Chapter 4. The Chapare

Three days north from Rosario we encountered the gigantic and terrible personality that we came to call Green Hell. It is a truly colossal block of forest, so vast that the mind refuses to grasp the immensity of its range. .... it is horrible, a dense, fever-stricken thicket, shimmering in the heat with a perpetual glassy haze dancing through the topmost branches. It is evil, swampy, miasmic, like a warm, festering wound.
-        J. Duguid, Green Hell: Adventures in the Mysterious Jungles of Eastern Bolivia

<u>Introduction</u>

The region along the base of the Cordillera Oriental (Eastern Range) of the Bolivian Andes in the Departamento of Cochabamba is colloquially referred to as the Chapare. At times, the Andean slopes are also included in the delineation of the Chapare (e.g., Guyot and Watson 1994; Solomon 1989), but the name is most often used solely in reference to the lowlands, a usage that is also applied here. The Chapare (Figure 2-4) occupies the transition between the Andes and the extensive floodplain that extends northwards through the Departamento of Beni and eastwards to the Brazilian Shield. The largest part of this floodplain, the Beni basin (Plafker 1964), is characteristically quite level and occupies elevations between 150-250 m (Killeen et al. 1993). Topography in the Chapare is more variable, with low hills creating a dissected relief. Although the Chapare region includes territory from three provinces (Chapare, Tiraque, and Carrasco) the colloquial name for the region is quite functional, circumscribing an area characterized by high rainfall, high temperatures, low elevations, and (previously) extensive tracts of rainforest. Although the precise geographic limits are not clearly defined, the Chapare has area of approximately 3000 (Henkel 1995) to 4000 km2 (determined from maps using the "cut and weigh method", cf. Lind 1985).

The Chapare is situated in an "inside corner" of the Andes, formed by a change from an approximately southwest to northeast orientation to a more eastern bearing. This region and the adjacent Andean slopes receive the highest amount of rainfall in Bolivia. Maximum precipitation in the Chapare reaches an estimated 4900 mm yr-1, with a maximum hydrologic year of 6900 mm (Morris et al. 1983). Precipitation is even greater in the lower Andean slopes just above the Chapare, where it is estimated to reach 6000

(Moraes and Beck 1992) to 7000 mm yr-1 (Guyot and Watson 1994). Rainfall decreases northwards away from the mountains and eastwards toward the City of Santa Cruz (Morris et al. 1983). Thus, in the approximately 70 km between the two most disjunct Chapare study sites (see Materials and Methods) mean annual precipitation ranged from > 4500 mm to about 2500 mm (estimated from isohyets presented in Morris et al. 1983). Despite the abundant precipitation, the region still experiences a few months of low rainfall (roughly, June to August), such that many of the area's small ponds and roadside ditches dry out completely. Mean monthly temperatures range from 20° to 38°C (Henkel 1995), with a mean annual temperature of 21.8° (Maldonado et al. 1996) to 25°C (Killeen et al. 1993). Temperatures in the region always remain above 0° C.

The slopes of the Cordillera Oriental are precipitous, with the transition between montane peaks (> 4500 m) and the lowlands occurring over a short distance (ca. 30-40 km, linea recta). The slopes above the Chapare are characterized by deposits of sedimentary rocks that consist primarily of shales and may be greater than 200 m in thickness (Morris et al. 1983). These substrata and their derived soils are unstable and tend to erode rapidly when stripped of vegetation (Morris et al. 1983), although rates of erosion are extremely variable, ranging from an estimated 1,000-20,000 t km-2 yr-1 (Guyot and Watson 1994). At the base of the mountains, the shales are overlain by deposited alluvial materials (Guyot and Watson 1994). These deposits are generally arrayed sequentially from coarse materials at the foothills to finer-grained sediments away from the mountains (Morris et al. 1983).

The rivers draining the steep Andean slopes arrive at the Chapare with abundant force and upon reaching the easily erodible soils are extremely dynamic. Erosion and sedimentation occur rapidly (Morris et al. 1983), with lateral channel migrations being a constant feature of the Chapare's rivers. Salo et al. (1986) analyzed channel dynamics in Peruvian Amazonia by comparing aerial photographs from 1962-63 with a 1976 LANSAT image. They estimated that, for their area of study in lowland Peru, the mean lateral erosion rate of meander bends was 12 m yr1 (Salo et al. 1986) during this period. It seems reasonable that channel migration in the Chapare rivers would be of a similar magnitude.

The rivers of the Beni basin are characteristically very turbid (Guyot and Watson 1994), corresponding to white-water rivers (sensu Sioli 1975). On the floodplain, the rivers are an opaque brown from their large load of suspended fine particles, however, river water in the Chapare is generally much more transparent. This is presumably because the rivers and streams that drain the Andean slopes are generally clear, and only carry large amounts of sediments when the vegetative cover, which protects the weathered substratum, is subjected to landslides and other large-scale disturbances (cf. Sioli 1984).

Historically, the Chapare's terrestrial vegetation was dominated by tall forest, characterized by high diversity (Killeen et al. 1993). During the 1960's and 70's, however, the government advanced colonization of the region, constructing roads to and within the Chapare and apportioning 202,000 ha of land for new colonists (Henkel 1995). Logging has been extensive and large portions of the region have been cleared for agriculture, with approximately 80% of the land dedicated to the cultivation of coco (*Erythroxylum coca*) and the remaining 20% to other crops (Henkel 1995). Consequently, the greatest part of the Chapare's remaining forested habitats are secondary forest, characteristically dominated by *Cecropia peltata* L. (Cecropiaceae), *Ochroma pyramidale* (Cav. ex Lam.) Urb. (Bombacaceae), *Inga* spp. and *Copaifera* sp. (Fabaceae), and *Sapium* spp. (Euphorbiaceae).

There have been few limnological investigations of the Chapare's aquatic habitats and references to the aquatic flora are nearly nonexistent. Limnological studies were undertaken by Barra et al. (1990), Cadima (1990), and Maldonado et al. (1996). Of these, the sole reference to the vascular flora was from Maldonado et al. (1996), who listed some of the macrophytes encountered in a series of lakes on the Río Ichilo floodplain. Additional information on Chapare wetland species was presented by Jiménez (1984), who included various wetland species in his account of the flora of the Departamento of Cochabamba.

As part of my Bolivian research, I undertook a botanical survey of the wetlands of the Chapare. My specific objectives were as follows: 1) to prepare a provisional checklist of the vascular plant species associated with Chapare wetland habitats; 2) to identify rare or

noteworthy species from these habitats; 3) to estimate the range of site-level vascular plant species richness, as represented by a series of study sites; 4) to compare species richness in the Chapare wetland flora to lowland regions in Bolivia and other South American countries; and, 5) to examine floristic similarities among the Chapare wetland flora and these regions. To these ends, the flora of the Chapare wetlands is listed and noteworthy species are discussed. Comparisons of species richness and floristic similarity are made between study sites. At the regional level, comparisons are made among the Chapare wetland flora and seven lowland regions in Amazonia and extra-Amazonian South America.

Materials and Methods

The Study Area

Within the Chapare, seven wetland systems were established as study sites (Table 4-1; Figure 4-1), with field research being concentrated on these systems. Descriptions of the study sites are presented in Appendix A. Additional botanical collecting was also undertaken in a variety of wetland types (e.g., small marshes, streams, rivers, oxbow lakes, strand lakes, and inundated roadside ditches).

Vegetation Sampling

Sampling focused on compiling comprehensive site floras. The study sites were fairly limited in size, with the largest system occupying approximately 30 ha and the others ranging from 0.2-1.5 ha (Table 4-1). Due to their relatively small size it was possible to survey each site in its entirety. Fieldwork was conducted intermittently during June, 1994 to November, 1996. Whenever possible, sites received multiple visits in order to view the systems under different hydrologic conditions and thus to maximize the number of species encountered. All sites received two to four visits, with the exception of the Valle de Sajta Curichi, which received a single visit. Preferably, fieldwork was scheduled so that sites were visited during seasons of high and low rainfall, but, due to various constraints, this was not always possible.

