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Phytosociology in Brazil

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ABSTRACT

A more or less random selection of the international journal literature on the subject of phytosociology in Brazil with publication dates from 1998 to 2007 is reviewed. The 90 papers are reviewed on the basis of three fundamental themes. First by their coverage of the various plant physiognomies that can be found in Brazil, and indeed throughout much of the Neotropics: phytoplankton, fungi, lichen, ferns, aroids, epiphytic orchids and bromeliads, Velloziaceae, palms, grasses, bamboo, succulents, stranglers, trees, shrubs and lianas. Then as representative of the Brazilian biomes: Amazon Biome, Cerrado Biome, Caatinga Biome, Pantanal Biome, Atlantic Forest Biome, and Coastal and Island Biome, there being none for the Pampa Biome. Finally, from a more critical viewpoint they are examined for their coverage of the environmental factors that help determine composition and structure of plant communities. The phytosociological methods for the predominantly woody plants and related multivariate data analysis are also briefly described. Many uses have been made of the results of phytosociological surveys, highlighting Brazil as a macrocosm of plant community ecology and vegetation science.

Keywords: plant communities, savanna, species identification, tropical forest, vegetation map, wetlands

CONTENTS

INTRODUCTION

Phytosociology aims to characterize and classify plant communities in terms of their composition and structure, and therefore has a place under Plant Ecology. In Brazil this area has been dominated by a generally uniform method of surveying the predominantly woody vegetation. The results of phytosociological surveys have been used to help classify the vegetation of Brazil (Veloso 1992) and they continue to contribute to phytogeography. These surveys are undertaken with painstaking care in Brazil and an enormous quantity of data has been accumulated.

A comprehensive review of the literature of phytosociology in Brazil would result in a book and the author had only three months in which to review the subject. The selection of the "review set" of 90 papers presented in the references was subject only to the following criteria. They are all journal articles with dates of publication between 1998 and 2007, they are written in English though most of the authors are Brazilian, and were discovered by the use of several internet bibliographic services allowing free full-text searching and free access to abstracts. Scielo provided title and abstract searching and free access to the full-text of many, but not all, peer reviewed Brazilian journals. The Boolean search strategy could not have been simpler (phytosoc* AND Brazil*) which may not have been comprehensive but it retrieved a set of documents that needed only a little filtering for relevance. An even larger literature was discovered by using Portuguese search terms (fitossoc* AND Brasil* – or equivalent) in Scielo. In this way a further 139 references were selected and scrutinized. Most of this literature in Portuguese relates to individual surveys of new areas or repeated surveys for studies of dynamics. They are often summaries of dissertations and theses of supervised university students on masters and doctorate programmes at Brazilian universities. This literature in Portuguese, was excluded from this review as its data and results in most cases would have been synthesized by the research team faculty members in the international journals and their findings will be reflected in the references presented here. For example, Santos *et al.* (2008) used the data of nine phytosociological surveys with publication dates in our window (1998-2007). Eight were published in Portuguese, at least three of these based on masters dissertations, and the remaining one was published in English by a Brazilian journal. Nevertheless, the literature in Portuguese represents a more first-hand experience of phytosociological surveys and analyses and would be well worth reviewing separately in Portuguese.

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Invited Review

PLANT PHYSIOGNOMIES IN BRAZIL

The earth's vegetation includes all plant forms wherever and whatever they may be, and most have yielded to a phytosociological approach of one type or another. Our literature search discovered a few references to **phytoplankton** research in Brazil (Melo and Huszar 2000; Reynolds *et al.* 2002; Moura *et al.* 2007). A further paper (Kruk *et al.* 2002) relates to research in neighbouring Uruguay but is included for its obvious relevance and for its clear exposition of the uniting theme of these papers which is the functional classification of phytoplankton. During successional changes in phytoplankton communities it has been found that to look only at the constituent taxonomic groups does not yield the best predictive models. A functional classification of Reynolds recognizing 31 associations based on morphology and certain ecological properties proved more predictive. Such concepts so assiduously applied to the polyphyletic phytoplankton may possibly be of application to other plant communities so it is worthwhile to draw attention to a new book by Reynolds (2006) on the ecology of marine and freshwater phytoplankton.

Mycorrhizal **fungi** are associated with the majority of vascular plants and play a vital role in helping the absorption of phosphorous and other nutrients. Their presence in the soil is thus essential for the regeneration of natural vegetation. Arbuscular mycorrhizal fungi were shown to have a greater association with pioneer tree species in open areas than with later successional species within forests in the South (Zangaro *et al.* 2000). Soil disturbances, for example, in the area of activity of a copper mine, can change species composition and reduce abundance in arbuscular mycorrhizal fungi communities (Silva *et al.* 2005).

A **lichen** species is a specific ascomycete fungus in symbiotic association with one or more species of alga. These algae may also be found in other species of lichen. Certain lichens therefore may well merit individual phytosociological treatments, not that our search found any such studies. What was found, were observations on epiphytic lichens and their phorophyte tree hosts. These have been studied in the understorey of the tropical rain-forest of the Northeast (Cáceres *et al.* 2007). Although no strongly delimited lichen communities were discovered, it was concluded that they were influenced by phorophyte bark characteristics and microclimate, and that the presence or absence of rare species in particular was largely the result of stochastic dispersal. Attempts have also been made to use epiphytic lichens as bioindicators of fire history in tropical savannas. However, the use of a key that was developed to assess fire history in areas of cerrado in Central Brazil was shown to be affected by other factors such as bark aluminium content, bark pH, and microclimatic factors (Mistry and Berardi 2005). Phorophyte species were therefore identified that were more reliable when using the key. One overriding factor was that the more severe the fire, the less influence other variables had on lichen establishment.

