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THE VEGETATION OF PRIORITY AREAS FOR CERRADO CONSERVATION IN SÃO PAULO STATE, BRAZIL

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Natural cerrado vegetation in São Paulo State now covers less than 7% of its original area and exists only as isolated fragments. Eighty-six sites in these priority cerrado conservation areas were surveyed using a rapid assessment technique. A total of 554 species of vascular plants, belonging to 77 families, was recorded. The vegetation types encountered comprised: campo sujo, campo cerrado, cerrado *sensu stricto*, cerradão, wet campo, riparian forest, swamp forest, ecotone cerrado/forest and seasonal semi-deciduous forest. Two-Way Indicator Species Analysis (TWINSPAN), Detrended Correspondence Analysis (DCA) and Unweighted Pair-Groups Method using Arithmetic Averages (UPGMA) revealed a weak similarity pattern based on geography, but divided the sites into two main structural groups:
(a) areas where more open forms of cerrado occur (cerrado *sensu stricto*, campo cerrado);
(b) areas where only forest physiognomies occur (cerradão, ecotone cerradão/seasonal semi-deciduous forest, or riparian forest).
The first group tends to be located in the east and the second in the west of São Paulo State.

Cerradão was the most frequent vegetation type, observed in 70% of the sites. Cerrado *sensu stricto* was recorded in only 31% of the sites. *Casearia sylvestris* and *Byrsonima intermedia* were the most widespread species, recorded in 90% and 88% of the sites, respectively. Only 10% of the species were found in 50% or more of the sites, while 19% of species were recorded at a single site only. There was a considerable difference in species number between sites, from a minimum of 29 at Taubaté to a maximum of 185 in one of those at Campos Novos Paulista. As shown in other studies, species richness is directly correlated with diversity of vegetation types occurring at a site (beta diversity). As expected, the seven richest fragments contain ecotonal vegetation, which combines both forest and cerrado elements.

Keywords. Beta diversity, Brazil, cerrado, conservation, multivariate analysis, species distribution.

Resumo

A vegetação de cerrado no Estado de São Paulo cobre atualmente menos de 7% da sua área original e existe apenas na forma de fragmentos isolados. Foram levantadas

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as espécies vegetais e descritos os tipos de vegetação, através de levantamentos rápidos, em 86 fragmentos considerados prioritários para conservação. No total foram amostradas 554 espécies, pertencentes a 77 famílias, ocorrendo em campo sujo, campo cerrado, cerrado, cerradão, campo úmido, mata ciliar, mata de brejo, ecótono cerrado/floresta e floresta estacional semidecidual. As analyses por meio de Two-Way Indicator Species Analysis (TWINSPAN), Detrended Correspondence Analysis (DCA) e Unweighted Pair-Groups Method using Arithmetic Averages (UPGMA) mostraram fraco padrão geográfico de similaridade, mas dividiram as áreas em dois grandes grupos:
(a) fragmentos onde ocorrem formas campestres de cerrado (cerrado, campo cerrado), geralmente localizados na porção leste do Estado;
(b) fragmentos onde a vegetação tem fisionomia florestal (cerradão, ecótono cerradão/floresta estacional semidecidual ou mata ciliar), geralmente localizados na porção oeste do Estado.

Cerradão foi a fisionomia mais freqüente, observada em 70% dos fragmentos e cerrado *sensu stricto* em apenas 31%. *Casearia sylvestris*, registrada em 90% dos fragmentos, foi a espécie de distribuição mais ampla, seguida de *Byrsonima intermedia*, com 88% de freqüência. Apenas 10% das espécies ocorreram em pelo menos 50% dos fragmentos, sendo que 19% das espécies foram observadas em um único local. Verificou-se diferença considerável entre fragmentos quanto ao número de espécies amostradas, variando desde um mínimo de 29 em Taubaté até o máximo de 185 espécies em Campos Novos Paulista. Conforme demonstrado em outros estudos, a riqueza está diretamente relacionada com a diversidade de tipos fitofisionômicos (diversidade beta). Os sete fragmentos com maior riqueza de espécies contêm vegetação ecotonal, com espécies de floresta e cerrado compartilhando o espaço.

Palavras-chaves. Análises multivariadas, Brasil, cerrado, conservação, distribuição de espécies vegetais, diversidade beta.

Introduction

The Cerrado Biome[1], before its large scale destruction by man, covered almost 23% of the total land area of Brazil (some 2 million km^2). A continuous core area of this formation occurs in the states of Minas Gerais, Mato Grosso do Sul, Mato Grosso, Goiás, Tocantins, Bahia, Maranhão and Piauí, with some extensions and disjunct areas in other states (Eiten, 1972).

In the early part of the twentieth century, 14% of São Paulo State was covered by cerrado vegetation, dispersed in patches across a landscape of mainly seasonal semi-deciduous forest. As described by Ratter (1992), the distribution of seasonal semi-deciduous forest and cerradão is related to soil conditions, the forest occurring on more fertile soils with higher levels of calcium and magnesium, and the cerradão on somewhat poorer soils.

[1] The concept of the Cerrado Biome adopted in this study includes the whole range of vegetation types occurring within the vast area where cerrado is the dominant vegetation (the so-called Domínio dos Cerrados) and is that described in Oliveira-Filho & Ratter (2002): 'The Cerrado Biome consists of savanna of very variable structure, termed cerrado *sensu lato*, on the well-drained interfluves, with gallery forests or other moist vegetation following the watercourses. In addition, areas of richer soils in the biome are clothed in mesophytic forests'.

Although they occupy the poorest soils in the state, areas of natural cerrado vegetation have been largely destroyed for agriculture, mainly for sugar cane, pine and eucalypt plantations, *Citrus* orchards, and pastures of African grasses. Government projects for agricultural settlements for the landless are also replacing cerrado vegetation (e.g. the already implemented, Martinópolis and Promissão, or those still planned, such as Colômbia). As a result, in a mere 30 years, the cerrado vegetation of São Paulo State has been reduced, principally by agricultural exploitation, from 33,929km^2 (Borgonovi & Chiarini, 1965) to 2379km^2 (Kronka *et al.*, 1998), i.e. to less than 7% of its original cover and less than 1% of the area of the state.

Two meetings were recently organized in Brazil with the aim of establishing strategies for cerrado conservation. The first of them, *Bases para a conservação e o uso sustentável dos cerrados do Estado de São Paulo*, was held in 1995 (Joly, 1997) and restricted to São Paulo State. The second was a national symposium in 1998, *Ações prioritárias para a conservação da biodiversidade do Cerrado e Pantanal* (Cavalcanti, 1999), that identified biodiversity hot spots for Cerrado Biome conservation in the country as a whole.

As a result of the first meeting, 23 areas were selected as maximum priorities for cerrado conservation in São Paulo State; these each comprise one large fragment or a group of fragments of usually different sizes. Each continuous area studied, large or small, was designated as a **site** in the following text. At the subsequent national symposium, some of these priority areas were maintained, some were removed, and others were added. Of the areas removed some did not contain cerrado vegetation. However, others not given high priority under the criteria adopted in the national meeting are in fact very important for cerrado conservation in São Paulo State. The newly added areas were not included for analysis at the first meeting, since there were then no maps or other information available.

The present paper provides floristic inventory information from 86 sites, located in the priority areas, representing approximately 10% of the remaining area covered by cerrado vegetation in São Paulo State.

This study is part of a major project entitled 'The conservation feasibility of the cerrado remnants in São Paulo State', one of the targeted projects of Program BIOTA funded by Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP).

Materials and methods

Location and description of survey sites

Eighty-six sites located in priority areas for cerrado conservation in São Paulo State were surveyed and designated by code letters (see Fig. 1 and Table 1). In each area, recent Landsat images provided the basis for selection of sites to be surveyed, which varied from a minimum of one to a maximum of eight per priority area. Sites were selected on the following principles:

(a) Where the vegetation cover was broken, all the larger fragments (400ha or over) were surveyed, if possible.

