Chapter 5. The Gran Pantanal

> The low, swampy country in which Corumbá is situated is a paradise for snakes. Big ones–luckily rare–were known to seize cattle at times, and even to pick men out of canoes at night. ..... Their weird cries could be heard at night, which is their normal feeding time.
> - Col. Percy Fawcett, Lost Trails, Lost Cities

Introduction

The Gran Pantanal de Mato Grosso is widely recognized as the world's largest wetland (Heckman 1998; Por 1995). For several centuries, it was thought that the Pantanal was an enormous lake, the 'Eupana Lacus', situated in the center of South America (Por 1995). This lake was at various times said to be the source of the Paraguay, São Francisco and Amazon rivers, and was depicted on European maps as early as 1559 (Por 1995). Although the name Gran Pantanal (literally "Great Swamp") evokes an image of a strictly marshy habitat, the system is markedly heterogeneous, consisting of a matrix of permanently and seasonally flooded habitats, interspersed by uplands and cut through by stream and river channels (Prance and Schaller 1982). Due in part to its complex morphology and large seasonal fluctuations in the extent of inundated territory, estimates of the Pantanal's area vary widely, ranging from 80,000 km2 (Bonetto 1975; van der Beck et al. 1996) to 250,000 km2 (Tundisi and Matsumura-Tundisi 1985). Recent estimates derived from the analysis of remotely sensed images place the area at 130,000 to 140,000 km2 (Hamilton et al. 1996).

The Pantanal is contiguous with a number of major vegetation types: the evergreen Amazonian forests to the north and northwest, the dry forest of the Chaco to the west and southwest and, the Brazilian Cerrado to the east (Ponce and Cunha 1993). These influences, in combination with the high habitat heterogeneity, have resulted in the Pantanal possessing a rich flora (Prance and Schaller 1982; Ponce and Cunha 1993).

Precipitation varies throughout the Pantanal, generally decreasing from north (1250 mm yr-1) to south (1100 mm yr-1) (Junk and Da Silva 1995). The region's annual hydrological deficit (i.e., net evaporative loss) is said to be about 300 mm (Por 1995). Thus, the Pantanal may be "the most important window of evaporative freshwater loss of the globe"(Por 1995, p. 19). Although reliable meteorological data are scarce for most parts of Bolivia, precipitation data were available for the town of Puerto Suárez in the Bolivian Pantanal. During 1949 to 1993, annual precipitation ranged from 642 to 1558 mm, with an average of 1077 mm (Servicio Nacional de Meteorología e Hidrología, La Paz). Average annual temperature is ca. 25ºC, with maximum temperatures reaching 40ºC and minimums approaching 0ºC (Junk and Da Silva 1995; Por 1995).

The Pantanal experiences a well defined wet-and-dry climate, with four distinct stages (Prado et al. 1994; Heckman 1998). Using the colloquial Portuguese names, Heckman (1994) elucidated these stages as follows: 1) enchente, the period of flooding associated with the beginning of the rainy season; 2) cheia, the high water period, which begins approximately 3-4 months after the onset of the rainy season and is maintained by daily rains; 3) vazante, the transition to the dry season during which time water levels drop rapidly and rainfall is diminished, but not completely ceased; and, 4) seca, the dry season. During the latter, many formerly inundated areas dry out completely and formerly fast-flowing, lotic systems are converted to lentic systems (Heckman 1994). The magnitude of seasonal changes in water level is on the order of 2-5 m (Junk and Da Silva 1995), which is significantly lower than the 5-10 m (maximum 15 m) annual fluctuations reported for the Central Amazon floodplain (Sioli 1984). Nevertheless, Prado et al. (1994) noted that in their northern Pantanal study area a fluctuation of less than a meter could correspond to a six month difference in the period of inundation.

Although the largest portion of the Gran Pantanal lies within Brazilian territory, the western limits of the system extend into Bolivia and Paraguay. Although substantially smaller, the Bolivian portion is said to be much better conserved than the Brazilian, with a higher concentration of wildlife (Halloy 1997). As with the uncertainty regarding the actual size of the Pantanal, the percentage of the system situated outside of Brazil is not precisely known, but it is clear that the Bolivian and Paraguayan portions have most often been substantially underestimated. Most likely, the extra-Brazilian portion of the Pantanal lies within the range of the estimates provided by Por (1995), who estimated that the Bolivian and Paraguayan portions accounted for 10% of the system's total area, whereas Halloy (1997) estimated that the Bolivian portion alone accounted for about 10% of the total area.

Aside from uncertainties regarding the size of the Pantanal, some confusion concerning the location of the system also exists. For example, in one recent report (Heckman 1998) the foothills of the Andes, which begin approximately 500 km to the west, were said to form the Pantanal's western border of the Pantanal. Similarly, van de Beck et al. (1996) listed the Andean foothills as a source of fluvial inputs to the Pantanal.

The first botanical collections from the Pantanal are said to have been those of Alexandre Rodriguez Ferreira in 1790 (Por 1995). With the notable exception of the work of F. C. Hoehne in the Pantanal in the middle part of this century, however, it is only in fairly recent times that any concentrated scientific investigations have taken place in this region. In a review of the status of socioeconomic and scientific knowledge of the Pantanal, Cadavid-García (1992, cited in Por 1995) noted that at least 820 publications dealing with the Pantanal had been published. Of these, approximately 85% were technical reports and 316 were said to pertain to the field of botany (Por 1995). Nevertheless, there appear to be have been relatively few studies of the Pantanal's wetland vegetation.

Prance and Schaller (1982) described the terrestrial and wetland plant communities of the Brazilian Pantanal in the area around Laguna La Gaiba. In contrast to their investigations of the terrestrial habitats, no phytosociological studies were undertaken in the wetland habitats. Nevertheless, the authors collected extensively in the wetlands and presented descriptions of the dominant vegetation formations of these habitats. Although this investigation was listed as a "preliminary study", it remains one of the more frequently cited accounts of the Pantanal's flora. Recent limnological studies were conducted in the Pantanal by Stephen Hamilton and associates (Hamilton, Sippel, and Melack 1995, 1996; Hamilton et al. 1997). Although these studies focused on characterizing the water's physicochemical properties and their effects on the aquatic biota, they also briefly described the most commonly encountered plant communities. Charles Heckman, Anajde do Prado and associates conducted a series of limnological investigations of the Gran Pantanal (Prado et al. 1994; Heckman 1994; 1998). Some of the most comprehensive studies of the Pantanal's vegetation are those of Vali and Arnildo Pott and colleagues (Pott et al. 1986; Pott et al. 1989; Pott et al. 1992; A. Pott and V. Pott 1997; V.

Pott and A. Pott 1997). The authors have worked extensively in both the terrestrial and inundated habitats of the Pantanal since the mid-1980's and their work has frequently served as a critical resource for other scientists working in the region.

In comparison with investigations in Brazilian territory, a minute amount of research has been carried out in the Bolivian portion of the Pantanal. Frey (1995) conducted an informal survey of the aquatic flora of Laguna Cáceres, one of the sites included in my research, but his investigations focused primarily on the flora of the *Ipomoeaeta* associations (communities dominated by *Ipomoea carnata* subsp. *fistulosa*). As part of the proposal for the creation of two “Protected Areas” within the Bolivian Pantanal (Áreas Protegidas Pantanal de Otuquis y San Matías) researchers from the Universidad Autónomo Gabriel Moreno conducted a study of the vegetation of this region (Halloy 1997). The investigators compared the floristic diversity of the various vegetation types in the region and attempted to identify and list predominant aquatic communities. Sampling in wetland habitats, however, was limited to twenty 1 m2 quadrats; hence sample size, as well as the total area sampled, were clearly insufficient to gain a representative sample of the wetland vegetation. As part of another study of the proposed Protected Areas, Navarro (1992) conducted investigations of Laguna Cáceres and the area around Puerto Suárez. Navarro listed the dominant associations of the terrestrial and wetland habitats; however, sampling at Laguna Cáceres was apparently limited to a single visit and no voucher specimens were cited.