Table 4-1. Study sites of the Chapare region, Bolivia, with province, elevation, approximate area, and approximate location.

| Study Site Name	Province	Elev. (m)	Area (ha)	Location
Mariposa Wetland	Carrasco	220	1.5	17°01'S 65°02'W
Ivirgarsama Wetland	Carrasco	200	0.7	17°01'S 64°50'W
Senda F Wetland	Carrasco	200	0.2	16°52'S 65°08'W
Villa Tunari Pond	Chapare	300	0.3	17°01'S 65°26'W
Sinahota Pond	Tiraque	240	0.15	17°00'S 65°18'W
Valle de Sajta Curichi	Carrasco	220	0.2	17°07'S 64°43'W
Puerto Villarroel Laguna	Carrasco	200	30	16°49'S 64°48'W
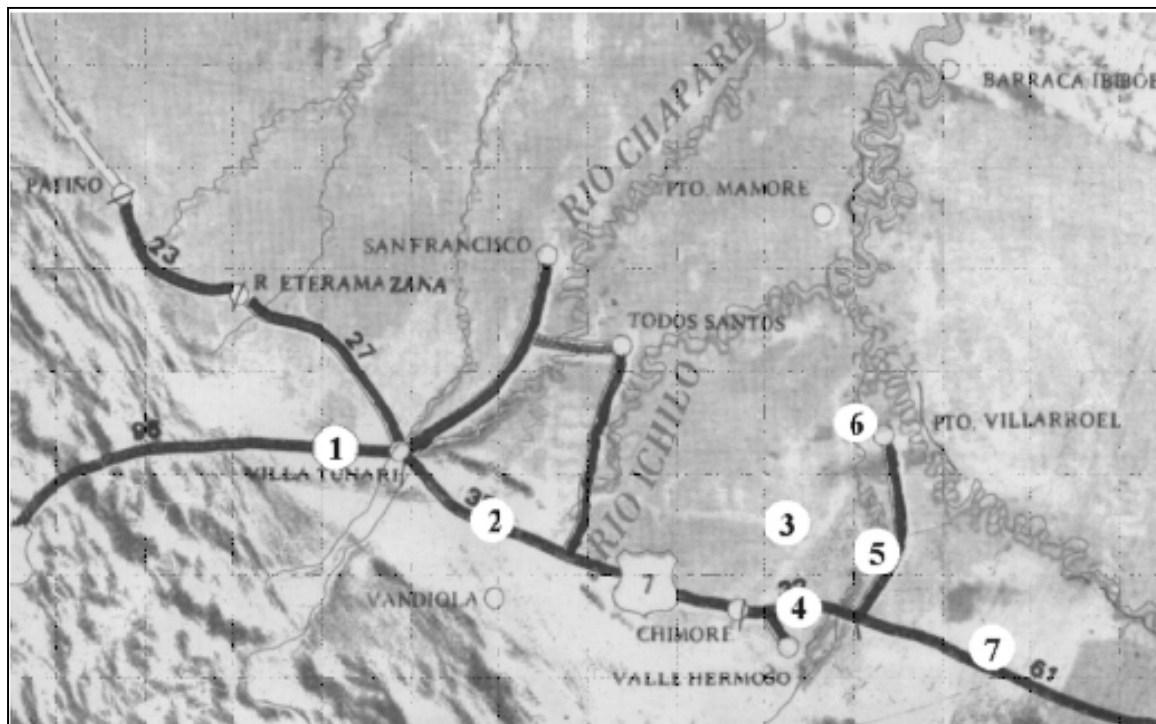
Figure 4-1. Location of the Chapare (Bolivia) study sites. 1. Villa Tunari Pond. 2. Sinahota Pond. 3. Senda F Wetland. 4. Mariposa Wetland. 5. Ivirgarsama Wetland. 6. Puerto Villarroel Laguna. 7. Valle de Sajta Curichi.

Floristic Comparisons

A regional checklist of wetland species was compiled from the study sites, augmented by data from general collecting in the Chapare, from the literature, and from exsiccatae listed in TROPICOS.   Published sources used to augment the checklist were Maldonado et al. (1996), which was incorporated in its entirety, and Jiménez (1984), which was reviewed for species which undoubtedly had been collected from the Chapare.

Floristic relationships were analyzed at two scales: 1) among study sites and, 2) among regions (macroregional scale sensu McLaughlin 1994). Regional comparisons were made among the flora of the Chapare and the following OGUs: the Gran Pantanal of Mato Grosso (Bolivia and Brazil), Central Amazonia (Brazil), lowland Amazonian Peru, and three regions in lowland Bolivia (the White-water Floodplain, Chiquitanía, and Andean Piedmont regions). The OGUs, with estimated total area, total wetland species, and mean annual precipitation are presented in Table 4-2. Descriptions of the Bolivian OGUs are presented in Appendix B and the extra-Bolivian OGUs are summarized in Appendix C.

Table 4-2. OGU's utilized in floristic comparisons, with estimated area, number of wetland species and estimated mean annual precipitation.

OGU	Approximate Area (km^2)	Wetland Flora (# of spp.)	Mean Annual Precipitation[A] (mm yr^{-1})
Chapare	4000	113	3500
Andean Piedmont	5000	244	1700
Whitewater Floodplain	325,000	464	1650
Chiquitanía	190,000	541	1200
Gran Pantanal (Bolivia and Brazil)	140,000	451	1100
Central Amazonia (Brazil)	70,700	429	2000
Lowland Amazonian Peru	533,100	255	2600
Río Paraná Delta	23,700	297	900
A. Precipitation data estimated from the following sources: the Chapare, Morris (1983); the White-water Floodplain, Andean Piedmont, and Chiquitanía Regions, Hanagarth (1993), Killeen et al. (1993), and the Servicio Nacional de Meteorología e Hidrología, La Paz; Central Amazonia, Ratisbona (1976); Peruvian Amazonia, Johnson (1976); Río Paraná Delta (Burkart 1957).			

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 solely to the distribution of species between the Chapare flora and

the other OGUs. Because floristic similarities (Sørensen's Index) between the Río Paraná Delta region and all other OGUs were uniformly low (see Results), the Río Paraná Delta region was excluded from the Frequency Analysis.

Results

Vegetation Description

One hundred forty one species, in 50 families and 100 genera, were identified as being associated with Chapare wetlands. Of these, 113 species were considered to be "wetland species" (Appendix D).   The Poaceae (13 genera, 23 spp.) and Cyperaceae (8 genera, 17 spp.) were the best-represented families, while *Panicum* (Poaceae, 9 spp.) and *Ludwigia* (Onagraceae, 7 spp.) were the best-represented genera (Appendix G). A checklist, including life-form and species abundances at each site, is presented in Appendix G.

Biodiversity

The number of species encountered at the individual sites varied considerably (5-49 spp., Table 4-3). Species richness was not consistently correlated with system area, with the largest site (the Puerto Villarroel Laguna) possessing the fewest species (5) and the second largest site possessing the greatest number of species (49). At the regional level (Table 4-4), OGU wetland floras ranged from 113-541 species, with the Chapare the most species-poor region and the Chiquitanía the most speciose (i.e., possessing the greatest number of species).