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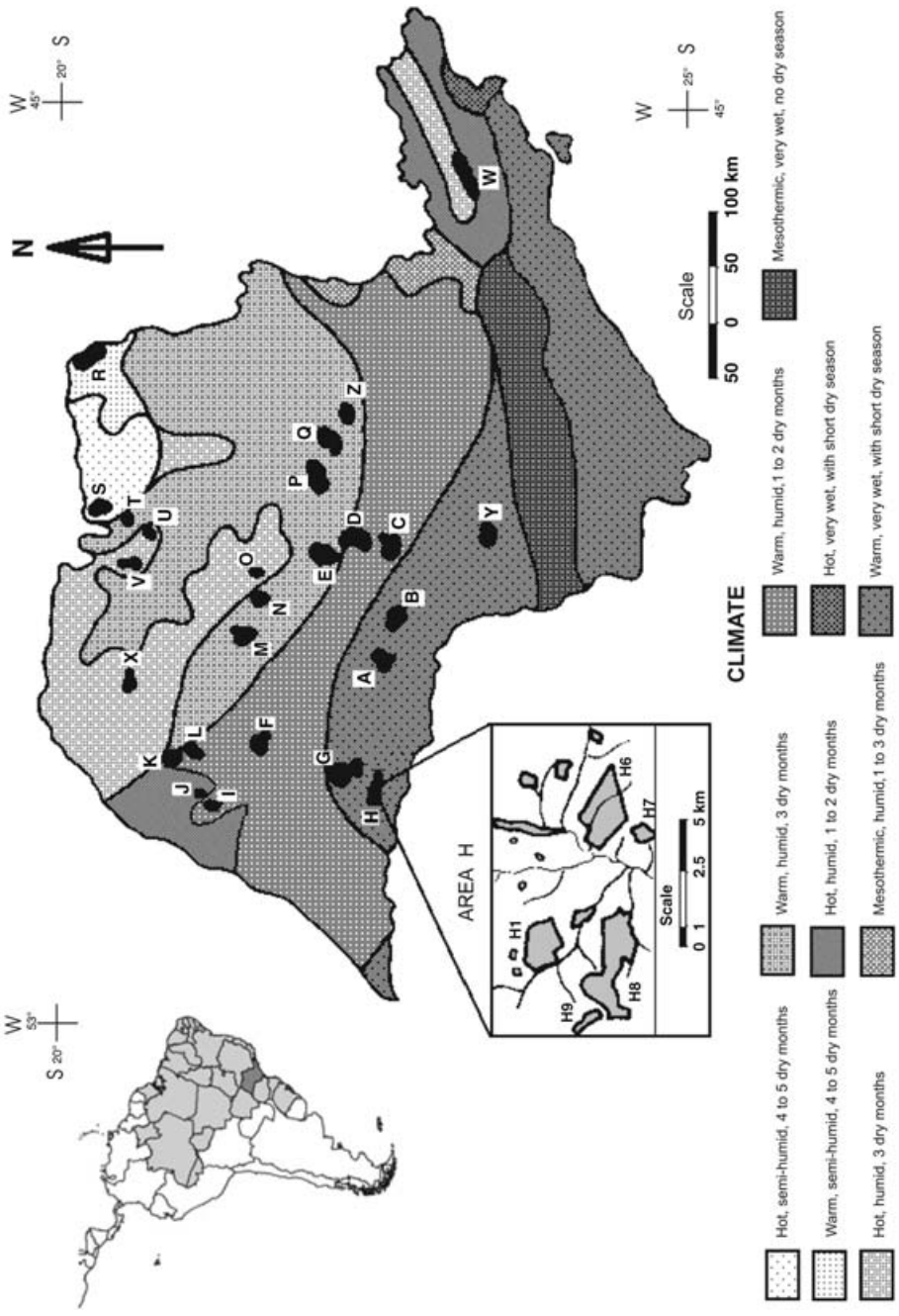

FIG. 1. Priority areas for cerrado conservation in São Paulo State. The letters on the map are those of the site codes in Table 1. Inset, as an example: location of the surveyed sites within Area H. The shading shows the climatic zones of São Paulo State, according to IBGE (1990).

TABLE 1. Location, area and vegetation types of the 86 sites. N = total species number; RA = rare species (recorded in only one site); RE = species with restricted distribution

Code	Locality	Coordinates	Area (ha)	N	RA	RA (%)	RE	RE (%)	Vegetation types
A1	Campos Novos Paulista	22°33′07″S, 50°04′43″W	1800	185	1	1	2	1	Cerrado *sensu stricto*, cerradão, riparian forest, swamp forest, wet campo, ecotone cerrado/seasonal semi-deciduous forest
A16	Campos Novos Paulista	22°31′24″S, 50°02′01″W	83	97	0	0	1	1	Wet campo, cerradão, riparian forest, swamp forest
A17	Campos Novos Paulista	22°31′49″S, 49°59′31″W	151	92	1	1	3	3	Wet campo, cerradão, riparian forest
A20	Campos Novos Paulista	22°32′49″S, 50°06′54″W	66	97	0	0	1	1	Cerradão, riparian forest
A29	Echaporã	22°33′29″S, 50°08′11″W	395	129	1	1	1	1	Cerrado *sensu stricto*, cerradão, riparian forest
A6	Ocauçu	22°29′11″S, 50°01′44″W	22	80	1	1	1	1	Ecotone cerrado/seasonal semi-deciduous forest
A8	Ocauçu	22°30′05″S, 50°00′58″W	320	113	1	1	1	1	Cerradão, riparian forest, swamp forest
B1	São Pedro do Turvo	22°41′13″S, 49°42′32″W	757	115	0	0	4	3	Cerradão, ecotone cerrado/seasonal semi-deciduous forest, riparian forest
B10	São Pedro do Turvo	22°41′45″S, 49°42′44″W	27	71	0	0	2	3	Ecotone cerrado/seasonal semi-deciduous forest
B16	São Pedro do Turvo	22°41′01″S, 49°44′05″W	49	71	0	0	3	4	Cerradão, ecotone cerrado/seasonal semi-deciduous forest
B2	Ubirajara, S. Pedro do Turvo	22°40′09″S, 49°37′21″W	818	84	0	0	4	5	Cerradão, riparian forest
B34	São Pedro do Turvo	22°38′37″S, 49°41′38″W	216	93	0	0	2	2	Cerradão, riparian forest, ecotone cerrado/seasonal semi-deciduous forest

TABLE 1. (*Cont'd*)

Code	Locality	Coordinates	Area (ha)	N	RA	RA (%)	RE	RE (%)	Vegetation types
B5	São Pedro do Turvo	22°41′31″S, 49°38′32″W	628	95	0	0	3	3	Cerradão, riparian forest
B6	São Pedro do Turvo	22°42′51″S, 49°40′50″W	328	105	0	0	2	2	Cerradão, riparian forest, ecotone cerrado/seasonal semi-deciduous forest
B9	São Pedro do Turvo	22°43′38″S, 49°41′11″W	27	72	0	0	2	3	Cerradão
C13	Agudos	22°36′24″S, 49°02′41″W	281	122	0	0	2	2	Cerradão, riparian forest, ecotone cerrado/seasonal semi-deciduous forest, seasonal semi-deciduous forest
C14	Agudos	22°34′11″S, 49°01′29″W	93	106	1	1	3	3	Cerradão, wet campo, riparian forest
C15	Agudos	22°36′15″S, 49°04′08″W	39	111	0	0	2	2	Cerradão
C2	Agudos	22°30′42″S, 48°59′44″W	304	120	2	2	2	2	Cerradão, riparian forest, ecotone cerrado/seasonal semi-deciduous forest
C22	Lençóis Paulista	22°37′17″S, 48°59′31″W	102	82	2	2	2	2	Ecotone cerrado/seasonal semi-deciduous forest
C30	Lençóis Paulista	22°39′03″S, 48°59′23″W	125	93	1	1	2	2	Cerradão, ecotone cerrado/seasonal semi-deciduous forest, riparian forest
D10	Pederneiras	22°14′25″S, 48°53′54″W	155	88	0	0	1	1	Cerradão, riparian forest
D14	Bauru; Pederneiras	22°16′44″S, 48°59′58″W	399	128	0	0	0	0	Cerradão, riparian forest
D17	Bauru	22°17′54″S, 48°59′58″W	20	106	3	3	0	0	Cerradão, riparian forest
D20	Bauru	22°19′52″S, 49°00′44″W	1155	176	2	1	3	2	Cerrado *sensu stricto*, cerradão, riparian forest, swamp forest, wet campo, ecotone cerrado/seasonal semi-deciduous forest