In the present study, a botanical survey of the large lakes of the Bolivian portion of the Gran Pantanal was undertaken during July 1998. Fieldwork was conducted during a joint expedition with researchers from the Museo de Historia Natural “Noel Kempff Mercado” (Santa Cruz, Bolivia), as part of efforts to gain an understanding of the biota of the two aforementioned proposed protected areas (now designated as Parque Nacional Otuquis and the Área de Manejo Integrado San Matías). I previously (July 1997) conducted some preliminary investigations of the aquatic flora of Laguna Cáceres. Data from this earlier visit were used to augment findings form the 1998 fieldwork.

My primary objectives were four-fold as follows: 1) to characterize and describe representative aquatic and wetland plant communities in the study sites; 2) to determine the range of plant species' diversity in these systems; 3) to prepare a preliminary checklist of species associated with the large lakes of the Bolivian Pantanal; and, 4) to examine the similarities of the aquatic flora of these systems to other regions in lowland South America. To these ends, the vegetation of the Bolivian Pantanal lakes is listed and described, and comparisons of floristic similarity and diversity are made among the study sites. Regional-scale floristic comparisons are made among the wetland flora of the Gran Pantanal (combined Bolivian and Brazilian portions), plus two lowland Bolivian regions and lowland regions in Argentina, Brazil, and Peru.

In light of the tremendous heterogeneity of the Pantanal and the seasonal changes in species composition and diversity which accompany the different hydrologic seasons, Heckman (1998) cautioned that any attempt to characterize the Pantanal based on investigations of a single habitat type, or from a single hydrological period, would be equivalent to the characterizations of the elephant produced by the blind men in Aesop's well-known fable. My field research in the Bolivian Pantanal was conducted primarily in lacustrine systems; hence it should not be considered as representative of the entire regional wetland flora. Still, although Por (1995, p. 29) noted that "more than anything else, the Pantanal is a land of lakes", there appear to have been few other studies that have focused on the region's lacustrine flora.

Materials and Methods

The Study Area

Five wetland systems (four large lakes and one riparian wetland) were established as study sites (Table 5-1; Figure 5-1), with my field research being restricted almost entirely to these systems. Descriptions of the study sites are presented in Appendix A.

Table 5-1. Study sites in the Bolivian Gran Pantanal region, with elevation, approximate area of the system, and approximate location.

System	Elevation (m)	Approximate Area (ha)	Approximate Location
Laguna Uberaba	90	30,000	57°44'W 17°34'S
Laguna La Gaiba	90	10,500	57°46'W 17°48'S
Laguna Mandioré	90	25,000	57°34'W 18°17'S
Laguna Cáceres	90	3500	57°46'W 18°57'S
Puesto Gonzalo	90	2	57°47"W 17°40'S

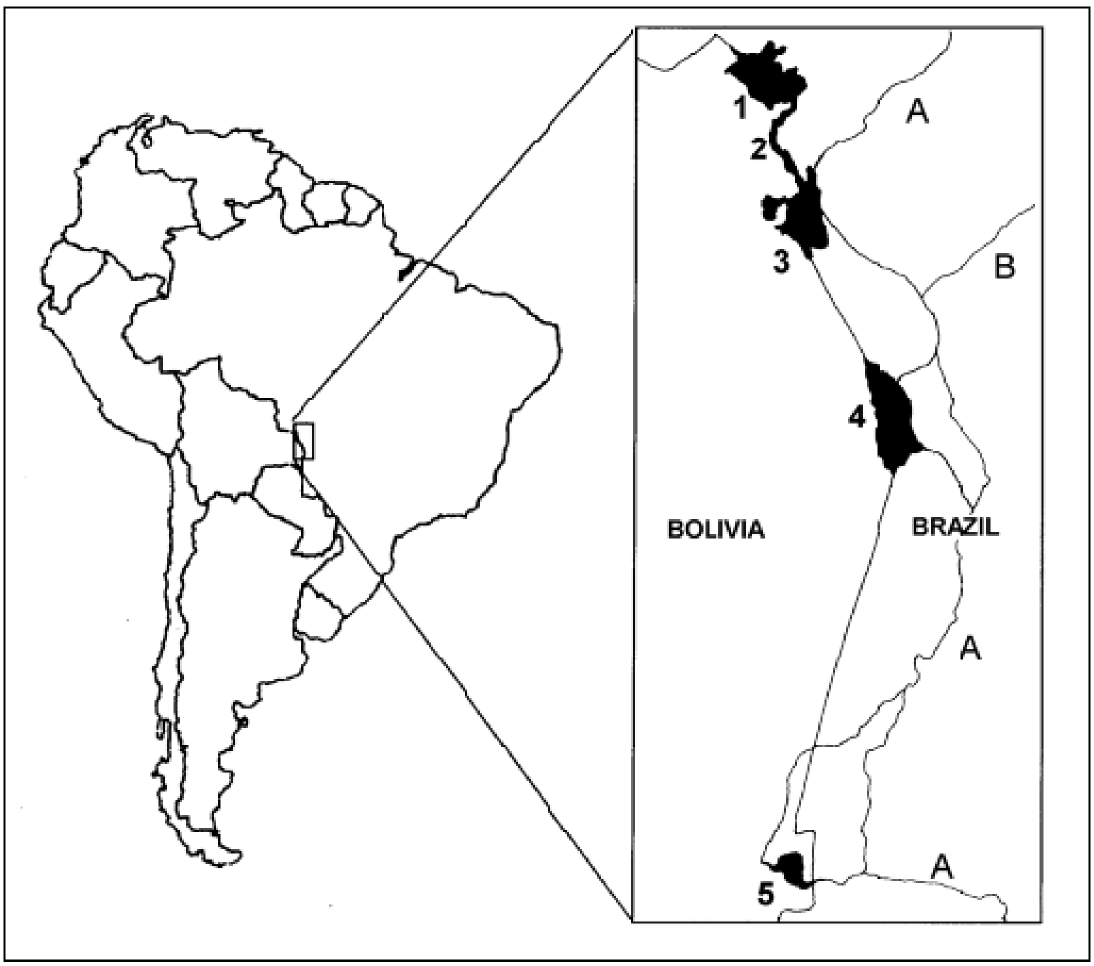

Figure 5-1. South America, with an inset of the study sites from the Bolivian Gran Pantanal. Study sites: 1. Laguna Uberaba. 2. Puesto Gonzalo. 3. Laguna La Gaiba. 4. Laguna Mandioré. 5. Laguna Cáceres. Rivers: A. Río Paraguay. B. Río Cuiaba.

Vegetation Sampling

Sampling focused on assembling comprehensive site floras. Ideally, all study sites would have been completely surveyed; however, with the exception of Puesto Gonzalo, the sites were too large for this approach. Therefore, sampling incorporated the identification of distinct communities and habitats (see Chapter 2), with surveying focused in these areas.

Floristic Comparisons

Floristic comparisons were analyzed at two scales: 1) between study sites; and, 2) between the Gran Pantanal and selected regions in the Neotropics ("macroregional scale" sensu McLaughlin 1994). Checklists for the Pantanal study sites were compiled primarily from field research; however, wetland species noted for Laguna Cáceres by Frey (1995), but which I hadn't observed in this system, were added to this system's checklist.

