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Biodiversity and phytogeography of Bolivia's wetland flora

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BIODIVERSITY AND PHYTOGEOGRAPHY OF BOLIVIA'S WETLAND FLORA

BY

NUR P. RITTER

B.S. University of New Hampshire, 1992

DISSERTATION

Submitted to the University of New Hampshire
in Partial Fulfillment of
the Requirements for the Degree of

Doctor of Philosophy
in Natural Resources

December, 2000

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8 December 2000

Date

DEDICATION

To Carlos and Anna Aliaga, without whose friendship and support
this work would not have been possible.

And to my wife, Martha Ritter.
A list of her contributions to this project, and to my life,
would exceed the length of this dissertation.

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ABSTRACT

BIODIVERSITY AND PHYTOGEOGRAPHY OF BOLIVIA'S WETLAND FLORA

by

Nur P. Rittter

University of New Hampshire, December 2000

The composition, diversity, and phytogeographic affinities of the vascular flora of Bolivia's wetlands were examined and compared with wetland floras from the other Neotropical countries and the New World Temperate region. Forty-six wetlands distributed throughout Bolivia and ranging in elevation from 90 m to > 4400 m were established as study sites. Regional and national wetland floras were compiled from field research, the literature, herbarium specimens, and available databases.

Two thousand and sixty species in 149 families and 666 genera were identified as associated with wetlands in Mesoamerica and tropical and subtropical South America. Of these, 1026 species in 126 families and 450 genera were noted for Bolivian wetlands. When considered both in terms of number of species per system and in comparisons of species-area curves, Bolivia's wetlands were found to be less diverse than wetlands of the New World Temperate region. At the macroregional level, both South and Central America were less diverse than the New World Temperate region. Thus, at both the system and regional scales, it appeared that phytodiversity in New World wetlands constituted an exception to the widely recognized latitudinal gradient in species richness.

Additionally, phytodiversity in Neotropical wetlands was generally not well-correlated with diversity in terrestrial habitats.

A large portion of the Neotropical wetland species possessed very broad ranges, and few endemic species were noted relative to the Neotropical terrestrial habitats. Similarity Indices were generally unsatisfactory for analyzing floristic similarities at the system level. Both Detrended Correspondence Analysis (DCA) and Frequency Analysis produced more satisfactory results. Species that typically tended towards dominance in Bolivian wetlands most often were extremely widely distributed, precluding the identification of regional wetland associations based on dominant species. Nevertheless, ordination of the study sites by DCA generally grouped wetlands from within the same Bolivian region. At the macroregional level, an ordination by DCA ordered the countries of the Neotropics into three groups: 1) Bolivia, Brazil and Peru; 2) Colombia, The Guianas, and Venezuela; and, 3) all Central American countries. Two countries, Mexico and Ecuador, were not clearly associated with any group.

CHAPTER I

INTRODUCTION

> Wetlands are a place of the alien reptilian 'other', even the home of monsters lurking in their murky depths. Rather than fascination, horror has been the typical patriarchal response to wetlands which have been seen as infested with malaria, miasma and melancholia.
> - R. J. Giblett, *Postmodern Wetlands. Culture, History, Ecology*

> ... there are certain water plants which are so striking and in places so abundant that in themselves they make scenes. Two of these (*Mourera fluviatilis* and *Lacis alata*) grow on the half-submerged rocks in most of the falls. As the water decreases in the dry season, the tall spikes of bright flowers of the former plant rise from their large leaves, the edges of which are cut and curled into the likeness of moss, which lie flat on the rocks; and at the same time and place, innumerable tiny pink stars rise an inch or two over the equally moss-like leaves of the *Lacis*. A rapid, apparently encircled by the forest, and with its rocks all reddened by these flowers, is very beautiful and noticeable.
> - E. F. Im Thurn, *Among the Indians of Guiana*

Bolivia

The Republic of Bolivia is situated in the approximate center of South America, between 10° and 23°S latitude (Fig. 1.1). The country occupies an estimated area of 1,098,581 km^2 (Central Intelligence Agency 2000), equivalent to approximately three times the area of Montana. Formerly, the country's borders extended to the Pacific coast, however during the late nineteenth century the coastal portion of the country was surrendered to Chile during a conflict. Hence, Bolivia is now, along with Paraguay, one of South America's two landlocked countries.

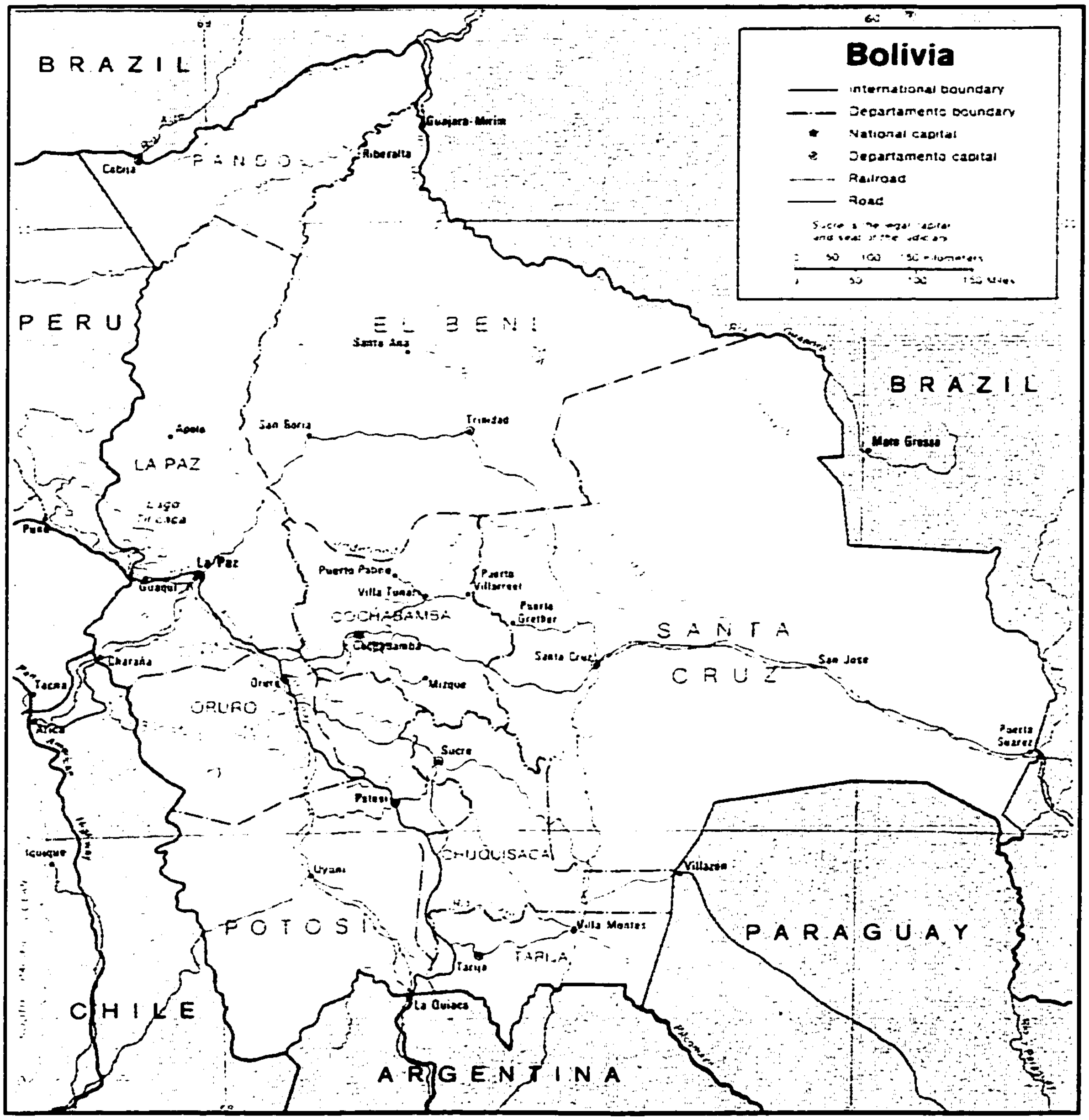


Figure 1.1. Bolivia, including major population centers and regionally important towns, primary roads, major water bodies, and political divisions (reproduced from The World Factbook, Central Intelligence Agency 2000). Uppercase names indicate the country's nine Departamentos (the highest level political division). The mountain range illustrated in the western portion of the country is the Andean range.

Bolivia constitutes an exemplary setting for botanical investigations. That is, due to the country's location in the center of the continent and to the presence of the Andes, the Bolivian flora contains elements from four phytogeographic regions: the Andean, Amazonian, Chaco, and Cerrado (Killeen *et al.* 1993). Topography is extremely variable, with elevations varying from greater than 6500 m in the Andes to less than 100 m in the lowlands (Nogales *et al.* 1991). Precipitation is also extremely variable, with annual average precipitation varying from less than 100 mm to greater than 6000 mm (Solomon 1989).

The country's topographic and climatic variability, in combination with its location and a varied geography, have provided Bolivia with a rich flora. Solomon (1989, p. 459) postulated that the Bolivian flora was "one of the most diverse for its area in all of South America", and estimated that the complete Bolivian flora might contain around 18,000 species. At the time of Solomon's estimate, approximately 10,000 species had been recorded for the country. Currently, estimates place its flora at ca. 16,800-17,300 species (P. Jørgensen, pers. com.).

Additional factors suggest that Bolivia might possess a particularly rich wetland flora. The country's rivers belong to three major hydrologic systems: the Amazon, the Paraná, and the Desaguadero (Fig. 1.2). The Río Iténez, which delineates the country's eastern border with Brazil, and the rivers that drain the eastern slopes of the Andes and the vast plains of northern and north-eastern Bolivia are all part of the Amazon river watershed (Fig 1.2). These areas constitute approximately three-quarters of the Río Madeira drainage basin (Guyot and Watson 1994); the Río Madeira is the Amazon's

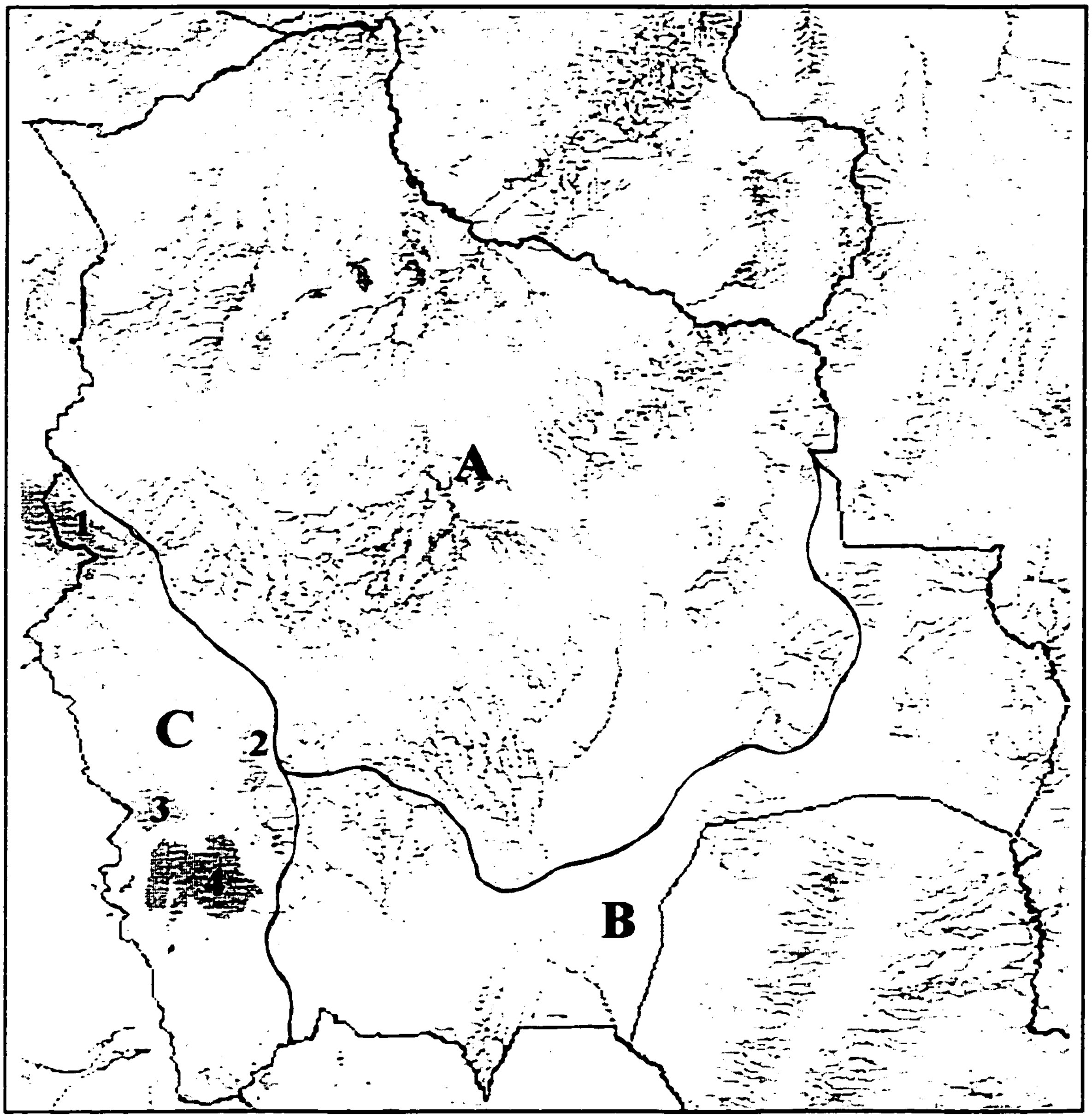


Figure 1.2. Hydrographic map of Bolivia. Watersheds: **A**. Amazon. **B**. Paraná. **C**. Desaguadero. Principal catchments: 1. Lago Titicaca. 2. Lago Poopo 3. Salar de Coipasa. 4. Salar de Uyuni. Map generated with AGIS (1999). Limits of the watersheds drawn as per Nogales et al. (1991).

second largest tributary and the world's sixth largest river based on discharge (Meade *et al.* 1991). Southeastern Bolivia and the southern portions of the Cordillera Central (Central Range) and Cordillera Oriental (Eastern Range) of the Andes are all part of the Río Paraná drainage (Fig 1.2). The Amazon river extends far northwards and the Paraná far to the south of Bolivia. These river systems should function as corridors for the immigration of wetland species from the tropical and temperate regions of South America.

The Río Desaguadero watershed (Fig 1.2) is composed of the aquatic systems of the Bolivian portion of the *Altiplano*, the high elevation (mean elevation ca. 3,800 m, Solomon 1989) plateau that is situated between the Cordillera Central and the Cordillera Oriental in Peru and Bolivia. Whereas the Río Desaguadero is neither as large nor as widely-known as the Amazon or the Paraná, two large and well-known lakes (Lago Titicaca and Lago Poopó) constitute the river's two primary catchments. The Desaguadero is essentially a closed watershed (Nogales *et al.* 1991), and, hence, does not function as a corridor for the immigration of species from extra-Bolivian regions. Nevertheless, the Altiplano is about 965 kilometers long, and Puna ecosystems (the characteristic vegetation of the southern High Andean region) extend for approximately 1400 km (Baied and Wheeler 1993), and it seems likely that the numerous water bodies that are scattered throughout the Altiplano would facilitate the migration of propagules.

General Botanical Research In Bolivia

Bolivia is said to be the least botanically investigated country of South America (Prance 1977a) and many areas of the country still remain completely unexplored botanically (Killeen *et al.* 1993; Solomon 1989). In the late 1970's Prance (*loc. cit.*) declared that little botanical collecting had been undertaken in Bolivia since Herzog's collections in the early part of the twentieth century. Solomon (1989) estimated that the total number of vascular plant collections from Bolivia was around 90,000 specimens. This was equal to about one-tenth of the collections made from Central America (Solomon 1989), which possesses only about one-half of the area of Bolivia. Based on this figure, collection density for Bolivia was equivalent to only 8 specimens per 100 km^2 (Solomon 1989). Considering that these collections were not distributed equally throughout the country, but were generally concentrated around the country's population centers and from a few other easily accessible areas (Solomon 1989), the lack of baseline botanical data is obvious. Surprisingly, despite the paucity of collections of vascular plants Bolivia's cryptogamic flora is said to be the best known of any of the Neotropical countries (Funk and Mori 1989).

Perhaps the most well-known botanical investigation in Bolivia was the Mulford Expedition to the Bolivian Amazon in 1921-1922, which was led by Dr. Henry H. Rusby of the New York Botanical Garden (Rusby 1922; White 1922). The Mulford expedition resulted in the description of numerous new species (Rusby 1922), and generated one well-known and particularly interesting anecdotal account (MacCreagh 1926). Because much of the research took place in a virtually unexplored area, many new species and genera were described from the approximately 2400 specimens that were collected during the expedition (Rusby 1922). Despite the intention to publish a comprehensive list of the species collected during the expedition (Rusby 1922), apparently no such list was ever published (Funk and Mori 1989). In accordance with the standards of the time, few, if any, specimens were deposited in the host country.

One of the participants of the Mulford expedition was Martín Cárdenas, at that time still a university student (Rusby, 1927). Dr. Cárdenas, who would become Bolivia's most well-known botanist, collected extensively in the region around his home in Cochabamba, however, despite a long and vigorous career as a botanist, it does not appear that he ever published any specific accounts of aquatic habitats. Cárdenas accumulated a large number of botanical specimens, but after his death his collection was entrusted to the herbarium at Tucumán (Argentina) and thus was not accessible for this study.

In the last 15 years or so, important collections of flowering plants have been made in Bolivia by the following researchers: Susana Arázola and Gonzalo Navarro (BOLV), Robin Foster (F), J. Richard Abbott (FLAS), Martha Serrano and John Wood (HSB), Steven Renvoize (K), Stephan Beck, Emilia Garcia E., and Monica Moraes (LPB), James C. Solomon (MO), Timothy Killeen (MO & USZ), Michael Nee (NY), and Rene Guillén, Mario Saldías, and Israel Vargas (USZ). A significant portion of this work was conducted in areas that had previously received little botanical attention. The research of most of these individuals, with the notable exceptions of Stephan Beck and Gonzalo Navarro, focused primarily on terrestrial habitats. Nevertheless, during these investigations a number of aquatic specimens were also collected. These latter specimens, many of which were deposited at LPB and USZ, were a valuable resource during the course of my study.

Killeen *et al.* (1993) noted that botanical research in Bolivia has accelerated greatly during the last twenty years, and that the number of collections made in the 10 years prior to 1993 was greater than those made in the preceding 100 years. Since the time of Killeen's comments, the rate of botanical research has, at the very least, continued apace. An excellent synopsis of plant collections from Bolivia was produced by Funk and Mori (1989). Foster (1958) compiled a checklist of the ferns and flowering plants for Bolivia that for many years remained the principal account of the country's flora. Given the recent increase in botanical research in Bolivia both of these publications are currently in need of revision.

Research In Bolivian Wetlands

Wetlands, in general, are uninviting, and tropical wetlands are perhaps more so, as they are frequently dangerous places that present many difficulties for plant collectors. Hence, it is not surprising that tropical macrophytes have been inadequately collected (*e.g.*, Prance 1977b). Although the majority of botanical expeditions have tended to avoid collecting in wetlands, nevertheless, some investigations of Bolivian wetlands have been undertaken. A brief synopsis of these activities is presented here.

The aforementioned Mulford Expedition (Rusby 1922) appears to have produced one of the earliest accounts of botanical research in Bolivia's wetlands. Approximately one month of the nearly two-year-long expedition was centered near Lago Rogagua, in the lowlands between the Río Mamoré and the Río Beni. Unfortunately, this portion of their expedition was during the "early spring" and the majority of the plants were not yet in flower (Rusby 1922). Nevertheless, White (1922) provided a short description of the vegetation in the savannas surrounding Lago Rogagua. Martín Cárdenas, one of the participants in this expedition, later returned to the Lago Rogagua area. Regrettably his account of this second journey (Cárdenas 1953) was primarily anecdotal and little description of the aquatic vegetation was given.

In more recent times, a number of floristic studies of Bolivian wetlands have been published. Examples are: Beck (1984), Cadima and Collot (1982), Estenssoro C. (1991), Franken (1991), Frey (1995), Haase (1989, 1990), Haase and Beck (1989), Hanagarth (1993), Justiniano M. (1998), Lara R. & Cazas (1996), Maldonado *et al.* (1996), Navarro (1993), and Raynal-Roques (1991). The studies of Stephan Beck and Ranier Haase in the Llanos de Moxos (an extensive complex of inundated savannas in the Bolivian lowlands) were particularly noteworthy. The Llanos de Moxos are said to be the largest area of inundated savannas in the Amazon basin (Hanagarth 1993) and Beck and Haase's research (Beck 1984; Haase 1989, 1990; Haase and Beck 1989) appears to constitute the first large-scale floristic investigation of this important ecosystem.

The Current Study

My interest in investigating phytodiversity in Neotropical wetlands was sparked by observations from a few researchers who noted that Neotropical wetlands were surprisingly species-poor. These observations were noteworthy for being contrary to the widely recognized latitudinal gradient in species richness (Blackburn and Gaston 1996; Brown 1988; France 1998; Qian 1998; Rosenzweig 1995; Stevens 1989), which holds that the Tropics are exceptionally rich in species.

The earliest published reference to Neotropical wetlands being noticeably poor in vascular species may be that of Black (1950), who noted that aquatic plants rarely occupied a position of much importance in the Amazonian flora ("as plantas verdadeiramente aquáticas, com poucas exceções, não ocupem posição de muita importância na flora da Amazônia", cited in Takeuchi 1962, page not specified). Three decades later, Haynes and Holm-Nielsen (1986, p. 14) observed that the Amazon basin possessed a "remarkably low diversity of fresh-water aquatic vascular plants." In a subsequent paper, Haynes and Holm-Nielsen (1989, p. 211) elaborated on this condition, noting that the Alismatidae (a subclass whose members are primarily associated with wetland habitats) was "almost completely absent from the Amazon basin." Later, Crow (1993, p. 229) determined that wetland floras throughout the Neotropics were relatively species-poor in comparison to northern temperate regions, stating that "a comparison of aquatic plant diversity on a latitudinal basis reveals a higher level of diversity at warm temperate latitudes and a surprisingly high, if not highest, level at cool temperate latitudes." Although I have presented the preceding observations in the order of their appearance in the literature, it was the work of Crow (1993) that first kindled my interest in the phytodiversity of Neotropical wetlands.

With a population of about 8,000,000 (July, 1999 estimate, Central Intelligence Agency 2000) and a national territory of more than 1,000,000 km^2, Bolivia possesses one of the lowest population densities in South America (7.2 persons per km^2), trailing only the three countries of the Guianas in this regard. Historically, the greatest portion of the population has been centered in the Altiplano and the Valles Secos region (a series of dry, Interandean Valleys that are situated at about 2800-2600 m). Hence, extensive areas of the country are still relatively unmodified by human activity. In recent years, however, many areas have been heavily altered by exploration for petroleum, large scale agricultural development, the construction of new roads, and the activities that accompany these new roads, such as logging and small scale agriculture. In addition, the Bolivian Pantanal is threatened by the proposed Hídrovia, a 3,400 km long waterway linking Bolivia, Paraguay, Brazil, Argentina and Uruguay (Halloy 1997). Therefore, as with almost all other areas of the underdeveloped world, there is an urgent need to maximize research in existing ecosystems before they are seriously disrupted. The 14 studies of Bolivian wetlands catalogued in the preceding section appear to represent the greatest portion of floristic research undertaken in the country's wetlands. Given the rudimentary state of Bolivian wetland research and the threats facing the country's natural habitats, the urgency for the baseline floristic data is clear.

Objectives

My study had five major objectives: 1) to identify species associated with wetland habitats in Bolivia; 2) to characterize and describe representative aquatic and wetland plant associations; 3) to determine the range of species richness in the wetland flora at the system, microregional, and macroregional scales; 4) to examine phytogeographic patterns among the study site floras and among the wetland floras of selected regions within Bolivia; and, 5) to compare phytogeographic patterns and relationships of the Bolivian wetland flora with selected New World countries and regions.

To these ends the wetland vegetation from various regions of Bolivia is listed and described. Phytodiversity is estimated from the range of species richness noted for a series of study sites, and from compiled regional wetland floras. Wetlands and regions that contained unique species or associations are identified. Floristic and phytogeographic analyses are made between study sites, between regions within Bolivia, and between regions and countries in tropical and subtropical South and Mesoamerica.

Descriptions and analyses are presented for all eight Bolivian regions considered in this study. Three of these, the Cloud Forest (Chapter 3), the Chapare (Chapter 4), and the Gran Pantanal (Chapter 5) are given expanded treatments. These regions were selected because they were either known to possess rich terrestrial floras (the Cloud Forest and the Chapare) or were expected to possess rich wetland floras (the Gran Pantanal).

CHAPTER II

MATERIALS AND METHODS

> Up to the age of 30 or beyond it, poetry of many kinds...gave me great pleasure, and even as a schoolboy I took intense delight in Shakespeare....formerly pictures gave me considerable, and music very great, delight. But now for many years I cannot endure to read a line of poetry: I have tried to read Shakespeare, and found it so intolerably dull that it nauseated me. I have also almost lost any taste for pictures or music.... I retain some taste for scenery, but it does not cause me the exquisite delight which if formerly did.... My mind seems to have become a kind of machine for grinding general laws out of large collections of facts, but why this should have caused the atrophy of that part of the brain alone, on which the higher tastes depend, I cannot conceive.... The loss of these tastes is a loss of happiness, and may possibly be injurious to the intellect, and more probably to the moral character, by enfeebling the emotional part of our nature.
>
> - Charles Darwin

> The investigation of nature is an infinite pasture-ground, where all may graze, and where the more bite, the longer the grass grows, the sweeter is its flavor, and the more it nourishes.
>
> - Thomas Henry Huxley (Cited in D. Boorstin, *The Discoverers*)

Study Site Selection

Potential wetland study sites were considered based upon a number of sources, including satellite images, vegetation maps, and topographic maps. Information was also obtained from other botanists, ecologists, ornithologists, and other researchers familiar with biological fieldwork in Bolivia. Additional input was sought from administrators of the Fundación Amigos de la Naturaleza (F.A.N.), the organization that manages a number of Bolivia's national parks, and from park guards and *guiás del campo* (field guides) in the National Park System. Potential study sites were also identified from site descriptions on herbarium specimens at the Museo Noel Kempff Mercado (USZ; Santa Cruz), the Herbario Nacional (LPB; La Paz), and the Herbario Forestal Martín Cárdenas (BOLV; Cochabamba). Study sites were chosen to create a reasonable representation of Bolivia's geographic, ecological, and elevational variability. At times, study site selections were weighted by necessity towards accessibility and the opportunity to coordinate with other ongoing biological investigations in the vicinity of the study sites.

Forty-six wetland systems were chosen as study sites (Table 2.1; Appendix A). Because meeting the objectives of this study necessitated establishing a large number of widespread study sites, it was critical to limit the types of wetland habitats included. Inundated riparian forest and seasonally inundated savanna can clearly be considered as wetlands (*sensu* Cowardin *et al.* 1979; Mitsch and Gosselink 1993), however, the inclusion of these types of habitats would have added enormously to the complexity of the project. It seemed that their exclusion would not detract significantly from attaining my study objectives, therefore, research focused on "traditional" (from a northern temperate viewpoint) aquatic habitats: those occupying basins or channels (*i.e.*, lakes, ponds, rivers, and streams) and those inundated throughout the greatest part of the year (*i.e.*, "marshes" and "swamps"). Nevertheless, although no inundated riparian forest or seasonally inundated savannas were included as study sites, general botanical reconnaissance and collecting were undertaken in these habitats and specimen data from this fieldwork were included in regional checklists (see Appendices B and C).

Table 2.1 Forty six study sites selected to represent Bolivian wetlands, with region, elevation, estimated area, Departamento (the 1st major political division), Provincia (the 2nd level political division), and major watershed.

Site [A]	Study Site	Region	Elev. (m)	Area (ha.)	Departamento	Provincia	Watershed
P	Laguna Toro	High-Andean	4420	2.5	Cochabamba	Ayopaya	Amazon
U	Huayalmarca Pond	High-Andean	4300	0.1	Oruru	Cercado	Desaguadero
Q	Laguna Saythu Khocha	High-Andean	4020	40	Cochabamba	Tiraque	Amazon
Q	Laguna Totora Khocha	High-Andean	3620	120	Cochabamba	Tiraque	Amazon
P	Laguna Larati	High-Andean	3540	124	Cochabamba	Chapare	Amazon
Q	Laguna Juntutuyo	High-Andean	3360	244	Cochabamba	Arani	Amazon
O	Río Candelaria	High-Andean	3165	1.0	Cochabamba	Chapare	Amazon
R	Laguna Chulichuncani	High-Andean	3160	20	Cochabamba	Carrasco	Amazon
P	Laguna Alalay	Valles Secos	2550	170	Cochabamba	Cercado	Amazon
S	Río Mizque Wetland	Valles Secos	1970	0.5	Cochabamba	Mizque	Amazon
V	Río Guadalquivir Wetland	Valles Secos	1800	0.5	Tarija	Cercado	Paraná
P	Tiquipaya Irrigation Canal	Valles Secos	2620	0.02	Cochabamba	Cercado	Amazon
O	Chimpa Huata Bog	Cloud Forest	2920	0.05	Cochabamba	Chapare	Amazon
O	Incachaca Pond	Cloud Forest	2385	1.0	Cochabamba	Chapare	Amazon
O	Laguna Khonchu - East	Cloud Forest	2620	0.07	Cochabamba	Chapare	Amazon
O	Laguna Khonchu - West	Cloud Forest	2620	0.09	Cochabamba	Chapare	Amazon
O	Corani Pampa Marsh	Cloud Forest	2470	0.02	Cochabamba	Chapare	Amazon
R	Siberia Marsh	Cloud Forest	2800	0.75	Cochabamba	Carrasco	Amazon
M	Mariposa Wetland	Chapare	220	0.8	Cochabamba	Carrasco	Amazon
M	Ivirgarsama Marsh	Chapare	220	0.7	Cochabamba	Carrasco	Amazon
M	Senda F Wetland	Chapare	220	0.1	Cochabamba	Carrasco	Amazon
N	Villa Tunari Pond	Chapare	300	0.3	Cochabamba	Chapare	Amazon
N	Sinahota Pond	Chapare	240	0.15	Cochabamba	Tiraque	Amazon
M	Valle de Sajta Curichi	Chapare	210	0.2	Cochabamba	Carrasco	Amazon
M	Puerto Villarroel Laguna	Chapare	190	30	Cochabamba	Carrasco	Amazon
A	Riberalta Ciénaga	White-Water Floodplain	170	150	Beni	Vaca Díez	Amazon
A	Laguna Tumechuqua	White-Water Floodplain	170	300	Beni	Vaca Díez	Amazon
B	Laguna Suarez	White-Water Floodplain	160	600	Beni	Cercado	Amazon
K	Bermudez Curichi	Andean Piedmont	430	15	Santa Cruz	Andres Ibañez	Amazon
K	Viru Viru Wetland	Andean Piedmont	430	15	Santa Cruz	Andres Ibañez	Amazon

Table 2.1 (continued).

Site [A]	Study Site	Region	Elev. (m)	Area (ha.)	Departamento	Provincia	Watershed
W	Laguna Yaguacua	Chaco	920	30	Chuquisaca	Luís Calvo	Paraná
G	Concepción Wetland	Chiquitanía	485	10	Santa Cruz	Ñuflo de Chavez	Amazon
E	Huanchaca Arroyo	Chiquitanía	760	0.04	Santa Cruz	Velasco	Amazon
F	La Toledo Curichi	Chiquitanía	220	6	Santa Cruz	Velasco	Amazon
F	Bahia Toledo	Chiquitanía	210	150	Santa Cruz	Velasco	Amazon
F	Río Paraguá	Chiquitanía	210	0.5	Santa Cruz	Velasco	Amazon
D	Cuatro Vientos Palm Swamp	Chiquitanía	205	690	Santa Cruz	Velasco	Amazon
C	Lago Caimán	Chiquitanía	200	575	Santa Cruz	Velasco	Amazon
H	Laguna Uberaba	Pantanal	85	30,000	Santa Cruz	Angel Sandoval	Paraná
H	Laguna La Gaiba	Pantanal	90	10,500	Santa Cruz	Angel Sandoval	Paraná
I	Laguna Mandioré	Pantanal	90	25,000	Santa Cruz	Angel Sandoval	Paraná
J	Laguna Cáceres	Pantanal	90	3,500	Santa Cruz	German Busch	Paraná
H	Puesto Gonzalo	Pantanal	90	2.0	Santa Cruz	Angel Sandoval	Paraná
L	Laguna Volcan	Transition	1150	3.0	Santa Cruz	Florida	Amazon
T	Yolosa Marsh	Lower Montane	1150	0.05	La Paz	Nor Yungas	Amazon
N	Cristalmayu Pond	Lower Montane	640	0.5	Santa Cruz	Andres Ibañez	Amazon

A. The letter appearing before the study site is the key to its location on Figure 2.1.

Additionally, data from studies of a variety of inundated forest types (*e.g.*, Foster *et al.* 1997; Junk 1989; Keel and Prance 1979; Klinge *et al.* 1990; Pires and Prance 1985; Worbes 1997) were utilized in the ascription of wetland species (see below).

The study sites encompassed a wide elevational range (Table 2.1), with the lowest site at about 90 m and the highest above 4400 m. Distribution of the study sites favored the lowlands. This distribution was partially due to the small number of wetlands in montane and dry valley habitats relative to the abundant lowland systems, and to the difficulties associated with locating wetlands in forested montane habitats. Moreover, as research progressed much more time was spent investigating the lowlands, as lowland systems generally proved to be richer and more interesting.

The study sites were also broadly distributed geographically throughout Bolivia (Fig. 2.1), although there was a strong correlation between study site density and proximity to the city of Cochabamba, my primary place of residence during the course of field research. Nevertheless, at least one study site was established in all but one of Bolivia's nine Departamentos (the principal political division, Table 2.1, Fig. 2.1), with Potosi the sole Departamento lacking a study site.

Vegetation Sampling

Initially, consideration was given to establishing a plot-based sampling methodology. In recent decades, researchers assessing phytodiversity in Neotropical terrestrial habitats have frequently employed standardized 0.1 hectare samples (*e.g.*,

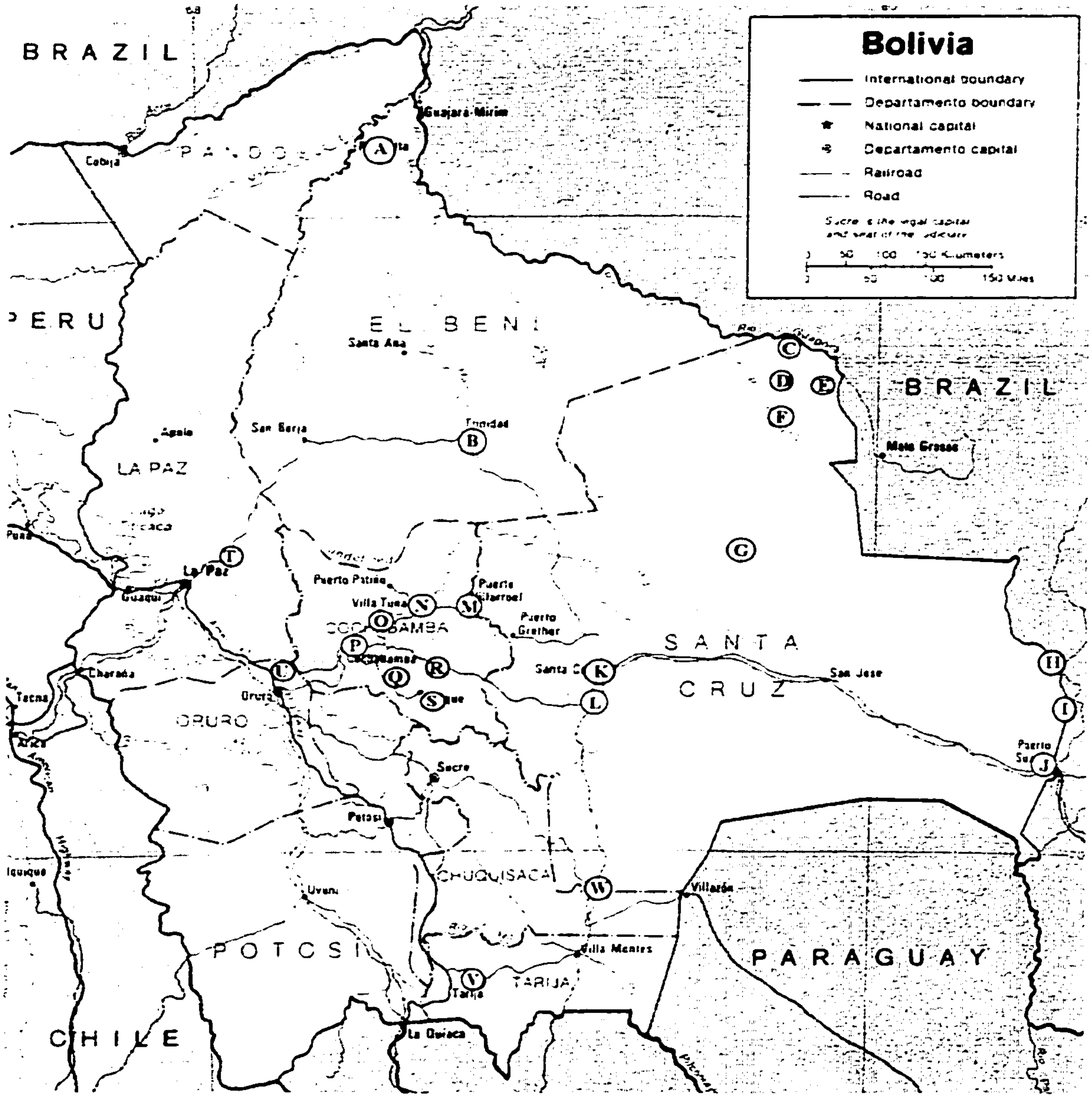


Figure 2.1. The forty-six Bolivian study sites. Letters in circles correspond to study sites as indicated in Table 2.1.

Gentry 1988a, 1995). In this approach, plants with dbh >2.5 cm (trees, "treelets", lianas and "even overgrown herbs" Gentry 1995) are censused from a series of 2 m X 50 m quadrats. Special problems are encountered in vegetation sampling in aquatic ecosystems; therefore, protocols developed for terrestrial habitats are often inadequate for aquatic research.

Some methodologies have been proposed specifically for floristic sampling in aquatic habitats. Crow (1993) cited the work of Gentry (1988a) and noted that no analogous approach had been developed for sampling in wetlands. Crow suggested that 0.01 ha might serve as an appropriate sample size in wetlands, as "a relatively quick means of gathering data sets to make comparisons (of species richness) between various aquatic habitats" (1993, p. 253). Apparently, a single 0.01 ha quadrat was assumed to be sufficient for any size system. Jensen proposed a methodology for sampling aquatic vegetation in lacustrine systems, with an aim toward developing "a rapid method to characterize and sample the macrophyte vegetation" (1977, p. 107). Sampling was limited to a series of nested relevés that were situated along a belt transect around the perimeter of the lake and along a series of profile transects. Relevé size was dependent upon the dominant life-form of the zone being sampled, while the number of profile transects were a function of shoreline length, system area, and fetch. Dubois *et al.* (1984) adopted the methods of Jensen (1977) and proposed some modifications for riverine systems.

Despite the demonstrated utility of some of these methods, applying any plot-based methodology to many of the Bolivian study sites would have been problematic. In some systems, the width of the vegetated zone from the marsh edge to open water approached 100 meters. This approach would have necessitated installing long, narrow quadrats barely a meter in width. The logistics of delineating such quadrats on the flexible and often weakly coalesced floating mats of vegetation that are characteristic of many lowland wetland habitats would have been daunting.

Furthermore, wetlands in the lowland Tropics are often extremely dynamic, with multiple "growing seasons" occurring in a single year due to seasonal changes in hydrology. Hence, an area dominated by a particular group of species during one set of hydrologic conditions may support an entirely different flora during a subsequent hydrologic period. In some systems, this process manifests as a seasonal change from hydrophytic to terrestrial vegetation. In other systems, however, different associations of hydrophilic vegetation may dominate the same area during different seasons. Clearly, in order to achieve a complete estimate of diversity a site should be sampled during as many different hydrologic stages as possible. Hence, additional difficulties would arise in any plot-based study because of the need to accurately re-locate quadrats during repeated sampling.

Although re-locating sampling areas might not present a significant problem in most temperate wetlands, floating mats in Neotropical wetlands frequently undergo physical changes, subsiding and rising in response to changes in water level, and foundering under certain conditions. Mats are also subject to other large-scale physical changes. For example, extensive sections of floating mats can break off and drift away and free-floating sections can merge with shore-bound mats. Therefore, in addition to the problems associated with delineating sampling areas on such a dynamic substratum, and in confidently re-locating quadrats, it is conceivable that a number of quadrats would be lost to migration or subsidence.

In addition to the need to devise a strategy to overcome the problems associated with sampling on floating mats and with seasonal variations in species composition, the question still would have remained as to whether plot-based sampling was the best approach for meeting the objectives of this study. Specifically, as the positive relationship between species richness and area has long been known (*e.g.*, Brown 1988; Rosenzweig 1995), it is obvious that sampling from the maximum possible area (*i.e.*, the entire system) would yield a more complete floristic account than sampling from only a portion of the system (*i.e.*, quadrats). A plot-based methodology would have added significantly to the amount of time required at each study site and would not have replaced the need to conduct broad floristic surveys of the systems; therefore, quantitative sampling was eschewed and fieldwork focused on assembling comprehensive site floras.

Whenever possible, each study site received multiple visits. Fieldwork was widely spaced temporally so that the sites were observed under varying hydrologic conditions and in different seasons. Sampling commonly commenced at a convenient point of entry and entailed a systematic survey of localized areas until no new species were encountered, or until the time available at the site had elapsed. Smaller (*i.e.*, < ca. 30 ha) systems were surveyed in their entirety; however, in many cases the sites were too large to allow this approach. Therefore, with large (*i.e.*, > ca. 30 ha) systems, sampling was preceded by the identification of distinct communities and habitats. Subsequently, surveying focused on these areas. Criteria used in identifying these areas were as follows: 1) differences in dominant species; 2) discernible differences in hydrology; 3) microtopographic variations (*i.e.* differences in substratum or differences in the degree of sedimentation of floating mats); and, 4) obvious disturbance. Large study sites also received as complete a survey as possible; however, time and resource limitations minimized this activity at many systems.

Specimen Collection and Preparation

Plant specimens were taken preferentially from fertile individuals but sterile specimens were collected whenever fertile material was lacking. Despite the contention that there is little value in collecting sterile aquatic specimens (Haynes 1984), sterile specimens were collected to document the presence of a species. If, for a particular species, only sterile material was encountered during the initial visit to a site, a concerted effort was made to locate fertile material on following visits. In the same manner, if poor quality specimens of fertile material were collected during an initial visit to a site, an attempt was made to obtain more suitable specimens during a subsequent visit.

Many aquatic species possess flowers that are very delicate and that make substandard specimens when normal pressing and drying procedures are employed. In these cases, the flowers were dried separately in small (ca. 8 cm x 14 cm) presses, with only light pressure applied to the closures (Haynes 1984). At times, delicate flowers were also preserved in vials of 70 percent ethanol.

Submerged macrophytes with highly-dissected leaves (*i.e.*, *Myriophyllum* spp., *Apalanthe* spp., and *Cabomba* spp.) often clump badly when pressed without special attention. Whenever possible, these species were "wet-mounted" (floated onto wet sheets of newsprint) to spread their leaf segments, and then dried using standard procedures (*cf.* Ceska and Ceska 1986; Haynes 1984; Taylor 1977). Additionally, for species with highly dissected leaves, cross-sections of stem nodes were also pressed to better present the leaves and leaf-arrangement (Haynes 1984).

Specimens were preferably dried in the field using a portable dryer with a propane stove as a heat source. In addition to yielding high quality herbarium specimens, this method preserves plant pigments, which can contain useful information (Ceska and Ceska 1986), and also allows for DNA samples to be taken from the herbarium specimens. If no portable drier were available, and if time and climatic conditions permitted, specimens were "sun-dried", with the plant presses placed in direct sun and the newspapers and blotters changed frequently. Given appropriate weather conditions, specimens produced by this method are equal in quality to those produced by gas drying, although this method was quite laborious and, hence, was utilized only when necessary. At certain times, such as on protracted expeditions to remote areas, field drying was not feasible. In these instances, specimens were pressed overnight and then placed in polyethylene bags containing a 70/30 mixture of alcohol and water (*cf.* Liesner 1990). Specimens remained in bags for the duration of the fieldwork, after which time they were removed and dried in a specimen dryer.

Although every attempt was made to collect voucher specimens of all species present at a site, in rare instances when the number of specimens exceeded the capacity of the portable field dryer and weather conditions precluded sun-drying, specimens of a few of the most common and easily identifiable species were discarded. Whenever possible, photo vouchers were taken to compensate for the absence of dried specimens.

Specimen Identification

Provisional identifications of specimens were made in the field. Frequently, there was some uncertainty as to the number of taxa present at the site (*e.g.*, as occurred with similar species in families with highly reduced and superficially similar flowers, such as the Poaceae and Cyperaceae). In these instances, specimens were taken from a number of different areas in the system and were given separate collection numbers. Further identifications and/or confirmations of specimens were carried out at the three primary herbaria in Bolivia (BOLV, LPB, USZ) and in the United States at the Hodgdon Herbarium (NHA), the Gray Herbarium at Harvard University (GH), and the Missouri Botanical Garden (MO). Specimens were also borrowed from other institutions when additional material was required. Voucher specimens were deposited at NHA and, depending on the region from which the collections were taken, at either USZ, LPB, or BOLV. When available, duplicates were also deposited at MO.

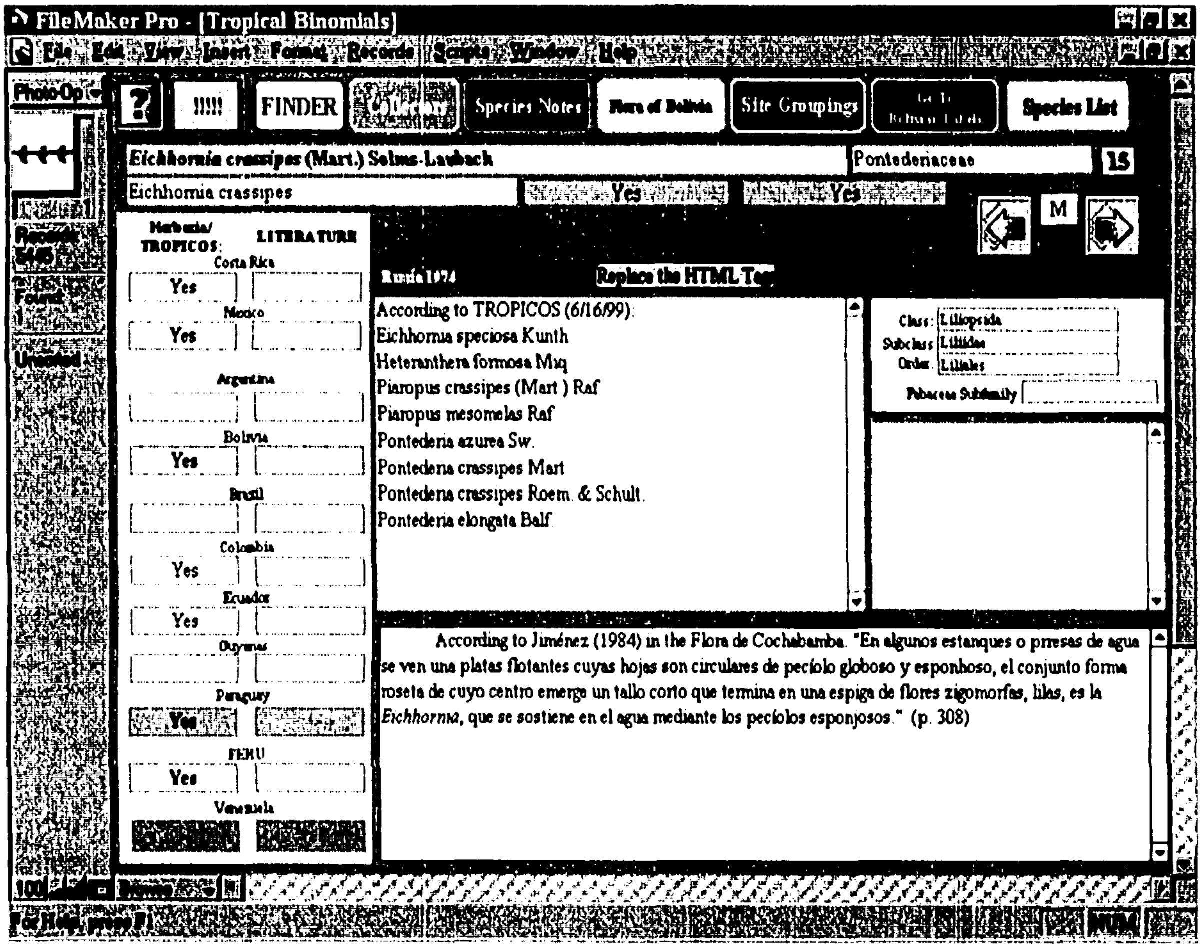
Whenever possible, all species noted at the study sites were included in the species richness estimates. When only sterile individuals of a particular species were encountered, and if clearly distinguishable from all other taxa at the site, that species was given a morphospecies name (*e.g.*, *Cyperus* #1) and was incorporated in the estimate of site diversity. Morphospecies names were also assigned to any fertile species that I was unable to confidently determine to the level of species. Frequently, it was not possible to ascertain whether or not a morphospecies corresponded to a morphospecies from another site (*e.g.*, it was not possible to differentiate between Poaceae #1 from site "A" and Poaceae #1 from site "B"). Hence, although these species were counted in the estimates of site diversity, they were excluded from floristic comparisons.

Wetland Species Database

To undertake floristic comparisons, a checklist of species associated with Neotropical wetlands was compiled and stored in a relational database (Ritter 2000). In assembling the checklist it was necessary to identify whether or not a particular species could be considered as a "wetland species". Ideally, these were both the truly aquatic species (those that spend nearly their entire life cycle in contact with water), as well as semi-aquatic species (those that require that the greatest part of their life cycle be spent in soils that are at least saturated, and which cannot survive extended periods of drought). This distinction was made to exclude those ruderal species that are tolerant of some inundation, but which are more characteristic of disturbed, terrestrial sites. It was often difficult to state with certainty whether or not a particular species met these criteria. In such cases, the species was designated as "possibly wetland" or "probably wetland", and further information regarding the species' typical habitat was sought. When information regarding the life history of a particular species was lacking, the habitat in which it was most often encountered was considered as an indicator of wetland affinity. Frequently, the delineation of wetland species in regions outside of Bolivia was based on habitat descriptions given by a single author. If it was unclear whether or not a habitat could be considered as a wetland (*i.e.*, if there was insufficient information given on innundation regime), the dominant vegetation was used as an indicator of wetland status. Hence, as a result of these uncertainties, a "wetland species" referred to a species that was strongly associated with inundated habitats.

A species that was recognized as a wetland species in one region was considered to be a wetland species throughout its range. Hence, it was possible to undertake comparisons of wetland floras at the regional and country level by obtaining or compiling species lists for these areas and querying the wetland species database as to the "wetland" status of each species.

Species lists from numerous published floristic studies of Neotropical wetlands were incorporated into the database (Figs. 2.2 and 2.3). Whenever possible, species lists were entered in their entirety, in order to accommodate changes in the ascription of wetland species. Thus, although a species might not be recognized as a "wetland species" at the time of the incorporation of data from a particular study, its presence in the region was still registered. Species lists from the following publications were entered in their entirety: Aristeguieta (1968), Armitage and Fassett (1971), Beck (1984), Bonilla-Barbosa and Novello R. (1995), Brandão *et al.* (1989), Bravo-Velásquez and Balslev (1985),



Eichhornia crassipes (Mart.) Solms-Laubach

Pontederiaceae

15

Eichhornia crassipes

Yes

Yes

Herbaria/ TROPICOS:	LITERATURE
Costa Rica	
Yes	
Mexico	
Yes	
Argentina	
Bolivia	
Yes	
Brasil	
Colombia	
Yes	
Ecuador	
Yes	
Guyanas	
Paraguay	
Yes	
PERU	
Yes	
Venezuela	

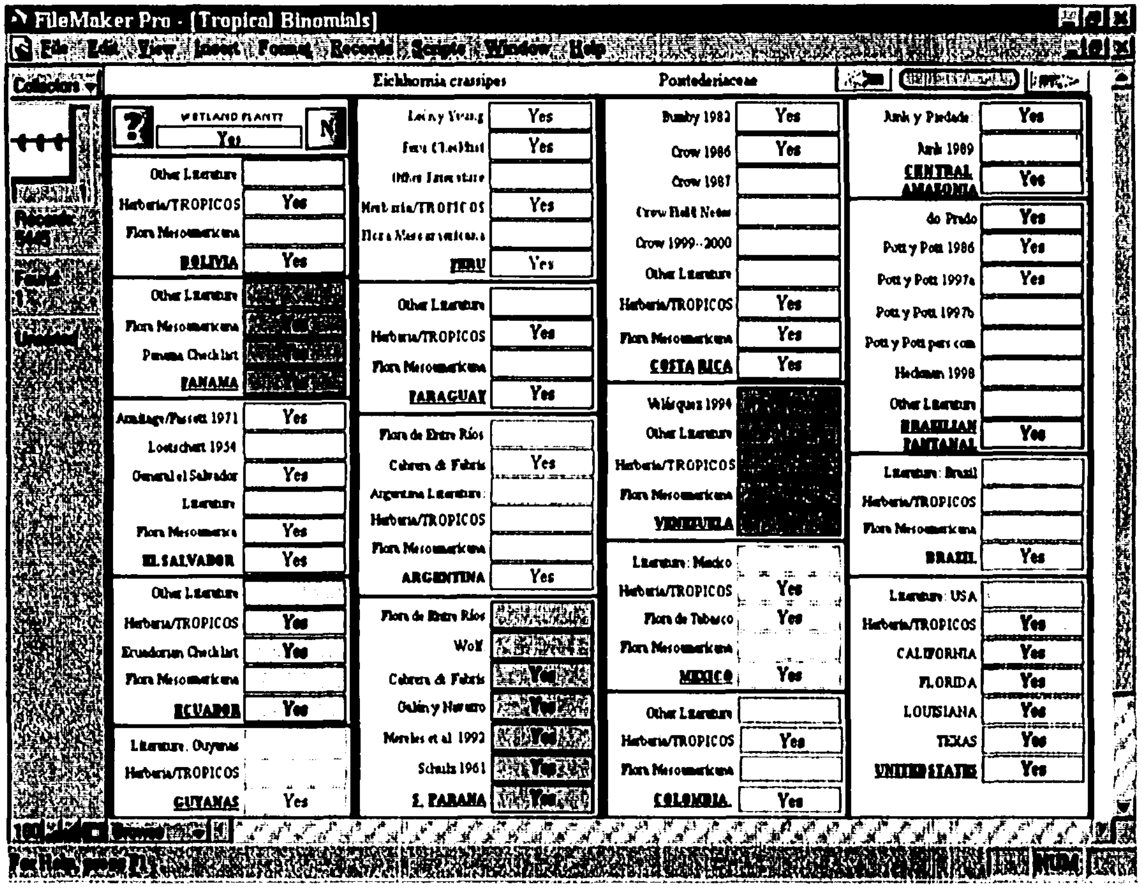
Rusda 1974

According to TROPICOS (6/16/99):
Eichhornia speciosa Kunth
Heteranthera formosa Miq
Piaropus crassipes (Mart) Raf
Piaropus mesomelas Raf
Pontederia azurea Sw.
Pontederia crassipes Mart
Pontederia crassipes Roem. & Schult.
Pontederia elongata Balf

Class: Liliopsida
Subclass: Liliidae
Order: Liliales
Fabaceae Subfamily:

According to Jiménez (1984) in the Flora de Cochabamba. "En algunos estanques o presas de agua se ven una platas flotantes cuyas hojas son circulares de pecíolo globoso y esponhoso, el conjunto forma roseta de cuyo centro emerge un tallo corto que termina en una espiga de flores zigomorfas, lilas, es la *Eichhornia*, que se sostiene en el agua mediante los pecíolos esponjosos." (p. 308)

Figure 2.2. A record from the Wetland Species database. Fields along the left hand edge indicate whether references to the species were encountered in the TROPICOS database, in herbarium specimens, or in the literature. The large field in the center of the image stores information on synonymy and other taxonomic notes. The large field in the lower right hand corner contains information on species' habitats.



Eichhornia crassipes

Pontederiaceae

WETLAND PLANTS
Yes

Other Literature	
Herbaria/TROPICOS	Yes
Flora Mesoamericana	
BOLIVIA	Yes
Other Literature	
Flora Mesoamericana	
Panama Checklist	
PANAMA	
Armitage/Fassett 1971	Yes
Loetschert 1954	
General el Salvador	Yes
Literature	
Flora Mesoamerica	Yes
EL SALVADOR	Yes
Other Literature	
Herbaria/TROPICOS	Yes
Ecuadorian Checklist	Yes
Flora Mesoamericana	
ECUADOR	Yes
Literature, Guyanas	
Herbaria/TROPICOS	
GUYANAS	Yes
Leiny Young	Yes
Ferr (Checklist)	Yes
Other Literature	
Herbaria/TROPICOS	Yes
Flora Mesoamericana	
PERU	Yes
Other Literature	
Herbaria/TROPICOS	Yes
Flora Mesoamericana	
PARAGUAY	Yes
Flora de Entre Ríos	
Cabrera & Fabris	Yes
Argentina Literature	
Herbaria/TROPICOS	
Flora Mesoamericana	
ARGENTINA	Yes
Flora de Entre Ríos	
Wolf	
Cabrera & Fabris	Yes
Galán y Navarro	Yes
Morales et al 1992	Yes
Schulz 1961	Yes
S. PARANA	Yes
Bunby 1982	Yes
Crow 1986	Yes
Crow 1987	
Crow Field Notes	
Crow 1999–2000	
Other Literature	
Herbaria/TROPICOS	Yes
Flora Mesoamericana	Yes
COSTA RICA	Yes
Velásquez 1994	
Other Literature	
Herbaria/TROPICOS	
Flora Mesoamericana	
VENEZUELA	
Literature: Mexico	
Herbaria/TROPICOS	Yes
Flora de Tabasco	Yes
Flora Mesoamericana	
MEXICO	Yes
Other Literature	
Herbaria/TROPICOS	Yes
Flora Mesoamericana	
COLOMBIA	Yes
Junk y Piedade	Yes
Junk 1989	
CENTRAL AMAZONIA	Yes
do Prado	Yes
Pott y Pott 1986	Yes
Pott y Pott 1997a	Yes
Pott y Pott 1997b	
Pott y Pott pers com	
Hedman 1998	
Other Literature	
BRAZILIAN PANTANAL	Yes
Literature: Brazil	
Herbaria/TROPICOS	
Flora Mesoamericana	
BRAZIL	Yes
Literature: USA	
Herbaria/TROPICOS	Yes
CALIFORNIA	Yes
FLORIDA	Yes
LOUISIANA	Yes
TEXAS	Yes
UNITED STATES	Yes

Figure 2.3. The same record from the Wetland Species database as in Figure 2.3. In this layout, the presence of the species in various countries and regions is displayed. Fields indicate the source of the species' references (*e.g.*, various published accounts, the TROPICOS and Flora Mesoamericana databases, herbarium specimens, etc.). Note: Only a small subset of the sources used in compiling species list for each OGU are presented in this layout.

Briones *et al.* (1997), Bumby (1982), Burkart (1957), Cabrera and Fabrís (1948), Cano *et al.* (1993), Conceiçâo and de Paula (1986), Crow and Rivera (1986), Crow *et al.* (1987), Estenssoro C. (1991), Franken (1991), Frey (1995), Galán de Mera (1989), Galán de Mera and Navarro (1992), Haase (1989, 1990), Haase & Beck (1989), Heckman (1998), Howard-Williams and Junk (1977) Junk (1983, 1986, 1989), Junk and Piedade (1997), Kalliola *et al.* (1991), Killeen (1990), Killeen and Nee (1991), Keel and Prance (1979), Klinge (1990), Lara R. & Cazas (1996), León *et al.* (1995), León and Young (1996), Loetschert (1954), López-Hernández (1993), Lot and Novelo R. (1988), Lot *et al.* (1986; 1999), Menalled and Adámoli (1995), Mereles *et al.* (1992), Navarro (1993), Neiff (1986), Pires and Prance (1985), Por (1995), A. Pott and V. Pott (1997), V. Pott and A. Pott (1997), Pott *et al.* (1986, 1989, 1992), Prado *et al.* (1994), Ramía (1974), Ramírez-García and Novelo R. (1984), Rangel & Aguirre (1983), Raynal-Roques (1991), Rojas and Novelo R. (1995), Sanabria and de Wilde (1998), Schulz (1961), Schmidt-Mumm (2000), Schulz (1961), Siebert (1994), Siebert and Menhofer (1992), Velásquez (1994), Wolf (1990), and Worbes (1997).

Information from the following regional floristic studies was also utilized in distinguishing wetland species: Burkart (1957, 1978), Davidse *et al.* (1994, 1995), Gómez (1984), Kahn (1993), Renvoize (1998), and Troncoso de B. *et al.* (1987). Although only a portion of the species lists from these sources were entered into the database, habitat descriptions were frequently used to identify wetland species and to resolve uncertainties regarding typical habitats of particular species. Likewise, habitat information from the many taxonomic treatments used during the identification of specimens was incorporated in the ascription of wetland species. Habitat data from herbarium specimens at BOLV, GH, LPB, MO, and USZ were also utilized in adjudging wetland species. Additional input on species' typical habitats came from discussions and written communications with other researchers working in tropical wetlands and from a query (for species associated with wetlands) of the Biological Diversity of the Guianas Database (the Biological Diversity of the Guianas project, National Museum of Natural History, Washington, DC.; see Appendix B). Information was incorporated from Reed's (1996) checklist of species associated with wetlands in the United States and its extra-continental protectorates and associated territories. The inclusion of material from this checklist was intended to help identify wetland species from those regions (*i.e.*, northern Mexico) which possess temperate and northern subtropical floristic elements. Based on the preceding sources, 2060 species in 149 families and 666 genera were identified as being associated with the OGS (*i.e.*, Mesoamerica and tropical and subtropical South America).

Phytogeographical Analysis

Floristic comparisons were made at three scales of "Operational Geographical Unit" or "OGU" (*cf.* Crovello 1981): 1) between study sites; 2) between regions within Bolivia ("mesoregional scale" *sensu* McLaughlin 1994); and, 3) between regions and countries in tropical and subtropical South and Mesoamerica ("macroregional scale" *sensu* McLaughlin 1994).

In his overview of quantitative biogeography, Crovello (1981) listed the potential purposes of quantitative biogeographical studies as follows: 1) to elucidate observed patterns among OGUs; 2) to account for the factors that produce and maintain these patterns; and, 3) to predict the effects of different conditions and events on future patterns. In this thesis, phytogeographical analyses are intended solely to address the first of these purposes, the elucidation of patterns among the OGU floras.

Regions Within Bolivia

Bolivia was divided into ten regions (Fig. 2.4). Sufficient study sites were present in eight of these to allow their inclusion in regional comparisons: three montane (High Andean, Valles Secos, and Cloud Forest) and five essentially lowland (Chapare, Andean Piedmont of Santa Cruz, White-water Floodplain, Chiquitania, and Gran Pantanal; Fig. 2.4).

Regions were delineated based on geographical features and predominant abiotic factors, principally precipitation. Descriptions of the regions are presented in the appropriate chapters. The Bolivian OGUs, their estimated area, range of elevation of the study sites within each OGU, and the watersheds present in each OGU are presented in Table 2.2.