TABLE 1. (*Cont'd*)

Code	Locality	Coordinates	Area (ha)	N	RA	RA (%)	RE	RE (%)	Vegetation types
D22	Pederneiras	22°19′24″S, 48°57′37″W	75	89	0	0	2	2	Cerrado *sensu stricto*, cerradão
D46	Pederneiras	22°17′17″S, 48°56′27″W	490	162	1	1	1	1	Cerradão, ecotone cerrado/seasonal semi-deciduous forest, riparian forest
E1	Reginópolis	21°59′55″S, 49°09′05″W	1255	178	2	1	1	1	Cerradão, ecotone cerrado/seasonal semi-deciduous forest, riparian forest, seasonal semi-deciduous forest
E10	Arealva	22°06′38″S, 49°00′15″W	70	121	1	1	0	0	Cerradão, riparian forest
E12	Bauru	22°07′28″S, 49°09′44″W	221	125	3	2	1	1	Ecotone cerrado/seasonal semi-deciduous forest, riparian forest, seasonal semi-deciduous forest
E16	Reginópolis	22°01′53″S, 49°09′55″W	149	107	0	0	1	1	Cerradão, ecotone cerrado/seasonal semi-deciduous forest, riparian forest
E7	Arealva	22°03′09″S, 48°59′28″W	75	64	0	0	1	2	Ecotone cerrado/seasonal semi-deciduous forest
F26	Salmourão	21°32′36″S, 50°50′31″W	650	81	3	4	6	7	Seasonal semi-deciduous forest
G0	Rancharia	22°22′18″S, 50°58′43″W	546	126	1	1	1	1	Cerrado *sensu stricto*, cerradão, riparian forest
G1	Martinópolis, Indiana	22°10′13″S, 51°12′31″W	341	96	0	0	1	1	Ecotone cerrado/seasonal semi-deciduous forest
G18a	Martinópolis, Rancharia	22°14′01″S, 51°06′30″W	507	100	1	1	2	2	Cerrado *sensu stricto*, cerradão, riparian forest
G18b	Martinópolis	22°13′21″S, 51°02′49″W	295	135	0	0	0	0	Cerradão
G2	Martinópolis	22°09′47″S, 51°08′36″W	50	120	0	0	0	0	Cerradão, cerrado, riparian forest

TABLE 1. (*Cont'd*)

Code	Locality	Coordinates	Area (ha)	N	RA	RA (%)	RE	RE (%)	Vegetation types
G32	Rancharia	22°14′23″S, 50°58′48″W	63	67	0	0	0	0	Cerradão
H1	Taciba	22°26′57″S, 51°17′30″W	389	103	2	2	3	3	Cerradão, riparian forest
H6	Martinópolis	22°28′56″S, 51°13′43″W	472	86	0	0	0	0	Ecotone cerrado/seasonal semi-deciduous forest, riparian forest
H7	Martinópolis	22°29′43″S, 51°14′47″W	51	67	0	0	0	0	Ecotone cerrado/seasonal semi-deciduous forest
H8	Taciba	22°28′46″S, 51°19′36″W	622	159	1	1	2	1	Cerradão, riparian forest, ecotone cerrado/seasonal semi-deciduous forest
H9	Taciba	22°28′35″S, 51°19′51″W	37	119	0	0	1	1	Cerradão, ecotone cerrado/seasonal semi-deciduous forest
I1	Guaraçaí	21°14′08″S, 51°22′01″W	690	72	0	0	7	10	Seasonal semi-deciduous forest
K17	Pereira Barreto, Mirandópolis	20°51′26″S, 50°57′47″W	850	79	1	1	5	6	Seasonal semi-deciduous forest
K19	Pereira Barreto	20°50′27″S, 50°56′41″W	50	84	0	0	2	2	Ecotone cerrado/seasonal semi-deciduous forest, riparian forest
L6	Valparaíso	21°00′38″S, 50°53′04″W	2127	97	3	3	10	10	Seasonal semi-deciduous forest
M41	Promissão	21°27′27″S, 49°49′11″W	117	90	0	0	5	6	Cerradão, swamp forest, riparian forest, ecotone cerrado/seasonal semi-deciduous forest
M47	Promissão	21°28′21″S, 49°50′39″W	526	124	2	2	4	3	Cerrado *sensu stricto*, cerradão, riparian forest, swamp forest
M0	Avanhandava	21°23′08″S, 49°57′28″W	20	86	2	2	2	2	Ecotone cerrado/seasonal semi-deciduous forest
M1	Avanhandava	21°24′00″S, 49°56′42″W	67	83	0	0	2	2	Cerrado *sensu stricto*, swamp forest, riparian forest
M4	Avanhandava	21°21′43″S, 49°55′35″W	150	130	2	2	6	5	Cerrado *sensu stricto*, cerradão, swamp forest

TABLE 1. (*Cont'd*)

Code	Locality	Coordinates	Area (ha)	N	RA	RA (%)	RE	RE (%)	Vegetation types
P0	Boa Esperança do Sul	22°00′31″S, 48°27′17″W	181	108	0	0	1	1	Cerradão
P10	Bocaina	22°05′37″S, 48°30′51″W	129	83	1	1	2	2	Cerradão, ecotone cerrado/seasonal semi-deciduous forest, riparian forest
P11	Bocaina	22°05′00″S, 48°31′42″W	460	93	1	1	2	2	Cerradão, ecotone cerrado/seasonal semi-deciduous forest, riparian forest
P7	Boa Esperança do Sul	21°59′33″S, 48°30′54″W	684	124	2	2	2	2	Cerrado *sensu stricto*, cerradão, riparian forest
Q18	Brotas	22°06′35″S, 48°01′23″W	499	131	5	4	7	5	Cerradão, ecotone cerrado/seasonal semi-deciduous forest, riparian forest
Q0	São Carlos	22°04′17″S, 48°00′50″W	133	84	16	19	3	4	Seasonal semi-deciduous forest
Q1	Ribeirão Bonito	22°06′20″S, 48°10′34″W	43	112	2	2	3	3	Cerradão, ecotone cerrado/seasonal semi-deciduous forest
Q12	São Carlos	22°02′45″S, 48°02′39″W	395	131	1	1	6	5	Cerradão, riparian forest
Q14	Ribeirão Bonito	22°06′30″S, 48°02′55″W	122	121	1	1	6	5	Cerradão, ecotone cerrado/seasonal semi-deciduous forest, riparian forest
Q7	Ribeirão Bonito	22°03′14″S, 48°08′31″W	700	143	1	1	3	2	Cerradão, ecotone cerrado/seasonal semi-deciduous forest, riparian forest, seasonal semi-deciduous forest
R1	Rifaina	20°07′10″S, 47°23′14″W	400	117	6	5	13	11	Cerrado *sensu stricto*, cerradão, wet campo, riparian forest
R2	Rifaina	20°05′47″S, 47°24′00″W	300	118	0	0	9	8	Cerrado *sensu stricto*, cerradão, swamp forest, riparian forest
R3	Rifaina	20°05′09″S, 47°26′17″W	13	101	1	1	9	9	Cerrado *sensu stricto*