Alexander von Humboldt can, among other professions, be thought of as an early international phytosociologist as he recognized 19 terrestrial plant physiognomic types during his travels in South America and published them in *Essai sur la géographie des plantes* in 1805 in Paris only a year after his return to Europe. With some rearrangement they are: ferns, conifers, aroids, lily, orchid, *Aloe*, palms, grass, banana, cactus, laurel, myrtle, Melastomataceae, willow, *Casuarina*, *Mimosa*, tree Malvaceae, Ericaceae and lianas. We must remember that these are only representative of certain physiognomies. *Aloe* and *Casuarina* are not Neotropical but they are commonly cultivated here.

Tree **ferns** of the genus *Cyathea* are often recorded during surveys of Atlantic forest (e.g. Vieira and Izar 1999). Six species from five families of less robust ferns, including *Pteridium aquilinum*, were recorded as invading 8-year-old fallow within a fragment of coastal lowland Atlantic forest in the South (Salimon and Negrelle 2001). Amongst the desiccation-tolerant vascular plants encountered on isolated Brazilian granitic and gneissic inselbergs throughout the Atlantic Forest the most prominent ferns and fern allies were the genera *Anemia*, *Doryopteris* and *Selaginella* (Porembski and Barthlott 2000).

The only **conifers** that will be found listed in Brazilian natural forest inventories are *Araucaria angustifolia*, *Podocarpus lambertii* and *P. sellowii*. They are concentrated in the highlands of the South with a more scattered distribution in the highlands of the Southeast, a distribution known as "paranense". The Paranense province was delimited by Cabrera and Willink in 1980 (Pennington *et al.* 2000).

Flowering plants dominate the terrestrial vegetation in the Tropics. The woody "basal angiosperms" such as the Annonaceae and Lauraceae, which are very diverse and common in Brazil, continue to be placed in the same physiognomic tree group as later-diverging woody dicots that share the same form and the same forests.

Within the monocots, the **aroids** (Araceae) are common and diverse in Brazilian forests with many epiphytic species. Many are zoochorous with fruits consumed and seeds dispersed by animals. In one major study the faeces of 2 primate species and 8 arboreal or semi-arboreal marsupials in a fragment of Atlantic forest in the Southeast were obtained from feeding stations and trapping respectively (Vieira and Izar 1999). An examination of the constituent seeds showed that both monkeys and 3 of the marsupials were feeding regularly on aroid fruits from the genera *Anthurium*, *Heteropsis*, *Monstera*, *Philodendron* and *Syngonium*. Most seeds tested viable and would thus be effectively dispersed. An abundance of **epiphytic orchids and bromeliads** and of three species of bamboo (non-epiphytic) was also noted for the same state park, as is typical of protected areas of Atlantic forest.

Members of the **Velloziaceae** are commonly found in "campo rupestre" and sandy restinga. Many are fire-resistant and some can branch and grow to more than a metre in height, a physiognomy that could be described as a dwarf grass-tree type. Most *Vellozia* species appear to be desiccation-tolerant and some species come to dominate mat-like communities on rocky slopes of inselbergs alongside desiccation-tolerant or xeromorphic Cyperaceae and Poaceae (Porembski *et al.* 1998; Porembski and Barthlott 2000).

Palms characterize the Tropics, not least in Brazil where they are found in diverse ecological situations. The family of trees with the highest density (stems per area) in a large majority of Amazonian and Guianan forests is either Arecaceae (Palmae) or Fabaceae and the forests of western Amazonia are particularly rich in palms (Terborgh and Andresen 1998). *Leopoldinia pulchra* was one of the most abundant species in an area of floodplain forest on the Rio Tapajós, Eastern Amazonia (Ferreira and Prance 1998). Floodplain forests in the Pantanal can be dominated by *Attalea phalerata* or *Copernicia alba* (Damasceno-Junior *et al.* 2005). In a fragment of lowland Atlantic forest in the Southeast, *Euterpe edulis* accounted for 21.8% of all individuals recorded (Guilherme *et al.* 2004).

Most tussock-forming Cyperaceae and Poaceae are found in **grassland** formations which principally occur in the Cerrado, Caatinga and Pampa biomes discussed below. **Bamboo** is exceptional among the Poaceae. Large forms of the Asian genera *Bambusa*, *Dendrocalamus* and *Gigantochloa* are cultivated, but more slender native species, including many species of *Chusquea*, *Merostachys* and *Guadua* occur in forests in São Paulo State (Longhi-Wagner *et al.* 2001) and elsewhere in Brazil. Bamboos have been considered to have a special role in the dynamics of canopy gaps (Tabarelli and Mantovani 2000; Martins *et al.* 2004).

In Brazil the order Caryophyllales is represented mainly by recognized **succulents** such as Cactaceae and Portulacaceae. Many succulents have crassulacean acid metabolism (CAM) which enables them to close their stomata during the day and open them for gas exchange and to fix carbon dioxide during the cool of the night thus reducing water loss by transpiration. Some species of bromeliads are CAM plants and *Clusia* is the only Neotropical tree to display CAM (Lüttge 2006).

Some species of *Clusia* (Clusiaceae) and *Ficus* (Moraceae) have a physiognomy known as **stranglers**. They start as epiphytes and can send out aerial roots many metres in length to reach the soil. Once fully established in this manner, they grow to the detriment and eventual death of host trees. Some can also establish on rock and rapidly cover a substrate normally associated with primary succession by lichens. Milliken (1998) recorded stranglers as a separate category in his survey of Amazon *terra firme* forest. *Clusia* has also recently been recognized as an important nurse plant for forest regeneration (Scarano *et al.* 2005).