In addition to data from the fieldwork, information on species' distributions were obtained from various other sources and incorporated into the regional wetland floras. Principal among these were: 1) published accounts of research in other Bolivian

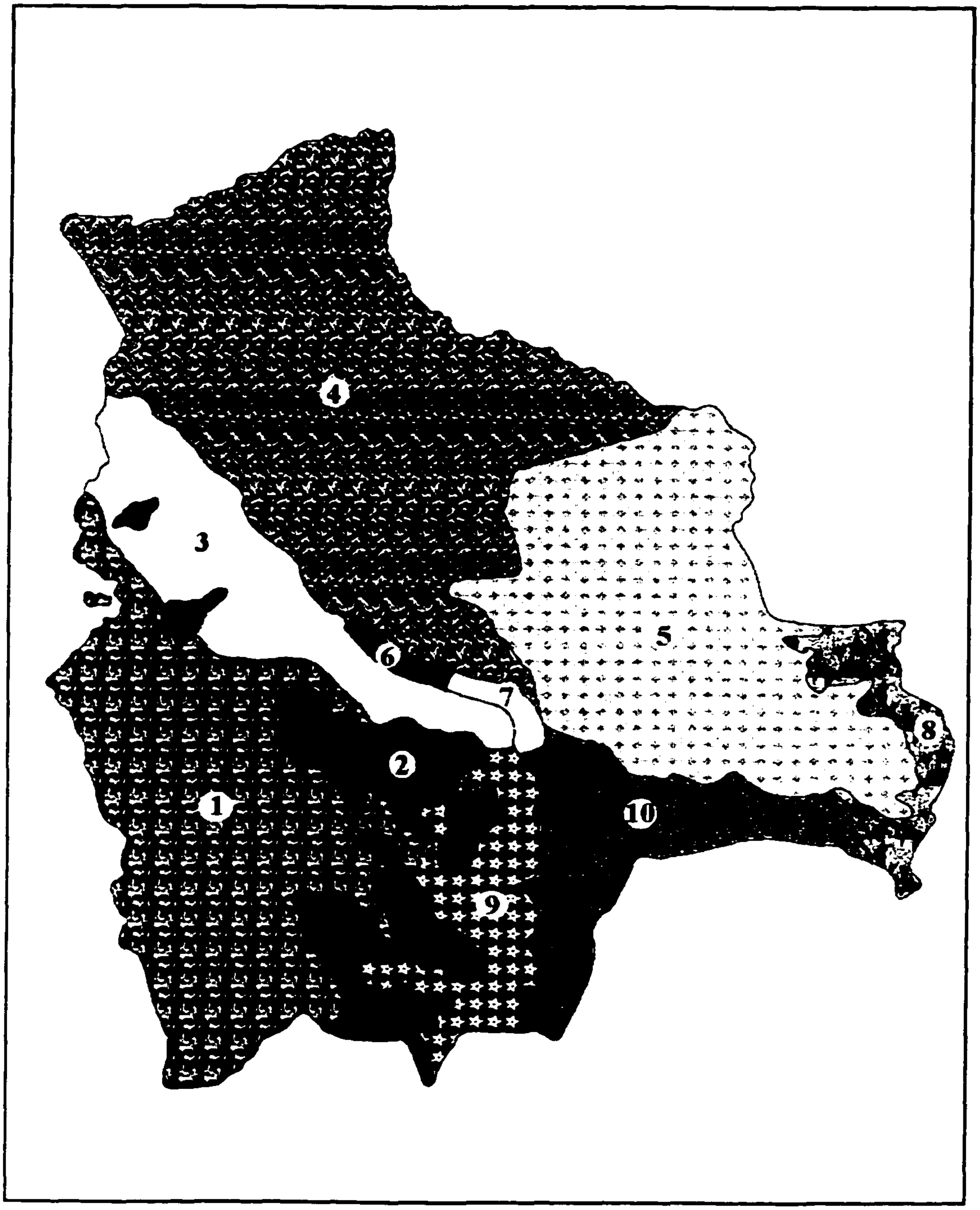


Figure 2.4. Bolivian Regions (modified from Killeen et al. 1993): 1) High Andean; 2) Valles Secos; 3) Cloud Forest; 4) White-water Floodplain; 5) Chiquitanía; 6) Chapare; 7) Andean Piedmont of Santa Cruz; 8) Gran Pantanal; 9) Tucumano-Boliviano; 10) Gran Chaco.

Table 2.2. The Bolivian regions, with estimated area, elevation range of the study sites, and major watersheds present in each region.

Region	Approximate Area (km^2)	Elevational Range[A] (m.a.s.l.)	Watershed(s)
High Andean	210,000	3100-4500	Desaguadero, Amazon, Paraná
Valles Secos	83,000	1800-2550	Amazon, Paraná
Cloud Forest	33,000	2400-2920	Amazon
Chapare	4000	200-230	Amazon
Andean Piedmont	5000	400-430	Amazon
Whitewater Floodplain	325,000	200-220	Amazon
Chiquitania	190,000	200-750	Amazon
Gran Pantanal	14,000	90-100	Paraná

A. Range of elevations of the study sites in the region. Regional checklists likely contain species which occur outside of this range.

wetlands; 2) data from Bolivian specimens listed in the Missouri Botanical Garden database TROPICOS. Specimen data from TROPICOS was obtained by querying the database for exsiccatae for each of the country's Departamentos. The selected records (ca. 61,000 records) were subsequently reviewed for locality errors (see Appendix C) and were apportioned to the proper region. At times, locality data from herbarium specimens and from floristic treatments were also incorporated into the regional checklists. A complete account of the sources used for compiling the Bolivian regional wetland floras is given in Appendix B. A checklist of the species associated with Bolivian wetlands (1026 species, in 126 families and 450 genera) plus regional presence/absence data is presented in Appendix D.

Extra-Bolivian Regions

Utilizing a diversity of sources, species checklists were either obtained or compiled for the following countries: Brazil, Colombia, Costa Rica, Ecuador, the Guianas (French Guiana, Guyana, and Suriname: treated here as a single OGU), Mexico, Panama, Paraguay, Peru, the United States, and Venezuela. The OGUs, their estimated area, total species, and total wetland species are presented in Table 2.3.

Preferably, complete species lists were obtained (in electronic format) for each country and incorporated into the database. When comprehensive checklists were unavailable for a country or region, representative floras were compiled from floristic studies, augmented by data from herbarium specimens, monographs, and other literature

Table 2.3. Countries and extra-Bolivian regions utilized in biodiversity and floristic comparisons, with estimated area, total species and total wetland species noted for each OGU. Sources used in compiling the Bolivian flora are given in Appendix B. Sources used in compiling the floras of extra-Bolivian OGUs are given in Appendix C.

OGU	Approximate Area [A] (km²)	All Species	Wetland Species
Central America			
"Mid-Central America" [B]	394,474	1527	696
Costa Rica	51,160	9265 [D]	708
Mexico	1,972,550	9942	778
Panama	78,200	7576 [D]	607
South America			
Río Paraná Delta (Argentina)	23,700	297	297
Bolivia	1,098,580	9539	1026
Brazil	8,511,965	.634	1007
Central Amazonia (Brazil)	4000	411	255
Gran Pantanal de Mato Grosso (Brazil)	140,000	1193	425
Colombia	1,138,910	1301	870
Ecuador	283,560	15,812 [D]	756
The Guianas [C]	378,331	14,088 [D]	845
Peru	1,285,220	18,687 [D]	903
Lowland Amazonian Peru	533,100	6014	429
Venezuela	912,050	1384	887
North America			
United States and Associated Territories	9,629,000	25,267	3284

A: World Factbook (Central Intelligence Agency 2000).
B: Belize, El Salvador, Guatemala, Honduras, and Nicaragua.
C: Guyana, French Guiana, and Suriname.
D: Presumed to represent relatively complete national floras.

as previously described. Checklists were also compiled for three South American regions: the Gran Pantanal de Mato Grosso, the Central Amazonian (Brazil) region, and the Río Paraná Delta region. A checklist for a fourth region, Lowland Amazonian Peru, was compiled by querying the Peruvian checklist (see Appendix B) for all species not restricted to coastal habitats whose lower distributional limit was 0 m (*e.g.*, 0-1000 m). A complete account of the sources used to compile the country and regional floras is presented in Appendix B.

Additional information regarding species' distributions was obtained from the Flora Mesoamericana checklist (Davidse *et al.* 1999) that was downloaded from the Missouri Botanical Garden website and converted to database format. In this form, the checklist contained only species and family names, however, it was possible to obtain distribution data for individual species by querying the Missouri Botanical Garden's online database for the Flora Mesoamericana (http://www.mobot.org). To this end, a program was written to direct the computer to automatically submit queries to the website and transfer results to the wetland species database. In this manner, the website was systematically queried for each species, thereby compiling distributions (in the form of presence/absence for each country in Meso- and South America) for the approximately 12,000 species in the Flora Mesoamericana checklist.

Complete locality data from the following floristic treatments were entered into the database: Balslev (1996), Cialdella (1989), Galán de Mera and Navarro (1989), Haynes and Holm-Nielsen (1994), Wiersema (1987), Van Royen (1951, 1953, 1954), and

Zardini and Raven (1991). Additionally, distribution data for all species listed for the Neotropics by Taylor (1989) were entered.

The wetland flora of the United States was also incorporated in floristic comparisons. The 1996 National List of Vascular Plant Species That Occur in Wetlands (Reed 1996) was downloaded as a text file and converted to a database (see Appendix B for an elaboration). Of the 7000+ species included in the checklist, 2034 were characterized as "Obligate Wetland Species" (OBL), *i.e.*, those that under natural conditions almost always occur in wetlands (Reed 1996). Species that were categorized as OBL in any region were treated as associated with wetlands throughout their range.

Analytical Methods

Similarity Indices

Degrees of similarity were analyzed using Sørensen's Index (Magurran 1988):

$$\mathbf{S = 2\,j\,/\,(a + b)};$$

where a is the total number of species noted for OGU 1, b is the total number of species noted for OGU 2, and j is the number of species common to both OGUs.

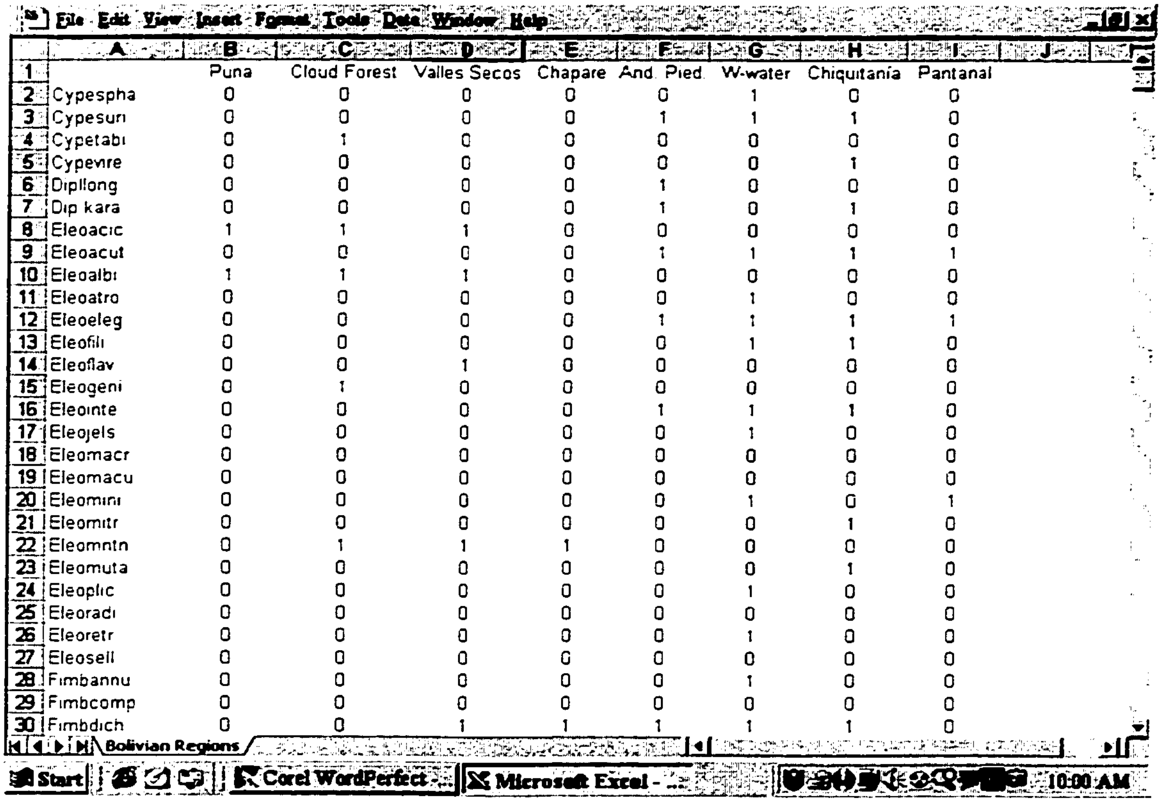
During the initial stages of statistical analysis, data from selected regions were also analyzed using Ochiai's index (McLaughlin 1994), with the resulting similarity matrix compared to that produced by Sørensen's index (*cf.* Hubálek 1982). Although some small differences were noted between the matrices generated by the two indices, ultimately, Sørensen's index was selected because it was one of the more commonly used indices (McLaughlin 1994). Morever, as this index has been used in various other wetland studies it allowed comparisons between these studies and the Bolivian data.

Ordination

In order to express floristic relationships among all OGUs simultaneously, data were organized into a binary matrix (see Fig. 2.5) of OGUs versus species (recorded as presence/absence values) and ordinated using Detrended Correspondence Analysis (DCA, Hill and Gauch 1980). Ordinations were conducted using the software package, PC-ORD (McCune and Mefford 1997).

Initially, two approaches were used to test the validity of the ordinations. First, random draws from the original data were performed, thereby creating data sets in which each OGU possessed half as many species as in the actual flora. Ordinations were then performed on these sets. Next, for each species, presence/absence data were replaced by randomly generated numbers. These randomly generated data sets were subsequently sorted, reconverted to presence/absence data, and ordinated. The number of species present in each OGU was maintained, *i.e.*, for each OGU the number of species after randomization equaled the number of species in the original data set. Each of these methods was repeated three times, and the resulting ordinations were compared to the ordination of the actual data.

Attempts at appraising the stability of the ordination were inconclusive. Ordinations of randomly drawn data sets (half-sized sets of the actual data) were often



	A	B	C	D	E	F	G	H	I
1		Puna	Cloud Forest	Valles Secos	Chapare	And. Pied.	W-water	Chiquitanía	Pantanal
2	Cypespha	0	0	0	0	0	1	0	0
3	Cypesuri	0	0	0	0	1	1	1	0
4	Cypetabi	0	1	0	0	0	0	0	0
5	Cypevire	0	0	0	0	0	0	1	0
6	Dipllong	0	0	0	0	1	0	0	0
7	Dip kara	0	0	0	0	1	0	1	0
8	Eleoacic	1	1	1	0	0	0	0	0
9	Eleoacut	0	0	0	0	1	1	1	1
10	Eleoalbi	1	1	1	0	0	0	0	0
11	Eleoatro	0	0	0	0	0	1	0	0
12	Eleoeleg	0	0	0	0	1	1	1	1
13	Eleofili	0	0	0	0	0	1	1	0
14	Eleoflav	0	0	1	0	0	0	0	0
15	Eleogeni	0	1	0	0	0	0	0	0
16	Eleointe	0	0	0	0	1	1	1	0
17	Eleojels	0	0	0	0	0	1	0	0
18	Eleomacr	0	0	0	0	0	0	0	0
19	Eleomacu	0	0	0	0	0	0	0	0
20	Eleomini	0	0	0	0	0	1	0	1
21	Eleomitr	0	0	0	0	0	0	1	0
22	Eleomntn	0	1	1	1	0	0	0	0
23	Eleomuta	0	0	0	0	0	0	1	0
24	Eleoplic	0	0	0	0	0	1	0	0
25	Eleoradi	0	0	0	0	0	0	0	0
26	Eleoretr	0	0	0	0	0	1	0	0
27	Eleosell	0	0	0	0	0	0	0	0
28	Fimbannu	0	0	0	0	0	1	0	0
29	Fimbcomp	0	0	0	0	0	0	0	0
30	Fimbdich	0	0	1	1	1	1	1	0

Figure 2.5. Sample of the binary matrix of species versus OGU's. The top row indicates OGUs. The lefthand column lists the species, with species names abbreviated to 8 characters, in order to accommodate the restrictions of the statistical program (PC-Ord). The remaining columns contain presence/absence data for each species.

consistent with the complete data set. In these instances, the OGUs maintained their same relative configuration with the only differences limited to small-scale migrations of the data points. At other times, ordinations of the randomly drawn data were not faithful with that of the full data set. Moreover, ordinations of the randomly *generated* data sets were extremely problematic. In these tests, the three OGUs with the fewest species were strongly associated with axial endpoints (*i.e.*, in most iterations the least species-rich OGUs formed the axial endpoints).

Clearly, the orientation of the OGUs in ordination space was influenced to a significant degree by sample size. Therefore, in order to establish a frame of reference for interpreting the ordinations of the actual data a null data set was created and classified by DCA. In this data set one half of the species in each OGU were shared with the other OGUs and the other half of the species were restricted to a single OGU. Floristic affinities were then interpreted by comparing the position of the actual data to the ordered data set.

Cluster Analyses

Initially, OGU floras were also classified by cluster analysis using PC-ORD (McCune and Mefford 1997) with Sørensen's Index distance and nearest neighbor linkage. Stability of the clustering was tested using sets of randomly generated presence/absence data as per the preceding analysis. In this manner, it was determined that cluster analysis of the data was particularly sensitive to flora size. The OGUs with the smallest floras always occupied the outermost branches of the dendrograms generated both from actual data and from the three iterations of randomly generated data. Although cluster analysis is a common tool of biogeographical research (McLaughlin 1994), it was clear that differences in flora size had too large an effect for the results to be interpreted with confidence in this study.

Frequency Analyses

Although similarity indices are regularly used in phytogeographical analysis (McLaughlin 1994, Simberloff and Connor 1979), it should be recognized that these are *ad hoc* constructs (Simberloff and Connor 1979), *i.e.*, they are not derived from any hypothesis regarding the factors that determine species' distributions. In most of these indices floristic similarities are calculated from the entire flora; however, the presence of shared rare species in a pair of OGUs can also serve as the criterion for adjudging similarity (Simberloff and Connor 1979). Therefore, a method was developed for graphically representing the relative contribution of species classes (*e.g.*, species present in all OGUs, species restricted to 2 OGUs, etc.) to overall similarity (see Fig. 2.6 for an illustration of this method).

In the following three chapters, descriptions and analyses are presented for three Bolivian regions selected for comprehensive analysis (the Cloud Forest, Chapter 3; the Chapare, Chapter 4; and, the Gran Pantanal, Chapter 5). Subsequently (Chapter 6), site-level diversity for all 46 Bolivian study sites is examined. In the final chapter,

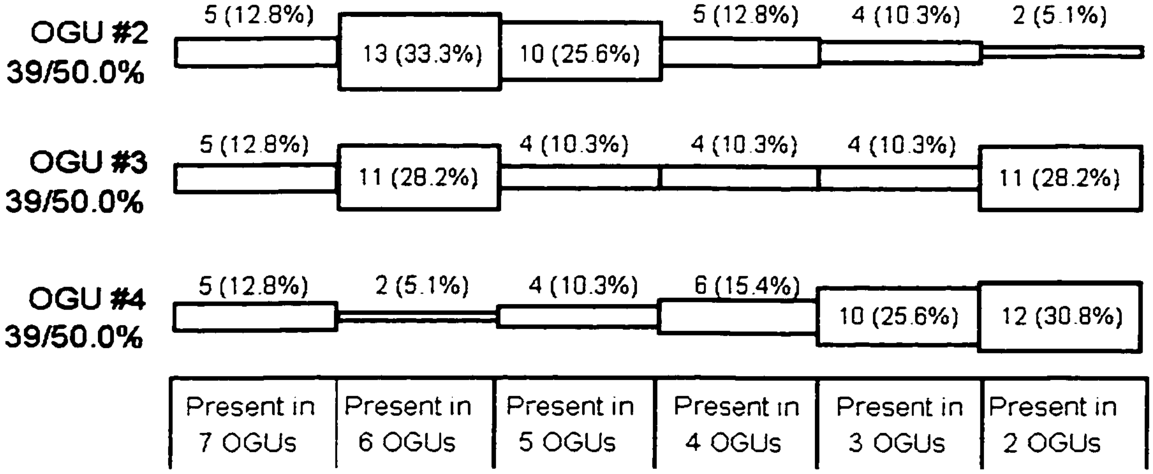


Figure 2.6. Frequency of species shared between a subset of hypothetical OGUs. Figures below the OGU names indicate the number of species shared between that OGU and OGU #1, followed by percent floristic similarity (Sørensen's Index) of the two floras. The boxes correspond to species classes (i.e., number of OGUs in which the species was present), as indicated by the key along the bottom edge of the figure. The vertical dimension of each box is proportional to the number of species that it represents. Figures associated with the boxes indicate the number of species that occurred in both the OGU and OGU #1, followed by the percentage that this portion of the flora contributed to the total species shared between the OGU and OGU #1. For example, considering the relationship between OGU #1 OGU #2, the initial (lefthand-most) box represents the 5 species that were present in all seven OGUs. These accounted for 12.8% of the species shared between these two OGUs. Continuing from left to right, the second box represents the 13 species that were present in both OGU #1 and OGU #2 and that occurred in exactly 6 OGUs. These accounted for 33.3 % of the species shared between these two OGUs. Note: due to rounding off, the percentages may not add up to exactly 100%.

comparisons of macroregional-scale diversity are made among Bolivian regions, among the countries of the Neotropics, and between the Neotropical region and the New World temperate regions.

CHAPTER III

CLOUD FOREST

> The cold through which we have passed–thank Heaven!–is the cold of altitude. So when things begin to grow they grow suddenly in all the profusion of the tropical belt. We are still too high up for tropical jungle; but there is an overall confusion of everything else. And everything is strange and new.
>
> - Gordon MacCreagh, *White Waters and Black*

Introduction

Tropical montane cloud forests (TMCFs) constitute one of the world's most threatened ecosystems (Aldrich *et al.* 1998). Globally, these habitats are said to be at least as threatened as lowland rainforest (Kricher 1997; Wuetrich 1993). Habitat loss is particularly pronounced in the Andean range, and it has been estimated that as much as 90% of the montane cloud forests of the northern Andes may have already been lost (Hamilton, Juvik, and Scatena 1995; Wuetrich 1993).

Although the term "cloud forest" lacks a strict scientific definition, it appears widely in the literature. Here, the terms "cloud forest", "montane cloud forest", and "tropical montane cloud forest" will be treated as synonyms. The capitalized form is used when referring to a particular region (*e.g.*, the Bolivian Cloud Forest). Stadtmüller (1987) presented the following working definition of cloud forests:

> Cloud forests include all forests in the humid tropics that are frequently covered in clouds or mist; thus receiving additional humidity, other than rainfall, through the capture and/or condensation of water droplets (horizontal precipitation), which influences the hydrological regime, radiation balance, and several other climatic, edaphic and ecological parameters. (Stadtmüller 1987, p. 14)

Historically, cloud forests have received surprisingly little botanical investigation (Gentry 1995). In recent years, however, a heightened awareness of their threatened status, in addition to the recognition of these habitats as centers of high diversity and endemism (Aldrich *et al.* 1998; Gentry 1995), has resulted in a substantial increase in cloud forest research (Churchill *et al.* 1995; Stadtmüller 1987). Nevertheless, as is typical for botanical research in the tropics, which tends to disproportionally favor terrestrial over aquatic habitats (Crow 1993), there have been few investigations of wetland habitats in cloud forests.

In Bolivia, cloud forest formations occur along the wet, eastern slopes of the Cordillera Oriental ("Eastern Range") of the Andes. These forests were divided into two primary formations, the Bosque Montano Húmedo and the Bosque Tucumano-Boliviano, by Killeen *et al.* (1993). The Bosque Montano Húmedo occupies the northern portion of the Bolivian Andes, and shares affinities with northern Andean formations, whereas the Bosque Tucumano-Boliviano occupies the southern portion and demonstrates strong affinities with the forests of southern South America (Killeen *et al.* 1993).

The Bosque Montano Húmedo, which is commonly referred to as the Yungas, extends for nearly 600 km (Solomon 1989) and is situated in parts of four Departamentos: La Paz, Cochabamba, Beni and Santa Cruz (Fig. 3.1). In contrast to other areas of the Neotropics, in which research has most often focused on lowland habitats, the greatest part of Bolivian botanical research has taken place in these montane habitats (Killeen *et al.* 1993). The primary area of my investigations in the Bolivian cloud forest was on the slopes descending from the mountains to the east of the Cochabamba valley to the Amazon basin, an area that has received little botanical investigation relative to montane habitats situated nearer to La Paz. Although none of the study sites were located in the cloud forest in the northern Yungas, nevertheless, data were incorporated from general collecting in wetlands (primarily streamside pools and seeps) in this area.

In Bolivia, cloud forest formations characteristically occur on very steep slopes. Because of the effects of frequent landslides and hydric erosion, the cloud forest is composed of a matrix of successional stages (Killeen *et al.* 1993). The flora is considered to be quite rich, although the epiphytic component is not as diverse as in comparable habitats in Ecuador and Peru (Solomon 1989). Cloud forest structure is thought to be as complex as that of lowland forest, with three or more strata present (Killeen *et al.* 1993). The most important arborescent families are said to be the Cyatheaceae, Lauraceae, Podocarpaceae, Solanaceae, Cunoniaceae, Piperaceae, Myrsinaceae, and Melastomataceae (Killeen *et al.* 1993).

In general, the forest around the study sites appeared to have a reasonably equivalent composition. The Podocarpaceae, however, was not an important component

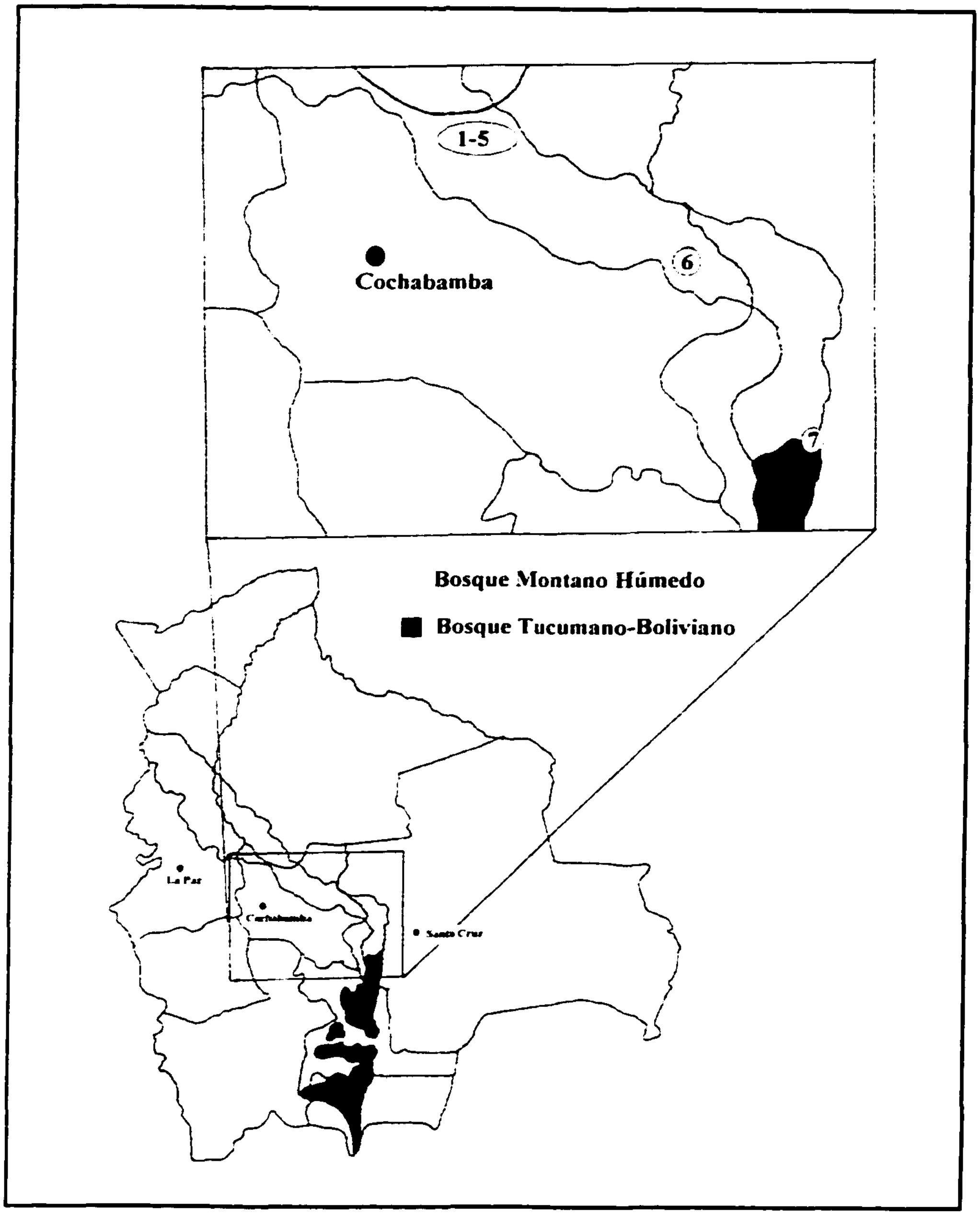


Figure 3.1. The Bolivian Cloud Forest study sites. 1-5. Chimpa Huata Bog, Lagunas Khonchu East and West; Corani Pampa Marsh, and Incachaca Pond. 6. Serranía de Siberia Marsh. 7. Laguna Volcan.

around most sites, except for the disjunct Siberia Marsh. In the general area around this system, remnant patches of *Prumnopitys*- and *Podocarpus*-dominated forest were in evidence. Additionally, the slopes above the Chimpa Huata Bog, as with a few remnant patches of undisturbed forest above Incachaca Pond, were noteworthy for their large populations of the arborescent *Columellia oblonga* Ruiz & Pavón (Columelliaceae). Representatives of this family had been so infrequently collected in Bolivia that the family was omitted from Killeen *et al.*'s (1993) guide to the country's trees.

The cloud forest study site area exhibited a distinct seasonality. Although detailed meteorological data for this region are lacking, Killeen *et al.* (1993) estimated that annual rainfall in the Bolivian cloud forest typically does not surpass 2000 mm. Although the cloud forests typically receive orographic precipitation throughout the year (Solomon 1989), the area is noticeably drier during the austral "winter" (June-August). At this time, the forest dries sufficiently to allow clearing for agriculture by slash and burn. Despite this seasonality, water levels at the majority of the study sites appeared to experience only small-scale fluctuations over the course of the year. Laguna Khonchu West, however, was observed to dry down to the point where standing water was completely absent from parts of the system during the dry season. Nevertheless, changes in water level were much less pronounced than in lowland wetlands, where seasonal variations can be on the order of 3-5 m.

Wetland habitats in tropical montane cloud forests have only rarely been described. This paucity of studies can be attributed to a general absence of wetlands (other than streams and rivers) on montane slopes. In the Bolivian Andes, slopes were extremely precipitous, with changes in elevation of 4500 m occurring over distances of 30-40 km. Nevertheless, small wetlands, such as marshes, bogs, and ponds, can occur on the infrequent level stretches on mountainsides, but these wetlands were typically absent from topographical maps, and those that were shown were often incorrectly located. Further difficulties in locating cloud forest wetlands arose because the dense forest cover limited accessibility and concealed their presence; hence wetlands not within close proximity to a trail or a clearing could easily go undetected.

Although the areas around most of the study sites were still relatively unpopulated, the forest was used for the free-range raising of cattle. Some small amount of trampling along system edges constituted the only visible impact of livestock on these sites. Nevertheless, since the initiation of my fieldwork in this area (1994), there has been a steady flow of immigration and significant amounts of forests have been cleared for subsistence agriculture. Thus, it seems likely that these sites will be subjected to more serious perturbation in the future.

In this chapter, my three primary objectives were: 1) to identify the plant species associated with wetland habitats in the Bolivian Cloud Forest region; 2) to determine the level of vascular plant species richness in these systems; and, 3) to examine the similarities of the region's wetland flora to those of other selected regions. To these ends, the flora of wetlands in the Bolivian Cloud Forest is listed and described, and comparisons of species richness and floristic similarity are made between the study sites. Regional-scale comparisons are made among the Bolivian Cloud Forest wetland flora, other Bolivian regions, and selected tropical and subtropical montane areas.

Materials and Methods

The general methodology followed the procedures outlined in Chapter 2. Six wetland systems served as the principal study sites in the Cloud Forest (Table 3.1; Fig. 3.1). The Cloud Forest study sites all occurred within the Bosque Montano Húmedo (northern Andean) vegetation type. Data were also introduced from Laguna Volcan (Table 3.1), a wetland situated in the transition zone between the Bosque Montano Húmedo and Bosque Tucumano-Boliviano (southern Andean) vegetation types, in order to compare these two montane areas. Descriptions of the seven systems are presented in Appendix A. Additional data were incorporated from general collecting in a variety of other wetlands, such as small marshes, streams, rivers, inundated roadside ditches, and vernal pools.

Due to the scarcity of accessible wetlands in the Cloud Forest, study site selection was somewhat serendipitous; hence some sites were included that, had they been located in areas where wetlands were more common, would most likely have been rejected as being too highly impacted by humans. All study sites were sufficiently small (0.02-3.0 ha) to allow them to receive complete floristic surveys. Each site received three to five visits, except for the Siberia Marsh, which was visited only once. Fieldwork was scheduled to ensure that sites were visited under different hydrologic conditions (*cf.* Chapter 2).

As outlined in Chapter 2, comparisons of floristic similarities (Sørensen's Index) were made among the seven study sites. An ordination (DCA) of all 46 Bolivian study

Table 3.1. Study sites in the Bolivian Cloud Forest region, with elevation, approximate system area, approximate location, and number of vascular species noted for the system.

System	Elevation (m)	Area (ha.)	Location	No. spp.
Chimpa Huata Bog	2920	0.05	65˚55'W 17˚12'S	23
Incachaca Pond	2385	1.0	65°49'W 17°15'S	26
Laguna Khonchu - East	2620	0.07	65˚56'W 17˚09'S	12
Laguna Khonchu - West	2620	0.09	65˚56'W 17˚09'S	13
Corani Pampa Marsh	2470	0.02	65°58'W 17°06'S	26
Serranía de Siberia Marsh	2800	0.75	64°45"W 17°51'S	7
Laguna Volcan	1150	3.0	63˚39'W 18˚08'S	39

sites was also introduced (see Appendix I) to examine site-level floristic affinities of the Cloud Forest sites within a country-wide context.

Floras from the study sites were combined with data from general collecting to approximate a regional wetland flora for the Cloud Forest (see Appendix B). The latter was compared with wetland floras from four Bolivian regions and from other montane regions in the New World tropics and subtropics (Mexico, Colombia, and Costa Rica). The Bolivian regions introduced into the comparisons included two additional montane regions (the High Andean and Valles Secos), and two regions situated at the base of the Andes (the Chapare and Andean Piedmont).

The wetland flora of the Mexican Cloud Forest was compiled from a study of eight ponds in Parque Nacional Lagunas de Zempoala, Mexico (Bonilla-Barbosa and Novelo R. 1995). These systems ranged in area from 0.5-10.6 ha and were situated at elevations between 2750 and 3010 m, with all but one site below 2825 m.

The wetland flora of Costa Rican montane regions was compiled from unpublished data gathered over several years (1985-present) by Dr. Garrett E. Crow (University of New Hampshire) in the Cordillera de Talamanca. Additional species were those listed by Bumby (1982) as having been collected in the transition between lower montane and montane zones.

An investigation of Colombia's Lago de Tota (Rangel and Aguirre 1983) was used to represent the wetland flora of the Colombian Cloud Forest. With an area of approximately 5620 ha, this system was substantially larger than any of the others included in the comparison. Furthermore, Lago de Tota was situated at a somewhat higher elevation (3020 m) than any of the other sites and received lower average annual precipitation (Rangel and Aguirre 1986). Consequently, the terrestrial vegetation in the areas surrounding the lake contained a flora more characteristic of Bosque Ceja de Monte, the transition zone between cloud forest and Puna (alpine) vegetation, than of true cloud forest. Nevertheless, because of the paucity of other published studies of Neotropical cloud forest wetlands, the Lago de Tota study provided a useful point of comparison.

As with the site-level comparisons, floristic similarities were examined among the various regions using both a similarity matrix (Sørensen's Index) and ordinated by Detrended Correspondence Analysis. In order to obtain a relatively stable ordination, it was necessary to downweight rare species and to reduce the number of segments from 26 (the default value) to 20. A null data set was created and ordinated by DCA, however, as it was consistently unstable along both the first and second axes it was discarded.

Results

Vegetation Description

A total of 74 vascular species, in 29 families and 50 genera, was identified as occurring in wetland habitats in the Bolivian Cloud Forest region. An annotated checklist including life-form, abundance, habitat, distribution, and specimen citations is given in

Appendix F. Of the 74 species, 57 were considered to be true wetland species (Appendix D).

Biodiversity

Site-level species richness was extremely variable, ranging from 7 to 26 species (Table 3.2). The disjunct Laguna Volcan (39 spp.) was appreciably richer than the Bosque Húmedo Montano sites (Table 3.2).

At the regional level, the Cloud Forest wetland flora was the most species-poor (57 species; Table 3.3) of the Bolivian regions included in the comparison. Nevertheless, this level of species richness was comparable to, or greater than, the number of wetland species noted for Cloud Forest and upper montane regions in the extra-Bolivian areas considered in these comparisons (Table 3.3).

Floristic Similarities

At the site-level, floristic similarities (Sørensen's Index) between the Cloud Forest sites were generally low, ranging from 0 to 50% (Table 3.2). The disjunct Laguna Volcan shared very few species with the Cloud Forest systems, with similarities ranging from 0 to 4% (Table 3.2). No species occurred in all study sites. Only one species, *Juncus microcephalus*, was present in as many as five sites, while *Eleocharis acicularis* and *Ranunculus flagelliformis* were present in four sites. Despite the generally low floristic similarities, all six Cloud Forest systems were situated in close proximity in ordination space in an ordination (DCA) of all 46 Bolivian study sites (Fig. 3.2). Laguna

Table 3.2. Comparison of richness and floristic similarity (Sørensen's Index) between study site floras. Figures in bold along the main diagonal indicate the number of species encountered at each site. Figures above the diagonal indicate the number of species in common to both sites. Figures in the shaded cells indicate percent floristic similarity between sites.

	Chimpa Huata Bog	Incachaca Pond	Laguna Khonchu E.	Laguna Khonchu W.	Corani Pampa Marsh	Serranía de Siberia Marsh	Laguna Volcan
Chimpa Huata Bog	**23**	6	7	9	8	4	0
Incachaca Pond	**24.5**	**26**	4	3	10	1	0
Laguna Khonchu E.	**40.0**	**21.1**	**12**	5	4	1	1
Laguna Khonchu W.	**50.0**	**15.4**	**40.0**	**13**	3	0	1
Corani Pampa Marsh	**32.7**	**38.5**	**21.1**	**15.4**	**26**	1	0
Serranía de Siberia Marsh	**26.7**	**6.1**	**10.5**	**0.0**	**6.1**	**7**	0
Laguna Volcan	**0.0**	**0.0**	**3.9**	**3.9**	**0.0**	**0.0**	**39**

Table 3.3. Comparison of diversity and floristic similarity (Sørensen's Index) between vascular wetland floras of the Bolivian cloud forest and other Bolivian and Extra-Bolivian regions. Figures in bold along the main diagonal indicate the number of species noted for each region. The numbers above the main diagonal indicate the number of species shared by both regions. Numbers in the shaded cells indicate the percent floristic similarity between areas. Regions: BCF - Bolivian Cloud Forest; HA - Bolivian High Andean Region; VS - Bolivian Valles Secos Region; CH - Bolivian Chapare Region; AP - Bolivian Andean Piedmont Region; MCF - Mexican Cloud Forest; CRCF - Costa Rican Cloud Forest; COLM - Colombian Montane Region

	BCF	HA	VS	CH	AP	MCF	CRCF	COLM
BCF	**57**	35	24	3	13	9	2	8
HA	**40.2**	**117**	45	0	8	14	1	10
VS	**29.3**	**40.1**	**107**	7	30	12	1	12
CH	**3.5**	**0.0**	**6.4**	**113**	60	2	0	3
AP	**8.6**	**4.4**	**17.1**	**33.6**	**244**	10	1	5
MCF	**15.4**	**15.8**	**14.4**	**2.3**	**6.6**	**60**	2	11
CRCF	**5.6**	**1.5**	**1.6**	**0.0**	**0.8**	**5.3**	**15**	2
COLM	**17.0**	**13.0**	**16.7**	**4.0**	**3.6**	**22.7**	**7.7**	**37**

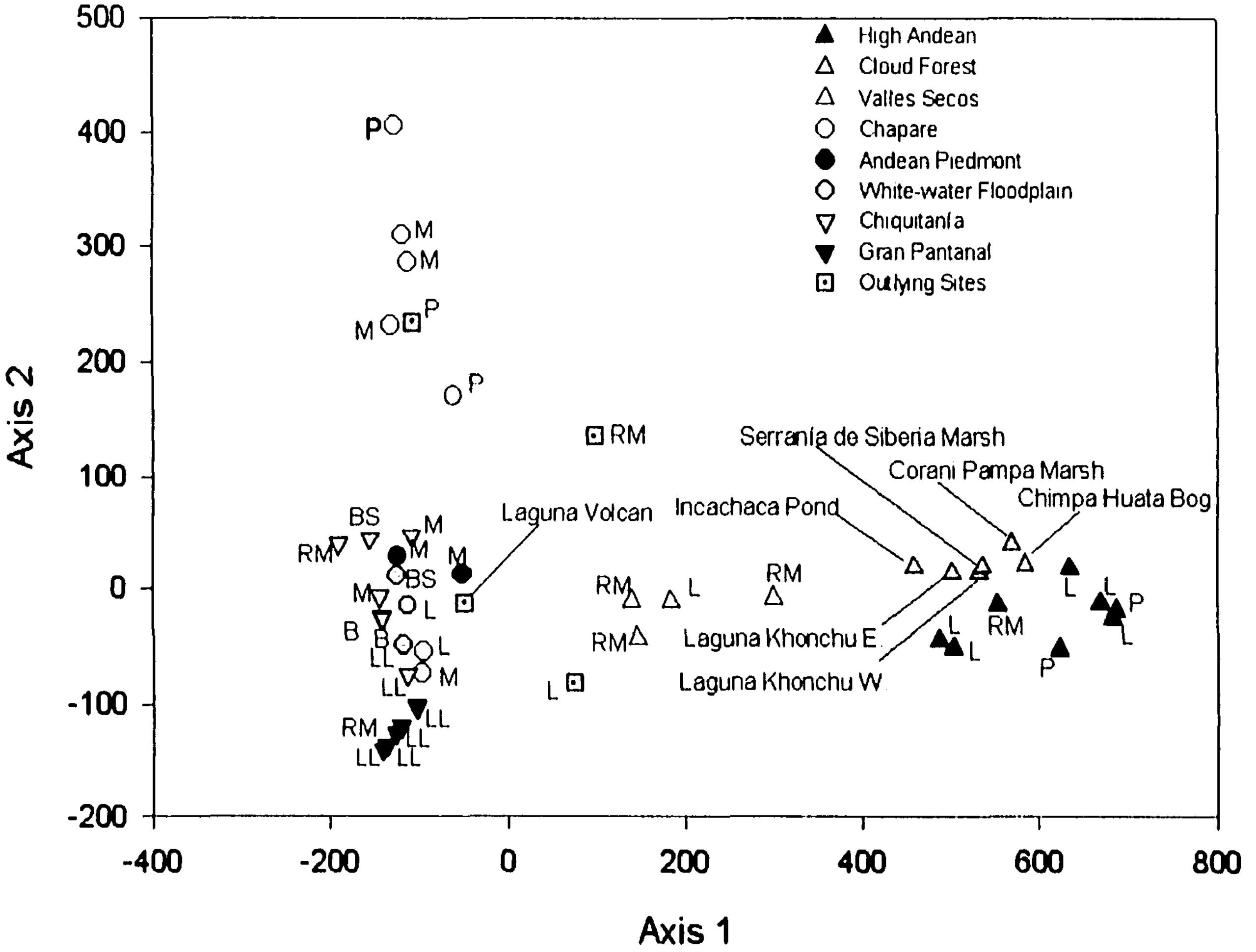


Figure 3.2. Ordination by Detrended Correspondence Analysis (DCA) of the 46 Bolivian study sites. The six Cloud Forest study sites and one outlying montane system (Laguna Volcan) are identified by name. Key to wetland types: B- bahía; BS - basin swamp; L - small lake (< 500 ha); LL - large lake (> 500 ha); M - marsh; P - pond; RM - riparian marsh.

Volcan, however, occupied a fairly disjunct position relative to the Cloud Forest study sites (Fig. 3.2).

At the regional level, floristic similarities (Sørensen's Index) between the wetland flora of the Bolivian Cloud Forest and the other OGUs were quite variable, ranging from 3.5-40.2% (Table 3.3). The strongest similarities were with the High Andean (50%) and Valles Secos (33%) regions (Table 3.3). Floristic similarities between the Bolivian Cloud Forest and two disjunct regions, the Colombian Montane region (17.0%) and the Mexican Cloud Forest region (15.4%), were much higher than between the Bolivian Cloud Forest and two proximal Bolivian regions, the Chapare (3.5%) and the Andean Piedmont region (8.6%; Table 3.3).

These relationships were generally reflected in the ordination of the 8 OGUs (Fig. 3.3). The Bolivian Cloud Forest occupied an approximately central position in ordination space, with the Valles Secos and High Andean regions the two nearest OGUs (Fig. 3.3). The Chapare and Andean Piedmont were disjunct from the three Bolivian montane OGUs, with the Chapare forming one of the first axile endpoints (Fig. 3.3). The three extra-Bolivian OGUs formed the remaining 3 axile endpoints, with the Costa Rican Cloud Forest occupying the closest position to the Bolivian Montane OGUs (Fig. 3.3).

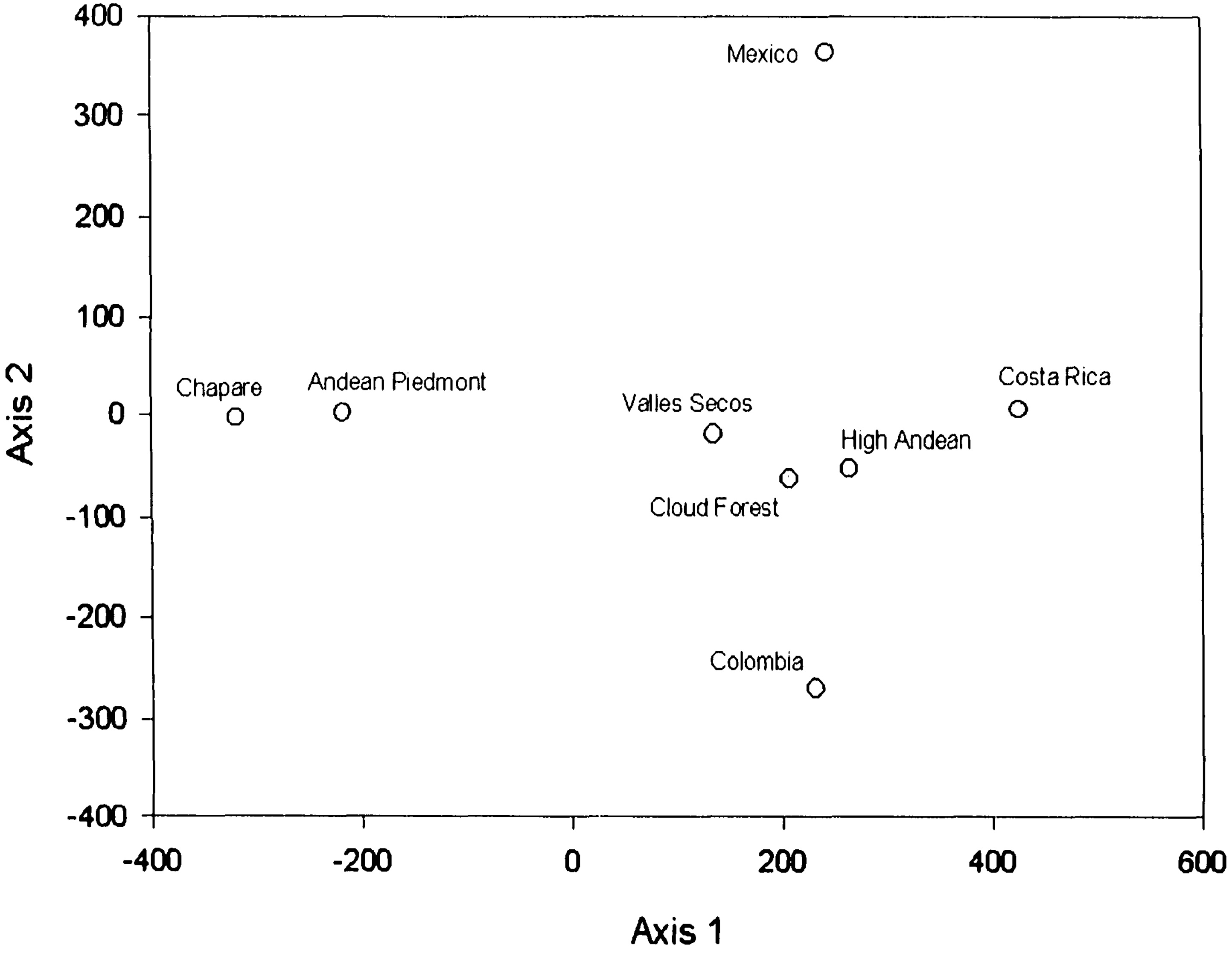


Figure 3.3. Ordination by Detrended Correspondence Analysis of the Bolivian Cloud Forest wetland flora and the wetland floras of selected regions.

Discussion

Vegetation Description

The wetland flora of the Bolivian Cloud Forest consisted of a mixture of aquatic species typical of the high Andean region and of more or less ruderal species that were commonly encountered in wet habitats subject to disturbance (*i.e.*, seeps, depressions, and roadside ditches) (Appendix F). In contrast to the wetlands of the Bolivian lowlands, which typically supported a diverse woody flora, woody species were nearly absent from the Bolivian Cloud Forest wetlands. The only exceptions were *Ludwigia peruviana*, which was encountered in a few flooded roadside ditches and in a small streamside marsh, plus the sub-woody *Baccharis trimera*, which was present at two of the systems (Appendix F).

Submerged species were also poorly represented in the Cloud Forest systems. The aquatic pteridophyte *Isoëtes herzogii* (Isoëtaceae) was the only submersed species observed in fairly deep water (*i.e.*, > 0.5 m), although small submersed herbs, such as *Callitriche albomarginata*, *C. heteropoda*, *Elatine* aff. *peruviana*, *E. triandra*, and *Crassula venezuelensis* were often fairly abundant in shallow water (Appendix F). By contrast, wetlands in the dry Interandean valleys situated on the western side of the Cordillera Oriental, were often dominated by submerged species, such as *Potamogeton* spp. and *Myriophyllum quitense*. Nevertheless, although the Cloud Forest systems were located at similar elevations as the Valles Secos sites, these species apparently did not become established in the more acidic, darker (from suspended humic acids) water of the Cloud Forest wetlands.

Surprisingly, no species of Melastomataceae were encountered in the Cloud Forest wetlands. Gentry (1995) recognized this family as the second most species-rich representative of Andean montane forests. Likewise, Killeen *et al.* (1993) listed the family among the most important arborescent families of the Bolivian Cloud Forest. This family was fairly well-represented in wetlands in the Bolivian lowlands, with 23 species (in 11 genera) noted in these systems (Appendix D). Despite the rich melastome flora in terrestrial habitats adjacent to the study sites, and despite the purported affinity of wetland species of the Melastomataceae for acidic conditions (A. Pott and V. Pott 1997), no members of this family were observed in Cloud Forest wetlands.

Although wet montane forests are recognized as centers of diversity for pteridophytes, this group was poorly represented in the Bolivian Cloud Forest wetlands. Moran (1995) demonstrated that in the Neotropics, as in other tropical areas that possess extensive mountain ranges, the greatest diversity of pteridophytes clearly occurs in montane habitats. Moran estimated that about 2000 fern species occur in the Andes, versus approximately 300 ferns in the Brazilian Amazon. Moraes and Beck (1992) noted that in the Bolivian Yungas pteridophytes constitute approximately 13-30% of the flora, whereas in the lowlands they account for no more than 5%. By contrast, although 40 species of pteridophytes were identified as being associated with Bolivian wetland habitats (Appendix D), the greatest portion of these occurred in lowland systems, with only 3 species encountered in the Bolivian Cloud Forest wetlands (Appendix F).

Tropical montane cloud forests are recognized as centers of endemism (Aldrich *et al.* 1998). Nevertheless, only a single species known to be endemic to Bolivia, *Calceolaria aquatica* (Molau 1988), was encountered in the Cloud Forest wetlands. Additionally, *C. aquatica* was the sole species listed in the IUCN Red List of Threatened Plants (world status: rare; Walter and Gillett 1998). A second species, *Juncus fuscocapitatus* (Juncaceae), is endemic to montane habitats in both Bolivia and Peru (Balslev, 1996).

Numerous new taxa were described from collections from terrestrial habitats in the Bolivian cloud forest by Rusby and others (see Funk and Mori 1989) during the early part of the twentieth century, and this region continues to yield species that are new to science or represent new records for the country (Moraes and Beck 1992). By contrast, no undescribed species or new Bolivian records were encountered in my fieldwork in the little-investigated cloud forest wetland habitats. Nevertheless, Neotropical wetlands seem to characteristically contain fewer rare species than Neotropical terrestrial habitats: thus, the paucity of noteworthy species in the cloud forest wetlands was not entirely unexpected.

Biodiversity

Site-level Diversity. The Cloud Forest sites were species-poor (13-26 spp.) relative to wetlands in most parts of the Bolivian lowlands. These lowland systems typically support on the order of 40-70 species, with 124 species present in the richest study site (Table

6.1). An exception is found in the wetlands in the very high-precipitation region in the Chapare (see Chapter 4), which possess a more equivalent diversity (6-49 species; Table 4.1). The low species-richness of the Cloud Forest sites was also conspicuous when compared to systems in the dry Interandean valleys (Valles Secos), which ranged from 16-66 taxa (Table 6.1). On the other hand, some Cloud Forest wetland systems are more diverse than many systems in the Bolivian High Andean Region. Species richness in the High Andean study sites ranged from 3-31 species (Table 6.1). Furthermore, a number of other low-diversity wetlands (*i.e.*, 1-5 vascular species noted) were encountered during fieldwork in the High Andean region that were not designated as study-sites.

In all of the preceding comparisons no consideration was given to the positive relationship between area sampled (*i.e.*, system area) and species richness (*e.g.*, Rosenzweig 1995). Many of the lowland systems were significantly larger than the Cloud Forest study sites: therefore, it is not unexpected that these might possess a richer flora (see Chapter 6). In order to account for the effects of system size on species richness in Bolivian wetlands, a species-area curve was plotted from data from all 46 study sites (see Chapter 6) and a linear regression fitted to the points. Study sites were classified by wetland type (*e.g.*, pond, marsh, large lake; see Chapter 6) in order to ascertain whether particular wetland types might be characteristically species-rich or -poor. The plot is reproduced here, modified so that the Cloud Forest study sites and Laguna Volcan are identified by name (Fig. 3.4).

When interpreting Fig. 3.4, the study sites situated below the regression line can be considered as relatively species-poor and those above as relatively species-rich. Thus,

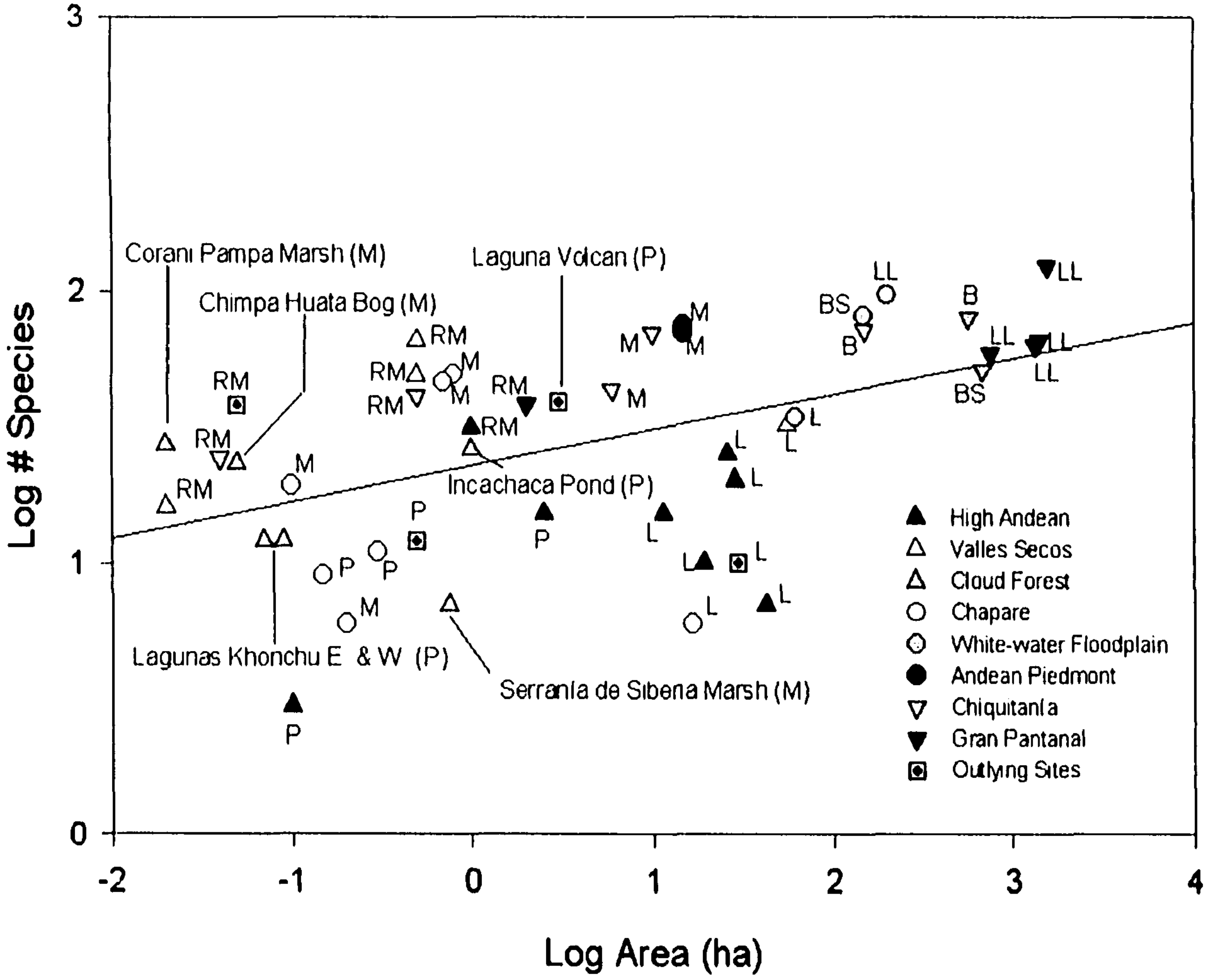


Figure 3.4. Species-area curve plotted from 46 Bolivian wetland study sites. Wetland types: **B**-bahía; **BS** - basin swamp; **L** - small lake; **LL** - large lake (> 500 ha); **M** - marsh; **P** - pond; **RM** - riparian marsh. Linear regression: log S = 1.35 + 0.13 log A; r² = 0.2441098499.

the Cloud Forest wetlands were not as unquestionably species-poor as they appeared when considering merely the number of species per system. Three of the systems were species-poor (*i.e.*, situated below the regression line) and the remaining three sites species-rich (*i.e.*, situated above the line, Fig. 3.4). As discussed in Chapter 6 the various wetland types can also be characterized as species-rich or -poor; hence, this aspect of diversity must also be considered. Two species-poor systems, Lagunas Khonchu East and West, were ponds, a wetland type that was found to be characteristically species-poor (Chapter 6). The third species-poor site, the Serranía de Siberia Marsh, was a species-rich wetland type (Chapter 6). Nevertheless, fieldwork at this site was limited to a single visit; hence, the actual flora of the site was almost certainly under-represented. Accordingly, it was not unexpected that these three sites might be somewhat depauperate. On the other hand, two of the three species-rich Cloud Forest study sites were representatives of a species-rich wetland type (marshes; Chapter 6); hence, it was expected that these would be relatively species-rich.

The Cloud Forest wetlands were noticeably richer than the High Andean wetlands, all but one of which were below the regression line (Fig. 3.4). Nevertheless, the Valles Secos study sites appeared to be richer than the Cloud Forest sites, with all of the former situated above the regression line (Fig. 3.4). Likewise, the Cloud Forest study sites were characteristically less diverse than the lowland regions, with the exception of the aforementioned species-poor Chapare region. Thus, although the Cloud Forest systems were somewhat richer than was suggested by the number of species per system, nevertheless, site-level species-richness was low relative to wetlands in most Bolivian regions.

Because all Cloud Forest study sites were situated at roughly the same elevation, it could be argued that perhaps a greater diversity of wetland species might exist in cloud forests on lower elevation montane slopes. For example, Moraes and Beck (1992) placed the greatest diversity of woody species in Bolivian montane habitats at between 500-2000 m. Likewise, Gentry (1995) found that at above 1500 m in Neotropical montane forests there was a linear decrease in species richness with elevation. Because the Bolivian Cloud Forest study sites were located well above this altitude, it is reasonable to hypothesize that more diverse wetlands might be present at lower elevation montane zones. This hypothesis appeared to be supported by the noticeably richer flora of Laguna Volcan (39 spp., Table 3.2), which was situated at about 1150 m. An examination of Laguna Volcan's flora, however, indicated that the strongest affinities were with lowland regions.

Diversity at the Regional Scale. As noted in the results, the Cloud Forest wetland flora was the most depauperate of the Bolivian regions included in the regional comparison, and was approximately as rich, or richer, than the extra-Bolivian montane regions (Table 3.3). These estimates, however, are based solely on the number of species noted for each region and, as with the comparisons of site-level diversity, it is also necessary to consider regional area in order to make meaningful comparisons of diversity at the regional scale.

Furthermore, it is preferable to consider the area of wetlands present in each region, rather than total regional area. Estimates of wetland area were made for the lowland Bolivian regions and a species-area curve plotted for these regions (see Chapter 6), but I was unable to do the same for the montane regions (Bolivian and extra-Bolivian) with any degree of confidence. Hence, the preceding characterization of the Bolivian Cloud Forest wetland flora as species-poor (relative to other Bolivian regions) is provisional, as it was based solely on differences in flora size. Nevertheless, diversity in Bolivian Cloud Forest wetlands does not appear to approximate that of the region's terrestrial flora, which is said to perhaps constitute the most diverse of Bolivia's forest formations (Killeen *et al.* 1993).

Floristic Similarities

Site-level Similarities. As noted, floristic similarities between the Cloud Forest study sites were generally low (Table 3.2). Nevertheless, despite the low floristic similarities, all Cloud Forest study sites were located in close proximity in an ordination of all Bolivian study sites (Fig. 3.2). Hence, the low floristic similarities were most likely an artifact of system size, as all of the Cloud Forest sites were quite small (*i.e.*, 1.0 ha or less). To elaborate, regions will possess a number of common species that will serve to elevate calculated floristic similarities. As the number of species in small sites will, on average, be less than in large sites, the number of common (and thus, commonly shared) species encountered in small areas will, on average, be less than in large areas.

The Lagunas Khonchu seemed to provide an excellent example of this relationship. These ponds were situated next to each other, separated by a narrow (ca. 5 m wide) strip of upland. The same stream flowed into both systems, and the two basins were similar in size (ca. 0.7 and 0.9 ha). Although there were some differences in sediment characteristics and system heterogeneity, it was expected that these systems would essentially be capable of supporting the same species. Nevertheless, the floristic similarity (Sørensen's Index) between the two systems was only 40% (Table 3.2).

Regional Similarities. The flora of the Bolivian Cloud Forest had the strongest floristic similarities (Sørensen's Index) with the Bolivian High Andean (40.2%; Table 3.3) and Valles Secos regions (29.3%, Table 3.3). A close relationship among these regions was corroborated by the ordinations of both the study site and regional floras (Figs. 3.2, 3.3). In the ordination of regional floras, the High Andean was the most proximal region to the Bolivian Cloud Forest and the Valles Secos region was the second most proximal (Fig. 3.3). Likewise, the High Andean study sites were all situated in close proximity to the Cloud Forest study sites, with the Valles Secos sites being somewhat more distal (Fig. 3.2).

A close floristic relationship among the Bolivian montane regions was not surprising, as they were in close proximity and occupied fairly comparable elevations relative to the elevational differences between the montane and lowland regions. The extremely low floristic similarity between the Bolivian Cloud Forest and the Chapare region (3.5%), however, was somewhat surprising as the former was located directly upslope from the latter, with the closest study sites (the Incachaca Pond and the Villa Tunari Pond) being separated by only about 50 km. Additionally, the high annual precipitation of the Chapare (see Chapter 4) more closely approximated meteorological conditions in the Bolivian Cloud Forest region than those of the dry High Andean and Valles Secos regions. Nevertheless, only three species (*Polygonum hydropiperoides, P. punctatum*, and *Utricularia gibba*; Appendix D) were present in the wetlands of both the Bolivian Cloud Forest and the Chapare. Corroboration of the low floristic similarity between the Bolivian Cloud Forest and the Chapare was seen in the ordinations of both the regional (Fig. 3.3) and study site data (Fig. 3.2). In both instances, the Chapare occupied the furthest position from the Bolivian Cloud Forest. Curiously, the other Bolivian lowland region considered in these comparisons, the Andean Piedmont region, showed somewhat stronger floristic associations to the Bolivian Cloud Forest (8.6%) than the Chapare, this despite being drier than the Chapare and situated further away from the Bolivian Cloud Forest.

Despite the large geographical distance between the Bolivian Cloud Forest and the extra-Bolivian montane regions, floristic similarities were greater (17.0%, Colombian montane, and 15.4%, Mexican montane; Table 3.3) than those between the Bolivian Cloud Forest and the two regions at the base of the Bolivian Andes. The ordination of regional floras (Fig. 3.3) offered some corroboration of a closer relationship between the Bolivian Cloud Forest and the extra-Bolivian montane regions, as both occupied somewhat closer positions to the Bolivian Cloud Forest than did either the Andean Piedmont or the Chapare (Fig. 3.3).

CHAPTER IV

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*

Introduction

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 (Fig. 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 km^2 (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 yr^{1} (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) (Henkel 1995).

