHLITTLER, F.H.M., CÉSAR, O. & MONTEIRO, R. 1997. Aspectos florísticos e fitossociológicos de um remanescente de brejo no Município de Brotas, SP. Arquivos de Biologia e Tecnologia 40:263-270.

DORNELES, L.P.P. & WAECHTER, J.L. 2004. Fitossociologia do componente arbóreo na floresta turfosa do Parque Nacional da Lagoa do Peixe, Rio Grande do Sul, Brasil. Acta Botanica Brasilica 18:815-824.

DURIGAN, G., RATTER, J.A., BRIDGEWATER, S., SIQUEIRA, M.F. & FRANCO, G.A.D.C. 2003. Padrões fitogeográficos do cerrado paulista sob uma perspectiva regional. Hoehnea 30:39-51.

GAUCH, H.G. & WHITTAKER, R.H. 1981. Hierarchical classification of community data. Journal of Ecology 69:135-152.

GOMES, B.Z., MARTINS, F.R. & TAMASHIRO, J.Y. 2004. Estrutura do cerradão e da transição entre cerradão e floresta paludícola num fragmento da International Paper do Brasil Ltda., em Brotas, SP. Revista Brasileira de Botânica 27:249-262.

GUARINO, E.S.G. & WALTER, B.M.T. 2005. Fitossociologia de dois trechos inundáveis de matas de galeria no Distrito Federal, Brasil. Acta Botanica Brasilica 19: 431-442.

HILL, M.O. & GAUCH, H.G. 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio 42:47-58.

IVANAUSKAS, N.M., RODRIGUES, R.R. & NAVE, A.G. 1997. Aspectos ecológicos de uma mata de brejo em Itatinga, SP: florística, fitossociologia e seletividade de espécies. Revista Brasileira de Botânica 20:139-153.

KÖPPEN, W.P. 1948. Climatologia. Fondo de Cultura Economica, Mexico.

LEITÃO FILHO, H.F. 1982. Aspectos taxonômicos das florestas do Estado de São Paulo. Silvicultura em São Paulo 16A:197-206.

LIEBERMAN, M., LIEBERMAN, D., HARTSHORN, G.S. & PERALTA, R. 1985. Small-scale altitudinal variation in lowland wet tropical forest vegetation. Journal of Ecology 73:505-516.

LOURES, L., CARVALHO, D.A., MACHADO, E.L.M. & MARQUES, J.J.G.S.M. 2007. Florística, estrutura e características do solo de um fragmento de floresta paludosa no sudeste do Brasil. Acta Botanica Brasilica 21:885-896.

MARQUES, M.C.M., SILVA, S.M. & SALINO, A. 2003. Florística e estrutura do componente arbustivo-arbóreo de uma floresta higrófila da bacia do rio Jacaré-Pepira, SP, Brasil. Acta Botanica Brasilica 17:495-506.

MARTINS, S.V., BRITO, E.R., OLIVEIRA FILHO, A.T. SILVA, A.F. & SILVA, E. 2008. Floristic composition of two wetland forests in Araguaian plain, state of Tocantins, Brazil, and comparison with other áreas. Revista Árvore 32:129-141.

MCCUNE, B. & MEFFORD, M.J. 1999. PC-ORD. Multivariate analysis of ecological data, version 4.0. MjM Software Design, Oregon Glaneden Beach.

NOGUEIRA, M.F. & SCHIAVINI, I. 2003. Composição florística e estrutura da comunidade arbórea de uma mata de galeria inundável em Uberlândia, MG, Brasil. Bioscience Journal 19:89-98.

NUNES, Y.R.F., MENDONÇA, A.V.R., BOTEZELLI, L., MACHADO, E.L.M. & OLIVEIRA FILHO, A.T. 2003. Variações da fisionomia, diversidade e composição de guildas da comunidade arbórea em um fragmento de floresta semidecidual em Lavras, MG. Acta Botanica Brasilica 17:213-229.

OLIVEIRA FILHO, A.T. 2006. Catálogo das árvores nativas de Minas Gerais: mapeamento e inventário da flora nativa e dos reflorestamentos de Minas Gerais. Editora UFLA, Lavras.