Humboldt's laurel, myrtle, Melastomataceae, tree Malvaceae and *Mimosa* remain practical ways to distinguish the very diverse Neotropical **dicot trees** using leaf physiognomy. He effectively delimited trees with simple leaves and alternate phyllotaxy or opposite phyllotaxy or Melastomataceae venation from trees with compound leaves in digitate or pinnate forms. The present author has also employed this traditional way of describing trees in combination with other easily observed vegetative characters and constructed a computer-aided plant characterization and identification system in Portuguese called CARipé (Hargreaves 2005, 2006), which can at present greatly facilitate the identification of 570 tree species in the Atlantic forest. Tree species identification has been highlighted as one of the principle areas needing more resources in studies of the Atlantic forest (Caiafa and Martins 2007).

In one hectare of Amazonian *terra firme* forest 16 **lianas** representing 14 species, 13 genera, and 8 families were recorded (Milliken 1998). Marimon *et al.* (2002) recorded trees and lianas in a gallery forest in the Amazon-Cerrado ecotone.

PHYTOSOCIOLOGICAL METHODS

Here it seems appropriate to briefly describe the principal phytosociological methods used for woody plant communities in Brazil. The predominant method of sampling is the multiple plot method but the quarter method has been found to encounter more species for less effort though it gives less accurate estimates of population densities (Caiafa and Martins 2007). In the plot method all the individual trees attaining a certain minimum size are labelled, and the circumference at breast height (CBH) measured with a tape. Standard breast height is taken as 1.3 m above the soil surface. The minimum size criterion can be variable and is often given as a diameter, with ≥ 5 cm DBH being much the most common for the coastal Atlantic forest (Caiafa and Martins 2007) and a sample of our references confirms this is also true for forest outside the Amazon. Smaller minimum size criteria and height of measurement are used in cerrado and caatinga as we will see. The heights of individual trees are also estimated and can be used to partition the data for studies of vertical stratification. Basal areas of individuals are calculated from diameter or circumference measurements and then summed for each species. Species are identified in the field or samples obtained for identification in the herbarium.

For each species in each plot, phytosociological parameters can be calculated. The *relative density* of a species is the number of its individuals expressed as a percentage of the total number of individuals of all species. Similarly, the *relative dominance* of a species is its total basal area as a percentage of the total basal area of all species. Counts per area are called *absolute densities* and expressed in units of hectares (ha^{-1}). Likewise, a species basal area per unit sample area gives its *absolute dominance* (m^2 ha^{-1}). In addition, we can calculate a *cover value index* (CVI) (e.g. Aidar *et al.* 2001) for each species as the sum of its *relative density* and *relative dominance.*

Usually there are multiple plots per site. For each site additional data accrue. The number of plots in which a species is present is called its frequency. The *relative frequency* of a species is its frequency as a percentage of the sum of the frequency values for all species. This is in addition to the parameters described for plots, as these can be recalculated for sites. The *importance value index* (IVI), or often simply called *importance value* (IV), of a species is calculated as the sum of its *relative density*, *relative dominance* and *relative frequency*. This is taken as an indication of overall ecological importance or impact and indeed all the parameters above are considered ecologically relevant in different though not yet completely understood ways. It is also necessary to be aware that ethnobotany studies use another type of importance value based on the utility of species by local populations (e.g. Santos *et al.* 2008).

To provide other perspectives, data of species can be combined by genera and family but analyses by species and family are more common. In the last ten years the use of multivariate analysis software has been universally applied by students and faculty alike. FITOPAC software (Shepherd 1996) has been a popular choice for data entry, organisation and calculation of phytosociological parameters, while others have preferred a more hands-on approach with Microsoft Excel spreadsheet or Microsoft Access database management software. Both FITOPAC and PC-ORD for Windows (e.g. Scudeller *et al.* 2001) have been popular sources of classification techniques such as UPGMA (e.g. Pinder and Rosso 1998; Silva and Albuquerque 2005) using a choice of similarity coefficients but often Sorensen's, and also of ordination using Principal Components Analysis (PCA) (e.g. Miranda *et al.* 2003; Damasceno-Junior *et al.* 2005; Pinto *et al.* 2005). Two-way indicator species analysis (TWINSPAN) (e.g. Ferraz *et al.* 2004; Damasceno-Junior *et al.* 2005; Marimon *et al.* 2006) has completed a set of three analyses that have been commonly used together to reciprocally confirm or clarify their individual outputs. In addition Canonical Correspondence Analysis (CCA) (e.g. Pivello *et al.* 1999b; Kruk *et al.* 2002; Fortney *et al.* 2004; Pinto *et al.* 2005) and Detrended Correspondence Analysis (DCA) (e.g. Terborgh and Andresen 1998; Guilherme *et al.* 2004; Costa Filho *et al.* 2006; Marimon *et al.* 2006; Toledo and Bush 2007) have commonly been used to analyse species distributions in relation to available or specially gathered environmental data. Particularly see Scudeller *et al.* (2001) who use all the methods from UPGMA through to DCA. Traditional statistical tools such as Chi-squared tests of association have also been useful (e.g. Fortney *et al.* 2004). At the other extreme, there have been experiments with parsimony analysis to study fragmented forests (Pellens *et al*. 2007).

BRAZILIAN BIOMES AND VEGETATION

At least seven biomes are recognized in Brazil. All of them, with the exception of the Pampa Biome consisting of grasslands, are found in our evaluation set of 90 references and are listed in **Table 1** that also shows the distribution of our references in relation to biomes and regions. A map of the Brazilian biomes, states and regions is shown in **Fig. 1**, which has been constructed from official sources (IBGE 2008).

Amazon Biome

The Amazon region occupies approximately 6 million km^2 in South America of which 65% consists of *terra firme* forest that does not suffer inundation (Oliveira and Amaral 2004).