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; Fig. 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

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

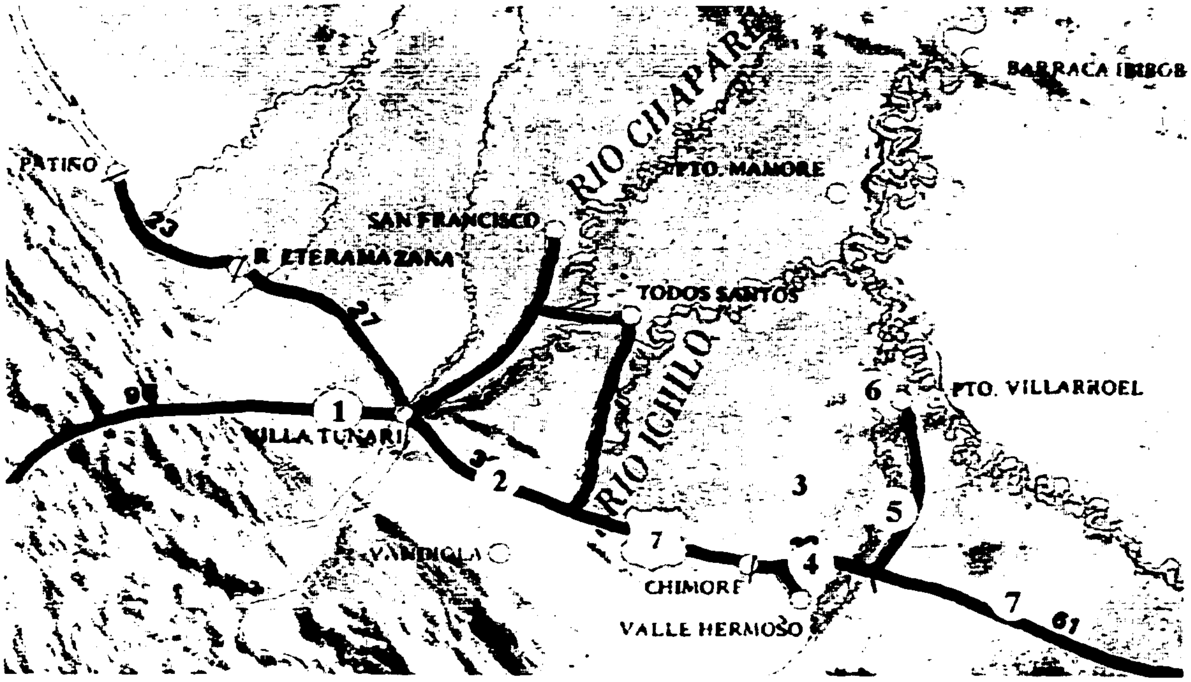


Figure 4.1. Location of the Chapare (Bolivia) study sites. 1. Villa Tunari Pond. 2. Sinahota Pond. 3. Senda F Wetland. 4. Mariposa Wetland. 5. Ivirgarsama Wetland. 6. Puerto Villarroel Laguna. 7. Valle de Sajta Curichi.

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.

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.

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.

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).

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).

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 in the shaded cells indicate the percent floristic similarity between sites.

	Mariposa Wetland	Ivirgarsama 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	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**6**	2
Puerto Villarroel	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**36.4**	**5**

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 in the shaded cells 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	**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**

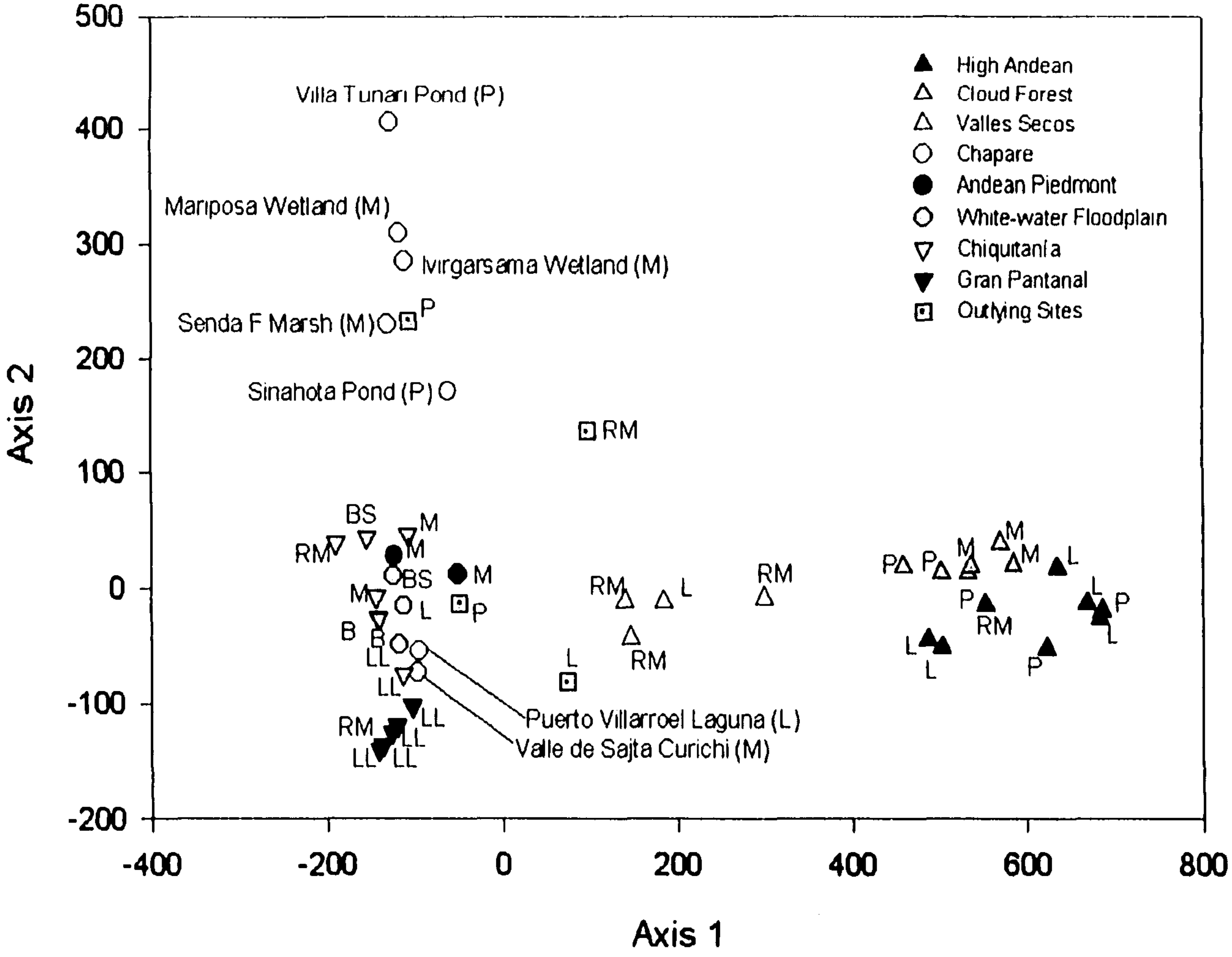


Figure 4.2. Ordination by Detrended Correspondence Analysis (DCA) of the 46 Bolivian study sites. The seven Chapare study sites are identified by name. Key to wetland types: B- bahía; BS - basin swamp; L - small lake (< 500 ha); LL - large lake (> 500 ha); M - marsh; P - pond; RM - riparian marsh.

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 (Fig. 4.2).

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% (Table 4.4). 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%) regions (Table 4.4).

The ordination of the regions by Detrended Correspondence Analysis (Fig. 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 (Fig. 4.3, circles), 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 space (Fig. 4.3,

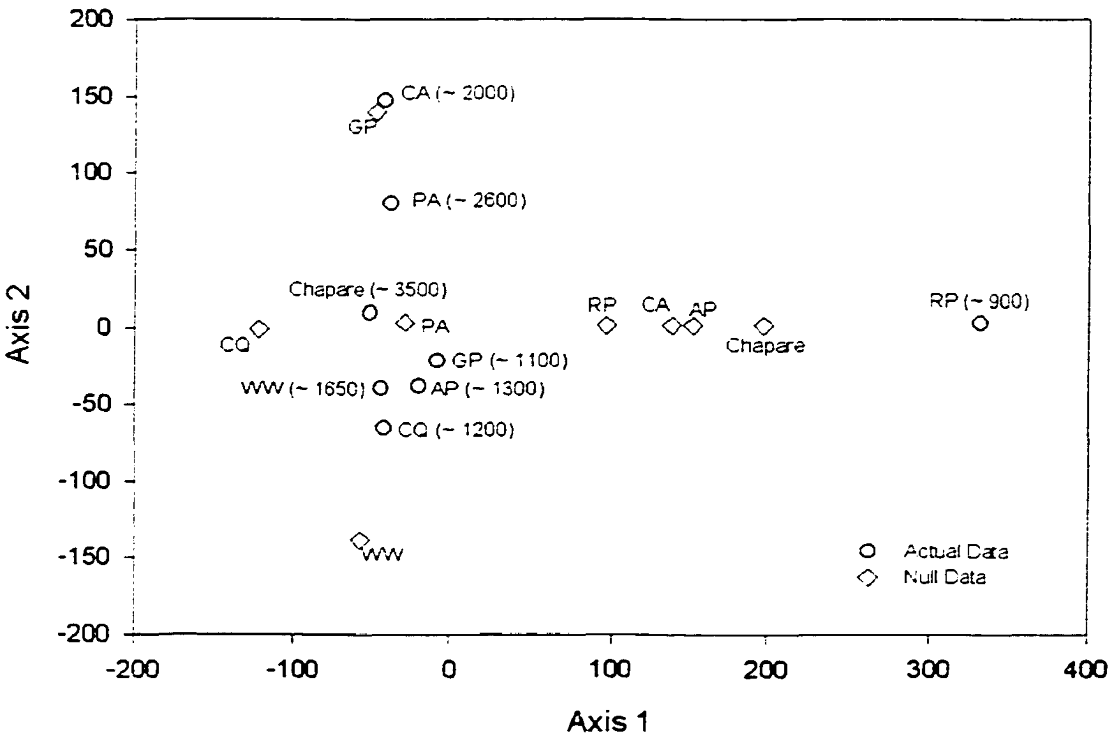


Figure 4.3. Ordination of the OGUs by Detrended Correspondence Analysis (DCA). OGUs: AP - Andean Piedmont; CA - Central Amazonia; CQ - Chiquitanía; GP - Gran Pantanal; PA - Lowland Amazonian Peru; RP - Río Paraná Delta; WW - White-water Floodplain. Values in parentheses indicate estimated mean annual precipitation (mm).

circles). The Río Paraná Delta region formed the other first axial endpoint, occupying a position far removed from all other OGUs (Fig. 4.3 circles). 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 (Fig. 4.3 circles). The ordination of the null data set (Fig. 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 (Fig. 4.3, circles) were far removed from their respective positions in the ordination of the null data (Fig. 4.3, diamonds). Hence, it appears that differences in floristic composition among the regions were sufficiently strong to surmount any effects of sample size.

The graphical representation of the species frequency "classes" (Fig. 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 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 (Fig. 4.4). 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 (Fig. 4.4). In all cases, rarely shared species contributed relatively little (1.9-13.4%, Fig. 4.4) to overall floristic similarity.

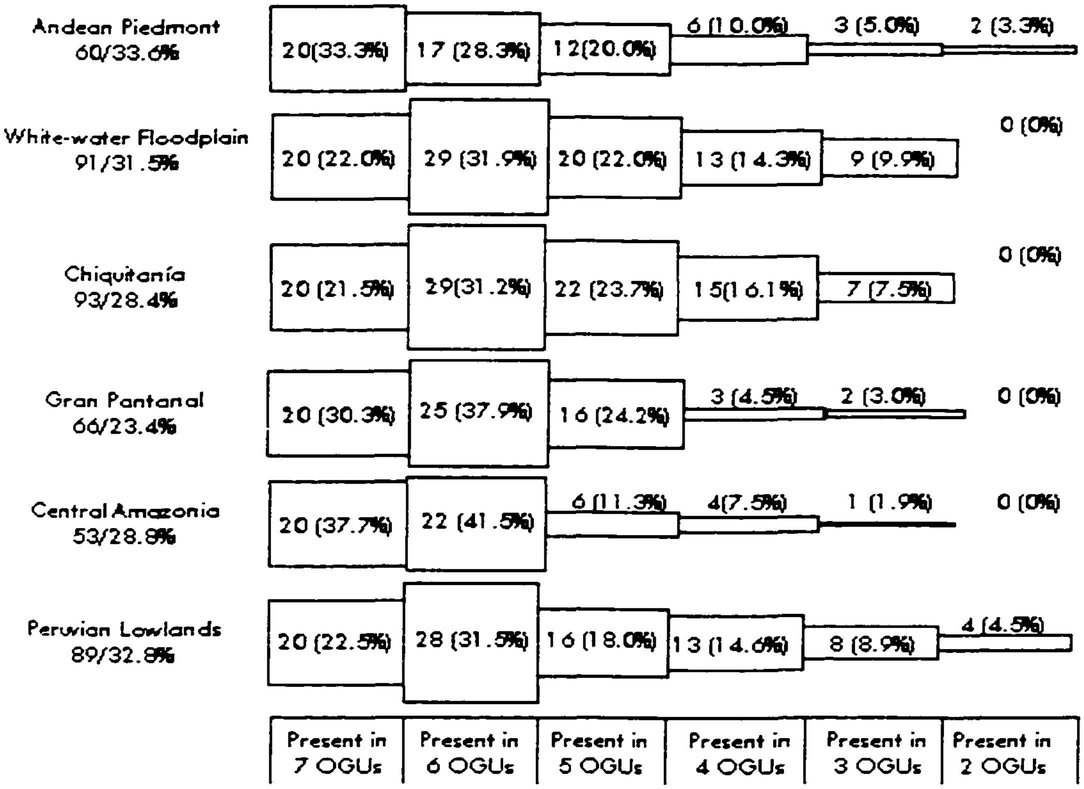


Figure 4.4. Frequency of species shared between the Chapare and the other OGUs. Figures below the OGU name indicate the number of species present in both the OGU and the Chapare, followed by floristic similarity (Sørensen's Index). Boxes correspond to species classes (i.e., the number of OGUs in which 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.

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 (México 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 (Fig. 4.5).

Study sites situated above the regression line (Fig. 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 (Fig. 4.5). Of the remaining systems, one was located just above the regression line, and two were situated well above the line (Fig. 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

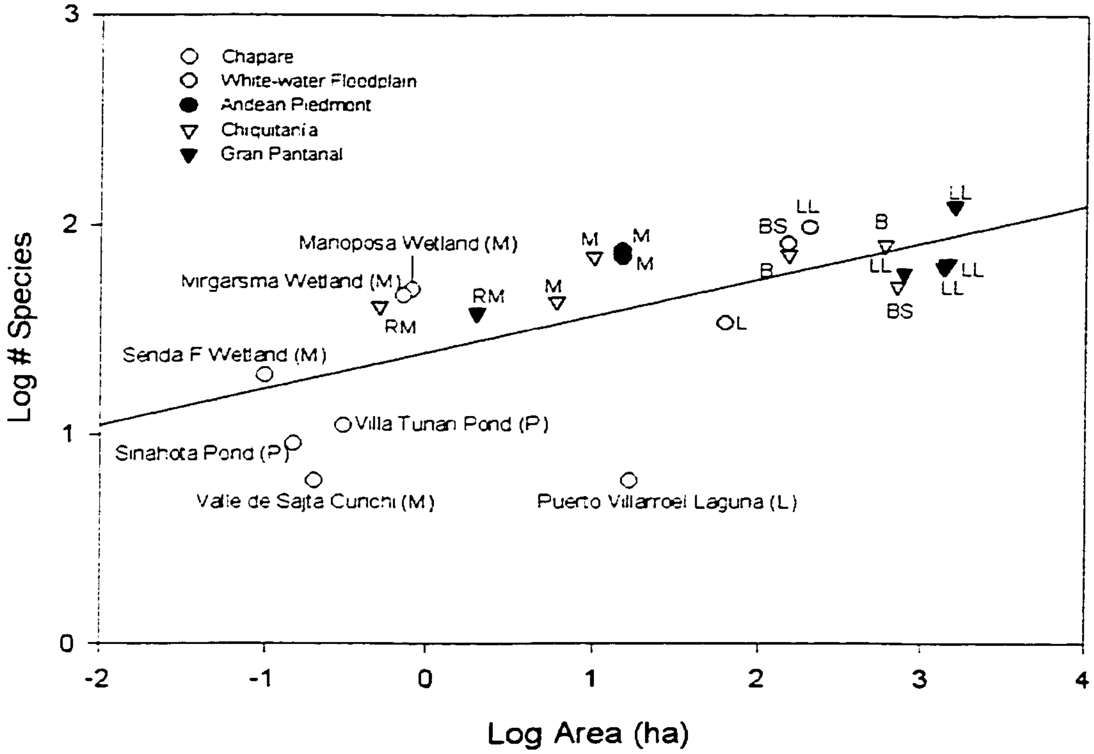


Figure 4.5. Species-area curve plotted from the 23 lowland Bolivian study sites, with the Chapare study sites identified by name. Wetland types: **B**- bahía; **BS** - basin swamp; **L** - small lake (< 500 ha); **LL** - large lake (> 500 ha); **M** - marsh; **P** - pond; **RM** - riparian marsh. Linear regression: Log S = 1.39 + 0.17 Log A. $r^2 = 0.44$.

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 (Fig. 4.6). Discrete species-area data from the Chapare and the other OGUs considered here were added to the plot (Fig. 4.6). 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 (Fig. 4.6). Other species-poor OGUs were lowland Amazonian

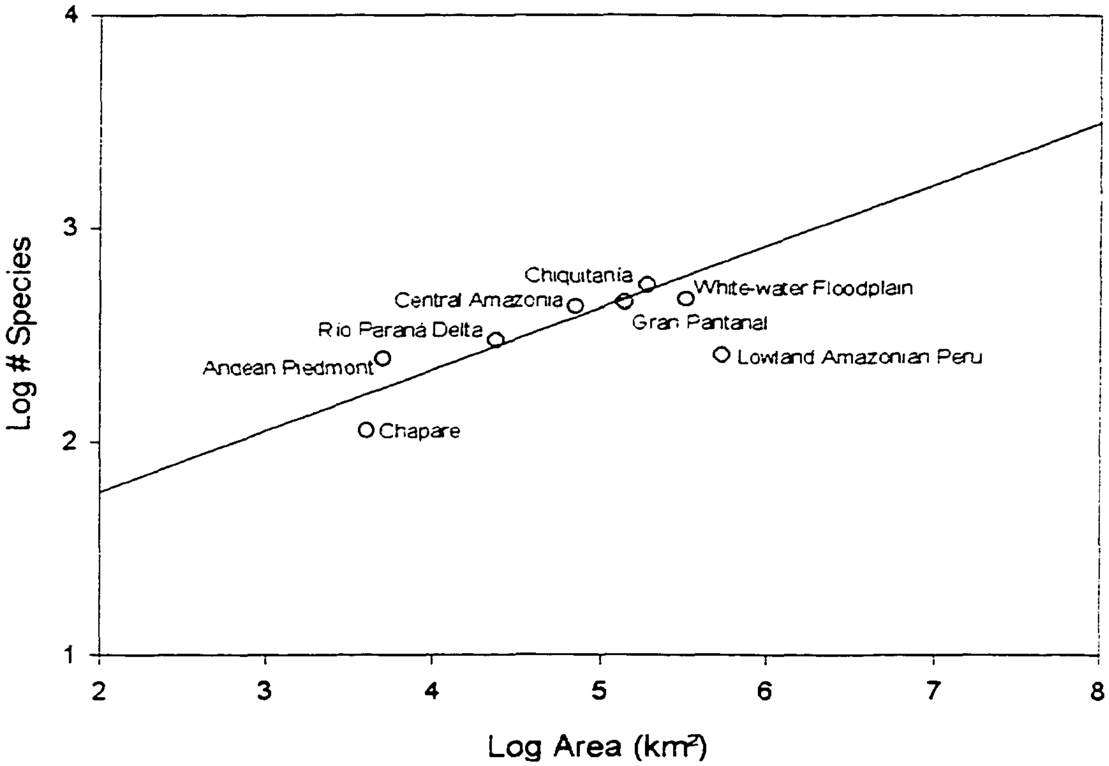


Figure 4.6. Species diversity of the OGUs considered in comparisons with the Chapare (Bolivia) wetland flora. Diversity is relative to a regression line fitted to a species-area curve plotted from cumulative species-area data from the Neotropical countries, including Mexico (see Chapter 6). Linear regression: Log S = 1.46 + 0.25 Log A; $r^2 = 0.99$.

Peru and the White-water floodplain (Fig. 4.6). By contrast, the Andean Piedmont region, which is contiguous with the Chapare, was the most diverse (Fig. 4.6).

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.

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 (Fig. 4.7). A trend toward fewer species with increased precipitation was apparent (Fig. 4.7), 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

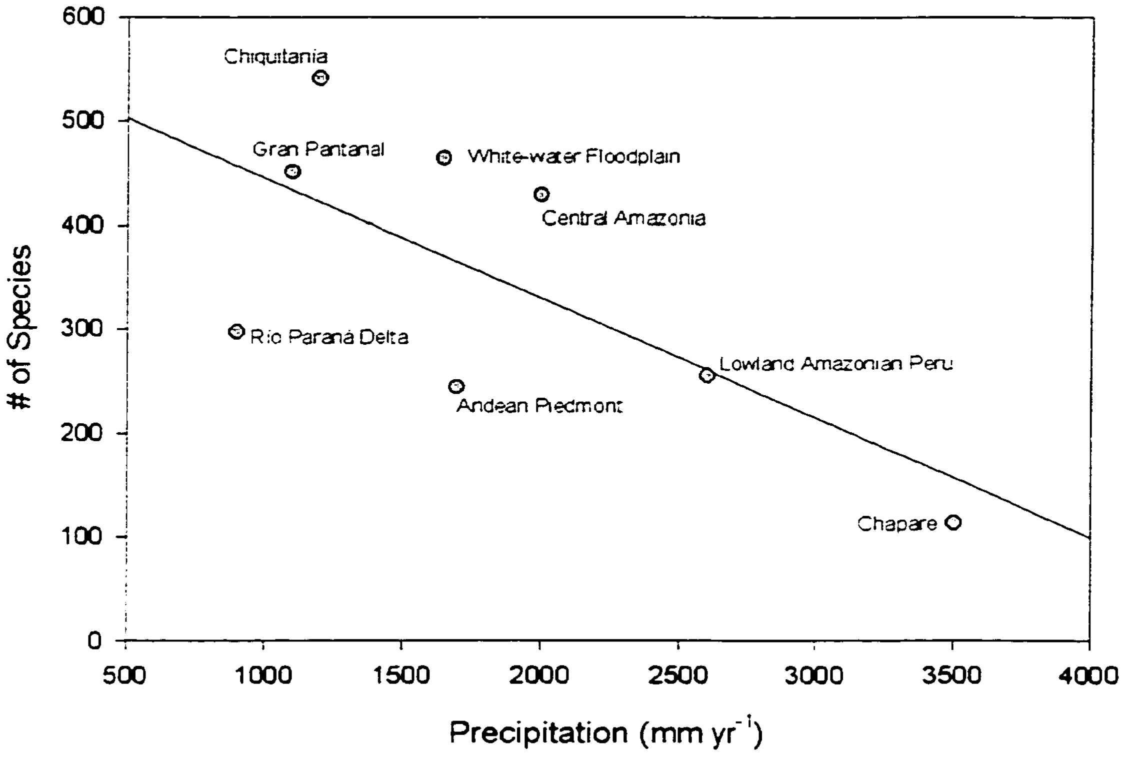


Figure 4.7. The relationship between precipitation and species richness. Linear regression: $S = 560.8 - 0.12\ P$; $r^2 = 0.48$.

diversity in 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 (244spp.) as the Chapare (113 spp.). Furthermore, in the comparison with the general trend of diversity in the Neotropical wetland flora (Fig. 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 km^2), 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.

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 β-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 (Fig. 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 (Fig. 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} (Fig. 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

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

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 (Table 4.5). 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.

Although the ordination by DCA (Fig. 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 (Fig. 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 (Fig. 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.

CHAPTER V

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 km^2 (Bonetto 1975;

van der Beck *et al.* 1996) to 250,000 km^2 (Tundisi and Matsumura-Tundisi 1985). Recent estimates derived from the analysis of remotely sensed images place the area at 130,000 to 140,000 km^2 (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. 25°C, with maximum temperatures reaching 40°C and minimums approaching 0°C (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 innundation.

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 m^2

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; Fig. 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

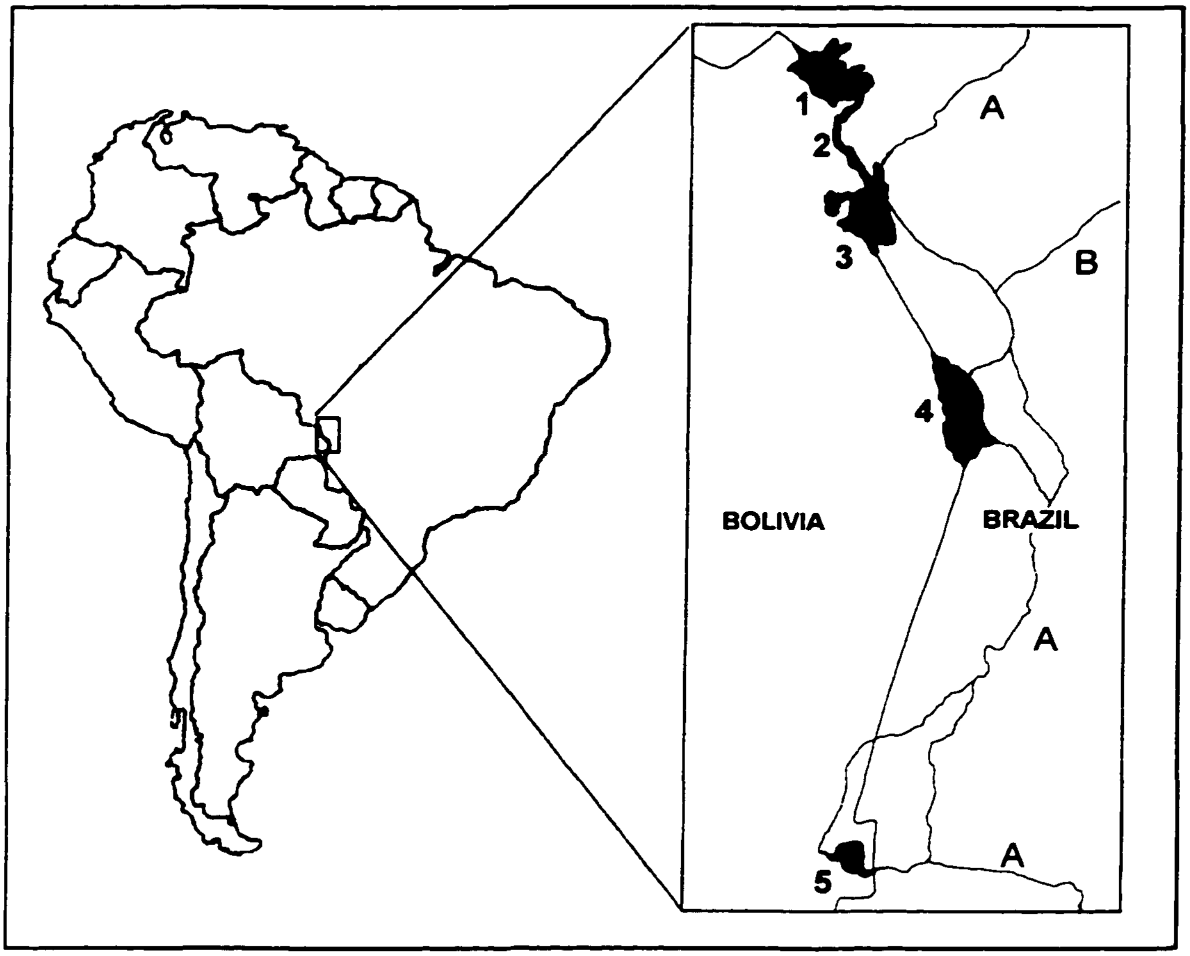


Figure 5.1. South America, with an inset of the study sites from the Bolivian Gran Pantanal. Study sites: 1. Laguna Uberaba. 2. Puesto Gonzalo. 3. Laguna La Gaiba. 4. Laguna Mandioré. 5. Laguna Cáceres. Rivers: A. Río Paraguay. B. Río Cuiaba.

Floristic 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 (Table 5.2). 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., Table 5.3). The Central Amazonian region possessed the fewest species (255 spp., Table 5.3).

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

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 in the shaded cells indicate the percent floristic similarity between OGUs.

	Lagune 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 in the shaded cells 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**

Puesto Gonzalo site demonstrated strong floristic similarities to the lacustrine study sites (39.5-48.5%, Table 5.2). 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 (Fig. 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% (Table 5.3). The Gran Pantanal flora demonstrated the strongest floristic affinities to the Chiquitanía (55.8%) and White-water Floodplain regions (54.9%, Table 5.3).

Ordination of the OGU's by Detrended Correspondence Analysis (Fig. 5.3) produced a plot that, for the most part, corresponded well with floristic similarities as expressed by Sørensen's Index (Table 5.3). The Río Paraná Delta region formed one of the first axial endpoints, and was far removed from all other OGUs (Fig. 5.3). The remaining OGUs were roughly aligned along the second axis, with the Chiquitanía and Lowland Amazonian Peru forming the axial endpoints (Fig. 5.3). The White-water Floodplain and the Chiquitanía, the OGUs that showed the strongest floristic similarities (Sørensen's Index, Table 5.3) to the Pantanal, were also closest to the Pantanal in

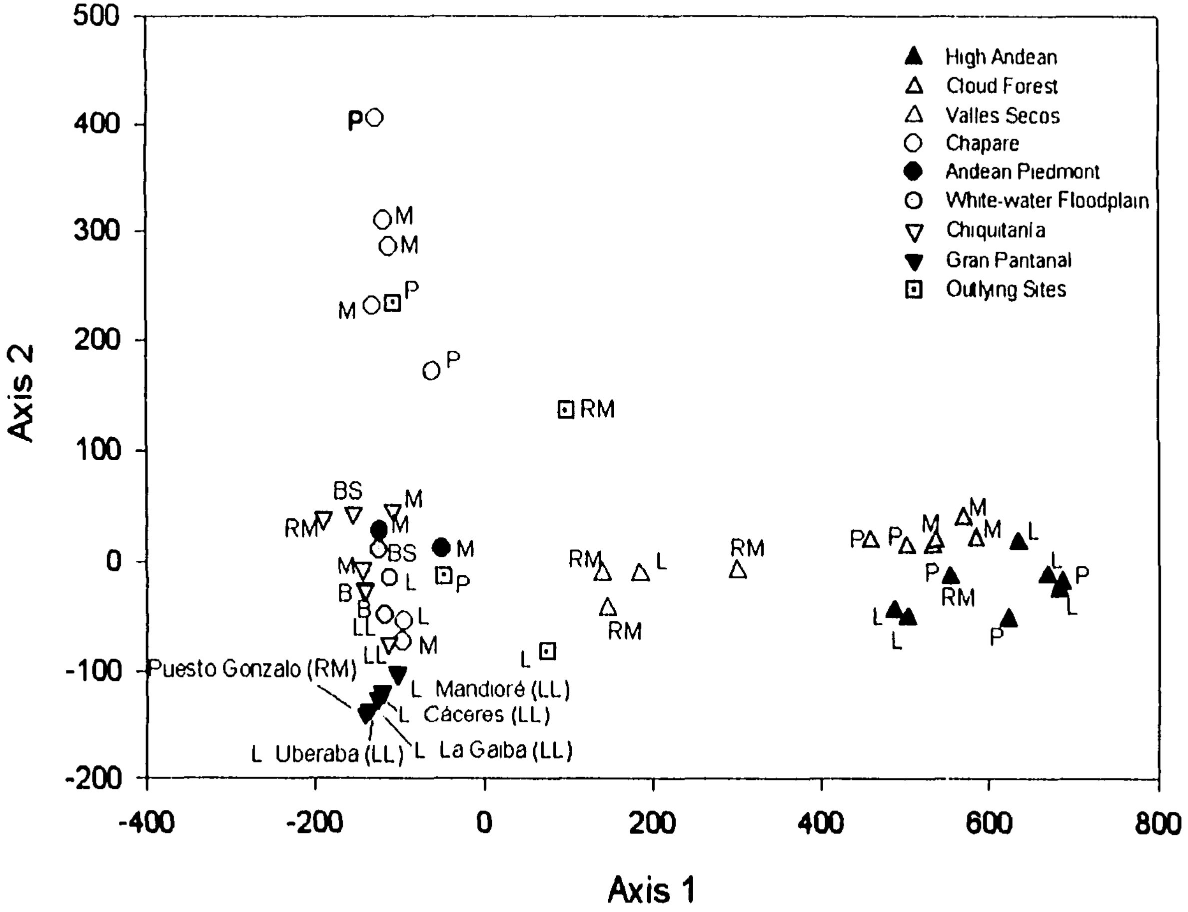


Figure 5.2. Ordination by Detrended Correspondence Analysis (DCA) of the 46 Bolivian study sites. The five study sites from the Bolivian Gran Pantanal are identified by name. Key to wetland types: B- bahía; BS - basin swamp; L - small lake (< 500 ha); LL - large lake (> 500 ha); M - marsh; P - pond; RM - riparian marsh.

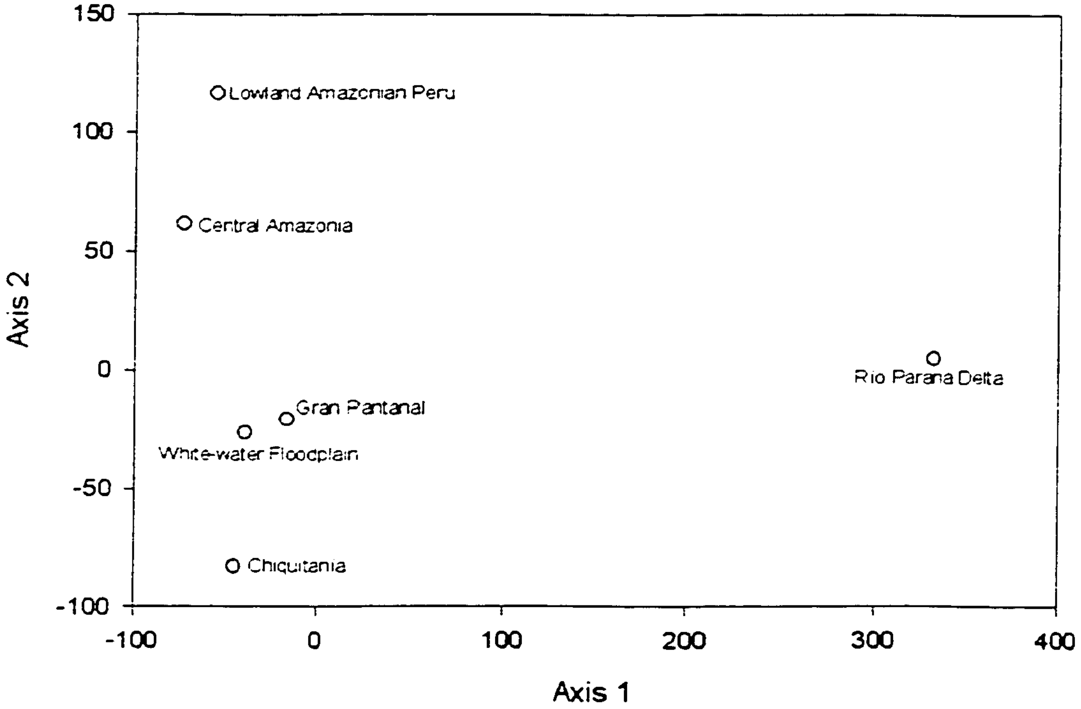


Figure 5.3. Ordination of the OGUs Detrended Correspondence Analysis (DCA). OGUs are those used in floristic comparisons with the Gran Pantanal. The wetland flora of the Gran Pantanal was compiled from species recorded from the Bolivian and Brazilian portions of this system.

ordination space (Fig. 5.3). Their position, however, was not strictly as suggested by Sørensen's Index (Table 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.

A histogram of the species frequency "classes" (Fig. 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 (Fig. 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' distributions; rather they refer solely to species distributions within this particular set of OGUs.

Floristic similarities between the Gran Pantanal and both Central Amazonia and Lowland Amazonian Peru were, in large part, derived from the presence of many

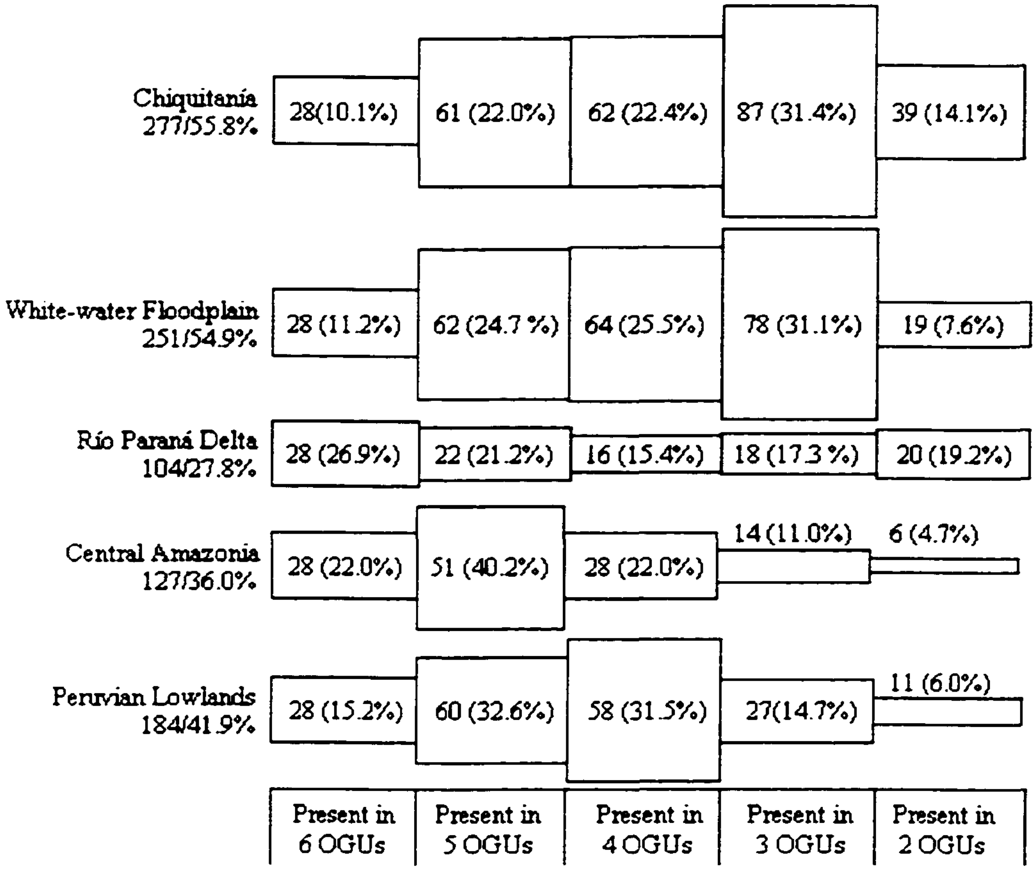


Figure 5.4. Frequency of species shared between the Gran Pantanal (Bolivian and Brazilian portions) and the other OGUs utilized in floristic comparisons. Figures below the OGU name indicate the number of species present in both the OGU and the Gran Pantanal, followed by floristic similarity (Sørensen's 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.

ubiquitous and widely distributed species (Fig. 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 (Fig. 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%, Fig. 5.4). 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%, Fig. 5.4) 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 (Fig. 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.

As in the preceding chapters, sites situated above the regression line (Fig. 5.5) were considered to be relatively species-rich and those below the line as relatively

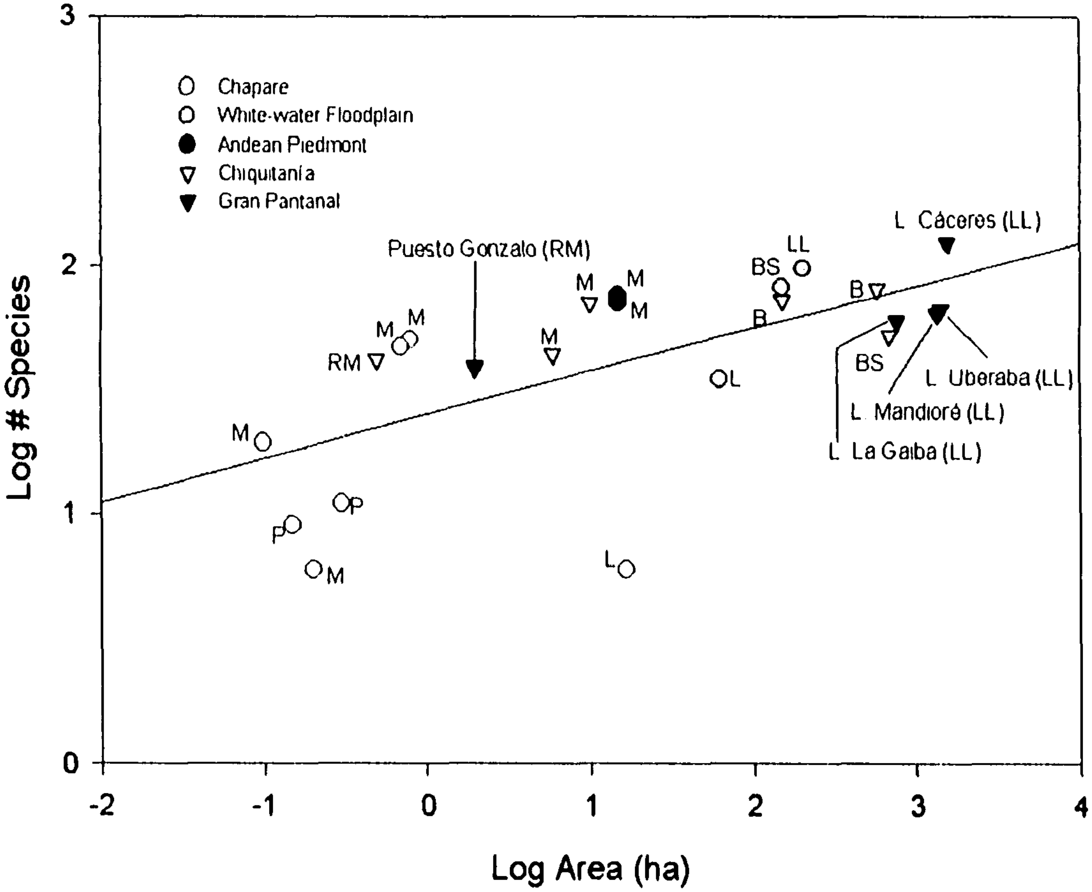


Figure 5.5. Species-area curve plotted from the 23 Bolivian lowland study sites, with the Gran Pantanal study site identified by name. Wetland types: B - bahía; BS - basin swamp; L - small lake (< 500 ha); LL - large lake (> 500 ha); M - marsh; P - pond; RP - riparian marsh. Linear regression: Log s = 1.39 + 0.17 log A; $r^2 = 0.44$.

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 above (Fig. 5.5). 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 (Fig. 5.5) 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; Table 5.3) 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 (Fig. 4.6) to represent the general trend in wetland species-richness throughout the Neotropics, is also used here (Fig. 5.6). This construction of this curve is discussed in detail in Chapter 7.

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 (Fig. 5.6). As discussed in Chapter 6, however, a more

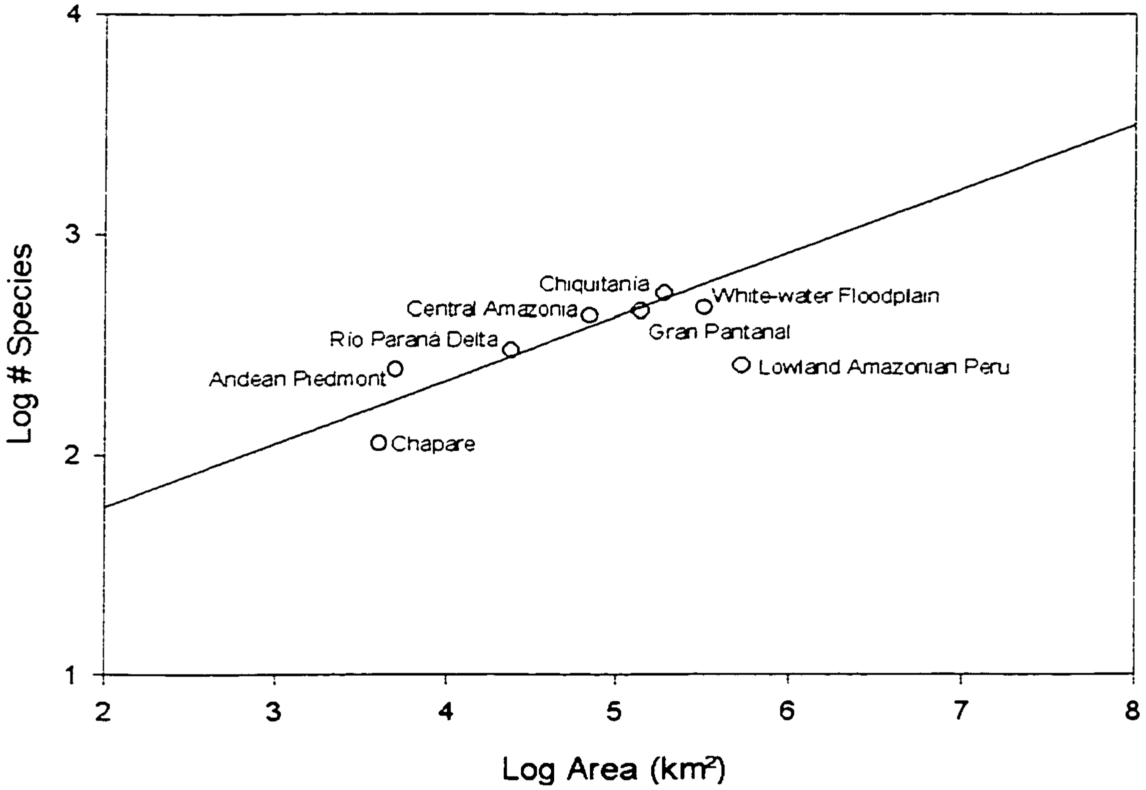


Figure 5.6. Phytodiversity of the OGUs considered in comparisons with the wetland flora of the Gran Pantanal (Bolivian and Brazilian portions). Diversity is relative to a regression line fitted to a species-area curve plotted from cumulative species-area data from the Neotropical countries, including Mexico (see Chapter 6). Linear regression: Log S = 1.46 + 0.25 Log A; $r^2 = 0.99$.

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 Fig. 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 (Fig. 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 (Fig. 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 (Fig. 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%, Table 5.3). 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 (Fig. 5.3).

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 (Fig. 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 (Fig. 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 (Fig. 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.

CHAPTER VI

SITE-LEVEL BIODIVERSITY

> Not only are islands impoverished relative to the mainlands, but small islands are more severely impoverished than large ones. That last bit of insight became famed as the species-area relationship. During your lifetime and mine, the science of ecology has responded to it as oceans and coyotes respond to the moon.
>
> - David Quammen, *The Song of the Dodo*

Introduction

In the last three chapters, phytodiversity in the wetland floras of three specific Bolivian regions was examined. Principal objectives were to estimate site- and regional-scale phytodiversity in the region's wetland floras and to examine how this compared with either diversity in the region's terrestrial flora (the Cloud Forest and the Chapare) or with what had previously been noted for the region's wetland flora (the Gran Pantanal). Attention was also given to the description of site and regional floras and to the examination of phytogeographic affinities.

In this chapter, diversity at the system level is examined in more detail. A brief discussion of general biodiversity research in the Neotropics is presented. Consideration is then given to sampling methodology and to patterns and processes in Neotropical wetlands that may affect estimates of diversity. Site-level diversity in the 46 Bolivian wetland systems is then examined, commencing with the most basic estimation (number of species) and proceeding through more elaborate approaches. In the final sections, site-level diversity in Bolivian wetlands is compared with diversity in Neotropical terrestrial habitats and with wetlands from the New World Temperate region. As comparisons were concerned specifically with these region's wetland habitats, "species" and "species-richness" refer solely to the wetland component of the flora unless otherwise noted. Similarly, although species-richness is but one component of diversity (and a simple one, at that), for utility's sake "species richness" and "diversity" are applied here as synonyms.

As noted in Chapter 1, my interest in phytodiversity in Neotropical wetlands was engendered by observations from a few researchers (Black 1950; Crow 1993; Haynes and Holm-Nielson 1986,1989) who perceived that Neotropical wetlands were surprisingly species-poor. Although the portrayal of Neotropical wetlands as species-poor is surprising, it is important to note that even the investigation of Amazonian diversity in terrestrial ecosystems is still in its beginning stages. As of the mid-1980's, just a single complete site inventory of terra firme forest, which is now though to constitute Amazonia's richest habitat type, had been accomplished (Gentry 1988b). Furthermore, although we now have an appreciation of Amazonian forests as phenomenally rich in species, until recently the ranking of the worlds richest terrestrial ecosystems was still a matter of debate (Gentry 1988b). Until the mid-1980's, it was widely held that the greatest diversity of trees was to be found in the rain forests of Southeast Asia (Gentry 1988b). Concurrently, much debate was centered on which ecosystem was the most species-rich, with various researchers nominating a wide range of forested and non-forested habitats (see Gentry & Dodson 1987, for a review).

Although Amazonia is undeniably rich in vascular plant species, this same relationship is not evident for all groups of organisms. For example, Mares (1992) investigated the distribution of mammals in South America. The continent was partitioned into six major "macrohabitats": 1) drylands; 2) Amazon lowlands; 3) Southern mesophytic forests; 4) uplands semideciduous forest; 5) western montane forests; and, 6) Atlantic rain forest. Species-richness and number of endemic taxa were calculated for each region. Mares (1992) determined that the Amazonian lowlands supported fewer taxa (at all taxonomic levels) than did the South America drylands. Furthermore, approximately 70% of the continent's endemic mammalian species (defined as species restricted to a single macrohabitat) were from regions outside the Amazonian lowlands.

Nevertheless, the Neotropical lowlands possess extensive areas of permanently- and seasonally-inundated habitat, and intuitively it seems that these should support a rich wetland flora. Furthermore, Amazonia is said to possess the world's "greatest diversity of fresh water vertebrates" (Haynes and Holm-Nielson 1986, p. 14), and it is not unreasonable to assume that the same might also hold true for the vascular flora.

Methodological Considerations

Floristic sampling in this study was intended to address multiple objectives (see Introduction). Meeting these objectives necessitated maximizing the number of species encountered and, therefore, the number of systems and regions visited. Thus, rather than employ quadrat-based sampling, (putatively) comprehensive site floras were compiled (see Chapter 2). Although it was unquestionably faster to sample in this manner there were a number of shortcomings associated with this approach.

One obvious problem is that it is generally much easier to detect all species present in a series of quadrats than it is to encounter all the species that occur in an entire system. If the system is small (*e.g.*, on the order of a few hectares), it seems likely that the greatest part of the flora can be encountered in a reasonable amount of time. In larger systems, however, it becomes less likely that all parts of the system can be surveyed with the same degree of thoroughness as can a smaller portion of the flora (*i.e.*, quadrats).

During the first year or so of fieldwork in Bolivia, it seemed reasonable to attempt to compile complete site floras, as many of the study sites were on the order of one ha or less and the larger sites (*e.g.*, Laguna Juntutuyo, 244 ha; Laguna Alalay, 170 ha; Laguna Totora Khocha, 120 ha) were sufficiently limited in area so that it was possible to survey the entire perimeter in a day. Additionally, the study sites from that time period generally contained few species due to their location in regions with relatively depauperate wetland floras (*i.e.*, the montane regions and the Chapare). As fieldwork progressed, however, and investigations shifted to larger, more complex (physiognomically and vegetatively) systems, it was frequently not possible to examine more than a small portion of the system. Thus, in all likelihood, a significant portion of the flora was not encountered in these systems.

Nevertheless, if after spending a certain amount of time investigating a system no additional species are immediately encountered, there *is* a natural tendency to feel as if a relatively complete site flora has been compiled. While undeniably comforting, it is not possible to ascertain whether these impressions are warranted or whether they are merely the outcome of wishful thinking. An example of the unreliability of this type of impression comes from the fieldwork in Laguna Cáceres, in the Bolivian Pantanal (Chapter 5). Initial fieldwork at this site was conducted by myself, Dr. Garrett Crow (UNH), and a field assistant during July 14-15, 1997. Merely 41 species were observed at this time, a relatively small number for such a large (ca. 3,500 ha), heterogeneous, lowland system. Dr. Crow and I shared the impression that, although we obviously had not encountered every species present at the site, the number that we had encountered was sufficiently representative of the overall flora so that we could confidently characterize the system as (surprisingly) species-poor. During the subsequent visit to the site (July 18-20, 1998), however, we encountered an additional 76 species and, thus, were both induced to consider the system as species-rich.

Additional difficulties in assessing species richness stem from the seasonal changes in floristic composition and abundance that are typical of many Neotropical wetlands. In order to account for this variability, study sites received multiple visits whenever possible, with fieldwork scheduled so that sites were observed during different hydrologic seasons. Nevertheless, it was frequently either impractical or impossible to adhere to these guidelines.

Short-lived herbaceous species, which develop during the latter stages of the rainy season, appear to be especially under-represented in floristic surveys of Neotropical wetlands. Seasonally inundated savannas (Sarmiento *et al.* 1996) and shallow ponds and pools (Heckman 1994), in particular, are recognized as supporting rich assemblages of ephemerals. For example, Sarmiento (1984) noted 18 ephemeral species in the flooded savannas at the Biological Station of the Guianas (Venezuela). Likewise, sampling from two seasonally inundated savannas in Parque Nacional Noel Kempff Mercado at a time when standing water had just recently receded yielded 19 herbaceous species that I had not previously encountered in many months of fieldwork in the park. Of these, 11 were new records for the Park, one was putatively new to science, two were definitely new records for Bolivia, four more were possibly new country records, and three were previously known for Bolivia from only one or two other collections. These discoveries were made despite the fact that both savannas had previously been the site of repeated botanical collecting from a number of researchers, with one savanna also serving as the study area for at least two student theses.

Although seasonal changes in floristic composition in Neotropical wetlands are well-known (*e.g.*, Prado *et al.* 1994; Heckman 1994, 1997; A. Pott and V. Pott 1997), studies aimed at assembling site floras in Neotropical wetlands often appear to have completely ignored this factor in their methodology, whereas others have neglected to even mention the existence of these cycles (*e.g.*, Crow 1993). One study that did pay particular attention to the effects of these seasonal changes was that of Prado *et al.* (1994) in the Brazilian Gran Pantanal. Sampling was conducted during each of the four hydrologic stages (see Chapter 5), enabling the authors to track seasonal variations in floristic diversity and similarity. Forty-eight species were encountered during a year's sampling in a 0.25 ha study area. The greatest number of species encountered at any one season (37 spp., during the *vazante*, the transition between the rainy and dry seasons) was equal to just 77% of the total observed (year-round) flora, whereas the fewest species encountered at any one season (31, during the *cheia*, or dry season) was only about 65% of the observed flora.

Another example of seasonal differences in floristic composition can be evidenced from my fieldwork at Lago Caíman, a large (ca. 575 ha) study site in Parque Nacional Noel Kempff Mercado (Appendix A). Seven days were spent on floristic sampling at the end of the rainy season (April and May,1996). Fifty-seven species were encountered and it seemed to me that the greatest portion of the flora had likely been encountered, given the large amount of sampling conducted. A subsequent visit was made to Lago Caimán under drier conditions (June, 1998) and twenty-three additional species were encountered. Although a portion of these had, in all likelihood, been present (but not observed) during the initial visit to the system, it seems likely that many were either absent during the first visit or were present in such low abundance that they were not observed.

It would be misguided to assume that the results from just two investigations (Lago Caimán and the quadrat of Prado *et al.*, 1994) approximate the average magnitude of seasonal fluctuations in floristic composition. Nevertheless, it is clear that the season during which fieldwork is conducted can potentially have a significant influence on the level of species richness encountered.

Site-Level Diversity

As noted in Chapter 2, researchers assessing phytodiversity in Neotropical terrestrial habitats have frequently employed a methodology utilizing 0.1 and 1.0 hectare samples. No equivalent standardized methodology appears to have been adopted for investigations in Neotropical wetlands, however, with the exception of seasonally inundated forests, which are capable of being sampled with the same methodology developed for upland forest. Citing this lack of standardized data sets from wetlands, Crow (1993) suggested that regional differences in wetland floristic diversity could be assessed by comparing system-level diversity from a series of wetlands. Although a reasonable starting point for estimating diversity, a serious shortcoming with this type of comparison is that by treating wetland "systems" as fixed units no consideration is given to the contribution of sample area toward species richness. In the following sections both approaches to evaluating diversity are employed and compared. Diversity is first evaluated in terms of number of species per site; subsequently, system area is factored into the evaluations.

The Bolivian study sites were categorized by wetland type and listed, along with region, elevation, area, and number of species (Table 6.1). Wetlands were grouped into seven categories: 1) ponds; 2) small lakes (area < 500 ha); 3) large lakes (area > 500 ha); 4) bahías; 5) basin swamps; 6) marshes; and, 7) riparian marshes. For most wetland types, the entire area of the system was considered to be the " vegetated area". Lacustrine study sites, however, generally contained extensive areas of open water that were characteristically unvegetated. For these systems, the potentially vegetated area was

Table 6.1. Bolivian study sites, with wetland type, region, elevation, estimated vegetated area (EVA), and number of vascular plant species. Wetland types: **B**- bahía; **BS** - basin swamp; **L** - small lake; **LL** - large lake (> 500 ha); **M** - marsh; **P** - pond; **RM** - riparian marsh. Regions: **HA** - High Andean; **VS** - Valles Secos; **CF** - Cloud Forest; **CP** - Chapare; **WW** - White-water Floodplain; **AP** - Andean Piedmont; **CQ** - Chiquitanía; **GP** - Gran Pantanal; **NA** - Not associated with one of these eight regions.

Study Site	Wetland Type	Region	Elev. (m)	Area (ha)	EVA (ha)	# of spp.
Laguna Toro	P	HA	4420	2.5	2.5	15
Huayalmarca Pond	P	HA	4300	0.1	0.1	3
Laguna Saythu Khocha	L	HA	4020	40	19.5	10
Laguna Totora Khocha	L	HA	3620	120	29.0	20
Laguna Larati	L	HA	3540	124	26.5	25
Laguna Juntutuyo	L	HA	3360	244	43.0	7
Río Candelaria	RM	HA	3165	1	1.0	31
Laguna Chulichuncani	L	HA	3160	20	11.5	15
Laguna Alalay	L	VS	2550	170	56.7	32
Río Mizque Wetland	RM	VS	1970	0.5	0.5	66
Río Guadalquivir Wetland	RM	VS	1800	0.5	0.5	49
Tiquipaya Irrigation Canal	RM	VS	2620	0.02	0.0	16
Chimpa Huata Bog	M	CF	2920	0.05	0.05	23
Incachaca Pond	P	CF	2385	1	1.0	26
Laguna Khonchu - East	P	CF	2620	0.07	0.07	12
Laguna Khonchu - West	P	CF	2620	0.09	0.09	13
Corani Pampa Marsh	M	CF	2470	0.02	0.02	26
Siberia Marsh	M	CF	2800	0.75	0.75	7
Mariposa Wetland	M	CP	220	0.8	0.8	49
Ivirgarsama Marsh	M	CP	220	0.7	0.7	46
Senda F Wetland	M	CP	220	0.1	0.1	19
Villa Tunari Pond	P	CP	300	0.3	0.3	11
Sinahota Pond	P	CP	240	0.15	0.15	9
Valle Sajta Curichi	M	CP	210	0.2	0.2	6
Puerto Villarroel Laguna	L	CP	190	30	16.8	6
Riberalta Ciénaga	BS	WW	170	150	150.0	81
Laguna Tumi Chuqua	L	WW	170	300	62.8	34
Laguna Suarez	LL	WW	160	600	200.0	97
Bermudez Curichi	M	AP	430	15	15.0	70
Viru Viru Wetland	M	AP	430	15	15.0	75
Concepción Wetland	M	CQ	485	10	10.0	70

Table 6.1 (continued).

Study Site	Wetland Type	Region	Elev. (m)	Area (ha)	EVA (ha)	# of spp.
Huanchaca Arroyo	RM	CQ	760	0.04	0.04	24
La Toledo Curichi	M	CQ	220	6	6.0	43
Bahia Toledo	B	CQ	210	150	150.0	72
Río Paraguá	RM	CQ	210	0.5	0.5	41
Cuatro Vientos Palm Swamp	BS	CQ	205	690	690.0	51
Lago Caimán	B	CQ	200	575	575.0	80
Laguna Uberaba	LL	GP	85	30,000	1410.0	66
Laguna La Gaiba	LL	GP	90	10,500	760.0	59
Laguna Mandioré	LL	GP	90	25,000	1350.0	63
Laguna Cáceres	LL	GP	90	3,500	1560.0	124
Puesto Gonzalo	RM	GP	90	2	2.0	38
Laguna Yaguacua	P	NA	920	30	30.0	10
Laguna Volcan	P	NA	1150	3	3.0	39
Yolosa Marsh	RM	NA	1150	0.05	0.05	38
Cristalmayu Pond	P	NA	640	0.5	0.5	12

estimated from an approximately 50 m wide band around the perimeter of the basin plus the (frequently extensive) areas of seasonally inundated marsh adjacent to the basin. Basin perimeter and associated seasonally inundated areas were determined from topographic maps or from other images. In one instance, system area was reduced in this manner from 600 to 200 ha; however, this system, Laguna Suarez, still retained its status as a "large lake." Additionally, although bahías (lakes with a seasonal connection to a riparian system) are also lacustrine, the two bahía study sites had a much greater ratio of vegetated area to open water than did other lacustrine sites. Therefore, the system area of the bahías were not recalculated, as per the lakes and large lakes. Additionally, one lake, Laguna Alalay, was unusual in that large portions of the open water zone supported submersed vegetation. In this instance, the potentially vegetated area of the system was estimated as one third of the total basin area.

The number of species at the study sites was extremely variable, ranging from 3-124 spp. (Table 6.1). Study sites were grouped by region and wetland type, with the range and mean of system-level species-richness calculated for each region and wetland type (Table 6.2; Table 6.3). The High Andean region possessed the most species-poor sites (3-31 spp.; $\bar{x} = 15.8$), with the Cloud Forest (7-26 spp.; $\bar{x} = 17.8$) and the Chapare (6-49 spp.; $\bar{x} = 20.9$) nearly as depauperate (Table 6.2). The Andean Piedmont (70-75 spp.; $\bar{x} = 72.5$), White-water Floodplain (34-97 spp.; $\bar{x} = 70.7$), and Gran Pantanal (38-124 spp.; $\bar{x} = 70$) possessed the highest site-level richness (Table 6.2). These estimates should be considered as preliminary, however, as consideration has not yet been given to the number of systems in each region and to average system area. Large lakes constituted

Table 6.2. Distribution of the 42 [A] study sites located in the eight Bolivian regions considered in floristic comparisons, with the number of study sites from each region, the range of species richness among the region's sites, and mean species richness for the region.

Region	**# of Systems**	**Range of Species**	$\bar{x}$
High Andean	8	3-31	15.8
Valles Secos	4	16-66	40.8
Cloud Forest	6	7-27	17.8
Chapare	7	6-49	20.9
Andean Piedmont	2	70-75	72.5
White-water Floodplain	3	34-97	70.7
Chiquitanía	7	24-80	54.4
Gran Pantanal	5	38-124	70

A. Data from the four Bolivian study sites situated outside of these eight regions were not included in these tabulations.

Table 6.3. Distribution of wetland types in the Bolivian study sites, with number of systems pertaining to each type, etc.

Wetland Type	# of Systems	Range of Species	$\bar{x}$
Pond	10	3-39	14.9
Small Lake	8	6-34	18.6
Large Lake	5	59-124	81.8
Bahía	2	72-80	76.0
Basin Swamp	2	51-81	66.0
Marsh	11	6-75	39.5
Riparian Marsh	8	16-66	37.8

* Data from the four Bolivian study sites situated outside of these eight regions were not included in these tabulations.

the most species-rich wetland type (59-124 spp.; $\bar{x} = 81.8$), with bahías (72-80 spp.; $\bar{x} = 76.0$), and basin swamps (51-81 spp.; $\bar{x} = 66$) next (Table 6.3). Ponds (3-39 spp.; $\bar{x} = 14.9$) and small lakes (6-34; $\bar{x} = 18.6$) were the least rich (Table 6.3). Again, as with the regional comparisons, these estimates were preliminary.

The next step was to consider the influence of sample area on species-richness. The species-area relationship, which has been expressed succinctly as "you will find more species if you sample a larger area" (Rosenzweig 1995, p. 8), is perhaps ecology's oldest generalization (Quammen 1996). Without being able to account for the contribution of sample area to species-richness, it is not possible to know how the level of diversity at one site compares to another. As the Bolivian study sites varied in area by nearly six orders of magnitude (0.04-30,000 ha), comparisons of species-richness that failed to consider system area would have been little more than metaphysical.

A graphical illustration of the importance of considering system area is presented using three "rich" study sites (Fig. 6.1): 1) Laguna Cáceres, the study site with the greatest number of species; 2) the Viru Viru Wetland, a species-rich "mid-sized" study site; and, 3) the Huanchaca Arroyo, a species-rich "diminutive" site (Table 6.4). Considering just the number of species at each site, Laguna Cáceres (124 spp.) would have to be considered the richest system, as it was nearly 60% richer than the Viru Viru wetland (75 spp.) and more than five times as rich as the Huanchaca Arroyo (24 spp.). As Laguna Cáceres was more than 100 times larger than the Viru Viru Wetland, and approximately 39,000 times as large as the Huanchaca Arroyo study site (Table 6.4), however, the actual relative differences in species richness are not so apparent.