Regional-scale comparisons were made among the Gran Pantanal wetland flora plus two regions in lowland Bolivia (the Chiquitanía and White-water Floodplain regions), the Río Paraná Delta region (Argentina), Central Amazonia (Brazil), and Lowland Amazonian Peru. For these comparisons, the wetland flora from the Bolivian and Brazilian portions of the Gran Pantanal were combined to create a single OGU. This was necessary because the region's wetland flora was undoubtedly under-represented in the checklist assembled from just the five Bolivian study sites. Descriptions of the extra-Bolivian OGUs and the sources used to compile OGU floras are presented in Appendix B, whereas Appendix C summarizes the Bolivian OGUs and the sources used to compile OGU floras.

Data Analysis

Degrees of floristic similarity among OGUs were analyzed using Sørensen's Index (Magurran 1988), Detrended Correspondence Analysis (DCA), and "Frequency Analysis", as per Chapter 2. Frequency Analysis was not conducted among all OGUs; rather it was restricted to the distribution of species between the Gran Pantanal wetland flora and the other OGUs.

Results

Vegetation Description

A total of 178 species, in 50 families and 123 genera, were identified as being associated with aquatic habitats in the five study sites (Appendix H). The most frequently encountered families were the Fabaceae (21 spp./14 genera), Poaceae (18 spp./13 genera), Cyperaceae (13 spp./7 genera), and Asteraceae (11 spp./10 genera). *Ludwigia* (8 species) was the best-represented genus. The Polygonaceae (4 species/3 genera) was well-represented at the generic level. However, the genus *Polygonum*, which frequently can have 4-5 species in a single system in other areas of the Bolivian lowlands, was surprisingly poorly represented, with three of the five sites having a single species, and two sites with only two species.

Biodiversity

The number of species encountered at the individual sites varied considerably, ranging from 61-124 species in lacustrine sites (Table 5-2). Puesto Gonzalo, the sole riverine study site, was poorer (38 spp.) than any of the lacustrine systems. Diversity in the richest system, Laguna Cáceres (124 spp.), was clearly enhanced by the presence of a greater variety of habitats than were present in the other systems, as well as by the addition of a number of species that I did not encounter but which were observed by Frey (1995). Furthermore, the species list for Laguna Cáceres was augmented by collections from my visit during the previous year, at which time I encountered a number of species that were not observed in my subsequent visit. Additionally, the initial visit allowed me to familiarize myself with the system, so that I was better able to identify potentially diverse areas.

At the regional level, OGU wetland floras ranged from 255-541 species (Table 5-3), with a mean of 406.2 species. The Gran Pantanal (451 spp.) was the third most speciose region, trailing the Chiquitanía (541 spp.) and the White-water Floodplain (464 spp.). The Central Amazonian region possessed the fewest species (255 spp).

Table 5-2. Comparison of richness and floristic similarity (Sørensen's Index) between study sites. Numbers in bold along the main diagonal indicate the number of wetland species noted for each OGU. The numbers above the main diagonal indicate the number of wetland species shared by both OGUs. Numbers below the main diagonal indicate the percent floristic similarity between OGUs.

	Laguna Cáceres	Laguna Uberaba	Laguna La Gaiba	Laguna Mandioré	Puesto Gonzalo
Laguna Cáceres	**124**	44	36	44	32
Laguna Uberaba	46.3	**66**	30	26	21
Laguna La Gaiba	38.9	47.2	**61**	36	24
Laguna Mandioré	47.1	40.3	58.1	**63**	20
Puesto Gonzalo	39.5	40.4	48.5	39.6	**38**

Table 5-3. Comparison of richness and floristic similarity (Sørensen's Index) among the OGUs. Numbers in bold along the main diagonal indicate the number of wetland species noted for each OGU. The numbers above the main diagonal indicate the number of wetland species shared by both OGUs. Numbers below the main diagonal indicate the percent floristic similarity between OGUs. OGUs” GP - Gran Pantanal (combined Bolivian and Brazilian portions); CQ - Chiquitanía; WW - White-water Floodplain; RP - Río Paraná Delta; CA - Central Amazonia; LP - Lowland Amazonian Peru.

	GP	CQ	WW	RP	CA	LP
GP	**451**	277	251	104	127	184
CQ	55.8	**541**	325	82	146	244
WW	54.9	64.7	**464**	76	152	232
RP	27.8	19.6	20.0	**297**	51	79
CA	36.0	36.7	42.3	18.5	**255**	166
LP	41.9	50.4	52.0	21.8	48.6	**429**

Floristic Similarities

At the site-level, floristic similarities (Sørensen’s Index) among all of the Bolivian Pantanal systems were relatively high, ranging from 39-59% (Table 5-2). Even the Puesto Gonzalo site demonstrated strong floristic similarities to the lacustrine study sites (39.5-48.5%). These strong similarities were unexpected because this site, which was composed of a side channel of the Río Pedro I, constituted a significantly different habitat from the other systems. A close floristic association among the Gran Pantanal study sites was substantiated by an ordination (by Detrended Correspondence Analysis) of the 46 Bolivian study sites (Figure 5-2), with all five systems being closely grouped in ordination space.

At the regional level, the Gran Pantanal flora (combined Bolivian and Brazilian portions) showed the least floristic similarity (Sørensen’s Index) to the Río Paraná Delta region (27.8%, Table 5-3). Nevertheless, this was the strongest relationship for the Río Paraná Delta region, as floristic affinities between this region and the remaining OGUs were consistently low, ranging from 18.5-21.8%. The Gran Pantanal flora demonstrated the strongest floristic affinities to the Chiquitanía (55.8%) and White-water Floodplain regions (54.9%).