Rivers and lakes are, nevertheless, important parts of the Amazon Biome. When a floodplain lake is > 4 m deep, thermal stratification of the water column can have a major influence on the distribution of phytoplankton populations, including nano-algae (Melo and Huszar 2000).

Amazon floodplain forest has evolved under challenging environmental conditions. Rivers in the Amazonian region have annual water level fluctuations varying from 6 to 20 m, and the flooding period ranges from 50 to 270 days between the rising and falling phases. The number of tree

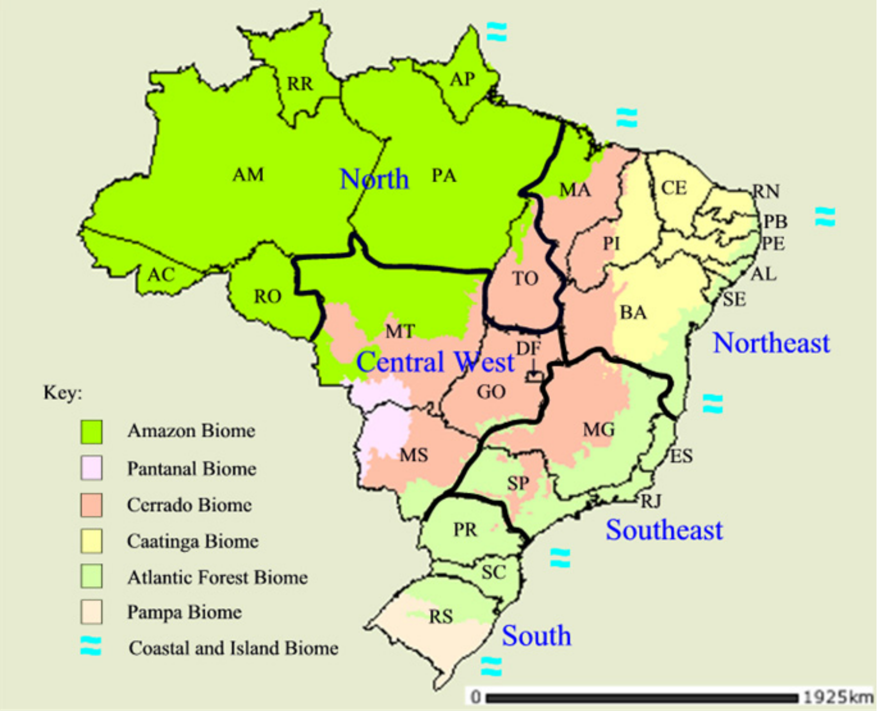

Fig. 1 Map of Brazilian biomes with states and regions. Adapted from IBGE 2008.

State	Abbrev.	Region
Acre	AC	North
Amapá	AP	North
Amazonas	AM	North
Pará	PA	North
Rondônia	RO	North
Roraima	RR	North
Tocatins	TO	North
Alagoas	AL	Northeast
Bahia	BA	Northeast
Ceará	CE	Northeast
Maranhão	MA	Northeast
Paraíba	PB	Northeast
Pernambuco	PE	Northeast
Piauí	PI	Northeast
Rio Grande do Norte	RN	Northeast
Sergipe	SE	Northeast
Mato Grosso	MT	Central West
Mato Grosso do Sul	MS	Central West
Goiás	GO	Central West
Federal District	DF	Central West
Espírito Santo	ES	Southeast
Minas Gerais	MG	Southeast
Rio de Janeiro	RJ	Southeast
São Paulo	SP	Southeast
Paraná	PR	South
Rio Grande do Sul	RS	South
Santa Catarina	SC	South

Table 1 Distribution of selected "Phytosociology in Brazil" literature (1998-2007) among Brazilian biomes and regions; N – North, CW – Central West, NE – Northeast, SE – Southeast, S – South, n/a – categories not applicable.

Biome or other	Brazilian Regions						
ecological category	**N**	**CW**	**NE**	**SE**	**S**	**n/a**	
Amazon Biome	12	2					*14*
Amazon-Cerrado ecotone		4					*4*
Cerrado Biome		7	1	5			*13*
Caatinga Biome			9				*9*
Atlantic Forest Biome		1	6	14	5	5^a	*31*
Pantanal Biome		6					*6*
Coastal and Island Biome			1	2	1		*4*
Lake phytoplankton	1		1			2^a	*4*
n/a						5	*5*
	13	*20*	*18*	*21*	*6*	*12*	*90*

a – more than one region covered by reported studies

species ranged from 21 to 30 ha^{-1}. Fabaceae was the most abundant and dominant family (Ferreira and Prance 1998).

Amazon *terra firme* forest is much more diverse. In one hectare of forest in the State of Amazonas the woody plants with stems ≥ 10 cm DBH were inventoried and 201 tree species, 14 liana species, and 1 strangler were registered. The dominant families of trees present were the Fabaceae, Lecythidaceae, Sapotaceae, Burseraceae, and Moraceae (Milliken 1998). In a survey in the State of Pará of 0.75 ha, using a smaller minimum size criterion of ≥ 7 cm DBH, 222 tree species were identified. However, they also described their data from the viewpoint of a minimum size criterion of ≥ 10 cm DBH and reported only 162 tree species (Mackensen *et al.* 2000).

On the Guayana Shield it appears that non-gramineous herbaceous communities, including endemic genera of the monocot families Rapateaceae, Bromeliaceae, Xyridaceae, Eriocaulaceae and Cyperaceae have evolved to occupy extremely nutrient poor sites at all altitudinal levels whilst grasses (Poaceae) dominate herbaceous communities on richer soils (Huber 2006).

