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Discriminant analysis of the spatial distribution of plant species occurrences: II. Distribution of major tree communities in Paraguay

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ABSTRACT

SPICHIGER, R., C. CALENGE & B. BISE (2005). Discriminant analysis of the spatial distribution of plant species occurrences II. Distribution of major tree communities in Paraguay. *Candollea* 60: 577-593. In English, English and French abstracts.

This paper is the second of two articles describing theoretical and practical aspects of discriminant analysis of species distributions in a given area. Here we present a practical case study using herbarium specimens. The geographical zonation of tree species in Paraguay was identified and used to describe both the vegetation structures and their spatial organization. Data on the spatial distribution of these species came from the herbarium databases of the Botanical Garden of Geneva (Switzerland) and Missouri Botanical Garden (St. Louis, USA). Thirty-two of the most common tree species in Paraguay ("ballast species") were selected for the analysis to homogenize the samples analysed. Discriminant Analysis on Eigenvectors of Neighbourhood Operator (DAENO) was used to identify the main vegetation structures. According to the scale, this study shows that the Paraguayan ecotone is composed of several communities rather than by a continuous change in vegetation composition. The analysis highlighted two main vegetation types in Paraguay, the Chaco and Paraná, both of which were composed of several "sub-structures". At the extreme West of the Chaco, the plant community belongs to the typical xeromorphic flora with *Aspidosperma quebracho-blanco* Schltdl. as the dominant tree species. The centre of the Paraguayan Chaco is occupied by a more psammophilous community, with *Schinopsis quebracho-colorado* (Schltdl.) F. A. Barkley & T. Mey. as the dominant tree species. The last of the Chaco community types highlighted in this study are the xeromesophilous forests of the wet Chaco, characterized by temporarily waterlogged soils and a wetter climate. Two Paranean communities have also been highlighted on the eastern bank of the Río Paraguay: (i) the typical Paranean forests, mainly composed of *Lauraceae*, and (ii) in the extreme North of Paraguay, a mixture of Paranean species and of cerrado-related species (savannah species). This mosaic constitutes a transition area between the Paranean forests and southern Brazilian cerrados. The Chaco and the typical Paranean forests are separated by an other ecotone characterized by a very high species diversity on the eastern bank of the Río Paraguay. The relationship between scale and heterogeneity is a fundamental issue in community studies. The congruence of these results with previous findings in the literature represents a strong argument in favour of the use of herbarium data in biogeographical studies.

RÉSUMÉ

SPICHIGER, R., C. CALENGE & B. BISE (2005). L'analyse discriminante de la distribution spatiale d'occurrences d'espèces végétales: II. Distribution des communautés d'espèces majeures d'arbres du Paraguay. *Candollea* 60: 577-593. En anglais, résumés anglais et français.

Cet article est le second d'une série de deux articles décrivant les aspects théoriques et pratiques de la discrimination spatiale des distributions de plusieurs espèces sur une zone donnée. Nous présentons ici un cas d'étude pratique utilisant des données d'herbier. Nous avons étudié la zonation géographique

des espèces arborées au Paraguay, afin d'identifier les communautés végétales et leur organisation spatiale dans ce pays. Des données sur la distribution spatiale de ces espèces ont été rassemblées dans les bases de données des herbiers de Genève (Suisse) et de Saint Louis (Missouri, USA). Nous avons choisi de travailler sur les 32 espèces les plus communes au Paraguay (espèces "ballasts"), pour homogénéiser l'échantillon analysé. Nous avons ensuite utilisé une Analyse Discriminante sur Vecteurs Propres du Graphe de Voisinage (ADVPGV) pour identifier les principales structures végétales rencontrées dans ce pays. Suivant l'échelle adoptée, cette étude souligne que l'écotone paraguayen est caractérisé par plusieurs communautés, et non par un changement continu de la composition de la végétation. Nous avons mis en lumière deux types végétaux principaux au Paraguay, le Chaco et le Paraná, eux-mêmes constitués de plusieurs «sous-structures». A l'extrême ouest du Chaco, une première communauté correspond à la flore xéromorphe typique, dont *Aspidosperma quebrachoblanco* Schltdl. est une espèce caractéristique. Le centre du Chaco paraguayen est occupé par une communauté plus psammophile, avec *Schinopsis quebracho-colorado* (Schltdl.) F. A. Barkley & T. Mey. comme espèce arborée dominante. La dernière communauté chaqueéenne mise en évidence dans cette étude est formée des forêts xéromésophiles du «Chaco humide», caractérisées par des sols temporairement inondés et un climat plus humide. Deux communautés paranéennes ont également été mises en évidence, sur la rive orientale du Río Paraguay : (i) les forêts paranéennes typiques, principalement constituées par des représentants de la famille des *Lauraceae*, et (ii) à l'extrême nord du Paraguay, un mélange d'espèces paranéennes et d'espèces liées aux «cerrados» (espèces de savane). Cette mosaïque constitue une zone de transition entre les forêts paranéennes et les cerrados du Sud-Bราซิล. Le Chaco et les formations typiques paranéennes sont séparés par un autre écotone caractérisé par une diversité très importante, sur la rive orientale du Río Paraguay. La relation entre le concept d'échelle et celui d'hétérogénéité est un problème essentiel en phytosociologie. L'accord entre ces résultats et ceux de la littérature constitue un argument fort en faveur de l'utilisation des données d'herbiers dans les études de biogéographie.

KEY-WORDS: Biogeography – Neotropics – Paraguay – Paraná – Chaco – Discriminant Analysis on Eigenvectors of Neighbourhood Operator (DAENO) – Floristic communities – Scale – Herbarium data

Introduction

The study of the geographical zonation of the distribution ranges of species lies at the very core of biogeography. It helps biologists to develop hypotheses on many aspects of the ecology of a region, including environmental and historical factors. However, at the scale of a country or continent it is often hard to carry out systematic sampling across the whole area (e.g. using a grid of quadrats). As a result of this many biologists try to develop hypotheses on the organization of vegetation using data originating from other sources. Herbarium specimens may be of great use in this context because each sample represents an occurrence of a species (GIMARET-CARPENTIER, 1999). In the first paper (see CALENGE & al., 2005) we noted that several statistical methods exist to analyse such lists of occurrences, and therefore to identify the geographical zonation of selected species in a given area. Here we use one of these methods to analyse herbarium data from specimens collected in Paraguay.

Paraguay has long been of major interest to botanists and several studies have described the flora and vegetation of this country (CHODAT & VISCHER, 1916; BERNARDI, 1984; BERNARDI, 1985; LOPEZ & al., 1987; RAMELLA & SPICHIGER, 1989; SPICHIGER & al., 1991; SPICHIGER & al., 1992; SPICHIGER & al., 1995). A considerable quantity of herbarium specimens have been collected by botanists in this area and most of these specimens are entered in the herbarium databases of Missouri Botanical Garden (St. Louis, U.S.A.) and the Botanical Garden of Geneva (Switzerland).