OLIVEIRA FILHO, A.T. & FONTES, M.A. 2000. Patterns of floristic differentiation among Atlantic forests in southeastern Brazil and influence of climate. Biotropica 32:793-810.

OLIVEIRA FILHO, A.T. & RATTER, J.A. 1995. A study of the origin of Central Brazilian forests by the analysis of plants species distribution patterns. Edinburgh Journal of Botany 52:141-194.

OLIVEIRA FILHO, A.T. & RATTER, J.A. 2002. Vegetation physiognomies and woody flora of the Cerrado Biome. *In* The Cerrados of Brazil: ecology and natural history of a Neotropical savanna (P.S. Oliveira & R.J. Marquis, eds.). Columbia University Press, New York, p.91-120.

OLIVEIRA FILHO, A.T., RATTER, J.A. & SHEPHERD, G.J. 1990. Floristic composition and community structure of a Brazilian gallery forest. Flora 184:103-117.

OLIVEIRA FILHO, A.T., VILELA, E.A., CARVALHO, D.A. & GAVILANES, M.L. 1994. Differentiation of streamside and upland vegetation in an area of montane semideciduous forest in southeastern Brazil. Flora 189:287-305.

OLIVEIRA FILHO, A.T., CURI, N., VILELA, E.A. & CARVALHO, D.A. 2001. Variation in tree community composition and structure with changes in soil properties within a fragment of semideciduous forest in southeastern Brazil. Edinburgh Journal of Botany 58:139-158.

PAGANO, S.N., LEITÃO FILHO, H.F. & SHEPHERD, G.J. 1987. Estudo fitossociológico em mata mesófila semidecídua no município de Rio Claro (Estado de São Paulo). Revista Brasileira de Botânica 10:49-61.

PASCHOAL, M.E.S. & CAVASSAN, O. 1999. A flora arbórea da mata de brejo do ribeirão do Pelintra, Agudos, SP. Naturalia 24:171-191.

RIBEIRO, J.F. & WALTER, B.M.T. 2008. As principais fitofisionomias do bioma Cerrado. *In* Cerrado: ecologia e flora (S.M. Sano, S.P. Almeida & J.F. Ribeiro, eds.). Embrapa, Brasília, p.151-212.

ROCHA, C.T.V., CARVALHO, D.A., FONTES, M.A.L., OLIVEIRA FILHO, A.T., VAN DEN BERG, E. & MARQUES, J.J.G.S.M. 2005. Comunidade arbórea de um *continuum* entre floresta paludosa e de encosta em Coqueiral, Minas Gerais, Brasil. Revista Brasileira de Botânica 28:203-218.

RODRIGUES, R.R. & NAVE, A.G. 2000. Heterogeneidade florística das matas ciliares. *In* Matas ciliares: conservação e recuperação (R.R. Rodrigues & H.F. Leitão Filho, eds.). Edusp/Fapesp, São Paulo, p.45-71.

SALIS, S.M., SHEPHERD, J.G. & JOLY, C.A. 1995. Floristic comparison of mesophytic semideciduous forests of the interior of the state of São Paulo, southeast Brazil. Vegetatio 119:155-164.

SANTOS, K. & KINOSHITA, L.S. 2003. Flora arbustivo-arbórea do fragmento de floresta estacional semidecidual do Ribeirão Cachoeira, Município de Campinas, SP. Acta Botanica Brasilica 17:325-341.

SCARANO, F.R. 2002. Structure, function and floristic relationships of plant communities in stressful habitats marginal to the Brazilian Atlantic rainforest. Annals of Botany 90:517-524.

SCARANO, F.R. 2006. Plant community structure and function in a swamp forest within the Atlantic rain forest complex: a synthesis. Rodriguésia 57:491-502.

SCUDELLER, V.V., MARTINS, F.R. & SHEPHERD, G.J. 2001. Distribution and abundance of arboreal species in the Atlantic ombrophilous dense forest in Southeastern Brazil. Plant Ecology 152:185-199.