TABLE 1. (*Cont'd*)

Code	Locality	Coordinates	Area (ha)	N	RA	RA (%)	RE	RE (%)	Vegetation types
R4	Pedregulho	20°14′22″S, 47°23′44″W	450	121	7	6	11	9	Campo cerrado, cerrado *sensu stricto*, cerradão, wet campo, riparian forest
R5	Pedregulho	20°10′56″S, 47°18′25″W	120	123	3	2	9	7	Cerrado *sensu stricto*, cerradão
S11	Colômbia	20°16′58″S, 48°46′14″W	1600	73	1	1	4	5	Cerradão, ecotone cerrado/seasonal semi-deciduous forest, riparian forest
S15	Colômbia	20°17′38″S, 48°43′32″W	320	58	1	2	2	3	Cerradão
S10	Colômbia	20°14′23″S, 48°42′18″W	71	56	1	2	2	4	Cerradão, swamp forest
T1	Barretos	20°29′14″S, 48°52′16″W	207	108	1	1	4	4	Cerradão, riparian forest
T3	Barretos	20°29′27″S, 48°48′37″W	563	106	0	0	3	3	Cerradão, riparian forest
U2	Olimpia	20°38′20″S, 48°57′09″W	500	95	0	0	6	6	Ecotone cerrado/seasonal semi-deciduous forest, riparian forest
V12	Nova Granada	20°33′28″S, 49°15′05″W	913	140	1	1	8	6	Ecotone cerrado/seasonal semi-deciduous forest, riparian forest
W207	Taubaté	23°03′58″S, 45°37′10″W	13	72	4	6	8	11	Campo cerrado, cerrado *sensu stricto*, ecotone cerrado/dense evergreen forest
W200	São José dos Campos	23°12′30″S, 45°51′46″W	200	75	5	7	13	17	Campo sujo, campo cerrado, cerrado *sensu stricto*, cerradão
W201	São José dos Campos	23°16′55″S, 45°51′37″W	50	60	1	2	8	13	Campo sujo, campo cerrado, cerrado *sensu stricto*, swamp forest
W206	Caçapava	23°04′15″S, 45°38′21″W	10	65	1	2	7	11	Cerrado *sensu stricto*, cerradão, riparian forest
W209	Taubaté	23°00′56″S, 45°31′29″W	10	29	0	0	2	7	Campo sujo, campo cerrado
Z1	Itirapina	22°10′35″S, 47°52′32″W	300	120	1	1	2	2	Cerrado *sensu stricto*
Z2	Brotas	22°11′38″S, 47°53′59″W	300	85	1	1	1	1	Campo cerrado, cerrado *sensu stricto*, wet campo, riparian forest
Y3	Paranapanema	23°21′42″S, 48°55′27″W	792	112	0	0	2	2	Cerradão, riparian forest
Y2	Paranapanema	23°22′20″S, 48°59′45″W	359	99	1	1	1	1	Cerrado *sensu stricto*
Y1	Angatuba	23°22′43″S, 48°31′20″W	399	100	1	1	1	1	Campo cerrado, cerrado *sensu stricto*, wet campo, cerradão, riparian forest
Y4	Paranapanema	23°20′08″S, 48°49′11″W	347	102	3	3	3	3	Cerradão, wet campo, riparian forest

(b) Fragments of different sizes (large, medium, small) were surveyed in each area, wherever possible.
(c) Sites representing all vegetation types present in an area were surveyed; these were classified as follows:
campo sujo: a dry grassland with a scattering of shrubs;
campo cerrado: numerous trees and shrubs present but still with a large grassland component;
cerrado *sensu stricto*: obviously dominated by trees and shrubs, but still with a fair amount of herbaceous vegetation between them;
cerradão: an almost closed woodland made up of trees of cerrado species, often of 8–12m or even taller, casting a considerable shade so that ground vegetation is much reduced;
cerrado *sensu lato*: collective term for campo sujo, campo cerrado, cerrado *sensu stricto* and cerradão;
wet campo: a wet grassland without shrubs or trees;
riparian forest: a closed woodland on non-flooded substrates along watercourses;
swamp forest: a closed woodland on permanently flooded areas;
ecotone cerrado/forest: a closed woodland with cerrado and forest species intermixed.
Geographical co-ordinates using GPS (Global Positioning System) were recorded in each site and descriptions of vegetation type and conservation state were made.

Rapid botanical assessment

The floristic inventory included all woody species and also some non-woody species with potential for economic management, since exploitation of the latter is one of the overall objectives of the project. The rapid survey method adopted was first used by Ratter *et al.* (2000a,b), in other cerrado areas in Brazil, and the following description comes from Ratter *et al.* (2003).

Rapid survey technique
Because of the constraints of time, a rapid survey technique was used, developed as a refinement of 'wide-patrolling' and with some relationship to 'caminhamento' (Filgueiras *et al.*, 1994). The adoption of this technique was based on experience of working in a large team in the states of Maranhão, Pará, Mato Grosso do Sul and Goiás in 1993. During this fieldwork, groups of up to eight people worked on numerous transects and plots, while usually a single person carried out wide-patrolling of the vegetation of the area. To our surprise, the transect/plot groups never recorded a single species unnoticed by the wide-patroller, but on the other hand the latter frequently noted 50% more species than them. Thus wide-patrolling represents a particularly effective method for producing comprehensive floristic data rapidly, providing, of course, that the patroller has a very good knowledge of the flora.

The method used was refined by introducing a timing element so that a species/time

curve could be produced, giving a quantitative measurement for judging the correct time to end a survey. The survey is carried out usually by a team of three or four, one of whom acts as a recorder and also registers 15-minute intervals, while the others shout out the species observed. Typically, species recording occupies four to eight intervals (60–120 minutes), according to floristic diversity, size and topography of the area.

In our study we regarded the survey as complete when no more than five new species were added in a 15-minute interval, but in any case a 1-hour (four-interval) survey was considered as the minimum necessary.

All species which could not be identified with certainty in the field were collected for subsequent herbarium determination, and a full description of the vegetation of every site was made.

Floristic inventories from all the sites were analysed, with the aim of understanding floristic affinities and phytogeographic patterns to assist conservation evaluation within São Paulo State.

Data analysis

The floristic matrix was compiled using the program EXCEL (Microsoft 1997), with the data entered in simple binary form, i.e. presence/absence. Three multivariate techniques were used to analyse the data in an attempt to identify floristic patterns within the matrix. These were:

(a) a divisive hierarchical classification by Two-Way Indicator Species Analysis (TWINSPAN) (Hill, 1979);

(b) an agglomerative hierarchical classification by Unweighted Pair-Groups Method using Arithmetic Averages (UPGMA) using Jaccard's coefficient as a measure of similarity (Sneath & Sokal, 1973);

(c) Detrended Correspondence Analysis (Hill & Gauch, 1980).

The versions of TWINSPAN and DCA used were contained in the statistical package for windows PC-ORD (Version 4.17) (McCune & Mefford, 1999). Multivariate Statistical Package – MVSP (Version 3.1) was used for UPGMA analysis. Jaccard's coefficient was applied, since it is a very simple mathematical expression of similarity and has been recommended for qualitative data (Kent & Coker, 1992). Species observed in only a single site (unicates) were excluded from the analysis, since they provide no basis for comparison.