Paraguay is a huge transition area where various vegetation types, floras and faunas compete together. The biogeographical situation of the Paraguay-Paraná basin does not allow for a high level of isolation and therefore of speciation. The large rivers such as the Río Paraná, Río Pilcomayo or Río Paraguay and some of their tributaries served as migration routes for the modern flora and fauna (BERNARDI, 1984). Altitudinal belts of vegetation are scarce because of the rarity of topographical relief. The climatic and edaphic dryness is much higher in the Andean

Piedmont than in the surroundings of the Río Paraná. This results in a division of the Paraguayan territory into two biomes separated by the Río Paraguay (Fig. 1A). The Chaco extends westward from the bank of the Río Paraguay to the Bolivian border and the Paraná area is located to the East of the country, between Río Paraguay and Río Paraná. The Paraguayan vegetation changes from semi-deciduous forests in the southeast, to xeromorphic forests and thickets in the northwest.

A recent study of the distribution across South America of the predominant tree-species growing in Paraguay highlighted four dispersal centres on the continent (SPICHIGER & al., 2004). The Columbian pole and the Paranean pole were characterized by a rather wet climate, whereas the Chaco and the São Francisco poles were characterized by a drier climate. Gradients, or continuous changes in vegetation composition, have been highlighted between the Columbian pole and the São Francisco pole ("peri-Amazonian" gradient), between the Paraná and the São Francisco poles, and between the Chaco and the three other poles. This study also confirmed the position of Paraguay as an ecotone between the Chaco, the Paraná and the southern Brazilian cerrados ecosystems. Many of the species growing in the Paraguay-Paraná basin are habitat generalists seen as having wide ecological amplitudes (OLIVEIRA-FILHO & RATTER, 1995). Using the terminology of MUELLER (1973) the generalist species are polycentric (related to two, three or four dispersal centres) whereas others are monocentric (belonging to either the Paraná or to the Chaco area). However, uncertainty remains concerning the spatial organisation of these communities within Paraguay at the country scale. It is now widely accepted that an ecological process may have different effects at different spatial scales (LEVIN, 1992). This is a significant point because Paraguay is at the crossroads of the four dispersal centres identified in South America.

We used herbarium specimens collected in Paraguay to emphasize the geographical zonation of tree species. This study had two objectives: (i) to determine whether the Paraguayan ecotone consisted of one or several gradients with continuous changes of the vegetation composition, or if it was composed of several homogenous communities that were distinct; (ii) to determine whether the analysis of herbarium data was congruent with other findings in the literature, i.e. those derived from the analysis of more "traditional" data.

Material and methods

We gathered data from databased specimens of the Botanical Garden of Geneva and Missouri Botanical Garden. Each herbarium specimen is a species occurrence which is characterized by three variables: the longitude, the latitude, and the species to which it belongs. There are more than 500 tree species in Paraguay and the databased herbarium specimens may have been collected for a wide variety of reasons (conservation, systematics, etc.). All species may not have the same value for the collectors of samples, and this value may vary depending on the context of collection. The databases thus contain very heterogeneous data. It is likely that the probability of sampling an occurrence at a given place varies between species which violates the most important assumption of the analyses used here (see CALENGE & al., 2005). For this reason we defined a particular class of tree species which we termed "ballast species". This class included only the most common tree species encountered in Paraguay. We used our knowledge of the region to select the species belonging to this class (RAMELLA & SPICHIGER, 1989). For example, *Balfourodendron riedelianum*, a common species along the banks of the Paraná and Uruguay rivers, and one that is also exploited for commercial timber was considered to be a ballast species. By focusing only on these ballast species we restricted the analyses to a more homogeneous set of species, based on their sampling probability. Even if there is no definitive means to ensure that the hypothesis of equal sampling probability between species is correct we have assumed that it is so in this paper. The commonness of these species also ensured that the spatial distribution of their occurrences approximately covered the geographic range of the species. At least 5 occurrences were required for each species for them to be included in the analysis.

The final database contained 669 occurrences belonging to 32 species (full species names and name abbreviations are in Table 1). We analysed the geographical zonation of these tree species using Discriminant Analysis on Eigenvectors of Neighbourhood Operator (DAENO). The principle of this analysis and the reasons for choosing it are detailed in CALENGE & al., (2005). This method is a discriminant analysis of the species according to synthetic variables describing the spatial position of occurrences within the study area. These synthetic variables are derived from a network of neighbouring relationships relating the occurrences to each other. We used the Delaunay triangulation algorithm to generate this network (RENKA, 1996; CALENGE & al., 2005). DAENO assigns a score to each occurrence such that two species with a similar distribution have a similar average score, and two species with very different distributions have very different average scores. A typology of the species and of the area can then be derived.

The area around Asunción, the capital of Paraguay, was more extensively sampled than any other part of the country (Fig. 1B). We stress here that the non-uniform sampling effort in our study area does not limit the use of the method. DAENO discriminates between tree species according to their spatial distribution. Even if sampling effort varies across the area the method is still valid provided that the sampling probability is the same for all species at any given point in the study area (CALENGE & al., 2005).

We tested the pertinence of this analysis using a randomisation test. This test was performed by comparing the eigenvalues of DAENO of the actual data set with the eigenvalues of DAENO of simulated data sets of random distributions of the selected ballast species within Paraguay. These data sets were generated by randomly permuting the levels of the factor species while keeping the table of eigenvectors of the neighbourhood operator fixed.

All analyses were carried out using the R software (IHAKA & GENTLEMAN, 1996). We used the packages “ade4” and “adehabitat” for the analyses, and “tripack” for the computation of neighbouring relationships. These three programs are freely available (see ade-4 package for R software, downloadable at <http://cran.r-project.org>).

Results

Spatial structures

We performed a discriminant analysis on the first 12 eigenvectors of the neighbourhood operator by the factor species. This analysis (which is a DAENO) produced two highly significant factors ($p < 0.001$). The percentage of geographical variation explained by the species was 66% and 30% for the first and second factorial axes respectively. This percentage sharply decreased for the subsequent factors (21%, 19% and 17% for the third, fourth and fifth axes respectively). We therefore restricted our interpretation to the first two factors. The distribution of the species occurrences on the first factor is markedly bimodal (Fig. 2A). The low density of occurrences with a score of about -0.5 indicates the presence of a “frontier” separating two distinct communities. The Chaquean biome, on the negative side, is opposite to the biome of the southeast of Paraguay (Paraná) which is on the positive side (Fig. 2B). The boundary between these two areas is formed by Río Paraguay. The strong difference between the two areas invalidates the hypothesis of a gradient in vegetation composition. The difference between the Chaco (western Paraguay) and the Paraná (eastern Paraguay) is the main vegetation structure revealed by the data and should not be ignored in the interpretation of the second factor. We interpreted the meaning of the second factor, while simultaneously taking into account the strong difference identified by the first factor, by studying the distribution of the points on the first factorial plane (plane F1-F2, Fig. 3).