SHEPHERD, G.J. 1994. FITOPAC 1. Manual do usuário. Departamento de Botânica. Universidade Estadual de Campinas, Campinas.

SILVA, A.C., VAN DEN BERG, E., HIGUCHI, P. & OLIVEIRA FILHO, A.T. 2007. Comparação florística de florestas inundáveis das regiões Sudeste e Sul do Brasil. Revista Brasileira de Botânica 30:257-269.

SILVA, L.F.G. & LIMA, H.C. 2007. Mudanças nomenclaturais do gênero *Tachigali* Aubl. (Leguminosae – Caesalpinioidea) no Brasil. Rodriguésia 58: 397-401.

SOUZA, L.B.G. 2003. Avaliação do efeito do entorno na integridade ecológica de uma mata de galeria inundável no Distrito Federal. Dissertação de mestrado, Universidade de Brasília, Brasília.

SOUZA, V.C. & LORENZI, H. 2005. Botânica sistemática – guia ilustrado para identificação das famílias de angiospermas da flora brasileira, baseado em APG II. Instituto Plantarum, Nova Odessa.

SZTUTMAN, M. & RODRIGUES, R.R. 2002. O mosaico vegetacional numa área de floresta contínua da planície litorânea, Parque Estadual da Campina do Encantado, Pariquera-Açu, SP. Revista Brasileira de Botânica 25:161-176.

TEIXEIRA, A.P. 2008. Composição florística e distribuição de espécies arbóreas em florestas paludosas interioranas do sudeste e centro-oeste do Brasil. Tese de doutorado, Universidade Estadual Paulista, Rio Claro.

TEIXEIRA, A.P. & ASSIS, M.A. 2005. Caracterização florística e fitossociológica do componente arbustivo-arbóreo de uma floresta paludosa no Município de Rio Claro (SP), Brasil. Revista Brasileira de Botânica 28:467-476.

TEIXEIRA, A.P. & ASSIS, M.A. 2009. Relação entre heterogeneidade ambiental e distribuição de espécies em uma floresta paludosa no Município de Cristais Paulista, SP, Brasil. Acta Botanica Brasilica 23:843-853.

TEIXEIRA, A.P. & RODRIGUES, R.R. 2006. Análise florística e estrutural do componente arbustivo-arbóreo de uma floresta de galeria no Município de Cristais Paulista, SP, Brasil. Acta Botanica Brasilica 20:803-813.

TEIXEIRA, M.I.J.G., ARAÚJO, A.R., VALERI, S.V. & RODRIGUES, R.R. 2004. Florística e fitossociologia de área de cerrado s.s. no Município de Patrocínio Paulista, nordeste do Estado de São Paulo. Bragantia 63:1-11.

TEIXEIRA, A.P., ASSIS, M.A., SIQUEIRA, F.R. & CASAGRANDE, J.C. 2008. Tree species composition and environmental relationships in a Neotropical swamp forest in Southeastern Brazil. Wetlands Ecology and Management 16:451-461.

TEIXEIRA, A.P., ASSIS, M.A. & LUIZE, B.G. 2011. Vegetation and environment relationships in a Neotropical swamp forest in southeastern Brazil (Itirapina, SP). Aquatic Botany 94:17-23.

TONIATO, M.T.Z., LEITÃO FILHO, H.F. & RODRIGUES, R.R. 1998. Fitossociologia de um remanescente de floresta higrófila (mata de brejo) em Campinas, SP. Revista Brasileira de Botânica 21:197-210.

TORRES, R.B., MATTHES, L.A.F. & RODRIGUES, R.R. 1994. Florística e estrutura do componente arbóreo de mata de brejo em Campinas, SP. Revista Brasileira de Botânica 17:189-194.

TORRES, R.B., MARTINS, F.R. & KINOSHITA, L.S. 1997. Climate, soil and tree flora relationships in forests in the state of São Paulo, southeastern Brazil. Revista Brasileira de Botânica 20:41-49.

WALTER, B.M.T. 1995. Distribuição espacial de espécies perenes em uma mata de galeria inundável no Distrito Federal: florística e fitossociologia. Dissertação de mestrado, Universidade de Brasília, Brasília.