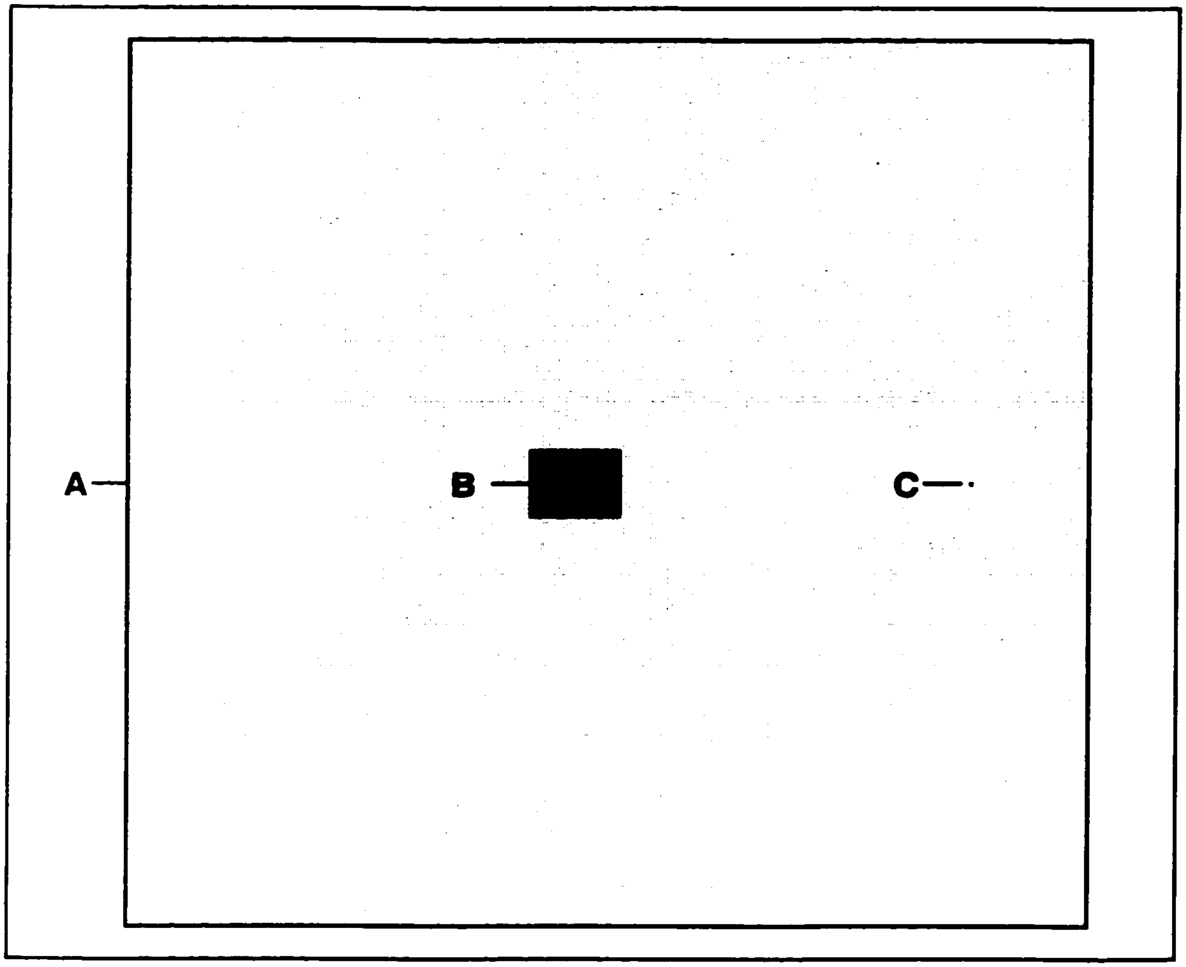


Figure 6.1. Comparison of three systems. **A**: Laguna Cáceres. **B**: Viru Viru Wetland. **C**: The Huanchaca Arroyo. All areas drawn approximately to scale.

Table 6.4. Comparison of area and species richness among three Bolivian wetland systems.

Study Site	Approximate Area (ha)	# of Species
Laguna Cáceres	1,560 ha.*	124
Viru Viru Wetland	15	75
Huanchaca Arroyo	0.04	24

* Estimated from the "potentially vegetated area" of the system, as described below.

From Fig. 6.1 it seems that, rather than being richer than the two smaller systems, Laguna Cáceres was actually much poorer. Nevertheless, although a large system may be many orders of magnitude larger than a small one it is not expected that the number of species would differ by the same magnitude (*e.g.*, that Laguna Cáceres should possess 39,000 times as many species as the Huanchaca Arroyo), as the relationship between species richness and area is non-linear. Thus, to approximate the expected level of species-richness at a site with a specific area one must plot a species-area curve.

Using data from the study sites (Table 6.1) log number of species was plotted versus log area (Fig. 6.2) and a linear regression was fitted to the data. In the resulting plot (Fig. 6.2), study sites occurring above the regression line can be considered as relatively species-rich, while those below are species-poor. A number of patterns were evident, both as regards regional differences in richness and differences among wetland types.

Ponds were almost always species-poor, regardless of where they occurred (Fig. 6.2). All ponds were located in species-poor regions (the High Andean, Cloud Forest, and Chapare; see Chapter 7), and it is not yet possible to know the independent roles of wetland types and regional richness. Small lakes (area < 500 ha) were species-poor, regardless of region. Seven of the eight lakes were from species-poor regions (*e.g.*, High Andean, 5 systems; Valles Secos, 1 system; and, Chapare, 1 system; see Chapter 7), it is not unexpected that these might be depauperate. The remaining small lake was situated in the species-rich White-water Floodplain region; thus, the species-poor character of this system suggests that this may be characteristic of small-lakes, in general.

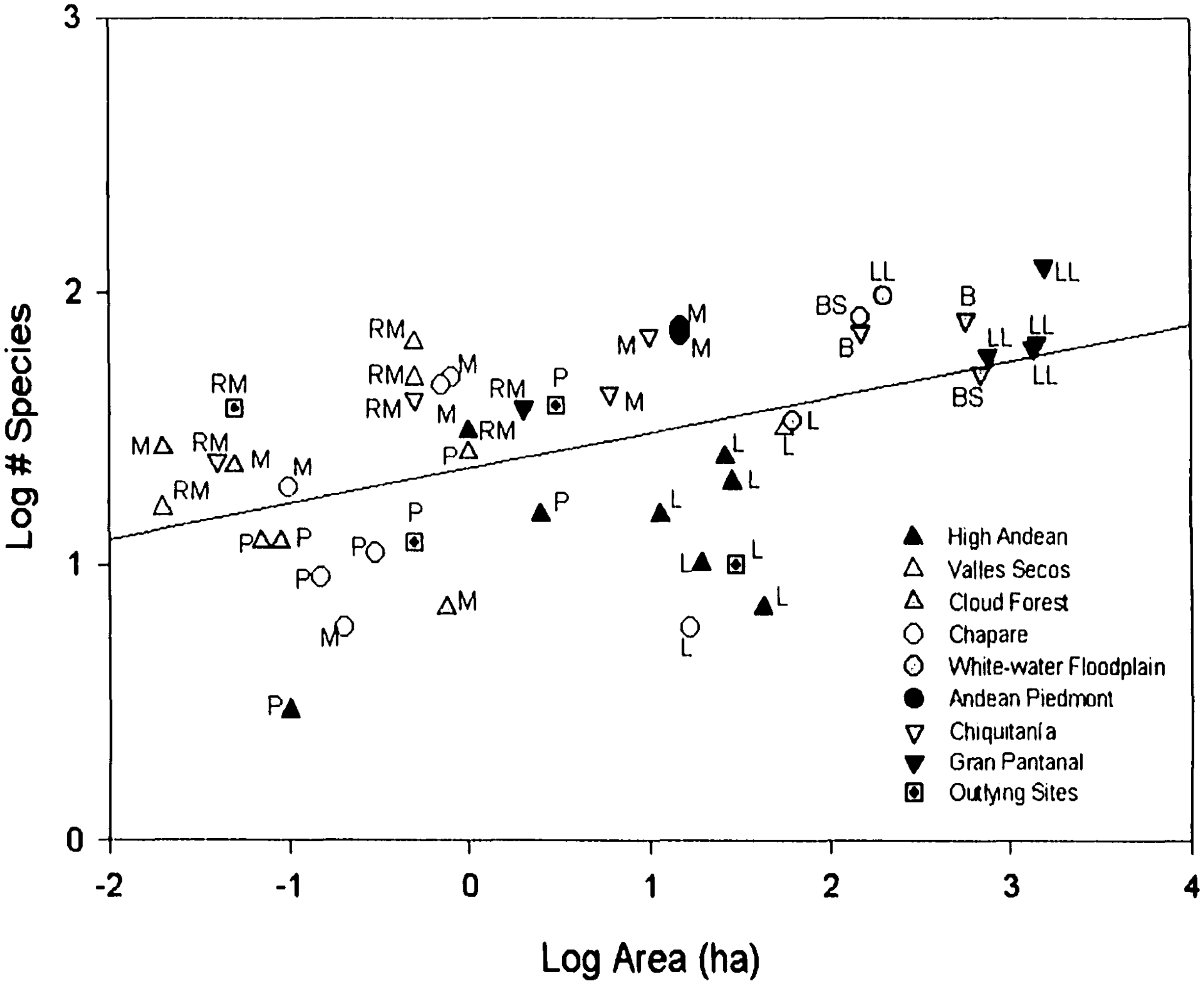


Figure 6.2. Species-area curve for the 46 Bolivian study sites. Wetland types: **B**- bahía; **BS** - basin swamp; **L** - small lake; **LL** - large lake (> 500 ha); **M** - marsh; **P** - pond; **RM** - riparian marsh. Linear regression: log S = 1.35 + 0.13 log A; $r^2 = 0.24$.

Large lakes appeared to be fairly species-rich, as two of the five systems were situated well above the regression line, with the other three systems situated on, or just below, the line. As all five large lakes were located in lowland regions, a second plot was prepared, using data from only the (23) lowland study sites (Fig. 6.3). In this case, the richness of large lakes does not seem to be exceptional, as three of the five systems were approximately as far below the regression line as the two remaining large lakes were above the line. As noted in Chapter 5, additional difficulties arose in interpreting either plot as four of the five large lakes were all from the same region (the Gran Pantanal), and three of these received just a single visit (*i.e.*, their checklists were most likely significantly incomplete).

All bahía and basin swamp study sites were restricted to the lowlands, so the plot of just the lowland data was used to adjudge their species-richness. Bahías appeared to be fairly species-rich, as both systems were situated a bit above the regression line (Fig. 6.3), but small sample size precluded strong inference. Additionally, both bahías were from the Chiquitanía, a species-rich region (see Chapter 7), further muddying interpretation. Basin swamps appeared to be somewhat species-poor, with the two systems situated on either side of the regression line, and the one below the line further away than the one above (Fig. 6.3). This level of diversity was still higher than expected, however, as basin swamps were the most difficult systems to sample comprehensively and, therefore, most likely had the least complete checklists. Moreover, water at these systems was very dark and acidic, due to the buildup of acids from the slow decomposition of accumulated plant matter ("secondarily blackwater") and blackwaters

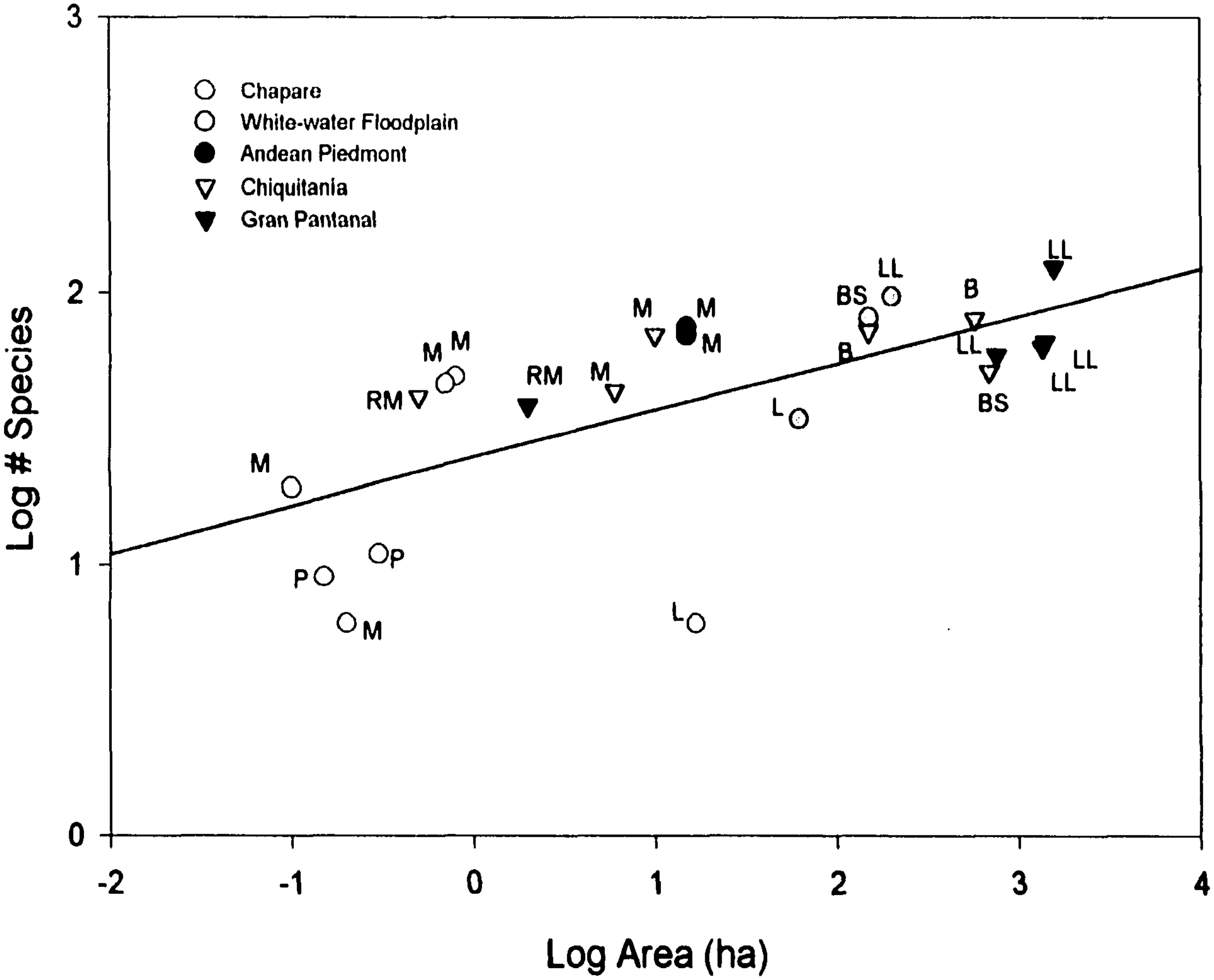


Figure 6.3. Species-area curve for the 23 lowland Bolivian study sites. Wetland types: **B**- bahía; **BS** - basin swamp; **L** - small lake; **LL** - large lake (> 500 ha); **M** - marsh; **P** - pond; **RM** - riparian marsh. Linear regression: Log S = 1.39 + 0.17 Log A. $r^2 = 0.44$.

are generally considered to be species-poor (Junk 1970: Junk and Howard-Williams 1984).

The remaining two wetland types, marshes and riparian marshes, had representatives in both lowland and montane regions. Therefore, the species-area curve plotted from all study sites will be referenced (Fig. 6.2). Both marshes and riparian marshes were characteristically species-rich, with most systems located on or above the regression line (Fig. 6.2).

Having plotted a species-area curve for the Bolivian study sites, it was now possible to reexamine the relative differences in species-richness among the three study sites previously singled out (Table 6.4; Fig. 6.1). It was clear from a plot of the data (Fig. 6.4), that (surprisingly) Laguna Cáceres was relatively richer than the other sites, as it was located furthest from the regression line.

Although intra-Bolivian regional differences in site-level diversity were apparent (Figs. 6.2; 6.3), interpretations were confounded by the inequitable distributions of either species-rich or species-poor wetland types within a particular region (*i.e.*, the large number of ponds included in the Chapare study sites). An attempt was made to assess the contribution of various regions on perceived diversity by plotting species-area curves for each of the three montane regions (High Andean, Valles Secos, and Cloud Forest), fitting regression lines to each curve (Fig. 6.5). Although three additional montane study sites were present (Laguna Volcan, Laguna Yaguacua, and the Yolosa Wetland), these occurred outside of these three regions and, hence, were not included in the plots.

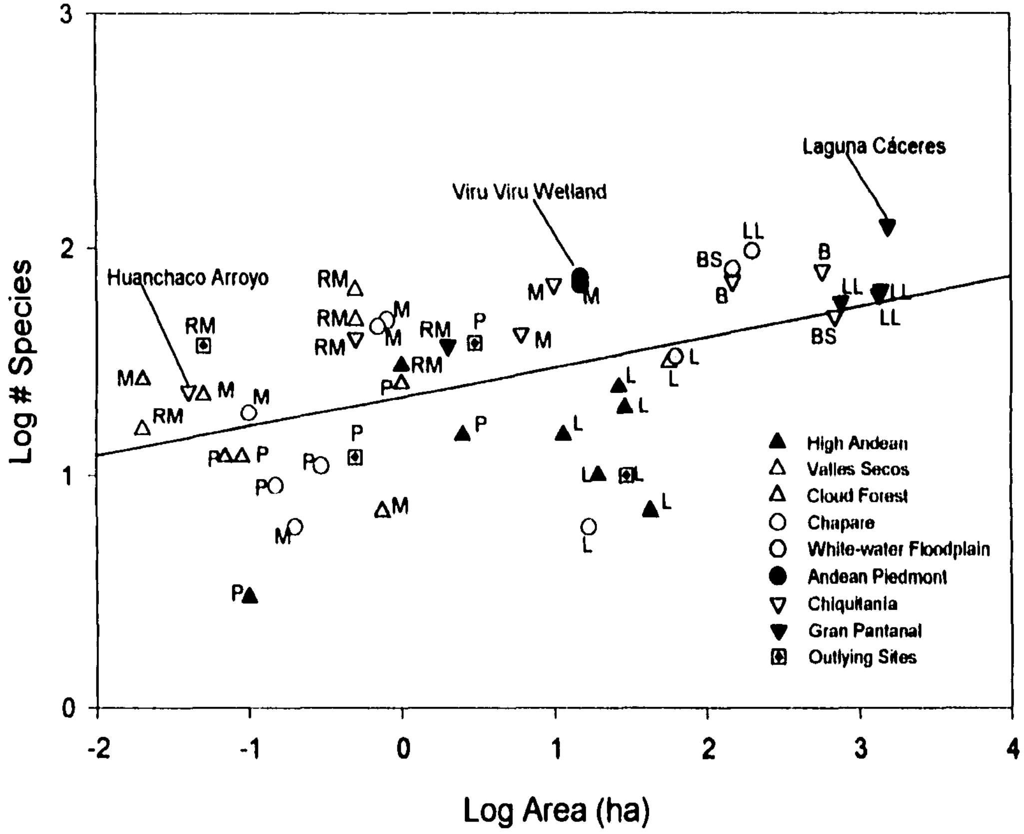


Figure 6.4. Species-area curve for the 46 Bolivian study sites. The three sites which were used in the example of the influence of area on richness are identified. Wetland types: **B**-bahía; **BS** - basin swamp; **L** - small lake; **LL** - large lake (> 500 ha); **M** - marsh; **P** - pond; **RM** - riparian marsh. Linear regression: log S = 1.35 + 0.13 log A; $r^2 = 0.24$.

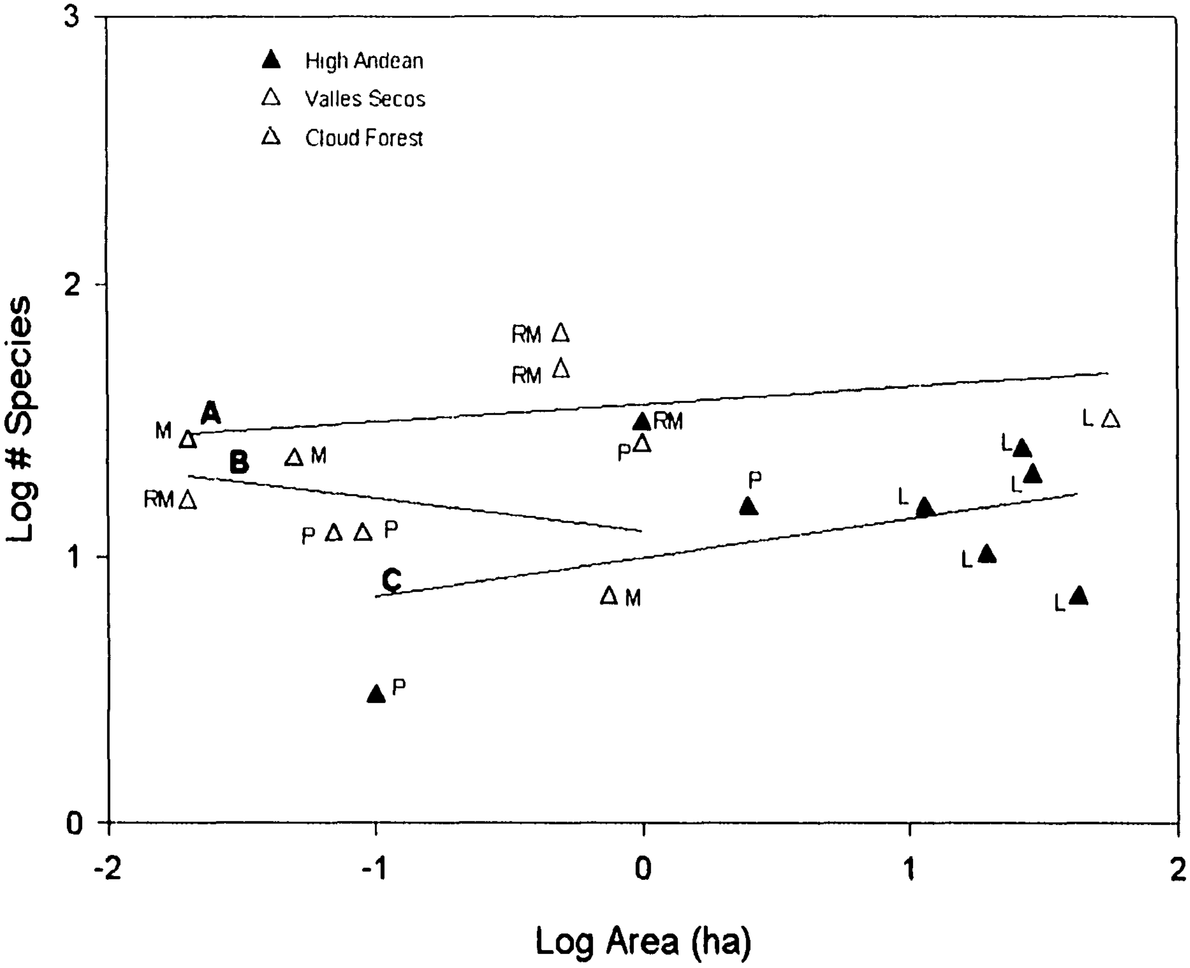


Figure 6.5. Species-area curves for the Bolivian montane study sites. A. Valles Secos. Log S = 1.6 + 0.04 Log A. $r^2 = 0.12$. B. Cloud Forest. Log S = 1.09 -0.12 Log A. $r^2 = 0.12$. C. High Andean Region. Log S = 0.99 + 0.15 Log A. $r^2 = 0.16$. Wetland types: L - small lake; M - marsh; P - pond; RM - riparian marsh.

Although Fig. 6.5 perhaps had some utility in illustrating the differences in site-level species-richness among the three montane regions, there were some obvious anomalies that resulted from an insufficient number of data points per curve (*e.g.*, the apparently negative correlation between area and diversity in the Cloud Forest sites, Fig. 6.5). Thus, it appeared that the plot of all the data (*i.e.*, from the 46 study sites) was a more accurate point of reference. The following discussion, therefore, pertains primarily to that figure (Fig. 6.2).

The High Andean region was clearly species-poor, with all but one system below the regression line and the remaining site on the line (Fig. 6.2). The Valles Secos region appeared to be fairly species-rich, with three of the four systems situated above the regression line; however, all three systems were riparian marshes, a species-rich wetland type (Fig. 6.2). The Cloud Forest sites were characteristically species-poor, with four of the six systems situated below the regression line (Fig. 6.2). Three of these were ponds, a species-poor wetland type, and undoubtedly this contributed to the depauperate character of the region's study sites. A plot of separate regression lines for each region (Fig. 6.5) suggested that the Valles Secos and High Andean study sites were of approximately equal richness (*i.e.*, the two lines possessed similar slopes), but the Valles Secos data set was composed of a small number (4) of sites and these were widely disparate with respect to the regression line. Thus, this interpretation should only be accepted with caution. The regression line for the Cloud Forest study sites was anomalous in that species richness was shown to decrease with an increase in system area (Fig. 6.5). This, however, was clearly an artifact of the relatively small number of systems (6), and the fairly large degree of difference in the number of species present at the sites (7-26, Table 6.1).

Differences in site-level species-richness among the lowland regions were seemingly best interpreted from the plot of the lowland data alone (Fig. 6.3), thereby avoiding the confounding effects of the montane sites. The Chapare sites were characteristically species-poor, with all but two of the sites on or below the regression line (Fig. 6.3). Five of the eight systems were of species-poor wetland types (*e.g.*, ponds and lakes), which undoubtedly influenced the region's overall trend. Still, even the three marsh sites (a species-rich wetland type) were situated on or just slightly above the regression line (Fig. 6.3). The Andean Piedmont sites were both very species-rich (Fig. 6.3), but this region was represented by just two sites, both marshes (*i.e.*, a species-rich wetland type). Thus, this should be considered as an extremely provisional characterization. The White-water Floodplain study sites were generally species-rich, with two sites above the regression line and one below (Fig. 6.3). As with the Andean Piedmont region, however, the number of sites from this region was not sufficiently large to bring this characterization above the provisional. The sites of the Chiquitanía were nearly all species-rich, with five systems situated above the regression line and two below (Fig. 6.3). The Chiquitanía was represented by a sufficient number of systems (7) and by a sufficient variety of wetland types (6) to allow this characterization to be made with confidence. Finally, the study sites of the Gran Pantanal were probably best characterized as somewhat species-poor, with all but one of the five systems situated on or below the regression line (Fig. 6.3).

A comparison of the estimates of diversity obtained using species number alone versus considering both species and system area is presented in Table 6.5. Although there was some congruence there was also much disagreement. It is clear that the species-area curves produced a much more accurate estimate of diversity. Additionally, correlations between region and wetland type were much more readily seen from the species-area curves (*e.g.*, Figs. 6.2, 6.3) than from the tables of species counts (Tables 6.2 & 6.3).

Comparison of Species-Richness With Neotropical Terrestrial Habitats.

One of the most striking aspects of the Bolivian wetland systems was how much more depauperate they were than Neotropical terrestrial habitats. In order to quantify this difference, species-area data were compiled from published accounts of 11 Neotropical forests. Most often, plot- and transect-based studies in tropical forests have censused only woody species (*i.e.*, trees, shrubs, and woody lianas), however, in these 11 studies complete floristic inventories were made. Study areas were located in both Central and South America and ranged in size from 0.1 ha study-plots to 2000 ha blocks of forest, with site-level species-richness ranging from 169-1740 species (Table 6.6). Species-richness in the four 0.1 ha study-plots ranged from 169-442 species (Table 6.6); the richest of these, El Amargal (coastal Colombia), is believed to possess the greatest number of species ever recorded for a 0.1 ha quadrat (Galeano *et al.* 1998). By contrast, the richest Bolivian wetland study site of comparable area (the Senda F Wetland, 0.1 ha)

Table 6.5. Comparison of the difference in characterizations of diversity produced by considering: A. the number of species present at a system; B. number of species and system area.

Wetland Type	A	B
Pond	Poorest	Poor
Small Lake	Poor	Poor
Large Lake	Richest	Intermediate
Bahía	Rich	Rich
Basin Swamp	Rich	Intermediate
Marsh	Intermediate	Rich
Riparian Marsh	Intermediate	Richest

Table 6.6. Species richness and area of selected neotropical forests utilized in comparisons of diversity with neotropical wetlands.

Site	Area (ha)	No. spp.
Capeira (Amazonian Ecuador)[3]	0.1	169
El Amargal (Coastal Colombia)[1]	0.1	442
Juaneche (Amazonian Ecuador)[3]	0.1	173
Río Puerto Viejo (lowland Costa Rica)[7]	0.1	233
Coquí (Coastal Colombia)[1]	0.4	489
Nuquí (Coastal Colombia)[1]	0.4	488
Cuyabeno (Amazonian Ecuador)[2]	1.0	942
Barro Colorado Island (Panama)[5]	1500	966
La Selva (lowland Costa Rica)[6]	1500	1740
Río Palenque (Amazonian Ecuador)[3]	1700	1033
Manu Floodplain (Amazonian Peru)[4]	2000	1215

1. Galeano et al. 1998
2. Balslev et al. 1998
3. Gentry and Dodson 1987
4. Foster 1990, cited in Balslev et al. 1998
5. Foster and Hubbell 1990, cited in Balslev et al. 1998
6. Hammel 1990, cited in Balslev et al. 1998
7. Whitmore et al. 1985, cited in Balslev et al. 1998

contained only 19 species (Table 6.1). The single 1.0 ha Neotropical forest site (Cuyabeno, in the Ecuadorean Amazon; Balslev *et al.* 1998) possessed an astonishing 942 species. The three Bolivian wetlands of approximately comparable area (the Ivirgarsama Marsh, 0.7 ha; Mariposa Wetland, 0.8 ha; and the Río Candelaria, 1.0 ha) were almost pathetically depauperate in comparison, ranging in richness from only 31-49 species (Table 6.1).

In order to better determine the differences in diversity between Neotropical forests and wetlands, a species-area curve was plotted using the data from the selected Neotropical forests (Table 6.6) and the Bolivian lowland wetlands (Table 6.1). A linear regression was fitted to the data and interaction between area and data source (*i.e.*, forest or wetland) was evaluated by an Analysis of Variance (ANOVA) test. Results indicated that the interaction between data sources was significant, thus, separate regression lines were fitted to each data set (Fig. 6.6). Viewed in this manner, Neotropical forested ecosystems were (as expected from the tabular data) unequivocally richer than Neotropical wetlands (Fig. 6.6). Although the slopes of the regression lines were extremely close (0.15, forests; 0.17, wetlands; Fig. 6.6), the difference between the y intercepts was 1.21 (log scale, Fig. 6.6). Thus, a Neotropical forest would generally be expected to possess more than ten times the species of a Neotropical wetland of comparable area.

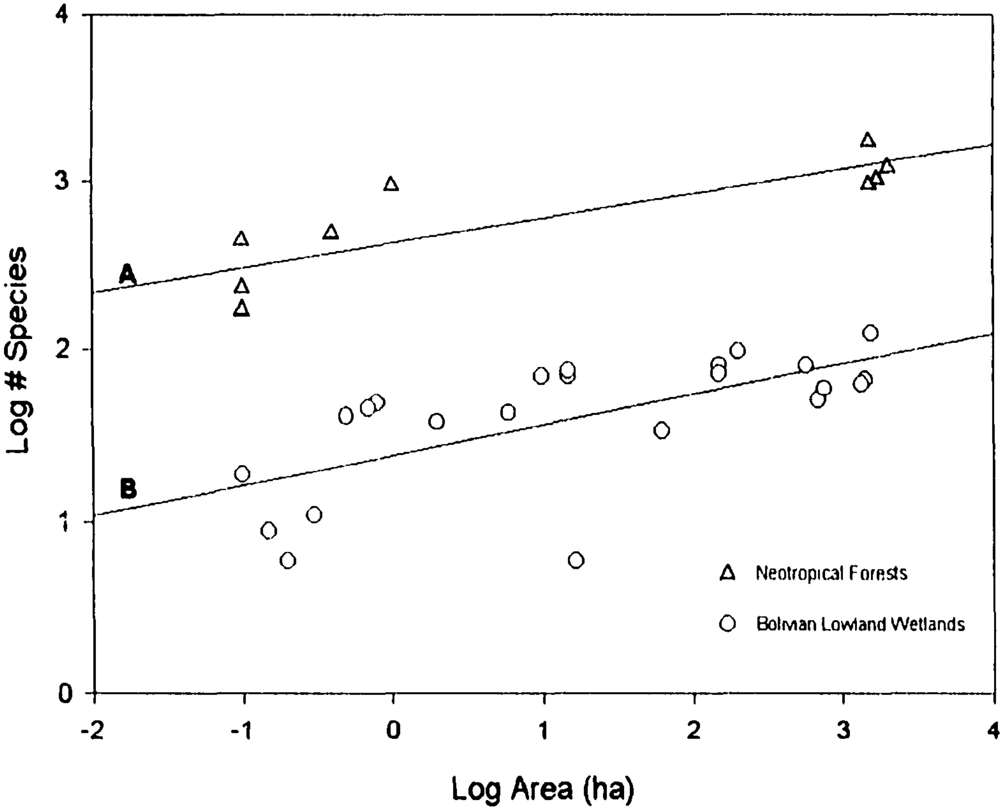


Figure 6.6. Comparison of a species-area curve plotted from 11 Neotropical forest sites with a species-area curve from 23 wetlands in the Bolivian lowlands. **A**: Linear regression of the forest data. Log S = 2.6 + 0.15 log A; $r^2 = 0.7$. **B**: Linear regression of the wetland data. Log S = 1.39 + 0.17 log A; $r^2 = 0.44$. Note: although 11 forest sites were plotted, two pairs of sites possessed sufficiently similar characteristics such that only 9 plotted symbols are distinguishable.

Comparison With Temperate Wetlands

As noted, the original stimulus for my investigations of phytodiversity in Neotropical wetlands was Crow's (1993) study of latitudinal patterns in species diversity in the aquatic vascular flora. Crow examined latitudinal differences in species-richness at the site level by comparing a series of Costa Rican wetlands with temperate North American wetlands of the same physiognomic "type" (*e.g.*, peatlands, marshlands, etc.). Based on these comparisons, Crow (1993) suggested that temperate wetlands may well be richer in vascular species than wetlands in the tropics. At the time, this conclusion was provisional, as only a few wetlands of each type were compared and no consideration was given to system area. Nevertheless, as Neotropical forests are generally recognized as being an order of magnitude more diverse than temperate forests (Gentry 1988a), the hypothesis was intriguing.

In continuing this line of inquiry, data from investigations of wetlands in the northeastern (cool temperate) and southeastern (warm temperate) regions of the United States were compiled and compared to the Bolivian lowland study sites. New England wetlands were represented by 31 systems (Dunlop 1983; Fahey 1993; Hellquist 1971; McMaster and McMaster 2000; Miller 1996; Searcy and Hickler 1999; Sperduto and Ritter 1994; Table 6.7). All New England wetlands were located in either New Hampshire or Massachusetts, as the selection of studies for inclusion in these comparisons, rather than representing an exhaustive literature search, was somewhat serendipitous. With one exception (Ossipee Lake, Hellquist 1971), the "potentially vegetated area" of each system was represented by the total area of each system. The

Table 6.7. Wetlands selected to represent New England (U.S.) in comparisons of site-level species richness among New World temperate and Neotropical regions, with source of data, system name, state, elevation, area, and number of species recorded for the site. Sources: A - Sperduto & Ritter 1994; B - Hellquist 1971; C - Miller 1996 - D, Fahey 1993; E - Dunlop 1983 ; F -Searcy and Hickler 1999; G - McMaster and McMaster 2000.

Source	System	State	Elev (m)	Area (ha)	No. spp.
A	Newton Cedar Swamp	New Hampshire	37	14.2	73
A	Locke Pond	New Hampshire	9	7.3	72
A	Rye Townline Swamp	New Hampshire	6	2.4	65
A	Portsmouth Cedar Swamp	New Hampshire	6	8.1	64
A	Country Swamp Pond East	New Hampshire	30	8.5	60
A	Newton-Kingston Cedar Swamp	New Hampshire	37	20.2	58
A	Bakie Swamp	New Hampshire	38	8.5	55
A	Lovern's Mill Swamp	New Hampshire	317	46.5	50
A	Ring Brook Swamp	New Hampshire	287	5.7	50
A	Bradford Bog	New Hampshire	270	4.0	49
A	Manchester Cedar Swamp	New Hampshire	106	17.0	43
A	Barrington Cedar Swamp	New Hampshire	76	6.1	40
A	Cedar Swamp Pond	New Hampshire	34	16.2	39
A	Cooper Cedar Woods	New Hampshire	158	6.9	39
B	Ossipee Lake	New Hampshire	124	503.0	120
C	Spruce Hole Bog	New Hampshire	45	1.0	37
D	Pequawket Bog	New Hampshire	124	9.9	109
D	Heath Pond Bog	New Hampshire	124	16.2	70
E	Mud Pond	New Hampshire	206	48.0	102
F	Poutwater Pond	Massachusetts	212	3.9	76
G	Ashfield 1	Massachusetts	417	3.8	45
G	Ashfield 2	Massachusetts	417	1.4	34
G	Ashfield 3	Massachusetts	393	2.5	45
G	Ashfield 4	Massachusetts	453	6.2	54
G	Ashfield 5	Massachusetts	453	2.5	39
G	Conway 1	Massachusetts	369	1.8	52
G	Conway 2	Massachusetts	362	2.5	32
G	Conway 3	Massachusetts	338	3.2	59
G	Conway 4	Massachusetts	329	1.0	70
G	Williamsburg 1	Massachusetts	220	7.8	45
G	Williamsburg 2	Massachusetts	164	0.6	54

Table 6.8. Wetlands selected to represent the Southeastern United States in comparisons of site-level species richness among New World temperate and Neotropical regions, with source of data, system name, state, elevation, area, and number of species recorded for the site. Source: A - MacRoberts & MacRoberts, 1988; B - MacRoberts & MacRoberts, 1990; C - MacRoberts & MacRoberts, 1991; D - MacRoberts & MacRoberts, 1992; E - MacRoberts & MacRoberts, 1993

Source	System	State	Elev (m)	Area (ha)	No. Spp.
A	Strange Road Bog	Louisiana	60	0.4	97
A	Middle Branch Bog	Louisiana	84	3.0	104
B	Woodstock Bog	Louisiana	90	0.8	102
B	Fixit Bog	Louisiana	90	0.4	98
C	Frog Arrow Bog	Louisiana	100	2.4	106
C	Bog 360 A	Louisiana	100	2.2	104
C	Bog 360 B	Louisiana	100	0.9	97
D	RCW	Louisiana	~ 85	0.0	68
D	Vine Bog	Louisiana	~ 85	0.1	69
D	Sparrow Bog	Louisiana	~ 85	0.0	63
D	Robin Bog	Louisiana	~ 85	0.0	62
E	Cooter's Bog	Louisiana	N.A.	3.2	134

potentially vegetated area of Ossipee Lake, a large lacustrine system, was determined as per the Bolivian large lakes, based on the site map in Hellquist (1971).

Wetlands of the Southeastern United States (Table 6.8) were represented by 12 bogs in Louisiana's Kisatchee National Forest (MacRoberts and MacRoberts 1988, 1990, 1991, 1992, 1993). As with the New England data, there was no conscious attempt to limit the representative wetlands of the Southeastern region to a single state; rather, this was due to time limitations resulting in a less than comprehensive literature search.

Species-richness ranged from 34-120 species in the New England systems (Table 6.7), and from 62-134 species in the Southeastern U.S. systems (Table 6.8). Therefore, considering just the number of species present, the systems of the warm temperate and cool temperate regions appeared to be somewhat richer than those of lowland Bolivia (6-124 spp., Table 6.1). This assessment, however, did not take into account the area of the systems. Rather, it was based solely on the observation that the most speciose systems from all three regions were approximately equal in number of species, whereas the poorest lowland Bolivian systems possessed significantly fewer species (*e.g.*, 6-9 spp.; Table 6.1) than did the most species-poor systems from the two temperate regions (*e.g.*, New England 34-39 spp., Table 6.7; Southeastern U.S. 62-69 spp., Table 6.8).

In order to consider species-richness within the context of system area, a species-area curve was plotted using data from the two sets of temperate wetlands and the lowland Bolivian systems. A linear regression was fitted to the data, and interaction between area and data source (*i.e.*, New England, Southeastern U.S., Bolivia) was

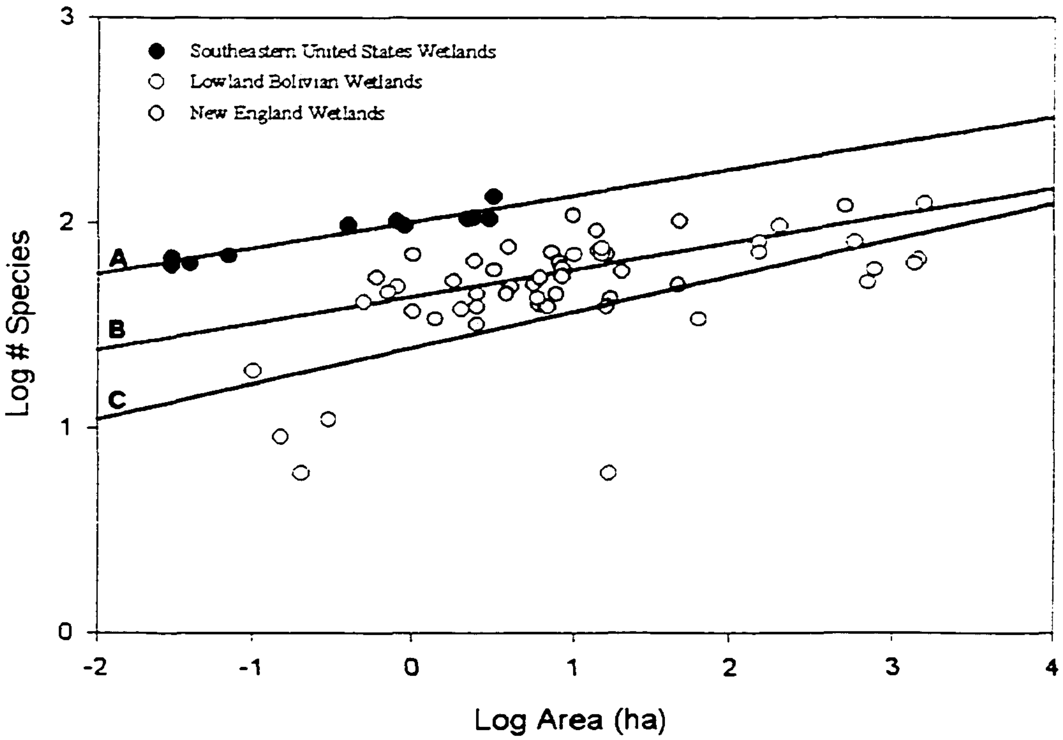


Figure 6.7. Comparison of species-area curves of wetlands from three New World regions. **A**. Linear regression of the Southeastern U.S. wetland data. Log S = 2.00 + 0.13 Log A; $r^2 = 0.90$. **B**. Linear regression of the New England wetland data. Log S = 1.6 + 0.13 Log A; $r^2 = 0.27$. **C**. Linear regression of the Lowland Bolivian wetland data. Log S = 1.4 + 0.17 Log A; $r^2 = 0.44$.

evaluated by an Analysis of Variance (ANOVA) test. Results indicated that the interaction between data sources was significant, therefore, separate regression lines were fitted to each data set (Fig. 6.7). From this figure, it was evident that wetlands from the Southeastern United States were markedly richer than those from lowland Bolivia (Fig. 6.7). The smallest Southeastern U.S. wetlands were at least three times as rich as comparably sized systems in lowland Bolivia, whereas the most speciose Southeastern U.S. system was approximately twice as rich as Bolivian systems of comparable area (Fig. 6.7). The New England systems were generally somewhat richer than those of lowland Bolivia, as evidenced by the regression line (B, Fig. 6.7) of the former being situated above that of the latter (C, Fig. 6.7).

Despite the differences in site-level species richness among the three regions, the slopes of all three regression lines were quite similar (0.13, Southeastern U.S.; 0.13 New England; and, 0.17 Lowland Bolivia; Fig. 6.7); thus, the rate of increase in number of species with increased area appears to be fairly constant on both continents. Of further interest, from the perspective of island biogeography these slopes were much lower than expected for a group of "islands" (*i.e.*, small areas of a particular habitat isolated by much larger expanses of unsuitable habitat). This is discussed in more detail in Chapter 7.

CHAPTER VII

REGIONAL SCALE BIODIVERSITY

> The species-area curve may be the first diversity pattern described by ecology, but the latitudinal gradient is the most famous. The Tropics, if not the seat of life, are the center of its richest display.
>
> - M. Rosenzweig, *Species Diversity in Space and Time*

Diversity Within Bolivia

In this chapter, mesoregional and macroregional-scale (*sensu* McLaughlin 1994) patterns in diversity in the Neotropical and New World Temperate wetland floras are examined and compared. Regional-scale diversity within Bolivia is first examined, followed by investigations of regional-scale diversity throughout the Neotropics and in the New World Temperate region. As comparisons were concerned specifically with these region's wetland habitats, "species" and "species-richness" refer solely to the wetland component of the flora unless otherwise noted. Similarly, while recognizing the species-richness is but one component of diversity, for utility's sake "species richness" and "diversity" are applied here as synonyms.

The number of species noted for the eight Bolivian regions considered in this study varied by nearly an order of magnitude (Table 7.1). Based solely on number of

Table 7.1. The eight Bolivian regions utilized in floristic comparisons, with estimated regional area, elevation range of the study sites, and total wetland species noted for each region.

Region	Approximate Area (km2)	Elevational Range[A] (m)	No. Spp.
High Andean	210,000	3100-4500	117
Cloud Forest	33,000	2400-2920	57
Valles Secos	83,000	1800-2550	107
Chapare	4000	200-230	113
Andean Piedmont	5000	400-430	244
Whitewater Floodplain	325,000	200-220	463
Chiquitania	190,000	200-750	541
Gran Pantanal	14,000	90-100	174

A. Elevational range of study sites within the region. In most cases, regional territories encompassed a somewhat greater range than listed here.

species (Table 7.1), the Cloud Forest was the most species-poor region (57 species), and the Chiquitanía the most species-rich (541 species). Differences in regional area, however, were even greater than differences in number of species, varying by close to two orders of magnitude (*e.g.*, 4.0 X 10^3 km^2 in the Chapare to 3.25 X 10^5 km^2 in the White-water Floodplain; Table 7.1). Hence, as with the estimates of site-level diversity, accurate estimates of regional diversity were necessarily based on the number of species per unit area.

In a study involving wetland habitats, it seems that the most accurate approximation of species-richness would be calculated from the area of inundated habitat. A few estimates of the extent of wetlands in Bolivia were available, but these varied to such a degree as to render them unserviceable. For example, Flores (1986) estimated that only 5,812 km^2 of wetlands were present in all of the Bolivian lowlands, whereas Allenby (1988) estimated that the Beni basin alone (*i.e.*, the White-water Floodplain region, excluding the Pando) contained roughly 250,000 km^2 of wetlands.

Eventually, it seemed best to formulate my own estimates of regional wetland areas based on information from maps, Landsat images, various published sources, and from my impressions from fieldwork and travel. Estimates were restricted solely to the five Bolivian lowland regions considered in this study, as I was unable to confidently estimate wetland areas for the three montane regions. Estimated wetland areas for the lowland regions are presented in Table 7.2.

A species-area curve was constructed for Bolivia with cumulative wetland species plotted against both cumulative estimated wetland area and cumulative total area (Fig.

Table 7.2. Area, estimated wetland area, number of wetland species, and the cumulative totals of these three parameters for the five regions and one regional sub-sample used in plotting species-area curves for the Bolivian lowlands. OGU abbreviations: CM - Chimoré; CH - Chapare; AP - Andean Piedmont; WW - White-water Floodplain; CQ - Chiquitanía; GP - Gran Pantanal.

OGU	Area (km^2)	Estimated Wetland Area (km^2)	Wetland Spp.	Cumulative Area (km^2)	Cumulative Wetland Area (km^2)	Cumulative Wetland Spp.
CM	20	7	23	20	7	23
CH	4000	2000	113	4000	2000	113
AP	5000	1250	244	9000	3250	297
WW	325,000	130,000	463	334,000	132,500	559
CQ	190,000	47,500	541	524,000	180,000	736
GP	14,000	10,000	174	538,000	190,000	763

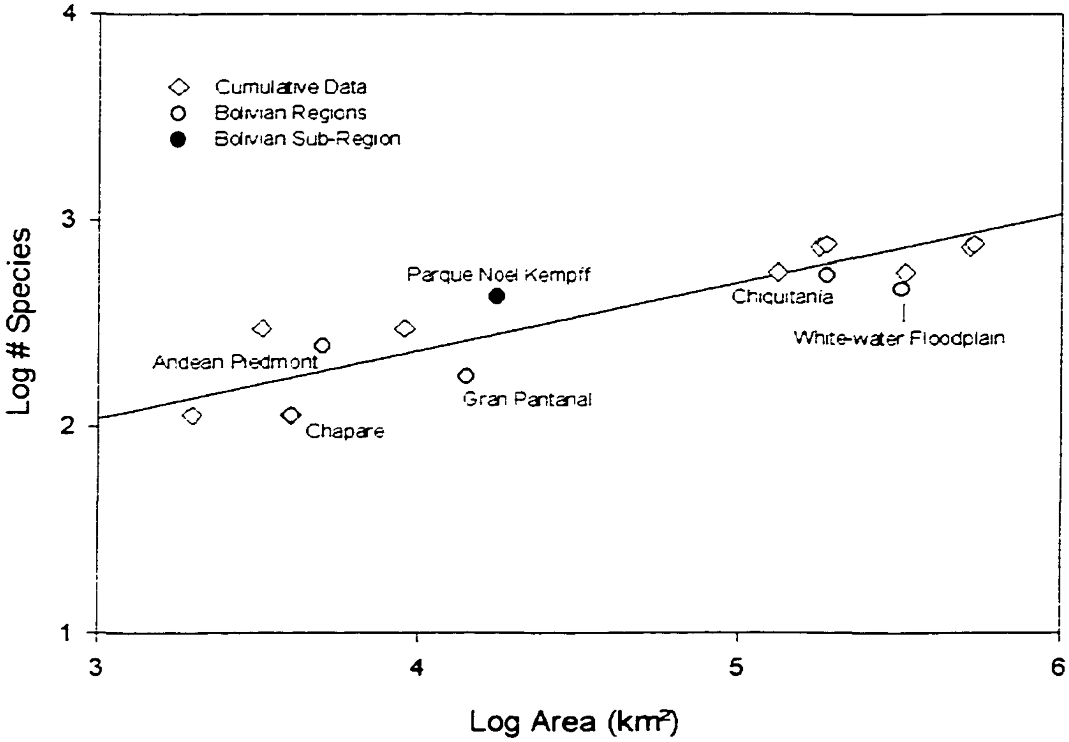


Figure 7.1. Species-area curves plotted from cumulative totals from the five Bolivian lowland regions considered in this study. Linear regression: Log S = 1.04 + 0.33 log A, $r^2 = 0.97$.

7.1). The curve was constructed commencing with a localized area (an approximately 20 km^2 area around the town of Chimoré, in the Chapare) and continuing through the addition of successively larger, contiguous areas (*cf.* Rosenzweig 1995), as indicated in Table 7.2. A linear regression was fitted to the data, and interaction between area and data source (*i.e.*, total regional area, regional wetland area) was evaluated by an Analysis of Variance (ANOVA) test. Results indicated that interaction between area and area type (regional verus wetland) was insignificant. Thus, as slopes of the regression lines were not different, total regional area was deemed to be an acceptable surrogate for regional wetland area.

Discrete (*i.e.*, non-cumulative) regional species-area data were plotted for each lowland region (Fig. 7.1, gray circles). As with the species-area curves for site-level data, regions above the regression line were considered as relatively species-rich and those below as relatively species-poor. Fig. 7.1 was previously referenced in Chapters 4 (the Chapare) and 5 (the Gran Pantanal), where it was used to establish the species-poor character of these two regions. It can also be seen that the White-water Floodplain regions, despite possessing a large flora (463 spp., Table 7.1), was somewhat species-poor, when considered in terms of overall regional area (Fig. 7.1). The Chiquitanía, the region with the largest wetland flora (541 spp., Table 7.1), was also somewhat species-poor in terms of its position to the regression line (Fig. 7.1). The Andean Piedmont was seemingly the most species-rich region (*i.e.*, furthest above the regression line) of the Bolivian lowlands (Fig. 7.1).

The preceding characterizations should be accepted provisionally, as regional checklists were undoubtedly influenced by differences in density of botanical collecting. Solomon (1989) identified the areas of highest collection density as the vicinity of La Paz (habitats in both the Altiplano and the upper slopes of the Yungas), the Cochabamba Valley, the vicinity of Lago Titicaca, and to a lesser extent, the areas around the cities of Santa Cruz and Tarija. Since the time of Solomon's report, the focus of botanical collecting has shifted to the lowlands, with the Departamento of Santa Cruz receiving a disproportionately large amount of the lowland research. Thus, the region with the most wetland species, the Chiquitanía (Table 7.1), and the most species-rich Bolivian lowland region, the Andean Piedmont (Fig. 7.1), were both within one of the most heavily investigated (botanically) Departamentos. The Bolivian Gran Pantanal was also situated within the Departamento of Santa Cruz. As noted in Chapter 5, however, the Gran Pantanal has received relatively little botanical investigation in comparison with the Departamento's more heavily researched areas (*e.g.*, Parque Nacional Noel Kempff Mercado and the Andean Piedmont region).

The White-water Floodplain region has also been the site for a significant portion of the botanical research conducted in the Bolivian lowlands, and a number of the published floristic accounts from this region were from wetlands (*e.g.*, Beck 1984; Haase 1989, 1990; Haase and Beck 1989; Hanagarth 1993). Botanical investigations in the White-water Floodplain, however, have seemingly been restricted to fewer areas than in the Departamento of Santa Cruz, with most studies located either in a few parts of the Llanos de Moxos and, to a lesser extent, in the area around the town of Riberalta, and in the Pando. Hence, it appears probable that the White-water Floodplain flora was somewhat under-represented relative to the number of botanical collections made from this region.

Although differences in collection density make these regional comparisons somewhat qualified, nevertheless, their utility is undeniable. To illustrate, the relative diversity of Parque Nacional Noel Kempff Mercado (PNNK), a particularly speciose "sub-region" of the Chiquitanía was examined (Table 7.3)

Table 7.3. Comparison of area and flora size for three Bolivian OGUs.

OGU	Approximate Area (km^2)	# of Wetland Species
Bolivia	1,098,580	1026
The Chiquitanía	190,000	541
Parque Nacional Noel Kempff M.	17,500	424

Four hundred and twenty four wetland species were noted for PNNK (Table 7.3); thus, this area possessed approximately 41% of Bolivia's wetland flora (1026 species, Table 7.3) in an area equivalent to just 1.6% of the national territory. Within the regional context, PNNK possessed nearly four fifths (78.3%) of the Chiquitanía's wetland species (541 species, Table 7.3) in less than a tenth (9.2%) of the region's area. As the diminutive (by comparison) PNNK contained such a large portion of the regional and national wetland floras, it seemed likely that it would prove to be an extremely high diversity area (*i.e.*, that it would occupy a position well above the regression line of the

Bolivian lowlands species-area curve). Locating the datum from PNNK on Fig. 7.1 demonstrated that this area was indeed species-rich, but not nearly as much as might be expected, based on the magnitude of the areal differences.

Macroregional Diversity

In order to undertake macroregional-scale comparisons of diversity in the Neotropical wetland flora, the next logical step was to construct a species-area curve using national data. A number of publications were encountered that offered partial or complete estimates of wetland area for various Neotropical countries and regions (*e.g.*, Aselman and Crutzen 1989; Junk 1993; Olmsted 1993; Olson *et al.* 1998; Naranjo 1995; Scott and Jones 1995). Regrettably, there was a large amount of variance among these estimates, and data were incomplete for most countries, and entirely lacking for some. Hence, it was necessary to rely on a country's total area as a surrogate for wetland area. In the preceding inter-Bolivian regional-scale comparison total regional area was found to be an acceptable surrogate for regional wetland area. Before proceeding with the Neotropical comparisons, the correlation between these two elements was first analyzed in another data set, the North American data.

Although compiling a comprehensive checklist of the wetland flora of North America would have far exceeded the scope of this project, fortunately, a checklist for the wetland flora of the United States was available (Reed 1996) and in a form (*e.g.*, electronic text file) that was readily convertible to database format. Data were also available regarding the estimated area of wetlands for each state (Fretwell *et al.* 1996). No comparable data set was encountered for Canada (although such data may well be available); therefore, the wetland flora of the coterminous United States, alone, served to represent the New World Temperate region.

Data (regional area, regional wetland area, and number of species) were tabulated for the ten regional groupings utilized by Reed (1996) for the coterminous United States. Not all species listed by Reed were used in the comparisons; rather, species were adjudged as wetland species based on various criteria (see Appendix C). A species-area curve was constructed commencing with a single state (Maine) and continuing through the stepwise addition of successively larger, contiguous areas (*cf.* Rosenzweig 1995). Initial additions involved 2-3 states, until all states in the initial region (New England) were added. Subsequent additions generally consisted of a single region; however, in two instances adjacent regions were combined as each contained a portion of the same state (see Table 7.4). OGUs, their stepwise order, cumulative area, cumulative wetland area, and cumulative wetland species are given in Table 7.4. A linear regression was fitted to the data and interaction between area and area type (*i.e.*, total regional versus regional wetland) was evaluated by an Analysis of Variance (ANOVA) test. Results indicated that the interaction between data sources was significant; thus, it was uncertain that total regional area could function as a suitable surrogate for regional wetland area in North America.

To examine the differences between the two measures of area, separate species-area curves were plotted and regression lines fitted to each set of data (Fig. 7.2). The line

Table 7.4. United States OGUs used in plotting a species-area curve for the wetland flora of the coterminous United States, with cumulative total area, cumulative wetland area. and cumulative wetland species noted for each OGU.

OGUs	Cumulative Area (km^2)	Cumulative Wetland Area (km^2)	Cumulative Wetland Spp.
ME	80.170	20.068	601
ME & NH &VT	127.474	23.598	667
ME & NH &VT & MA & RI & CT	163.091	29.316	782
ME & NH &VT & MA & RI & CT & NY & PA	402.110	40.664	908
N-E	826.183	56.765	1201
N-E & S-E	1.936.421	252.391	1736
N-E & S-E & N-C	2.991.606	325.960	1772
N-E & S-E & N-C &S-P	3.848.011	360.360	1857
N-E & S-E & N-C &S-P & C-P & I-M	5.023.802	378.456	2108
N-E & S-E & N-C &S-P & C-P & I-M & N-W & N-P	6.662.543	416.050	2312
N-E & S-E & N-C &S-P & C-P & I-M & N-W & N-P & CA	7.067.337	417.887	2516
N-E & S-E & N-C &S-P & C-P & I-M & N-W & N-P & CA & S-W	7.657.565	422.777	2543

Regions:
N-E (Northeast): CT. DE. KY. MA. MD. ME. NH. NJ. NY. OH. PA. RI. VA. VT. WV
S-E (Southeast): AL. AR. FL. GA. LA. MS. NC. SC. TN
N-C (North Central): IA. IL. IN. MI. MO. MN. WI
N-P (North Plains): ND. MT (Eastern). SD. WY (Eastern)
C-P (Central Plains): CO (Eastern). KS. NE
S-P (South Plains): OK. TX
S-W (Southwest): AZ. NM
I-M (Intermountain): CO (Western). NV. UT
N-W: (Northwest): ID. MT (Western). OR. WA. WY (Western)
CA (California): CA

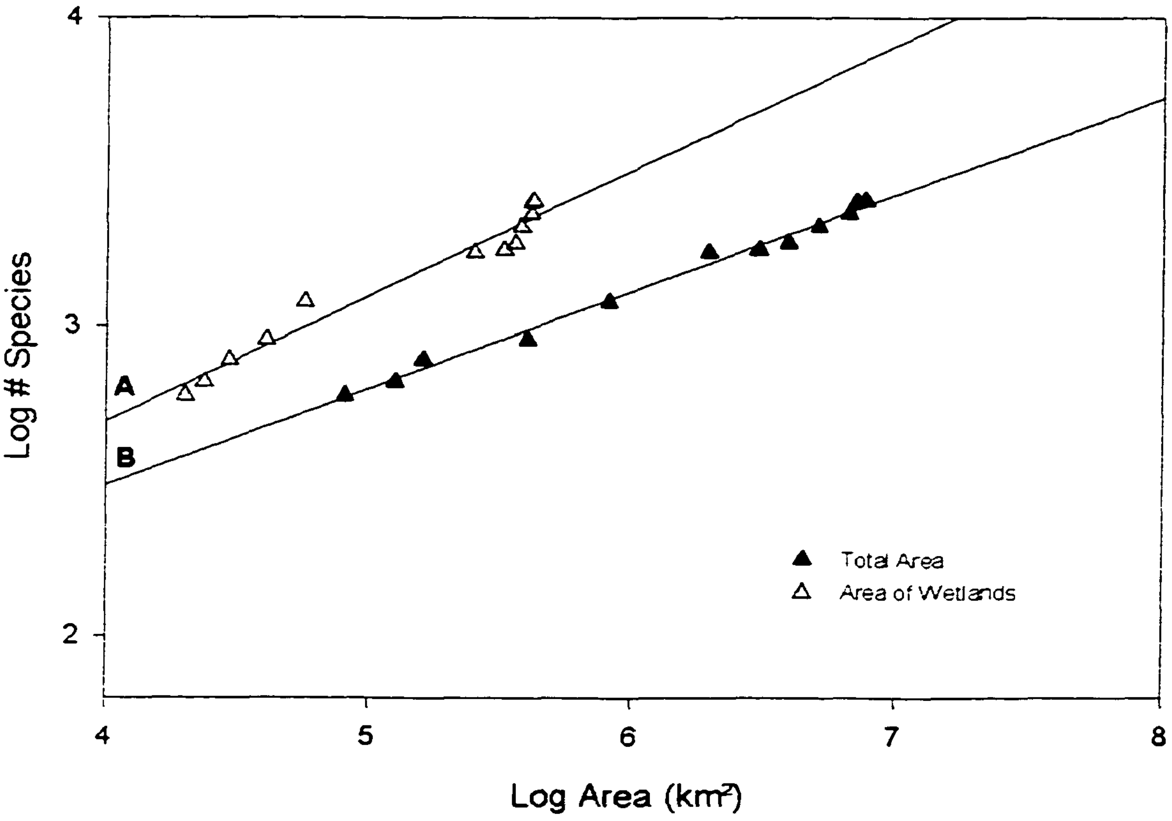


Figure 7.2. Species-area curves for the wetland flora of the coterminous United States. Species-area curves generated from cumulative data (Table 7.4). A. Area of wetlands within each region. Linear regression: Log S = 1.07 + 0.41 Log A, $r^2 = 0.96$. B. Total regional area. Linear regression: Log S = 1.24 + 0.31 Log A, $r^2 = 0.99$.

fitted to the wetland area data (A, Fig. 7.2) possessed a lower y-intercept (1.07) than that for the total area data (B, Fig. 7.2) and the slope was somewhat greater (0.41, A; 0.31 B). Still, the slopes of the two lines seemed to be sufficiently similar for total regional area to serve as a reasonable surrogate for regional wetland area.

The congruence of the two areal measures was further investigated by adding plots of discrete (*i.e.*, non-cumulative) regional species-area data to the plots of the cumulative data (Fig. 7.3). It seemed that if total regional area were indeed a reasonable surrogate for regional wetland area, then regions (as represented by plotted discrete data) would consistently be either species-rich or species-poor relative to both sets of data. Although this relationship held true for some regions, more often than not regions varied considerably in their position relative to both the regression lines (Fig. 7.3). The most radical discrepancies were with the Californian and Southwest regions. When referenced to the curve generated from cumulative wetland area (A, Fig. 7.3), California and the Southwest both appeared to be species-rich (*i.e.*, above the regression line), with California by far the most species-rich of all the regions. When referenced to the curve generated from total regional area (B, Fig. 7.3), however, California was of average richness (*i.e.*, situated on the regression line), whereas the Southwest was the most species-poor region. The large differences in relative species-richness in California was perhaps partially attributable to its having lost about 90% of its original wetlands (Dahl 1990). It seems probable that at the regional scale the rate of species loss must lag behind wetland loss, as it seems unlikely that California once supported ten times as many wetland species as at present. Thus, the position of California far above the regression

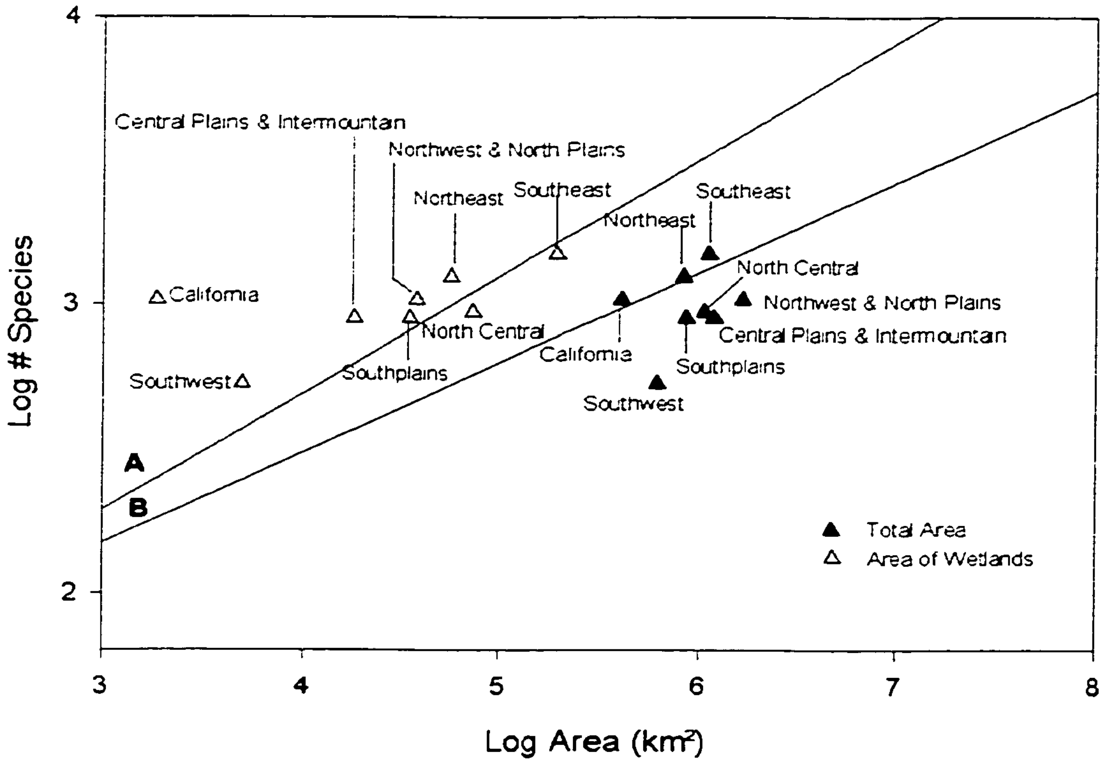


Figure 7.3. Species-area curves for the wetland flora of the coterminous United States, with discrete regional data added to the plots. A. Total regional area. Linear regression: Log S = 1.07 + 0.41 Log A, $r^2 = 0.96$. B. Area of wetlands within each region. Linear regression: Log S = 1.24 + 0.31 Log A, $r^2 = 0.99$. Regression lines were fitted to species-area curves generated from cumulative data (Table 7.4), but in order to avoid visual clutter data points from the cumulative data are not shown.

line for the species-area curve generated from regional wetland area (Fig. 7.3, A) is most likely an exaggeration of its relative diversity.