Roraima savannas located on the Amazon-Orinoco Plateau are heavily used for cattle ranching. Extensive sampling showed that the woody vegetation was poor in species in relation to other savanna areas such as found in the Cerrado Biome discussed below. In 40 plots totalling 6.75 ha scattered throughout the State but excluding the much impacted central area, only 71 woody plant species were found (Miranda *et al.* 2003). However, as the sampling took place only along the main highways the biodiversity may have been underestimated (Barbosa *et al.* 2007).

A series of studies has been carried out in the Amazon-Cerrado ecotone (Marimon *et al.* 2001a, 2001b, 2002). A further study was made of the transition between the Amazon and Cerrado Biomes on the Serra do Roncador in the northeast of Mato Grosso State and it was reported that no species of ≥ 15 cm CBH was common to the samples of communities of forest, cerradão and cerrado (Marimon *et al.* 2006).

Our references include others that report studies in the Amazon Biome (Terborgh and Andresen 1998; ter Steege *et al.* 2000; Ivanauskas *et al.* 2003; ter Steege *et al.* 2003; Rodrigues *et al.* 2004; Vieira *et al.* 2004; Parmentier *et al.* 2007; Toledo and Bush 2007).

Cerrado Biome

The Cerrado Biome covers approximately 2 million km^2 and principally consists of cerrado vegetation which is often called Brazilian savanna. Cerrado physiognomies are given as campo limpo, campo sujo, campo cerrado (or campo ralo), cerrado *sensu stricto* and cerradão, which are viewed as describing an ecotonal transition between grassland and tall forest (Batalha *et al.* 2001 {citing Coutinho 1978}; Ratter *et al.* 2003).

Most studies of cerrado have described only the woody plant component which therefore excludes areas of campo limpo. An extensive analysis was carried out of the floristic composition of all the Brazilian cerrado *sensu lato*, a working definition including all the physiognomies except campo limpo (Ratter *et al.* 2003; Bridgewater *et al.* 2004). A comparison was made of 376 areas including disjunct areas in the Amazon such as the already mentioned Roraima savannas. Thus, six cerrado phytogeographic provinces (southern, central and south-eastern, central-western, far-western, north-eastern, disjunct Amazonian) were delimited using a consensus classification derived from the use of multivariate analysis software TWINSPAN and UPGMA. It is clear that the names of the proposed cerrado provinces have been carefully chosen to reflect their positions with respect to the Brazilian regions. The main casualty is São

Paulo State which is placed in the southern province when it is part of the Southeast region. This should not present a problem to specialists on cerrado but will limit their use in wider ranging works such as this review, which is already using states, regions and biomes.

In a study of plots of cerrado *sensu stricto* at 15 sites in Goiás, the Federal District, northern Minas Gerais and Bahia (two cerrado provinces or three regions) using a minimum size criterion of ≥5 cm diameter measured with a caliper at 0.3 m from the ground level, the number of species of woody plants ranged between 55 to 97 ha $^{-1}$ (Felfili *et al.* 2004). Six "land systems" from the earlier RADAM-BRASIL zoning of the region based on climate, soils, relief, topography and vegetation physiognomy were compared against the vegetation classification by TWINSPAN of the 15 sites, and conformed well enough to recommend the adoption of those land systems as an additional tool to set up conservation strategies. The dynamics of cerrado *sensu stricto* both in the Federal District (Felfili *et al.* 2000) and near the Cerrado-Caatinga ecotone in Bahia (Roitman *et al.* 2008) has also been studied.

The herbaceous component and the necessarily antagonistic woody component of three cerrado physiognomies were surveyed in the Southeast (Batalha *et al.* 2001). Rigorous analyses of both components independently confirmed a floristic transition between the cerrado physiognomies from campo cerrado to cerrado *sensu stricto* to cerradão. In the same nature reserve the invasion of exotic grasses (Pivello *et al.* 1999b) was also studied.

In the Cerrado Biome other vegetation types can be found. Dry semideciduous or deciduous forests occupy 20% of the area and indicate base rich soils high in calcium whereas the savanna physiognomies and gallery forest generally occur on acid soils. A phytosociological survey of trees ≥15 cm CBH, was carried out in a dry deciduous forest located on a hillside at the margin of a small river in the Southeast (Souza *et al.* 2007). In the 1 ha site 59 species were recorded, and *Myracrodruon urundeuva* (Anacardiaceae) and *Tabebuia roseo-alba* (Bignoniaceae) were species with high importance values. In the same local region the dynamics of a dry forest were elucidated (Werneck and Franceschinelli 2004). Not on base rich soils, one of many valley forests found in the Cerrado Biome was studied in the Chapada dos Guimarães National Park, Mato Grosso State (Pinto *et al.* 2005).

Our references include other studies on the Cerrado Biome (Pivello *et al.* 1999a; Mistry and Berardi 2005; Nardoto *et al.* 2006).

Caatinga Biome

Araújo *et al.* (2007) have already reviewed the Caatinga Biome in regional detail. Apart from our other references, the information of this section is adapted from their review. The Caatinga Biome is located mainly in the Northeast, often appearing as thorn scrub with some succulents and represents Brazilian semi-arid vegetation. It occupies approximately 800,000 km^2 or half the area of the Northeast region. The mean annual rainfall for the biome is 620 mm. Precipitation is seasonal and varies geographically and unpredictably. Caatinga vegetation is represented by the physiognomic types: parkland, scrub, scrub-woodland and woodland – when necessary, a prefix of semi-arid would identify them as belonging to the Caatinga.