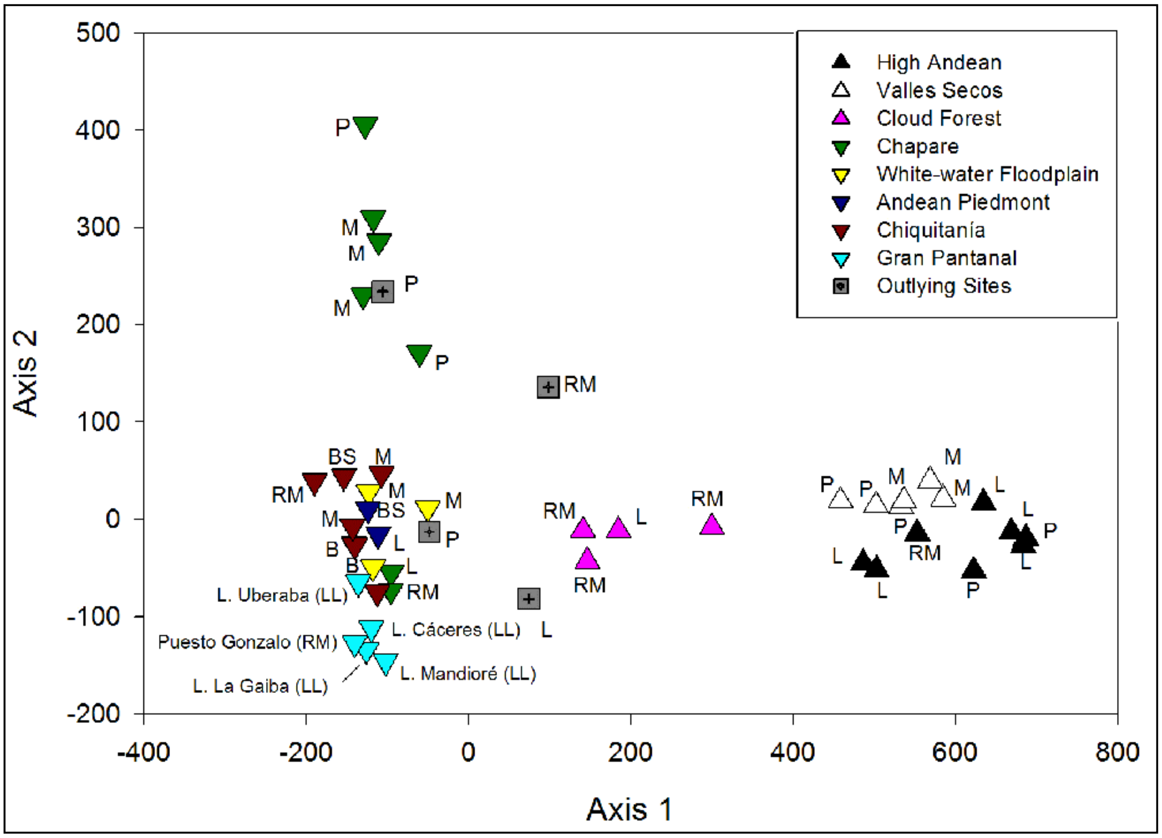

Figure 5-2. Ordination by Detrended Correspondence Analysis (DCA) of the 46 Bolivian study sites. The five study sites from the Bolivian Gran Pantanal are identified by name. Key to wetland types: B- bahía; BS - basin swamp; L - small lake (< 500 ha); LL - large lake (> 500 ha); M - marsh; P - pond; RM - riparian marsh.

Ordination of the OGU's by Detrended Correspondence Analysis (Figure 5-3) produced a plot that, for the most part, corresponded well with floristic similarities as expressed by Sørensen's Index (Figure 5-3). The Río Paraná Delta region formed one of the first axial endpoints, and was far removed from all other OGUs (Figure 5-3). The remaining OGUs were roughly aligned along the second axis, with the Chiquitanía and Lowland Amazonian Peru forming the axial endpoints. The White-water Floodplain and the Chiquitanía, the OGUs that showed the strongest floristic similarities (Sørensen's Index, Figure 5-3) to the Pantanal, were also closest to the Pantanal in ordination space (Figure 5-3). Their position, however, was not strictly as suggested by Sørensen's Index (Figure

5-3), as the White-water Floodplain (54.9%) was closer to the Pantanal than was the Chiquitanía (55.8%). An ordination of a null data set was attempted in order to approximate the effects of sample size on the distribution of OGUs (see Chapter 2). Regrettably, I was unable to find a configuration that resulted in a stable ordination; thus, I was forced to forgo this comparison.

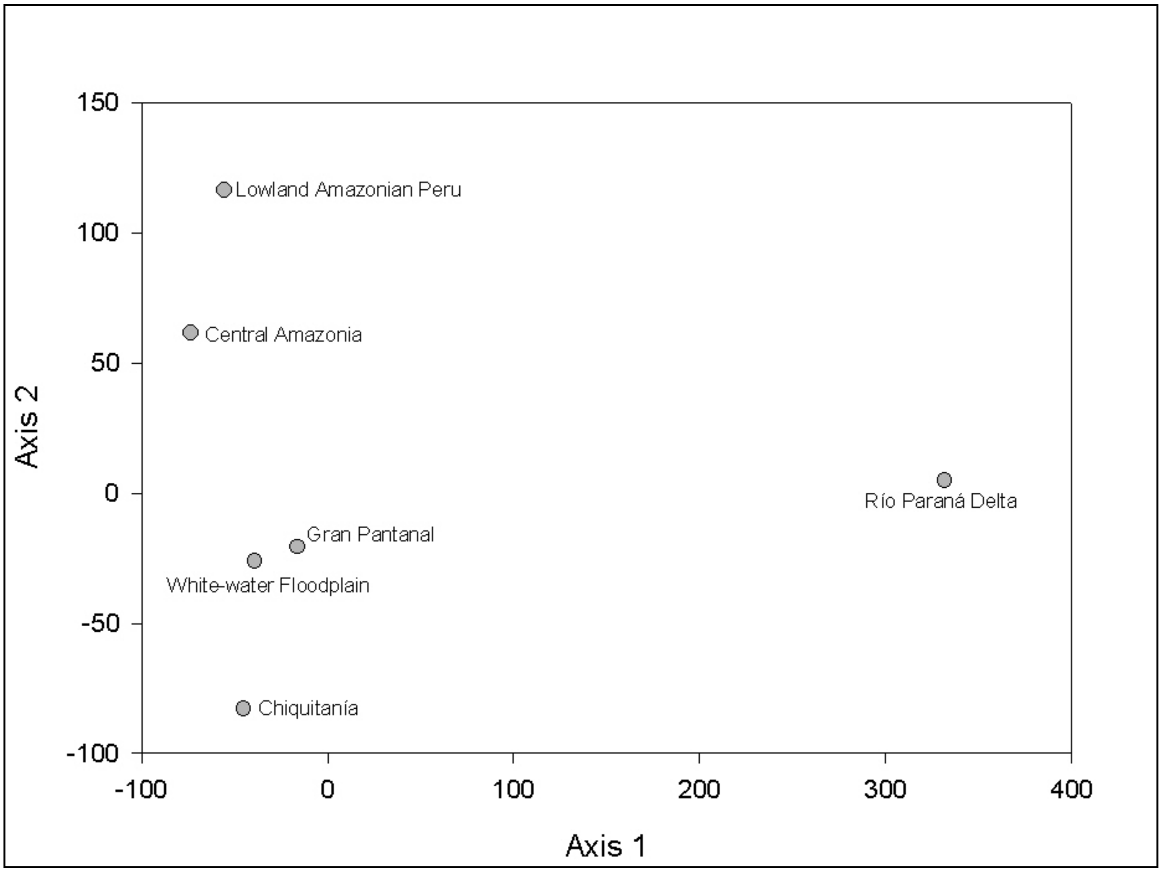

Figure 5-3. Ordination of the OGUs Detrended Correspondence Analysis (DCA). OGUs are those used in floristic comparisons with the Gran Pantanal. The wetland flora of the Gran Pantanal was compiled from species recorded from the Bolivian and Brazilian portions of this system.

A histogram of the species frequency "classes" (Figure 5-4), indicated that the contributions of the different classes to floristic similarities between the Chapare and the other OGUs were extremely variable. This variability was immediately evident from the shape of the histograms, some of which tapered from left to right (i.e., the greatest portion of shared species were from the more commonly encountered species), others from right to left, and one that possessed a fairly equitable width throughout (Figure 5-4). By contrast, frequency histograms constructed from comparisons of the Chapare flora and various OGUs (Chapter 4) all tapered from left to right. In order to facilitate discussion of these relationships, descriptive names were assigned to the four "classes" of species: 1) 'ubiquitous', present in all OGUs; 2) 'widely distributed', present in five OGUs; 3) 'intermittent', present in 3-4 OGUs; and, 4) 'rarely shared', restricted to 2-3 OGUs. It should be noted that these labels were not intended to represent actual species' rather they refer solely to species distributions within this particular set of OGUs.