Having accepted (with some provisions) total regional area as a valid surrogate for regional wetland area, it was then possible to examine macroregional-scale diversity in the Neotropics. Data (cumulative species and cumulative total area) were compiled for all Neotropical countries (Table 7.5). Although northern Mexico was not strictly within the Neotropics, species and area data from the entire country were used (Table 7.5). The inclusion of the entire country was necessary because distribution data in sources used in compiling the wetland species database frequently indicated little more than the species presence in the country. The three countries that constituted "the Guianas" (French Guiana, Guyana, and Suriname) were treated as a single OGU (Table 7.5), because references (*e.g.*, literature and herbarium labels) occasionally failed to differentiate between them. Additionally, five Central American countries (Belize, El Salvador, Guatemala, Honduras, and Nicaragua) were considered as a single OGU, designated here by the decidedly inelegant appellation "Mid-Central America" (Table 7.5). These countries were grouped because their checklists were obviously incomplete relative to the other OGUs and I thought it better to have one large, under-represented OGU, rather than five small, contiguous, under-represented OGUs.

A species-area curve was constructed commencing with a localized area (the Andean Piedmont, Bolivia) and continuing through the addition of successively larger, contiguous areas (*cf.* Rosenzweig 1995) and a linear regression was fitted to the data (Fig. 7.4). The order of additions was as indicated in Table 7.5. Discrete regional species-area

Table 7.5. OGUs used in plotting a species-area curve for the Neotropical (South America, Central America, and Mexico) wetland flora, with OGU area, number of wetland species noted for each OGU, cumulative wetland area, and cumulative wetland species.

OGU	Area (km^2)	Wetland Spp.	Cumulative Area (km^2)	Cumulative Wetland Spp.
Andean Piedmont	5000	244	5000	244
Chiquitania	190,000	541	195,000	613
Bolivia	1,098,580	1026	1,098,580	1026
Peru	1,285,220	903	2,383,800	1246
Ecuador	283,560	756	2,667,360	1303
Brazil	8,511,965	1007	11,179,325	1541
The Guianas [A]	378,331	845	11,557,656	1678
Venezuela	912,050	887	12,469,706	1761
Colómbia	1,138,910	870	13,608,616	1818
Panama	78,200	607	13,686,816	1840
Costa Rica	51,160	708	13,737,976	1863
Mid-Central America" [B]	394,474	696	14,132,450	1911
Mexico	1,972,550	778	16,105,000	1993

A. Guyana, French Guiana, Suriname.
B. Belize, El Salvador, Guatemala, Honduras, and Nicaragua.

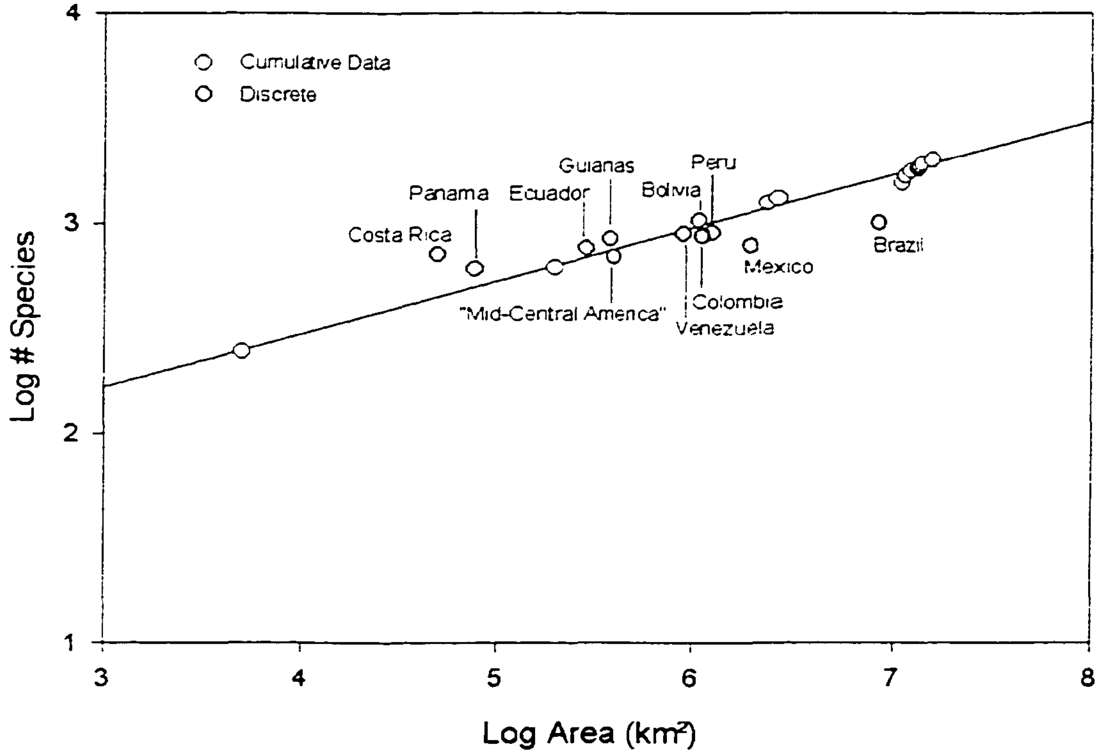


Figure 7.4. Species-area curve for the wetland flora of the Neotropics. Linear regression: Log S = 1.46 + 0.25 Log A, $r^2 = 0.99$. The linear regression was fitted to the species-area curve generated from cumulative data (Table 7.5).

data were then plotted for each lowland region (Fig. 7.4, gray circles). As with the preceding species-area curves, regions above the regression line were considered as relatively species-rich and those below as relatively species-poor.

The slope of the regression line (0.25, Fig. 7.4) was slightly lower than those from both the inter-Bolivian regional data (0.33, Fig. 7.1) and the regional data from the coterminous United States (0.31, Fig. 7.3). I can think of no processes that would affect regional-scale diversity in both Bolivia and the United States without also operating in the Neotropics, as a whole. Therefore, it seemed reasonable to consider all three slopes as roughly equivalent.

The slopes from the regression lines fitted to the regional data were much steeper than those from the three sets of site-level data (0.13, Southeastern U.S.; 0.13 New England; and, 0.17 Lowland Bolivia; Fig. 6.7). These results were striking, as they were the inverse of what was expected. Assuming that individual wetlands are functionally islands (*i.e.*, small areas of a particular habitat isolated by much larger expanses of unsuitable habitat), then the species-area curves generated from the site-level data were expected to possess slopes approximating those known for islands (*e.g.*, 0.25-0.33, Rosenzweig 1995). Instead, the site-level species area curves all fell within the range known for "mainlands" (*e.g.*, 0.13-0.17, Rosenzweig 1995). Conversely, the species-area curves from the macroregional data, rather than corresponding to those known for mainlands, were analogous to those expected for islands. This incongruity was particularly puzzling as the two macroregional data sets (*i.e.*, the Neotropics, and the coterminous United States) both were constructed from sufficiently large areas such that they were expected to possess even steeper slopes than the figures cited for mainlands (Rosenzweig 1995). I am unable to suggest a mechanism that would account for these anomalies.

The discrete regional data formed a tight fit to the regression line of the cumulative data (Fig. 7.4). Costa Rica and Panama were found to be the two most diverse countries (*i.e.*, situated furthest above the regression line). In general, Central America appeared to possess a somewhat higher diversity than South America. An exception was Mid-Central America, which was situated just below the regression line, however, the species checklist for this OGU was most likely very incomplete, as relatively little botanical work seems to have taken place in the wetlands of the constituent countries.

The characterization of Central America as more diverse than South America was confounded by indications that the smallest OGUs (and, hence, Central America) were generally represented by more complete floristic accounts. This pattern was evidenced from two trends in the plot of the discreet regional data (Fig. 7.4, gray circles). First, diversity was (generally) negatively correlated with area. The most diverse OGUs (*i.e.*, OGUs situated above the regression line) were generally the smallest, whereas the largest OGUs (Mexico and Brazil) were the least diverse (i.e, OGUs situated below the regression line, Fig. 7.4). It would seem that, rather than representing some heretofore unrecognized facet of biodiversity, this was simply a function of a much greater percentage of the area of the smaller countries having been surveyed. The second pattern was that OGUs represented by putatively complete national checklists (Costa Rica, Ecuador, the Guianas, Panama, and Peru) were generally the most diverse (exception, Peru), whereas those that were represented by checklists that I compiled (Bolivia, Brazil, Colombia, Mexico, Mid-Central America, and Venezuela) were the least diverse. In some cases (*e.g.*, Brazil), I recognized that the wetland flora was most likely significantly incomplete, but in other instances I felt as if a substantial portion of the wetland flora was probably accounted for. For example, the number of wetland species noted for Mexico (778 species, Table 7.5) was of the same order as the 747 species noted for Mexico by Lot *et al.* (1993). Still, they noted that large gaps remained in the country's floristic inventory. Thus, it may well be that a significant portion of the Mexican wetland flora was not accounted for in the wetland species database.

Although the OGUs varied in how completely their floras were represented in the wetland species database, the characterization of Central America as more diverse than South America appears warranted, if somewhat qualified. Because (the aptly named) Central America occupies a position proximal to two larger land masses and, as wetland plants frequently possess extremely large distributions (Arber 1920), it was not unexpected that this region would possess a diverse wetland flora. Still, it is antithetical to the latitudinal gradient, which predicts a greater diversity for South America. Furthermore, four countries in Meso- and South America (Brazil, Colombia, Mexico, and Peru) have been identified as "megadiversity" countries (Mittermeier and Werner 1990), *i.e.*, countries that possess large numbers of species, high levels of endemism, or both. Based on Fig. 7.4., however, none of these could be characterized as possessing a particularly diverse wetland flora.

At this point, it was possible to again address the question that originally kindled my interest in Neotropical wetlands. How does diversity in the Neotropical wetland flora compare with that of the New World Temperate region? The data (cumulative species and cumulative total regional area) that were previously used to generate the species-area curves for these regions were combined and the interaction between area and data source (*i.e.*, Neotropics versus coterminous United States) was evaluated by an ANOVA test. Results indicated that the interaction between data sources was significant; thus, separate regression lines were fitted to the data (Fig. 7.5). Although the two regression lines varied slightly, the New World Temperate region was the more diverse. The y-intercept of the regression line for the Neotropics (1.46) was higher than that for the New World Temperate region (1.24); thus, below a certain area (ca. 10,000 km^2) the regression line for the former was situated above the line for the latter. It did not appear that this represented a difference in regional-scale diversity in smaller areas, as Neotropical wetlands were also determined to be less diverse than New World Temperate at a smaller scale (*i.e.*, the comparison of site-level diversity; Fig. 6.7). Rather, it most likely was the result of the "starting point" for the New World Temperate region species-area curve (*i.e.*, Maine) being an order of magnitude or so larger than the smallest unit for the Neotropics, and as such it can be ignored.

A more important consideration is what portion of each region's wetland flora was included in the data. Although the checklist used to represent the wetland flora of the United States (Reed 1996) was considered to be a draft, the United States has unquestionably been subjected to a much more comprehensive floristic investigation than

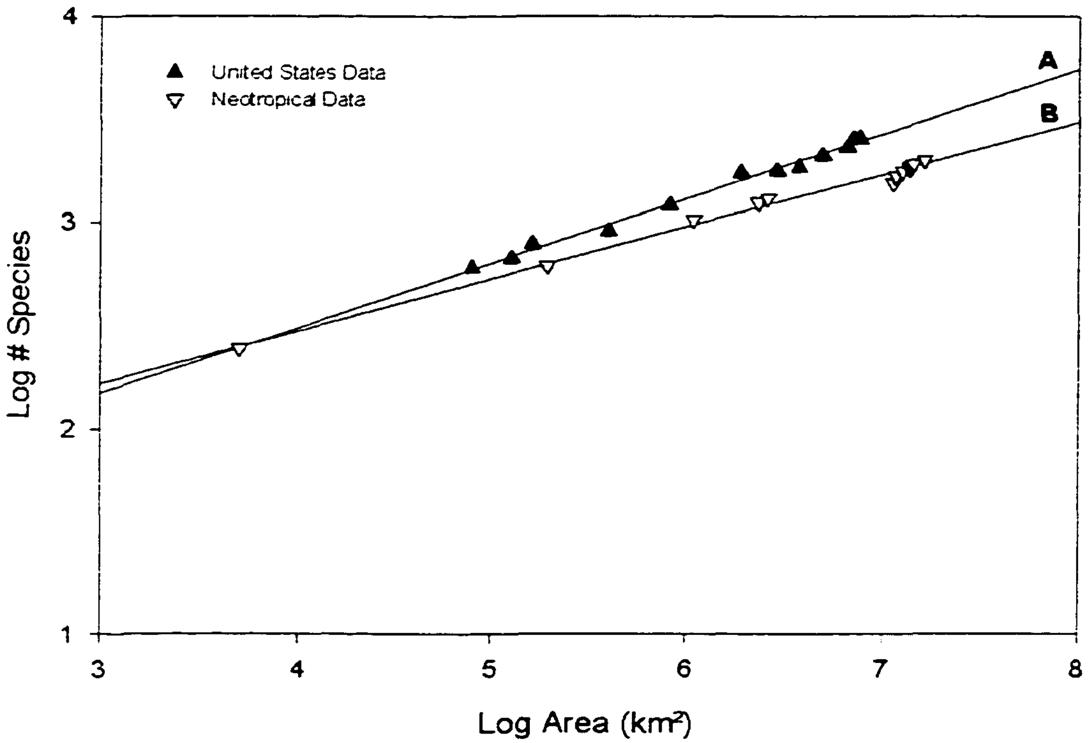


Figure 7.5. Species-area curves for the wetland floras of the coterminous United States and the Neotropics. A. Coterminous United States. Linear regression: Log S = 1.24 + 0.31 Log A, $r^2 = 0.99$. B. The Neotropics. Linear regression: Log S = 1.46 + 0.25 Log A, $r^2 = 0.99$.

have any of the Neotropical countries. The checklist assembled here to represent the Neotropical wetland flora (Ritter 2000) was compiled from a portion of the floristic accounts from what were, generally, incompletely surveyed countries, and can only be considered as embryonic relative to the checklist of Reed (1996).

In an attempt to assess how completeness of the Neotropical wetland species database may have affected the preceding analysis (Ritter 2000), data regarding the evolution of the database were compiled and tabulated (Table 7.6). Ideally, the condition of the database (*e.g.*, number of wetland species entered, etc.) would have been recorded at regular intervals throughout the duration of the research. Regrettably, this was not the case. Instead, the data presented in Table 7.6 represents an *ex post facto* reconstruction based on versions of the database that had been fortuitously archived on various computers. January 23, 1994 (the date of the first botanical collections I made in Bolivia), was designated as the starting date for the compilation of the database.

A few observations regarding the evolution of the database should be made. First, the longer I looked, the more wetland (and provisional wetland) species I encountered. Over time, an increasingly smaller fraction of wetland species was derived from the total taxa entered; nevertheless, there were no indications that the rate at which new wetland species were encountered was approaching an asymptote. Thus, there is no question that with further work a substantial number of wetland species would have been added to the checklist. Secondly, the data from the second tabulation (*i.e.*, May 25, 1999) represented the status of the database at the time when I first felt that a reasonable approximation of the number of Neotropical wetland species had been achieved. This perception was

Table 7.6. Evolution of the Wetland Species Database.

Date[A]	Total Taxa[B]	Wetland Species	Provisional Wetland Species	Wetland Species: Bolivia	Provisional Wetland Species: Bolivia
10/0/1998	1155	907	171	591	22
5/25/1999	2319	1111	264	671	187
11/29/1999	3452	1414	497	753	288
9/20/2000	5713	2060	1034	1026	527

A. The first species were added to the database on January 23, 1994.
B. Total taxa entered in the database, including accepted taxa, synonyms, invalid names, sub-specific taxa, non-wetland species, etc.

Table 7.7. OGUs used in plotting a species-area curve for the Neotropics (South America, Central America, and Mexico), with cumulative OGU area, cumulative wetland species, cumulative wetland and provisional wetland species, and percent increase resulting from the inclusion of provisional wetland species.

OGU	Cumulative Area (km^2)	Cumulative Wetland Spp.	Cumulative Wetland and Provisional Wetland Spp.	% Increase
Andean Piedmont	5000	244	304	24.6
Chiquitania	195,000	613	854	39.3
Bolivia	1,098,580	1026	1553	51.4
Peru	2,383,800	1246	1913	53.5
Ecuador	2,667,360	1303	2013	54.5
Brazil	11,179,325	1541	2364	53.4
The Guianas [A]	11,557,656	1678	2522	50.3
Venezuela	12,469,706	1761	2609	48.2
Colómbia	13,608,616	1818	2670	46.9
Panama	13,686,816	1840	2728	48.3
Costa Rica	13,737,976	1863	2805	50.6
Mid-Central America" [B]	14,132,450	1911	2868	50.1
Mexico	16,105,000	1993	2985	49.8

A. Guyana, French Guiana, Suriname.
B. Belize, El Salvador, Guatemala, Honduras, and Nicaragua.

primarily based on this estimate (1,111 spp.) corresponding to the number of species noted for South America (ca. 1,100) in a checklist compiled by Conservation International and the Chicago Field Museum (Tyana Wachter, Field Museum, pers. com.). Nevertheless, after two additional years of work on the database the number of wetland species had nearly doubled (2,060 spp., Table 7.6). This suggests a rule of thumb, "when you've reached the point where you think the checklist is reasonably complete, you might be halfway there." In other words, although I feel confident that the levels of diversity presented here for the various Neotropical OGUs are reasonably representative, I have been wrong before.

Therefore, it seemed appropriate to augment the number of species listed for the Neotropical OGUs and reexamine the differences in diversity between the Neotropical and New World Temperate regions. The provisional wetland species noted for each OGU were used to augment the checklists (Table 7.7). I originally considered increasing the species list for each OGU by a uniform 50%, but it seemed that the provisional wetland species might better represent actual diversity patterns in the OGUs. As it turned out, both methods would have been more or less equivalent, as the average percent increase in the floras was 47.8%, with relatively little variance (Table 7.7).

A species-area curve was plotted using the augmented floras for the Neotropical OGUs, a regression line was fitted to the data and the resulting plot added to the existing species-area curves for the Neotropics and the New World Temperate regions (Fig. 7.6). Despite the floras of the Neotropical OGUs having been increased by nearly 50%, the level of diversity was no more than equivalent to that of the New World temperate region.

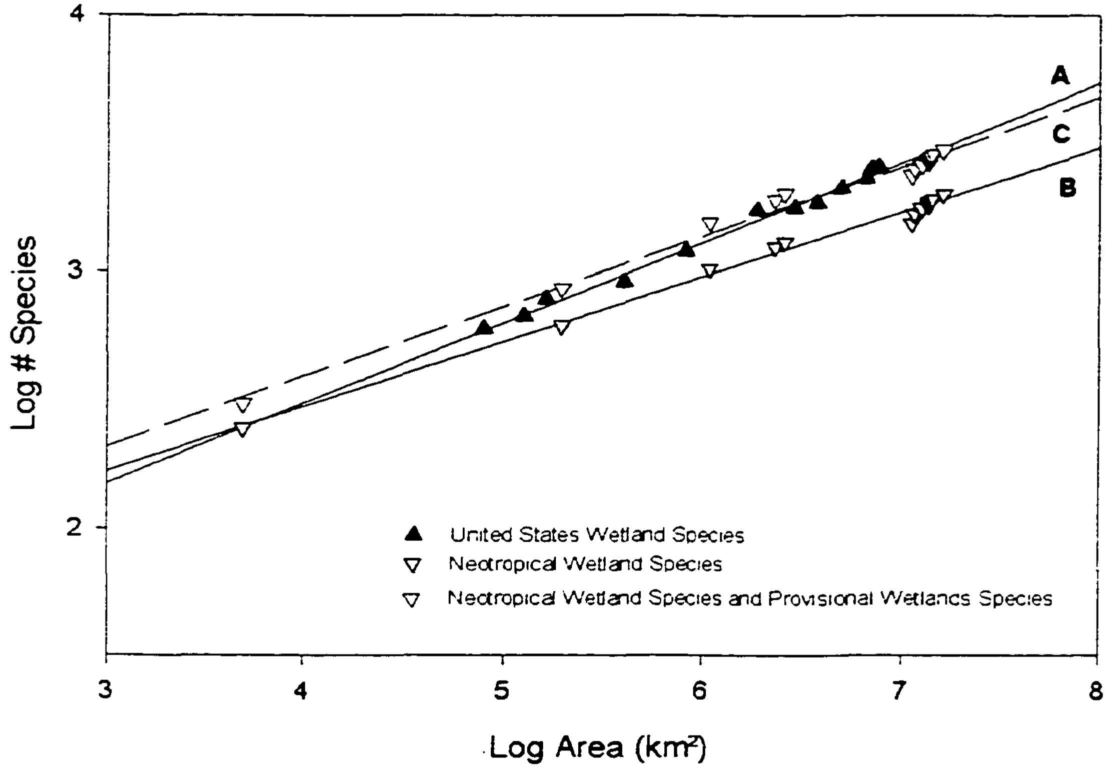


Figure 7.6. Species-area curves for the wetland floras of the coterminous United States and the Neotropics, and for the combined wetland and potentially wetland species of the Neotropics. **A**. Coterminous United States. Linear regression: Log S = 1.24 + 0.31 Log A, $r^2 = 0.99$. The Neotropics: **B**. Wetland Species. Linear regression: Log S = 1.46 + 0.25 Log A, $r^2 = 0.99$. **C.** Wetland and Provisional Wetland Species. Linear regression: Log S = 1.50 + 0.27 log A, $r^2 = 0.99$.

The (approximately) 50% increase in species engendered by the addition of the provisional wetland species undoubtedly exceeds the actual diversity of the Neotropical wetland flora. Hence, I am confident in the assessment of the wetland flora of the Neotropical region as not demonstrably richer than that of the New World Temperate region.

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APPENDICES

APPENDIX A: THE STUDY SITES

This appendix contains descriptions of the 46 systems which served as the principal foci of field investigations, along with notes on the composition and structure of the vegetation. Note that descriptions of the study site floras from the three regions which were examined in detail (the Cloud Forest, Chapter 3; the Chapare, Chapter 4; and, the Gran Pantanal, Chapter 5) were presented in these chapters.

High Andean

Despite the semi-arid to arid conditions that are characteristic of the Bolivian High Andean region, various types of wetlands (*i.e.*, lakes, ponds, streams, small rivers, riparian marshes, and marshes) were common. The larger systems were often fairly accurately located on maps, and, as the paucity of woody vegetation in the Puna allowed for expansive vistas, wetlands were easily encountered during general reconnaissance. This region possessed such a large number of study sites due to both the close proximity of High Andean habitats to the my home in Cochabamba, and to the relative ease with which these systems were encountered. Eight study sites were established in the High Andean region (Table A.1): five lakes (four created or modified by impoundments, and one natural lake), two ponds, and one riparian wetland.

Table A.1. Study sites in the High Andean region (Bolivia), with elevation, approximate area of the system, approximate location, and number of species noted for each site.

System	Elev. (m)	Approximate Area (ha)	Approximate Location	No. Spp.
Laguna Toro	4420	2.5	66°23'W 17°11'S	15
Huayalmarca Pond	4300	0.1	66°41W 17°39'S	3
Laguna Saythu Khocha	4420	40	65°39'W 17°23'S	7
Laguna Totora Khocha	3620	120	66°38'W 17°27'S	20
Laguna Larati	3540	124	66°02'W 17°21'S	25
Laguna Juntutuyo	3360	244	65°39'W 17°34'S	7
Río Candelaria	3165	1	65°56'W 17°16'S	31
Chulichuncani Laguna	3160	20	65°22W 17°34'S	15

Laguna Toro
Elevation: 4420 m. Watershed: Amazon Number of species: 15
Dates visited: Sep 23, 1994; Mar 9, 1995; Dec 1, 1996

Laguna Toro, the highest elevation study site (ca. 4420 m), was an approximately 2.5 ha pond, with a maximum depth of about 3 m. The Río Khullarijoni– which was hardly more than a stream (maximum width, ca. 2.5 m) in the area around Laguna Toro–provided a year-round, low volume flow through the system. Directly upstream from where the Khullarijoni entered the system, the river took a sinuous path, forming a small marsh. The basin was bordered by steep slopes on the southern and western edges, and runoff from these slopes drained into the system.

The pond basin possessed a complex morphometry, with the southern half flat-bottomed and shallow (ca. 0.5-1.0 m), and the remainder deeper, with sharply sloped sides. The shallows were vegetated by small, submerged species. Typical species were

Crassula venezuelensis (Crassulaceae), *Lilaeopsis macloviana* (Apiaceae), *Lilaea scilloides* (Juncaginaceae), *Isoëtes lechleri* and *I. herzogii* (Isoëtaceae), and *Pilularia americana* (Marsileaceae). *Calamagrostis eminens* (Poaceae) formed a series of hummocks in this part of the system, and other emergent herbs, such as *Schoenoplectus californicus* (Cyperaceae) and *Alopecurus aequalis* (Poaceae) were common. The deeper parts of the basin were dominated by the submerged macrophyte *Myriophyllum quitense* (Haloragaceae). Another submerged species, *Ruppia filifolia* (Ruppiaceae), was fairly common in this zone.

No rare species were observed at Laguna Toro. Nevertheless, the population of *Myriophyllum quitense* was noteworthy for possessing some unusual characteristics (see Appendix E). Laguna Toro was located in an area of low population density, and appeared to be subjected to only a small amount of anthropogenic disturbance; generally from fishing and grazing livestock (predominantly llamas).

Huayalmarca Pond

Elevation: 4300 m Watershed: Desaguadero Number of species: 3
Dates visited: Jun 4, 1994; Feb 25, 1995

The Huayalmarca Pond was a small (ca. 0.1 ha) pond situated downslope from the highway between Cochabamba and La Paz. The system was shallow, with a maximum depth of less than 0.75 m, nevertheless, it apparently contained water throughout the year. The pond received inputs of water from runoff draining the adjacent slopes, and from a small seep at one end of the basin, which also appeared to be wet year-round. Pond water was rich in suspended material, and water color was an opaque white.

Although the Huayalmarca Pond was very species-poor (3 spp.), it was selected as a study site because of the extreme alkalinity (pH 10.0-10.4) of the water. Despite the low species richness, aquatic vegetation filled the basin, with two submerged macrophytes, *Myriophyllum quitense* and *Stuckenia filiformis* (Potamogetonaceae) present in abundance.

No rare or noteworthy species were observed at this site. Anthropogenic disturbance appeared to be limited to the road construction, and the resultant erosion, above the site.

Laguna Saythu Khocha

Elevation: 4020 m. Watershed: Amazon Number of species: 10
Dates visited: Jul 2, 1994; Oct 11, 1994

Laguna Saythu Khocha was located on the eastern Cordillera near the lower limits of the Puna vegetation zone. The lake was a fairly large (ca. 40 ha), artificial system that was formed by damming the shallow end of a natural depression. The dam appeared to be of fairly recent origin (*i.e.*, within the last 5-20 years). Presumably, some type of wetland served as the "nucleus" for the system. Overflow from the system passed through a stream (unnamed on the topo map) which flowed into the Río Talpasale. Lake water was clear and somewhat acidic (pH = 6.5). Although water levels were controlled by a floodgate, at the time of the second visit to the site (well into the dry season) water levels were about 2.5 m below the floodgate. Maximum depth of the system was not determinable.

Although Laguna Saythu Khocha was somewhat richer in species (10 spp.) than many of the high elevation lakes encountered in this study, vegetative cover was generally sparse. No emergent species were noted; rather, the flora was composed almost entirely of submerged species. Common species were *Crassula venezuelensis* (Crassulaceae), *Limosella* sp. (Scrophulariaceae), *Elodea potamogeton* (Hydrocharitaceae), *Myriophyllum quitense*, and *Isoëtes* sp. (Isoëtaceae). As noted, during the dry season water levels dropped substantially, exposing a broad band (varying from ca. 5-20 m) of relatively flat lake bottom and allowing short-lived annual herbs (primarily, *Alchemilla* sp., Rosaceae) to become established. No rare or noteworthy species were observed at this system.

A small agrarian community was located on the western side of the mountains, a few kilometers downslope from Laguna Saythu Khocha, and villagers passed by the lake on their way to harvest firewood from the forested areas (Ceja de Monte, and Cloud Forest) on the eastern side of the Cordillera. Nevertheless, other than the modifications to the original system and the control of water levels, there were no obvious indications of anthropogenic disturbance to the system.

Laguna Totora Khocha

Elevation: 3620 m. Watershed: Amazon Number of species: 20
Dates visited: Jun 28, 1994; Jul 2, 1994; Apr 26, 1995

Laguna Totora Khocha was a large (ca. 120 ha) lake. Previously, the lake was significantly smaller, but in 1991 construction of a dam was completed on the southern end of the system, thereby greatly increasing the system's area and depth. According to a sign posted along the edge of the lake, the system possessed a maximum depth of 18 m and a volume of 22,000,000 m^3. Lake water was basic ($pH = 8.1$), with abundant filamentous algae. Outflow from Laguna Totora Khocha formed the Río Jatun Mayu.

The vascular flora consisted primarily of submerged species. Typical species were *Crassula venezuelensis* (Crassulaceae), *Myriophyllum quitense* (Haloragaceae), *Elodea potamogeton* (Hydrocharitaceae), *Isoëtes boliviensis* (Isoëtaceae), and *Potamogeton pusillus* (Potamogetonaceae). With the exception of *Poa annua* (Poaceae), no emergent species were observed. Vascular species were generally limited to a fairly narrow band around the perimeter of the lake, however, during the dry season, small islands were exposed as water levels dropped. These islands supported populations of diminutive herbs, many of which are typical of streams and marshes in the area and others which were of uncertain ecological affinity. Typical "island" species were *Spergula arvensis* (Caryophyllaceae), *Erodium cicutarium* (Geraniaceae), *Paspalum pygmaeum* (Poaceae), and *Cotula australis* (Rosaceae). No rare or noteworthy species were observed.

Anthropogenic disturbance appeared to be limited to modifications of the original system and the continued control of water levels. Although Laguna Totora Khocha most likely once possessed large reed beds ("totora" is Quechua for *Schoenoplectus californicus*), the construction of the dam apparently resulted in the extirpation of this species from the site.

Laguna Larati

Elevation: 3540 m. Watershed: Amazon Number of species: 25
Dates visited: May 29, 1994; Jul 14, 1994; May 5, 1995, Oct 5, 1995

Laguna Larati was another large (ca. 124 ha), high elevation lake that had been modified by the construction of a dam. The dam had clearly been in existence longer than dams of the other high elevation systems of anthropogenic origin (probably 30-50 years), allowing macrophytes to become well-established. At least two seasonal streams flowed into the basin and others may be present. Lake water was cloudy white, with abundant solids in suspension. Outflow from the system formed the Río Apacheta Mayu, which in the area around Laguna Larati was scarcely more than 1.5 meters wide. Species encountered in the lake basin and in the "river" just below the spillway were included in the site checklist.

Laguna Larati possessed a rich flora (25 spp.) for a high-elevation system. Submerged species were abundant along the edges of the system, occupying depths up to ca. 2.5 m. Common species were *Myriophyllum quitense* (Haloragaceae), and *Potamogeton illinoensis*, and *P. pusillus* (Potamogetonaceae). The submerged herbs *Callitriche heteropoda* (Callitrichaceae) and *Elodea potamogeton* (Hydrocharitaceae) were locally abundant below the spillway and in quiet areas along the stream banks.

Emergent species were common, with *Juncus arcticus var. andicola*, J. fuscocapitatus, and *J. pallescens* (Juncaceae), and *Polypogon interuptus* (Poaceae) representative. Two aquatic ferns were present. *Marsilea crotophora* (Marsileaceae) was abundant in the shallows and in depths up to ca. 1.2 m and *Azolla mexicana* (Salviniaceae) was common in the area beneath the spillway.

Small islands (at least some of which were seasonally submerged) were present and these supported a distinct flora. Species typical of this habitat were *Hydrocotyle ranunculoides* (Apiaceae), *Eleocharis acicularis* (Cyperaceae), *Ludwigia peploides* (Onagraceae), and *Castilleja pumila* (Scrophulariaceae). Island surfaces that were still slightly inundated at the time of the fieldwork supported dense populations of the diminutive herb *Limosella subulata* (Scrophulariaceae).

Laguna Larati was atypical for a Bolivian high Andean system. The flora possessed an extremely complex structure for a high altitude site. Life-forms noted included emergent, submerged, free-floating, rooted with floating leaves, and rooted with floating stems. Many of the species encountered at this site were not observed in other Bolivian wetlands during this study, although none were new country records. Two species noteworthy for their presence in a high altitude system were *Ludwigia peploides* and *Potamogeton illinoensis* (see Appendix E).

The land surrounding the lake was utilized for farming and grazing, and the community of Larati was large by high Andean standards (ca. 300-500 residents). Nevertheless, little anthropogenic disturbance was noted at the site, although, agricultural run-off might have had a negative impact on the system. Grazing from livestock generally appeared to be minimal. An exception was *Marsilea polycarpa*, which was grazed when the plants became easily accessible in the dry season due to subsiding water levels. A much greater threat to Laguna Larati came from the city of Cochabamba, which was located approximately 15 km from the system. In 1995, it was decided to increase the area of the lake in order to incorporate Laguna Larati into the city's municipal water supply. The proposed plan entailed raising the level of the dam by a number of meters, a modification that clearly would negatively impact existing aquatic vegetation. Species associated with the seasonally inundated islands would be particularly vulnerable.

Laguna Juntutuyo
Elevation: 3360 m. Watershed: Amazon Number of species: 7
Dates visited: Sep 9, 1994; Apr 3, 1995; May 27, 1995

Laguna Juntutuyo, was a large (ca. 244 ha) lacustrine system located in a dry, high elevation valley situated between the Cochabamba valley and the Mizque valley. This system was the third largest of a complex of six large lacustrine systems; these most likely were once a single system. Water color was an opaque brown, and the water had a distinct saline taste. Maximum depth of the system was not determined, but it exceeded 3.5 meters (the length of a pole used to propel the log raft that was utilized during botanical collecting).

Despite Laguna Juntutuyo's large size, the flora was quite species-poor (7 spp.). The submerged herb *Myriophyllum quitense* (Haloragaceae) was by far the most abundant species; *Stuckenia filiformis* and *S. striata* (Potamogetonaceae) were common. Although compact, submerged species (*e.g.*, *Crassula venezuelensis*, Crassulaceae; *Elatine* spp., Elatinaceae) are frequently abundant in the shallows of high Andean lakes, no species with this life-form were noted in Laguna Juntutuyo. *Schoenoplectus californicus* (Cyperaceae) was the sole abundant emergent species. Large populations of this species were present along the edges of the basin, growing in depths of ca. 0.5-2.0 m. The free-floating fern *Azolla caroliniana* (Salviniaceae) was fairly abundant at one end of the system; this species is said to be extremely abundant, at times (A. Zabala Alvarado, pers. com). No rare or noteworthy species were observed at this system.

Laguna Juntutuyo was subjected to some anthropogenic disturbance. A number of small agrarian communities (*e.g.*, Estancia Juntutuyo, Estanica Chimpa Khocha, Estancia Juntutuyo Pampa) were located within a few kilometers of Laguna Juntutuyo. During the dry season, cattle were driven into the lake to browse, with *Myriophyllum quitense* and *Stuckenia striata* the preferred species. Additionally, *Schoenoplectus totora* was harvested for use as roofing thatch, and for building traditional Andean reed boats.

Río Candelaria

Elevation: 3165 m. Watershed: Amazon Number of species: 31
Dates visited: May 27, 1994; Feb 9, 1995; May 30, 1995

The Río Candelaria study site was a section of a high elevation river located on a plateau on the Cordillera Oriental, between the Cochabamba valley and the descent to the Amazon basin. The river was fed by run-off from the steep slopes bordering the area and experienced intense hydrologic pulses during periods of rain. Consequently, the river was fairly dynamic, and during the course of this study deposition and erosion changed the structure and floristic composition of some of the areas included in the study site. A section of the Río Candelaria approximately 0.5 km long (total area ca. 1.0 ha) was surveyed. This section was selected for study because it possessed a fairly complex morphology, with small strand lakes (or, more properly, "strand ponds") present in areas formerly occupied by the main channel and with marshy habitats present in low-lying adjacent areas. The main channel of the river possessed water throughout the year, however, at least some of the strand lakes and marshes were subject to dry-down during the dry season.

Río Candelaria supported a rich flora (31 spp.) for a high elevation system. Emergent species were the predominant life-form. Representative species were *Eryngium* cf. *coronatum* (Apiaceae), *Pycreus niger* (Cyperaceae), *Juncus ebracteatus* and *J. bufonius* (Juncaceae), *Polypogon viridis*, and *Deyeuxia rigescens* (Poaceae), and *Rumex conglomeratus* (Polygonaceae). *Hydrocotyle ranunculoides* (Apiaceae) was extremely abundant along the edges of the strand lakes, where it formed loosely coalesced floating mats. Submerged species were much less abundant than emergents, with *Lilaeopsis macloviana* (Apiaceae), *Callitriche* sp. (Callitrichaceae), *Crassula venezuelensis* (Crassulaceae), and *Isolepis inundata* (Cyperaceae) representative species. *Alchemilla pinnata* (Rosaceae), *Cotula australis* (Asteraceae), and *Mimulus glabratus* (Scrophulariaceae) were present along the river banks. As water levels dropped, sand bars became exposed and these supported various herbaceous species, a number of which were not observed elsewhere in the system. Representative species were *Sagina procumbens* (Caryophyllaceae), *Equisetum bogotense* (Equisetaceae), *Plantago buchtienii* (Plantaginaceae), *Poa annua* (Poaceae), and *Limosella aquatica* (Scrophulariaceae). These areas were particularly vulnerable to erosion and deposition. The sole noteworthy species encountered at Río Candelaria was the cosmopolitan weed *Sagina procumbens* (see Appendix E).

The system appeared to experience some anthropogenic disturbance, primarily from livestock grazing in the marshes. Nevertheless, impacts from human activities were clearly small-scale relative to the hydrologic disturbances (*e.g.*, deposition of sediments, and channel migration) which were characteristic of this system.

Chulichuncani Laguna

Elevation: 3160 m. Watershed: Amazon Number of species: 15
Date visited: Apr 26, 1995

The Chulichuncani Laguna was an approximately 20 ha, artificial lake, situated on the slopes (the Cerro Macho Corral) above the community of Estancia Chulichuncani. The system was situated above the old highway to Santa Cruz, ca. 50 km east of the Serranía de Siberia Wetland. Although the terrestrial vegetation immediately around the laguna was Puna, Cerro Macho Corral was situated in the transition between the Valles Secos and the Cloud Forest. The system appeared to receive greater inputs of atmospheric water (precipitation and fog) than did high Andean systems in the Cordillera del Tunari.

The lake was created by damming the Río Chulichuncani. A deep basin occupied the western half of the lake. Maximum depth was not determinable, however, the dam was approximately 12-15 m tall at its highest point. The eastern half of the basin was characterized by a much more shallow topography, and depths did not exceed 2 meters. Seasonally inundated marsh was present along the south and southwestern edges of the basin. It was difficult to determine the magnitude of annual fluctuations in water level, although the presence of species such as *Crassula venezuelensis* (Crassulaceae) and

Elatine peruviana (Elatinaceae) along the gradually sloping edges suggests that these areas are inundated throughout much of the year. Therefore, annual variations in water level most likely were not large-scale. At the time of the visit to the site (in the first few months of the dry season) the water level was just slightly below the level of the spillway.

The sides of the basin along the deeper (western) end of the system were quite steep and vegetation was scarce. The shallowly sloped, eastern portion of the basin supported a number of species, although vegetation was often sparse. Common emergents were *Juncus microcephalus* (Juncaceae), and *Agrostis perennans* and *Amphibromus scabrivalvis* (Poaceae). Small submerged species were also fairly common, with *Crassula venezuelensis* (Crassulaceae), *Elatine peruviana* (Elatinaceae), and *Limosella aquatica* (Scrophulariaceae) representative species. The seasonally inundated marshes supported an abundance of herbaceous vegetation. Common species were *Cotula mexicana, Gamochaeta americana, Gnaphalium dombeyanum,* and *Hypochoeris apargioides* (Asteraceae), *Spergula arvensis* (Caryophyllaceae), *Plantago australis* (Plantaginaceae), and *Ranunculus flagelliformis* (Ranunculaceae). The sole species of note at the Chulichuncani Laguna was *Amphibromus scabrivalvis,* an aquatic grass with lax semi-floating culms, which was common in the shallow end of the system (see Appendix E).

Anthropogenic disturbance appeared to be minimal, other than the control of water levels. Abundant livestock were noted in the area, but there were other water sources nearby and these appeared to be more heavily frequented than the Chulichuncani Laguna.

This system was worthy of more than the single visit it received, but the site's inaccessibility served as a deterrent to return visits. A particular incentive to continued fieldwork in the Chulichuncani Laguna was provided by the boiled potatoes, hard-boiled eggs, and "locoto" (*Capsicum pubescens*) that residents of the nearby community of Khewiña Pampa offered for sale along the highway. These are highly recommended as a source of comfort to researchers whose chest-waders may have recently been filled with water from a high Andean lake.

Valles Secos

Four systems served as study sites in the Valles Secos (Table A.2): one lake, two riparian marshes, and one irrigation channel. Additionally, general collections were made from other wetlands in the Valles Secos, principally seasonal ponds, riparian habitats, and irrigation channels and ditches.

Table A.2. Study sites in the Valles Secos region (Bolivia), with elevation, approximate area of the system, approximate location, and number of species noted for each site.

System	Elevation (m)	Approximate Area (ha)	Approximate Location	No. Spp.
Laguna Alalay	2550	175	66°08'W 17°24'S	32
Río Mizque Wetland	1970	0.5	65°18'W 17°56'S	65
Río Guadalquivir Wetland	1800	0.05	64°44'W 21°32'S	49
Tiquipaya Irrigation Canal	2620	0.02	66°13'W 17°21'S	16

Laguna Alalay

Elevation: 2550 m Watershed: Amazon Number of species: 33
Dates visited: Apr 6, 1994; May 25, 1994; Mar 18, 1995; Apr 1, 1995; Jan 10, 1996; Oct 3, 1996; Oct 23, 1996; Jun 24, 1997

Laguna Alalay was a large (ca. 175 ha) basin system located within the city of Cochabamba. The basin was shallow throughout: average water depth was estimated at 69.8 cm (Maldonado and Goitia 1989). Maximum depth was on the order of ca. 2.0 m. Water conditions were basic, with average measured pH ranging from 9.8-10.3 (Maldonado and Goitia 1989). Water was dark brown. Basin sediments were soft and deep, averaging 54.5 cm in areas without macrophytes and 72.7 cm in areas with macrophytes (Maldonado and Goitia 1989).

When fieldwork commenced in Laguna Alalay, vegetation was abundant throughout much of the system. Subsequent human activities, however, greatly affected the distribution of vegetation (see below). The most abundant emergent species were *Schoenoplectus californicus* and *S. americanus* (Cyperaceae), *Echinochloa crus-pavonis* (Poaceae), *Polygonum lapathifolium* and *P. punctatum* (Polygonaceae), and *Typha domingensis* (Typhaceae). Species typical of seasonally inundated habitats along the edge of the system were *Baccharis juncea, Eclipta prostrata, Pluchea sagittalis* (Asteraceae), and *Tessaria integrifolia* (Asteraceae), *Heliotropium curassavicum* (Boraginaceae), *Pycreus niger* and *Schoenoplectus americanus* (Cyperaceae), *Chenopodium ambrosioides* (Chenopodiaceae), and *Rumex crispus* (Polygonaceae). *Tessaria integrifolia* was the sole woody species observed in the system. Following major changes to the system's hydrology (see below), *Heliotropium curassavicum* and *Chenopodium ambrosioides* were particularly abundant, dominating large-areas of the recently exposed lake bed.

Free-floating species were *Lemna gibba, Wolffia columbiana* and *Wolffiella oblonga* (Lemnaceae), and *Azolla caroliniana* (Salviniaceae). At times, *A. caroliniana* was extremely abundant, covering extensive areas (ca. 40-50 ha) of the system; at other times this species was inconspicuous. The sole rooted species with floating stems was *Ludwigia grandiflora* (Onagraceae), which formed small, loosely-knit floating assemblages in one part of the system. Despite the dark water and the episodic blanketing of the surface by *Azolla caroliniana*, submerged species were abundant. Submerged species were *Myriophyllum quitense* (Haloragaceae), and *Potamogeton pusillus, Stuckenia striata* and *S. pectinata* (Potamogetonaceae). In extensive areas of the system, dense populations of filamentous algae were present, although this varied seasonally (see Maldonado and Goitia 1989). No rare species were observed at Laguna Alalay, but a few species were noteworthy, either for possessing unusual characteristics or for approaching the known elevational limits of their distribution (see Appendix E).

Laguna Alalay was heavily impacted by human activities. The system served as an informal dumping ground for all manner of refuse and most likely received raw sewage from the surrounding neighborhoods. In recent years, Laguna Alalay has experienced severe perturbation. In 1995 the lake was partially drained in an attempt to install a system to facilitate the aeration of the typically stagnant, foul-smelling water. Water levels, therefore, were lower than normal during the dry season and a much larger than normal area of basin was exposed during dry down. Additionally, in 1997 the city initiated dredging the lake. A dike was constructed, bisecting the basin, water was drained from one side of the system, and the basin was deepened. The dredged portion of the system was left without water for a long period (a year or two), and was subsequently refilled. This process was then repeated for the area on the other side of the dike.

The close proximity of Laguna Alalay to my home in Bolivia facilitated numerous visits to the site. Despite this accessibility, the system's deep, mushy sediments–which were of decidedly suspicious, anthropogenic origin–and the site's powerful stench, assured that the system was visited no more often than was absolutely necessary.

Río Mizque Wetland
Elevation: 1970 m Watershed: Amazon Number of species: 65
Dates visited: Jan 8, 1995; Apr 6, 1995; May 28, 1995, Nov 11, 1996

The Río Mizque wetland was a riparian wetland, situated ca. 2 km south of the town of Mizque. The wetland was structurally complex, and incorporated a series of meander scrolls, intervening marshy areas, and three streams which passed through these areas on their way to the Río Mizque. The system was also hydrologically complex. Many parts were annually flooded during the rainy season when the river level rose. Some areas were only temporally inundated, however, the three streams provided year-round water to other parts of the system. One section of the wetland also received ground water from a hillside seep. Soils were variable, ranging from compacted silty sand to soft, fairly deep deposits of silt. An approximately 300 m long section of the river, including areas along both banks, was selected for study. Total study area was about 0.5 ha.

The site supported a species-rich flora (65 spp.), with slightly more than half (55.4%) of these contributed by three families: the Poaceae (14 spp.; 21.5%), Asteraceae (12 spp.; 18.5%), and Cyperaceae (10 spp.; 15.4%). Emergent species were the dominant life form. The most abundant emergents were *Pluchea sagittalis* and *Tessaria* *integrifolia* (Asteraceae), *Eleocharis flavescens*, *E. montana*, and *Pycreus bipartitus* (Cyperaceae). *Juncus microcephalus* (Juncaceae), *Echinochloa* crus-pavonis, *Imperata tenuis*, and *Paspalum distichum* (Poaceae), *Polygonum punctatum* (Polygonaceae), *Pityrogramma trifoliata* (Pteridaceae), and *Salix humboldtiana* (Salicaceae). Two emergent species, *Commelina* sp. (Commelinaceae) and *Dalea cliffortiana* (Fabaceae), were common in shallowly inundated areas along the upland edge of the system. The creeping semi-aquatic herbs *Bacopa monnieri* (Scrophulariaceae), *Mimulus glabratus* (Scrophulariaceae), and *Rorippa nasturtium-aquaticum* (Brassicaceae) were abundant along the upland edge of the system and in shallow pools. *Ludwigia peploides* (Onagraceae) was extremely abundant in shallow pools alongside the main river channel, occurring both as a creeping herb and as a rooted macrophyte with floating stems.

Submerged species were nearly absent, with a small population of *Callitriche* sp. (Callitrichaceae) the only example of this life-form noted. Free-floating species were well-represented. The water hyacinth, *Eichhornia crassipes*, was extremely abundant, completely covering the surface of some meander scrolls. Other free-floating species were *Azolla caroliniana* and *A. filiculoides* (Salviniaceae), and *Lemna aequinoctialis* and *L. minuta* (Lemnaceae). The sole climber noted was *Mikania micrantha* (Asteraceae). Despite the rich flora relative to other Valles Secos wetlands, no rare or noteworthy species were observed.

The Río Mizque Wetland was periodically subjected to anthropogenic disturbance. At times, cows were tethered in the meander scrolls to graze. In the 1990's, a concrete bridge was built over the wetland, and was rebuilt a few years later (see below). These construction activities must have impacted the wetland; however, the largest disturbances to the wetland appeared to come from the Río Mizque itself. During the rainy season, when water velocities are high, a portion of the substantial bed load transported by the river will be spread through sections of the wetland. Additionally, the river can periodically rise far above its normal flood level and move through the study site area with great force. For example, the first bridge that was built over the wetland during the early 1990's lasted only a few years until it was destroyed by an unusually high flood. This magnitude of flood (ca. 3 m over the water's "normal" height during the rainy season) must have flooded the entire study site area.

Río Guadalquivir Wetland

Elevation: 1800 m Watershed: Paraná Number of species: 49
Dates visited: Dec7, 1996; Dec 9, 1996; Dec 10, 1996.

The Río Guadalquivir Wetland, another riparian wetland, was the southernmost study site. The portion of the Río Guadalquivir that was selected for study was situated in the northwestern section of the city of Tarija. Two separate areas comprised the study site. The first, located along the west bank of the Río Guadalquivir, was structurally similar to the Río Mizque Wetland. Predominant features were: 1) meander scrolls; 2) seasonally inundated areas directly adjacent to the main river channel, with numerous, scattered pools; and, 3) small streams. The second area was located along the east bank, approximately 300 m upstream from the first. The predominant feature of this area was a shallowly inundated (ca. 0.7 m) marsh. Total area included in the study site was approximately 0.5 ha This system was quite dynamic hydrologically, as per the Río Mizque Wetland.

The flora was species-rich (49 spp.) and was dominated by emergent vegetation. The most abundant emergent species were *Gnaphalium dombeyanum* (Asteraceae), *Chenopodium ambrosioides* (Chenopodiaceae), *Juncus microcephalus* and *J. tenuis* (Juncaceae), *Luziola peruviana* and *Paspalum distichum* (Poaceae), *Polygonum* punctatum and *P. persicaria* (Polygonaceae), *Salix humboldtiana* (Salicaceae), *Typha domingensis* (Typhaceae), and *Veronica anagallis-aquatica* (Scrophulariaceae). The shrub *Baccharis salicifolia* (Asteraceae) and the herb *Acicarpha tribuloides* (Calyceraceae) were common in the transition between wetland and upland.

The sole submerged species was *Myriophyllum aquaticum* (Haloragaceae), which also possessed an erect, semi-terrestrial form in formerly inundated areas. Free floating species were *Eichhornia crassipes* (Pontederiaceae), *Spirodela intermedia* and *Lemna* sp. (Lemnaceae), and *Azolla mexicana* (Salviniaceae). *Eichhornia crassipes* was particularly abundant, at times nearly covering the surface of meander scrolls. The two noteworthy species observed at this site were *Myriophyllum aquaticum* and *Oenothera tarijensis* (see Appendix E).

Due to its location in an urban area, this system has been heavily impacted by anthropogenic activities. The edges of the wetland were used for dumping trash and construction material. Chemical pollution was probably the most significant threat to the site, as the Río Guadalquivir is said to be highly contaminated (Óscar Barrenachea, PROMETA, pers. com.).

Irrigation Canal at Tiquipaya
Elevation: 2620 m. Watershed: Amazon Number of species: 16
Dates visited: Apr 5, 1994; Apr 21, 1994

This study site was a section of a network of irrigation and drainage canals in the community of Tiquipaya (Cochabamba valley). Irrigation canals and ditches are common in populated areas of the Valles Secos. These frequently support hydrophytic species and species tolerant of some inundation along their edges and on channel bars. The hydrologic regime in these systems is extremely variable. Water flow is controlled by floodgates and it is not uncommon for water levels to change by a meter, or more, in a brief period. Hence, areas immediately adjacent to the canals, which spend the greatest part of the year above water, can suddenly be inundated, and at times, non-hydrophilic species can be encountered growing under water.

A stretch of canal approximately 50 m long was surveyed. No submerged or free-floating species were observed; rather the flora consisted entirely of emergent species and erect, weedy species growing under saturated conditions. The most abundant species were *Cyperus eragrostis, Eleocharis montana*, and *Schoenoplectus californicus* (Cyperaceae), *Echinochloa crus-pavonis* (Poaceae), and *Polygonum persicaria* (Polygonaceae).

In addition to their anthropogenic origin, these systems were continually heavily impacted by human activities and thus would appear to be poor candidates for the vegetation study. Nevertheless, these canals most likely functioned as corridors for the dispersal of macrophytes throughout the Valles Secos, hence their inclusion in this study.

Cloud Forest

Six wetland systems served as the principal study sites in the Cloud Forest (Table A.3). Additional data were incorporated from general collecting in a variety of other wetlands, such as small marshes, streams, rivers, inundated roadside ditches, and vernal pools.

Table A.3. Study sites in the Cloud Forest region (Bolivia), with elevation, approximate area of the system, approximate location, and number of species noted for each site.

System	Elev. (m)	Approximate Area (ha)	Approximate Location	No. Spp.
Chimpa Huata Bog	2920	0.05	65˚55'W 17˚12'S	23
Incachaca Pond	2385	1	65°49'W 17°15'S	26
Laguna Khonchu - East	2620	0.07	17˚09'S 65˚56'W	12
Laguna Khonchu - West	2620	0.09	17˚09'S 65˚56'W	13
Corani Pampa Marsh	2470	0.02	65°58'W 17°06'S	26
Serranía de Siberia Marsh	2800	0.75	64°45"W 17°51'S	7

Chimpa Huata Bog

Elevation: 2920 m. Watershed: Amazon Number of species: 23
Dates visited: Jul 5, 1994; Aug 26, 1994; Feb 14, 1995; May 31, 1995; Dec 7, 1995

The Chimpa Huata Bog was a small (ca. 0.05 ha) *Sphagnum* bog located on the slopes of the Cerro Chimpa Huata, directly alongside the ancient Incan roadway leading from the community of Candelaria to the community of Corani Pampa. Although small populations of *Sphagnum* spp. were often present in seeps and in protected areas alongside rivers and streams in upper montane habitats, this was one of the few systems I encountered that possessed a well-developed floating *Sphagnum* mat. The bog mat, although fairly thick, was noticeably weaker than mats of New England bogs and frequently proved incapable of supporting a person's weight.

The bog occupied a small depression at the base of a steep section of slope. The area surrounding the bog was a mixture of relatively undisturbed forest, secondary forest, and patches of open grassland, some of which were maintained by seasonal burning. Water at the site was stained a very dark brown and had a maximum depth of about 2 meters. Sediments were organic overlying clay. The site was visited under varying hydrologic conditions: during relatively dry conditions in July and August of 1994, and under wetter conditions in February, May, and December of 1995. The bog appeared to suffer little direct anthropogenic disturbance, although livestock were observed stepping through the bog mat to drink from the system.

Incachaca Pond

Elevation: 2385 m Watershed: Amazon Number of species: 26
Dates visited: Oct 2, 1994; Oct 30, 1994; Feb 12, 1995; Apr 2, 1995; June 7, 1995; Jul 14, 1997

The Incachaca Pond was an artificial system, with an area of ca. 1.0 ha. The system was fairly shallow throughout, with a maximum depth of about 1.2 m. Water was a transparent brown. Sediments were deep and very soft. The pond received year-round inflow through a concretized channel leading from a nearby river, with outflow occurring through a small stream at the end of the pond farthest from the inflow. The terrain above the northern edge of the system was fairly steep, and undoubtedly a significant amount of runoff drained into the pond from this area during the wetter seasons.

The Incachaca Pond was the most heavily impacted of the Cloud Forest study sites. The area surrounding the Incachaca Pond formerly supported primary cloud forest, however, in recent decades the forest has been severely fragmented by human activities. During the 1950s or thereabouts, the area surrounding the pond was logged and converted to pasture as part of a program to introduce livestock production to the region. This activity was apparently unsuccessful, and only a small number of cows and pigs are now in evidence in the area. Subsequently, the largest part of the cleared land was left fallow, and these areas developed into a shrub-scrub dominated by a weedy species of *Lepechinia* (Lamiaceae). In a later development program, a large (ca. 5-10 ha) area directly upslope from the pond was planted with *Pinus radiata*. Currently, the pond and its environs are the site of a substantial amount of recreational activity, from day visitors from the nearby (ca. 2 hours) city of Cochabamba (population 900,000) who frequent the area for hiking and fishing.

Lagunas Khonchu East and West

Elevation: 2620 m Watershed: Amazon Number of species: 12/13
Dates visited: Aug 31, 1994; Feb 4, 1994; Jun 1, 1995

The Lagunas Khonchu East and West were two ponds, located about 5 km downslope from the Chimpa Huata Bog and situated alongside the same trail as that system. While the name "Lagunas Khonchu" appears on a topographical map of the area, the descriptive names "east" and "west" have been applied here to differentiate between the two systems and refer to their orientation relative to the trail.

Laguna Khonchu East was a small pond, approximately 0.07 ha in area, with a shallowly sloped basin. Laguna Khonchu West was slightly larger (ca. 0.09 ha) and was more heterogeneous, with a shallow central basin fringed by a matrix of marshy areas and small open channels at either end of the system. Maximum depth of both basins was less than 1 m. Although somewhat opaque, the water at these sites was much clearer than that of the Chimpa Huata Bog. Sediments were silt and clay. The surrounding terrestrial vegetation was relatively undisturbed primary forest, and anthropogenic disturbance at the two wetlands appeared to be minimal.

Corani Pampa Marsh

Elevation: 2470 m. Watershed: Amazon Number of species: 26
Dates visited: Sept 7, 1994; Apr 14, 1995; May 25, 1995

The Corani Pampa Marsh was a small streamside marsh. The marsh developed when streamflow was restricted by the installation of a culvert at the downstream end of the marsh. The marsh had a length of approximately 25 m and a maximum width of about 6 m. Depth of inundation ranged from shallowly inundated areas to a small pool greater than 1.5 m deep. Substrata were variable, ranging from firm sand and gravel areas along the edges, to deep, mushy sediments in the more permanently inundated areas.

Serranía de Siberia Marsh

Elevation: 2800 m Watershed: Amazon Number of species: 7
Date visited: Feb 3, 1996

The Serranía de Siberia marsh was a small *Sphagnum* dominated marsh. Although the other Cloud Forest study sites were situated on the eastern slope of the Cordillera Oriental, the Serranía de Siberia Marsh was located on the generally drier, western side of the Cordillera. Nevertheless, the area around the town of Siberia receives significant amounts of precipitation and fog during the year and undisturbed terrestrial habitats in the area typically support elfin forest with an extremely closed canopy and abundant epiphytes.

This system was situated along the "Old Highway" from Cochabamba to Santa Cruz, an unpaved road that formerly constituted the principal route between these cities. The system consisted of a small, shallow pond bordered on three sides by marshy habitat. Total area was approximately. 0.75 ha. The pond and marsh supported a variety of emergent species, particularly members of the Cyperaceae and Juncaceae. This site received a single visit in February of 1996. At this time, which was well into the rainy season, maximum depth of the pond was about 0.75 m. Despite the close proximity to the road, this system appeared to be little-disturbed.

Although a single visit to this site was insufficient for a total inventory of the flora, this system's disjunct location, as well as the presence of a number of species not encountered elsewhere, warranted the inclusion of the Serranía de Siberia Marsh as a study site.

The Chapare

Seven wetland systems were established as study sites in the Chapare (Table A.4), and field research was concentrated on these systems.

Table A.4. The Chapare Study Sites (Bolivia), with elevation, approximate area of the system, approximate location, and number of species noted for each site.

Study Site Name	Elev. (m)	Approximate Area (ha)	Approximate Location	No. Spp.
Mariposa Wetland	220	1.5	65°02'W 17°01'S	49
Ivirgarsama Marsh	200	0.7	64°50'W 17°01'S	46
Senda F Wetland	200	0.2	65°08'W 16°52'S	19
Villa Tunari Pond	300	0.3	65°26'W 17°01'S	11
Sinahota Pond	240	0.15	65°18'W 17°00'S	9
Valle de Sajta Curichi	220	0.2	64°43'W 17°07'S	6
Puerto Villarroel Laguna	200	30	64°48'W 16°49'S	6

Additional collections were made from a variety of other wetlands, including inundated roadside ditches, streams, small rivers, and seasonal ponds and pools.

Mariposa Wetland

Elevation: 220 m Watershed: Amazon Number of species: 49
Dates visited: Nov 27, 1994; Mar5, 1995; Jun 8, 1995; Nov 1, 1996

The Mariposa Wetland was located alongside the highway from the Chapare to Santa Cruz, approximately 1.5 km east of the community of Mariposa. The system consisted of two small (<0.3 ha) ponds fringed with a strip of marshy habitat. The ponds occupied shallow depressions (ca. 2 m deep) that were created when fill for an adjacent highway was excavated from the site. The marsh was situated between the ponds and the highway and was essentially a particularly wide (ca. 50 m) section of the "borrow canals" that typically flanked the highway and other roads in the region. Although these canals extend for many kilometers, investigations of the Mariposa "system" were limited to an approximately 200 m long section of marsh, centered on the two ponds. A small, seasonal stream delineated the western edge of the study site. Total study site area was ca. 0.8 ha.

In contrast to many similar small bodies of water in the Chapare, the ponds contained water throughout the year, suggesting that they received some subsurface water inflow. During the dry season, standing water disappeared from most areas of the marsh, and soil conditions varied from fairly dry to saturated during this period. Although this system undoubtedly received substantial inputs of runoff from adjacent uplands during the rainy season, there were no large rivers near the site. Thus, the system did not appear to receive the periodic influxes of water-borne sediment that were characteristic of many of the Chapare's aquatic habitats.

Ivirgarsama Marsh

Elevation: 220 m. Watershed: Amazon Number of species: 46
Dates visited: Feb 23, 1996; May 10, 1996; Oct 27, 1996

The Ivirgarsama Marsh was located alongside the unpaved road that connected the highway to Santa Cruz with the town of Puerto Villarroel. The system was composed of a small (ca. 0.2 ha), shallow pond, with an adjoining (ca. 0.5 ha) marshy area in the area between the pond and the road. Smaller sections of marsh were also present along the other edges of the pond. A narrow stream flowed through the system, entering the pond at its southern end and discharging through the marsh at the far end of the system. As with the Mariposa Wetland, the marsh was essentially a widening of a typical roadside borrow canal, however the pond at the Ivirgarsama Marsh appeared to be of natural origin.

The Ivirgarsama Marsh was unique among the Chapare study sites because of the well-developed floating mats of vegetation that were present along the edges of the pond. Although floating mats are a characteristic feature of aquatic habitats throughout most parts of the Bolivian lowlands, they appeared to be uncommon in the Chapare.

Senda F Marsh
Elevation: 220 m. Watershed: Amazon Number of species: 19
Dates visited: Jun 1, 1994; Nov 11, 1994; Mar 4, 1995.

The Senda F Marsh was located alongside the unpaved road that originated in the town of Chimoré, proceeding north through a series of small communities (Comunidades Senda A-Senda F) until it reached the zone of influence of the Río Chapare. The Senda F Marsh was contiguous with the borrow canals which flanked the road. The area surveyed was approximately 80 m long with a maximum width of about 15 m on either side of the road. A small stream flowed into the southeast corner of the marsh and a number of small, fairly deep pools were present. Thus, habitat heterogeneity was much higher than was typical for the region's roadside canals. Water levels at the site fluctuated seasonally and standing water was absent from parts of the marsh during the driest portions of the year.