The occurrences are not homogeneously distributed on this plane, and clusters of points can be identified. These clusters correspond to several communities in the two main biomes. We visually defined a typology of these occurrences according to their position on the first factorial

plane (plane F1-F2, Fig. 3) to make the subsequent interpretation of patterns easier. Tree occurrences have been categorized into six major types: three Chaquean types, labelled A0, A1 and A2, and three Paranean types, labelled B0, B1, and B2. Each type is a community characterized by a rather homogeneous floristic composition (except the group B0, see below), and is geographically well-delimited (Fig. 4A). Two points are worth noting concerning the definition of these communities. Firstly, community B0 seems to be formed of two parallel structures. This is an artefact of the strong sampling effort around Asuncion (Fig. 1B). The lower part is exclusively made up of these occurrences and the upper part is composed of the rest of the area covered by this group. We grouped these two parts together to form a single unit. Secondly, the definition of the communities was problematic for a small isolated group of occurrences (emphasized by an arrow on Fig. 3A). This group corresponded to a small number of occurrences located at the extreme North of the eastern part of Paraguay. From their position on the factorial plane, it was not clear whether this group should be included in community B1 or B2, or even if a new community (e.g. "B3") should be defined. Several biological arguments led us to assign these occurrences to community B2. These occurrences were from specimens that had been collected from an area characterized by a high frequency of cerrados species (pers. obs.). Because community B2 was mainly characterized by a mixture of cerrados and Paranean species (see below) we considered that this community should include the outlying group of occurrences.

Note that the shape of the distribution of points on the first factorial plane should not be confused with the classical arch or horseshoe effect (HILL & GAUCH, 1980). The arch effect is the result of long gradients in vegetation composition and is characterized by a homogeneous cloud of points distributed in a U-shape on the factorial plane. We proved that the variations in vegetation composition were not homogeneous: a clear frontier exists between two major kinds of vegetation. This is evident from the histogram of the occurrence scores on the first factor of the analysis (bimodal distribution, Fig. 2A), from the distribution of points on the factorial plane (very clustered occurrence pattern, Fig. 3A), and from the point of view of the vegetation composition (Fig. 4B). All these arguments strengthen the hypothesis that the species are distributed between several distinct communities and not along homogeneous gradients.

Floristic composition of the structures

The Chaco and the Paraná areas are clearly separated based on their floristic composition (Fig. 4). Most of the tree species studied are either exclusively Chaquean or exclusively Paranean but a few, such as *Jacaranda cuspidifolia*, *Astronium urundeuva*, or *Calycophyllum multiflorum*, are encountered in both regions. The Paraná and the Chaco are each composed of three communities. The Chaquean communities were labelled A0, A1, and A2, and the Paranean communities were labelled B0, B1, and B2 (Fig. 4).

Chaquean Flora

The community A2 (Fig. 4A) covers a huge geographical area. The restricted area occupied by A2 on the factorial plane (Fig. 3B) indicates that its floristic composition is very homogeneous, in other words the floristic composition does not vary spatially. This community is made up mainly of *Capparis retusa*, *Aspidosperma quebracho-blanco* and *Schinopsis quebracho-colorado*. The species *Capparis speciosa*, *Cercidium praecox*, *Anadenanthera colubrina* var. *cebil*, *Geoffroea striata* and *Tabebuia nodosa* are common in this community type (Fig. 4B). Other elements of the Chaquean flora are also encountered in this community type, although to a lesser extent. The community A1 is located in the centre of the Chaco (Fig. 4A). This assemblage contains the same species encountered in the community A2 but their relative frequencies are different. Thus, *Capparis retusa* and *Aspidosperma quebracho-blanco* are less common in this community (Fig. 4B). The most frequent species are *Schinopsis quebracho-colorado*, *Acacia praecox*, *Cercidium praecox* and *Capparis speciosa*. The Chaquean community, A0, is well-delimited

in both geographical space and on the factorial plane (Fig. 3B, 4A). Its species composition is very different from that of the two previously described communities. The most common species are *Schinopsis balansae*, *Acacia caven* and *Diplokeleba floribunda*. Other Chaquean species are also encountered, although to a lesser extent.

Paranean Flora

The type B0 represents the ecotone separating the Chaco (western Paraguay) and the Paraná (eastern Paraguay) (Fig. 4A). The frequencies of the two types of species are similar in this area. This assemblage covers a large area on the first factorial plane (Fig. 3B), indicating that the floristic composition is spatially heterogeneous. The even distribution of the occurrences on the factorial plane revealed the presence of a gradient, which forms the ecotone between the community A0 and B1. The areas close to the Chaco are richer in Chaquean species, and conversely the areas adjacent to the Paraná are dominated by Paranean species. The floristic diversity of this area is the highest in Paraguay. The community B1 occupies the largest part of eastern Paraguay (Fig. 4A). The small area covered by this community on the first factorial plane indicates that the floristic composition is spatially homogeneous (Fig. 3B). The main species encountered include *Nectandra megapotamica*, *Sorocea bonplandii*, *Balfourodendron riedelianum*, and to a lesser extent *Trichilia elegans*, *Chrysophyllum marginatum* and *Chrysophyllum gonocarpum* (Fig. 4B). Other species that are characteristic of the Paraná are also present, although they are less common (*Cochlospermum regium*, *Patagonula americana*, *Tabebuia nodosa*, etc.). The community B2 covers a small part of the Paraná (Fig. 4A), i.e. the northeastern part of the Paraná. It is characterized by a lower floristic richness (only 11 species), and by the frequent presence of *Cochlospermum regium*. Species typical of the Paraná are quite frequent in this area, especially *Nectandra megapotamica*, *Balfourodendron riedelianum* and *Sorocea bonplandii*. The small area covered by this community on the factorial plane (Fig. 3B) indicates a homogeneous spatial distribution of the species.

Discussion

The use of herbarium data allowed us to identify the main biogeographical structures in the complex Paraguayan transition area. To assess the efficiency of the use of herbarium data to identify the vegetation structures our results can be compared with those in existing literature. The Paraguayan vegetation does not change continuously from the East to West of Paraguay, instead it is structured into sharply defined communities. The analysis of tree species occurrences revealed six communities in Paraguay, which form the two main biomes separated by an ecotone. The Chaco is composed of three communities: (i) the typical xeromorphic forests of the Chaco at the extreme West (A2), (ii) the psammophilous vegetation with *Schinopsis quebracho-colorado* (A1) and (iii) the wet Chaco, on the West side of the Río Paraguay (A0). The Paraná is composed of two communities: the Paranean semi-deciduous forests (B1), and the forest-cerrados mosaic of northeastern Paraguay (B2). The Chaco and the Paraná formations are separated by an ecotone (B0), in the Paraguay-Paraná delta (eastern side of the Río Paraguay), where species of the two main communities are intermingled.