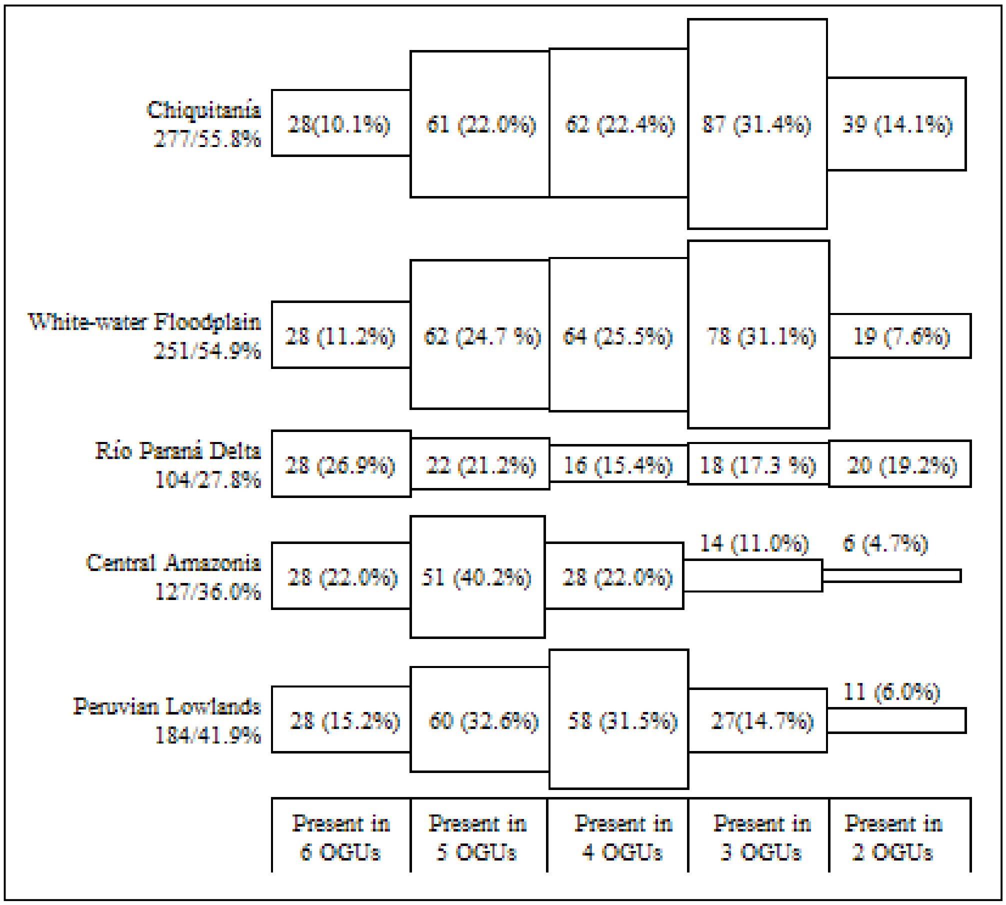

Figure 5-4. Frequency of species shared between the Gran Pantanal (Bolivian and Brazilian portions) and the other OGUs utilized in floristic comparisons. Figures below the OGU name indicate the number of species present in both the OGU and the Gran Pantanal, followed by floristic similarity (Sørensen's Index). Boxes correspond to species classes (i.e., the number of OGUs in which the species was present) as indicated by the key along the bottom of the figure. The vertical dimension of each box is proportional to the number of species that it represents. Values associated with the boxes indicate the number of species in that class that occurred in both the OGU and the Gran Pantanal, followed by the percentage that this portion of the flora contributed to the total species shared between the OGU and the Gran Pantanal.

Floristic similarities between the Gran Pantanal and both Central Amazonia and Lowland Amazonian Peru were, in large part, derived from the presence of many ubiquitous and widely distributed species (Figure 5-4). By contrast, floristic similarities between the Gran Pantanal and both the Chiquitanía and the White-water floodplain region were enhanced by a large number of "rarely shared" species (Figure 5-4). This frequency class accounted for more than a third of the species shared between the Gran Pantanal and both the White-water Floodplain (38.7%) and the Chiquitanía (35.5%). Although the floristic similarity (Sørensen's Index) between the Gran Pantanal and the Río Paraná Delta was fairly low (27.8%, Table 5.3), more than a third of this (36.5%) was attributable to rarely shared species.

Discussion

Vegetation Description

GENERAL DESCRIPTION. As is common for lakes in tropical lowland areas, extensive floating mats of aquatic vegetation frequently occupied the edges of the systems. Common mat-forming species were *Hymenachne amplexicaulis*, *Oxycaryum cubense*, and *Eleocharis acutangula*. Many areas along the edge of Laguna Cáceres contained thick mats dominated by the grass *Leersia hexandra*. The mats were distinct from floating mats that I observed in other areas of Bolivia and appear to correspond to those described from Central Amazonia by Junk (Junk 1970, 1973, 1983). The wetland sedge, *Fuirena umbellata*, which was a conspicuous mat-former in many of the wetlands in other parts of lowland Bolivia, was only observed at a single site, Laguna Uberaba (Appendix H).

The outer edges of the mats were frequently dominated by populations of *Eichhornia azurea* and *Pontederia rotundifolia*. At times, the grass *Imperata tenuis* and the floating herbs *Eichhornia crassipes*, *Limnobium laevigatum*, and *Alternanthera philoxeroides* also formed large populations in this zone. Additionally, the edges of a stream that flowed into Laguna Mandioré contained floating mats of the aquatic fern, *Marsilea crotophora*, and plus an unidentified, mat-forming species of *Commelina*. A few species appeared to be restricted to the floating mats, e.g., *Barrosoa confluentis*, *Erechtites hieracifolia*, *Piper fuligineum*, and *Pontederia triflora*.

In parts of some systems, the floating mats lacked a clear zonation of species, as is common in many wetlands in the Bolivian lowlands. Rather, they were composed of a mosaic of species. This lack of zonation was conceivably due to the combined effects of strong winds and the long fetch of the lakes resulting in the mats being continuously broken apart, translocated, and recombined.

Frequently, large populations of emergent species were present along the edges of the lakes. The grass, *Echinochloa polystachya,* was often present in this zone. This species is reported to be common in Central Amazonia and the Brazilian Pantanal, but I rarely encountered it in other areas of the Bolivian lowlands. Some seasonally inundated areas around the edge of Laguna Cáceres were notable for extensive tracts of the emergent grass *Paspalum wrightii* (see discussion of noteworthy species below). Emergent shrubs were very abundant around the edges of the four lacustrine systems. Common emergent species included the legumes *Mimosa pigra, Discolobium pulchellum, Sesbania exasperata, Rudgea cornifolia, Alchornea castaneifolia*, and *Combretum lanceolatum*. Emergent species were growing in depths of up to about 2.0 meters at the time of fieldwork, and although these areas may dry out during part of the year, they were clearly inundated for a large part of the year.

Small trees were also present along the edge of the lakes, frequently in areas that were inundated to depths greater than 1 m. Common arborescent species in these habitats were *Triplaris gardneriana, Bergeronia sericea, Simira rubescens, Rheedia brasiliensis*, and *Myrcia fallax*. An abundance and variety of shrubs and small trees growing in inundated habitats is at odds with what has previously been reported by some researchers. For example, Prado et al. (1993, p. 570) observed that in the Pantanal, "woody plants are confined to the small areas of woods that establish themselves on isolated, elevated mounds and river banks that are almost never inundated".

In large areas of some systems the palm *Copernicia alba* was extremely abundant. This species, which is sufficiently abundant in this region to have been termed "the species symbolic of the Pantanal" (Conceiçâo and de Paula 1986, p. 110), is widely distributed in the southern half of South America (Moraes 1991) and reaches the southern limits of

Amazonia (Henderson 1995). In Bolivia, extensive areas of the lowlands are occupied by populations of C. alba, which are known locally as palmares in Bolivia (Moraes 1991) or carandazais in Brazil (Por, 1995). This species is subjected to some harvesting pressure, as it is frequently utilized for fence posts (Moraes, 1991) and telephone poles (Killeen et al., 1993); however, no evidence of harvesting was seen in the study sites.