Floristic Similarities

Floristic similarities (Sørensen's Index) between study sites were quite variable, ranging from 0-43.0% (Table 4-3). In general, floristic similarities were extremely low, with only two pairs of sites having similarities greater than 20% (Table 4-3). Despite the generally low floristic similarities, five of the seven Chapare study sites were closely situated in ordination space in an ordination (DCA) of the 46 Bolivian study sites (Figure 4-2).
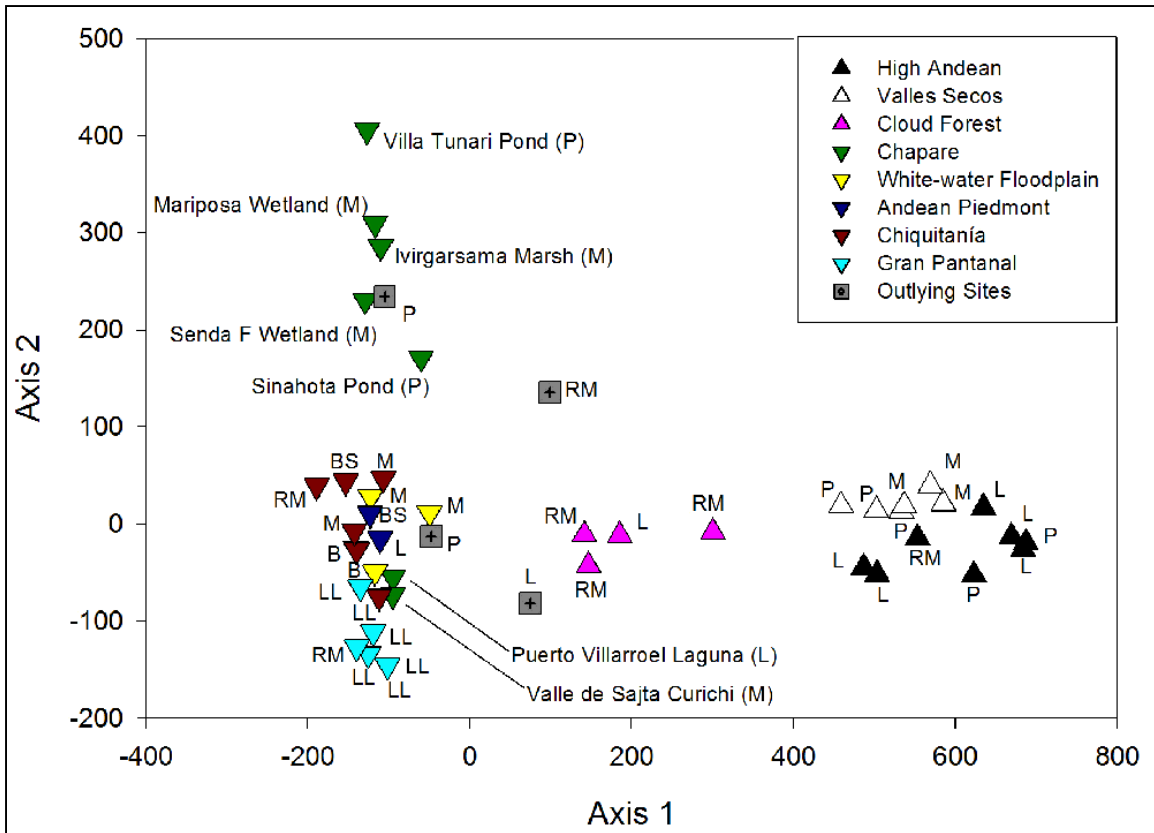
Figure 4-2. Ordination by Detrended Correspondence Analysis (DCA) of the 46 Bolivian study sites. The seven Chapare study sites are identified by name. Key to wetland types: B- bahía; BS - basin swamp; L - small lake (< 500 ha); LL - large lake (> 500 ha); M - marsh; P - pond; RM - riparian marsh.

Table 4-3. Comparison of richness and floristic similarity (Sørensen's Index) between study sites in the Chapare, Bolivia. Figures in bold along the main diagonal indicate the number of wetland species noted for each site. Numbers above the main diagonal indicate the number of wetland species shared by both areas. Numbers below the main diagonal indicate the percent floristic similarity between sites.

	Mariposa Wetland	Ivirgarsam a Marsh	Senda F Wetland	Villa Tunari Pond	Sinahota Pond	Valle de Sajta Curichi	Puerto Villarroel Laguna
Mariposa Wetland	**49**	20	5	3	2	0	0
Ivirgarsama Marsh	43.0	**44**	5	3	2	0	0
Senda F Wetland	14.7	15.9	**19**	3	2	0	0
Villa Tunari Pond	10.0	10.9	20.0	**11**	1	0	0
Sinahota Pond	6.9	7.6	14.3	10.0	**9**	0	0
Valle de Sajta Curichi	0.0	0.0	0.0	0.0	0.0	**6**	2
Puerto Villarroel Laguna	0.0	0.0	0.0	0.0	0.0	36.4	**5**

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At the regional level, the Chapare showed the least floristic similarity (Sørensen's Index) to the Río Paraná Delta region (10.7%, Table 4-4); however, the latter region showed few floristic affinities to any of the OGUs (10.7-27.8%, Table 4-4). Floristic similarities between the Chapare and the remaining OGUs showed little variability, ranging from 23.4-33.6. The Chapare was most similar to the Andean Piedmont (33.6%), but this was scarcely higher than the similarities between the Chapare and Lowland Amazonian Peru (32.8%) and White-water Floodplain (3.7%) .

Table 4-4. Comparison of richness and floristic similarity (Sørensen's Index) among selected OGUs. Figures in bold along the main diagonal indicate the number of wetland species noted for each region. The numbers above the main diagonal indicate the number of wetland species shared by both regions. Numbers below the main diagonal indicate the percent floristic similarity between regions.

	Chapare	Andean Piedmont	White-water Floodplain	Chiquitanía	Gran Pantanal	Peruvian Amazonia	Central Amazonia	Río Paraná Delta
Chapare	**113**	60	91	93	66	89	53	22
Andean Piedmont	33.6	**244**	160	172	136	127	76	61
White-water Floodplain	31.5	45.2	**464**	325	251	232	152	76
Chiquitanía	28.4	43.8	64.7	**541**	277	244	146	82
Gran Pantanal	23.4	39.1	54.9	55.9	**451**	184	127	104
Peruvian Amazonia	32.8	37.7	52.0	50.3	41.8	**429**	166	79
Central Amazonia	28.8	30.5	42.3	36.7	36.0	48.5	**255**	51
Río Paraná Delta	10.7	22.6	20.0	19.6	27.8	21.8	18.5	**297**

The ordination of the regions by Detrended Correspondence Analysis (Figure 4-3, circles) suggested that the floristic relationships between the Chapare and the other OGUs were more complex than suggested by the Similarity Index. The Chapare formed one of the first axial endpoints a short distance removed from the remaining lowland Bolivian OGUs (the White-water Floodplain, Chiquitanía, Andean Piedmont and Gran Pantanal), which were grouped in close proximity in ordination. The Río Paraná Delta region

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formed the other first axial endpoint, occupying a position far removed from all other

OGUs. Central Amazonia formed one of the second axial endpoints, while Lowland

Amazonian Peru was situated in ordination space approximately midway between this

OGU and the Chapare. The ordination of the null data set (Figure 4-3, diamonds) was

intended to approximate the effects of sample size on the distribution of OGUs. The

locations of all OGUs in the ordination of the actual data (Figure 4-3, circles) were far

removed from their respective positions in the ordination of the null data (Figure 4-3,

diamonds). Hence, it appears that differences in floristic composition among the regions

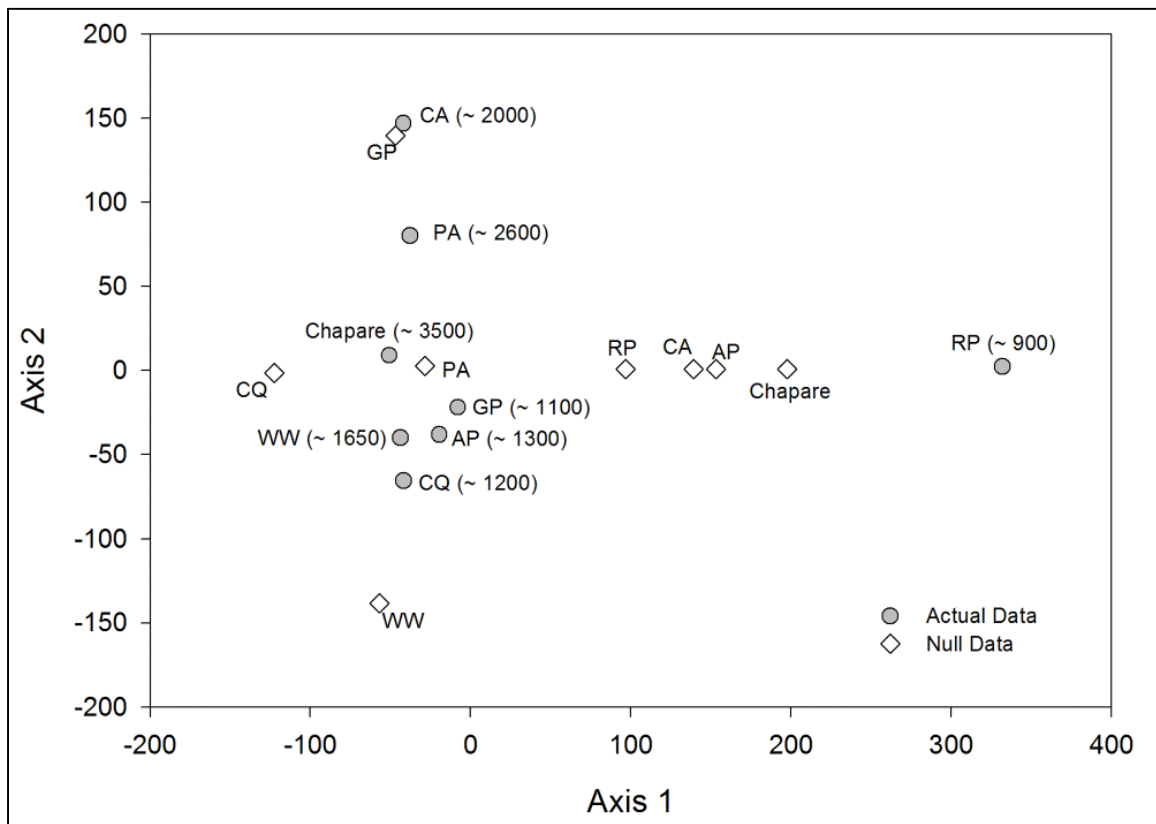were sufficiently strong to surmount any effects of sample size.