Villa Tunari Pond
Elevation: 300 m. Watershed: Amazon Number of species: 11
Dates visited: Nov 12, 1994; Mar 5, 1995; Jun 8, 1995

The Villa Tunari Pond was a small pond located alongside the Cochabamba-Santa Cruz highway, approximately 4 km east of the town of Villa Tunari. Due to its location at the start of the ascent of the Cordillera Oriental (Eastern Range) of the Andes, this system was at a slightly higher elevation (300 m) than the other Chapare sites. During the dry season, the pond basin occupied an area of approximately 0.3 ha with a maximum depth of about 2.0 m. During the rainy season, large portions of the upland areas adjacent to the pond become shallowly inundated and the limits of the "system" were indistinct. Water levels dropped significantly during the dry season. Although the system was never observed to be entirely without standing water, it seems likely that this might occur during dry years.

Sinahota Pond

Elevation: 240 m Watershed: Amazon Number of species: 9
Dates visited: Nov 12, 1994; Jun 8, 1995

The Sinahota Pond was another small (approximately 0.15 ha), seasonal pond situated alongside the Cochabamba-Santa Cruz highway, ca. 2 km west of the town of Sinahota. Maximum depth during the rainy season was about 2.0 m; during the dry season the system dried out completely. The basin was fairly steep-sided and, in contrast to the Villa Tunari Pond, inundation did not appear to extend to the surrounding areas during high water stages.

Valle de Sajta Curichi

Elevation: 210 m. Watershed: Amazon Number of species: 6
Date visited: Mar 20, 1995

In the Bolivian lowlands, a "curichi" is a system that occupies a section of a former river channel, and which normally does not dry down completely during the dry season (Beck 1984). The Valle de Sajta Curichi consisted of two small ponds separated by a narrow (10 m) strip of land. The ponds originally were part of a river channel, most likely the nearby Río Zabala, and developed into their present form after being stranded due to channel migration. This system was said to contain water year-round, and the ponds appeared to be connected by an subterranean passage.

Puerto Villarroel Laguna

Elevation: 190 m. Watershed: Amazon Number of species: 6
Dates visited: Mar 19, 1995; Nov 1, 1996

The Puerto Villarroel Laguna, a large curichi, was the largest and deepest of the Chapare study sites. Despite being located in a region of "white-water' (*sensu* Sioli 1975), the water was stained dark from organic acids. Maximum depth was difficult to determine, but appeared to be at least 4 m. The lake's area was estimated using the cut and weight method (Lind 1985) on a topographical map (scale 1:100,000). By this method, the system was found to occupy 70 ha, however during visits to the site, the area was visually estimated at about 15 ha. As a compromise, 30 ha was selected as a rough approximation of the system's size.

Andean Piedmont

Two study sites were established in the Andean Piedmont region (Table A.5). A small amount of additional fieldwork was conducted in the region, principally in seasonal ponds, riparian wetlands, and seasonally inundated grasslands.

Table A.5. Study sites in the Andean Piedmont of Santa Cruz (Bolivia), with elevation, approximate area of the system, approximate location, and number of species noted for each site.

System	Elev. (m)	Approximate Area (ha)	Approximate Location	No. Spp.
Bermudez Curichi	430	15	63°16'W 17°46'S	70
Viru Viru Wetland	430	15	63°16'W 17°40'S	75

Bermudez Curichi
Elevation: 430 m Watershed: Amazon Number of species: 70
Dates visited: May 6, 1995; May 8, 1995; Jun 3, 1995; Nov 25, 1996; June 26, 1997; July 28, 1998

The Curichi at Bermudez was a crescent-shaped system, located in the grassy plains west of the outskirts of the city of Santa Cruz. The Bermudez Curichi occupied a section of the former channel of the Río Piray–which currently passes a kilometer, or so, to the east of the system. After the Río Piray shifted its course, the system appears to have been no more than a shallow pond. At some point, however, a dike was constructed along the low end of the basin, deepening the system appreciably. Total area of the system was about 15 ha. Inputs from rainfall and groundwater through a hillside seep at the western end of the system were sufficient to fill and maintain the basin to the level of the overflow in the dike (maximum depth ca. 2.5 m). When first visited in 1995, the Curichi was a magnificent (from a botanical point of view), rich system, however it has since been significantly altered (see below). The following description of the flora represents the system before these alterations.

The vegetation of the Bermudez Curichi was rich (71 spp.) and structurally complex. The eastern end of the system exhibited an extremely marked zonation. Moving from open water toward the upper limits of the system, the zones were: 1) deepest water dominated by submerged species; 2) shallower water dominated by rooted macrophytes with floating leaves; 3) 1-3 distinct zones dominated by different emergent herbaceous species; and, 4) a shrub-dominated zone. In many areas, the zone closest to open water was occupied by loosely coalesced floating mats of vegetation. The central portion of the Curichi was more shallowly inundated than was either end. During the rainy season, this central area was inundated to a depth of ca. 1.0 m; during the dry season standing water was scarce or absent, although the soil appeared to remain saturated. The western end of the Curichi was similar to that of the eastern end, although zonation of the vegetation was not nearly so evident.

Submerged species were *Mayaca longipes* and *M. fluviatilis* (Mayacaceae), and *Bacopa aquatica* (Scrophulariaceae). "Nymphaeaceous" species (*i.e.*, rooted macrophytes with floating leaves) were particularly well-represented. Species were *Sagittaria guayanensis* (Alismataceae), *Hydrocleys nymphoides* and *H. parviflora* (Limnocharitaceae), *Nymphoides indica* (Menyanthaceae), and *Ludwigia sedoides* (a rooted macrophyte with its upper leaves crowded toward the tip of the stem and forming floating "rosettes"). Surprisingly, no free-floating species were observed, although the free-swimming herb *Utricularia foliosa* (Lentibulariaceae) was abundant in some parts of the system. Species which formed loosely-coalesced floating mats were *Eichhornia azurea* and *P. subovata* (Pontederiaceae), and, to a lesser degree, *Hydrocotyle bonariensis* (Apiaceae).

Emergent species were particularly well-represented. The most abundant emergent herbaceous species were *Eleocharis interstincta, Fuirena umbellata,* and *Scleria setuloso-ciliata* (Cyperaceae), *Syngonanthus caulescens* (Eriocaulaceae), *Limnocharis flava* (Limnocharitaceae). *Thalia geniculata* (Marantaceae), *Andropogon bicornis. Homolepis aturensis,* and *Panicum schwackeanum* (Poaceae), and *Polygonum ferrugineum* (Polygonaceae). Emergent shrubs and shrubby herbs were *Aeschynomene fluminensis* (Fabaceae). *Hydrolea spinosa* (Hydrophyllaceae), *Rhynchanthera grandiflora* (Melastomataceae). and *Ludwigia martii* (Onagraceae). Climbing species were not abundant, nor diverse, and were represented by only two species *Aniseia martinicensis* and *Ipomoea regnellii* (Convolvulaceae). A number of noteworthy species were encountered in the Bermudez Curichi *Apalanthe granatensis, Bacopa aquatica, Ludwigia martii,* and *Mayaca longipes* (see Appendix E).

As noted, the Bermudez Curichi has been subjected to significant disturbance. In 1996, the owner of the land initiated a process to deepen the system by the breaching the dike, thereby draining much of the basin. A number of small, primarily seasonal pools remained, however, and these supported some of the species which had been abundant before the disturbance. Additionally, weedy hydrophilic species, such as *Torulinium odoratum* and *Kyllinga odorata* (Cyperaceae), became established around pool edges. The system remained in this condition for approximately a year, after which the dike was repaired and the basin allowed to refill. It was not apparent whether or not the basin was deepened during this process. Of note, some of the more noteworthy species, such as *Mayaca longipes* and *Bacopa aquatica*, which were not observed at the site during the "drying down period", were both abundant after the dike had been restored. Furthermore, two submerged species not observed before modifications to the system, *Cabomba furcata* (Cabombaceae) and *Apalanthe granatensis* (Hydrocharitaceae), were both common afterwards.

Viru Viru Wetland
Elevation: 430 m Watershed: Amazon Number of species: 75
Dates visited: Jun 4, 1995; Jan 14, 1996; May 25, 1996; Aug 2, 1996; Jun 28; 1997

The Viru Viru Wetland was a marsh located near the Santa Cruz International Airport. The wetland had an area of approximately 15 ha, and was structurally complex incorporating a variety of permanently and seasonally inundated marshy habitats, and a small (ca. 0.75 ha), but fairly deep (maximum depth > 2.5 m) pond. The system was also hydrologically complex, with some areas fed by runoff and groundwater from adjacent slopes and other sections apparently relying on rainwater as the major water input.

The Viru Viru Wetland supported a rich flora (75 spp.), with a particularly rich pteridophyte component (11 spp.). Common emergent herbaceous species were *Commelina diffusa* (Commelinaceae), *Eleocharis minima* and *E. mutata* (Cyperaceae), *Imperata contracta*, *Leersia hexandra*, and *Luziola peruviana* (Poaceae), *Polygonum punctatum* and *P. acuminatum* (Polygonaceae), and *Acrostichum danaeifolium* and *Pityrogramma trifoliata* (Pteridaceae). Emergent shrubs and shrubby herbs were represented by *Aeschynomene sensitiva* (Fabaceae), *Hydrolea spinosa* (Hydrophyllaceae), *Hibiscus sororius* (Malvaceae), *Ludwigia peruviana* (Onagraceae), and *Piper aduncum* and *P. gaudichaudianum* (Piperaceae).

Floating mats, composed principally of either *Oxycaryum cubense* or *Typha domingensis*, were characteristic of many areas. These provided a substratum for colonization by other species, and were often sufficiently buoyant and adherent to support a person's weight. Species commonly associated with floating mats, either as secondary colonizers or growing in openings in the mat matrix, were *Hydrocotyle ranunculoides* (Apiaceae), *Begonia fischeri* (Begoniaceae), *Utricularia gibba* (Lentibulariaceae), *Erythrodes* sp. and *Xylobium* sp. (Orchidaceae), *Pityrogramma calomelanos* (Pteridaceae), and *Thelypteris interrupta* and *T. serrata* (Thelypteridaceae). Small individuals of the arborescent *Sapium glandulosum* (Euphorbiaceae) grew on *Typha* mats in one area.

Free-floating macrophytes were common and fairly diverse. Species were *Limnobium laevigatum* (Hydrocharitaceae), *Lemna aequinoctialis* and *L. valdiviana* (Lemnaceae), *Ludwigia helminthorrhiza* (Onagraceae), *Ceratopteris pteridoides* (Pteridaceae), and *Azolla mexicana* and *Salvinia minima* (Salviniaceae). Additionally, the free-floating liverwort *Ricciocarpus natans* (Ricciaceae) was locally abundant in one area. Nymphaeaceous species were poorly represented, with *Hydrocleys nymphoides* (Limnocharitaceae) the sole representative of this life-form. In contrast to the Bermudez Curichi, which supported a rich submerged flora, no submerged species were observed at the Viru Viru wetland.

Climbers were common, with Asclepiadaceae Indet., *Mikania congesta* (Asteraceae), *Ipomoea ramosissima* and *Merremia umbellata* (Convolvulaceae), *Centrosema pubescens* and *Vigna adenantha* (Fabaceae), and *Odontocarya* sp. (Menispermaceae) representative species. Common species in the seasonally inundated transition zone along the upper edge of the system were *Pycreus bipartitus* (Cyperaceae), *Teucrium vesicarium* (Lamiaceae), *Ammannia latifolia* (Lythraceae), *Anagallis pumila* (Primulaceae), and *Stemodia hyptoides* (Scrophulariaceae). Despite the rich flora, the only species of note encountered at the Viru Viru Wetland was the robust emergent fern *Acrostichum danaeifolium* (see Appendix E).

Conspicuous seasonal changes in floristic composition were observed in parts of the system. During the rainy season, some areas were nearly completed covered by free-floating macrophytes. These species disappeared as water levels subsided, with the areas then supported abundant emergent herbs.

The Viru Viru Wetland was located in a fairly high population area, nevertheless, direct anthropogenic disturbance did not appear to be significant. The edges of the system were used for dumping refuse, but few impacts beyond this were noted.

White-water Floodplain

Three study sites–two lakes, and one basin swamp–were established in the White-water Floodplain region (Table A.6). Additionally, general collections were made from other wetlands in the region, principally streams, rivers, roadside marshes, and curichis and ponds.

Table A.6. Study sites in the White-water Floodplain Region (Bolivia), with elevation, approximate area of the system, approximate location, and number of species noted for each site.

System	Elev. (m)	Approximate Area (ha)	Approximate Location	No. Spp.
Riberalta Ciénaga	170	150	66°03'W 11°02'S	81
Laguna Tumi Chuqua	170	300	66°11'W 11°08'S	34
Laguna Suarez	160	560	64°52'W 14°53'S	97

Riberalta Ciénaga
Elevation: 170 m Watershed: Amazon Number of species: 81
Dates visited: Oct 11-13, 1996; Jul 5, 1997

The Riberalta Ciénaga (swamp) was a large (150 ha), steep-sided basin swamp, located on the outskirts of the town of Riberalta in northern Bolivia. The system occupied a section of the former channel of the Río Beni. Rivers can be very dynamic in this region, but the Río Beni clearly migrated long ago and there were no indications that the Ciénaga is ever flooded by overflow from the river. The Río Beni was a whitewater system, however, owing to the buildup of acids from the slow decomposition of accumulated plant matter, the Riberalta Ciénaga water was better classified as a "secondarily blackwater" system.

The flora was quite rich (81 spp). Large portions of the system support swamp forest, many parts of which appeared to be inundated year-round. Arborescent species were *Tabebuia insignis* (Bignoniaceae), *Diospyros nur* (Ebenaceae), *Hevea brasiliensis* (Euphorbiaceae), *Macrolobium acaciifolium* and *Pterocarpus santalinoides* (Fabaceae), *Hasseltia floribunda* (Flacourtiaceae), *Cariniana* sp. (Lecythidaceae), *Lueheopsis hoehnei* (Tiliaceae), and *Mauritia flexuosa* (Arecaceae). Shrubs and shrubby perennials were fairly abundant, particularly along the edge of the system, and were well-represented. Species were *Combretum lanceolatum* (Combretaceae), *Hyptis lacustris* (Lamiaceae), *Aeschynomene ciliata*, *A. fluminensis*, and *Mimosa schrankioides* (Fabaceae), *Hibiscus furcellatus* (Malvaceae), *Cybianthus longifolius* (Myrsinaceae), and *Ludwigia nervosa* (Onagraceae).

Floating mats occurred throughout the system, both in areas below the canopy, and in non-forested areas. *Eleocharis acutangula*, *Fuirena umbellata*, and *Oxycaryum cubense* (Cyperaceae) were the most common mat-forming species, with *F. umbellata* the most abundant, particularly in areas beneath the canopy. *Eichhornia azurea* (Pontederiaceae), another mat-forming species which is often abundant in Bolivian lowland aquatic habitats, was not observed in Riberalta Ciénaga, nor were any other members of the Pontederiaceae. Their exclusion was most likely due to the system's acidic conditions. Species commonly associated with floating mats were *Chromolaena laevigata*, *Eclipta prostrata*, *Enhydra anagallis*, and *Pacourina edulis* (Asteraceae), *Begonia fischeri* (Begoniaceae), *Cyperus haspan* (Cyperaceae), *Irlbachia alata* (Gentianaceae), *Sinningia sceptrum* (Gesneriaceae), *Habenaria* aff. *repens* and *H. sartor* (Orchidaceae), *Panicum grande* (Poaceae), and *Alectra aspera* (Scrophulariaceae).

Common emergent herbs were *Erechtites hieracifolia* (Asteraceae), *Urospatha sagittifolia* (Araceae), *Rhynchospora* corymbosa (Cyperaceae), *Andropogon bicornis*, *Homolepis aturensis*, *Isachne polygonoides*, and *Panicum hylaeicum* (Poaceae), Polygonum *acuminatum* (Polygonaceae), *Thelypteris interrupta* (Thelypteridaceae), and *Xyris laxifolia* (Xyridaceae). One portion of the basin was characterized by a channel and hummock topography, with the emergent fern *Thelypteris serrata* (Thelypteridaceae) the dominant species. The perennial herb *Hypolytrum longifolium* (Cyperaceae) was common in seasonally inundated areas along the system edge.

Free-floating species were *Pistia stratiotes* (Araceae), *Limnobium laevigatum* (Hydrocharitaceae), *Lemna valdiviana* and *Wolffiella lingulata* (Lemnaceae), *Azolla caroliniana*, *Salvinia auriculata* and *S. minima* (Salviniaceae). The free-floating liverwort, *Ricciocarpus natans* (Ricciaceae) was also present. No rooted macrophytes with floating leaves were observed.

Climbers were particularly diverse, with *Rhabdadenia macrostoma* (Apocynaceae), *Mikania congesta* (Asteraceae), *Combretum laxum* (Combretaceae), *Ipomoea regnellii* and *Tetralocularia pennellii* (Convolvulaceae), *Melothria pendula* (Cucurbitaceae), *Senna pendula* and *Vigna longifolia* (Fabaceae), *Odontocarya tamoides* (Menispermaceae), and *Cissus erosa* (Vitaceae) representative species. The semi-climbing sedge, *Scleria flagellum-nigrorum* (Cyperaceae) formed dense, nearly impenetrable tangles in some parts of the transition between wetland and upland.

Access to the swamp was frequently quite difficult and moving through the system was particularly trying. Therefore, many parts of the system were not investigated. Arborescent species were most likely particularly under-represented in the site checklist. A single noteworthy species, *Diospyros nur*, was observed at this system (see Appendix E).

The Riberalta Ciénaga is fringed on two sides by the town of Riberalta; however, direct human impacts to the system appeared to be minimal. Among local residents, the system was reputed to contain enormous anacondas (*e.g.*, 15 m long, with diameters greater than a meter). Fortunately, I was unable to corroborate their existence.

Laguna Tumi Chuqua
Elevation: 170 m Watershed: Amazon Number of species: 34
Approximate center of the system: 66°11'W 11°08'S
Dates visited: Oct 14, 1996; Jul 8, 1997

Laguna Tumi Chuqua was a large (ca. 300 ha) oxbow lake, located in the northern Departamento of Beni, approximately 40 km south of the town of Riberalta. As with the Riberalta Ciénaga, the system occupied a section of a former channel of the Río Beni. During high water stages, the Río Beni periodically breaches the uplands that separate the laguna from the current main channel. Local residents indicated that this occurs approximately every 12-15 years. During the initial site visit, the lake water possessed the crystalline green color that was characteristic of numerous lakes viewed during overflights of the region. The second visit to the site occurred during a particularly rainy year, shortly after the Río Beni had overflowed into the laguna. There were abundant sediments in suspension, and the water had much more the appearance of a "whitewater" system.

Species richness was low for an Amazonian system of this size (34 spp.), although this may be partially accounted for by the site having received only two visits. The genus *Ludwigia* was particularly well-represented, with six species.

The system contained numerous floating mats; these were generally weakly coalesced, and were not extensive. Mat-forming species were *Leersia hexandra* and *Paspalum repens* (Poaceae), and *Eichhornia crassipes* and *Pontederia rotundifolia*

(Pontederiaceae). Some mats were sufficiently adherent to support secondary colonizers. These included *Cyperus surinamensis* and *Torulinium odoratum* (Cyperaceae), *Limnocharis* flava (Limnocharitaceae), *Ludwigia leptocarpa* (Onagraceae), *Phlebodium decumanum* (Polypodiaceae), *Sphenoclea zeylanica* (Sphenocleaceae), and *Thelypteris interrupta* (Thelypteridaceae).

Submerged macrophytes (*e.g.*, *Potamogeton pusillus*, Potamogetonaceae; *Najas arguta*, Najadaceae) were abundant in depths up to ca. 1.5 m during the first visit to Laguna Tumi Chuqua. During the second visit (*i.e.*, after sediment-rich water from the Río Beni had poured into the system), however, no submerged species were encountered. Free-floating species were generally rare and were poorly represented, with *Ludwigia helminthorrhiza* (Onagraceae), and *Salvinia auriculata* and *S. minima* (Salviniaceae) the only species noted. *Nymphaea amazonum* (Nymphaeaceae) and *Ludwigia sedoides* (Onagraceae) were the sole "Nymphaeaceous" species.

Due in part to the steep basin sides, emergent species were generally not very abundant. In general, these were restricted to marshy edge habitats, and in seasonally inundated areas along the banks. Emergent herbaceous species were *Gymnocoronis spilanthoides* (Asteraceae), *Ludwigia hyssopifolia* (Onagraceae), *Dactyloctenium aegyptium* (Poaceae), *Polygonum acuminatum* (Polygonaceae), and *Lindernia crustacea* (Scrophulariaceae). Shrubs and shrubby perennials were common in marshy edge habitats, with *Mimosa xanthocentra* and *Sesbania exasperata* (Fabaceae), *Cuphea melvilla* (Lythraceae), *Hibiscus peruvianus* (Malvaceae), and *Ludwigia affinis* (Onagraceae) representative species. Climbers were abundant in a few areas, yet diversity in this life-form was low, with *Mikania congesta* (Asteraceae) and *Centrosema vexillatum* (Fabaceae) the sole species noted. Despite the relatively small flora, Laguna Tumi Chuqua possessed two noteworthy species: *Potamogeton pusillus* (Potamogetonaceae) and *Ludwigia hyssopifolia* (Onagraceae) (see Appendix E).

A small community was present along the eastern end of Laguna Tumi Chuqua, however, anthropogenic impacts to the system appeared to be minimal.

Laguna Suarez
Elevation: 160 m Watershed: Amazon Number of species: 97
Approximate center of the system: 64°52'W 14°53'S
Dates visited: Jun 15, 1996; Jun 17-20, 1996; Aug 4, 1996; Aug 6, 1996; Nov 18, 1996; July 1-2, 1997

Laguna Suarez was a large (ca. 600 ha) lake located in the southeastern corner of the Llanos de Moxos, the seasonally inundated savannas of the central Departamento of Beni. Laguna Suarez belongs to the class of "oriented fault lakes"– lacustrine systems with strait edges, which are oriented in a SW to NE alignment (Allenby 1988)– which characteristically occur in the Beni Basin. Despite it's large area, Laguna Suarez was extremely shallow throughout, with maximum depths during the rainy season said to be no more than about 1.5 m. The basin contains water year-round; seasonal fluctuations in water levels appeared to small scale (ca. 0.5 m). The water was an opaque brown, and contained abundant sediments in suspension. Laguna Suarez was bordered on three sides by extensive inundated savannas, dominated by the tall emergent herb *Cyperus giganteus* (Cyperaceae). In a number of areas, more deeply inundated marshy habitats dominated by species other than *C. giganteus*, were present between the lake basin and the *C.*

giganteus marsh. Additionally, small amounts of seasonally inundated gallery forest occupied a raised spit of land along the western edge of the system.

Laguna Suarez possessed a rich flora (97 spp.). Much of the basin was fringed with floating mats. The most abundant mat-forming species was *Panicum elephantipes* (Poaceae), which formed extensive mats along the northern and eastern basin edges. Most often, these were loosely coalesced, but in some areas the mats were sufficiently adherent to permit secondary colonizers to become established. Other mats were dominated by *Oxycaryum cubense* (Cyperaceae), *Eichhornia azurea, E. crassipe*s, and *Pontederia rotundifolia* (Pontederiaceae), with *Hydrocotyle ranunculoides* (Apiaceae), *Hymenachne donacifolia* and *Paspalum repens* (Poaceae) present in lesser amounts. Species associated with the mats were *Gymnocoronis spilanthoides* (Asteraceae), *Begonia fischeri* (Begoniaceae), *Cyperus haspan* and *Torulinium odoratum* (Cyperaceae), *Ludwigia leptocarpa* (Onagraceae), *Habenaria* aff. *repens* (Orchidaceae), *Andropogon bicornis* (Poaceae), *Pityrogramma calomelanos* (Pteridaceae), *and Alectra aspera* (Scrophulariaceae). Despite the shallow basin, no submerged species were noted. Likewise, rooted species with floating leaves were nearly absent, with *Ludwigia sedoides* (Onagraceae) the sole representative.

Free floating species were well-represented. Within the lake basin, these were generally restricted to small "pools" formed by openings in the floating mats, and in among the small interstices between the mat-forming species. Representative free-floating species were *Alternanthera philoxeroides* (Amaranthaceae), *Pistia stratiotes* (Araceae), *Limnobium laevigatum* (Hydrocharitaceae), *Lemna valdiviana* and *Wolffiella* *lingulata* (Lemnaceae), *Ludwigia helminthorrhiza* (Onagraceae), *Ceratopteris pteridoides* (Pteridaceae), and *Azolla mexicana, Salvinia auriculata* and *S. minima* (Salviniaceae). The free-floating liverwort *Ricciocarpus natans* (Ricciaceae) was also present.

Arborescent species were fairly common. *Erythrina fusca* (Euphorbiaceae) grew in the shallows and in the adjacent marshes; *Laetia americana* (Flacourtiaceae) was occasional in the latter habitat. Other arborescent species were *Ocotea cernua* and *Nectandra amazonum* (Lauraceae) and an unidentified Fabaceae. Shrubs and shrubby perennials were abundant in many areas. Common species were *Aeschynomene fluminensis, A. sensitiva, Senna alata* and *Sesbania exasperata* (Fabaceae), *Hydrolea spinosa* (Hydrophyllaceae), *Hyptis lorentziana* (Lamiaceae), and *Rhynchanthera novemnervia* (Melastomataceae).

Climbers were abundant and particularly speciose. Representative species were *Rhabdadenia* sp. (Apocynaceae), *Sarcostemma clausum* (Asclepiadaceae), *Mikania congesta* (Asteraceae), *Aniseia martinicensis, Ipomoea rubens* and *Merremia umbellata* (Convolvulaceae), *Cayaponia citrullifolia* (Cucurbitaceae), *Vigna lasiocarpa* (Fabaceae), *Odontocarya tamoides* (Menispermaceae), *Paullinia pinnata* (Sapindaceae), and *Cissus spinosa* (Vitaceae).

Emergent herbaceous species were most abundant in marshy habitats, but were also present in the basin, most often in shallowly inundated areas that lacked floating mats. Common emergent herbs were *Echinodorus grandiflorus* subsp. *aureus* and *E. macrophyllus* subsp. *scaber* (Alismataceae), *Enhydra anagallis* (Asteraceae), *Canna glauca* (Cannaceae), *Rhynchospora* cf. *gigantea* and *R. corymbosa* (Cyperaceae), *Caperonia castaneifolia* (Euphorbiaceae), *Ludwigia decurrens* (Onagraceae), *Hymenachne amplexicaulis*, *Panicum mertensii*, and *Steinchisma hians* (Poaceae), *Polygonum acuminatum*, *P. ferrugineum*, *P. hispidum*, and *P. punctatum* (Polygonaceae), and *Thelypteris interrupta* (Thelypteridaceae). Two tall emergents, *Thalia geniculata* (Marantaceae) and *Ipomoea alba* subsp. *fistulosa* (Convolvulaceae), were frequently present in the transition between the *Cyperus giganteus* marsh and more open marshy areas.

Various species were strongly associated with shallow water along the basin edge; these increased in abundance as water levels subsided during the dry season. Representative species were *Xanthosoma* cf. *sagittifolium* (Araceae), *Cyperus imbricatus* and *Eleocharis interstincta* (Cyperaceae), *Heliconia marginata* (Heliconiaceae), *Marsilea* sp. (Marsileaceae), *Panicum dichotomiflorum* (Poaceae), and *Sphenoclea zeylanica* (Sphenocleaceae).

Some areas supported markedly different floras during different hydrologic seasons. For example, at the end of the rainy season one of the marshes adjoining the lake was covered with free-floating (principally, *Limnobium laevigatum* and *Salvinia auriculata*) and free-swimming (*Utricularia gibba*) species, intermixed with young plants of *Oxycaryum cubense*. During the dry season, this same area was dominated by the spiky-leaved emergent herb *Pacourina edulis* (Asteraceae).

Despite the rich flora at Laguna Suarez, no rare or particularly uncommon species were encountered. Laguna Suarez was subjected to low levels of anthropogenic disturbance. The system was situated about 6 km to the south of the city of Trinidad, and portions of the system were used for recreation–primarily swimming and fishing–however, the impacts from these activities appeared to be minimal. The vegetation of the lake was directly impacted by livestock, which were periodically herded into the system to graze, and by logging (selective cutting) in gallery forest along system edges.

Chiquitanía

Seven study sites were established in the Chiquitanía region: one large pond with associated marsh, two bahías, one basin swamp, one riparian wetland, one streamside marsh, and one curichi (Table A.1).

Table A.7. Study sites in the Chiquitanía Region (Bolivia), with elevation, approximate area of the system, approximate location, and number of species noted for each site.

System	Elev. (m)	Approximate Area (ha)	Approximate Location	No Spp.
Concepción Wetland	485	10	62°01'W 16°08'S	70
Huanchaca Arroyo	760	0.04	65°56'W 17°16'S	24
La Toledo Curichi	220	6	61°8'W 14°42'S	42
Bahía Toledo	210	150	61°07'W 14°42'S	72
Río Paraguá	210	0.5	61°10'W 14°40'S 61°10'W 14°37'S	40
Cuatro Vientos Palm Swamp	205	690	61°11'W 14°32'S	50
Lago Caimán	200	575	60°55'W 13°35'S	80

Additionally, general collections were made from other wetlands in the region, including seasonally inundated gallery forest, streams, rivers, roadside marshes and pools, and curichis and ponds. Some particularly useful collections were made in the inundated savannas in the La Toledo and Flor de Oro areas.

Concepción Wetland

Elevation: 485 m Watershed: Amazon Number of species: 70
Dates visited: Sep 6, 1995; Aug 20, 1996; Dec 4, 1996; Jun 18, 1998

The Wetland at Concepción was a small (ca. 10 ha) wetland complex, located alongside the unpaved highway leading from the town of Concepción to San Ignacio de Velasco. The system was composed of two ponds, separated by a deeply inundated (ca. 1.5-2.0 m) marsh. The wetland was bisected by a road which was raised well above water levels, and the two halves of the system were interconnected through a single culvert. Additional marshy habitat was present around the edges of both ponds. A stream passed through the system; year round flow was evident. Annual variation in water levels was on the order of 2.5 m (as judged from the high-water mark on pilings in the back pond). The ponds and deeply inundated sections of marsh contained water year round, although standing water was absent from the edges of the system during the dry season. Nevertheless, soil conditions remained moist to saturated in many edge areas.

The Concepción Wetland supported a rich flora (70 spp.). The predominant vegetation was markedly different in the two ponds. The front (adjacent to the highway) pond was dominated by large populations of the emergent herb *Pontederia cordata* subsp. *ovalis* (Pontederiaceae), which in deep water areas formed loosely-coalesced floating mats. At times, these were sufficiently buoyant and had accumulated sufficient sediment to be colonized by other species. Species associated with floating mats of *Pontederia* *cordata* subsp. *ovalis* were *Utricularia gibba* (Lentibulariaceae), *Habenaria* aff. *repens* (Orchidaceae), and *Polygonum meisnerianum* (Polygonaceae). The back pond was characterized by floating mats of *Eleocharis quadrangulata* (Cyperaceae), a common mat-forming species. Species associated with floating mats of *Eleocharis acutangula* were *Echinodorus bolivianus* and *E. grandiflorus* (Alismataceae), *Erechtites hieracifolia* (Asteraceae), *Begonia fischeri* (Begoniaceae), *Pycreus lanceolatus* (Cyperaceae), *Caperonia palustris* (Euphorbiaceae), *Mayaca sellowiana* (Mayacaceae), *Pterolepis glomerata* (Melastomataceae), *Ludwigia peploides* and *L. torulosa* (Onagraceae), *Erythrodes* sp. (Orchidaceae), *Bacopa salzmanii* and *B. tweedii* (Scrophulariaceae), *Thelypteris interrupta* (Thelypteridaceae), and *Xyris laxifolia* (Xyridaceae).

Scattered arborescent species were present, and were represented by *Mauritia flexuosa* (Arecaceae), *Tabebuia insignis* (Bignoniaceae), *Sapium glandulosum* (Euphorbiaceae), *Ocotea cernua* (Lauraceae), and *Myrsine umbellata* (Myrsinaceae). The sub-arborescent herb, *Philodendron bipinnatifidum* (Araceae) was a conspicuous component, growing on small hummocks in various parts of the system. The wetland fern, *Thelypteris serrata* (Thelypteridaceae) was frequently present on the hummocks. Shrubs and shrubby perennial species were *Desmodium subsecundum* and *Mimosa* cf. *pigra* (Fabaceae), *Hydrolea spinosa* (Hydrophyllaceae), *Adenaria floribunda* (Lythraceae), *Hibiscus sororius* (Malvaceae), *Rhynchanthera novemnervia* (Melastomataceae), *Ludwigia leptocarpa* and *L. martii* (Onagraceae), and *Paullinia pinnata* (Sapindaceae).

A number of life-forms were poorly represented. Submerged species were *Cabomba furcata* (Cabombaceae) and *Mayaca sellowiana* (Mayacaceae). The latter, however, was more frequently observed growing in interstices in the *Eleocharis acutangula* mats. The sole free-floating species observed was *Pistia stratiotes* (Araceae). This species was abundant in the front half of the system, and was observed serving as the substratum for germinating seedlings of an undetermined species of Cyperaceae (the "epiphytic" pathway of floating mat formation, *sensu* Tur 1965; Tur 1969). The free-swimming macrophyte, *Utricularia gibba* (Lentibulariaceae) was abundant in both halves of the system. The sole Nymphaeaceous species was *Nymphaea amazonum* subsp. *amazonum* (Nymphaeaceae). Climbers were also poorly represented, with *Vigna longifolia* (Fabaceae) and *Smilax fluminensis* (Smilacaceae) the only species noted.

Emergent herbs were abundant, particularly along the edges of the system. Common species were *Pityrogramma calomelanos* (Adiantaceae), *Eclipta prostrata* (Asteraceae), *Canna glauca* (Cannaceae), *Carex* sp., *Cyperus haspan, C. meyenianus, Eleocharis mutata, Rhynchospora* cf. *scutellata, R. corymbosa, Scleria macrophylla* and *S. mitis* (Cyperaceae), *Hyptis recurvata* (Lamiaceae), *Andropogon bicornis* and *Panicum laxum* (Poaceae), *Polygonum acuminatum* and *P. punctatum* (Polygonaceae), and *Typha domingensis* (Typhaceae).

Species of note at the Concepción Wetland were *Ludwigia martii, Ludwigia torulosa,* and *Carex* indet. (see Appendix E). The system experienced some perturbation from human activities, principally bathing and washing of clothes. The area between the edge of the back pond and the road were periodically trimmed or grazed. Additionally, the back pond was almost certainly used at times for watering cattle.

Huanchaca Arroyo

Elevation: 760 m Watershed: Amazon Number of species: 24
Date visited: Aug 16, 1996

The "Huanchaca Arroyo" was a stream situated on the Serranía de Huanchaca, the massive, steep-sided plateau which forms the eastern border of Noel Kempff National Park. This plateau, known locally as the "Meseta", is approximately 150 km long with a maximum width of about 50 km (Litherland and Power 1989), and a maximum elevation of about 900 m (Killeen 1996).

The stream was generally fairly narrow (ca. 1-2 m), widening in a few areas to form small, still pools. Although the stream was most often shallow, maximum depths reached 1.5 m in a few pools. The bottom varied between sand and exposed bedrock, although some of the deeper pools possessed accumulations of sediment and organic material. Bank topography, while generally steep, was variable; at times being sufficiently low and gradual to allow the seasonal flooding of small areas adjacent to the channel. The surrounding area was open savanna with scattered trees, corresponding to Campo Limpio *sensu* Killeen (1996). An approximately 200 m section of the stream was surveyed.

The Huanchaca Arroyo possessed a rich flora (24 spp.) for such a small study area. Floristic composition varied among the different habitats. Deeper pools were dominated by the rheophytic herb *Utricularia neottioides* (Lentibulariaceae), and by the submerged form of *Sagittaria rhombifolia* (Alismataceae). The submerged herb *Mayaca fluviatilis* (Mayacaceae) and the semi-aquatic grass *Isachne polygonoides* (Poaceae) were also common in this habitat. Where the stream widened to form shallow pools, the edges characteristically contained populations of emergent species, such as *Urospatha sagittifolia* (Araceae), *Eleocharis filiculmis* (Cyperaceae), *Syngonanthus densiflorus* (Eriocaulaceae), and *Xyris* cf. *asperula* (Xyridaceae).

Steep-sided sections of the bank supported small populations of *Drosera communis* (Droseraceae), *Trichomanes hostmannianum* (Hymenophyllaceae), a rheophytic fern, an unidentified Hepaticae, and small populations of *Sphagnum* sp. Numerous wet seeps were present along the stream. Typical species in this habitat were *Genlisea guianensis*, *Utricularia amethystina*, *U. pusilla*, and *U. nana* (Lentibulariaceae), *Siphanthera foliosa* (Melastomataceae). Small, semi-aquatic ephemerals, such as *Polygala microspora* (Polygalaceae) and *Burmannia flava* (Burmanniaceae), were also present in this habitat. A few species from the Huanchaca Arroyo were particularly noteworthy: *Genlisea guianensis*, *Utricularia nana*, and *Siphanthera foliosa* (see Appendix E).The Huanchaca Arroyo was relatively inaccessible and was situated far any human settlements; hence, anthropogenic disturbance was minimal, with the largest threats to the system perhaps coming from botanists.

La Toledo Curichi

Elevation: 220 Watershed: Amazon Number of species: 43
Dates visited: Sep 30, 1995; Aug 10, 1996; Aug 11, 1996

The La Toledo Curichi was large. horseshoe-shaped wetland, which occupied a portion of an abandoned course of the Río Paraguá, about 0.5 km to the west of the current position of the river. The Curichi was approximately 1.6 km long, with an average width of about 40 m; total area was on the order of 6 ha. Maximum water depth during visits to the site was about 1.5 m, with an average depth of 0.75-1.0 m. Water conditions were intermediate between clear-water and secondarily black-water.

The Curichi was ringed with a narrow belt of seasonally inundated gallery forest, beyond which were large expanses of seasonally inundated savanna interspersed with narrow forested "islands". The Río Paraguá annually overflows its banks during the rainy season, flooding the surrounding savannas (Killeen 1996). Water from the Río Paraguá flowing across the savannas at the beginning of the rainy season undoubtedly carried a pulse of cations to the Curichi (*cf.* Furch *et al.* 1983). Additionally, a portion of the accumulated organic acids was probably flushed from the basin at this time.

The La Toledo Curichi was somewhat species-poor (43 spp.). The system was a patchwork of different "successional" stages: sections of open water alternated with areas completely covered by floating mats of vegetation. Emergent vegetation was present along system edges, and in irregular "bands" growing on sediment bars oriented transversely across the basin.

Floating mats were well-developed. Mat-forming species were *Eleocharis acutangula*, *Fuirena robusta*, and *Oxycaryum cubense* (Cyperaceae), and *Eichhornia azurea* (Pontederiaceae). Accumulated sediments were particularly abundant in mats dominated by *F. umbellata*. These mats were capable of supporting shrubs (*e.g.*, *Rhynchanthera novemnervia*, Melastomataceae), and small trees, such as *Tabebuia insignis* (Bignoniaceae), and *Pterocarpus santalinoides* (Fabaceae). Other species associated with floating mats were *Echinodorus bolivianus* (Alismataceae), *Erechtites hieracifolia* (Asteraceae), *Begonia fischeri* (Begoniaceae), *Torulinium odoratum* (Cyperaceae), *Ludwigia nervosa* and *L. torulosa* (Onagraceae), *Cyrtopodium paludicolum* (Orchidaceae), *Imperata brasiliensis* and *Saccharum trinii* (Poaceae), *Pityrogramma calomelanos* (Pteridaceae), *Alectra aspera* (Scrophulariaceae), *Thelypteris interrupta* (Thelypteridaceae), and *Xyris laxifolia* (Xyridaceae).

Emergent vegetation was fairly abundant. Shrubs and shrubby perennials were *Aeschynomene fluminensis* and *Mimosa pigra* (Fabaceae), *Ludwigia nervosa* (Onagraceae), and *Melochia arenosa* (Sterculiaceae). Common emergent herbs were *Thalia geniculata* (Marantaceae), *Andropogon bicornis*, *Hymenachne amplexicaulis*, *Isachne polygonoides*, and *Leersia hexandra* (Poaceae), and *Polygonum acuminatum* (Polygonaceae). The climbers *Rhabdadenia pohlii* (Apocynaceae), *Aniseia martinicensis*, *Ipomoea subrevoluta*, and *Tetralocularia pennellii* (Convolvulaceae) were common along system edges and on floating mats. The sole free-floating species noted was *Salvinia auriculata* (Salviniaceae). Free-swimming species were represented by *Utricularia breviscapa* and *U. gibba* (Lentibulariaceae); both of which were common. Two Nymphaeaceous species, *Hydrocleys nymphoides* (Limnocharitaceae) and *Nymphaea amazonum* subsp. *pedersenii* (Nymphaeaceae), were fairly common in shallow water. Species of note were *Cyrtopodium paludicolum* and *Ludwigia torulosa* (see Appendix E).

In general, the La Toledo Curichi appeared to experience little anthropogenic disturbance. At times, however, the system was subjected to unintentional burning when fires set in adjoining grasslands outside the limits of Parque Noel Kempff Mercado spread to the La Toledo savannas. During fieldwork in La Toledo, one such fire burnt through the area. The fire arrived at the La Toledo Curichi, burnt across a large section of floating mat, and spreading across adjacent savanna. All of the mat's "standing vegetation" was destroyed, including the living shoots *Fuirena umbellata*, the principal mat component. The mats retained sufficient structural integrity to support a person's weight, however, and within a week new shoots of *F. umbellata* were apparent. During a return visit to this site approximately a year later, the mats had regained full vegetative growth.

Bahía Toledo

Elevation: 210m Watershed: Amazon Number of species: 72
Dates visited: Sep 10-13, 1995; Aug 12, 1996

Bahía Toledo was a large wetland complex formed by the divergence of the Río Paraguá into a series of channels. Three primary channels were present; these were linked by smaller side channels, forming a complex reticulate system. Downstream from Bahía Toledo, the Río Paraguá reintegrated into a single channel. The large size and complicated morphology of the Bahía made an accurate estimate of system area difficult. Based on coordinates taken from a handheld GPS, and on extrapolation from a LANDSAT image, Bahía Toledo occupied an area of ca. 150 ha.

Year-round (albeit reduced) flow occurred in much of the system; however, some of the secondary channels were transformed into "backwaters" during the dry season, when they became isolated by water levels dropping below the level of sediment dams. Additionally, some connecting waterways were most likely ephemeral during dry years. Annual variation of water levels appeared to be on the order of 1.5-2.5 meters. Water conditions were intermediate between clear- and blackwater. The system was fairly steep-sided along most of its perimeter, however, the upland areas which separated the main channels possessed a more gradual slope. Additionally, some areas between the channels were scarcely higher than the channel beds and were apparently inundated year-round. These topographical differences, in combination with variation in the amounts of sedimentation and build up of organic matter in the channels and backwaters, conferred a high degree of habitat heterogeneity to the system. The areas surrounding Bahía Toledo were essentially as described for the La Toledo Curichi. Hence, Bahía Toledo likely experienced a similar pulse of cations at the start of the rainy season.

Bahía Toledo supported a rich flora (72 spp). Furthermore, due to the system's complex morphology of this system, it is expected that many additional species that were present at the site were not encountered. Much of the system supported extensive floating mats. Principal mat-forming species were *Oxycaryum cubense* and *Eleocharis acutangula* (Cyperaceae). *Fuirena robusta* (Cyperaceae) and *Paspalum repens* (Poaceae) also contributed to mat formation, but were not nearly so abundant as the former species. *Eichhornia azurea* (Pontederiaceae) was abundant, frequently forming the outermost zone of floating mats. Species associated with floating mats were *Erechtites hieracifolia*

(Asteraceae), *Begonia cucullata* (Begoniaceae), *Commelina diffusa* (Commelinaceae), *Cyperus haspan* (Cyperaceae), *Ludwigia affinis* (Onagraceae), *Cyrtopodium paludicolum*, *Erythrodes* sp., and *Habenaria* aff. *repens* (Orchidaceae), *Imperata brasiliensis* and *Isachne polygonoides* (Poaceae), *Pityrogramma calomelanos* (Pteridaceae), *Alectra aspera* and *Bacopa stricta* (Scrophulariaceae), *Thelypteris interrupta* (Thelypteridaceae), and *Xyris laxifolia* (Xyridaceae).

Arborescent species were poorly represented, with *Tabebuia insignis* ("tajibo", Bignoniaceae) and *Genipa americana* (Rubiaceae) the sole trees noted. Scattered individuals of *Tabebuia insignis* were present on floating mats, and one area contained a small "tajibal" (a swampy area dominated by *T. insignis*). Some species, such as *Echinodorus macrophyllus* (Alismataceae), *Rhynchospora rugosa* (Cyperaceae), and *Luziola bahiensis* (Poaceae), were only observed in this habitat.

Climbers were common, and were most abundant on floating mats. Representative species were *Rhabdadenia pohlii* (Apocynaceae), *Aniseia martinicensis, Ipomoea carnea, Ipomoea subrevoluta, Operculina hamiltonii*, and *Tetralocularia pennellii* (Convolvulaceae), *Centrosema vexillatum*, *Senna splendida*, and *Vigna luteola* (Fabaceae), *Passiflora* sp. (Passifloraceae), and *Cissus spinosa* (Vitaceae).

Two submerged species were noted. *Najas arguta* (Najadaceae) was locally abundant in a few areas, and tended to occur in large expanses of open water, in depths up to ca. 2.0 m. *Eichhornia diversifolia* (Pontederiaceae), was also locally abundant, but occurred in areas with shallow, still water.

Free-floating species were well-represented, with *Pistia stratiotes* (Araceae), *Limnobium laevigatum* (Hydrocharitaceae), *Lemna* sp. (Lemnaceae), *Eichhornia crassipes* (Pontederiaceae), *Ceratopteris pteridoides* (Pteridaceae), and *Salvinia auriculata* (Salviniaceae). The free-floating liverwort *Ricciocarpus natans* (Ricciaceae) was also present. *Utricularia gibba* (Lentibulariaceae), was the only free-swimming species noted. *Hydrocleys nymphoides* (Limnocharitaceae) was the sole "Nymphaeaceous" species encountered.

Emergent species were uncommon along the edges of the main channels, as these were generally steep-sided, and frequently served as anchoring points for floating mats. Areas with a more gradual topography, such as the edges of the secondary channels and seasonally inundated sediment bars, and shallowly inundated marshes, supported abundant emergent species. Common shrubs and shrubby perennials were *Mimosa pellita* and *Sesbania exasperata* (Fabaceae), *Hydrolea spinosa* (Hydrophyllaceae), *Rhynchanthera novemnervia* (Melastomataceae), *Piper fuligineum* (Piperaceae), and *Ludwigia leptocarpa* and *L. nervosa* (Onagraceae). Common emergent herbs were *Echinodorus paniculatus*, and *E. subalatus* subsp. *subalatus* (Alismataceae), *Alternanthera lanceolata* (Amaranthaceae), *Eleocharis elegans, E. filiculmis, Rhynchospora corymbosa* and *Scleria microcarpa* (Cyperaceae), *Andropogon bicornis*, *Hymenachne donacifolia*, and *Oryza grandiglumis* (Poaceae), and *Polygonum acuminatum* (Polygonaceae).

The system contained three species of note: *Operculina hamiltonii, Tetralocularia pennellii* and *Cyrtopodium paludicolum* (see Appendix E). In general, Bahía Toledo appeared to be subjected to little anthropogenic disturbance, other than small-scale fishing by local residents. As with the La Toledo Curichi, however, the edges of this system were perhaps vulnerable to fires in adjoining savannas.

Río Paraguá

Elevation: 210 m Watershed: Amazon Number of species: 41
Dates visited: Sep 13, 1995; Mar 22, 1996; Aug 13, 1996; Jun 20-21, 1996

This study site was composed of two sections of the Río Paraguá. The first was located approximately 5 km from Bahía Toledo, and incorporated the area where a blackwater stream, the Arroyo Toledo, entered the river. The second which incorporated the east bank of river adjacent to the community of Florida, was located approximately 7 km further downstream. At the first site, the "Arroyo Toledo sub-site" (61°10'W 14°40'S), an approximately 150 m long section of the Río Paraguá, and ca. 60 m of the Arroyo Toledo were surveyed. At the second site, the "Florida sub-site" (61°10'W 14°37'S), sampling was conducted over an approximately 100 m long section of the river. Total area sampled was roughly 0.5 ha.

At the Arroyo Toledo sub-site, the banks of the Río Paraguá were frequently steep, however some areas were shallow and supported scattered emergent vegetation. The main river channel possessed a strong current, however, the current was much reduced in the area directly around the mouth of the Arroyo Toledo, and floating mats were well-developed. During the two visits to the site, the Arroyo Toledo possessed a continuous flow, but this stream was said to dry down substantially during the dry season, to the point where it is reduced to a series of isolated pools. Maximum water depth in this section of the Río Paraguá was about 2.0 m during the first visit (September, 1995), and was at least 1.0 m deeper during the subsequent visit (June, 1998). Based on the high water mark in adjacent seasonally inundated forest, maximum depth of inundation appeared to be at least three m above this.

Vegetation at the Arroyo Toledo sub-site was more species-rich and structurally complex than at the Florida sub-site. Principal mat forming species were *Oxycaryum cubense* (Cyperaceae) and *Eichhornia azurea* (Pontederiaceae). *Hydrocotyle ranunculoides* (Apiaceae) was frequently a component of the mats. Species associated with the mats were *Hibiscus sororius* (Malvaceae), *Ludwigia affinis* and *Ludwigia leptocarpa* (Onagraceae), *Habenaria* aff. *repens* (Orchidaceae), and *Pityrogramma calomelanos* (Pteridaceae). Climbers were fairly abundant on the floating mats, with *Mikania micrantha* (Asteraceae), *Ipomoea subrevoluta* (Convolvulaceae), *Cayaponia* sp. (Cucurbitaceae), and *Centrosema bifidum* and *Vigna longifolia* (Fabaceae) representative species.

Free-floating species were common in interstices of the floating mats, or in small eddies among fallen, partially submerged tree trunks. Representative species were *Pistia stratiotes* (Araceae), *Lemna valdiviana*, *Spirodela intermedia*, and *Wolffiella lingulata* (Lemnaceae), and *Azolla mexicana* and *Salvinia auriculata* (Salviniaceae). The free-floating liverwort *Ricciocarpus natans* (Ricciaceae) was also present. The sole submerged species noted was *Eichhornia diversifolia* (Pontederiaceae), which was present in shallowly inundated areas along the stream. The sole Nymphaeaceous species was *Hydrocleys parviflora* (Limnocharitaceae). Common emergent species were

Echinodorus subalatus subsp. *subalatus* (Alismataceae), *Melanthera latifolia* (Asteraceae), *Torulinium odoratum* (Cyperaceae), *Senna pendula* (Fabaceae), *Homolepis aturensis* (Poaceae), and *Polygonum acuminatum* and *P. hispidum* (Polygonaceae).

At the Florida sub-site, the Río Paraguá was broader, and the current was reduced. The banks were generally shallow, enabling free-floating and submerged vegetation to develop. Floating mats were poorly developed in this area, although fairly large expanses were visible along the (unsampled) eastern bank. Rather, the vegetation was dominated by submerged and free-swimming species. Submerged species were *Cabomba furcata* (Cabombaceae), *Websteria confervoides* (Cyperaceae), *Egeria najas* (Hydrocharitaceae), and *Najas arguta* (Najadaceae). The rare *Nymphaea oxypetala* (Nymphaeaceae)–an unusual member of the genus which possesses submerged leaves–was locally abundant. The free-swimming species *Utricularia breviscapa* and *U. foliosa* (Lentibulariaceae) were abundant locally.

Rare or noteworthy species encountered at the Río Paraguá were *Egeria najas*, *Nymphaea oxypetala*, and *Websteria confervoides* (see Appendix E). The Río Paraguá was subjected to a certain amount of anthropogenic disturbance. The community of Florida utilized the river for bathing and for washing clothes, and maintained areas along the banks free from floating mats to facilitate these activities. During the same general period as fieldwork, commercial fishermen working the Río Paraguá used the Arroyo Toledo as an embarkation point. Although no visible effects on the aquatic vegetation were noted, fishing clearly impacted more than the ichthyofauna as wild birds were shot and used for bait. The remains of a blue and gold Macaw beside the Arroyo Toledo were a particularly disturbing indicator of the damages effected by these activities.

Cuatro Vientos Palm Swamp

Elevation: 205 m Watershed: Amazon Number of species: 50
Dates visited: Oct 1. 1995; Aug 14, 1996

The Cuatro Vientos Palm Swamp was a basin swamp dominated by the palms *Mauritiella armata* and *Mauritia aculeata*. The system occupied a large, shallow basin, estimated to be roughly 690 ha in area. Water at the site was very dark brown, with abundant humic acids in suspension, and extremely low transparency, and corresponded to either blackwater or secondarily blackwater. Depth at the time of the visits to the site ranged from approximately 0.8-2.0 m, with an average depth of ca. 1.0 m. The basin contained water throughout the year; seasonal variations in water level appeared to be fairly small-scale, probably on the order of 0.5-1.0 m.

With a total of only 51 species, Cuatro Vientos gave the appearance of being somewhat depauperate for a large lowland system. As with the Riberalta Ciénaga, however, maneuvering through the system was extremely problematic, and large areas of Cuatro Vientos were not surveyed. During the second visit to the site, more than 30 species were noted that weren't encountered during the initial visit, therefore, it seemed probable that numerous additional species were present but not encountered.

The system was structurally heterogeneous. Basin sides were steep, and a lagg (narrow band of open water) was present along the outer edge of the basin. A substantial portion of the system was covered with floating mats of vegetation. Peat deposits beneath the mats reached 1 m, or greater (F. Mayle, pers. com). The mats were dissected by broad channels, at least some of which led to two large expanses of open water. Few emergent species appeared capable of growing in the channels. Exceptions were *Ludwigia torulosa* (Onagraceae), *Panicum schwackeanum* (Poaceae), and *Pontederia cordata* var. *lancifolia* (Pontederiaceae).

Trees were well-represented at Cuatro Vientos. *Mauritiella armata* and *Mauritia aculeata* (Arecaceae) were abundant, growing on hummocks throughout the system. In addition to these two palms, arborescent species were *Tapirira guianensis* (Anacardiaceae), *Tabebuia insignis* (Bignoniaceae), *Diospyros yomomo* (Ebenaceae), *Pterocarpus santalinoides* (Fabaceae), and *Genipa americana* (Rubiaceae). With the exception of *G. americana*, these grew on floating mats and were small in stature (ca. 2.5 m tall). *G. americana* was present in the lagg and in seasonally inundated forest surrounding the swamp, and attained heights of about 5 m.

Floating mats varied in composition, with *Fuirena cf. robusta* (Cyperaceae) the most abundant and *Eleocharis acutangula* (Cyperaceae) the second-most abundant mat-forming species. Mats with a large *Oxycaryum cubense* component were also present. These tended to occur adjacent to the lagg, in the (presumably) more nutrient rich water. It appeared that different mat types were often colonized by different species, however, some species appeared to be "mat generalists". Additionally, as large sections of mats were composed of both *Fuirena* cf. *robusta* and *Eleocharis acutangula*, it was often not possible to identify species growing on these mats as favoring a particular mat type. Species encountered growing on *Eleocharis acutangula* mats were *Anthurium* *atropurpureum* (Araceae), *Drosera communis* (Droseraceae), *Syngonanthus caulescens* (Eriocaulaceae), *Irlbachia caerulescens* (Gentianaceae), *Lycopodium clavatum* (Lycopodiaceae), *Mayaca fluviatilis* (Mayacaceae), *Macairea radula* (Melastomataceae), and *Pityrogramma calomelanos* (Pteridaceae). Species observed growing on *Fuirena robusta* mats were *Philodendron brevispathum* and *P. imbe* (Araceae), *Blechnum serrulatum* (Blechnaceae), *Calyptrocarya luzuliformis, Cyperus haspan* and *Eleocharis elegans* (Cyperaceae), *Diospyros yomomo* (Ebenaceae), *Aeschynomene fluminensis* (Fabaceae), *Utricularia tricolor* (Lentibulariaceae), *Miconia* sp. (Melastomataceae), *Alectra aspera* (Scrophulariaceae), and *Thelypteris interrupta* (Thelypteridaceae). Species commonly encountered on both *Eleocharis acutangula* and *Fuirena* cf. *robusta* mats were *Urospatha sagittifolia* (Araceae), *Rhynchospora* corymbosa (Cyperaceae), Piper *fuligineum* (Piperaceae), and *Xyris laxifolia* (Xyridaceae).

No free-floating species were observed, although the free-swimming *Utricularia gibba* (Lentibulariaceae) was present in low abundance. The sole submerged species was *Isoëtes panamensis* (Isoëtaceae). Only a few individuals of *I. panamensis* were noted; these grew in a small opening in an *Eleocharis acutangula* dominated mat. *Nymphaea gardneriana* (Nymphaeaceae), which was common in the channels, was the only rooted macrophyte with floating leaves encountered. Climbers were infrequent, and species-poor, with *Tassadia* sp. (Asclepiadaceae), and *Combretum laxum* (Combretaceae) the representatives noted. Additionally, some of the species of Araceae present at Cuatro Vientos possessed an elongated trailing life form.

Cuatro Vientos possessed a number of rare and/or noteworthy species: *Calyptrocarya luzuliformis*, *Cyrtopodium paludicolum*, *Diospyros yomomo*, which was recently described from this system (Wallnöfer 1999), *Isoëtes panamensis*, and *Ludwigia torulosa* (see Appendix E). This system appeared to suffer little anthropogenic disturbance, with almost all human activity apparently associated with scientific investigation.

Lago Caimán

Elevation: 200 m Watershed: Amazon Number of species: 80
Dates visited: Mar 30, 1996; Apr 5, 1996; Apr 9-10, 1996; Apr 14, 1996; Apr 18, 1996; Jun 25-26, 1998

Lago Caimán was a large (ca. 575 ha) basin system located at the base of the extreme northern end of the Serranía de Huanchaca. Although the name "Lago Caimán" suggests a lake, the system was more properly a "bahía": a lacustrine system that is seasonally connected with a river. The system occupied a section of a former course of the Río Iténez. During the rainy season, water from the river entered Lago Caimán through a narrow channel. During the highest water stages, inflow and outflow also occurred through broad sections of the seasonally inundated forest bordering Lago Caimán. The bed of the inflow channel was elevated above the low water levels of both the Río Iténez and Lago Caimán, hence, during the dry season as water levels in the river subsided, Lago Caimán became isolated from the river.

Lago Caimán was approximately 8-9 kilometers long, and had the shape of an elongated fishhook with a sinuous shank. The dimensions of the basin were quite variable, with the narrowest stretches approximately 150 m wide, and the widest areas on the order of half a kilometer. Because many parts of the basin were steep-sided in, there most likely was not a substantial fluctuation in system area between wet and dry seasons. Annual fluctuations in water level appeared to be on the order of 3 m. The system's water possessed the visual characteristics of clearwater, with a slight brown tint.

Lago Caimán was tremendously heterogeneous. Along the edge which abutted the base of the Serranía, the basin was extremely steep-sided, with little macrophyte development, other than small assemblages of wind-blown, free-floating aquatics. Other parts of the system were characterized by a more gradual topography; these frequently served as anchoring points for large expanses of floating mats. The eastern edge of the basin possessed an irregular profile, with various small "bays". At times, floating mats were sufficiently large to span the mouths of these bays, thereby transforming them into isolated backwaters (*remansas*). Differences in water movement throughout the system, also contributed to habitat heterogeneity, with the areas of the strongest current possessing distinctive floras.

Lago Caimán possessed a rich flora (80 spp.). Submerged species were very well-represented with *Cabomba* cf. *furcata* (Cabombaceae), *Websteria confervoides* (Cyperaceae), *Egeria najas* (Hydrocharitaceae), *Mayaca longipes* and *M. sellowiana* (Mayacaceae), *Najas arguta* (Najadaceae), *Eichhornia diversifolia* (Pontederiaceae), and *Limnophila perdiemensis* Ritter sp. nov. (Scrophulariaceae). The submerged form of *Ludwigia inclinata* (Onagraceae) was abundant around the mouth of the channel that connected Lago Caimán with the Río Iténez.

Numerous free-floating species were present. Representative species were *Pistia stratiotes* (Araceae), *Limnobium laevigatum* (Hydrocharitaceae), *Lemna aequinoctialis* (Lemnaceae), *Ceratopteris pteridoides* (Pteridaceae), and *Azolla microphylla*, *Salvinia auriculata* and *S. minima* (Salviniaceae). The free-floating liverwort, *Ricciocarpus natans* (Ricciaceae), was also present, and floating clusters of the moss cf. *Vesicularia* sp. (Hypnaceae), were occasionally observed. Free-swimming species were common, and well-represented with *Utricularia breviscapa*, *U. foliosa*, *U. gibba*, and *U. hydrocarpa* (Lentibulariaceae).

Much of the system was characterized by the presence of large, well-developed floating mats. Principal mat forming species were *Eleocharis acutangula* and *Oxycaryum cubense* (Cyperaceae). In a few areas, *Leersia hexandra* (Poaceae) formed weakly-coalesced floating mats. Outer edges of the floating mats were frequently formed by *Eichhornia azurea*. At times, *Floscopa glabrata* (Commelinaceae), *Isachne polygonoides* (Poaceae), *Polygonum acuminatum* (Polygonaceae), and *Pontederia rotundifolia* (Pontederiaceae) also occupied the outermost zone. Species associated with floating mats were *Erechtites hieracifolia* and *Gymnocoronis spilanthoides* (Asteraceae), *Cyperus haspan*, *Pycreus unioloides* and *Torulinium odoratum* (Cyperaceae), *Syngonanthus caulescens* (Eriocaulaceae), *Aeschynomene fluminensis* (Fabaceae), *Hydrolea spinosa* (Hydrophyllaceae), *Utricularia tricolor* (Lentibulariaceae), *Cuphea melvilla* (Lythraceae), *Hibiscus sororius* (Malvaceae), *Ludwigia nervosa* and *L. leptocarpa* (Onagraceae), *Cyrtopodium paludicolum* (Orchidaceae), *Pityrogramma calomelanos* (Pteridaceae), *Diodia multiflora* (Rubiaceae), *Alectra aspera*

(Scrophulariaceae), and *Xyris laxifolia* (Xyridaceae). The shrub *Rhynchanthera novemnervia* (Melastomataceae) was common on floating mats, and frequently formed a distinct zone a few meters from the edge. Additionally, a few small individuals of the arborescent *Macrolobium acacifolium* (Fabaceae), were growing in conjunction with the mats. It could not be determined whether these were actually supported by the mats, or whether they were rooted in the basin and merely surrounded by mat.

Climbers were common along system edges and on floating mats. Representative species were *Sarcostemma clausum* (Asclepiadaceae), *Mikania micrantha* (Asteraceae), *Ipomoea regnellii, I. subrevoluta,* and *Operculina hamiltonii* (Convolvulaceae), *Pseudocyclanthera australis* (Cucurbitaceae), *Vigna peduncularis* and *V. longifolia* (Fabaceae), and *Cissus* sp. (Vitaceae). *Pseudocyclanthera australis* was particularly abundant, covering large areas along island edges, where water levels had subsided.

Emergent species were generally uncommon, although in a few areas they were fairly abundant. Representative species were *Justicia laevilinguis* (Acanthaceae), *Echinodorus grisebachii* and *E. tenellus* (Alismataceae), *Scleria melaleuca* (Cyperaceae), *Caperonia castaneifolia* (Euphorbiaceae), *Hymenachne amplexicaulis, Oryza grandiglumis,* and *Panicum pilosum* (Poaceae), and *Pontederia cordata* var. *ovalis* (Pontederiaceae). The shrub *Senna aculeata* (Fabaceae), was locally abundant around the mouth of the inflow channel, growing in fairly deep (ca. 2.0 m) water, with a strong current. *Oryza grandiglumis* was also abundant in this area.

Noteworthy species present at Lago Caimán were *Cyrtopodium paludicolum, Egeria najas, Floscopa glabrata, Limnophila perdiemensis* Ritter, sp. nov., *Nymphaea* *jamesoniana*, ***Operculina hamiltonii***, and ***Websteria confervoides*** (see Appendix E). Lago Caimán was fairly isolated, and access to the system was well-hidden, nevertheless, local fishermen and hunters were familiar with the system and made occasional use of it, although anthropogenic impact appeared to be minimal.

Gran Pantanal

Five study sites were established in the Bolivian portion of the Gran Pantanal: four large lacustrine systems and one riparian marsh (Table A.8). The four lacustrine study sites are said to be remnants of much larger "pluvial" lakes (Por 1995), and are interconnected by either the Río Paraguay, or through channels that connect with the river. Three of these lakes, Lagunas Uberaba, La Gaiba and Mandioré, are said to also receive inputs from the overflow of the Río Cuiaba system (Por 1995).

Table A.8. Study sites in the Bolivian Gran Pantanal region, with elevation, approximate area of the system, approximate location, and number of species noted for each site.

System	Elev (m)	Approximate Area (ha)	Approximate Location	No. Spp.
Laguna Uberaba	90	30000	57°44'W 17°34'S	66
Laguna La Gaiba	90	10500	57°46'W 17°48'S	61
Laguna Mandioré	90	25000	57°34'W 18°17'S	63
Laguna Cáceres	90	3500	57°46'W 18°57'S	124
Puesto Gonzalo	90	2	57°47"W 17°40'S	38

Laguna Uberaba
Elevation: 90 m. Watershed: Paraná Number of species: 66
Approximate center of the system: 57°44'W 17°34'S
Dates visited: Jul 10-11, 1998

Laguna Uberaba, the northernmost of the Gran Pantanal study sites, was once thought by the Spanish Conquistadors to be an inland sea: the "Sea of the Xaraes" (Por 1995). The lake is situated in both Brazil and Bolivia, with approximately 60% occurring in Bolivian territory (Justiniano M. 1998). The area of Laguna Uberaba has been variously estimated as being from 91 km^2 (Justiniano M. 1998) to 400 km^2 (Por 1995). The basin appeared to be fairly shallow throughout, with a maximum depth of perhaps 3 m at the time of fieldwork.