Distribution of species

According to their geographical distribution, species were classified as rare (recorded at only a single site), restricted, regional, or of wide distribution, using the following index:

$$Ds = (S-1)\,A^{-2}$$

where S = number of sites (Table 1) where the species occurs,
A = number of areas (Fig. 1) where the species occurs,
Ds = geographic distribution index, as follows:

Restricted distribution: $Ds \geqslant 1.0$
Regional distribution: $0.3 < Ds < 1.0$
Wide distribution: $0 < Ds \leqslant 0.3$
Rare species (only one site): $Ds = 0$.

Results and discussion

A list of the sites surveyed with descriptions of vegetation types, species numbers and scores for occurrence of rare species or species with restricted distribution is presented in Table 1. There was no cerrado vegetation in seven of the 26 areas visited (Fig. 1: F, I, J, L, N, O and X), and although these may have priority status for forest conservation they are clearly not relevant to cerrado protection. These areas were selected erroneously during the São Paulo State symposium in 1995 (Joly, 1997) on the basis of remote sensing. Satellite images do not always provide an easy method of distinguishing between different, but structurally similar, vegetation types, and ground-truthing is essential to differentiate precisely between the similar physiognomies of cerradão and secondary forests. However, data from three of these (F, I and L) were included in the matrix, since they could be useful in characterizing the floristic transition from cerrado to seasonal semi-deciduous forest.

The frequency of vegetation types occurring in all 86 sites is presented in Table 2. Cerradão was the most frequent vegetation type, followed by other forest types such as riparian forests and ecotonal vegetation of cerrado/seasonal semi-deciduous forest. Cerrado *sensu stricto* was recorded in only 27% of the sites, while the other more open forms of cerrado (campo cerrado, campo sujo) are even rarer.

These observations differ from older studies of the São Paulo cerrado. Chiarini & Coelho (1969) mapped the cerrado vegetation of the state using photointerpretation

Table 2. Frequency of vegetation types. N = number of sites; F = % occurrence in the 86 sites

Vegetation types (see footnote, p. 218)	N	F
Campo sujo	3	3.5
Campo cerrado	7	8.1
Cerrado *sensu stricto*	23	26.7
Cerradão	60	69.8
Wet campo	10	11.6
Riparian forest	52	60.5
Swamp forest	11	12.8
Ecotone cerrado/seasonal semi-deciduous forest	32	37.2
Seasonal semi-deciduous forest	11	12.8
Ecotone cerrado/dense evergreen forest	1	1.2

of aerial photographs taken in 1962 and concluded that cerrado *sensu stricto* was the commonest physiognomy (75% of total cerrado area), followed by campo (16%) and cerradão (9%). Subsequently, Kronka *et al.* (1993) mapped the cerrado remnants by remote sensing, using images produced in 1992, and found 68.9% of cerrado *sensu stricto*, 30.5% cerradão and 0.6% campo cerrado. We concluded from these figures that the remaining vegetation of cerrado *sensu lato* in São Paulo State has become denser during the last 40 years, probably as a consequence of the suppression of fires. This process of thickening of cerrado vegetation was noticed by Durigan *et al.* (1987), using sequential aerial photographs of the same area from 1962 to 1984 in Assis, western São Paulo State, where cerradão seems to be the climax vegetation. It has also been observed at Angatuba, São Paulo, by Ratter *et al.* (1988) and in the Federal District (Ratter, 1992). Rizzini (1963, 1979) and Warming (1892) regarded cerradão as the dominant form of cerrado vegetation before the human disturbance of the last centuries, a theory supported by the relatively rapid recuperation which often occurs when this disturbance is relaxed.

Floristic analysis

Floristic surveys of the 86 sites resulted in a total record of 554 species in 77 families, comprising 383 species of trees, 64 treelets, 74 shrubs, 14 subshrubs, 12 palms and seven herbs. However, only those subshrubs and herbs of potential economic value were recorded in the study. Records of all species and their site occurrence can be obtained from the authors or on the internet site of Programa BIOTA: http://sinbiota.cria.org.br/atlas/. The most common species (those occurring in 50% or more of the sites) are listed in Table 3.

Only 167 species were trees typical of cerrado vegetation *sensu lato*, where trees are defined as woody plants taller than 2m, with a distinct trunk. The other arboreal species were 'accessories', more characteristic of forests and/or riparian habitats; as would be expected, they were particularly abundant in ecotonal vegetation.

Casearia sylvestris Sw. and *Byrsonima intermedia* A. Juss. were the most widespread species, recorded in 90% and 88% of the sites, respectively. Only 10% of the species occurred in $\geqslant$50% of the sites and 19% of the species were recorded in only a single site. A number of species occurring in more than one site showed restricted geographic distribution (Table 4).

There were considerable differences between sites in the number of species recorded, from a minimum of 29 in Taubaté to a maximum of 185 in one of the fragments at Campos Novos Paulista (Table 1). As expected, the seven richest sites in terms of species number contain ecotonal vegetation, with floras comprising elements of both forest and cerrado habitats.

Site richness, therefore, was directly correlated with the diversity of vegetation types present in the area. This relates to 'beta diversity', which can be defined as the difference in species composition between habitats (Whittaker, 1972; Magurran, 1988) or how species composition changes with distance (Condit *et al.*, 2002). Since

TABLE 3. Plant species recorded in 50% or more of the sites. N = number of sites; F = frequency of occurrence (% of sites); Ds = geographic distribution index ($Ds = (S-1)A^{-2}$; see pp. 228–229)

Species	Family	N	F	Ds
Casearia sylvestris Sw.	*Flacourtiaceae*	78	90	0.2
Byrsonima intermedia A. Juss.	*Malpighiaceae*	76	88	0.2
Copaifera langsdorffii Desf.	*Caesalpiniaceae*	76	87	0.2
Gochnatia barrosii Cabrera	*Asteraceae*	75	86	0.2
Tabebuia ochracea (Cham.) Standl.	*Bignoniaceae*	74	85	0.2
Siparuna guianensis Aubl.	*Monimiaceae*	73	81	0.2
Bromelia balansae Mez	*Bromeliaceae*	70	81	0.2
Machaerium acutifolium Vogel	*Fabaceae*	70	80	0.2
Platypodium elegans Vogel	*Fabaceae*	69	79	0.2
Roupala montana Aubl.	*Proteaceae*	68	79	0.3
Stryphnodendron obovatum Benth.	*Mimosaceae*	68	78	0.3
Miconia albicans (Sw.) Triana	*Melastomataceae*	67	78	0.3
Syagrus romanzoffiana (Cham.) Glassman	*Arecaceae*	67	77	0.2
Bauhinia rufa (Bong.) Steud.	*Caesalpiniaceae*	66	76	0.1
Tapirira guianensis Aubl.	*Anacardiaceae*	65	76	0.3
Xylopia aromatica (Lam.) Mart.	*Annonaceae*	65	74	0.3
Solanum paniculatum L.	*Solanaceae*	64	72	0.2
Terminalia glabrescens Mart.	*Combretaceae*	62	72	0.3
Vochysia tucanorum (C.K. Spreng.) Mart.	*Vochysiaceae*	62	71	0.2
Baccharis dracunculifolia DC.	*Asteraceae*	61	71	0.3
Luehea grandiflora Mart.	*Tiliaceae*	61	70	0.3
Acosmium subelegans (Mohl.) Yakovlev	*Fabaceae*	60	70	0.2
Didymopanax vinosum March.	*Araliaceae*	60	67	0.3
Anadenanthera peregrina (L.) Speg. var. *falcata* (Benth.) Altschul	*Mimosaceae*	58	66	0.1
Gochnatia polymorpha (Less.) Cabrera	*Asteraceae*	57	66	0.3
Ocotea corymbosa Mez	*Lauraceae*	57	66	0.3
Protium heptaphyllum March.	*Burseraceae*	57	65	0.1
Aegiphila lhotskiana Cham.	*Verbenaceae*	56	65	0.2
Cecropia pachystachya Trécul	*Cecropiaceae*	56	64	0.2
Brosimum gaudichaudii Trécul	*Moraceae*	55	63	0.2
Bredemeyera floribunda Willd.	*Polygalaceae*	54	63	0.1
Matayba elaeagnoides Radlk.	*Sapindaceae*	54	63	0.3
Tabernaemontana hystrix (Steud.) DC.	*Apocynaceae*	54	62	0.3
Qualea grandiflora Mart.	*Vochysiaceae*	53	60	0.1
Dimorphandra mollis Benth.	*Caesalpiniaceae*	52	60	0.2
Miconia stenostachya DC.	*Melastomataceae*	52	59	0.3
Duguetia furfuracea (A. St.-Hil.) Benth. & Hook.f.	*Annonaceae*	51	59	0.2
Myrcia albotomentosa DC.	*Myrtaceae*	51	59	0.2
Styrax camporum Pohl	*Styracaceae*	51	59	0.2
Zanthoxylum rhoifolium Lam.	*Rutaceae*	51	58	0.1
Caryocar brasiliense Cambess.	*Caryocaraceae*	50	58	0.2