Figure 4-3. Ordination of the OGUs by Detrended Correspondence Analysis (DCA). OGUs: AP - Andean Piedmont; CA - Central Amazonia; CQ - Chiquitanía; GP - Gran Pantanal; PA - Lowland Amazonian Peru; RP - Río Paraná Delta; WW - White-water Floodplain. Values in parentheses indicate estimated mean annual precipitation (mm).

The graphical representation of the species frequency "classes" (Figure 4-4), demonstrated that the contribution of the different classes to floristic similarities between the Chapare and the other OGUs was variable. In order to facilitate discussion of these relationships, descriptive names were assigned to the four "classes" of species: 1) 'ubiquitous', present
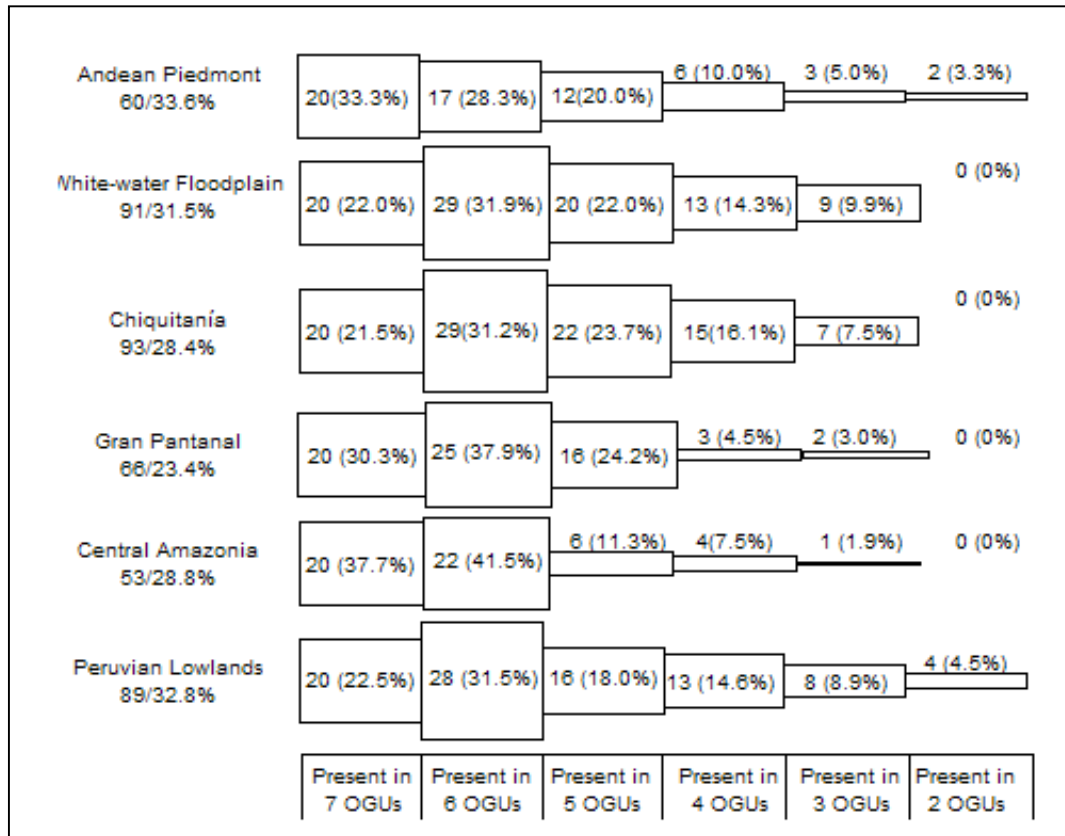

Figure 4-4. Frequency of species shared between the Chapare and the other OGUs. Figures below the OGU name indicate the number of species present in both the OGU and the Chapare, followed by floristic similarity (Sørensen's Index). Boxes correspond to species classes (i.e., the number of OGUs in which 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 Chapare, followed by the percentage that this portion of the flora contributed to the total species shared between the OGU and the Chapare. For example, considering the relationship between the Chapare and the Andean Piedmont, the initial (lefthand-most) box represents the 20 species that were present in all seven OGUs. These species accounted for 33.3% of the species shared between these two OGUs. Continuing from left to right, the second box represents the 16 species that were present in both the Chapare and the Andean Piedmont and that occurred in exactly 6 OGUs. These accounted for 28.3% of the species shared between these two OGUs.

in all OGUs; 2) 'widely distributed', present in six OGUs; 3) 'intermittent', present in 4-5 OGUs; and, 4) 'rarely shared', restricted to 2-3 OGUs. These labels were not intended to represent actual species distributions; they refer to species distributions within this

particular set of OGUs. In all cases, ubiquitous and widely shared species contributed the greatest amount to floristic similarity (53.7-79.2%), with intermittent species accounting for the greatest portion (18.8-39.8%) of the remaining similarity. In all cases, rarely shared species contributed relatively little (1.9-13.4%, Figure 4-4) to overall floristic similarity.

Discussion

Vegetation Description

The Chapare wetlands were distinct from wetlands of the other Bolivian lowlands regions, both in floristic composition and structure. The aquatic herb *Eichhornia azurea* (Pontederiaceae) is ubiquitous throughout most of the Bolivian lowlands, where it frequently contributes to the formation of extensive floating mats of vegetation. Yet, *E. azurea* was not noted in the Chapare. A closely related species, the free-floating macrophyte *Eichhornia crassipes*, is commonly encountered in the wetlands of lowland Bolivia, also occurring in abundance in some wetlands of the dry Interandean Valleys of the Bolivian Andes. Yet, *E. crassipes* was rare in the Chapare. It was not encountered during fieldwork for this study, nor was it listed for the region by Jiménez (1984). Apparently, the population cited by Maldonado et al. (1996) is the sole record for this species in the Chapare.

The Lentibulariaceae was very poorly represented, with the ubiquitous Utricularia gibba the sole species encountered. By contrast, this family was well-represented in the Chiquitanía (17 spp., in two genera), Gran Pantanal (10 spp.), and White-water Floodplain (8 spp.) regions. Submerged macrophytes were also poorly represented, with only three species noted, *Myriophyllum mattogrossense, Mayaca longipes, and Eichhornia diversifolia*. The genus *Ludwigia* was well-represented with seven species (Appendix G). Nevertheless, *L. helminthorrhiza* and *L. sedoides*, two aquatic species sensu stricto that are very common in most of the Bolivian lowlands, were not encountered in the Chapare.

Floating vegetation mats, a typical feature of lowland Neotropical wetlands (e.g., Junk 1970, 1983), were conspicuously absent from the most of the Chapare wetlands.