Most areas along the edges of the system supported either well developed floating mats of vegetation or fairly dense populations of emergent species. The edges of the lake possessed a few areas of marshy habitat, with these almost always associated with inflowing streams. In one area, however, a large back-swamp had formed behind a low "dike" of highly sedimented floating mat that, having come to rest as water levels subsided, served to isolate this swamp from the main body of the lake. This habitat was inundated to a depth of about 1 m, and was dominated by emergent shrubs, herbs, and climbers. A few small, scattered islands were present in the lake, and at least one of these contained a well-developed marsh along one edge.

Laguna La Gaiba
Elevation: 90 m Watershed: Paraná Number of species: 61
Approximate center of the system: 57°46'W 17°48'S
Dates visited: Jul 9, 1998; Jul 13-14, 1998

Laguna La Gaiba was located at the southern end of the Río Pedro II, a river which connected this system with Laguna Uberaba. Laguna La Gaiba was situated in both Brazil and Bolivia, with approximately 60% occurring in Bolivian territory (Justiniano M. 1998)). Laguna La Gaiba is said to cover 105 square kilometers during high water, diminishing to 55 square kilometers during the dry season (Por, 1995), and large areas of the system are said to be less than 1 m deep (Por, 1995). At the southern end of the system, a small cove, "Bahía Preseverancia", was separated from the main body of the lake by an narrow spit of land. This cove was much more protected from wave and wind action than were the other parts of the system.

Laguna Mandioré

Elevation: 90 m Watershed: Paraná Number of species: 63
Approximate center of the system: 57°34'W 18°17'S
Dates visited: Jul 15-17, 1998

Laguna Mandioré was located almost entirely within Bolivian territory. Various estimates place the seasonal fluctuations in area of this system at between 89 and 200 km^2 (Por, 1995), or between 80 and 300 km^2 (Justiniano M. 1998). Laguna Mandioré was connected to the río Paraguay by a navigable channel, which flowed southward from the lake. Another channel flowed from the Río Paraguay to the northeastern corner of the lake, but this was said to be non-navigable and flow may have been seasonal.

Laguna Mandioré possessed greater habitat heterogeneity than did Lagunas Uberaba and La Gaiba. A raised spit of land partially separated the southern end of the system from the main body of the lake, forming a large, somewhat-protected cove. A few small streams entered the lake along its western edge; at the time of fieldwork, flow was negligible and floating vegetation covered much of the water's surface. In some sections of the streams, small marshes occupied the transition zone between stream edge and upland. The area around the mouth of the outflow channel had a particularly complex morphology, with a series of small channels anastomosing along the main channel. Additionally, a back-swamp was present along one section of the northwestern edge of the basin. Water in this habitat was about 1 m deep and was stained very dark brown.

Laguna Cáceres

Elevation: 90 m Watershed: Paraná Number of species: 124
Approximate center of the system: 57°46'W 18°57'S
Dates visited: Jul 14-15, 1997; Jul 18-20, 1998

Laguna Cáceres, the southernmost of Gran Pantanal study sites, was located entirely within Bolivian territory. The system had an area of approximately 35 km^2 (3,500 ha). Laguna Cáceres was the sole Pantanal study site situated near any appreciable human populations, with the communities of Puerto Suárez and Puerto Qiharro–where the Bolivian Navy maintained a port–located along its southern edge. Additionally, the city of Corumbá (Brazil) was situated approximately 15 km east of the lake. Activities associated with these population centers, in particular shipping, had some effect on the aquatic vegetation. For example, crewmen from a lumber barge were observed using a smaller boat to remove sections of floating mat to maintain an navigable channel between an access road and open water.

Although the other Gran Pantanal lacustrine study sites were all "overflow lakes" (Por 1995), Laguna Cáceres was one of a series of deeper lakes which are thought to be of karstic origin (Por 1995). These are said to be characterized by smaller scale fluctuations in water level (Por 1995), however, local lore has it that Laguna Cáceres dried out completely at one point during the 1930's. Likewise, Por (1995) noted that during a particularly dry year (1994) Laguna Jacadigo, another deep lake, also dried down completely.

Laguna Cáceres was the most heterogenous of the Gran Pantanal study sites. Two rivers, the Río Pimiento and Río Sicurí, flowed into the lake. Upstream from the lake's basin these were sinuous and were flanked by a series of braided side channels. Overflow from these rivers during high water stages flooded large parts of the adjacent floodplains, forming what appeared (from images) to be complex and potentially interesting marshlands. Unfortunately, at the time of both visits to this system (July 1997, 1998), the mouth of the Río Pimiento was completely blocked by mats of floating vegetation, and it was not possible to access these areas. The main channel of the Río Sicurí was also blocked with floating mats at various points, however, it did prove possible to clear pathways through these, enabling sampling to be conducted for a few km upriver. Outflow from the lake was through the Tamengo canal, which connected Laguna Cáceres with the Río Paraguay.

Puesto Gonzalo
Elevation: 90 m. Watershed: Paraná Number of species: 38
Approximate center of the collecting area: 57°47"W 17°40'S
Date visited: Jul 12, 1998

Puesto Gonzalo was an outpost of the Bolivian Navy, situated along a side channel of the Río Pedro II. The two ends of this channel were said to be connected with the Río Pedro II during high water stages, and water conditions are said to be lotic at this time.

At the time of the fieldwork, the sole connection with the main body of the river was through a small lateral channel, and water conditions were lentic. Total area surveyed was approximately 2 ha.

In general, Puesto Gonzalo lacked the substantial populations of emergent woody and herbaceous species characteristic of the lacustrine study sites, however, a few emergent herbs were present. In most areas, channel edges contained floating mats of vegetation. At times, small openings were present in the mats and these supported either submerged species (*e.g. Cabomba furcata*) or rooted macrophytes with floating leaves (*e.g. Nymphaea* spp.). The area between the floating mats and non-inundated uplands was shallowly inundated at the time of the fieldwork, and supported dense populations of free-floating herbaceous macrophytes.

Outlying Sites

Laguna Volcan

Elevation: 1150 m. Watershed: Amazon Number of species: 39
Approximate center of the collecting area: 63°39'W 18°08' S
Dates visited: Feb 4, 1996; Jul 17, 1996; Jun 29, 1997

Laguna Volcan was a montane pond (elev. 1150 m) situated in a small saddle in the eastern Andean foothills. Bolivian vegetation maps (Killeen *et al.* 1993; Ribera *et al.* 1994) depict the general area of Laguna Volcan as falling within the transition between the southern (Bosque Tucumano-Bolivian) and northern (Bosque Montano Húmedo) wet montane forest types. As in the Bosque Montano Húmedo, wetlands appear to be uncommon in the Bosque Tucumano-Boliviano. For example, in the account of the RAP

(Rapid Assessment Protocol) survey of this vegetation type (Schulenberg and Awbrey 1998) references to wetlands were limited to streams.

The system occupied a natural basin, but the basin had been deepened by the creation of a low earthen dike at it's shallow most end. A billboard at the base of the road leading to Laguna Volcan marked the area of the system at 7.0 ha, but I estimated the area as closer to 3.0 ha. Inputs of water to the system appeared to be limited to runoff and groundflow from adjacent slopes. Pond water was stained a dark brown, yet fairly transparent. Maximum depth was on the order of 3.5-4.0 m. A few marshy areas adjoined the pond basin. One of these contained a spongy, floating mat dominated by *Cyperus papyrus* (Cyperaceae) and *Typha domingensis* (Typhaceae). The emergent sedge, *Schoenoplectus californicus* (Cyperaceae), was the most abundant species in other marshy habitats.

Much of the basin was dominated by submerged vegetation. Three species, *Potamogeton gayii* and *P. illinoensis* (Potamogetonaceae), and *Najas guadalupensis* (Najadaceae), were noted; all were abundant. The submerged alga, cf. *Nitella* sp. (Characeae), was also common. Submerged species grew to depths of about 2.0-2.5 m.

Two species of rooted macrophytes with floating leaves, *Nymphoides verrucosa* (Menyanthaceae) and *Nymphaea lingulata* (Nymphaeaceae), were common in the basin. A few free-floating species were present. *Lemna valdiviana* (Lemnaceae) and *Limnobium laevigatum* (Hydrocharitaceae) were both common. *Spirodela intermedia* (Lemnaceae) was also present, but only a single frond was noted.

Emergent vegetation was well-represented with: *Hygrophila costata* (Acanthaceae), *Echinodorus bolivianus* and *E. paniculatus* (Alismataceae), *Acmella brachyglossa* (Asteraceae), *Cyperus haspan*, *Rhynchospora gigantea*, *Schoenoplectus californicus*, and *Torulinium odoratum* (Cyperaceae), *Hydrolea* cf. *elatior* (Hydrophyllaceae), and *Leersia hexandra* (Poaceae). Species which occupied the shallows, increasing in abundance as water levels dropped were *Echinodorus bolivianus* and *E. paniculatus* (Alismataceae), *Drymaria glandulosa* (Caryophyllaceae), *Commelina diffusa* (Commelinaceae), *Eleocharis minima*, (Cyperaceae), *Ludwigia leptocarpa* and *L. octovalvis* (Onagraceae), *Polygonum meisnerianum* (Polygonaceae), and *Bacopa salzmannii* (Scrophulariaceae).

Species associated with the *Typha domingensis/Cyperus giganteus* mat were *Hydrocotyle verticillata* (Apiaceae), *Begonia cucullata* (Begoniaceae), *Carex* sp. and *Cyperus surinamensis* (Cyperaceae), *Polygonum acuminatum*, *P. hispidum*, and *Polygonum punctatum* (Polygonaceae), and *Physalis* sp. (Solanaceae).

Woody species were poorly represented, although the shrub *Ludwigia peruviana* (Onagraceae) was abundant along one edge of the system. Two poorly represented taxonomic groups were the Pteridophytes (with no species noted), and grasses, which had a single representative (*Leersia hexandra*).

Laguna Volcan was the sole wetland encountered in the Bosque Tucumano-Boliviano, other than a few, essentially unvegetated streams. Therefore, it is unclear whether or not the flora was representative of other wetlands in this vegetation type. Moreover, Laguna Volcan was located near the borders of two other primary vegetation types. the Bosque Serrano Chaqueño and the Bosque Semideciduo Chiquitano (Killeen *et al.* 1993), and elements from these were undoubtedly present.

Noteworthy species encountered at Laguna Volcan were *Carex* sp., *Echinodorus bolivianus* and *E. paniculatus, Hydrocotyle verticillata, Nymphaea lingulata, Nymphoides verrucosa,* and *Potamogeton gayii* (see Appendix E). Formerly, anthropogenic impacts appeared to be small-scale. The system was used for recreation by tourists from the nearby (ca. 40 km) city of Santa Cruz, with these activities generally limited to boating and fishing. Recently, however, residential development was initiated in the areas immediately surrounding Laguna Volcan. At the time of the last visit to the site (June, 1997) the road which led to this area had been extended to the pond. It is uncertain how many structures are planned, but erosion from clearing the slopes and nutrient inputs from sewage almost certainly will pose threats to the system.

Yolosa Wetland

Elevation: 1150 m Watershed: Amazon Number of species: 38
Approximate center of the collecting area: 16°16'04"S 67°44'14"W
Dates visited: Feb 26, 1995; May 21, 1995; May 18, 1996; July 29, 1996

The Yolosa Wetland was composed of a series of riverside and streamside marshy habitats associated with the Río San Juan, in the area around the town of Yolosa. Approximately 100 m of the river were surveyed. Included within the study site were two distinct areas: 1) a small stream which flowed out of the Río San Juan, passed through a culvert under a highway, and re-entered the river; and, 2) seasonally inundated areas along the banks of the river. The total area surveyed was approximately 0.05 ha.

The Yolosa Wetland flora was fairly species-rich (38 spp.), and was composed almost entirely of herbaceous species. Exceptions were the small tree, *Tessaria integrifolia* (Asteraceae) and the shrub *Ludwigia peruviana* (Onagraceae), both of which grew along the upper edges of the system, and the climber, *Mikania* sp. (Asteraceae), which was abundant in the stream and associated marshy areas. The spreading herb *Heteranthera reniformis* (Pontederiaceae) was locally abundant in one broad, shallow area, where it formed a very loosely-coalesced, more or less floating assemblage. The remainder of the flora was composed of emergent herbs, the most abundant of which were *Eclipta prostrata* (Asteraceae), *Drymaria glandulosa* (Caryophyllaceae), *Cyperus iria, C. luzulae, C. prolixus, Eleocharis montana*, and *Kyllinga odorata* (Cyperaceae), *Ludwigia octovalvis* (Onagraceae), *Chloris radiata, Echinochloa colona, Eleusine indica, Melinis minutiflora* and *Pennisetum purpureum* (Poaceae) *Polygonum hydropiperoides* (Polygonaceae), and *Pityrogramma calomelanos* (Pteridaceae).

No species of note were encountered at the Yolosa wetland; rather, the flora was composed almost entirely of common weedy species. Of note, however, was the population of the endemic "rockweed", *Apinagia boliviana* (Podostemaceae), which was encountered in the Río Coroico, a few kilometers below the point where the Río San Juan entered this system (see Appendix E).

The Yolosa Wetland was significantly impacted by human activities. All manners of refuse were deposited along the edges of the system, and the upper portions of the stream were commonly used for washing clothes. Additionally, Yolosa was the site of a police checkpoint, and the buses that passed through this area on their way to and from La

Paz were often required to stop at the checkpoint for extended periods. Consequently, the portion of the stream nearest the road was frequently called into service as a public bathroom. How these activities may have impacted the flora is not certain, but it can be stated unequivocally that they served to minimize botanical reconnaissance in this part of the system.

Laguna Yaguacua
Elevation: 920 m Watershed: Paraná Number of species: 10
Approximate center of the collecting area: 20°26'S 63°27'W
Date visited: Nov 24, 1996

Laguna Yaguacua was located in Serranía de Aguarague–a low range which comprises the first foothills of the Andes–at an elevation of 920 m. The system had an area of about 30 ha, and was shallow throughout, with a maximum depth (near the end of the dry season) of about 1.0 m. Water was a cloudy brown.

The vegetation was dominated by herbaceous species. An exception was the arborescent *Salix Humboldtiana* (Salicaceae), numerous individuals of which were present along the edge the system and along a seasonally inundated spit of land which intruded into the basin. Many species were sterile at the time of the visit, hence, species which could normally be easily identified (*e.g.*, *Schoenoplectus californicus*) were given only provisional determinations. Emergent species (listed in approximate order of decreasing abundance) were *Thalia* sp. (Marantaceae), *Polygonum paraguayense* (Polygonaceae), *Eleocharis macrostachya* (Cyperaceae), cf. *Schoenoplectus californicus* (Cyperaceae), *Eclipta prostrata* (Asteraceae), cf. *Echinodorus* (Alismataceae) and *Cleome hassleriana* (Capparidaceae). *Lemna aequinoctialis* (Lemnaceae) was the sole free-floating species. No true submerged species were present, but young plants of *Ludwigia peploides* (Onagraceae) had the aspect of *Callitriche*, with most of the plant submerged, and leaves crowded toward the tip of the plant and floating on the water's surface. The lack of submerged species was surprising, since two other shallow ponds in the same general area supported fairly dense populations of *Stuckenia striata* (Potamogetonaceae).

Anthropogenic disturbance appeared to be limited to grazing by cattle, which ranged freely in the area. No rare or noteworthy species were present, at least as could be determined from the numerous sterile species. Nevertheless, as fieldwork at this site represented conditions during a single hydrologic stage, the composition and structure of the vegetation during the rainy season is expected to be significantly different. At the time of the visit, a striking feature of the system was the presence of 20-30 flamingos (presumably, the Andean flamingo, *Phoenicopterus andinus*).

Cristalmayu Wetland

Elevation: 640 m. Watershed: Amazon Number of species: 12
Approximate center of the collecting area: 65°38'W 17°00'S
Dates visited: Oct 30, 1994; May 14, 1995; Jun 7, 1995

The Cristalmayu Wetland consisted of a small artificial pond, formed by damming a stream which passed through the basin. The pond was situated in a notch at the base of two hills. A poorly constructed road ran above the pond and a large amount of material from the eroding hillside was washed into the pond during the (prolonged) rainy season. Basin sediments were soft and deep. Total area of the system was approximately 0.5 ha.

The Cristalmayu Wetland was the lowest montane study site. Due to the steep topography, few bodies of standing water were encountered in the lower Andean slopes, and the rivers and streams draining these slopes were generally fast moving, and supported few macrophytes.

The stream passed through thick forest and was heavily shaded in the areas immediately above and below the pond. No vascular species were observed in the stream in the immediate vicinity of the pond, but a small population of *Heteranthera rotundifolia* (Pontederiaceae) was noted where the stream crossed a highway (ca. 0.3 km below the pond). Small marshy areas were present around the mouth of the stream, and in a few additional areas along the edge of the pond basin. These contained the greatest portion of the wetland vegetation at the site. Species noted in these habitats were *Justicia comata* (Acanthaceae), *Hydrocotyle leucocephala* (Apiaceae), *Drymaria glandulosa* (Caryophyllaceae), *Commelina diffusa* (Commelinaceae), *Cyperus luzulae, Scleria melaleuca*, and *Torulinium odoratum* (Cyperaceae), *Hymenachne donacifolia, Panicum polygonatum,* and *P. stoloniferum* (Poaceae), *Pennisetum purpureum* (Poaceae), and *Ludwigia affinis* (Onagraceae).

Pennisetum purpureum (Poaceae), was common along the edge of the pond, and extended over open water by means of floating culms. No submerged, or free-floating species were observed at the site.

No noteworthy species were encountered at the Cristalmayu Wetland. The system was heavily impacted by human activities. By the time of the second visit, the streamside marsh had been modified by the deposition of sand and gravel from roadside erosion above the pond, and the species previously observed in this habitat were no longer evident. Because of heavy erosion upslope from the system, the future prognosis for the Cristalmayu pond is poor.

APPENDIX B: EXTRA-BOLIVIAN REGIONAL AND NATIONAL WETLAND FLORAS

In addition to the sources listed below, regional and country floras were augmented by species distributions noted from taxonomic treatments, from herbarium specimens viewed at BOLV, LPB, MO, and USZ , and from distribution data obtained from queries of two online databases: the Flora Mesoamericana checklist (Davidse *et al.* 1999; http://mobot.mobot.org), and the Missouri Botanical Garden database TROPICOS (http://mobot.mobot.org).

Argentina

Río Paraná Delta Region

A number of references pertaining to wetlands in the southern Río Paraná region were available. The following were entered in their entirety:

Burkart, A. 1957. Ojeado sinóptica sobre la vegetación del Delta del Río Paraná. Darwiniana 11: 457-561.

Cabrera, A. L. and H. A. Fabrís. 1948. Plantas Acuáticas de la Provincia de Buenos Aires *In:* Publ. Tec. Min. Hac. Econ. Prev. Cont. Ser. D.A.G.I. 5.

Menalled, F. D. and J. M. Adámoli. 1995. A quantitative phytogeographic analysis of species richness in forest communities of the Parana River Delta, Argentina. Vegetatio 120: 81-90.

Additional wetland species were noted from the following sources. Although the complete species lists from these volumes were not incorporated into the database, each volume was reviewed for the presence of species already included in the "Wetland Species Database" and for additional species whose descriptions suggested that they were strongly associated with wetland habitats.

Burkart, A., ed. 1974. Flora Ilustrada de Entre Ríos (Argentina). Parte VI: Dicotiledoneas Metaclamideas (Gamopétalas), B. Rubiales a Campanuales (incluso Compuestas). Instituto Nacional de Tecnología Agropecuaria, Buenos Aires, Argentina.

——— 1978. Flora Ilustrada de Entre Ríos (Argentina). Parte V : Dicotiledoneas Metaclamideas (Gamopétalas), A. Primulales a Plantaginales. Instituto Nacional de Tecnología Agropecuaria, Buenos Aires, Argentina.

Troncoso de B., N. S. and N. M. Bacigalupa eds. 1987. Flora Ilustrada de Entre Ríos (Argentina). Parte III: Dicotiledóneas Arquiclamídeas, A. Salicales a Rosales (Incluso Leguminosas). Instituto Nacional de Tecnología Agropecuaria, Buenos Aires, Argentina.

Brazil

Central Amazonia

The wetland flora of Central Amazonia was represented by the following sources:

Howard-Williams, C. and W. J. Junk. 1977. The chemical composition of central Amazonian aquatic macrophytes with special reference to their role in the ecosystem. Arch. Hydrobiol. 79: 446-464.

Junk, W. J. 1983. Ecology of Swamps on the Middle Amazon. pp. 269-294. *In:* Ecosystems of the World 4B. Mires: Swamp, Bog, Fen and Moor. Gore, A. J. P., ed. Elsevier, Amsterdam, The Netherlands.

——— 1986. Aquatic plants of the Amazon system. pp. 319-337. *In:* The Ecology of River Systems. Davies, W. B., ed. Dr. W. Junk Publishers, Dordrecht, The Netherlands.

——— 1989. Flood tolerance and tree distribution in central Amazonian floodplains. pp. 47-64. *In:* Tropical Forests. Botanical Dynamics, Speciation and Diversity. Haynes, R. R., Holm-Nielsen, L. B. and Balslev, H., eds. Academic Press, London.

——— and M. T. F. Piedade. 1993. Herbaceous plants of the Amazon floodplain near Manaus: species diversity and adaptations to the flood pulse. Amazoniana 7: 467-484.

Keel, S. H. K. and G. T. Prance. 1979. Studies on the vegetation of a white-sand black-water igapó (Río Negro, Brazil). Acta Amaz. 9: 645-6555.

Worbes, M. 1997. The forest ecosystem of the floodplain. pp. 223-265. *In:* The Central Amazon Floodplain. Junk, W. J. (ed.) . Springer-Verlag, Berlin, Heidelberg.

Gran Pantanal de Mato Grosso

The following sources were used to identify wetland species in the Gran Pantanal and to compile a regional flora. Additional species were from data provided by Vali Pott (personal communication).

Conceição, C. d. A. and J. E. de Paula. 1986. Contribuição para o conhecimento da flora do Pantanal Mato-Grossense e sua relação com a fauna e o homem. pp. 107-130. *In:* Anais 1° Simpósio Recursos Naturais e Sócio-Econômico do Pantanal. EMBRAPA-CPAP, Corumbá, Brasil.

Heckman, C. W. 1998. The Pantanal of Pocone - Biota and Ecology in the Northern Section of the World's Largest Pristine Wetland. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Por, F. D. 1995. The Pantanal of Mato Grosso (Brazil). Kluwer Academic Publishers, Dordrecht.

Pott, A. and V. J. Pott 1997. Plants of Pantanal. EMBRAPA-SPI, Corumbá, Brasil.

Pott, V. J. 1998. A família Nymphaeaceae no Pantanal, Mato Grosso e Mato Grosso do Sul, Brasil. Acta. Bot. Bras. 12: 183-194.

——, S. C. de Almeida Rego and A. Pott. 1986. Plantas uliginosas e aquáticas de Pantanal arenoso. 6. EMBRAPA, CPAP, Corumbá, Brasil.

——, N. C. Bueno, R. A. C. Pereira, S. M. De Salis and N. L. Vieira. 1989. Distribuição de macrófitas aquáticas numa lagoa na fazenda Nhumirim, Nhecolândia, Pantanal, MS. Acta. Bot. Bras. 3: 153-168.

——, N. C. Bueno and M. Pereira da Silva. 1992. Levantamento florístico e fitossociológico de macrófitas aquáticas em lagoas da Fazenda Leque, Pantanal, MS. Anais 8° Cong. SBSP : 91-99.

—— and A. Pott. 1997. Checklist do macrófitas aquáticas do Pantanal, Brasil. Acta. Bot. Bras. 11: 215-227.

Prado, A. L., do, C. W. Heckman and F. R. Martins. 1994. The seasonal succession of biotic communities in wetlands of the tropical wet-and-dry climatic zone: II. The aquatic macrophyte vegetation in the Pantanal of Mato Grosso, Brazil. Int. Rev. Gesamten. Hydrobiol. 79: 569-589.

Other Brazil

Additional Brazilian wetland species were ascribed from:

Brandão, M., J. P. Laca-Buendia and M. L. Gavilanes. 1989. Plantas palustres e aquáticas que se comportam como invasoras, no estado de Minas Gerais. Acta. Bot. Bras. 2 (1) supl. Anais do XXXIX Congresso Nacional de Botânico: 255-265.

Klinge, H., W. J. Junk and C. J. Revilla. 1990. Status and distribution of forested wetlands in tropical South America. For. Ecol. Manag. 33/34: 81-101.

Pires, J. M. and G. Prance. 1985. The vegetation types of the Brazilian Amazon. pp. 109-145. *In:* Key Environments: Amazonia. Prance, G. T. and Lovejoy, T. E. eds. Pergamon Press, Oxford, England.

No comprehensive checklist of the flora of Brazil was encountered. Therefore, a provisional Brazilian flora was approximated by combining the preceding sources with the following general checklists:

Espécies Arbóreas da Estação Ecológica dos Caetetus. Estação Ecológica dos Caetetus Gália/Alvinândia, SP. Base de Dados Tropical. http://www.bdt.org.br/mata.atlantica/flora/caetetus/listagalia. Date Accessed: September 12, 2000.

Floristics and Economic Botany of Acre, Brazil. New York Botanical Garden and Universidade Federal do Acre. http://www.nybg.org/bsci/acre/title.html (Date Accessed: June 27, 2000)

Listagem de Espécies da Flora do Cerrado. Espécies da flora de Cerrado do Estado de São Paulo. Base de Dados Tropical. http://www.bdt.org.br/cerrado/flora/sp/especies. Date Accessed: September 12, 2000.

Mata da Esperança. New York Botanical Garden: http://www.nybg.org/bsci/res/bahia/ME-chkl.html (Date Accessed: 6/27/2000)

Monte Pascoal National Park. New York Botanical Garden: http://www.nybg.org/bsci/res/bahia/MP-chkl.html (Date Accessed: 6/27/2000)

Serra Grande forest/Serra do Condurú State Park. New York Botanical Garden: http://www.nybg.org/bsci/res/bahia/SG-chkl.html (Date Accessed: 6/27/2000)

Una Biological Reserve. New York Botanical Garden: http://www.nybg.org/bsci/res/bahia/Checkli1.html (Date Accessed: 6/27/2000)

Colombia

No comprehensive checklist of the flora of Colombia was encountered. Sufficient references were available, however, to allow the compilation of a national checklist of wetland species. The checklist of Colombian macrophytes provided by Profesor Udo Schmidt-Munn was a particularly critical resource.

Sources were as follows:

Rangel, O. and J. Aguirre. 1983. Comunidades acuáticas altoandinas - I: Vegetación sumergida y de ribera en el Lago de Tota, Boyacá, Colombia. Caldasia 13: 719-742.

Rangel, O. and J. Aguirre. 1986. La vegetación de la cuenca del Lago de Tota (Boyacá). Caldasia 15: 263-311.

Sanabria, M. J. and A. De Wilde. 1998. Humedales del Departamento del Quindío. Inventario preliminar. (doc. intern.). Corporación Autónoma Regional del Quindío. CRQ, Armenia, Colombia.

Schmidt-Mumm, U. 2000. Macrófitos Acuáticos y Palustres de Colombia. Unpublished checklist. Date created: March 19, 2000.

Costa Rica

The following sources were used in the ascription of Costa Rican wetland species:

Bumby, M. J. 1982. A survey of aquatic macrophytes and chemical qualitites of nineteen locations in Costa Rica. Brenesia 19/20: 487-535.

Crow, G. E. and D. I. Rivera. 1986. Aquatic vascular plants of Palo Verde National Park, Costa Rica. Uniciencia 3: 71-78.

———, D. I. Rivera and C. Charpentier. 1987. Aquatic vascular plants of two Costa Rican ponds. Selbyana 10: 31-35.

Gómez, L. D. 1984. Las Plantas Acuáticas y Anfibias de Costa Rica y Centroamérica. Editorial Universidad Estatal A Distancia, San José, Costa Rica.

The complete Costa Rican flora was represented by:

Grayum, M., B. Hammel and N. Zamora. 1987 to present. Species list for the Manual to the Plants of Costa Rica. Database maintained at INBio. Access Date: Sep. 3, 1999. (http://www.inbio.ac.cr/bims/PLANTAE.html).

This checklist was obtained from the authors as a text file, and was converted to a database.

Ecuador

The following sources were used to identify Ecuadorian wetland species:

Bravo-Velásquez, E. and H. Balslev. 1985. Dinámica y adaptaciones de las plantas vasculares de dos ciénegas tropicales en Ecuador. Reports from the Botanical Institute, University of Aarhus 11: 1-50.

Briones, E. E., A. Flachier, J. Gómez, D. Tirira, H. Medina, I. Jaramillo and C. Chiriboga 1997. Inventario de Humedales del Ecuador. Primera Parte: Humedales Lénticos de las Provincias de Esmeraldas y Manabí. EcoCiencia/INEFAN/Convención de Ramsar, Quito, Ecuador.

The complete Ecuadorean flora was represented by:

Jørgensen, P. M. and S. León-Yánez (eds.). 1999. Catalogue of the Vascular Plants of Ecuador. Monographs in Systematic Botany from the Missouri Botanical Garden, St. Louis, Missouri.

The checklist was obtained from the authors as a text file, and was converted to a database. Data pertaining to species habitat, elevational range and geographical range were obtained by querying the "Catalogue of the Vascular Plants of Ecuador" (http://www.mobot.org/MOBOT/research/ecuador/welcome.htm) at the Missouri Botanical Garden website. A program was written to direct the computer to automatically submit queries to the website and to transfer query results to the database of Ecuadorian species (Dates accessed: August 20-25, 2000).

El Salvador

Due to insufficient data, it was not possible to compile a complete national checklist for El Salvador. Information from the following published accounts of Salvadorian wetlands was used in the ascription of wetland species:

Armitage, K. B. 1957. Lagos de la Planicie Costera de El Salvador. Comun. Inst. Trop. Invest. Ci. Univ. El Salvador 6: 5-8.

——— 1958. Lagos Volcánicos de El Salvador. Comun. Inst. Trop. Invest. Ci. Univ. El Salvador 7: 39-48.

——— and N. C. Fassett. 1971. Aquatic plants of El Salvador. Arch. Hydrobiol. 69: 234-255.

Loetschert, W. 1954. La Laguna de Alegría. Comun. Inst. Trop. Invest. Ci. Univ. El Salvador 3: 173-175.

The Guianas

French Guiana, British Guyana, and Suriname, the three countries which constitute "the Guianas", were treated as a single OGU. Although this region possesses a rich wetland flora, no reports of Guianan wetlands were encountered, other than references in various taxonomic treatments. Therefore, additional Guianan wetland species were distinguished by a query of the exsiccatae in the Biological Diversity of the Guianas Database (performed by Tom Hollowell, of the Department of Botany at the Smithsonian Institution, Washington, DC) using the following terms: Like "*bog*" Or Like "*wetland*" Or Like "*marsh*" Or Like "*fen*" Or Like "*swamp*" Or Like "*seep*" Or Like "*flooded*".

The complete flora of the Guianas was represented by:

Boggan, H., V. Funk, C. Kelloff, M. Hoff, G. Cremers and C. Feuillet 1997. Checklist of the Plants of the Guianas. The Biological Diversity of the Guianas Program, Dept. of Botany, National Museum of Natural History, Washington, DC.

The checklist was acquired in database format from the Biological Diversity of the Guianas project, National Museum of Natural History, Washington, DC. (Access Date: February 2, 2000).

Mexico

No comprehensive checklist of the flora of Mexico was available. Checklists for various state and regional floras, however, were encountered on the World Wide Web. These, along with species lists from a number of published studies of Mexican wetlands, were downloaded and incorporated into a database. Additional species records from the Flora Mesoamerican database (Davidse *et al.* 1999) were combined with these sources. Although this checklist was undoubtedly an incomplete representation of the country's flora, it contained over 10,000 species. As many of the studies used in compiling the list were of wetland habitats, it seems probable that a significant portion of the country's wetland species were represented. Sources were:

Bonilla-Barbosa, J. R. and A. Novelo R. 1995. Manual de Identificación de Plantas Acuáticas del Parque Nacional Lagunas de Zempoala, México. Instituto de Biología, Universidad Nacional Autónoma de México, México, D. F., México.

Breedlove, D. E. 1986. Listados Florísticos de México II: Flora de Chiapas. Instituto de Biología, Universidad Nacional Autónoma de México. Access Date: Nov. 21, 1999. (http://www.ibiologia.unam.mx/publicaciones/lfl4.html).

Cowan, C. P. 1983. Listados Florísticos de México I: Flora de Tabasco. Instituto de Biología, Universidad Nacional Autónoma de México. Access Date: Aug. 8, 1999. (http://www.ibiologia.unam.mx/publicaciones/lfl1.html).

Dávila Aranda, P., J. L. Villasenor Ríos, R. Medina Lemos, A. Ramírez Roa, A. Salinas Tovar, J. Sánchez-Ken and P. Tenorio Lezama. 1993. Listados Florísticos de México X: Flora del Valle de Tehuacán-Cuicatlan. Instituto de Biología, Universidad Nacional Autónoma de México. Access Date: Nov. 23, 1999. (http://www.ibiologia.unam.mx/publicaciones/lfl10.html).

López-Hernández, E. 1993. Aspectos de la vegetación de los Pantanos de Centla, Tabasco, México. Universidad y Ciencia 10: 43-56.

Lot, A., A. Novelo R. and P. Ramírez-García. 1986. Listados Florísticos de México V. Angiospermas Acuáticas Mexicanas 1. Instituto de Biología, Universidad Nacional Autónoma de México. Access Date: Sep. 20, 1999. (http://www.ibiologia.unam.mx/publicaciones/lfl5.html).

——— and A. Novelo R. 1988. Vegetación y flora acuática del Lago de Pátzcuaro, Michoacán, México. Southw. Natur. 33: 167-175.

——— A. Novelo Retana, M. Olvera García and P. Ramírez-García 1999. Catálogo de Angiospermas Acuáticas de México. Hidrófitas estrictas emergentes, sumergidas y flotantes. Instituto de Biología. Universidad Nacional Autónoma de México, México, D. F.

Ramírez-García, P. and A. Novelo R. 1984. La vegetación acuática vascular de seis lagos-cráter del estado de Pueblo, México. Bot. Soc. Bot. México 46: 75-88.

Rojas, J. and A. Novelo R. 1995. Flora y vegetación del Lago de Cuitzeo, Michoacán, México. Act. Bot. Mex. 31: 1-17.

Sousa S., M. and E. F. Cabrera C. 1983. Listados Florísticos de México II: Flora de Quintana Roo. Instituto de Biología, Universidad Nacional Autónoma de México. Access Date: Nov. 19, 1999. (http://www.ibiologia.unam.mx/publicaciones/lfl2.html).

Tellez Valdes, O. and E. F. Cabrera Cano. 1987. Listados Florísticos de México VI: Florula de la Isla de Cozumel, Q.R. Instituto de Biología, Universidad Nacional Autónoma de México. Access Date: Nov. 24, 1999. (http://www.ibiologia.unam.mx/publicaciones/lfl6.html).

——— , G. Flores Franco, A. Martinez Rodriguez, R. E. Gonzalez Flores, G. Segura Hernandez, R. Ramirez Rodriguez, A. Dominguez Mariani and I. Calzada. 1995. Listados Florísticos de MéxicoXII. Flora de la Reserva Ecológica Sierra de San Juan, Nayarit, México. Instituto de Biología, Universidad Nacional Autónoma de México. Access Date: Nov. 22, 1999. (http://www.ibiologia.unam.mx/publicaciones/lfl12.html).

Panama

The Panamanian flora was represented by:

D'Arcy, W. G. 1987. Flora of Panama. Missouri Botanical Garden. Access Date: Aug. 7, 1999. (http://mobot.mobot.org/Pick/Search/index/panamaa.html.)

As this checklist included only flowering plants, the presence and absence of wetland pteridophytes in Panama were determined from: 1) online queries of the Flora Mesoamerican database (Davidse *et al.* 1999; http://mobot.mobot.org); 2) exsiccatae listed in TROPICOS; 3) specimens encountered in herbaria; and, 4) species distributions from the literature.

No reports of Panamanian wetlands were encountered. Nevertheless, as numerous accounts of wetlands and wetland species in countries near Panama (*i.e.*, countries in Central America and northern South America) were incorporated into the Wetland Species Database it seems likely that the greatest part of the Panamanian wetland flora was accounted for. Additionally, Gómez (1984) listed various wetland species known for Panama, and this information was also incorporated into the compiled Panamanian wetland flora.

Paraguay

The following sources were used in the ascription of wetland species, and for compiling a representative wetland flora for Paraguay:

Galán de Mera, A. and G. Navarro. 1992. Comunidades vegetales acuáticas del Paraguay occidental. Caldasia 17: 35-46.

Mereles, F., R. Degen and N. López de Kochalca. 1992. Humedales en el Paraguay: breve reseña de su vegetación. Amazoniana 12: 305-316.

Wolf, A. 1990. Vegetationshundliche Beobachtungen en Flachwasserseen nahe der Mündung des Río Ypané, Paraguay. Amazoniana 11: 167-184.

Peru

The following sources were used in the ascription of Peruvian wetland species:

Cano, A., B. León and K. R. Young. 1993. Plantas vasculares de los Pantanos de Villa, Lima. pp. 177-208. *In:* Las Plantas Vasculares en las Aguas Continentales del Perú. Kahn, F., León, B. and Young, K. R., eds. IFEA (Instituto Francés de Estudios Andinos), Lima, Perú.

Galán de Mera, A. 1989. Notas florísticas sobre el litoral y los Andes del Perú (Departamento de Lima). Lazaroa 11: 193-196.

Kahn, F., B. León and K. R. Young, eds. 1993. Las Plantas Vasculares en las Aguas Continentales del Perú. IFEA (Instituto Francés de Estudios Andinos), Lima, Peru.

Kalliola, R., J. Salo, M. Puhakka and M. Rajasilta. 1991. New site formation and colonizing vegetation in primary succession on the western Amazon floodplains. J. Ecol. 79: 877-901.

León, B., A. Cano and K. R. Young. 1995. La flora vascular de los Pantanos de Villa, Lima, Perú: adiciones y guía para las especies comunes. Publ. Mus. Hist. Nat. UNMSM (B) 38: 1-39.

——— and K. R. Young. 1996. Aquatic plants of Peru: diversity, distribution and conservation. Biodivers. Conserv. 5: 1169-1190.

The complete Peruvian flora was represented by:

Brako, L. and J. L. Zarucchi 1993. Catalogue of the Flowering Plants and Gymnosperms of Peru. Missouri Botanical Garden, St. Louis, Missouri.

The checklist was downloaded from the Missouri Botanical Garden website (http://www.mobot.org/MOBOT/Research/peru.html: Access date: August 20, 1999) and converted to database format. This file contained the complete range of data (i.e, life-form, principal habitat, elevational range) contained in the published checklist. Thus, it was possible to produce "regional" checklists (*i.e.*, the Lowland Amazonian Peru OGU) by querying the database.

As pteridophytes were not included in Brako and Zarucchi's (1993) checklist, the presence and absence of wetland pteridophytes in Peru were determined from: 1) exsiccatae listed in TROPICOS; 2) online queries of the Flora Mesoamerican database (Davidse *et al.* 1999; http://mobot.mobot.org); 3) specimens encountered in herbaria; and, 4) monographs and other literature.

United States and Associated Territories

The 1996 National List of Vascular Plant Species That Occur in Wetlands (Reed 1996) was downloaded as a text file and converted to a database. This checklist enumerated the wetland status for 7437 species from the United States *sl.* and catalogued the status for each species in 11 regions from the Continental United States (Northeast, Southeast, North Plains, North Central, Central Plains, South Plains, Southwest, Intermountain, Northwest, California, and Alaska), and for associated territories in the Caribbean (Puerto Rica and the U.S. Virgin Islands) and Pacific regions (the Hawaiian Islands, American Samoa, the Federated States of Micronesia, Guam, the Marshall Islands, the Northern Mariana Islands, Palau, and U.S. Minor Outlying Islands).

Of the 7000+ species included in the checklist, 3284 were selected here as being "wetland species". Of these, 2034 were characterized as "Obligate Wetland Species" (OBL), *i.e.*, those that, under natural conditions, almost always occur in wetlands (Reed 1996). The remaining 1250 species were those that possessed a national status of "Facultative Wetland Species" (FACW), *i.e.*, those that usually occur in wetlands (estimated probability 67%-99%, Reed 1996). In most cases, species that had a "mixed" national status indicating both wetland and upland affinities (*i.e.*, FACU, FACW) were not considered as wetland species. Thirty-four species had a mixed national status that indicated that each was an obligate wetland species in part of its range (*i.e.*, FACU, OBL), and these were treated as wetland species. To allow comparisons on the sub-regional level, the presence and absence of wetland species from various states were ascertained by downloading state checklists from the National Plant Data Center website (USDA & NRCS 1997) and incorporating this information into the database.

The complete flora of the United States and associated territories was obtained by downloading the PLANTS National Database checklist:

USDA, NRCS 1997. The PLANTS database. (http://plants.usda.gov). National Plant Data Center, Baton Rouge, LA. (Downloaded July 9, 2000).

The checklist was downloaded as a text file and was converted to a database.

Venezuela

The following sources were used to compile a representative wetland flora for the country:

Aristeguieta, L. 1968. Consideraciones sobre la flora de los Morichales Llaneros al norte del Orinoco. Acta Bot. Venez. 3: 19-38.

Colonnello, G., S. Castroviejo and G. López. 1986. Comunidades vegetales asociadas al río Orinoco en el Sur de Monagas y Anzoátegui (Venezuela). Mem. Soc. Ci. Nat. La Salle 46: 127-165.

Ramía, M. 1974. Plantas de las sabanas llaneras. Monte Avila Editores, Caracas, Venezuela.

Velásquez, J. 1994. Plantas Acuáticas Vasculares de Venezuela. Universidad Central de Venezuela, Consejo de Desarrollo Científico y Humanístico, Caracas.

APPENDIX C: THE BOLIVIAN REGIONS

In addition to species lists compiled from my field research, wetland floras for the Bolivian regions were augmented by the work of other researchers whenever possible. In some cases (*e.g.*, the White-water floodplain region), data from these sources equaled or exceeded data from my fieldwork. In addition to data taken from studies of specific wetlands, regional checklists were augmented by specimens listed in the general literature (*e.g.*, monographs and local floras and florulas) that could be confidently ascribed to a that region.

The Missouri Botanical Garden's database TROPICOS also served to augment the regional checklists. Data from TROPICOS were obtained by querying the database for the exsiccatae collected from each of Bolivia's nine Departamentos. The selected records (ca. 61,000) were subsequently apportioned to the proper region. As with any database, a portion of the records from TROPICOS contained errors from incorrectly entered data. Errors in locality data were located by exporting the records to a spreadsheet and performing a series of sequential sortings. In this way, specimen records with outlying locations (*i.e.*, latitudes or longitudes) or improperly recorded political divisions (*e.g.*, Provincias which did not correspond to the Departamento for which they were listed) were identified. Whenever possible, incorrect data for these records were emended, but when it was not possible to make corrections the record was discarded.

In the following sections, the eight Bolivian regions considered in floristic comparisons are described and sources used in compiling the regional wetland floras are listed.

High Andean

The High Andean "region" incorporates territory from the country's three major watersheds (Desaguadero, Amazon, and Paraná). In Bolivia, the greatest portion of high Andean (Puna) vegetation occurs within one large contiguous region (the "Altiplano" and adjacent peaks), with outlying high Andean ecosystems occurring on high elevation habitats in the Cordillera Central ("central range") and the Cordillera Oriental ("eastern range") of the Andes (*i.e.*, the montane peaks situated above the Valles Secos).

The Altiplano, which has a mean elevation of 3800 m (Solomon 1989), is an extensive interior basin bounded by the Cordillera Occidental ("western range") and the Cordillera Central. The Altiplano and bordering montane slopes comprise the Desaguadero watershed, which is essentially a closed watershed. High-elevation habitats from the mountain peaks above the Valles Secos (Dry Interandean Valleys) are characterized by alpine vegetation similar to that of the Altiplano (Solomon 1989), and these habitats have been grouped with the high-altitude sites from the Río Desaguadero watershed. The greatest part of these belong to the Amazon watershed, although the southern sections of the mountains drain to the Río Paraná system. With a single exception (Huayalmarca Pond Desaguadero watershed) the High-Andean study sites were all situated within the Amazon watershed. Auxiliary collections, however, were made from other high-elevation wetlands in the Desaguadero watershed in the areas around the city of La Paz and Lago Titicaca. Additional botanical reconnaissance was conducted in high-elevation habitats of the Paraná watershed, but no study sites were established in this area.

The High Andean region is characterized by low (<500 mm) average annual precipitation and by an annual average temperature of less than 10°C. (Killeen *et al.* 1993). The vegetation of the High-Andean zone is termed *puna*; an association which extends southwards into Chile and Argentina and northwards into Peru (Solomon 1989). In Bolivia, puna formations occur between elevations of 2550-4800 m (Killeen *et al.* 1993). The puna is characteristically dominated by graminoids and herbaceous dicotyledons (Killeen *et al.* 1993), although a variety of shrubs and short trees are also often present.

Sources used to augment the checklist for the High Andean region were:

Estenssoro C., E. S. 1991. Los bofedales de la cuenca alta del valle de La Paz. pp. 109-116. *In:* Historia Natural de un Valle en Los Andes: La Paz. Forno, E. and Baudoin, M., eds. Instituto de Ecología, Universidad Mayor de San Andrés, La Paz, Bolivia.

Franken, M. 1991. Plantas Acuáticas. pp. 511-520. *In:* Historia Natural de un Valle en Los Andes: La Paz. Forno, E. and Baudoin, M., eds. Instituto de Ecología, Universidad Mayor de San Andrés, La Paz, Bolivia.

Lara, R. R. and A. L. Cazas. 1996. Caracterización ambiental de las vegas altoandinas en Los Lipez - Potosí. Revista Boliviano de Ecología 1: 60-68.

Pestalozzi Schmid, H.-U. A. 1998. Flora ilustrada Altoandina: la relación entre hombre, planta y medio ambiente en el Ayllu Majasaya Mujlli (Prov. Tapacarí, Depto. Cochabamba, Bolivia). Herbario Forestal "Martín Cárdenas", Herbario Nacional de Bolivia, Cochabamba and La Paz, Bolivia.

Raynal-Roques, A. 1991. Las Plantas Superiores. pp. 233-239. *In:* El Lago Titicaca: Síntesis del Conocimiento Limnológico Actual. Dejoux, C. and Iltis, A., eds. ORSTOM, La Paz, Bolivia.

Siebert, P. v. and X. Menhofer. 1992. Die Vegetation des Wohngebietes der Kallawaya und des Hochlandes von Ulla-Ulla in den bolivianischen Anden. Teil I. Phytocoenologia 20: 289-438.

Cloud Forest

A description of the Bolivian Cloud Forest region is presented in Chapter 3. No published accounts of wetlands in the Cloud Forest were encountered; hence, the region's species checklist was compiled almost entirely from my fieldwork in the region, with a few species added from TROPICOS specimens and from the taxonomic literature.

Valles Secos

"Valles Secos" is the name given to the series of tablelands, peaks and valleys which occupy portions of the Central and Eastern Ranges (Cordillera Central and Cordillera Oriental) of the Andes. In the Andes south of about 18° the orientation of the mountains changes to a nearly north-south alignment, the mountains are lower, orographic precipitation is lessened, and there is a shift in weather patterns (Solomon 1989). This results in the Valles Secos being in rainshadow, with the region having a dry season of at least six to eight month duration (Killeen *et al.* 1993). The terrestrial vegetation is a matrix of xerophytic thorn woodland, thorn scrub, and dry forest (Killeen *et al.* 1993). The Valles Secos have been inhabited since pre-Incan times, and now face a number of serious problems, such as erosion, desertification, loss of vegetative cover, and lack of water during the prolonged dry season (Navarro *et al.* 1996).

Although aquatic habitats do not constitute a large portion of the Valles Secos, lakes and ponds are not uncommon, and the edges of streams and rivers frequently contain marshy habitats. These range in size from tens of square meters to a few hectares (and possibly much larger). The sole published floristic account of a Valles Secos wetland that I encountered was Cadima's (1989) study of Laguna Alalay. This system was also one of my study sites. Cadima listed three species for Laguna Alalay that I did not encounter, but I felt that the identity of these was questionable. No voucher specimens were cited; hence, I was unable to satisfactorily resolve the questions I had regarding their identity. These species, therefore, were not added to the regional checklist.

Chapare

A description of the Chapare region is presented in Chapter 4. Sources used to augment the checklist for the Chapare region were:

Jiménez, A. M. 1984. Flora de Cochabamba. Imprenta Los Huerfanos, Santa Cruz de la Sierra, Bolivia.

Maldonado, M., E. Goitia, F. Acosta, M. Cadima and D. Castellon. 1996. Caracterización limnológica de lagunas en la llanura alluvial del río Ichilo (Cochabamba). Rev. Bol. de Ecol. 1: 30-38.

Andean Piedmont

The Andean Piedmont region is a small (ca. 4500 km^2) region situated along the area at the base of the Andes directly east of the Chapare. As defined here, this region comprises the lowland portions of the areas around the city of Santa Cruz (the Provincias of Sarah, Santiesteban, Warnes, and Ibanez). Elevations are somewhat higher than the Chapare, with a minimum of ca. 400 m. For this study, a maximum elevation of 600 m was chosen as the upper limit for the region.

In contrast to the Chapare, which is situated in an "inside corner" of the Andes, the Andean Piedmont region is located in an "outside corner", formed as the orientation of the mountains changes from an approximately eastern to a southern bearing. Hence, the eastern portion of the Andean Piedmont region is situated in the transition between the mountains and the vast plains which extend from south-central Bolivia southwards through Paraguay and Argentina. Because of its position in the transition between the humid forests of Amazonia and the dry forests of the Chiquitanía and the Chaco, the Andean Piedmont region supports a matrix of terrestrial vegetation types (Killeen *et al.* 1993).

As with the Chapare, annual precipitation varies significantly over a fairly short distance, ranging from ca. 2400 mm yr^{-1} at the town of Yapacaní near the western limits of the region to 1300 mm yr^{-1} in the area around the city of Santa Cruz (Servicio Nacional de Meteorología e Hidrología, La Paz). Isohyets shown in a map prepared by Roche and Rocha (1985) suggest that the eastern portion of the region is even drier, reaching about 900 mm yr^{-1} in the area south of the city of Santa Cruz.

Sources used to augment the checklist for the Andean Piedmont region were:

Foster, R. C. 1946. Studies in the Flora of Bolivia, -- I. Contributions From The Gray Herbarium Of Harvard University, No. CLXI : 3-18.

——— 1948. Studies in the Flora of Bolivia, II. Contributions From The Gray Herbarium Of Harvard University, No. CLXVI : 28-43.

——— 1965. Studies in the flora of Bolivia, III. Cyperaceae, Part 1. Rhodora 67: 97-138.

——— 1966. Studies in the flora of Bolivia, IV. Gramineae. Rhodora 68: 97-120; 233-358.

White-water Floodplain

Northern and northeastern Bolivia, is characterized by an extensive plain, cut-through by a network of rivers which drain the eastern slope of the Andes. In this study, the greatest part of this plain was treated as the "White-water Floodplain" region. As defined here, this region corresponds roughly to the area extending from near the base of the Andes northwards to the country's borders with Peru and Brazil, and is composed of the Departamentos of Beni and Pando, and most of the lowland portions of the Departamentos of La Paz and Cochabamba. The name "white-water" refers to the highly turbid rivers which drain the Andes, as per the classification of Amazonian water types presented by Sioli (1975).

The floodplain varies from 150-250 meters in elevation, with areas of local relief located near the base of the mountains (Killeen *et al.* 1993). Annual precipitation is variable, with rainfall generally decreasing northwards. Mean annual precipitation from seven meteorological stations ranged from 1800 mm at Riberalta (yearly totals: 975-2430 mm) to about 2200 mm at Rurrenabaque (yearly totals:1155-3512 mm; Servicio Nacional de Meteorología e Hidrología, La Paz). Based on records for precipitation in the adjacent Chapare region– where mean annual precipitation can reach at least 6000 mm (Moraes and Beck 1992)–the southernmost portions of the White-water Floodplain undoubtedly experience annual rainfall of greater than 3,000 mm. Average annual temperature is on the order of 25°C (Killeen *et al.* 1993).

Large areas of the floodplain contain wetland ecosystems. Allenby (1988) estimated that this region (excluding the Pando) contained roughly 250,000 km^2 of "swampland". Included in this region are the "Llanos de Mojos", an extensive complex of seasonally flooded savanna, which covers approximately 100,000 km^2 (Haase and Beck 1989) and which constitutes the largest area of seasonally inundated savanna ("sabanas hiperestacionales") in the Amazon basin (Hanagarth 1993). Lacustrine systems are plentiful, with many characteristically containing one or more straight edge (*i.e.*, the "aligned, rectangular lakes of the Beni Basin" *sensu* Allenby 1988).

Sources used to augment the checklist for the White-water Floodplain region were:

Beck, S. G. 1984. Comunidades vegetales de las sabanas inundadas en el NE de Bolivia. Phytocoenologia 12: 321-350.

Haase, R. 1989. Plant communities of a savanna in northern Bolivia I. Seasonally flooded grassland, and gallery forest. Phytocoenolgia 18: 55-81.

——— 1990. Plant communities of a savanna in northern Bolivia II. Palm swamps, dry grassland, and shrubland. Phytocoenolgia 18: 343-370.

——— and S. G. Beck. 1989. Structure and composition of savanna vegetation in northern Bolivia: A preliminary report. Brittonia 41: 80-100.

Hanagarth, W. 1993. Acerca de la Geoecología de las Sabanas del Beni en el Nordeste de Bolivia. Instituto de Ecología - Bolivia, La Paz.

Helme, N. A. and L. Kruger. 1995. Preliminary Field Report. The Bolivian Pampas de Heath - An International Conservation Priority for Neotropical Savannas. Proposed Madidi National Park, Dpto. La Paz, Prov. Iturralde,

Chiquitanía

The Chiquitanía is a large (ca. 170,000 km^2, Killeen 1990) region in eastern lowland Bolivia. The Chiquitanía occupies the extreme western edge of the Brazilian shield (Killeen 1990) and is composed of the provinces of Velasco, Chiquitos, and Ñuflo de Chavez. The region experiences a pronounced dry season (ca. 5 months, Killeen 1990) during the austral winter. Precise meteorological data are lacking for the region, however, mean annual precipitation from two weather stations (Concepción and San Ignacio de Velasco) ranged from about 1150-1250 mm, with yearly totals ranging from 700-1600 mm (Servicio Nacional de Meteorología e Hidrología, La Paz). Conditions are progressively wetter toward the northeast, with mean annual precipitation in the Parque Nacional Noel Kempff Mercado area estimated at between 1400-1500 m (Killeen and Schulenberg 1999). Mean annual temperatures are around 25°-26°C, with highs of 38° and lows of 3°C recorded for Concepción (Killeen and Schulenberg 1999).

The central portion of eastern Bolivia is essentially a zone of climatic transition between the wet conditions of the Amazon basin and the drier climate of southern South America. The terrestrial vegetation in this area reflects a gradual change from the evergreen forest of Amazonia to the dry forest of the Chaco, and has been delineated as "Bosque Semideciduo Chiquitano" (Killeen *et al.*, 1993). The Chiquitanía possesses a variable topography (ca. 300-1,240 m), and is characterized by a mixture of forest, savanna, savanna wetlands, and vegetated rock outcroppings and is considered to be a part of the Cerrado biogeographic region (Killeen *et al.*, 1993). No wetland complex on the scale of the Llanos de Mojos is present in Chiquitanía, nevertheless, wetlands are fairly common throughout the region.

Sources used to augment the checklist for the Chiquitanía region were:

Killeen, T. J. 1990. The grasses of Chiquitanía, Santa Cruz, Bolivia. Ann. Missouri Bot. Gard. 77: 125-201.

——— and M. Nee. 1991. Catálogo de las plantas sabaneras de Concepción, Depto. de Santa Cruz, Bolivia. Ecol. Bolivia 17: 53-71.

——— and T. S. Schulenberg eds. 1999. A Biological Assessment of the Parque Nacional Noel Kempff Mercado, Bolivia. RAP Working Paper 10. Conservation International, Washington, DC.

Gran Pantanal

The Gran Pantanal region is described in Chapter 5. Sources used to augment the checklist for the Gran Pantanal region were:

Frey, R. 1995. Flora and vegetation of "Las Piedritas" and the margin of Laguna Cáceres, Puerto Suárez, Bolivian Pantanal. Bull. Torrey Bot. Club 122: 314-319.

Halloy, S. 1997. Áreas Protegidas Pantanal de Otuquis y San Matías. Ministerio de Desarrollo Sostenible y Medio Ambiente, Santa Cruz, Bolivia.

Additional Sources Incorporated Into The Bolivian Wetland Species Database

Species listed in the following two reports for the Reserva de Vida Silvestre Rios Blancos y Negros were incorporated in the wetland species database. This reserve is situated in the transition zone between the White-water floodplain and the Chiquitanía, therefore, I was unable to confidently ascribe species listed for the Reserva to either region.

Navarro, G. 1992. Informe: Sectorizacíon Ecológica Previa de la Reserva Memoria y Mapa de Unidades Ambientales. Proyecto de Protección Ríos Blanco y Negro. Departamento de Botánica, Universidad Complutense, Madrid, Spain.

——— 1993. Informe: Tipificación de Ambientes Acuáticos y Clasificación de la Vegetación de la "Reserva de Vida Silvestre Ríos Blanco y Negro". Proyecto de Protección Ríos Blanco y Negro. Departamento de Botánica, Universidad Complutense, Madrid, Spain.

APPENDIX D. SPECIES ASSOCIATED WITH BOLIVIAN WETLANDS

OGUs: HA) High Andean; CF) Cloud Forest; VS) Valles Secos; CP) Chapare; AP) Andean Piedmont of Santa Cruz; WW) White-water Floodplain; CQ) Chiquitanía; GP) Gran Pantanal; AS) Andean Slopes, without a clear association; TB) Bosque Tucumano-Boliviano (presumed); GC) Gran Chaco. Species lacking reference to any OGU are those which are known for Bolivia, but which I was not able to confidently assign to a particular region. **Habit**: HR, Rheophytic herb; HL, Lithophytic herb; CF, Cushion-forming herb; HT, Trailing Herb; HA, Annual Herb; HP, Perennial Herb; HA/P, Annual or Perennial Herb; HF-F, Free-Floating Herb; HS, Submerged herb; HSA, Suspended Aquatic Herb; HF-S, Herb with floating stems and/or petioles; FM-F, Floating Mat-forming Herb; RFL, Rooted macrophyte with floating leaves; H, Herb; PS-W, Sub-woody Perennial; PSF, Suffrutescent Perennial; S-S, Sub-shrub; S, Shrub; TU, Understory Tree; T, Tree; CL, Climber; LN, Liana. Life-forms were as could be determined from descriptions in the literature, live material, and herbarium specimens.