The less studied herbaceous component mainly comes from the families Poaceae, Convolvulaceae, Asteraceae, Fabaceae, Euphorbiaceae, Cyperaceae, Malvaceae, Scrophulariaceae and Rubiaceae. Its richness is generally three times that of the woody component (Araújo *et al.* 2007). The usual minimum size criteria for surveying the woody component is a diameter at soil level of 3 cm (DSL ≥3 cm) which reflects the smaller stature in relation to cerrado and forest formations. There are approximately 1100 species of tree and shrub and 318 are endemic. The most common families are Euphorbiaceae, Fabaceae, Cactaceae and Anacardiaceae. The Fabaceae species *Caesalpinia pyramidalis* and *Anadenanthera colubrina*, and the Anacardiaceae species *Schinopsis brasiliensis* and *Myracrodruon urundeuva* are widespread in the Caatinga (Araújo *et al.* 2007). The predominance of *Anadenanthera colubrina*, in particular, possibly links the Caatinga to other seasonally dry tropical forests, in a southern arc through Southeast and Central West regions of Brazil and as far as coastal Ecuador (Pennington *et al.* 2000; Prado 2000).

Our references include other studies on the Caatinga Biome (Nascimento *et al.* 2003; Pereira *et al.* 2003; Machado and Lopes 2004; Silva and Albuquerque 2005; Silva *et al.* 2005; Machado *et al.* 2006; Reis *et al.* 2006; Santos *et al.* 2008).

Pantanal Biome

The Pantanal is an approximately 140,000 km^2 Quaternary floodplain located mainly in the Central West region of Brazil with some extensions into Paraguay and Bolivia. Floodplains present plant communities ranged along an inundation gradient that is in some places gradual and in other situations abrupt.

Floating aquatic macrophyte species at two environmentally distinct river bays in the Brazilian Pantanal were resolved into 4 groups at one site and 2 in the other using Chi-squared analysis along depth gradients (Fortney *et al.* 2004). CCA gave similar results at the first site but not at the second. *Eichhornia azurea* and *Salvinia auriculata* occurred most frequently as dominant or co-dominant species at both sites.

In the south-eastern Pantanal, the point-quadrat method of sampling, UPGMA and Correspondence Analysis (possibly CCA) were used to characterize the following floodplain plant formations: marsh pond, waterlogged basin, short grassland, tall grassland, scrub, and forest edge (Pinder and Rosso 1998). The forest edge separated well from the other formations and was described as consisting of diverse species including lianas, and *Chomelia obtusa*. In the present author's experience this widespread shrub may possibly characterize forest edge with a high water table. Pinder and Rosso (1998) noted that the very small semideciduous forest patches encountered were never flooded.

However, riparian forest of the Paraguay river near Corumbá does experience periodic inundation. In general the riparian forests are located at convex curves of meanders where sets of narrow sediment banks are deposited during floods (Damasceno-Junior *et al.* 2005). Species richness was 37 ha^{-1} when using a minimum tree size of ≥15 cm CBH, and 29 ha^{-1} for an inclusion criterion ≥31 cm CBH. *Inga vera* ssp. *affinis* (Fabaceae) was dominant (IVI = 116.9) and *Vochysia divergens* (Vochysiaceae) that is frequently dominant in Pantanal floodplain vegetation was also ecologically important (IVI = 14.56).

Our references include other studies on the Pantanal Biome (Guarim *et al.* 2000; Damasceno-Junior *et al.* 2004; Julião *et al.* 2004). Riparian forests on the upper Paraná river are considered under the Atlantic Forest Biome.

Atlantic Forest Biome

The Atlantic Forest Biome occurs in a wide band along the Brazilian coast from 7° S to 29° S and covers approximately 1 million km^2. At present only 7% remains of its estimated original forested area and exploitation of the forest has left it much fragmented. According to a recent review, geographical coverage of research on the Atlantic Forest *sensu stricto* is also patchy (Caiafa and Martins 2007) and our own literature search confirmed this.

In the Northeast the usual suite of multivariate analysis software was used on a binary matrix of species presence-absence data to enable the grouping of various forest tree communities (Ferraz *et al.* 2004). The main separation was between montane (≥700 m) semi-deciduous forest and ombrophilous mainly lowland forest.

Previously in the State of São Paulo in the Southeast, two floristic-structural species groups were recognized in the ombrophilous dense forest: coastal province and Atlantic plateau (Scudeller *et al.* 2001). The list of more cover-dominant species for the Atlantic plateau group was immediately recognizable to the present author as showing strong affinities to semi-deciduous or dry forests of the neighbouring highlands in the south of Minas Gerais. The semi-deciduous forest has stronger similarity with the ombrophilous mainly lowland forest than either have with cerrado or Amazon forest. Its floristic differences are associated with a lower rainfall regime so that its characteristic species are better adapted to a dry-season (Oliveira-Filho and Fontes 2001). In one of these semi-deciduous forests a high floristic similarity between the lower tree strata and the canopy was observed (Souza *et al.* 2006).

Seasonally dry tropical forests grow on fertile soils, have woody floras dominated by the Fabaceae and Bignoniaceae and a sparse ground flora. They occur in disjunct areas throughout the Neotropics including the Caatinga Biome, semideciduous forests of the Paranense province in the Atlantic Forest Biome and the Cerrado Biome on areas of fertile soils (Pennington *et al.* 2000). The dry forests of the Northeast are found near the coastal zone and inland on isolated small mountains amid semi-arid vegetation. They were shown to represent two major vegetation transitions: (1) a humid forest/dry forest transition; and (2) a deciduous thorn-woodland/dry forest transition (Rodal and Nascimento 2006). The canopy of this dry-forest in the Northeast is mainly composed of deciduous species, while the understory is predominantly evergreen (Lopes *et al.* 2008). Other information on dry forests has already been presented under the Cerrado and Caatinga biomes. Prado (2000) proposed the separate recognition of a Tropical Seasonal Forests Region in South America.