The Chaco (western bank of the Río Paraguay)

The Chaco is a biogeographical region that has been extensively studied (for reviews see RAMELLA & SPICHTER, 1989; SPICHTER & al., 1991; PRADO, 1993a; PRADO, 1993b) under a wide variety of names: the "Chacoan Province" (TAKHTAJAN, 1986), the "Provincia Chaqueña" (CABRERA & WILLINK, 1973), the "Pantanal and Chaco Phytochorium" (PRANCE, 1989) and the "Regionen des Chaco und seiner Randgebiete" (HUECK, 1966). The Andean uplift during the

Oligocene caused the formation of a synclinal which was first occupied by the sea. When the sea withdrew salty marine sediments were left behind and Andean deposits accumulated on them (PUTZER, 1962). This particular substrate is now colonized by a xeromorphic flora that extends from northwestern Argentina up to northwestern Paraguay and southeastern Bolivia. The Chaco biome is thus likely to have been a Tertiary or early-Pleistocenic refuge, although this hypothesis is challenged by MUELLER (1973) who considers the Chaquean biome to be much younger.

Our present results agree with the literature on the Chaco (SPICHIGER & al., 1991; SPICHIGER & al., 1995). The distribution of the Chaquean species shows two distinct patterns. The communities A1 and A2 correspond to the dry Chaco, also named Boreal Chaco (MORELLO, 1967; ESKUCHE, 1986). It is centred in the northwestern Chaco, running along the Andean Piedmont and reaching almost to the centre of Argentina. On the other hand, the wet Chaco (community A0) is a transition area corresponding to the drainage of the lower Paraguay river and to higher annual precipitations.

The dry Chaco (communities A1 and A2)

The Paraguayan xeromorphic forests and thickets belong to the Chaquean communities of the Gran Chaco (PRADO, 1993b). These communities have been highlighted at the extreme West of Paraguay in our study (see Fig. 4). They are a northern extension of the “Quebrachales” type of vegetation (LEWIS & PIRE, 1981), which has a large number of names in the literature: “Bosques altos abiertos” (MORELLO, 1967; ESKUCHE, 1986), “Distrito chaqueño occidental” (CABRERA, 1953; CABRERA, 1976), “Monte” (CÁRDENAS, 1945), “Sukkulenten Dornbusche” or “Monte Alto Formationen” (ESSER, 1982), and “Parque Chaqueño” or “Monte Occidental” (TORTORELLI, 1967). In Paraguay, the Chaquean vegetation and flora is closely associated with loamy or loamy-clayey, alkaline and salty soils which can suffer from either temporary aridity or temporary water logging (SPICHIGER & al., 1991).

DAENO distinguished two kinds of Chaquean dry forests. Firstly, the typical “White Quebrachales” (A2) that is characterized by the predominant *Aspidosperma quebracho-blanco*. This medium-sized tree is one of the dominant species of the dry Chaquean forest and of its successional stages (“Quebrachales de quebracho-blanco” *sensu* SPICHIGER & al., 1991). The centre of distribution for this species is the Argentina-Paraguay Chaco with an extension to the eastern drainage system of the Río Paraguay and southeast Bolivia. Besides the most common species in this formation, such as *Aspidosperma quebracho-blanco* or *Schinopsis quebracho-colorado*, a lot of smaller trees, spiny shrubs and succulent plants constitute the understory (*Ruprechtia triflora* Griseb., *Cercidium praecox*, *Capparis spp.*). According to SPICHIGER & al. (1991), other species that were not studied here are also characteristic of this understory vegetation (*Bougainvillea spp.*, *Zizyphus spp.*, *Cactaceae*, *Bromeliaceae*, etc.).

Secondly, located on the eastern side of the typical “White Quebrachales”, the community A1 corresponds to a more psammophilous forest, characterized by a high frequency of *Schinopsis quebracho-colorado* (“Quebrachal de coronillo”) and more or less the same understory species (Fig. 4B). According to MUÑOZ (1990), the “Quebrachal de coronillo” and the related thickets grow in the most xeric areas. Spiny thickets are found in the younger or impoverished stages of both the above-mentioned vegetation types. In the wettest areas, species more related to the wet Chaco are encountered (*Tabebuia nodosa*, *Prosopis spp.*, *Acacia spp.*). In the saltiest areas (“peladares”), a halophilous steppic vegetation with *Cactaceae*, *Amaranthaceae* and *Celastraceae* thrives (SPICHIGER & al., 1991).

Some generalist species are also encountered in the dry Chaco (*Astronium urundeuva*, *Maclura tinctoria*, etc., see Fig. 4). These species, related to the Paraná-São Francisco gradient and to the peri-Amazonian gradient (SPICHIGER & al., 2004), invade the dry Chaco in the areas where the substrate is suitable, mostly on rather well-drained and salt-less soils. Gallery-forests allow

the “extra-zonal” mesophilous species (*Astronium urundeuva*, *Maclura tinctoria*, *Diplokeleba floribunda*, *Calycophyllum multiflorum* and *Phyllostylon rhamnoides* (J. Poiss.) Taub.) to penetrate deeply into the Chaco area (OLIVEIRA-FILHO & RATTER, 1995). Extra-zonal mesophilous forests with *Anadenanthera colubrina* var. *cebil* and *Astronium urundeuva* grow on the hills and the low mountains (Cerro León and Cerro Cabrera). For the mesophilous generalists these hills, serranias and galleries act as barriers between the Paraná area and the Andean Piedmont, despite the fact that they are surrounded by xerophilous forests (SPICHIGER & al., 1991). Cerrado-related species (*Jacaranda cuspidifolia*, *Astronium fraxinifolium*) grow on top of the fossil sand dunes, serranias and cerros.