TABLE 3. (*Cont'd*)

Species	Family	N	F	Ds
Tocoyena formosa (Cham. & Schltdl.) K. Schum.	*Rubiaceae*	50	57	0.2
Ananas ananassoides (Baker) L.B. Smith	*Bromeliaceae*	49	57	0.2
Annona coriacea Mart.	*Annonaceae*	49	57	0.2
Campomanesia adamantium Cambess.	*Myrtaceae*	49	57	0.2
Ouratea spectabilis (Mart.) Engl.	*Ochnaceae*	49	56	0.2
Annona dioica A. St.-Hil.	*Annonaceae*	48	55	0.3
Acacia polyphylla DC.	*Mimosaceae*	47	55	0.1
Eugenia aurata O. Berg	*Myrtaceae*	47	55	0.2
Pouteria ramiflora (Mart.) Radlk.	*Sapotaceae*	47	52	0.2
Erythroxylum cuneifolium (Mart.) Schult.	*Erythroxylaceae*	45	52	0.2
Lacistema hasslerianum Chodat	*Lacistemaceae*	45	52	0.2
Memora axillaris K. Schum.	*Bignoniaceae*	45	52	0.2
Qualea multiflora Mart.	*Vochysiaceae*	45	51	0.2
Diospyros hispida DC.	*Ebenaceae*	44	51	0.1
Machaerium brasiliense Vogel	*Fabaceae*	44	51	0.3
Rapanea umbellata (Mart. ex DC.) Mez	*Myrsinaceae*	44	51	0.2
Luehea candicans Mart.	*Tiliaceae*	43	50	0.2

the botanical inventories extended over all the distinct physiognomies in each site, the richness values obtained should accurately reflect beta diversity.

The overall richness of the woody cerrado flora and the existence of distinct geographic patterns have been discussed by Castro & Martins (1999), Oliveira-Filho & Ratter (2002) and Ratter *et al.* (2003). On the other hand, relatively few studies have been focused on quantifying broad patterns of cerrado diversity, although Felfili & Felfili (2001) analysed alpha and beta diversity in patches of cerrado (*sensu stricto*) in Central Brazil. More research is certainly needed in this area to clarify patterns of beta diversity within the Cerrado Biome, and it would be interesting to compare these patterns with those hypothesized for tropical rainforest (see, for instance, Hubbel, 2001; Pitman *et al.*, 2001; Condit *et al.*, 2002).

Multivariate analyses

The multivariate analyses showed the expected correlation of species occurrence with vegetation type and demonstrated a distinct geographic pattern of distribution.

TWINSPAN

The TWINSPAN analysis of species distribution (Fig. 2) showed, in the first level of division, a distinct western group, containing sites where forest vegetation types prevail (cerradão and ecotonal), and an eastern group, dominated by more open forms of cerrado, although cerradão also occurs here.

For the western group of sites, the preferential species were mostly characteristic

TABLE 4. Species with restricted geographic distribution in São Paulo State ($Ds \geqslant 1.0$). Ds = geographic distribution index ($Ds = (S-1)A^{-2}$; see pp. 228–229 and Fig. 1); N = number of sites where the species occurs (see Table 1)

Species	Family	Ds	N	A
Eremanthus matogrossensis O. Kuntze	*Asteraceae*	4.0	5	R
Lippia lasiocalycina Cham.	*Verbenaceae*	4.0	5	M
Leucochloron incuriale (Vell.) Barneby & Grimes	*Mimosaceae*	3.0	4	W
Cereus hildmannianus K. Schum.	*Cactaceae*	3.0	4	P
Eriotheca candolleana (K. Schum.) A. Robyns	*Bombacaceae*	3.0	4	P
Cedrela odorata L.	*Meliaceae*	2.0	3	Q
Eremanthus sphaerocephalus Baker	*Asteraceae*	2.0	3	Y
Ficus gomelleira Kunth & Bouché	*Moraceae*	2.0	3	M
Hirtella hebeclada Moric.	*Chrysobalanaceae*	2.0	3	R
Ouratea hexasperma (A. St.-Hil.) Benth.	*Ochnaceae*	2.0	3	R
Sterculia striata A. St.-Hil. & Naud.	*Sterculiaceae*	2.0	3	K
Vochysia rufa Mart.	*Vochysiaceae*	2.0	3	R
Bauhinia pentandra D. Dietr.	*Caesalpiniaceae*	1.5	7	S, T
Zanthoxylum hyemale A. St.-Hil.	*Rutaceae*	1.5	7	A, B
Kielmeyera rubriflora Cambess.	*Clusiaceae*	1.3	6	D, R
Myrcia variabilis DC.	*Myrtaceae*	1.3	6	R, W
Sapium longifolium (Müll. Arg.) Huber	*Euphorbiaceae*	1.3	6	M, R
Casearia lasiophylla Eichler	*Flacourtiaceae*	1.2	12	B, C, Y
Annona tomentosa R.E. Fries	*Annonaceae*	1.0	2	R
Aspidosperma olivaceum Müll. Arg.	*Apocynaceae*	1.0	2	Q
Bauhinia brevipes Vogel	*Caesalpiniaceae*	1.0	2	T
Brosimum glaziovii Taub.	*Moraceae*	1.0	2	W
Diplusodon virgatus Pohl	*Lythraceae*	1.0	5	R, T
Erythrina verna Vell.	*Papilionaceae*	1.0	2	S, T
Ilex paraguariensis A. St.-Hil.	*Aquifoliaceae*	1.0	5	A, B
Laetia americana L.	*Flacourtiaceae*	1.0	2	S
Lonchocarpus muehlbergianus Hassler	*Papilionaceae*	1.0	2	B
Mandevilla illustris (Vell.) R.E. Woodson	*Apocynaceae*	1.0	2	W
Mauritia flexuosa L.	*Arecaceae*	1.0	2	R
Myrcia obtecta (O. Berg) Kiaersk.	*Myrtaceae*	1.0	2	W
Ouratea floribunda (A. St.-Hil.) Engl.	*Ochnaceae*	1.0	2	W
Podocarpus sellowii Endl.	*Podocarpaceae*	1.0	2	Q
Rhamnus sphaerosperma Sw.	*Rhamnaceae*	1.0	2	Q
Macairea radula (Bonpl.) DC.	*Melastomataceae*	1.0	2	R

of forest, such as: *Cupania tenuivalvis* Radlk., *Matayba elaeagnoides* Radlk., *Coutarea hexandra* (Jacq.) K. Schum., *Myrcia bella* Cambess., *Nectandra cuspidata* Nees and *Machaerium aculeatum* Raddi. For the eastern group, the preferential species were those typical of open types of cerrado: *Stryphnodendron adstringens* (Mart.) Cov., *Schefflera macrocarpa* (Seem.) D.C. Frodin, *Diptychandra aurantiaca* Tul., *Tabebuia aurea* S. Moore, *Attalea geraensis* B. Rodr., *Erythroxylum campestre* A. St.-Hil. and