Aidar *et al.* (2001) studied humid forest in the Southeast over calcareous substrate. Citing various sources they reported that humid forest on karsts or calcareous soils are rare in South America and absent from Africa. More than 30% of the earth's surface is covered by calcareous soils but in Brazil they only constitute 7% of the territory and most of this is in areas of cerrado or seasonally dry forest. The results of their survey suggested that *Tibouchina pulchra*, the most dominant tree in early successions in the local region and one that prefers acid soils was, on the calcareous soils, replaced by other species.

Riparian forests in the Pantanal have already been mentioned. Further south from there, riparian forests on the upper Paraná river were also described as seasonal semi-deciduous forest (Campos *et al.* 2000; Campos and Souza 2002; Costa Filho *et al.* 2006) and are considered as constituents of the Atlantic Forest Biome that enter the Central West.

In the South of Brazil, only 96 species ha^{-1} were recorded for both the herbaceous and woody strata for an old cultivation clearing that had been regenerating for 8 years surrounded by coastal Atlantic forest. However, it was reported that most of the species did not tolerate extreme conditions in the centre of the opening, and were slowly colonizing the area through the borders (Salimon and Negrelle 2001). Also in the South, woody species richness of 78 species was recorded for a seasonal deciduous Atlantic forest (Ruschel *et al.* 2007).

Some characteristics of the special vegetation of inselbergs in the Atlantic Forest Biome have been described when discussing the physiognomies of various herb groups (Porembski *et al.* 1998; Porembski and Barthlott 2000).

Various other methodological, ecological and conservation research topics on the Atlantic Forest Biome are covered by our other references (Vieira and Izar 1999; Tabarelli and Mantovani 2000; Zangaro *et al.* 2000; Grombone-Guaratini and Rodrigues 2002; Martins and Rodrigues 2002; França *et al.* 2004; Martins *et al.* 2004; Victor *et al.* 2004; Scarano *et al.* 2005; Cunha and Albuquerque 2006; Pinheiro *et al.* 2006; Cáceres *et al.* 2007; Ferreira-Júnior *et al.* 2007; Sambuichi and Haridasan 2007).

Coastal and Island Biome

Some may argue that restinga vegetation should be placed in the Atlantic Forest Biome with which it no doubt has some affinities, however, it is better for our purposes to use the Coastal and Island Biome as a convenient heading under which to discuss it. None of our references relate to the Brazilian islands. Restinga is associated with sandy beach ridges (Scheel-Ybert 2000) and sandy coastal plain (Matallana *et al.* 2005) and dunes. Charcoal analysis of six shell mounds along the south-eastern Brazilian coast used taxonomic determinations based on a reference collection of charred woods and a program for computer-aided identification. These shell mounds had been occupied by sedentary fisher–gatherer–hunters during the studied period 5500 to 1400 14C yr BP. Charcoal assemblages represented taxa from various restinga vegetation types, mangroves, xeromorphic coastal forest, and inland Atlantic forest. The restinga forest was much more abundant during the studied period than at present (Scheel-Ybert 2000). The local area of one restinga study, again in the Southeast, was described as a vegetation mosaic comprising nine plant formations, ranging from open types to forest (Matallana *et al.* 2005).

The "Todos os Santos" mangrove ecosystem in Bahia has a fringe physiognomy with low bearing, containing the species, *Laguncularia racemosa* (Combretaceae), *Rhizophora mangle*, and *Avicennia schaueriana* (Freitas *et al.* 2002).

South-west Atlantic saltmarshes are best characterized by the presence of the halophytic genera *Spartina* (Poaceae) and *Sarcocornia* (Chenopodiaceae). Cluster analysis showed three habitat types: saltmarshes dominated by (1) *Spartina densiflora* and brackish species, (2) *Spartina alterniflora* and *Sarcocornia perennis* and (3) *Spartina densiflora* only. The south-west Atlantic coast has decreasing mean annual rainfall (1200 to 196 mm) and increasing mean tidal amplitude (<0.5 to >2.5 m) from latitude 31° to 43° (Isacch *et al.* 2006). It was also noted that other phytosociological studies on saltmarshes have been carried out in southern Brazil (Reitz 1961; Danilevicz 1989; Costa 1997; all cited by Isacch *et al.* 2006).

ENVIRONMENTAL FACTORS

Environmental conditions are the main influences on the association of plants when taking into account their physiognomies, as the mapping of climatic, topographic and vegetation zones has clearly demonstrated (**Fig. 1**). However, studies of the effects of the environment on the distribution of individual species or species assemblages in patches of similar physiognomy, such as forest, perhaps not surprisingly, encounter more difficulties. Nevertheless, progress is being made to unravel the complexities of cause and effect in such plant communities.

We have already seen how climate influences the species composition of Atlantic forest so that the semi-deciduous dry forests can be distinguished from the ombrophilous coastal forest and this is associated with seasonal patterns of precipitation (Oliveira-Filho and Fontes 2000). Climate may also explain the lower tree α-diversity of African rain forests relative to Amazon forest (Parmentier *et al.* 2007). Changes of climate high in the watershed may influence the vegetation downstream, for example, the results of pollen and charcoal analysis of lake sediments in eastern Amazonia suggest that changes of climate in the Andes determined the Holocene distribution of savannas in the vicinity of those lakes (Toledo and Bush 2007).

Studies reporting on individual phytosociological surveys are usually the ones to highlight the influence of soil water regimes on the spatial distribution patterns of tree species (Pinto *et al.* 2005; Ferreira-Júnior *et al.* 2007). This is a common finding in soil-vegetation studies (Sollins 1998), also the majority of remaining forests, at least of

Atlantic forest, are located on slopes, with a corresponding environmental gradient of soil humidity.