NOTEWORTHY SPECIES

A number of rare and/or uncommon species were encountered during fieldwork. The rare night-blooming waterlily *Nymphaea oxypetala* (Nymphaeaceae) was collected at both Puesto Gonzalo and Laguna Cáceres. This species is endemic to South America, with only a few (7-10) known populations (Wiersema 1987). *Nymphaea oxypetala* was previously known for Bolivia from a single population along the Río Paraguá at Parque Nacional Noel Kempff Mercado (Ritter et al. 2000). The population at Laguna Cáceres was very large, with at least 100 individuals noted, and may constitute the largest known population of *N. oxypetala*.

Another waterlily, *Nymphaea belophylla*, a rare and extremely poorly known species, was also encountered in Laguna Cáceres. This species is also known from only a few sites (Wiersema 1987), and the population at Laguna Cáceres constitutes a first record for Bolivia (Ritter et al. 2000). Its presence in this area, however, was not entirely unexpected as *Nymphaea belophylla* had been previously reported for the Brazilian portion of the Pantanal (Pott 1998).

A population of the rare (or rarely collected) aquatic herb *Pontederia triflora* (Pontederiaceae) was encountered at Laguna Uberaba. Its presence in this system, where it was observed in a single area growing on and along the edge of a highly sedimented floating mat, constituted a new country record. Additionally, *P. triflora* was the only rare or noteworthy species encountered in association with the floating mats. Another addition to Bolivia's flora was the semi-aquatic grass *Leptochloa panichoides*. A single individual was observed in a marshy area alongside a stream that flowed into Laguna Mandioré. A further addition to the country's flora was the submerged macrophyte *Najas podostemon* (Najadaceae), which was abundant in the shallows at Puesto Gonzalo. As best as I can determine, these are the first records for all three species in the Pantanal system.

Four of the species encountered during this study were listed in the IUCN Red List of Threatened Plants (Walter and Gillett 1998). Three species, *Bergeronia sericea, Thevetia bicornuta* (Apocynaceae), and *Sphinctanthus hassleriana* (Rubiaceae), have a world status designation of "rare", while a fourth, *Paspalum wrightii*, has a world status of "endangered" (Walter and Gillett 1998). *Paspalum wrightii* has previously been noted for the Chiquitanía region (Killeen 1990), although it was said to be rarely encountered in that region. At Laguna Cáceres, this species was extremely abundant in at least one area, and a number of species that were collected in conjunction with P. wrightii, e.g., *Nymphaea oxypetala, N. belophylla*, and *N. gardneriana*, weren't observed elsewhere in the system.

A few aquatic species were encountered that are widely distributed in the Neotropics but which seemingly have been rarely collected in Bolivia. The free-floating macrophyte, *Neptunia natans*, was observed at three sites (Appendix H). Although *N. natans* possesses a nearly pantropical distribution (McVaugh 1987), this was the only Bolivian region in which I encountered this species. The wetland shrub *Neptunia plena*, another widespread species (McVaugh 1987), was also observed at Laguna Mandioré. As with *N. natans*, this was my first encounter with *N. plena* in Bolivia. The free-floating macrophyte *Phyllanthus fluitans* (Euphorbiaceae) is another widely distributed species, ranging from Paraguay to northern South America, with at least one disjunct population known for Mexico (Lot et al. 1980). Although this species has rarely been encountered in Bolivia, it was present at two of the Pantanal sites (Appendix H).

EFFECTS OF ANTHROPOGENIC IMPACT ON THE FLORA

A general tendency is to assume (most often, correctly) that human activities will have a negative impact on vulnerable species. Nevertheless, it appeared that anthropogenic impact might inadvertently be beneficial for the rare waterlily, *Nymphaea oxypetala*. In the two smaller Bolivian sites where this species was encountered (Puesto Gonzalo and the Comunidad de Florida at Parque Noel Kempff Mercado), it appeared that the populations may have been able to persist (and perhaps were able to become established), in part due to the activities of local residents. Specifically, it was a common practice in the two villages to keep small areas of the river's edge free of floating mats. It was only in these cleared areas where *N. oxypetala* was encountered. The large population at Laguna Cáceres, however, did not appear to rely on human intervention for its maintenance.

Additional evidence of a positive correlation between phytodiversity and human activities comes from A. Pott and V. Pott (1997) who noted that in seasonally inundated habitats in the Brazilian portion of the Gran Pantanal a number of species that can be shaded out by grasses are maintained by the grazing of cattle. Examples were, *Burmannia flava*, *Aniseia cernua*, and *Drosera sessilifolia* (A. Pott and V. Pott 1997).

Biodiversity

Based solely on number of species, Laguna Cáceres would be considered the most species-rich of the 46 Bolivian study sites with its 124 species (Table 5-3) surpassing the species count for all other sites (see Chapter 6). The remaining three Gran Pantanal lacustrine systems would be considered as moderately species-rich (61-66 spp, Table 5-3), in comparison with the other lowland study sites. Puesto Gonzalo (38 spp.) would be considered somewhat depauperate.

As noted, it is essential to consider system size when evaluating diversity. In the preceding chapter, diversity in the Chapare wetlands was evaluated relative to a species-area curve plotted from data for the 23 lowland Bolivian study sites. The curve is also used here as a reference point for diversity in the Gran Pantanal systems (Figure 5-5). Criteria used in compiling the data and adjudging system area are discussed more fully in Chapter 6, but one point bears mention here. For most wetland types, the entire area of the system was considered to be the “potentially vegetated area”. As the lacustrine study sites characteristically contained extensive areas of unvegetated, open water, the potentially vegetated area for these systems was estimated from an approximately 50 m wide band around the perimeter of the basin plus any areas of seasonally inundated marsh adjacent to the basin. Four of the five Gran Pantanal study sites were large lakes and their system areas were calculated as per above.