The wet Chaco (community A0)

The wet Chaco region is a transition area where many elements are intermingled: the dry Chaco trees, wet savannah species, mesophilous generalists, some scarce Paraná elements, and anthropogenous pan-American or cosmopolitan species (SPICHIGER & al., 1991; SPICHIGER & al., 1995). It is the southern limit of the Pantanal, which explains the use of the term “Chaco-Pantanal” for this region. This vegetation grows on the temporarily waterlogged soils of the flood plains of the Río Paraguay and Río Pilcomayo, and in the Paraná-Paraguay delta. The wet Chaco forests and the palm-savannahs form a forest-savannah mosaic landscape. The palm-savannahs occupy the part of the land flooded for 3 to 4 months of the year, whereas the Chaco forests grow on the higher more well-drained substrates (FIEBRIG & ROJAS, 1933). The forests growing in the Paraguayan wet Chaco are also called “xeromesophilous” forests (SPICHIGER & al., 1991), to distinguish them from the “xerophilous” forests of the dry Chaco. The species of the xeromesophilous forests are less frost-tolerant than those of the dry Chaco but they are more generalist. They grow on temporarily waterlogged basic and loamy soils as well on sandier and drier substrates. Our study indicates that *Schinopsis balansae*, the “quebracho-colorado”, is an important species of the wet Chaco forests (Fig. 4). It also occurs in community B0 of eastern Paraguay. A lot of generalist species (*Astronium urundeuva*, *Diplokeleba floribunda*, *Calycophyllum multiflorum*, *Phyllostylon rhamnoides*) are dominant trees, together with the Chaquean elements, in both the wet Chaco plateau forests and the gallery-forests. The wet Chaco is also an ecotone (SPICHIGER & al., 1995) between the Paraná area *sensu lato* and the dry Chaco, made up of a mosaic of forest patches intermingled with palm savannahs and marshes (see also SPICHIGER & al., 2004). Common savannah tree species, such as *Copernicia alba* Morong & Britton, were not well represented in the herbarium databases so we could not take them into account. In our analyses the presence of the marshy areas is indicated through the dominance of *Acacia caven*, and presence of the gregarious *Geoffroea decorticans* (“chañares”). The peri-Amazonian *Geoffroea spinosa* is also frequent in the wettest places of the dry Chaco, in the wet Chaco and on the eastern bank of the Río Paraguay. The wetness of this area combined with the closeness of the Paraná region may explain the presence of Paranean species, such as *Tabebuia heptaphylla*, in this area.

Eastern Paraguay (eastern bank of the Río Paraguay)

Eastern Paraguay corresponds to the area delimited by the Paraná and Paraguay rivers. This area is also named Paraguay-Paraná interfluve or Paraguayan Mesopotamy. It was originally covered by a tall semi-deciduous forest which has mostly been destroyed and replaced by pastures (SPICHIGER & al., 1995). This forest belongs to the “Misiones Nucleus” which is itself a fragment of the Residual Pleistocenic Seasonally Dry Forests (PRADO & GIBBS, 1993). The numerous authors that have worked on this area have given it a wide variety of names: the “Paraná Province” (TAKHTAJAN, 1986), the “Provincia Paranense” (CABRERA & WILLINK, 1973), the “Southern Brazil Phytochorium” (Prance, 1989), or the “Region des Ost- und Südbrasilianischen Wälder” (HUECK, 1966). The Paranean forests are spread over the Paraguayan-Upper Paranean-Upper Uruguayan basins (SPICHIGER & al., 1992; SPICHIGER & al., 1995).

The landscape of Eastern, Central and Northeastern Paraguay is made up of cerros and cordilleras, and of low undulations in other places. The soils are generally clayey in the Paraná drainage, sandier in the Paraguay drainage and rich in nutrients, as well as frequently hydromorphic, in the depressions. Three assemblages are highlighted by our analysis: the Paraná-Paraguay delta (B0); the Paranean semi-deciduous forests (B1); the forest-cerrados mosaic of northeastern Paraguay (B2).

The Paraná-Paraguay delta (community B0)

The Paraná-Paraguay delta ecotone spreads along the eastern bank of the Río Paraguay and across the Paraguay-Paraná delta. This area is a boundary between the Chaquean and the Paranean flora, and is characterized by very high species diversity. Thus, Chaquean elements such as *Schinopsis balansae*, *S. quebracho-colorado*, *Aspidosperma quebracho-blanco*, *Geoffroea decorticans*, *Acacia caven*, *A. praecox*, *Prosopis alba*, *P. nigra*, *Capparis retusa* or *Tabebuia nodosa* invade the eastern bank where they grow in association with Paraná-related species (*Trichilia elegans*, *Chrysophyllum gonocarpum*, *C. marginatum*, *Peltophorum dubium*, *Tabebuia heptaphylla*, *Astronium urundeuva*, *Sorocea bonplandii*, *Cedrela fissilis*, *Balfourodendron riedelianum*, etc.). Generalist species are also encountered there. Field observations indicate that these species grow along the gallery forests (*Calycophyllum multiflorum*, *Maclura tinctoria*, *Geoffroea spinosa*, etc.) and in the savannah patches (*Jacaranda cuspidifolia*, *Diplokeleba floribunda*, etc.). The species *Tabebuia heptaphylla*, together with *Astronium urundeuva* and *Chrysophyllum gonocarpum*, constitute the forest patches in the Paraguay-Paraná delta (ESKUCHE, 1982; SPICHIGER & al., 1992).

The Paraná forest (community B1)

The Paranean species constitute the Paranean semi-deciduous forest ("Floresta Ombrofila Mista" according to Brazilian authors). This forest is centred in the Upper Paranean-Upper Uruguayan basins. It extends from northeastern Argentina to southeastern Brazil and to the southern Planalto (Bolivia), along the Río Paraná and its tributaries. Even if some species show a much wider pattern of distribution, a lot of mesophilous species are strongly associated with the Paraná area (see Fig. 4B): *Cedrela fissilis*, *Balfourodendron riedelianum*, *Chrysophyllum gonocarpum*, *Chrysophyllum marginatum*, *Peltophorum dubium*, *Tabebuia heptaphylla*, *Astronium urundeuva*, *Xylopia aromatica* (Lam.) Mart., *Patagonula americana*, *Sorocea bonplandii* and *Nectandra megapotamica*. Due to the high frequency of *Lauraceae* species, these forests are called "Monte de Laurel", "Laurisilva", or "Parapiptadenia rigida-Nectandra saligna" forests (ESKUCHE, 1982; ESKUCHE, 1984). In Paraguay the *Lauraceae* - *Cedrela fissilis* - *Chrysophyllum gonocarpum* tall forests grow on the well-drained clayey soils and can be considered as the climax vegetation (SPICHIGER & al., 1992). Three vegetation types are usually distinguished in the Paranean forests (SPICHIGER & al., 1992): a typical aspect with *Balfourodendron riedelianum*; a riparian aspect with *Guarea kunthiana* A. Juss. and *Euterpe edulis* Mart.; and, a psammophilous aspect with *Heliopsis scabra* Benth. *Lauraceae* tall forests with *Luehea divaricata* Mart. and *Plinia rivularis* (Cambess.) A. D. Rotman are confined to the swampy substrates. We were unable to identify these associations since most of these species were not included in our study.

The forest-cerrado mosaic (Canendiyu, Concepcion and Amambay areas, community B2).