Exceptions were the Ivirgarsama marsh, which possessed a well-developed floating mat of *Eleocharis acutangula*, plus a few systems visited during general reconnaissance that possessed poorly developed mats of Poaceae spp. and *Polygonum acuminatum*.

Palm swamps, a type of wetland common throughout the greatest part of the Bolivian lowlands (e.g., Balslev and Moraes 1989; Beck 1984; Moraes 1991), were not encountered in the Chapare. Although these ecosystems may have been present in the region, none were observed during my fieldwork, nor were any of the "wetland palms" (e.g., *Copernicia alba, Euterpe precatoria, Mauritia flexuosa, Mauritiella armata*) listed for the Chapare by Balslev and Moraes (1989).

Despite the Chapare's small wetland flora, relative to other Bolivian lowland regions (Table 4-2), a number of noteworthy species were present. The semi-aquatic herb *Tonina fluviatilis* (Eriocaulaceae) covered large areas of the Mariposa Wetland. Although the Eriocaulaceae is fairly well-represented in Bolivia's wetlands, with 5 genera and 17 species, *T. fluviatilis* was the sole member of the family encountered in the Chapare. Although *T. fluviatilis* is widely distributed (Mexico to Central South America, Cuba and Trinidad; Huft 1994), the species is apparently known only from three widely separated sites in Bolivia: the Mariposa wetland, a wetland in the Pando (extreme northern Bolivia), and a recently encountered population in Parque Nacional Noel Kempff Mercado (eastern Bolivia). Despite the extensive fieldwork undertaken by Haase and Beck in the inundated savannas of central Bolivia (Beck 1984; Haase 1989; Haase 1990; Haase and Beck 1989), this species apparently has not yet been collected in that region.

The submersed macrophyte, *Apalanthe granatensis* (Hydrocharitaceae), was present in abundance in the Senda F Wetland, and it was observed in a number of roadside pools and marshes in the Chapare. Additional populations were noted in the Andean Piedmont region. Although this species possesses a fairly broad distribution (Colombia to Bolivia, Cook 1985), it was previously known for Bolivia from only a single population (Cook 1985).

The wetland shrub Ludwigia latifolia (Onagraceae) is also widely distributed, ranging from Nicaragua southwards to Brazil and Bolivia (Ramamoorthy and Zardini 1987). In

Bolivia, this species was previously only known from a single site in the Chapare along the Río Isarsama (Ramamoorthy and Zardini 1987). Nevertheless, L. latifolia appeared to be fairly common in this region, as it was encountered along three streams during this study.

Other noteworthy species were the rare *Myriophyllum mattogrossense* (Haloragaceae), a submersed macrophyte that had not been known for the country (see Crow and Ritter 1999), and the waterlily, *Nymphaea glandulifera* (Nymphaeaceae), which was only previously known for Bolivia from a single population in the White-water Floodplain region (see Ritter et al. 2000). In general, the Chapare appeared to constitute the southern distributional limit for a number of wetland species, e.g*., Nymphaea glandulifera*, *Ludwigia latifolia*, *Apalanthe granatensis, Myriophyllum mattogrossense*, and *Tonina fluviatilis*.

No members of the Podostemaceae (the 'rock-weed family') were encountered in the Chapare, despite numerous localities with the favored habitat for members of this family (i.e., well-aerated, clear water, boulder-strewn beds, and direct sunlight; Philbrick and Novelo R. 1995) and despite numerous attempts by myself and Dr. Garrett E. Crow (University of New Hampshire) to locate populations of this family. On the one hand, this was not entirely unexpected, as species of the Podostemaceae have rarely been reported for Bolivia. Still, populations of the rock-weed *Apinagia boliviana* (Podostemaceae) have been collected from higher elevation rivers (ca. 1000-1100 m) on the eastern slopes of the Andes and more diverse assemblages of Podostemads were encountered during this study in various rivers draining the Brazilian shield in eastern Bolivia. As members of the Podostemaceae require a period of low water to flower (Philbrick and Novelo R. 1995), it may be that the irregular hydrologic pulses that are characteristic of the Chapare's rivers preclude the successful development of rock-weed populations.

Also of note, although perhaps more from the social than the botanical perspective, a single individual of *Erythroxylon coca* (the species from which cocaine is derived) was encountered along the edge of the Ivirgarsama Marsh. Lamentably, although this plant

had managed to escape both the cocaine producers and the anti-drug police, it succumbed during the ravages of botanical sampling.

Biodiversity

Based solely on number of species, the Chapare study sites could be characterized as species-poor. These systems possessed only 5-49 species, whereas the number of species encountered in other Bolivian lowland study sites ranged from 25-124 species. Nevertheless, there were large differences in the area of the sites being compared (e.g., 0.15 ha in the smallest Chapare site to > 30,000 ha in the largest lowland Bolivian site) and, as noted in Chapter 3, larger sites would generally be expected to contain more species (e.g., Rosenzweig 1995). As in the preceding chapter, a species-area curve was plotted for the 23 lowland Bolivian study sites and a regression line fitted to the data (see Chapter 6). The plot is reproduced here, modified so that the Chapare sites are identified by name (Figure 4-5).
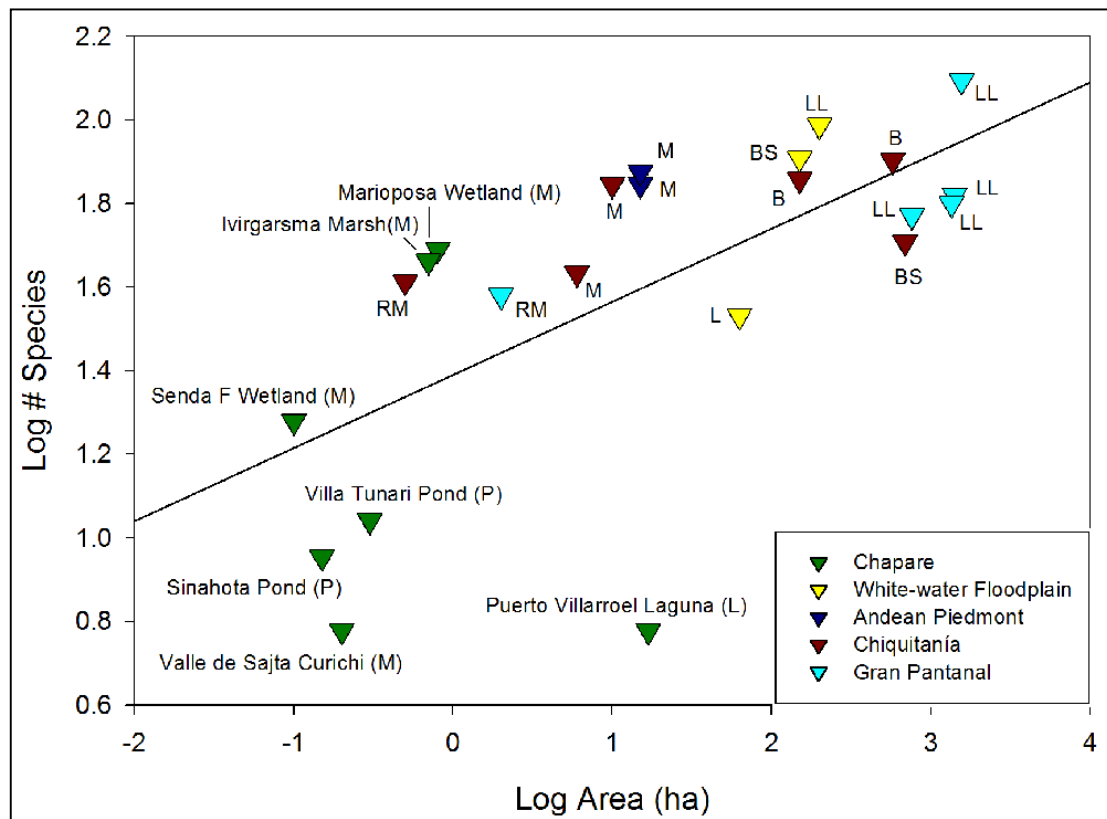

Figure 4-5. Species-area curve plotted from the 23 lowland Bolivian study sites with the Chapare study sites identified by name. Wetland types: B – bahia; BS – basin swamp; L – small lake (<500 ha); LL – large lake (> 500 ha); M – marsh; P – pond; RM – riparian marsh. Linear regression: Log S = 1.39 + 0.17 Log A. r^2 = 0.44, p = 0.00005.