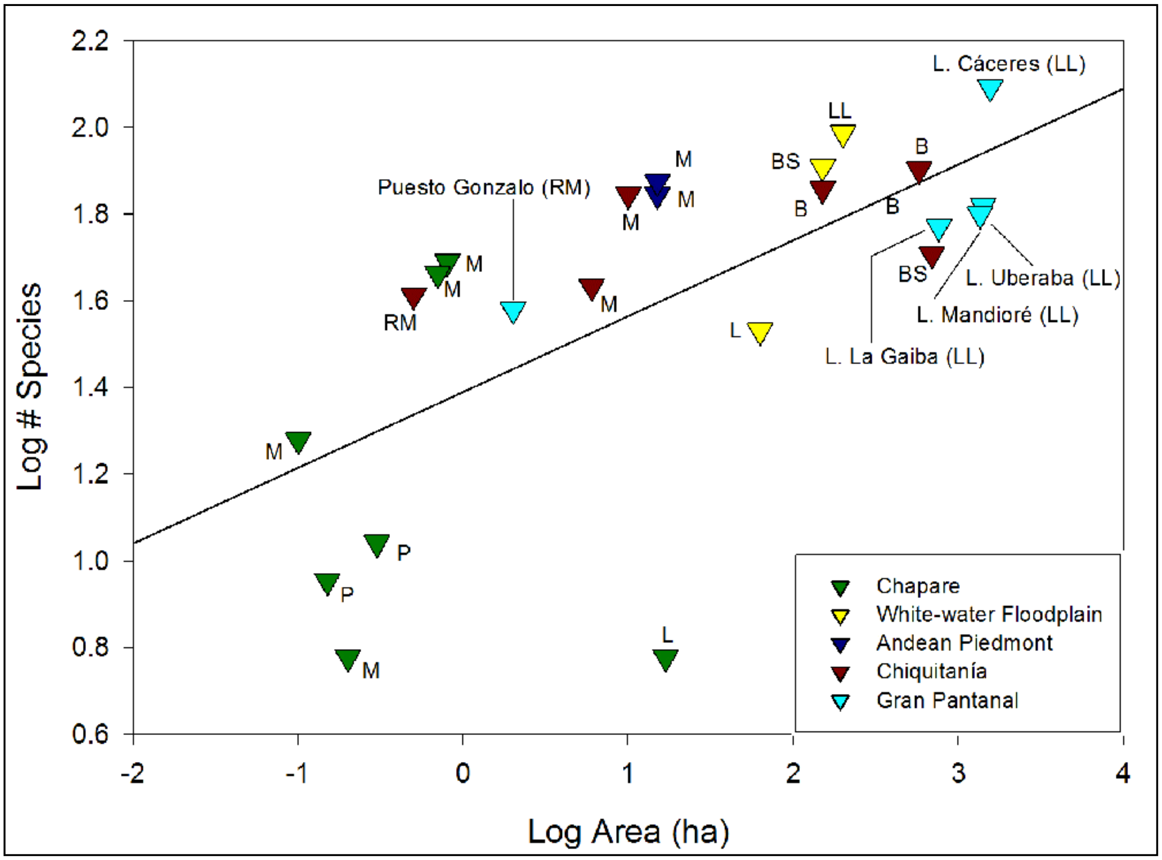

Figure 5-5. Species-area curve plotted from the 23 lowland Bolivian study sites with the Gran Pantanal study sites identified by name. Wetland types: B – bahia; BS – basin swamp; L – small lake (<500 ha); LL – large lake (> 500 ha); M – marsh; P – pond; RM – riparian marsh. Linear regression: Log S = 1.39 + 0.17 Log A. r^2 = 0.44, p = 0.00005.

As in the preceding chapters, sites situated above the regression line (Figure 5-5) were considered to be relatively species-rich and those below the line as relatively species-poor. Therefore, it appeared that the Gran Pantanal study sites could be characterized as somewhat species-poor, or perhaps as possessing intermediate richness, as three of the five systems were located below the regression line and two. Interpretation of the plot was compounded by four of the five study sites belonging to a (presumably) species-poor wetland type (large lakes; Chapter 6). Furthermore, true to their name, the large lakes were indeed large, and thus their species checklists were undoubtedly less complete than those of smaller wetlands. The three systems situated below the regression line all received just a single visit, further reducing the likelihood that they were represented by fairly complete checklists.

At the regional level, diversity in the Gran Pantanal (combined Bolivian and Brazilian portions) wetland flora was approximately intermediate between the most species-poor (Central Amazonia, 255 spp.; Table 5-3) and species-rich (the Chiquitanía, 541 spp) OGUs. This comparison was based solely on number of species and, as with the site-level comparisons of diversity, a true measure of diversity required that regional area also be considered. The species-area curve that was used in the preceding chapter (Figure 4.6) to represent the general trend in wetland species-richness throughout the Neotropics, is also used here (Figure 5-6). This construction of this curve is discussed in detail in Chapter 7.

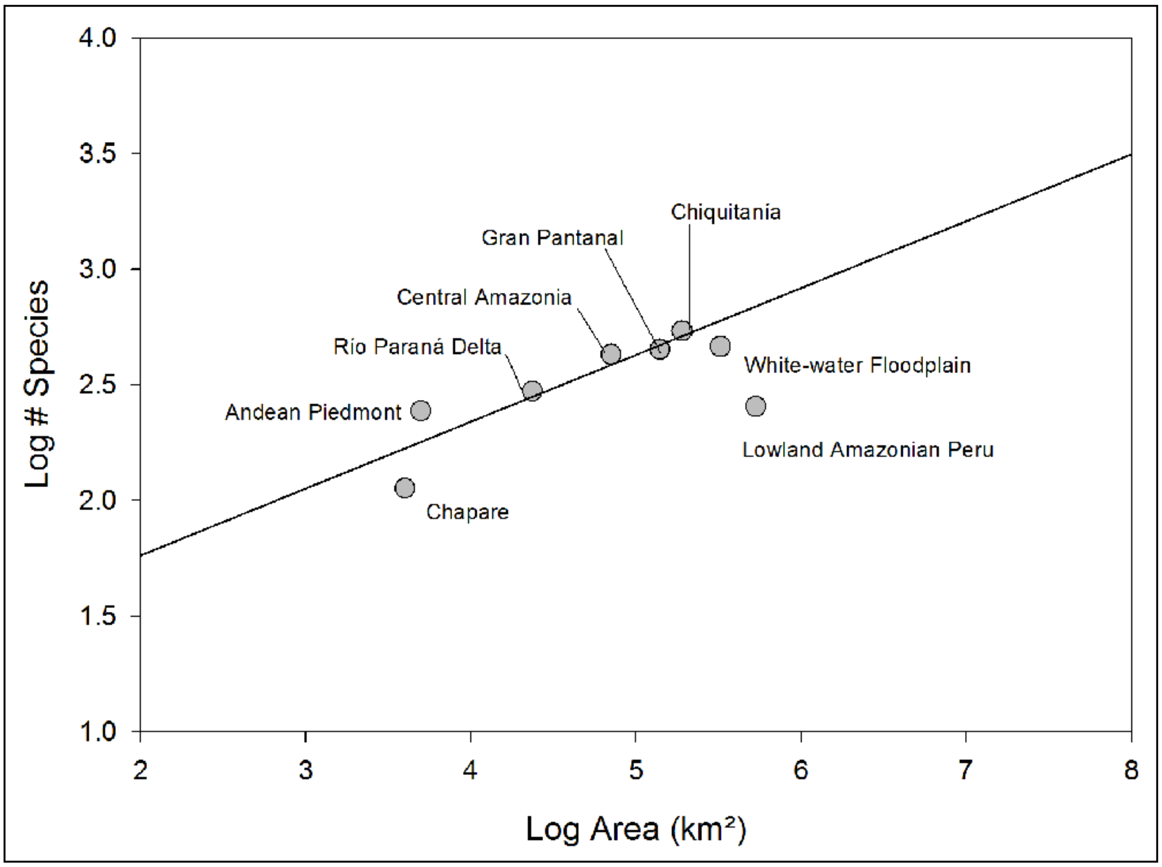

Figure 5-6. Phytodiversity of the OGUs considered in comparisons with the wetland flora of the Gran Pantanal (Bolivian and Brazilian portions). Diversity is relative to a regression line fitted to a species-area curve plotted from cumulative species-area data from the Neotropical countries, including Mexico (see Chapter 6). Linear regression: Log S = 1.19 + 0.29 Log A; $r^2 = 0.90$.

As with the site-level species-area curves, OGUs situated above the regression line were considered as species-rich and those below the line as species-poor. From this perspective, the Gran Pantanal appeared to be of average diversity, as it was situated directly on the regression line (Figure 5-6). As discussed in Chapter 6, however, a more accurate estimate of regional diversity would be calculated from just the area of inundated habitats within a region. Of the OGUs considered here, the Gran Pantanal most likely possessed the highest ratio of inundated to non-inundated territory. Furthermore, the Gran Pantanal has probably received the most complete botanical survey of all the OGUs. For these reasons, the actual diversity of its wetland flora was most likely lower than suggested by Figure 5-6.