Although at the scale of our study this community seemed rather homogeneous at a smaller scale the savannahs and tall *Lauraceae* forests outline a mosaic (*pers. field obs.*). This finding again stresses the importance of the spatial scale in ecological studies (LEVIN, 1992). This area is an ecotone between the cerrados of the southern Brazilian and the Paranean flora where the above-mentioned Paranean elements are intermingled with cerrado-related species (*Cochlospermum regium*, *Jacaranda cuspidifolia*). Other species characteristic of the cerrados are found there, although they were not included in this study (*Pradosia brevipes* (Pierre) T. D. Penn., *Anacardium*

humile A. St.-Hil., *Andira laurifolia* Benth., and other geoxylic sub-shrubs *sensu* PENNINGTON, 1990). These species grow in the patches of cerrados or in the low forests where *Myrtaceae* are predominant: ecocline belts between tall forests and savannahs, invasive forest-islets surrounded by grasslands, gallery-forests fringes (SPICHIGER & al., 2002).

Conclusions on the Paraguayan transition area

When viewed on a large scale the flora of Paraguay appears as an ecotone between the Brazilian cerrados, the xeromorphic Chaquean forests and the semi-deciduous Paranean forests. The changes in vegetation composition between these different types appear continuous. However, this research has shown that when studied on a smaller scale a more complex structure emerges. The Paraguayan flora is made up of two main vegetation types: the Chaco and the Paraná. Between these two forest masses a wide transition area made up of a mosaic of forest-patches intermingled with palm-savannahs, cerrados (Brazilian savannahs), pastures and cultivated land is found (SPICHIGER & al., 1995). This mosaic of vegetation types also constitutes a small scale ecotone where floristic elements of distinct origins are converging or diverging (SPICHIGER & al., 1995). The strong heterogeneity emphasized in this study underlines the importance of the concept of scale in ecology (LEVIN, 1992). A study of the spatial distribution of tree species could be carried out at an even smaller scale, e.g. that of the wet Chaco (A0), and a new level of heterogeneity may then appear. In the Chaco area the generalist species, such as *Callycophyllum multiflorum*, which appear to be associated with the Chaquean communities in this study, only grow in riverine forests, on hills and on low mountains. This close association may be more evident in a study carried out in an area of several hectares. The relationship between scale and heterogeneity is a fundamental issue in community studies and should be fully understood to gain further insight into the functioning of any ecosystem.

Conclusion on the use of herbarium data in biogeographical studies

The study of geographical zonation of vegetation on a large scale is often problematic. This is mainly because the large areas involved make systematic sampling difficult. Such studies become even more complicated in tropical regions where access to remote areas is difficult. Although herbarium data do not have the same quality as systematically sampled specimens they do carry information on the spatial distribution of species. Many questions arise over how representative herbarium specimens are of the studied species. The samples, available through herbarium databases, have been collected in a wide variety of contexts by a large number of biologists. For example, the herbarium of Geneva was created 180 years ago and botanists working all over the World have contributed to the development of its plant collection. The sources of specimens are so varied that the detection of bias from the data is practically impossible. The bias can be supposed by drawing hypotheses on the usual behaviour of the biologists in the field.

In tropical regions the sampling effort is not spatially uniform because many areas are inaccessible to biologists. Studies relying on herbarium data have to acknowledge that the distribution of the species occurrences is the result of both the species distribution and of sampling intensity, which is often unknown. The statistical methods used to analyse this type of data must therefore take into account this characteristic of the data. In this study, we suppose that the variation in sampling intensity is the same for all species, even if sampling probability varies from one place to another. However, the hypothesis of equal sampling probability among species remains questionable for herbarium data. By choosing *a priori* a subset of species in the herbarium databases based on a criterion of commonness we reduced these probabilities. It is likely that a small residual variation in probability remains but, as noted above, there is no means to measure this variation.

Another possible source of bias arises when botanists tend to collect and label a specimen according to their own preconceived ideas of vegetation types. In this case any analysis will return results that reflect of the biologist's beliefs. However, because herbarium specimens are collected

by numerous biologists over a long time period and all the biologists working on a given area do not necessarily have the same concept of its vegetation structures this effect is somewhat reduced. The pooling of all samples from the herbarium databases achieves a mixture of all the interpretations although we do not know in what proportions each is present. In this case the analysis of herbarium data may give a model of the system summarizing the different interpretations. Although results derived from herbarium databases are not by themselves definitive proof of the validity of a particular concept of the organization of vegetation they are one source of information which can be compared to results from the literature.

In our study the results were in agreement with all previous findings. Herbarium data therefore provided additional information which helped to build a conceptual model of the spatial organisation of the vegetation in Paraguay. We think that it is a strong argument in favour of the use of herbarium data in biogeographical studies.

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APPENDIX

Table 1. – The number of occurrences for each species is given in the table below with and abbreviations used throughout this paper

Species name	Abbreviation	Number
<i>Acacia caven</i> (Molina) Molina	Aca.cav	34
<i>Acacia praecox</i> Griseb.	Aca.pra	25
<i>Anadenanthera colubrina</i> var. <i>cebil</i> (Griseb.) Altschul	Ana.col.ceb	8
<i>Aspidosperma quebracho-blanco</i> Schltld.	Asp.que	28
<i>Astronium fraxinifolium</i> Schott	Ast.fra	9
<i>Astronium urundeuva</i> (Allemão & M. Allemão) Engl.	Ast.uru	10
<i>Balfourodendron riedelianum</i> (Engl.) Engl.	Bal.rie	32
<i>Bulnesia sarmientoi</i> Griseb.	Bul.sar	9
<i>Calycophyllum multiflorum</i> Griseb.	Cal.mul	38
<i>Capparis retusa</i> Griseb.	Cap.ret	37
<i>Capparis speciosa</i> Griseb.	Cap.spe	13
<i>Cedrela fissilis</i> Vell.	Ced.fis	9
<i>Cercidium praecox</i> (Ruiz & Pav.) Harms	Cer.pra	16
<i>Chrysophyllum gonocarpum</i> (Mart. & Eichler) Engl.	Chr.gon	17
<i>Chrysophyllum marginatum</i> (Hook. & Arn.) Radlk.	Chr.mar	36
<i>Cochlospermum regium</i> (Schrank) Pilg.	Coc.reg	13
<i>Diplokeleba floribunda</i> N. E. Br.	Dip.flo	37
<i>Geoffroea decorticans</i> (Hook. & Arn.) Burkart	Geo.dec	9
<i>Geoffroea striata</i> (Willd.) Morong	Geo.str	11
<i>Jacaranda cuspidifolia</i> Mart.	Jac.cus	11
<i>Maclura tinctoria</i> (L.) Steud.	Mac.tin	20
<i>Nectandra megapotamica</i> (Spreng.) Mez	Nec.meg	44
<i>Patagonula americana</i> L.	Pat.ame	21
<i>Peltophorum dubium</i> (Spreng.) Taub.	Pel.dub	11
<i>Prosopis alba</i> Griseb.	Pro.alb	11
<i>Prosopis nigra</i> (Griseb.) Hieron.	Pro.nig	14
<i>Schinopsis balansae</i> Engl.	Sch.bal	35
<i>Schinopsis quebracho-colorado</i> (Schltld.) F. A. Barkley & T. Mey.	Sch.que	26
<i>Sorocea bonplandii</i> (Baill.) W. C. Burger, Lanj. & Wess. Boer	Sor.bon	27
<i>Tabebuia heptaphylla</i> (Vell.) Toledo	Tab.hep	18
<i>Tabebuia nodosa</i> (Griseb.) Griseb.	Tab.nod	19
<i>Trichilia elegans</i> A. Juss.	Tri.ele	21