The same studies highlight the influence of soil fertility. Also we have already seen that the distribution of dry forests has been related to more fertile soils or those high in calcium. A monodominant forest of *Brosimum rubescens* (Moraceae) was found on soils with high concentrations of magnesium in the Amazon-Cerrado ecotone (Marimon *et al.* 2001a, 2001b) and indeed they reported that throughout the world monodominant forests have often been found on soils high in magnesium. According to Sollins (1998) the soil chemical properties most likely to influence species composition in lowland tropical rain forests are: availability of P, K, Ca, and Mg, and Al toxicity. However his analysis of 18 soil-vegetation studies measuring quantities of these elements showed that many authors did not report any trends of chemical concentrations in relation to species composition whilst of the several that report definite trends only three presented the evidence for such findings, and even from these three it was difficult to generalise findings. He made a plea for better designed, more intense, sampling methods.

Biotic environmental factors can take the form of obvious dependencies such as already seen for the fungus-algae symbiosis of lichens and the epiphyte-phorophyte interactions. Animal-plant interactions between mammals and aroids have already been mentioned. Also, Julião *et al.* (2004) studied the distribution and species richness of gall-forming insects in both the interior and edge of forests in the Pantanal.

Some biotic interactions are more subtle. Forests are often said to consist of two or three layers or strata but in many cases these are not easily delimited. DCA was successfully used to do just this in a lowland Atlantic forest in the Southeast. Stratum A (≥26 m) showed the lowest density, Stratum B (8 m < h < 26 m) had the greatest richness and diversity, and Stratum C (≤8 m) showed the highest density (Guilherme *et al.* 2004). However, in a semi-deciduous forest in the Southeast there was a great floristic similarity between canopy trees and a sub-canopy tree layer (Souza *et al.* 2006), suggesting that semi-deciduous forest is essentially two layered – canopy and understorey with young canopy trees at various intermediate heights. According to Miyawaki (2004) one of the most important challenges is the restoration of complex, multilayer forests.

Other biotic interactions are dynamic. The initial stages of both natural and old field successions in the humid tropics will depend on the surrounding vegetation matrix as well as other factors. Vegetation was observed on a temporary sandbank island in the river Paraná where an initial succession of pioneer trees was encountering no recruitment of either pioneer or later successional trees species. This arrested succession was possibly due to the presence of cattle (Campos and Souza 2002). Land degraded by mining in an Amazon forest area was surveyed three times in the 18 months after the area was abandoned. The number of individuals, species, families and diversity increased during the time interval studied and decreased with distance from the remnant fragment. These results are compatible with a model of succession by facilitation, where pioneers improve the ecological conditions for establishment of later successional species (Rodrigues *et al.* 2004). Old field succession will also be influenced by the type of crop and agricultural system at the time of abandonment. In the already mentioned study of Salimon and Negrelle (2001), a patch of forest had previously been cleared to cultivate mandioca for two years and burnt twice (presumably before and after cultivation) and then abandoned for 8 years before the phytosociological survey that showed a slow regeneration of natural vegetation in progress. Agroforestry systems on the other hand experience a more rapid regeneration of natural forest. Sambuichi and Haridasan (2007) describe the recovery of tree species richness after abandonment of cacao cultivated in modified Atlantic forest.

Some ecotones are clearly the result of environmental gradients such as the already mentioned inundation regimes experienced by riparian vegetation. However, over long periods such environmental gradients can shift position so that in one location there can be a succession of vegetation "over time" that reflects the environmental gradient "over space". Similarly, changing climates will influence the potential position of cerrado-forest ecotones. Short-term factors such as fire (Felfili *et al.* 2000; Cochrane 2003; Roitman *et al.* 2008) and other disturbances will determine the actual position of ecotones, with active biotic regeneration or succession in evidence whenever there is a respite.

We can at least hypothesize the existence of climax forest. However, this natural equilibrium state would have to include the dynamics of gap-phase regeneration (e.g. Martins and Rodrigues 2002). Bamboo occupies forests in individual clumps that sometimes attain large sizes and some species have long-period, synchronized flowering and seed-set followed by mortality so that suddenly gaps of various sizes are available for invasion and forest regeneration (Tabarelli and Mantovani 2000; Martins *et al.* 2004).

The dynamics of more or less homogeneous stands of vegetation are described in four of our references. A dry forest fragment after the exclusion of human disturbance demonstrated an increased density of shade-tolerant trees and a decline of pioneer species (Werneck and Franceschinelli 2004). The tree dynamics of a fire-protected cerrado *sensu stricto* surrounded by forest plantations, over a 13-year period showed that species number rose from 62 to 84, diversity increased significantly, there was an increase of many fire-sensitive species, and woody plants increased in density and basal area (Roitman *et al.* 2008). A study of the inter-annual variations in the floristic and population structure of an herbaceous community of caatinga vegetation highlighted the problem that seasonal climatic variations greatly modified the population structure so that long-term studies are needed in order to better understand inter-annual dynamics (Reis *et al.* 2006). The regular sampling of permanent plots that is necessary for the study of forest or cerrado dynamics means that most studies will have be situated near to centres of population and carried out on previously disturbed vegetation in active "build" or regeneration. However, studies of one area of cerrado *sensu stricto* over a nine-year period showed a nearly constant density and basal area (Felfili *et al.* 2000). Lewis *et al.* (2004) make an important methodological note – in studies of forest dynamics, tree mortality, recruitment and turnover rates require special methods for their calculation, interpretation and comparison when census intervals vary.

Further perusal of even this sample of journal literature will show that many other uses have been made of the results of phytosociological surveys, highlighting Brazil as a macrocosm of plant community ecology and vegetation science.

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