Study sites situated above the regression line (Figure 4-5 were considered to be relatively species-rich, whereas those below the line were considered to be relatively species-poor. The Chapare sites could generally be characterized as species-poor, as four of the seven systems were located well below the regression line (Figure 4-5). Of the remaining systems, one was located just above the regression line, and two were situated well above the line (Figure 4-5). As noted previously (Chapter 3), the various wetland types were also found to be characteristically species-rich or -poor (see Chapter 6 for an elaboration). Three of the four systems that were located below the regression line were either ponds or lakes, i.e., wetland types that were generally found to be species-poor (Chapter 6). Thus, the question arises whether or not the characterization of the wetlands of the Chapare as species-poor was due primarily to the regional sample having a fairly large proportion of species-poor wetland types. Still, the Chapare also possessed the two least diverse lowland marshes (a species-rich wetland type), which suggests that the region's wetlands were, indeed, species-poor.

Further corroboration of the species-poor nature of the Chapare's wetlands can be evidenced in the study of Maldonado et al. (1996) who investigated 11 lacustrine systems in the Río Ichilo floodplain, in the eastern Chapare. Although the primary objectives of the study were the characterization of the physicochemical condition of the lakes and the cataloging of the microflora and microfauna, the authors also compiled a checklist of the system's vascular plants. The systems were much larger than most of my Chapare sites, except for the Puerto Villarroel Laguna, ranging in area from 7.75-84.25 ha (Maldonado et al. 1996). In total, 29 species were noted, however, as not all specimens were identified the authors only presented a partial checklist of 19 species. Site-level species-richness from this portion of the flora ranged from 3-12 species; thus, species-richness could theoretically have ranged from 13-22 species if all ten of the unidentified species were present at every site. This level of diversity was even lower than what was encountered at my seven Chapare sites, and was much lower than equivalent-sized systems in other Bolivian lowland regions. For example, the two study sites from the Andean Piedmont region were each about 15 ha in area and possessed 71 and 76 species (Appendix A).

At the regional level, the Chapare was the most species-poor (113 spp.) and the Chiquitanía the most species-rich regions (541 spp, Table 4-2). As with the site-level comparisons of diversity, however, a true measure of diversity required that regional area also be considered. As is discussed in Chapter 6, it would be ideal in a study of wetland habitats if regional area were calculated from just the area of inundated habitats within a region. Although I was able to estimate the extent of inundated area for the Bolivian lowland regions (see Chapter 7), I was unable to confidently do so for all OGUs considered here. Thus, total regional area was substituted as a surrogate for regional wetland area. As demonstrated in Chapter 7, this approach appears to be sound.

In order to establish a point of reference for comparing diversity in the OGUs, a species-area curve was plotted using cumulative species (wetland species) and area (total area) for the countries of the Neotropics and Mexico. The construction of this curve is discussed in detail in Chapter 7. A regression line was fitted to the data, representing the general trend for wetland species richness throughout the Neotropics (Figure 4-6). Discrete species-area data from the Chapare and the other OGUs considered here were added to the plot. As with the site-level species-area curves, OGUs situated above the regression line were considered as species-rich and those below as species-poor. It was evident that the Chapare could, indeed, be considered species-poor, as it was situated well below the regression line. Other species-poor OGUs were lowland Amazonian Peru and the White-water floodplain. By contrast, the Andean Piedmont region, which is contiguous with the Chapare, was the most diverse.

Low aquatic species richness in the Chapare is not in accordance with what is known for terrestrial habitats in the Andean forelands (e.g., Gentry 1988b; Salo et al. 1986). Gentry (1988a) determined that phytodiversity in the Neotropics was strongly correlated with precipitation. The richest forests were found in high rainfall areas (3,000-4,000 mm) with an aseasonal distribution of precipitation (Gentry 1988a, 1992). Gentry (1988a) also noted that under very wet conditions the relationship became linear, with an asymptote reached at annual precipitation levels of around 4,000-4,500 mm. Nevertheless, a positive relationship between species richness in aquatic plants and a pronounced dry

season had previously been noted by Haynes and Holm-Nielsen (1989) in their study of Neotropical Alismatidae; thus, the low diversity of the Chapare wetlands was not entirely unexpected.
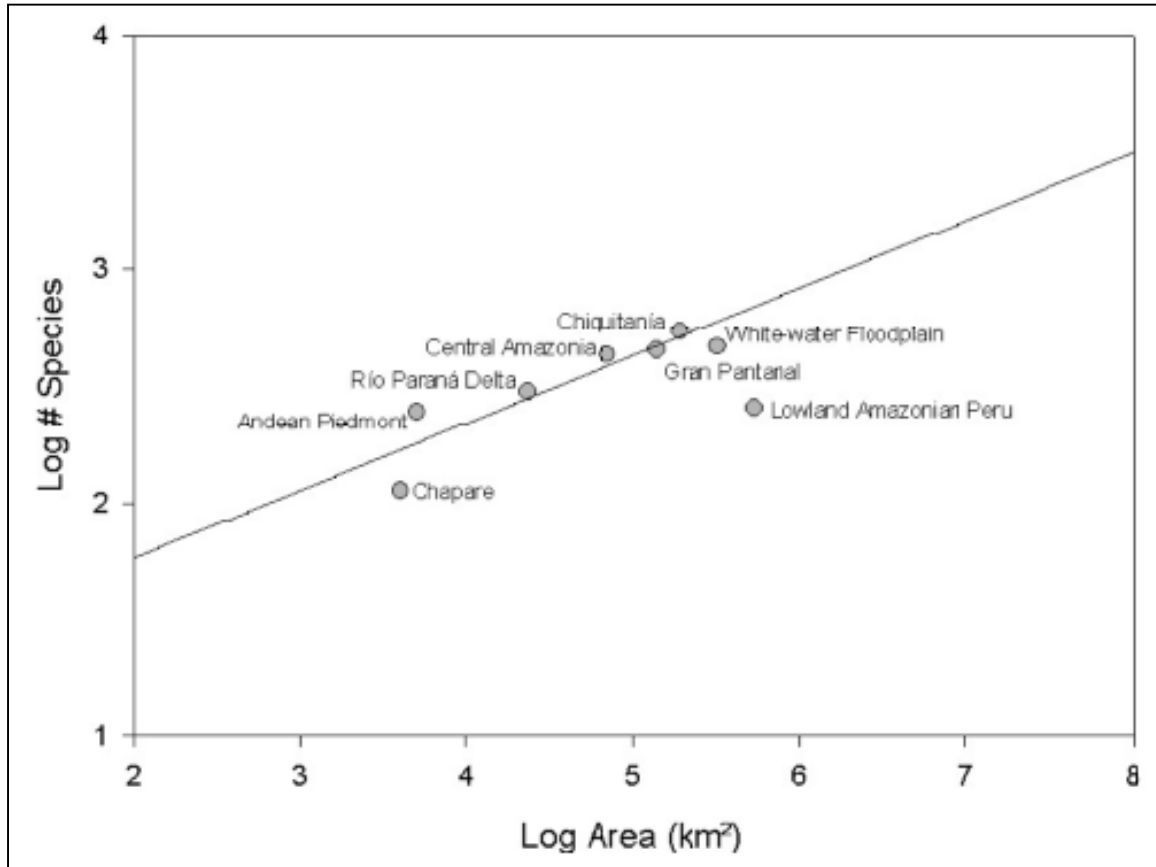

Figure 4-6. Species diversity of the OGUs considered in comparisons with the Chapare (Bolivia) wetland flora. Diversity is relative to a regression line fitted to a species-area curve plotted from cumulative species-area data from the Neotropical countries, including Mexico (see Chapter 6). Linear regression: Log $S = 1.46 + 0.25$ Log A; $r^2 = 0.99$.