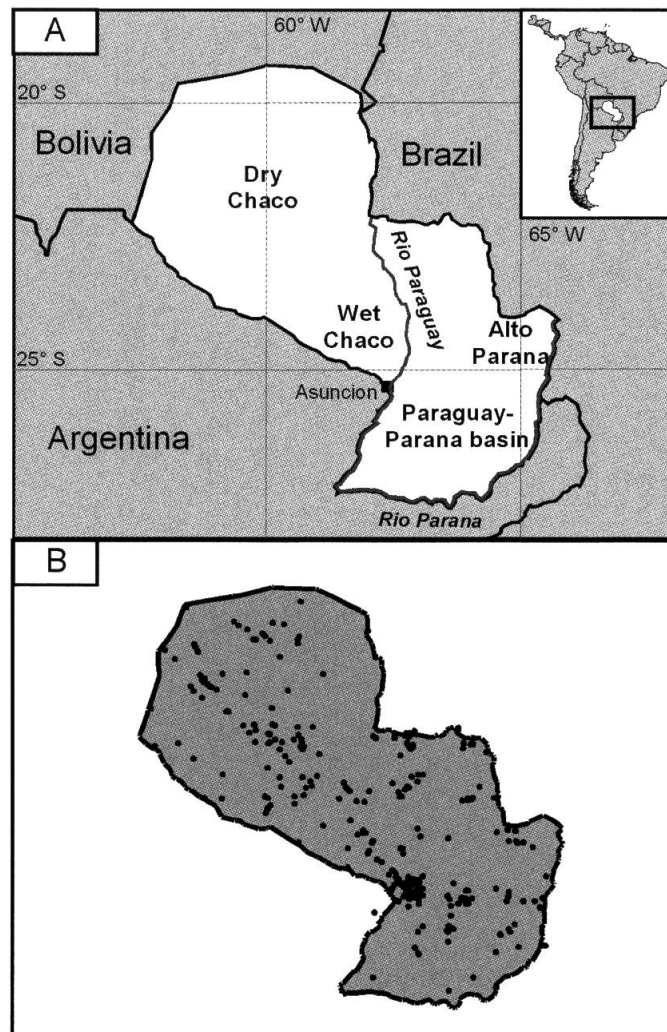


Fig. 1. – (A) Map of Paraguay; the main rivers and climatic areas are indicated. (B) Distribution of the 669 tree occurrences in Paraguay.

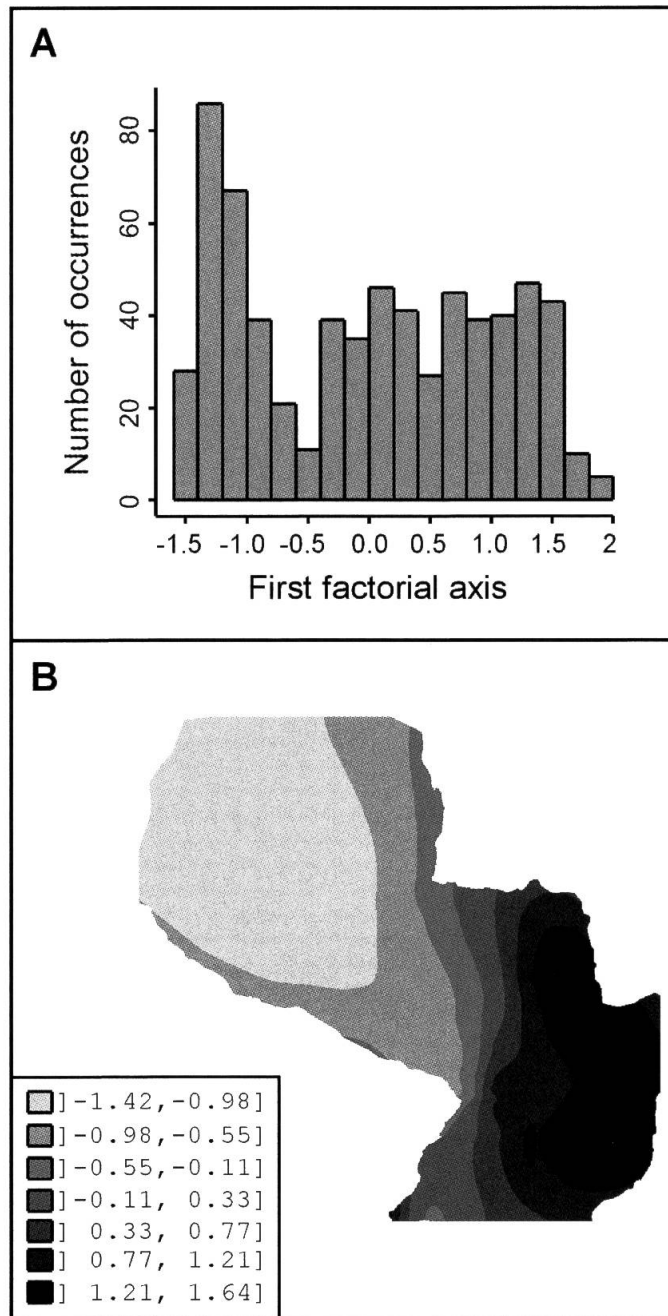


Fig. 2. – (A) Histogram of the distribution of tree occurrences on the first factor of the Discriminant Analysis on Eigenvectors of Neighbourhood Operator (DAENO) by the species. (B) Map of the distribution of the occurrence scores on the first factorial axis in Paraguay. The scores are smoothed using Lowess regression on 167 neighbours. The shades of grey reflect variation in occurrence scores (cf. insert).