The portrayal of the Gran Pantanal as possessing a rather poor wetland flora agrees with the observations of some other researchers. Prado et al. (1994) considered the Pantanal's wetland flora as quite poor, whereas the terrestrial flora was said to be enormously rich. This difference in diversity between the two components of the flora was presumed to result from geographical barriers severely limiting immigration of wetland species from adjacent regions (Prado et al. 1994). These same barriers were perceived to have no effects on terrestrial species, which could migrate freely from adjacent Cerrado and dry forest habitats (Prado et al. 1994). It appears that this impression of the Pantanal wetland habitats as being species-poor was based primarily on the authors having encountered only 48 species (in a 50 X 50 m quadrat) during a year's sampling, with an additional 19 species noted in the general area (Prado et al. 1994). The authors apparently assumed that these 57 species represented the largest part of the Pantanal's wetland species (as stated by Heckman 1997, one of the coauthors with Prado et al. 1994). Although it may be that the area of the Pantanal studied by Prado et al. (1994) was particularly depauperate in species, it is clear from floristic accounts of the Pantanal presented by Pott and Pott (A. Pott and V. Pott 1997, V. Pott and A Pott 1997, 1998) that the species encountered by Prado et al. represented only a small fraction of the Pantanal's wetland flora. Furthermore my impression from floristic surveys and general collecting in wetlands throughout Bolivia is that the level of richness noted by Prado et al. (i.e., 48 species in a 50 m X 50 m area 1994) was at least comparable to the richest areas I encountered.

Heckman (1997, p. 99) stated that, in general, "the water bodies of the wet-and-dry climatic zone seem to support a much less diverse biota than the neighboring equatorial regions" and maintained that the Gran Pantanal was considerably poorer in wetland species than the Amazonian region. Although Central Amazonia appears to be slightly richer than the Gran Pantanal (Figure 5-6), the difference in diversity between the two regions could not be accurately described as "considerable." Furthermore, as discussed in the preceding chapter, wetlands in the Chapare, the area of lowland Bolivia with the highest annual precipitation, were found to be much less floristically diverse than in the seasonally dry regions of the Bolivian lowlands.

Floristic Similarities

As noted, site-level, floristic similarities among all Bolivian Pantanal systems were relatively high (Sørensen's Index 39.5-58.1%, Table 5-3). Strong floristic affinities at the site level were corroborated by the Gran Pantanal study site's close proximity in ordination space in the ordination by DCA (Figure 5-2). Based on the ordination of the study sites, the Gran Pantanal systems were most closely associated with wetlands from the Chiquitanía and White-water Floodplain regions (Figure 5-2).

At the regional level, the wetland flora of the Gran Pantanal also appeared to be most closely allied with the Chiquitanía (55.8%, Table 5-3) and White-water Floodplain regions (54.9%). The Chiquitanía is contiguous with the western border of the Gran Pantanal and demonstrated a slightly higher floristic similarity (Sørensen's Index) to the Gran Pantanal than did the White-water Floodplain. Nevertheless, in the ordination by DCA the White-water Floodplain was situated closer to the Pantanal in ordination space than was the Chiquitanía (Figure 5-2).

As these regions were closest geographically to the Gran Pantanal it was not surprising that strong floristic associations were noted. Still, it has been hypothesized that the (presumed) low richness of the Pantanal wetland flora was the result of the surrounding dry regions limiting the immigration of wetland species by functioning as formidable geographical barriers (Prado 1993). Nevertheless, it was obvious from the frequency analysis (Figure 5-4) that a significant portion of the floristic similarities between the Gran Pantanal and both the Chiquitanía and the White-water Floodplain were due to the presence of a large number of rarely shared species (i.e., species that were present in only the Gran Pantanal and one other OGU). Moreover, of the 112 species that were restricted to exactly three OGUs (including the Gran Pantanal), 103 (91.9%) were present in the Chiquitanía and/or the White-water Floodplain. These observations suggest that migration of wetland species between the Gran Pantanal and western lowland Bolivia is not seriously impeded by either geographical or climatic barriers.

It was somewhat surprising that the floristic similarity between the Gran Pantanal and the Río Paraná Delta was relatively low (27.8%, Table 5-3) and that the two OGUs were separated by a large distance in the ordination by DCA (Figure 5-2). I anticipated stronger floristic affinities between the two regions as it seemed likely that the Paraná river would serve as a natural corridor for species migration from the south, and as Amazonian phytogeographic elements are known to extend to the Paraná river delta (Menalled and Adámoli 1995). Migration of macrophytes, however, might be favored in the downstream direction, limiting the immigration of species from the Río Paraná Delta region toward the Pantanal. Some evidence of a strong floristic association between these two regions was evidenced in the frequency analysis (Figure 5-4) as 20 species shared by these regions were absent from all other OGUs.

Other researchers have commented on the phytogeographic affinities of the Gran Pantanal wetland flora. Heckman (1997) stated that the strongest floristic and faunal similarities generally occur between adjacent geographical regions and that the biota of the Gran Pantanal showed the closest affinities to the Amazon basin and the south temperate section of the Río Paraná system. Nevertheless, it was clear from the comparisons made in here (Figure 5-2; Table 5-3) that the Gran Pantanal wetland flora was more closely associated with the Chiquitanía and the Whitewater Floodplain regions. In fairness to Heckman, however, it need be emphasized that hardly any floristic data from these Bolivian regions was available at the time of his study.

Many wetland species have large distributions, and a number of these (e.g., *Eichhornia crassipes, E. azurea, Pistia stratiotes, Eleocharis acutangula, Oxycaryum cubense, Hymenachne* spp.) can dominate large areas of wetland systems. Frequently, references to floristic affinities between the Gran Pantanal and other regions appeared to be weighted heavily by the presence of a few of these common and conspicuous wetland species. For example, Frey (1995) noted that, as expected, there were strong similarities between the flora of the Bolivian Pantanal and nearby areas of the Brazilian Pantanal. Frey identified 14 species as indicators of this phytogeographic association. Based on species distributions as recorded in the wetland species database (Ritter 2000), however, the majority of the 14 species are widely distributed in the Neotropics. Thirteen of these species were present in the Guianas; 12 in Ecuador, Panama, Peru, and Venezuela; and 11 in Colombia and Costa Rica (Ritter 2000). Clearly, estimates of phytogeographic affinities in Neotropical wetlands need take into account more than the dominant or most common species.

Various researchers have noted that the Gran Pantanal lacks endemic wetland species. Some evidence indicates that until recently (on a geological time scale) the Gran Pantanal was characterized by desert-like conditions (Klammer 1982, cited in Prado et al. 1994). Prado and colleagues (1994) stated that the relatively short history of the Pantanal as a wet environment accounted for the lack of an endemic flora in this region. According to their hypothesis there simply has not been sufficient time for an endemic flora to develop. Junk and da Silva (1995) also commented on the lack of endemic species in the Gran Pantanal and hypothesized that the semi-desertic condition of the Pantanal during the last period of glaciation may have resulted in the extinction of a number of aquatic organisms. Endemism in the Neotropical vascular plant flora, however, is apparently quite low relative to the terrestrial flora and undescribed species are seemingly encountered much less frequently. For example, Brako and Zarucchi (1993) calculated that 5353 (31.27%) of the 17,119 species of angiosperms known for Peru were national endemics. By contrast, only 3 of the 151 angiosperm species (1.98%) listed as being associated with Peruvian aquatic habitats by León and Young (1996) were recognized as endemic. Therefore, the absence of a large number of endemic wetland plants in the Gran Pantanal was in keeping with what has been observed elsewhere in the Neotropics.