In order to examine the correlation between precipitation and diversity, the number of species per OGU was plotted against precipitation and a regression line fitted to the data (Figure 4-7). A trend toward fewer species with increased precipitation was apparent, and an ANOVA test indicated that the relationship between precipitation and number of species was significant. Nevertheless, it was obvious that the Chapare strongly influenced the position of the regression line. When the Chapare was removed from consideration, an ANOVA indicated that the relationship between the two factors was no longer significant. Therefore, it did not seem that there was sufficient evidence to confidently state that annual precipitation was negatively correlated with diversity in

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Neotropical wetlands. Nevertheless, a negative correlation can be evidenced in the difference in diversity between the Chapare and the Andean Piedmont. These regions were approximately equal in area (Table 4-2) and were situated adjacent to each other along the base of the Andes. Yet, the markedly drier Andean Piedmont region (mean annual precipitation = ca. 1,700 yr^{-1}) possessed more than twice as many wetland species (244 spp.) as the Chapare (113 spp.). Furthermore, in the comparison with the general trend of diversity in the Neotropical wetland flora (Figure 4-6) the Andean Piedmont region was shown to be pronouncedly more diverse. I am inclined to think that if species and precipitation data were compiled from a series of small regions (i.e., 5000 km²), commencing with the Chapare and proceeding northwards and eastwards out onto the Beni basin, a negative correlation between these two factors would be demonstrated. Regrettably, the current state of both botanical and meteorological data from this region precludes this comparison.
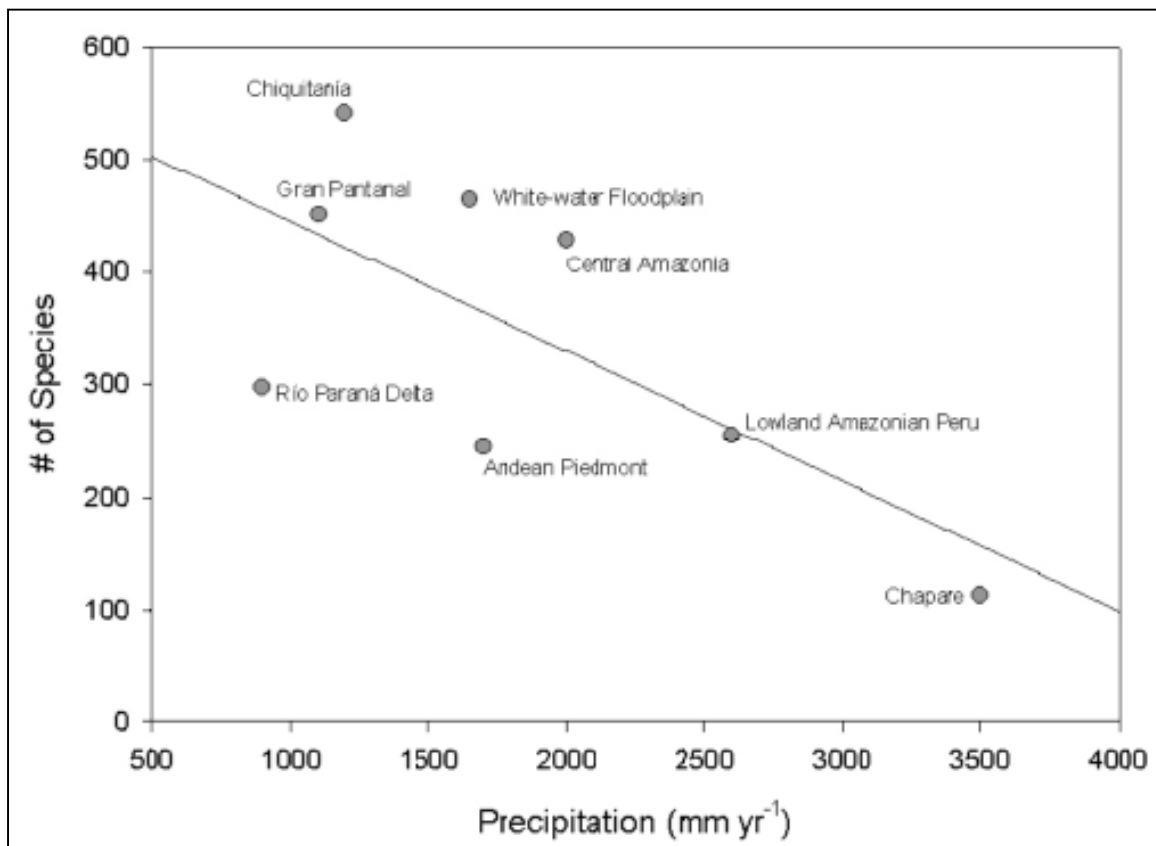

Figure 4-7. The relationship between precipitation and species richness. Linear regression: S = 560.8 - 0.12 P; r² = 0.48.

Factors other than high precipitation are thought to contribute to the high levels of phytodiversity in Amazonia. The long-held view of Amazonian rainforests has emphasized stability, with forest regeneration seen as occurring predominantly in gaps from treefall (Salo et al. 1986). In the last two decades, however, researchers investigating the effects of floodplain dynamics on lowland Amazonian forests have formulated various hypotheses regarding the contribution of hydrology to forest formation, structure, and diversity (e.g., Kalliola et al. 1991; Salo 1987; Salo et al. 1986; Puhakka et al. 1992). It is now recognized that a significant portion of lowland Amazonian forest is growing upon substrata of fluvial origin. In western Amazonia even forests that are currently unflooded have their origins in the processes that are characteristic along present-day rivers (Kalliola et al. 1991). The lateral erosion and channel migration of the meandering rivers in this region are thought to bring about large-scale natural disturbance and initiate primary succession (Salo et al. 1986). Accretion, erosion, and channel migration serve as a constant form of disturbance in this region, creating a mosaic of forests of different age structure. Approximately 0.2% of the area of the active meander plains and 0.02% of the Peruvian lowlands is eroded annually through these processes (Puhakka et al. 1992).

Salo et al. (1986) proposed that the high levels of disturbance associated with the effects of current and past river dynamics is partially responsible for the elevated biological diversity of the upper Amazon basin. They suggested that: 1) erosion and deposition created a variety of habitats which, as forest succession and erosion went forward, resulted in a mosaic of different aged forest and soil types; 2) competitive exclusion was precluded because these habitats were fairly short-lived and were highly stable in species composition; and, 3) there was a large degree of variation in water and soil chemistry, mode of sedimentation, and "case-historical biogeographical events" (Salo et al., 1986, p. 257). The authors also proposed that, as a result of the high site turnover, intense disturbance, and the resulting varied forest structure, fluvial dynamics might be a major factor in creating and maintaining the high -diversity characteristic of the upper Amazon basin. Nevertheless, as Puhakka et al. (1992) points out, the relationship between vegetation patterns and river types are poorly understood; hence, it is difficult to assess the influence that fluvial dynamics may have had on a region's biota.

Although fluvial dynamics may be positively linked with phytodiversity in lowland Amazonian terrestrial habitats, these forces appear to negatively impact the Chapare's wetlands. As river channels shift, oxbow and strand lakes are frequently formed. Many of these persist as lacustrine systems, but others may be reincorporated into the river's mainstem when the sediment dams separating them from the main channel are breached by flooding and erosion. The transitions can occur over a fairly short period of time. For example, during field research a journey was taken up the Río Ichilo to visit a large (ca. 8 km long) oxbow lake that had formed approximately two years previously (based on estimates provided by local fishermen). Upon arrival, it was found that the barriers separating the oxbow from the river had eroded, and the oxbow was once again joined with the Ichilo.

Nevertheless, many of these systems can persist as isolated basins and will undergo various stages of lake-fill (i.e., "successional stages") over time. I examined a number of such systems during this study and all appeared to be species-poor. The flora differed from system to system but, in contrast to what is known for Amazonian terrestrial habitats, it was not evident that there were particular sets of species associated with various successional stages. In Bolivian lowland wetlands it appeared that systems with well-developed floating mats of vegetation generally were the most speciose, in part because of the capability of these mats to become secondarily colonized by other taxa. As noted, floating mats were generally lacking or poorly developed in Chapare wetlands, and it seems likely that the aforementioned fluvial dynamics contributed to their paucity.