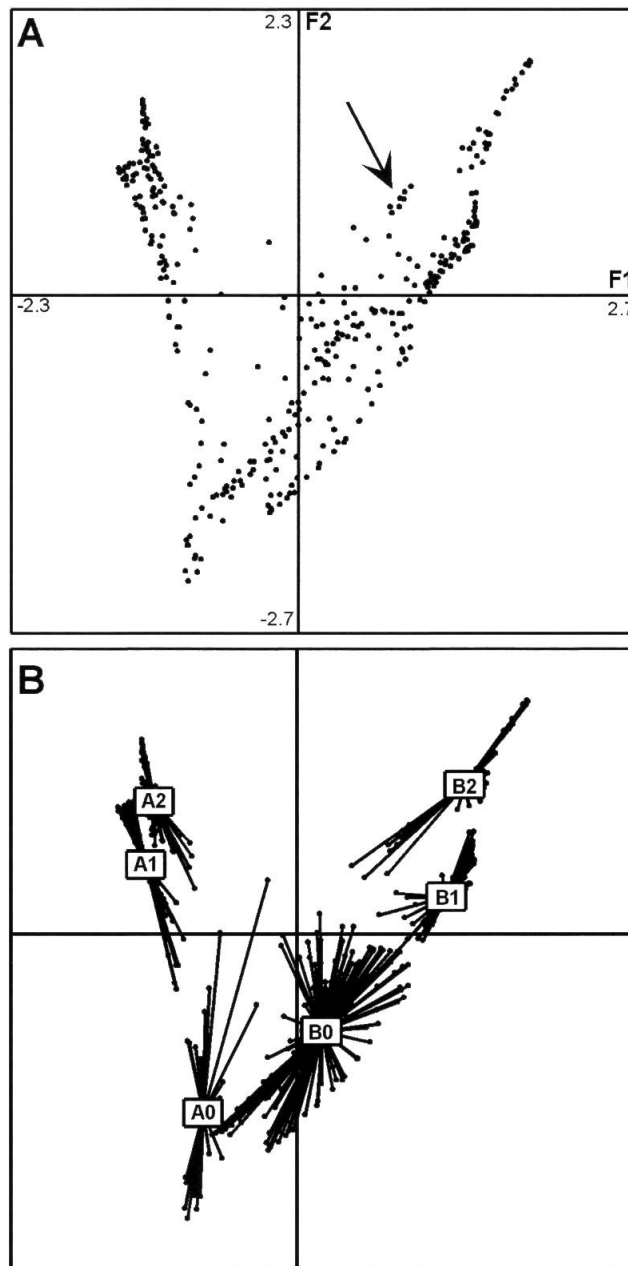


Fig. 3. – **(A)** Scatter plot of the occurrence scores on the F1-F2 factorial plane of the Discriminant Analysis on Eigenvectors of Neighbourhood Operator (DAENO) by the species. The arrow indicates the group of occurrences for which the definition of groups was problematic (see text). **(B)** Typology of the occurrences on the first factorial plane. Six groups of occurrences with a rather homogeneous floristic composition have been defined visually. Each group is identified by a star connecting all the occurrences of the group to its barycentre on the factorial plane.

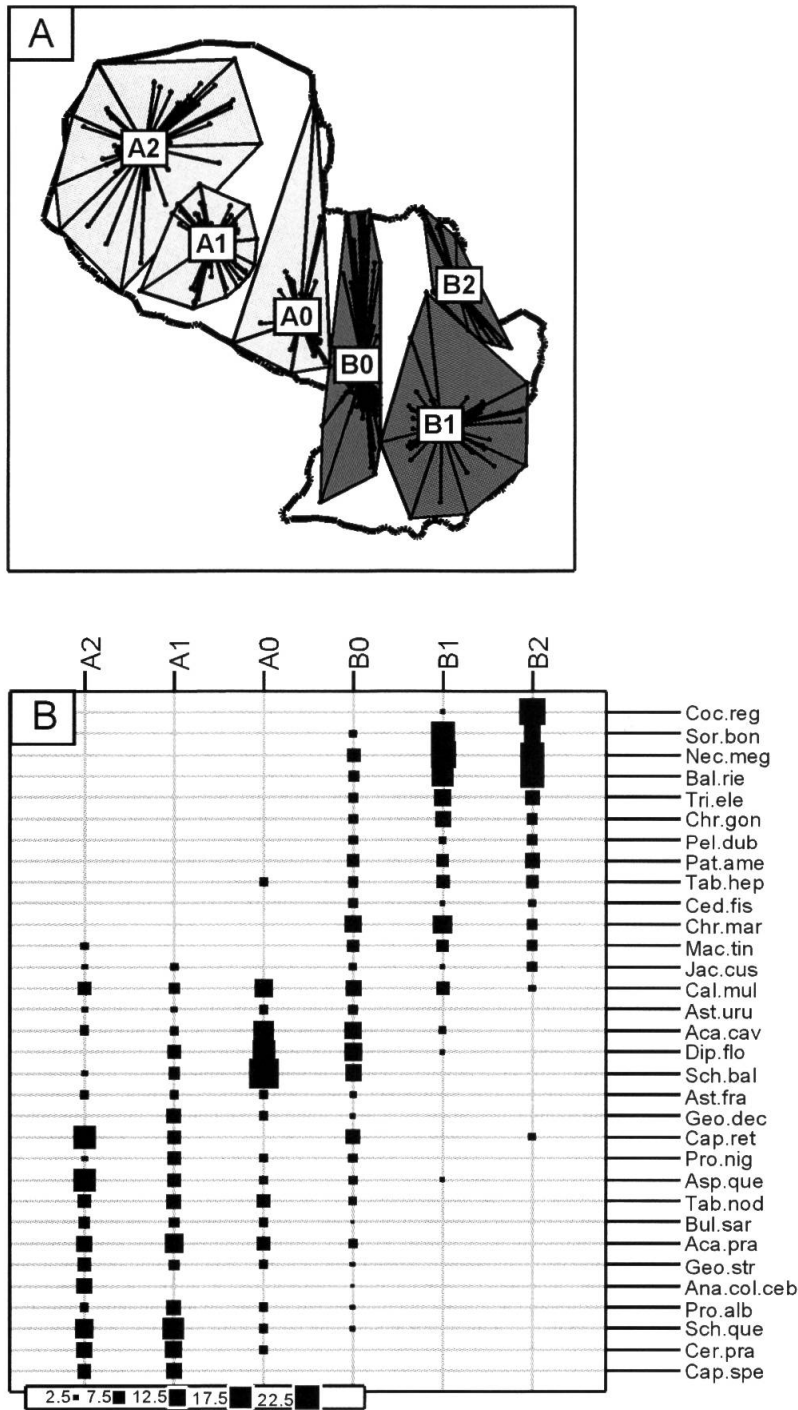


Fig. 4. – (A) Geographical position of the six groups of occurrences defined in Fig. 3. Each group is identified by a star connecting the occurrences to the geographical barycentre of the group. The contour polygon of each group is also displayed (light grey polygons correspond to the Chaquean communities, and dark grey polygons indicate the Paranean communities). (B) Species composition of the six groups of occurrences defined in Fig. 3. The importance of a species in a given community is represented by a black square. The square size is proportional to the percentage of the total number of occurrences of the community that is represented by this species (cf. insert).