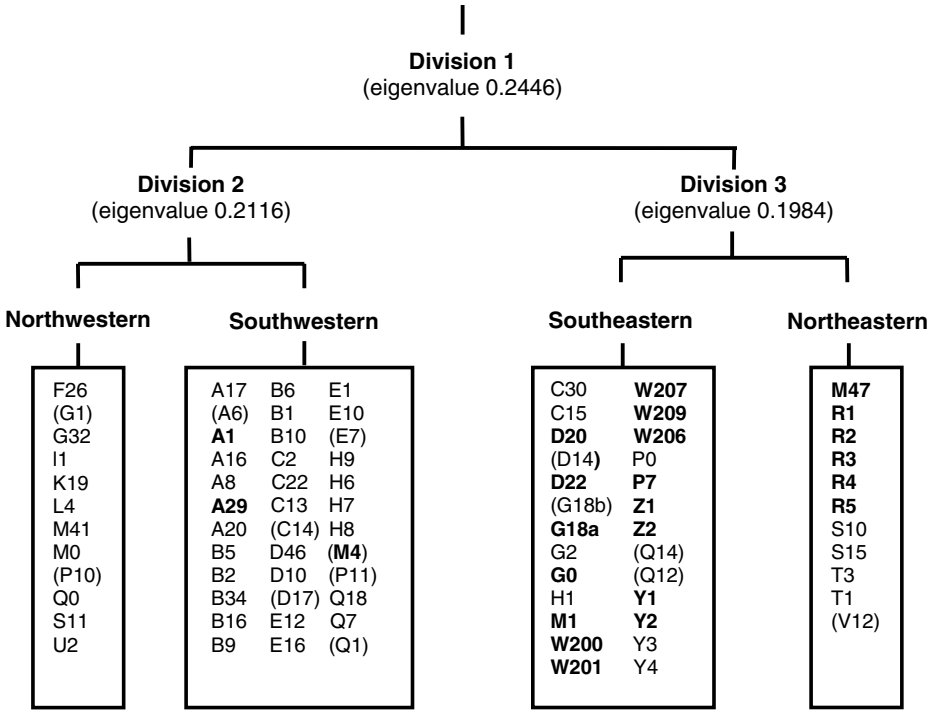

FIG. 2. Groups of cerrado sites in São Paulo State, resulting from TWINSPAN analysis. Site codes as in Table 1. Codes in parentheses refer to borderlines or are misclassified. Codes in bold refer to sites where open forms of cerrado exist.

Acosmium dasycarpum (Vogel) Yakovlev. As expected, non-preferential species were generally those that occur mainly in cerradão, the most widespread cerrado type in São Paulo State. Since vegetation types (physiognomies in the Brazilian sense) seem to be the primary factor influencing the grouping of sites, there are some western areas where more open cerrado vegetation occurs classified by the analysis in the eastern group (e.g. H1).

At the second level of division (Division 2 and Division 3), the groups seem to be determined more by geographic distribution than by physiognomy. There is a division of the western sites into northwestern (Salmourão, Guaraçaí, Pereira Barreto, Valparaíso, Olímpia) and southwestern (Campos Novos Paulista, São Pedro do Turvo, Taciba). The eastern group is divided into northeastern (Rifaina, Nova Granada, Barretos, Colômbia) and southeastern (São José dos Campos, Caçapava, Taubaté, Itirapina, Brotas, Paranapanema, Angatuba) sites. There is an intersection zone in the central region of the state where these four groups are mixed (Agudos, Bauru, Promissão, Martinópolis, Bocaina, Ribeirão Bonito). Although these four geographic groups are not strongly distinct, they do indicate floristic differences among regions, which will be useful in designing conservation strategies for cerrado vegetation in São Paulo State.

DCA

The distribution of the sites generated by DCA (Fig. 3) is very similar to the groups resulting from TWINSPAN.

The distribution of sites along the first axis is clearly determined by vegetation type, from the more open cerrado physiognomy in site W200 to the more dense forest in site Q0. The second axis also has ecological significance, correlated with climate (see Fig. 1), especially the duration of the dry season and temperature. Along this axis, sites are distributed from cooler and wetter zones (south) to warmer and drier zones (north).

As a result, there are four groups indicated by the two axes:

- open cerrado physiognomies in cooler and wetter climates (southeastern);
- open cerrado physiognomies in warmer and drier climates (northeastern);
- closed physiognomies (cerradão, ecotone and forest) in cool and wet climates (southwestern); and

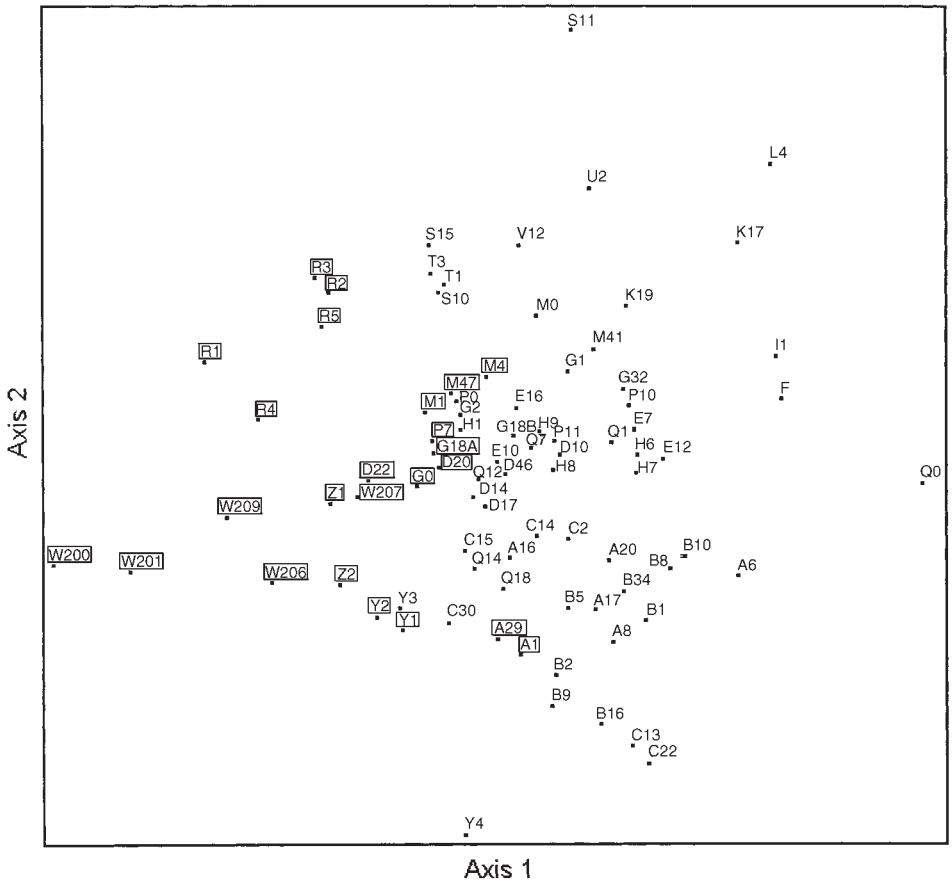

FIG. 3. A two-dimensional species ordination plot derived from DCA analysis of the 86 sites. Codes in boxes refer to sites which contain open forms of cerrado.

- closed physiognomies (cerradão, ecotone and forest) in warmer and drier climates (northwestern).

Clearly there is strong agreement between TWINSPAN and DCA analyses, both of which make the primary division on physiognomically related floristics.

UPGMA

The results obtained by UPGMA analyses (Fig. 4) are not as clearly distinct as those from TWINSPAN and DCA. However, the dendrogram does partially show the separation of cerradão sites from more open forms of cerrado.