In extensive areas of lowland South America, wetlands are subjected to large-scale, regular, seasonal hydrological pulses. Rather than functioning as a disturbance and therefore limiting species richness, some researchers consider that these regular, monomodal pulses enhance diversity (e.g., Junk et al. 1989; Prado et al. 1994). The rivers of the Chapare, however, do not experience regular seasonal pulses. Instead, they fluctuate in response to precipitation in the areas from which their tributaries flow. For example, a small river that contained a population of the rare *Myriophyllum mattogrossense* was visited at the beginning of the Chapare "dry season". Water levels had dropped sufficiently for the semi-terrestrial growth-form of this species to begin to

develop along the banks. A return visit was made to this site about a month later in an attempt to collect well-developed specimens of the semi-terrestrial form, but, despite the advanced dry season, water levels were approximately a foot higher.   Although it may be that the absence of a monomodal hydrologic pulse is associated with the low diversity of the Chapare wetlands, there is still some question as to whether or not these pulses have a positive effect on wetland phytodiversity.

Any discussion of Chapare ecosystems needs to take into account anthropogenic disturbance. As noted, extensive portions of the Chapare have been converted to the production of coca (*Erythroxylum coca*), with the greatest part intended for the manufacture of cocaine. Enormous quantities of various chemicals (e.g., ammonia, ether, kerosene, potassium permanganate, sodium bicarbonate, and sulfuric acid) are used each year in the extraction of coca paste (Henkel 1995), the first step of cocaine processing. As of the early 1990's, an estimated 4000-5000 coca paste-producing laboratories were operating in the Chapare (Henkel 1995), with the chemicals used in the extraction process disposed of on site. Although it seems likely that diversity in the Chapare might be negatively impacted by such extensive chemical pollution, there is some evidence that this is not yet the case (Southwest Research Associates Inc. 1993, cited in Henkel 1995). Nevertheless, the region has unquestionably been subjected to extensive anthropogenic modifications in recent decades, and the assumption that these activities must have had some negative impact on diversity in the region's wetlands seems warranted.

Floristic Similarities

At the site level, floristic similarities (Sørensen's Index) were generally low, ranging from 0-39% Table 4-3). By contrast, floristic similarities between study sites in the Bolivian portion of the Gran Pantanal of Mato Grosso ranged from 39-58% (see Chapter 5). All of the systems in the Pantanal study (with one exception) were much larger (i.e., 3000-20,000 ha) than the Chapare sites, all but one of which were less than 2 ha. Thus, their low floristic similarities (as with the Cloud Forest study sites) were undoubtedly partially attributable to sample size. Furthermore, despite their generally low floristic similarities, the majority of the Chapare study sites were situated in close proximity in an

ordination (DCA) of the 46 Bolivian study sites (Figure 4-2). The two systems (the Puerto Villarroel Laguna and the Valle de Sajta Curichi) that were disjunct from the other Chapare study sites had extremely small floras (5 and 6 species, respectively; Table 4-3). Therefore, their positions in the ordination were most likely due to their possessing one or two species that were common in most lowland systems but absent from the other Chapare sites.

At the regional scale, the Chapare wetland flora appeared to possess equivalent affinities with the more northern Amazonian OGUs (Lowland Amazonian Peru and Central Amazonia) as with the other Bolivian lowland regions. The positions of the OGUs in the ordination by DCA (Figure 4-3) appeared to be correlated to some degree with mean annual precipitation. Precipitation in the lowland Bolivian OGUs, with the exception of the Chapare, ranged from 1200-1650 mm yr-1 (Figure 4-3). The Chapare (ca. 3500 mm yr-1, Fig. 4.3), despite its close (geographical) proximity to the other Bolivian lowland OGUs, occupied a position in ordination space somewhat disjunct from these OGUs and toward the wetter Lowland Amazonian Peru (ca. 2000 mm yr-1) and Central Amazonia (ca. 2000 mm yr-1). The Río Paraná Delta region, which was disjunct geographically and in ordination space, was also characterized by the least annual precipitation (ca. 900 mm yr-1).

A close floristic association between the Chapare, Lowland Amazonian Peru, and Central Amazonia was suggested in the phytogeographic classifications given by Cabrera (1980) and Takhtajan (1986). In both classifications the whole of the lowland Amazon basin was treated as a single floristic region. A finer-scale classification was presented by Prance (1977b). Based on terra firme (upland) forests, Prance divided Amazonia into seven major floristic regions. Lowland Amazonian Peru, the White-water floodplain, and the western portion of the Chiquitanía were placed in the "Southwest Region", the eastern portion of the Chiquitanía was in the "Solimões-Amazonas West Region", and Central Amazonia was in the "Roraima-Manaus Region" (Prance 1977b). The Chapare and the Andean Piedmont were located just outside the area proscribed by this classification.

The former phytogeographical classifications were based primarily on the distributions of terrestrial species. Some general distributional patterns of South American wetland plants were presented by Haynes and Holm-Nielsen (1989). Although not intended as a formal phytogeographical classification, Haynes and Holm-Nielsen grouped the distribution patterns of Neotropical Alismatidae, a subclass of angiosperms whose members principally occur in aquatic or wetland habitats, into 7 categories as follows: (i) "north temperate species that extend into the tropics"; (ii) "species with distribution centers in Central America and the Caribbean Islands"; (iii) "bicentric species with centers in northern South America and on the Brazilian shield"; (iv) "species with centers in southern South America"; (v) "south temperate species that extend into the tropics"; (vi) "species restricted to the Andes; and, (vii) "species of wide-ranging distribution" (1989, p. 212). None of these categories, however, with the possible exception of the cosmopolitan species (i.e., "species of wide-ranging distributions"), suggest that a strong floristic association might be expected among the wetland floras of the Chapare, Central Amazonia, and Lowland Amazonian Peru.

Haynes and Holm-Nielsen (1989) noted a scarcity of species in the subclass Alismatidae in Neotropical regions that did not experience a pronounced wet-and-dry seasonality, and this pattern was evident among the OGUs considered here (Table 4-5). The Alismatidae was poorly represented in the Chapare relative to other Bolivian lowland regions. Central Amazonia was approximately as poor in members of the Alismatidae as the Chapare (Table 4-5), although the subclass was much better represented in Lowland Amazonian Peru. Within the subclass, the family Alismataceae was particularly poorly represented in both the Chapare and Central Amazonia, with a single species noted for each region. By contrast, 4-10 species were present in the other Bolivian OGUs, whereas 11 species were noted for Lowland Amazonian Peru (Table 4-5). Although both the Alismataceae and the Alismatidae were better represented in Lowland Amazonian Peru than in the other two "wet" OGUs (the Chapare and Central Amazonia), Lowland Amazonian Peru is contiguous with the White-water floodplain region and includes areas with relatively low annual precipitation (Instituto Geográfico Nacional 1989). Hence, it seems reasonable that at least a portion of the species of Alismatidae noted for this region were restricted to these drier areas.

Table 4-5. Presence of the Alismatidae and the Alismataceae in selected OGUs. Note: the Río Paraná Delta region was excluded from these comparisons because it is situated far outside of the limits of Amazonia.

Region	Families	Genera	Species	Alismataceae (spp.)
Chapare	3	4	4	1
Andean Piedmont	5	9	12	4
White-water Floodplain	5	8	15	9
Chiquitanía	5	8	15	10
Gran Pantanal	5	9	23	13
Lowland Amazonian Peru	5	9	18	11
Central Amazonia (Brazil)	3	3	3	1
Río Paraná Delta	5	10	17	4

Although the ordination by DCA (Figure 4-3) and the distribution of the Alismatidae both suggested a strong floristic association among the "wet" OGUs, this relationship was not apparent in the histograms of the species frequency classes (Figure 4-4). The relationships between the Chapare wetland flora and the other OGUs consistently followed the same general pattern, with "ubiquitous" (present in all OGUs) and "widely shared" species (present in six OGUs) contributing the greatest amount to floristic similarities (Figure 4-4). The largest contribution of "rarely shared" species (restricted to 2-3 OGUs) to floristic similarity was between the Chapare and Lowland Amazonian Peru (13.4%); however, the smallest percentage of floristic similarity attributable to this same species class was between the Chapare and the other "wet" OGU, Central Amazonia (1.1%). Thus, the presumed close relationship among the floras of the wet OGUs was neither supported nor refuted by the distribution of frequency classes.