There are six distinct groups of which four are small: Vale do Paraíba (five W sites); northeastern (five R sites); northern ecotone and cerradão (six sites); and forest vegetation (six sites). Of the two large groups with cerrado *sensu lato*, one has 42 sites with open forms of cerrado and the other has 18 sites without. Here again, physiognomy seems to be the main factor influencing the results, establishing floristic similarity between sites.

In all the analyses, the sites located in the Vale do Paraíba stand out as very distinct. This remarkable difference is a consequence of two factors. The first is the low species richness of these sites and consequent low similarity indices, as noted in a theoretical study of reciprocal averaging and DCA by Dargie (1986). These sites had an average of 60 species each (trees, shrubs and subshrubs), when the total average for the state as a whole was 103 species per site. Therefore, even if all the species present there had also occurred in another site, similarity would be low. The second factor is the high percentage of rare species or species of restricted distribution (see Table 1), corresponding to 14.1% of the species recorded in that region (18 out of 128, considering the five W sites together). These species were recorded in only one site or in a few geographically restricted sites.

The northeastern area (site code R) also has a high proportion of rare species or species with restricted distribution, 13.4% (28 out of 209 species recorded in the five sites), when the average of all the areas presented in Fig. 1 is only 4.0%. These sites also form a distinct group in DCA and in UPGMA.

Contrary to expectations, the five sites where the vegetation was entirely seasonal semi-deciduous forest did not form a distinct group. They were placed in the northwestern group by TWINSPAN and DCA, where there are also sites with closed cerrado structure under a warm and dry climate. These sites are grouped together in the UPGMA dendrogram, but there is low floristic similarity between them. This confirms the continuous floristic gradient from cerrado to seasonal semi-deciduous forest, with ecotonal sites containing variable proportions of cerrado/forest species, an observation well known to field workers.

The existence of two distinct groups related to physiognomy in the cerrado flora of São Paulo State has previously been documented by Castro (1994), using TWINSPAN. The first contained areas with denser cerrado forms (cerrado *sensu stricto*, cerradão and transition cerrado/forest) and the second comprised areas with

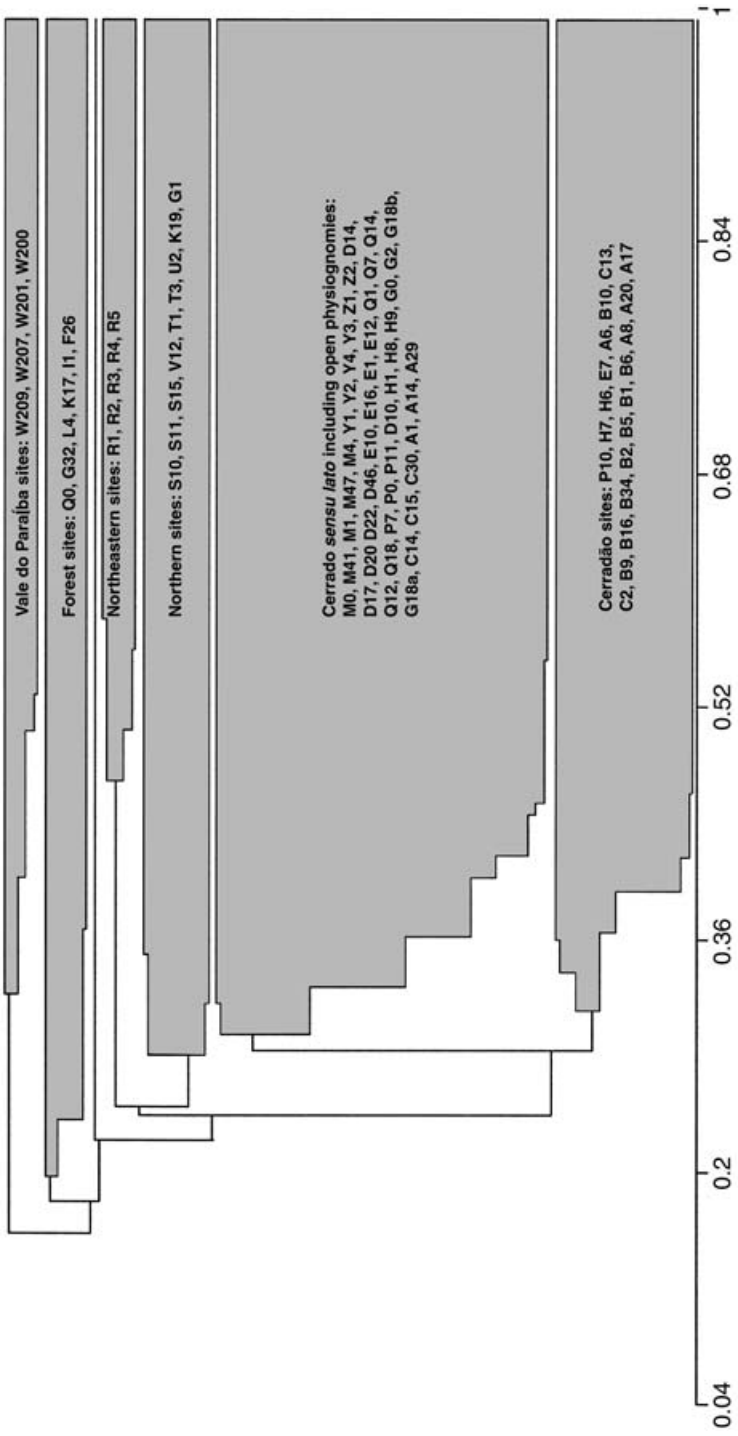

FIG. 4. Dendrogram resulting from UPGMA analysis of the 86 sites using Jaccard's similarity coefficient.

more open cerrado forms (campo sujo, campo cerrado, cerrado *sensu stricto* and cerradão).

Ratter *et al.* (1996), in a study applying multivariate analysis to 98 cerrado areas, included 10 São Paulo sites (based on previously published data); one of these appeared isolated and all the others formed an apparently very natural group distinct from those of the central core cerrado area. However, all nine sites in this group had more open vegetation, were located at the eastern side of the state, and seemed to correspond to the group of more open vegetation defined by the present study.

Conclusion

We conclude, on the basis of the multivariate analyses, that cerrado vegetation in São Paulo State can be divided into two main types: a western group, corresponding to cerradão, and an eastern group, corresponding to more open forms of cerrado. Distribution of species within São Paulo State correlates with the occurrence of cerrado physiognomies (cerradão and more open forms of cerrado, each having their own characteristic communities); thus the phytogeographic division of cerrado vegetation is a direct consequence of the distribution of these physiognomies.

Climate, especially the duration of the dry season, can explain the secondary pattern of distribution observed, with distinct variation of flora occurring from north to south inside the physiognomic groups.

Site richness was more strongly correlated with diversity of vegetation type than with fragment size, so that beta diversity (which corresponds to the variety of different habitats) is more important than area as a criterion to assist in identifying individual priority areas for cerrado conservation.

Several species are confined to restricted areas of São Paulo State, but so far evidence is insufficient to establish strong phytogeographic patterns on the basis of species distribution.

The floristic gradient from cerrado to seasonal semi-deciduous forest is continuous, sometimes extending for hundreds of kilometres, with variable proportions of forest and cerrado species, often making it hard to decide whether an area should be classified as belonging to the forest or the cerrado domain. As there are no specific policies or laws to protect ecotonal vegetation, it is difficult to decide whether to apply cerrado or forest legislation.

Prior to our work, western São Paulo State and, especially, its cerradão and ecotone between cerrado and seasonal semi-deciduous forest had been little studied and are thus poorly represented in protected areas. Efforts must be directed towards policies and strategies for conservation and study of the last remaining natural areas in this region.

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