Family	**Species**	**Habit**	**HA**	**CF**	**VS**	**CP**	**AP**	**WW**	**CQ**	**GP**	**AS**	**TB**	**GC**
Pteridophytes													
Adiantaceae	*Pityrogramma calomelanos* (L.) Link	H	-	-	-	+	+	+	+	+	+	-	-
	Pityrogramma trifoliata (L.) R. Tryon	H	-	-	+	-	+	-	-	-	-	-	-
Azollaceae	*Azolla caroliniana* Willd.	H	+	+	+	-	-	+	+	+	-	-	-
	Azolla filiculoides Lam.	H	-	-	+	-	-	-	+	-	-	-	-
	Azolla mexicana C. Presl.	HF-F	+	-	-	-	+	+	+	+	-	-	-
	Azolla microphylla Kaulf.	H	-	-	-	-	-	-	+	-	-	-	-
Blechnaceae	*Blechnum loxense* (H. B. K.) Solomon	H	-	-	-	-	-	-	-	-	-	-	-
	Blechnum serrulatum Rich.	H	-	-	-	-	-	+	+	-	-	-	-
Dennstaedtiaceae	*Dennstaedtia bipinnata* (Cav.) Maxon	H	+	-	-	-	-	-	-	-	-	-	-
Dryopteridaceae	*Dryopteris rivulariformis* Rosenst.	H	-	-	-	-	-	-	-	-	-	-	-
Equisetaceae	*Equisetum bogotense* Kunth	H	+	+	+	-	-	-	-	-	+	-	-
	Equisetum giganteum L.	H	-	-	+	-	+	-	-	-	-	-	-
	Equisetum pyramidale Goldm.	H	-	-	-	-	-	-	-	-	-	-	-
Isoëtaceae	*Isoëtes baculata* Hickey & Fuchs	HS	+	-	-	-	-	-	-	-	-	-	-
	Isoëtes boliviensis U. Webber	HS	+	-	-	-	-	-	-	-	-	-	-
	Isoëtes eshbaughii Hickey	HS	-	-	-	-	-	-	-	-	-	-	-
	Isoëtes glacialis E. Asplund	HS	+	-	-	-	-	-	-	-	-	-	-
	Isoëtes herzogii U. Weber	HS	+	+	-	-	-	-	-	-	-	-	-

Family	Species	Habit	HA	CF	VS	CP	AP	WW	CQ	GP	AS	TB	GC
	Isoëtes lechleri Mett.	HS	+	-	+	-	-	-	-	-	-	-	-
	Isoëtes panamensis Maxon & C. V. Morton	HS	-	-	-	-	-	-	+	-	-	-	-
	Isoëtes pedersenii H.P. Fuchs ex Hickey	HS	-	-	-	-	-	-	-	-	-	-	-
Lycopodiaceae	*Lycopodiella alopecuroides* (L.) Cranfill	H	-	-	-	-	-	-	+	-	-	-	-
	Lycopodiella caroliniana (L.) Pic. Serm.	H	-	-	-	-	-	+	+	-	-	-	-
	Lycopodiella pendulina (Hook.) B. Øllg.	H	-	-	-	-	-	-	+	-	-	-	-
Hymenophyllaceae	*Trichomanes hostmannianum* (Klotzsch) Kunze	HR	-	-	-	-	-	-	+	-	-	-	-
	Trichomanes radicans Swartz	H	-	-	-	-	-	-	-	-	-	-	-
Marsileaceae	*Marsilea ancylopoda* A. Br.	H	+	-	-	-	-	-	-	-	-	-	-
	Marsilea crotophora D. M. Johnson	RFL	+	-	-	-	-	+	-	+	-	-	-
	Marsilea polycarpa Hook. et Grev.	RFL	-	-	-	-	-	+	+	-	-	-	-
	Pilularia americana A. Braun	HS	+	-	-	-	-	-	-	-	-	-	-
Ophioglossaceae	*Ophioglossum nudicaule* L. f.	H	-	-	-	-	-	+	-	-	-	-	-
Parkeriaceae	*Ceratopteris pteridoides* (Hook.) Hieron	HF-F	-	-	-	+	+	+	+	+	-	-	-
Pteridaceae	*Acrostichum danaeifolium* Langsd. & Fisch.	H	-	-	-	-	+	+	-	-	-	-	-
Salviniaceae	*Azolla caroliniana* Willd.	H	+	+	+	-	-	+	+	+	-	-	-
	Azolla filiculoides Lam.	H	+	-	+	-	-	-	+	-	-	-	-
	Azolla mexicana C. Presl.	HF-F	+	-	-	-	+	+	+	+	-	-	-
	Azolla microphylla Kaulf.	H	-	-	-	-	-	-	+	-	-	-	-
	Salvinia auriculata Aubl.	HF-F	-	-	-	-	-	+	+	+	-	-	-
	Salvinia minima Baker	HF-F	-	-	-	+	+	+	+	+	-	-	-
Thelypteridaceae	*Macrothelypteris torresiana* (Gaudich.) Ching	HP	-	-	-	-	-	-	-	-	-	-	-
	Thelypteris angustifolia (Willd.) Proctor	HP	-	-	-	-	-	-	-	-	-	-	-
	Thelypteris interrupta (Willd.) Iwatsuki	H	-	-	-	+	+	+	+	-	-	-	-
	Thelypteris serrata (Cav.) Alston	H	-	-	-	+	+	+	+	-	-	-	-
Woodsiaceae	*Diplazium striatum* (L.) Presl.	H	-	-	-	-	-	-	-	-	-	-	-

Family	Species	Habit	HA	CF	VS	CP	AP	WW	CQ	GP	AS	TB	GC
Dicotyledons													
Acanthaceae	*Hygrophila costata* Nees (= *Hygrophila guianensis*)	HA/P	-	-	-	+	+	-	+	-	-	-	+
	Justicia calycina (Nees) V.A.W. Graham	H	-	-	-	-	-	+	+	-	-	-	-
	Justicia comata (L.) Sw.	H	-	-	-	+	+	+	+	-	-	-	-
	Justicia laevilinguis (Nees) Lindau	H	-	-	-	-	+	+	+	+	-	-	-
	Stenandrium dulce (Cav.) Nees	H	-	-	+	-	-	-	-	-	-	-	-
Aizoaceae	*Sesuvium portulacastrum* (L.) L.	H	-	-	-	-	-	-	-	-	-	-	-
Amaranthaceae	*Alternanthera aquatica* (D. Par.) Chodat	H	-	-	-	-	-	+	-	+	-	-	-
	Alternanthera caracasana H.B.K.	NK	+	-	-	-	-	-	-	-	-	-	-
	Alternanthera philoxeroides (Mart.) Griseb.	HF-S	-	-	-	-	-	+	+	+	-	-	-
	Alternanthera pilosa Moq.	H	-	-	-	-	-	-	-	-	-	-	-
	Alternanthera reineckii Briq.	H	-	-	-	-	+	-	-	-	-	-	-
	Amaranthus lividus L.	H	-	-	-	-	-	+	-	-	-	-	-
	Iresine diffusa Kunth	H	-	-	-	-	-	-	+	-	-	-	-
	Pfaffia stenophylla (Sprengel) Stuchlik	H	-	-	-	-	+	-	-	-	-	-	-
	Tapirira guianensis Aublet	T	-	-	-	+	-	+	+	-	-	-	-
Annonaceae	*Unonopsis guatterioides* (A. DC.) R. E. Fr.	T	-	-	-	-	-	+	-	-	-	-	-
Apiaceae	*Apium sellowianum* H. Wolff	H	-	-	+	-	-	-	-	-	-	-	-
	Conium maculatum L.	H	-	-	-	-	-	-	-	-	-	-	-
	Cyclospermum leptophyllum (Pers.) Sprague ex Britton & P. Wilson	NK	+	-	+	-	+	-	-	-	-	-	-
	Eryngium cf. *coronatum* Hook. & Arn.	H	+	-	-	-	-	-	-	-	-	-	-
	Eryngium ebracteatum Lam	H	-	-	+	-	+	+	+	-	-	-	-
	Hydrocotyle bonariensis Lam.	H	-	-	+	-	+	-	-	-	-	-	-
	Hydrocotyle bonplandii A. Rich	H	-	-	-	-	-	-	-	-	-	-	-
	Hydrocotyle leucocephala Cham. & Schltdl.	H	-	+	-	-	-	-	-	-	-	-	-
	Hydrocotyle pusilla A. Rich	H	+	+	-	-	-	-	-	-	-	-	-
	Hydrocotyle ranunculoides L.f	H	+	+	-	-	+	+	+	+	-	-	-
	Hydrocotyle verticillata Thunb.	H	-	-	-	-	+	-	-	-	-	-	+
	Lilaeopsis macloviana (Gandoger) A.W. Hill	HS	+	-	+	-	-	-	-	-	-	-	-
	Niphogeton dissecta (Benth.) F. Macbr.	NK	+	-	-	-	-	-	-	-	-	-	-

Family	Species	Habit	HA	CF	VS	CP	AP	WW	CQ	GP	AS	TB	GC
Apocynaceae	*Mesechites sanctae-crucis* (S. Moore) Woodson	NK	-	-	-	-	-	+	-	-	-	-	-
	Rhabdadenia biflora (Jacq.) Müell. Arg.	CL	-	-	-	-	-	-	+	-	-	-	-
	Rhabdadenia macrostoma (Benth.) Müell. Arg.	CL	-	-	-	+	-	+	+	-	-	-	-
	Rhabdadenia pohlii Müell. Arg.	CL	-	-	-	-	-	+	+	+	-	-	-
	Tabernaemontana catharinensis A. DC.	NK	-	-	-	-	-	+	-	-	-	-	-
	Tabernaemontana rupicola Benth.	S	-	-	-	-	-	-	-	-	-	-	-
	Thevetia bicornuta Müell. Arg.	S	-	-	-	-	-	-	-	+	-	-	-
Aquifoliaceae	*Ilex inundata* Poepp. ex Reissek	TU	-	-	-	-	-	+	+	-	-	-	-
Asclepiadaceae	*Cynanchum montevidense* Spreng.	CL	-	-	-	+	+	-	+	+	-	-	-
	Matelea rivularis Woodson	LH	-	-	-	-	-	-	-	-	-	-	-
	Sarcostemma clausum (Jacq.) Schult. in Roem. & Schult.	CL	-	-	-	-	-	+	+	+	-	-	-
	Tassadia cf. *grazielae* Fontana	CL	-	-	-	+	-	-	-	-	-	-	-
Asteraceae	*Acmella alba* (L'Hér.) R. K. Jansen	H	+	-	-	-	-	-	-	-	-	-	-
	Ageratum conyzoides L.	H	-	+	+	-	+	-	-	-	+	-	+
	Ambrosia peruviana Willd.	H	-	-	-	-	-	+	-	-	-	-	-
	Aspilia lucidula Blake	H	-	-	-	-	-	+	-	-	-	-	-
	Baccharis juncea (Lehm.) Desv.	H	+	+	+	-	+	-	-	-	-	-	-
	Baccharis salicifolia Nutt.	PS-W	-	-	+	-	-	+	-	-	-	-	-
	Baccharis trimera (Less) DC.	PS-W	-	+	-	-	-	-	-	-	-	-	-
	Barrosoa candolleana (Hook. & Arn.) R. M. King & H. Rob.	H	-	-	-	-	-	-	-	+	-	+	-
	Barrosoa confluentis (B. L. Rob.) R. M. King & H. Rob.	HP	-	-	-	+	+	+	+	+	-	-	-
	Bidens laevis (L.) Britton, Sterns & Poggenb.	H	-	-	+	-	-	-	-	-	-	-	-
	Chromolaena laevigata (Lam.) R. M. King & H. Rob	S	-	-	-	-	+	+	+	-	-	-	-
	Cotula australis (Sieb. ex Spreng) Hook.f	H	+	+	+	-	-	-	-	-	-	-	-
	Cotula coronopifolia L.	HF-S	+	-	+	-	-	-	-	-	-	-	-
	Cotula mexicana (DC.) Cabr.	H	+	+	+	-	-	-	-	-	-	-	-
	Eclipta prostrata (L.) L.	HA/P	-	-	+	+	+	+	+	+	+	+	-
	Emilia sonchifolia DC.	H	-	-	-	-	+	-	-	-	-	-	-
	Enhydra anagallis Gardner	H	-	-	-	-	+	+	+	+	-	-	-
	Erechtites hieraciifolia (L.) Raf. ex DC.	HA	-	-	-	+	-	+	+	+	-	-	-

Family	Species	Habit	HA	CF	VS	CP	AP	WW	CQ	GP	AS	TB	GC
	Gamochaeta americana (Miller) Wedd.	H	+	+	+	-	-	-	-	-	-	-	-
	Gymnocoronis spilanthoides DC.	H	-	-	-	-	+	+	+	-	-	-	-
	Jaegeria hirta (Lag.) Less.	H	-	-	-	-	-	-	-	-	+	-	-
	Lepidaploa remotiflora (L. C. Rich) H. Rob.	H	-	-	-	-	+	+	+	+	-	-	-
	Melanthera latifolia (Gardner) Cabrera	H	-	-	-	-	-	+	+	+	-	-	-
	Mikania congesta DC.	CL	-	-	-	+	+	+	+	-	-	-	-
	Mikania cordifolia Willd.	CL	-	-	-	-	-	-	-	+	-	-	-
	Mikania micrantha Kunth	CL	-	-	-	-	+	-	+	+	-	-	-
	Mikania psilostachya DC.	CL	-	-	-	+	-	+	+	-	-	-	-
	Milleria quinqueflora L.	NK	-	-	-	-	-	-	-	-	-	-	-
	Oritrophium limnophilum (Sch. Bip.) Cuatrec.	H	+	-	+	-	-	-	-	-	-	-	-
	Pacourina edulis Aubl.	H	-	-	-	-	-	+	-	+	-	-	-
	Plagiocheilus solivaeformis DC.	NK	-	-	-	-	-	-	-	-	-	-	-
	Pluchea absinthioides (Hook. & Arn.) H. Rob.	H	-	-	+	-	-	-	-	-	-	-	-
	Pluchea sagittalis (Lam.) Cabr.	H	-	-	+	-	+	+	+	-	-	-	-
	Senecio bonariensis Hook. & Arn.	H	-	-	+	-	-	-	-	-	-	-	-
	Sigesbeckia jorullensis H.B.K.	H	-	-	+	-	-	-	-	-	-	-	-
	Struchium sparganophorum (L.) Kuntze	H	-	-	-	-	-	-	+	-	-	-	-
	Tagetes filifolia Lag.	H	-	-	+	-	-	-	-	-	-	-	-
	Tessaria integrifolia Ruiz & Pavón	TU	-	-	+	+	+	+	-	-	+	-	-
	Trichospira verticillata (L.) Blake	H	-	-	-	-	-	+	-	-	-	-	-
	Vernonanthura brasiliana (L.) H. Rob.	S	-	-	-	-	-	+	+	+	-	-	-
	Vernonia rubricaulis H.B.K.	S	-	-	-	-	-	+	-	-	-	-	-
	Werneria marcida S. F. Blake	H	+	-	-	-	-	-	-	-	-	-	-
	Werneria pygmaea Gill ex. Hook.	H	+	-	-	-	-	-	-	-	-	-	-
	Werneria spathulata Wedd.	H	+	-	-	-	-	-	-	-	-	-	-
	Wulffia baccata O. Kuntz	H	-	-	-	-	-	+	+	-	-	-	-
Begoniaceae	*Begonia cucullata* Willd.	H	-	-	-	-	-	-	+	-	-	-	+
	Begonia fischeri Schrank	H	-	-	-	+	+	+	+	-	-	-	-
Bignoniaceae	*Arrabidaea bilabiata* (Sprague) Sandwith	CL	-	-	-	-	-	+	-	-	-	-	-

Family	Species	Habit	HA	CF	VS	CP	AP	WW	CQ	GP	AS	TB	GC
	Tabebuia barbata (E. Mey.) Sandwith	T	-	-	-	-	-	+	-	-	-	-	-
	Tabebuia heptaphylla (Vell.) Toledo	T	-	-	-	-	-	+	+	-	-	-	-
	Tabebuia insignis (Miquel) Sandw/	T	-	-	-	-	-	+	+	+	-	-	-
	Tabebuia nodosa Griseb.	T	-	-	-	-	+	+	-	-	-	-	-
Bombacaceae	*Ceiba pentandra* (L.) Gaertn.	T	-	-	-	-	+	-	+	-	-	-	-
	Pachira aquatica Aubl.	T	-	-	-	-	-	-	+	-	-	-	-
	Pseudobombax munguba (Mart. & Zucc.) Dugand	T	-	-	-	-	-	+	-	-	-	-	-
Boraginaceae	*Cordia tetrandra* Aubl.	T	-	-	-	+	+	+	+	-	-	-	-
	Heliotropium curassavicum L.	H	-	-	+	-	-	-	-	-	-	-	-
	Heliotropium filiforme Lehm.	H	-	-	-	-	-	+	-	-	-	-	-
	Heliotropium indicum L.	PS-W	-	-	-	-	-	+	+	-	-	-	-
	Heliotropium lagoense (Warm.) Gürke	H	-	-	-	-	-	+	-	-	-	-	-
	Myosotis scorpioides L.	H	+	-	-	-	-	-	-	-	-	-	-
Brassicaceae	*Cardamine bonariensis* Juss. ex Pers.	H	+	+	+	-	-	-	-	-	-	-	-
	Nasturtium officinale R. Br. (= *Rorippa nasturtium-aquaticum*)	H	+	-	+	-	-	-	-	-	-	-	-
	Rorippa bonariensis (Poiret) Macloskie	H	-	-	+	-	-	-	-	-	-	-	-
	Rorippa nana (Schltdl.) J.F. Macbr.	H	+	-	-	-	-	-	-	-	-	-	-
	Rorippa nasturtium-aquaticum (L.) Hayek	H	-	-	-	-	-	-	-	-	-	-	-
Cabombaceae	*Cabomba furcata* Schultes & Schultes.f	HS	-	-	-	+	+	+	+	+	-	-	-
Callitrichaceae	*Callitriche albomarginata* Fassett	HS	+	+	-	-	-	-	-	-	-	-	-
	Callitriche heteropoda Engelm. ex Hegelm.	HS	+	+	+	-	-	-	-	-	-	-	-
Calyceraceae	*Acicarpha tribuloides* Jussieu	H	-	-	+	-	-	-	-	-	-	-	-
Campanulaceae	*Sphenoclea zeylanica* Gaetrn.	HA/P	-	-	-	+	-	+	+	+	-	-	-
Capparaceae	*Cleome hassleriana* Chodat	H	-	-	-	-	-	-	-	-	-	-	-
	Cleome spinosa Jacq.	PS-W	-	-	-	-	-	-	+	+	-	-	-
	Crataeva tapia L.	TU	-	-	-	-	-	-	-	+	-	-	-
Caryophyllaceae	*Cerastium nutans* Raf.	H	+	+	-	-	-	-	-	-	-	-	-
	Cerastium rivulare Camb. in St.-Hil.	H	-	-	-	-	-	-	-	-	-	-	-
	Drymaria glandulosa C. Presl.	H	-	-	-	-	-	-	-	-	+	-	+
	Sagina procumbens L.	H	+	-	-	-	-	-	-	-	-	-	-

Family	Species	Habit	HA	CF	VS	CP	AP	WW	CQ	GP	AS	TB	GC
	Stellaria ovata Willd. ex Schlecht.	H	-	-	-	-	-	-	-	-	-	-	-
Celastraceae	*Hippocratea volubilis* L.	CL	-	-	-	-	+	+	+	-	-	-	-
	Peritassa laevigata (Hoffmsgg.) A. C. Smith	NK	-	-	-	-	-	+	+	-	-	-	-
Chenopodiaceae	*Chenopodium album* L.	H	-	-	-	-	-	-	-	-	-	-	-
Chrysobalanaceae	*Couepia uiti* Bentham	T	-	-	-	-	-	-	-	+	-	-	-
	Hirtella triandra Sw.	T	-	-	-	+	-	+	+	-	-	-	-
	Licania britteniana Fritsch	T	-	-	-	-	-	+	+	-	-	-	-
	Licania heteromorpha (C. Mart. ex Hook. f.) Benth.	T	-	-	-	-	-	+	+	-	-	-	-
	Parinari campestris Aubl.	S	-	-	-	-	-	-	+	-	-	-	-
Clusiaceae	*Calophyllum brasiliense* Cambess.	T	-	-	-	+	-	-	-	-	-	-	-
	Symphonia globulifera L.f.	T	-	-	-	-	-	-	+	-	-	-	-
	Vismia lauriformis (Lam.) Choisy	S	-	-	-	-	-	+	-	-	-	-	-
Combretaceae	*Buchenavia macrophylla* Eichler	T	-	-	-	-	-	-	+	-	-	-	-
	Combretum lanceolatum Pohl	S	-	-	-	-	-	+	+	+	-	-	-
	Combretum laxum Jacq.	LN	-	-	-	-	-	+	+	-	-	-	-
Convolvulaceae	*Aniseia cernua* Moric.	CL	-	-	-	-	-	+	+	-	-	-	-
	Aniseia martinicensis (Jacq.) Choisy	CL	-	-	-	-	+	+	+	+	-	-	-
	Ipomoea alba L.	CL	-	-	-	-	-	+	+	+	-	-	-
	Ipomoea anisomeres B.L. Rob. & Bartlett	CL	-	-	-	-	-	-	+	-	-	-	-
	Ipomoea carnea Jacq. subsp. *fistulosa* (Choisy) Austen	PS-W	-	-	-	-	-	+	+	+	-	-	-
	Ipomoea rubens Choisy	CL	-	-	-	-	+	+	-	+	-	-	-
	Ipomoea setifera Poir	CL	-	-	-	-	-	-	+	-	-	-	-
	Ipomoea squamosa Choisy in DC.	CL	-	-	-	-	-	-	+	-	-	-	-
	Ipomoea subrevoluta Choisy	CL	-	-	-	-	-	-	+	+	-	-	-
	Merremia umbellata (L.) Hall f.	CL	-	-	-	-	+	+	+	+	-	-	-
	Operculina hamiltonii (G. Don) D.F. Austin & Staples	CL	-	-	-	-	-	-	+	-	-	-	-
	Stictocardia tiliifolia (Desr.) Hallier f.	CL	-	-	-	-	-	-	-	+	-	-	-
	Tetralocularia pennellii O'Donnell	CL	-	-	-	-	-	+	+	-	-	-	-
Crassulaceae	*Crassula peduncularis* (Sm.) Meigen	H	+	-	-	-	-	-	-	-	-	-	-
	Crassula venezuelensis (Steyer.) Bywater & Wilkins	HS	+	+	+	-	-	-	-	-	-	-	-

Family	Species	Habit	HA	CF	VS	CP	AP	WW	CQ	GP	AS	TB	GC
Cucurbitaceae	*Cayaponia podantha* Cogn.	CL	-	-	-	-	-	-	-	+	-	-	-
	Cyclanthera hystrix (Gill.) Arn.	CL	+	-	+	-	-	-	-	-	-	-	-
	Melothria pendula L.	CL	-	-	-	-	+	-	+	-	-	-	-
Droseraceae	*Drosera communis* A. St. Hil.	H	-	-	-	-	-	-	+	-	-	-	-
	Drosera sessilifolia A. St. Hil.	H	-	-	-	-	-	-	+	-	-	-	-
Ebenaceae	*Diospyros nur* B. Walln.	T	-	-	-	-	-	+	-	-	-	-	-
	Diospyros yomomo B. Walln.	T	-	-	-	-	-	-	+	-	-	-	-
Elatinaceae	*Elatine peruviana* Baehni & Macbr.	HS	+	+	-	-	-	-	-	-	-	-	-
	Elatine triandra Schkuhr	HS	+	-	-	-	-	-	-	-	-	-	-
Euphorbiaceae	*Alchornea castaneifolia* (Willd.) A. Juss.	Shrub	-	-	-	-	-	+	-	+	-	-	-
	Alchornea schomburgkii Klotzsch	T	-	-	-	-	-	+	+	-	-	-	-
	Caperonia castaneifolia (L.) A. St.-Hil.	HF-S	-	-	-	-	+	+	+	+	-	-	-
	Caperonia palustris (L.) Saint-Hilaire	HA/P	-	-	-	+	+	+	+	+	-	-	-
	Chamaesyce hirta (L.) Millsp.	H	-	-	-	-	+	+	+	-	-	-	-
	Chamaesyce thymifolia (L.) Millsp.	H	-	-	+	-	-	+	+	-	-	-	-
	Croton argenteus L.	S	-	-	-	-	-	-	-	+	-	-	-
	Euphorbia peplus L.	H	-	-	+	-	-	-	-	-	-	-	-
	Hura crepitans L.	T	-	-	-	-	-	+	-	-	-	-	-
	Mabea nitida Spruce ex Benth.	T	-	-	-	-	-	+	+	-	-	-	-
	Maprounea guianensis Aubl.	T	-	-	-	-	-	-	+	-	-	-	-
	Phyllanthus fluitans Müell. Arg.	HF-F	-	-	-	-	-	+	+	+	-	-	-
	Phyllanthus hyssopifolioides Kunth	H	-	-	-	-	-	+	-	-	-	-	-
	Phyllanthus lindbergii Müell. Arg.	H	-	-	-	-	-	-	+	-	-	-	-
	Phyllanthus niruri L.	H	-	-	-	-	-	-	-	-	-	-	-
	Phyllanthus stipulatus (Raf.) Webster	H	-	-	-	-	+	+	+	-	-	-	-
	Sapium obovatum Klotzsch ex Müll. Arg.	T	-	-	-	-	-	+	-	-	-	-	-
	Sebastiania corniculata (Vahl) Müll. Arg.	H	-	-	-	-	-	+	+	-	-	-	-
Fabaceae	*Acacia farnesiana* (L.) Willd.	S	-	-	-	-	-	-	-	-	-	-	-
	Acosmium nitens (Vogel) Yakovlev	T	-	-	-	-	-	+	+	-	-	-	-
	Aeschynomene americana L.	H	-	-	-	-	-	+	-	-	-	-	-

Family	Species	Habit	HA	CF	VS	CP	AP	WW	CQ	GP	AS	TB	GC
	Aeschynomene ciliata Vog.	HA	-	-	-	-	-	+	-	-	-	-	-
	Aeschynomene denticulata Rudd	S	-	-	-	-	-	-	+	-	-	-	-
	Aeschynomene fluminensis Vell.	PS-W	-	-	-	-	+	+	+	+	-	-	-
	Aeschynomene montevidensis Vogel	NK	-	-	-	-	-	-	+	-	-	-	-
	Aeschynomene pratensis Small	PS-W	-	-	-	-	+	+	-	-	-	-	-
	Aeschynomene rudis Benth.	HP	-	-	-	+	-	+	+	-	-	-	-
	Aeschynomene scabra G. Don	S	-	-	-	-	-	+	-	-	-	-	-
	Aeschynomene sensitiva Swartz	H	-	-	-	-	+	+	+	+	-	-	-
	Albizia guachapele (Kunth) Dugand	T	-	-	-	-	-	-	-	-	-	-	-
	Albizia polyantha (Sprengel f.) G.P. Lewis	T	-	-	-	-	-	+	+	-	-	-	-
	Andira inermis (W. Wright) Kunth ex DC.	T	-	-	-	-	-	-	+	-	-	-	-
	Bauhinia bauhinioides (Mart.) J.F. Macbr.	T	-	-	-	-	-	-	+	+	-	-	-
	Bergeronia sericea Micheli	T	-	-	-	-	-	+	+	+	-	-	-
	Bowdichia virgilioides Kunth	T	-	-	-	-	-	+	+	-	-	-	-
	Calopogonium caeruleum (Benth.) Sauv.	CL	-	-	-	-	-	+	-	-	-	-	-
	Camptosema paraguariense (Chodat & Hassl.) Hassl.	CL	-	-	-	-	-	-	-	+	-	-	-
	Cassia grandis L. f.	T	-	-	-	-	-	-	+	-	-	-	-
	Centrosema bifidum Benth	CL	-	-	-	-	-	+	+	-	-	-	-
	Centrosema brasilianum (L.) Benth.	CL	-	-	-	-	-	+	+	-	-	-	-
	Centrosema pubescens Benth.	CL	-	-	-	-	+	-	+	-	-	-	-
	Centrosema vexillatum Benth.	CL	-	-	-	-	+	+	+	-	-	-	-
	Crotalaria pilosa Mill.	S	-	-	-	-	-	+	-	-	-	-	-
	Dalbergia riedelii (Benth.) Sandw.	TU	-	-	-	-	-	+	-	-	-	-	-
	Desmodium barbatum (L.) Benth.	PS-W	-	-	-	-	+	+	+	-	-	-	-
	Desmodium subsecundum Vogel	S	-	-	-	-	-	-	+	-	-	-	-
	Dioclea burkartii Maxwell	CL	-	-	-	-	-	-	-	+	-	-	-
	Discolobium pulchellum Benth.	S	-	-	-	-	-	-	-	+	-	-	-
	Dolichopsis paraguariensis Hassl.	HT	-	-	-	-	-	-	-	-	-	-	-
	Erythrina crista-galli L.	T	-	-	-	-	-	-	-	-	-	-	-
	Erythrina fusca Loureiro	T	-	-	-	-	-	+	-	-	-	-	-

Family	Species	Habit	HA	CF	VS	CP	AP	WW	CQ	GP	AS	TB	GC
	Goldmania paraguensis (Benth.) Brenan	T	-	-	-	-	-	+	+	-	-	-	-
	Inga edulis Mart.	T	-	-	-	-	-	+	+	-	-	-	-
	Inga umbellifera (Vahl) Steud. ex DC.	T	-	-	-	+	-	+	-	+	-	-	-
	Machaerium inundatum (Mart. ex Benth.) Ducke	T	-	-	-	-	-	-	+	-	-	-	-
	Machaerium leiophyllum (DC.) Benth.	T	-	-	-	-	-	+	+	-	-	-	-
	Macrolobium acaciifolium (Benth.) Benth.	T	-	-	-	-	-	+	+	-	-	-	-
	Macrolobium angustifolium (Benth.) R.S. Cowan	T	-	-	-	-	-	-	-	-	-	-	-
	Macrolobium multijugum (DC.) Benth.	T	-	-	-	-	-	+	+	-	-	-	-
	Macroptilium gracile (Poepp. ex Benth.) Urb.	NK	-	-	-	-	-	+	-	-	-	-	-
	Macroptilium lathyroides (L.) Urb.	H	-	-	-	-	-	+	+	+	-	-	-
	Mimosa debilis Humb. & Bonpl. ex Willd.	HP	-	-	-	-	+	+	+	-	-	-	-
	Mimosa pigra L. (= *Mimosa pellita* H. & B. ex Willd.)	S	-	-	-	+	+	+	+	+	-	-	-
	Mimosa schrankioides Benth.	S	-	-	-	-	-	+	-	-	-	-	-
	Mimosa weddelliana Benth.	S	-	-	-	-	-	-	-	+	-	-	-
	Mimosa xanthocentra C. Martius s.l.	S	-	-	-	-	-	+	+	+	-	-	-
	Neptunia natans (L.f.) Druce	HF-S	-	-	-	-	-	+	-	+	-	-	-
	Neptunia plena (L.) Benth.	S	-	-	-	-	-	+	-	+	-	-	-
	Parkinsonia aculeata L.	S	-	-	-	-	-	-	-	-	-	-	-
	Pithecellobium dulce (Roxb.) Benth.	T	-	-	-	-	-	-	-	-	-	-	-
	Pterocarpus santalinoides L'Her. ex DC.	TU	-	-	-	-	-	+	+	-	-	-	-
	Sclerolobium aureum (Tul.) Baill.	T	-	-	-	-	-	-	+	-	-	-	-
	Senna aculeata (Pohl ex Benth.) H.S. Irwin & Barneby	S	-	-	-	-	-	+	+	-	-	-	-
	Senna alata (L.) Roxb.	S	-	-	-	-	-	+	+	+	-	-	-
	Senna pendula (H. & B. ex Willd.) H. S. Irwin & Barneby	S	-	-	-	-	+	+	+	+	-	-	-
	Senna reticulata (Willd.) H.S. Irwin & Barneby	T	-	-	-	-	-	-	+	-	-	-	-
	Senna splendida (Vogel) H. S. Irwin & Barneby	S	-	-	-	-	-	-	+	+	-	-	-
	Sesbania exasperata Kunth	S	-	-	-	-	-	+	+	+	-	+	-
	Sesbania virgata (Cav.) Pers.	S	-	-	-	-	-	-	-	+	-	-	-
	Stylosanthes acuminata M. B. Ferreira & S. Costa	NK	-	-	-	-	-	-	+	-	-	-	-
	Trifolium amabile Kunth	H	+	-	-	-	-	-	-	-	-	-	-

Family	Species	Habit	HA	CF	VS	CP	AP	WW	CQ	GP	AS	TB	GC
	Vigna adenantha (G. F. Meyer) Maréchal	CL	-	-	-	-	+	-	-	-	-	-	-
	Vigna lasiocarpa (C. Mart. ex Benth.) Verdc.	CL	-	-	-	-	-	+	+	-	-	-	-
	Vigna longifolia (Benth.) Verdc.	CL	-	-	-	-	-	+	+	-	-	-	-
	Vigna luteola (Jacq.) Benth.	CL	-	-	-	-	-	-	+	+	-	-	-
	Vigna peduncularis Fawc. & Rendle	CL	-	-	-	-	-	-	+	+	-	-	-
	Zygia inaequalis (Humb. & Bonpl. ex Willd.) Pittier	TU	-	-	-	-	-	-	-	-	-	-	-
	Zygia latifolia (L.) Fawc. & Rendle	T	-	-	-	-	-	+	-	-	-	-	-
Flacourtiaceae	*Casearia aculeata* Jacq.	S	-	-	-	-	+	+	+	-	+	-	-
	Casearia grandiflora Cambess.	T	-	-	-	-	-	-	+	-	-	-	-
	Laetia corymbulosa Spruce ex Benth.	T	-	-	-	-	-	-	+	-	-	-	-
	Laetia suaveolens (Poeppig) Benth.	S	-	-	-	-	-	+	+	-	-	-	-
Gentianaceae	*Coutoubea ramosa* Aubl.	H	-	-	-	-	-	+	+	-	-	-	-
	Curtia tenuifolia (Aubl.) Knobl.	H	-	-	-	-	-	-	+	-	-	-	-
	Gentiana sedifolia Kunth (= *Gentiana prostrata* Haenke)	H	+	-	-	-	-	-	-	-	-	-	-
	Irlbachia caerulescens (Aubl.) Griseb.	H	-	-	-	-	-	-	+	-	-	-	-
	Schultesia australis Gris.	H	-	-	-	-	-	-	+	-	-	-	-
	Schultesia brachyptera Cham.	H	-	-	-	-	-	-	+	-	-	-	-
	Schultesia guianensis (Aubl.) Malme	H	-	-	-	-	-	+	+	-	-	-	-
Gesneriaceae	*Sinningia elatior* (Kunth) Chautems	H	-	-	-	-	-	-	+	-	-	-	-
	Sinningia sceptrum (Mart.) Wiehler	H	-	-	-	-	+	+	-	-	-	-	-
Haloragaceae	*Myriophyllum aquaticum* (Vellozo) Verdcourt	HS	-	-	+	-	-	-	-	-	-	-	-
	Myriophyllum mattogrossense Hoehne	HS	-	-	-	+	-	-	-	-	-	-	-
	Myriophyllum quitense H.B.K.	HS	+	-	+	-	-	-	-	-	-	-	-
Hydrophyllaceae	*Hydrolea elatior* Schott	PS-W	-	-	-	-	+	-	-	-	-	-	+
	Hydrolea spinosa L.	PS-W	-	-	-	-	+	+	+	-	-	-	-
Lamiaceae	*Hyptis atrorubens* Poir.	H	-	-	-	+	-	+	-	-	-	-	-
	Hyptis brevipes Benth.	HP	-	-	-	+	+	+	-	-	-	-	-
	Hyptis crenata Benth.	H	-	-	-	-	-	+	+	-	-	-	-
	Hyptis goyazensis Benth.	PS-W	-	-	-	-	-	-	+	-	-	-	-
	Hyptis lacustris St.-Hil. ex Bentham	PS-W	-	-	-	+	-	+	-	-	-	-	-

Family	Species	Habit	HA	CF	VS	CP	AP	WW	CQ	GP	AS	TB	GC
	Hyptis lantanifolia Poit.	HP	-	-	-	-	-	-	+	-	-	-	-
	Hyptis lappacea Benth.	H	-	-	-	-	-	+	-	-	-	-	-
	Hyptis lorentziana O. Hoffm.	H	-	-	-	-	+	+	-	-	-	-	-
	Hyptis microphylla Pohl ex Benth.	NK	-	-	-	-	-	+	+	-	-	-	-
	Hyptis mutabilis Brig.	H	-	-	-	-	+	-	+	-	-	-	-
	Hyptis parkeri Benth.	H	-	-	-	-	-	+	+	-	-	-	-
	Hyptis paupercula Epling	H	-	-	-	-	-	+	-	-	-	-	-
	Hyptis recurvata Poit.	HP	-	-	-	-	-	+	+	+	-	-	-
	Mentha aquatica L.	H	-	-	-	-	-	-	-	-	-	-	-
	Scutellaria racemosa Persoon	H	-	-	-	-	-	-	-	-	-	-	-
	Teucrium vesicarium Mill.	HP	-	-	-	-	+	-	+	-	-	-	-
Lauraceae	*Nectandra amazonum* Nees.	TU	-	-	-	-	-	+	+	-	-	-	-
	Ocotea diospyrifolia (Meissn.) Mez	TU	-	-	-	-	-	-	+	-	-	-	-
Lecythidaceae	*Eschweilera parviflora (Aubl.) Miers*	T	-	-	-	-	-	+	-	-	-	-	-
Lentibulariaceae	*Genlisea guianensis* N. E. Brown	H	-	-	-	-	-	-	+	-	-	-	-
	Utricularia amethystina Salzmann ex St. Hilaire & Girard	H	-	-	-	-	-	+	+	-	-	-	-
	Utricularia breviscapa Wright ex Grisebach	H	-	-	-	-	-	+	+	+	-	-	-
	Utricularia erectiflora A. St.-Hil. & Girard	H	-	-	-	-	-	+	-	-	-	-	-
	Utricularia foliosa L.	HSA	-	-	-	-	+	+	+	+	-	-	-
	Utricularia gibba L.	HSA	-	+	-	+	+	+	+	+	-	-	-
	Utricularia cf. *guyanensis* A. DC. in DC.	H	-	-	-	-	-	-	+	-	-	-	-
	Utricularia hispida Lam.	H	-	-	-	-	-	-	-	-	-	-	-
	Utricularia hydrocarpa Vahl	HSA	-	-	-	-	-	-	+	+	-	-	-
	Utricularia lloydii Merl.	H	-	-	-	-	-	+	-	-	-	-	-
	Utricularia meyeri Pilg.	H	-	-	-	-	-	-	+	-	-	-	-
	Utricularia myriocista A. St.-Hil. & Girard	HSA	-	-	-	-	-	-	+	-	-	-	-
	Utricularia nana St.-Hil.	H	-	-	-	-	-	-	+	-	-	-	-
	Utricularia neottioides A. St.-Hil.	H	-	-	-	-	-	-	+	-	-	-	-
	Utricularia nervosa G. Weber ex Benj. in Martius	H	-	-	-	-	-	-	+	-	-	-	-
	Utricularia oliveriana Steyermark	H	-	-	-	-	-	-	+	-	-	-	-

Family	Species	Habit	HA	CF	VS	CP	AP	WW	CQ	GP	AS	TB	GC
	Utricularia poconensis Fromm-Trinta	HSA	-	-	-	-	-	-	-	+	-	-	-
	Utricularia pusilla Vahl	H	-	-	-	-	-	-	+	-	-	-	-
	Utricularia simulans Pilger	H	-	-	-	-	-	-	+	-	-	-	-
	Utricularia subulata L.	H	-	-	-	-	-	+	+	-	-	-	-
	Utricularia trichophylla Spruce ex Oliver	H	-	-	-	-	-	-	-	-	-	-	-
	Utricularia tricolor A. St.-Hil.	H	-	-	-	-	+	-	+	-	-	-	-
	Utricularia triloba Benj. ex Mart.	H	-	-	-	-	-	-	-	-	-	-	-
	Utricularia warmingii Kamiénski	HSA	-	-	-	-	-	+	-	-	-	-	-
Loganiaceae	*Mitreola petiolata* (J.F. Gmel.) Torr. & A. Gray	H	-	-	-	-	-	-	+	-	-	-	-
	Strychnos darienensis Seem.	CL	-	-	-	-	-	-	-	-	-	-	-
Lythraceae	*Ammannia auriculata* Willd.	H	-	-	-	-	+	-	-	-	-	-	-
	Ammannia latifolia L.	H	-	-	-	-	+	-	-	-	-	-	-
	Cuphea antisyphilitica Kunth	H	-	-	-	-	-	+	+	-	-	-	-
	Cuphea carthagenensis (Jacq.) J. F. Macbr.	H	-	-	-	-	-	-	-	+	-	-	-
	Cuphea melvilla Lindl.	S	-	-	-	+	+	+	+	-	-	-	-
	Cuphea micrantha H.B.K.	H	-	-	-	-	-	-	+	-	-	-	-
	Cuphea odonellii Lourteig	NK	-	-	-	-	-	+	+	-	-	-	-
	Cuphea racemosa (L. f.) Spreng.	NK	-	-	+	-	-	-	-	-	-	-	-
	Cuphea repens Koehne	H	-	-	-	-	-	+	+	-	-	-	-
	Cuphea setosa Koehne	H	-	+	-	-	-	-	+	-	-	-	-
	Lythrum maritimum Kunth	H	-	-	-	-	-	-	-	-	-	-	-
	Rotala mexicana Schltdl. & Cham.	H	-	-	-	-	-	-	+	-	-	-	-
	Rotala ramosior (L.) Koehne	H	-	-	-	-	-	+	-	-	-	-	-
Malpighiaceae	*Byrsonima riparia* W. R. Anderson	TU	-	-	-	-	-	-	-	-	-	-	-
Malvaceae	*Hibiscus bifurcatus* Cav.	S	-	-	-	-	-	+	+	-	-	-	-
	Hibiscus furcellatus Lam.	S-S	-	-	-	-	-	+	+	+	-	-	-
	Hibiscus sororius L.	PS-W	-	-	-	+	+	-	+	+	-	-	-
	Hibiscus striatus Cav.	S	-	-	-	-	-	+	-	-	-	-	-
	Malachra radiata (L.) L.	PS-W	-	-	-	-	-	+	-	-	-	-	-
	Pavonia angustifolia Benth.	PS-W	-	-	-	-	-	+	+	-	-	-	-

Family	Species	Habit	HA	CF	VS	CP	AP	WW	CQ	GP	AS	TB	GC
	Pavonia fruticosa (Miller) Fawcett & Rendle	PS-W	-	-	-	+	-	+	+	-	-	-	-
	Pavonia paniculata Cav. var. *corymbosa* Gürke.	PS-W	-	-	-	-	-	-	-	-	-	-	-
	Peltaea riedelii (Gürke) Standley	PS-W	-	-	-	-	+	+	+	-	-	-	-
Melastomataceae	*Aciotis acuminifolia* (Mart. ex DC.) Triana	H	-	-	-	+	-	-	-	-	-	-	-
	Aciotis dichotoma (Benth.) Cogn.	H	-	-	-	-	-	+	+	-	-	-	-
	Acisanthera alsinaefolia (DC.) Triana	PS-W	-	-	-	-	+	-	+	-	-	-	-
	Acisanthera bivalvis (Aubl.) Cogn.	H	-	-	-	-	-	-	+	-	-	-	-
	Acisanthera crassipes (Naudin) Wurdack	H	-	-	-	-	-	-	+	-	-	-	-
	Acisanthera limnobios (DC.) Triana	H	-	-	-	-	+	-	+	-	-	-	-
	Acisanthera quadrata Pers.	PS-W	-	-	-	-	-	+	-	-	-	-	-
	Acisanthera uniflora (Vahl) Gleason	PS-W	-	-	-	-	-	-	+	-	-	-	-
	Clidemia bullosa DC.	S	-	-	-	-	-	+	+	-	-	-	-
	Clidemia capitellata (Bonpl.) D. Don	S	-	-	-	+	-	+	+	-	-	-	-
	Desmoscelis villosa (Aubl.) Naud.	HP	-	-	-	-	-	+	+	-	-	-	-
	Mouriri apiranga Spruce ex Triana	TU	-	-	-	-	-	-	+	-	-	-	-
	Mouriri guianensis Aubl.	T	-	-	-	-	-	+	+	-	-	-	-
	Macairea radula (Bonpl.) DC.	S	-	-	-	-	-	-	+	-	-	-	-
	Poteranthera pusilla Bong.	H	-	-	-	-	-	-	+	-	-	-	-
	Pterolepis glomerata (Rottb.) Miq.	H	-	-	-	-	-	-	+	-	-	-	-
	Rhynchanthera bracteata Triana	S	-	-	-	-	-	+	-	-	-	-	-
	Rhynchanthera gardneri Naudin	S	-	-	-	-	-	-	+	-	-	-	-
	Rhynchanthera grandiflora (Aubl.) DC.	S	-	-	-	-	+	+	-	-	-	-	-
	Rhynchanthera novemnervia (Martius) DC.	S-S	-	-	-	-	-	+	+	+	-	-	-
	Siphanthera foliosa (Naud.) Wurdack	H	-	-	-	-	-	+	+	-	-	-	-
	Tibouchina gracilis (Bonpl.) Cogn.	S	-	-	-	-	+	-	-	-	-	-	-
	Tibouchina spruceana Cogn.	S	-	-	-	-	-	+	-	-	-	-	-
Meliaceae	*Cedrela odorata* L.	T	-	-	-	-	-	-	-	-	-	-	-
	Trichilia singularis C. DC.	T	-	-	-	-	-	-	-	-	-	-	-
Menyanthaceae	*Nymphoides herzogii* A. Galán & G. Navarro	RFL	-	-	-	-	-	-	-	-	-	-	-
	Nymphoides indica (L.) O. Kuntze	H	-	-	-	-	+	+	+	-	-	-	-

Family	Species	Habit	HA	CF	VS	CP	AP	WW	CQ	GP	AS	TB	GC
	Nymphoides verrucosa (R. W. Fries) Galán de Mera et Navarro	RFL	-	-	-	-	-	-	-	-	-	-	+
Molluginaceae	*Glinus radiatus* (Ruiz y Pavón) Rohrb.	H	-	-	-	-	-	+	+	-	-	-	-
Moraceae	*Brosimum lactescens* (S. Moore) C. C. Berg.	T	-	-	-	-	-	-	+	-	-	-	-
	Cecropia latiloba Miq.	T	-	-	-	-	-	-	+	-	-	-	-
Myristicaceae	*Virola elongata* (Benth.) Warb.	T	-	-	-	-	-	+	+	-	-	-	-
Myrtaceae	*Calyptranthes fasciculata* O. Berg	TU	-	-	-	-	-	-	+	-	-	-	-
	Eugenia florida DC.	TU	-	-	-	+	-	+	+	-	-	-	-
	Myrcia fallax (Rich.) DC.	S	-	-	-	-	-	-	+	+	-	-	-
	Myrciaria dubia (Kunth) McVaugh	T	-	-	-	-	-	-	-	-	-	-	-
	Myrciaria floribunda (West ex Willd.) O. Berg	TU	-	-	-	-	-	+	+	-	-	-	-
Nymphaeaceae	*Nymphaea amazonum* Mart. & Zuccarini	RFL	-	-	-	+	-	+	+	+	-	-	-
	Nymphaea ampla (Salisb.) DC.	RFL	-	-	-	-	-	+	-	-	-	-	-
	Nymphaea belophylla Trickett	RFL	-	-	-	-	-	-	-	+	-	-	-
	Nymphaea gardneriana Planchon	RFL	-	-	-	-	-	-	+	+	-	-	-
	Nymphaea glandulifera Rodschied	RFL	-	-	-	+	-	+	-	-	-	-	-
	Nymphaea jamesoniana Planchon	RFL	-	-	-	-	-	-	+	-	-	-	-
	Nymphaea lingulata Wiersema	RFL	-	-	-	-	-	-	-	-	-	-	+
	Nymphaea oxypetala Planchon	H	-	-	-	-	-	-	+	+	-	-	-
	Nymphaea rudgeana G. F. W. Meyer	RFL	-	-	-	-	-	-	-	-	-	-	-
	Victoria amazonica (Poepp.) Sower	RFL	-	-	-	-	-	+	-	+	-	-	-
Ochnaceae	*Sauvagesia deflexifolia* Gardner	H	-	-	-	-	-	+	+	-	-	-	-
	Sauvagesia erecta L.	HA	-	-	-	+	+	+	+	-	-	-	-
	Sauvagesia nana Ule	H	-	-	-	-	-	+	-	-	-	-	-
Onagraceae	*Epilobium denticulatum* R. & P.	H	-	-	-	-	-	-	-	-	-	-	-
	Ludwigia affinis (DC.) Hara	HA/P	-	-	-	+	-	+	+	+	-	-	-
	Ludwigia bonariensis (Micheli) H. Hara	H	-	-	-	-	+	-	-	-	-	+	-
	Ludwigia bullata (Hassler) Hara	S	-	-	-	-	-	-	-	-	-	-	-
	Ludwigia decurrens Walt.	H	-	-	-	+	-	+	+	+	-	-	-
	Ludwigia densiflora (Micheli) H. Hara	HA	-	-	-	-	-	-	-	-	-	-	-
	Ludwigia elegans (Camb.) H. Hara	PSF	-	-	-	-	-	+	-	+	-	-	-

Family	Species	Habit	HA	CF	VS	CP	AP	WW	CQ	GP	AS	TB	GC
	Ludwigia erecta (L.) Hara	HA	-	-	-	-	-	+	+	-	-	-	-
	Ludwigia filiformis (Micheli) Ramamoorthy	H	-	-	-	-	-	-	+	-	-	-	-
	Ludwigia foliobracteolata (Munz) H. Hara	S	-	-	-	-	-	-	-	-	-	-	-
	Ludwigia grandiflora (Michaux) Greuter & Burdet	S	-	-	+	-	-	-	-	+	-	-	-
	Ludwigia helminthorrhiza (Mart.) Hara	HF-S	-	-	-	-	+	+	+	+	-	-	-
	Ludwigia hyssopifolia (G. Don) Exell	HP	-	-	-	-	-	+	-	-	-	-	-
	Ludwigia inclinata (L.f) Gómez	H	-	-	-	+	-	+	+	-	-	-	-
	Ludwigia latifolia (Benth.) Hara	S	-	-	-	+	-	-	-	-	-	-	-
	Ludwigia leptocarpa (Nutt.) Hara	PS-W	-	-	-	+	+	+	+	+	-	-	+
	Ludwigia longifolia (DC.) H. Hara	H	-	-	-	-	-	-	-	-	-	-	-
	Ludwigia martii (Micheli) Ramamoorthy	S	-	-	-	-	+	-	+	-	-	-	-
	Ludwigia nervosa (Poiret) Hara	S	-	-	-	+	+	+	+	+	-	-	-
	Ludwigia octovalvis (Jacq.) Raven	PS-W	-	-	-	+	+	+	+	-	+	-	+
	Ludwigia peploides (H.B.K.) Raven	S	+	-	+	-	-	-	+	-	-	+	-
	Ludwigia peruviana (L.) Hara	PSF	-	+	-	-	+	+	+	+	+	-	+
	Ludwigia rigida (Miquel) Sandw/	PSF	-	-	-	-	-	+	+	-	-	-	-
	Ludwigia sedoides (H. & B.) Hara	HP	-	-	-	-	+	+	+	+	-	-	-
	Ludwigia sericea (Cambess.) Hara	S	-	-	-	-	-	-	-	-	-	-	-
	Ludwigia tomentosa (Cambess.) H. Hara	S	-	-	-	-	-	-	-	+	-	-	-
	Ludwigia torulosa (Arnott) Hara	PS-W	-	-	-	-	-	+	+	-	-	-	-
Oxalidaceae	*Oxalis spiralis* Ruiz & Pavón ex G. Don	H	-	+	-	-	-	-	-	-	-	-	-
Passifloraceae	*Passiflora caerulea* L.	CL	+	-	-	-	-	-	-	-	-	-	-
Piperaceae	*Piper aduncum* L.	S	-	-	-	-	+	-	+	+	-	-	-
	Piper fuligineum Kunth	S	-	-	-	-	-	-	+	+	-	-	-
Plantaginaceae	*Plantago myosuros* Lam.	H	-	-	-	-	-	-	-	-	-	-	-
	Plantago rigida Kunth	H	+	+	-	-	-	-	-	-	-	-	-
	Plantago tubulosa Decne.	H	+	-	-	-	-	-	-	-	-	-	-

Family	Species	Habit	HA	CF	VS	CP	AP	WW	CQ	GP	AS	TB	GC
Podostemaceae	*Apinagia boliviana* P. Royen	HR	-	-	-	-	-	-	-	-	+	-	-
	Apinagia fluitans P. Royen	HR	-	-	-	-	-	+	-	-	-	-	-
	Apinagia cf. *pilgeri* Mildbraed	HR	-	-	-	-	-	-	+	-	-	-	-
	cf. *Mourera*	HR	-	-	-	-	-	+	-	-	-	-	-
	cf. *Podostemum*	HR	-	-	-	-	-	-	+	-	-	-	-
	Tristicha trifaria (Willd.) Spreng.	HR	-	-	-	-	-	-	+	-	-	-	-
Polygalaceae	*Polygala boliviensis* A.W. Benn.	H	-	-	-	-	+	-	+	-	-	-	-
	Polygala leptocaulis Torr. & A. Gray	H	-	-	-	-	+	+	+	-	-	-	-
	Polygala microspora Blake	H	-	-	-	-	-	-	+	-	-	-	-
	Polygala subtilis Kunth	H	-	-	-	-	-	+	-	-	-	-	-
	Polygala timoutou Aubl.	H	-	-	-	-	-	+	+	-	-	-	-
Polygonaceae	*Coccoloba densifrons* Mart. ex Meisn.	S	-	-	-	-	-	+	+	-	-	-	-
	Coccoloba ovata Bentham	S	-	-	-	-	-	-	-	+	-	-	-
	Muehlenbeckia sagittifolia (Ortega) Meisn.	S	-	-	-	-	-	-	-	-	-	-	-
	Polygonum acuminatum Kunth	H	-	-	-	-	+	+	+	+	-	-	+
	Polygonum ferrugineum Wedd.	HP	-	-	-	+	+	+	-	+	-	-	-
	Polygonum glabrum Willd.	H	-	-	-	-	-	+	-	-	-	-	+
	Polygonum hispidum Kunth	H	-	-	-	-	+	+	+	-	-	-	+
	Polygonum hydropiperoides Michx.	HP	-	+	+	+	+	+	+	+	+	-	-
	Polygonum lapathifolium Poir.	H	-	-	+	-	-	-	-	-	-	-	-
	Polygonum meisnerianum Cham. et Schltdl.	HP	-	-	-	+	-	-	+	-	-	-	+
	Polygonum paraguayense Wedd.	H	-	-	-	-	-	-	-	-	-	+	-
	Polygonum persicaria L.	H	-	-	+	-	-	-	-	-	-	-	-
	Polygonum punctatum Elliot	HA/P	-	+	+	+	+	+	+	+	-	-	+
	Rumex conglomeratus Murray	H	+	-	+	-	-	-	-	-	-	-	-
	Rumex crispus L.	H	-	-	+	-	-	-	-	-	-	-	-
	Rumex obtusifolius L.	H	-	-	-	-	-	-	-	-	-	-	-
	Symmeria paniculata Benth.	TU	-	-	-	-	-	+	+	-	-	-	-
	Triplaris americana L.	T	-	-	-	+	+	-	+	-	-	-	-
	Triplaris gardneriana Wedd.	T	-	-	-	-	-	-	+	+	-	-	-

Family	Species	Habit	HA	CF	VS	CP	AP	WW	CQ	GP	AS	TB	GC
Portulacaceae	*Montia fontana* L.	H	-	-	-	-	-	-	-	-	-	-	-
	Portulaca cryptopetala Speg.	H	-	-	-	-	-	+	-	-	-	-	-
Primulaceae	*Anagallis pumila* Sw.	H	-	-	-	-	+	-	-	-	-	-	-
Proteaceae	*Panopsis rubescens* (Pohl) Rusby	NK	-	-	-	-	-	+	+	-	-	-	-
Quiinaceae	*Quiina rhytidopus* Tul.	T	-	-	-	-	-	-	-	-	-	-	-
Ranunculaceae	*Ranunculus breviscapus* DC.	H	-	-	-	-	-	-	-	-	-	-	-
	Ranunculus flagelliformis Smith	H	+	+	+	-	-	-	-	-	-	-	-
	Ranunculus limoselloides Turcz.	H	+	-	-	-	-	-	-	-	-	-	-
	Ranunculus psychrophilus Wedd.	H	+	+	+	-	-	-	-	-	-	-	-
	Ranunculus sarmentosus Griseb.	H	-	+	-	-	-	-	-	-	-	-	-
	Ranunculus trichophyllus Chaix	H	+	-	-	-	-	-	-	-	-	-	-
Rosaceae	*Lachemilla aphanoides* (Mutis ex L. f.) Rothm.	HT	-	-	-	-	-	-	-	-	-	-	-
	Lachemilla diplophylla (Diels) Rothm.	H	+	-	-	-	-	-	-	-	-	-	-
	Lachemilla aphanoides (Mutis ex L. f.) Rothm.	HT	-	-	-	-	-	-	-	-	-	-	-
Rubiaceae	*Borreria capitata* (Ruiz & Pavón) DC.	H	-	-	-	-	+	+	+	-	-	-	-
	Borreria densiflora DC.	H	-	-	-	-	-	-	-	-	-	-	-
	Borreria scabiosoides Cham. & Schl.	H	-	-	-	-	-	-	+	-	-	-	-
	Borreria verticillata (L.) G. Mey.	H	-	-	-	-	-	+	-	-	+	-	-
	Calycophyllum spruceanum (Benth.) Hook. f. ex K. Schum.	T	-	-	-	-	-	-	+	-	-	-	-
	Chomelia barbellata Standley	TU	-	-	-	-	-	-	+	-	-	-	-
	Coccocypselum hirsutum Bartl. ex DC.	H	-	-	-	+	-	-	-	-	-	-	-
	Diodia kuntzei Schumann	H	-	-	-	-	-	+	+	-	-	-	-
	Diodia macrophylla K. Schum.	H	-	-	-	-	+	+	+	-	-	-	-
	Diodia multiflora DC.	H	-	-	-	-	-	+	+	-	-	-	-
	Genipa americana L.	T	-	-	-	+	+	+	+	+	-	-	-
	Genipa spruceana Steyerm.	T	-	-	-	-	-	-	+	-	-	-	-
	Hedyotis salzmannii (DC.) Steud.	H	-	-	-	-	+	-	-	-	-	-	-
	Hemidiodia ocymifolia (Willd. ex Roem. & Schult.) K. Schum.	H	-	-	-	-	+	+	+	-	-	-	-
	Limnosipanea spruceana Hook. f.	H	-	-	-	-	-	-	+	-	-	-	-
	Oldenlandia lancifolia (Schumach.) DC.	HA/P	-	-	-	+	-	+	+	-	-	-	-

Family	Species	Habit	HA	CF	VS	CP	AP	WW	CQ	GP	AS	TB	GC
	Perama hirsuta Aubl.	H	-	-	-	-	-	-	+	-	-	-	-
	Psychotria anceps Kunth	T	-	-	-	-	-	+	-	-	-	-	-
	Psychotria lupulina Benth.	S	-	-	-	-	-	+	+	-	-	-	-
	Rudgea cornifolia (Kunth) Standl.	TU	-	-	-	-	-	-	+	+	-	-	-
	Sabicea novo-granatensis K. Schum.	CL	-	-	-	+	-	-	-	-	-	-	-
	Sabicea villosa Willd. ex Roem. & Schult.	CL	-	-	-	+	-	+	+	-	-	-	-
	Sipanea acinifolia Spruce ex Sprague	H	-	-	-	-	-	+	-	-	-	-	-
	Sipanea hispida Benth. ex Wernham	H	-	-	-	-	-	+	+	-	-	-	-
	Spermacoce glabra Michx.	H	-	-	-	-	-	+	-	-	-	-	-
Salicaceae	*Salix humboldtiana* Willd.	TU	-	-	+	-	-	-	-	-	-	+	-
Sapindaceae	*Cupania cinerea* Poeppig & Endl.	T	-	-	-	-	-	+	+	-	-	-	-
	Paullinia pinnata L.	LN	-	-	-	+	-	+	+	+	-	-	-
Sapotaceae	*Manilkara inundata* (Ducke) Ducke	T	-	-	-	-	-	+	-	-	-	-	-
	Pouteria cuspidata (A. DC.) Baehni	T	-	-	-	-	-	+	+	-	-	-	-
	Pouteria elegans (A. DC.) Baehni	T	-	-	-	-	-	-	-	-	-	-	-
	Pouteria glomerata (Pohl ex Miq.) Radlk.	T	-	-	-	-	-	-	+	-	-	-	-
Scrophulariaceae	*Alectra aspera* (Cham. & Schltdl.) L. O. Williams	H	-	-	-	-	-	+	+	+	-	-	-
	Bacopa aquatica Aublet	HS	-	-	-	-	+	-	-	-	-	-	-
	Bacopa axillaris (Benth.) Standl.	H	-	-	-	-	-	+	+	-	-	-	-
	Bacopa laxiflora (Benth.) Wettst. ex Edwall	H	-	-	-	-	-	+	-	-	-	-	-
	Bacopa monnieri (L.) Pennell	H	-	-	+	-	-	+	-	-	-	-	-
	Bacopa monnierioides (Cham.) B.L. Rob.	H	-	-	-	-	-	+	-	-	-	-	-
	Bacopa myriophylloides (Benth.) Wettstein	H	-	-	-	-	-	+	+	-	-	-	-
	Bacopa reptans (Benth.) Wettst. ex Edwall	H	-	-	-	-	-	-	+	-	-	-	-
	Bacopa salzmannii (Benth.) Edwall	H	-	-	-	-	+	-	+	+	-	-	+
	Bacopa sp. nov. (?)	H	-	-	-	-	-	-	+	-	-	-	-
	Bacopa stricta (Scrad.) Edwall	H	-	-	-	-	-	+	+	+	-	-	-
	Bacopa tweedii (Bentham) Parodi	H	-	-	-	-	-	+	+	-	-	-	-
	Benjaminia reflexa (Benth.) D'arcy	HS	-	-	-	-	-	+	+	-	-	-	-
	Buchnera longifolia H.B.K.	HP	-	-	-	-	-	+	-	-	-	-	-

Family	Species	Habit	HA	CF	VS	CP	AP	WW	CQ	GP	AS	TB	GC
	Calceolaria aquatica A. Br. & Bouché	H	+	+	+	-	-	-	-	-	-	-	-
	Castilleja communis Benth. en DC.	H	-	-	-	-	-	-	-	-	-	-	-
	Castilleja pumila Wedd.	H	+	-	-	-	-	-	-	-	-	-	-
	Escobedia grandiflora (L. f.) Kuntze	NK	-	-	-	-	-	-	-	-	-	-	-
	Limnophila sp. nov.	HS	-	-	-	-	-	-	+	-	-	-	-
	Limosella aquatica L.	HS	+	-	-	-	-	-	-	-	-	-	-
	Limosella subulata Ives	HS	+	-	-	-	-	-	-	-	-	-	-
	Lindernia brachyphylla Pennell	H	-	-	-	-	-	-	+	-	-	-	-
	Lindernia crustacea (L.) F. Müell.	H	-	-	-	-	-	+	-	-	-	-	-
	Lindernia microcalyx Pennell & Stehle	H	-	-	-	-	-	+	-	-	-	-	-
	Mimulus glabratus Kunth	H	+	+	+	-	-	-	-	-	-	-	-
	Scoparia dulcis L.	H	-	-	-	+	+	+	+	-	+	-	-
	Scoparia nudicaulis Chodat	H	-	-	+	-	-	-	-	-	-	-	-
	Stemodia hyptoides Cham. & Schlecht.	H	-	-	+	-	+	-	-	-	-	-	-
	Torenia thouarsii (Cham. & Schltd.) O. Kuntze	HA	-	-	-	+	+	-	-	-	-	-	-
	Veronica anagallis-aquatica L.	H	+	-	+	-	-	-	-	-	-	-	-
	Veronica peregrina L.	H	-	+	+	-	-	-	-	-	-	-	-
	Veronica serpyllifolia L.	H	+	+	-	-	-	-	-	-	-	-	-
Solanaceae	*Solanum amygdalifolium* Steud.	CL	-	-	-	-	-	-	-	-	-	-	-
	Solanum glaucophyllum Desf.	S	-	-	-	-	-	-	+	+	-	-	-
	Solanum stramoniifolium Jacq.	NK	-	-	-	-	-	+	+	-	-	-	-
Sterculiaceae	*Byttneria divaricata* Benth.	S	-	-	-	-	-	-	+	-	-	-	-
	Byttneria filipes Mart.	PS-W	-	-	-	-	+	-	-	+	-	-	-
	Byttneria genistella Triana & Planchon	PS-W	-	-	-	-	-	+	+	-	-	-	-
	Byttneria scabra L.	PS-W	-	-	-	-	-	-	+	-	-	-	-
	Melochia arenosa Benth.	PS-W	-	-	-	-	-	+	+	+	-	-	-
	Melochia graminifolia St. Hil.	PS-W	-	-	-	-	-	+	+	-	-	-	-
	Melochia parvifolia Kunth	PS-W	-	-	-	-	-	+	+	-	-	-	-
	Melochia villosa (Mill.) Fawc. & Rendle	PS-W	-	-	-	-	-	+	+	-	-	-	-
Tiliaceae	*Corchorus hirtus* L.	NK	-	-	-	-	-	+	-	-	-	-	-

Family	Species	Habit	HA	CF	VS	CP	AP	WW	CQ	GP	AS	TB	GC
	Lueheopsis hoehnei Burret	T	-	-	-	-	-	+	+	-	-	-	-
	Mollia lepidota Spruce ex Benth.	T	-	-	-	-	-	+	+	-	-	-	-
	Muntingia calabura L.	T	-	-	-	-	-	-	-	-	-	-	-
Turneraceae	*Turnera melochia* Triana & Planch.	NK	-	-	-	-	-	+	-	-	-	-	-
Urticaceae	*Boehmeria cylindrica* (L.) Willd.	H	-	-	+	-	-	-	-	-	-	-	-
Verbenaceae	*Baillonia amabilis* Bocq.	S	-	-	-	-	-	-	+	+	-	-	-
	Lippia alba (Miller) N.E. Brown	S	-	-	-	-	-	+	+	+	-	-	-
	Phyla nodiflora (L.) Greene	H	-	-	-	-	-	-	+	+	-	-	-
	Stachytarpheta elatior Schrad. ex Schult.	H	-	-	-	-	-	-	-	+	-	-	-
	Verbena bonariensis L.	H	+	-	-	-	-	-	-	-	+	-	-
	Verbena hispida Ruiz & Pavón	H	-	-	-	-	-	-	-	-	-	-	-
	Vitex cymosa Bertero ex Spreng.	T	-	-	-	-	+	+	+	+	-	-	-
Vitaceae	*Cissus erosa* L.C. Rich.	CL	-	-	-	+	-	+	+	-	-	-	-
	Cissus palmata Poir.	CL	-	-	-	-	+	+	+	-	-	-	-
	Cissus spinosa Camb.	CL	-	-	-	-	-	+	+	+	-	-	-
	Cissus tweediana (Bak.) Planchon	CL	-	-	-	-	-	-	-	-	-	+	-
Vochysiaceae	*Vochysia divergens* Pohl	T	-	-	-	-	-	+	+	-	-	-	-
Monocotyledons													
Alismataceae	*Echinodorus aschersonianus* Graebner	H	-	-	-	-	-	-	+	-	-	-	-
	Echinodorus bolivianus (Rusby) Holm-Nielson	H	-	-	-	-	+	+	+	-	-	-	+
	Echinodorus grandiflorus (Cham. & Schltdl.) Micheli	H	-	-	-	-	+	+	+	-	-	-	-
	Echinodorus grisebachii Small	H	-	-	-	-	-	+	+	-	-	-	-
	Echinodorus macrophyllus (Kunth) Micheli ex A. & C. DC.	H	-	-	-	-	-	+	+	-	-	-	-
	Echinodorus paniculatus Micheli	H	-	-	-	-	-	+	+	+	-	-	+
	Echinodorus subalatus (Mart.) Grisebach	HP	-	-	-	+	-	+	+	-	-	-	-
	Echinodorus tenellus (Mart.) Buchenau	H	-	-	-	-	-	-	+	-	-	-	-
	Sagittaria guayanensis Kunth	RFL	-	-	-	-	+	+	+	-	-	-	-
	Sagittaria lancifolia L.	H	-	-	-	-	-	-	-	-	-	-	-
	Sagittaria montevidensis Chamisso & Schleectendal	H	-	-	-	-	+	+	-	-	-	-	-

Family	Species	Habit	HA	CF	VS	CP	AP	WW	CQ	GP	AS	TB	GC
	Sagittaria rhombifolia Chamisso	H	-	-	-	-	-	+	+	+	-	-	-
Amaryllidaceae	*Curculigo scorzonerifolia* (Lam.) Baker	H	-	-	-	-	-	-	+	-	-	-	-
Araceae	*Pistia stratiotes* L.	HF-F	-	-	-	+	+	+	+	+	-	-	-
	Philodendron tweedieanum Schott	H	-	-	-	-	-	-	+	-	-	-	-
	Urospatha sagittifolia (Rudge) Schott.	H	-	-	-	-	-	+	+	-	-	-	-
	Xanthosoma striatipes (Kunth & Bouché) Madison	H	-	-	-	-	-	+	+	-	-	-	-
	Zantedeschia aethiopica (L.) Spreng.	NK	-	-	-	-	-	-	-	-	-	-	-
Arecaceae	*Astrocaryum murumuru* Mart.	T	-	-	-	-	-	+	-	-	-	-	-
	Attalea maripa (Aubl.) Mart.	T	-	-	-	-	-	-	-	-	-	-	-
	Bactris glaucescens Drude	T	-	-	-	-	-	+	+	-	-	-	-
	Bactris major Jacq.	T	-	-	-	-	-	-	+	-	-	-	-
	Bactris maraja Mart.	T	-	-	-	-	-	-	-	-	-	-	-
	Bactris riparia Mart.	T	-	-	-	-	-	-	+	-	-	-	-
	Copernicia alba Mor. ex Mor. & Britt.	T	-	-	-	-	-	+	-	+	-	-	-
	Euterpe precatoria Mart.	T	-	-	-	-	-	-	-	-	-	-	-
	Mauritia flexuosa C. Mart.	T	-	-	-	-	-	+	+	-	-	-	-
	Mauritiella aculeata (Kunth) Burret	T	-	-	-	-	-	+	+	-	-	-	-
	Mauritiella armata (Mart.) Burret	T	-	-	-	-	-	+	+	-	-	-	-
	Oenocarpus bataua Mart	T	-	-	-	-	-	-	-	-	-	-	-
	Oenocarpus distichus Mart.	T	-	-	-	-	-	-	+	-	-	-	-
	Oenocarpus mapora Karst.	T	-	-	-	-	-	-	-	-	-	-	-
Burmanniaceae	*Burmannia bicolor* Mart.	HA	-	-	-	-	-	+	+	-	-	-	-
	Burmannia capitata (Walter ex J.F. Gmel.) Mart.	H	-	-	-	-	-	+	-	-	-	-	-
	Burmannia flava Martius	H	-	-	-	-	+	-	+	-	-	-	-
Cannaceae	*Canna glauca* L.	H	-	-	-	-	-	+	+	+	-	-	-
	Canna indica L.	H	-	-	-	-	-	-	+	-	-	-	-
Commelinaceae	*Commelina diffusa* Burm.f	H	-	-	-	-	+	-	+	-	-	-	+
	Commelina erecta Chapm.	H	-	-	-	-	+	+	+	+	-	-	-
	Floscopa glabrata (Kunth) Hassk.	H	-	-	-	-	-	-	+	-	-	-	-
Costaceae	*Costus arabicus* L.	HP	-	-	-	+	-	+	+	-	-	-	-

Family	Species	Habit	HA	CF	VS	CP	AP	WW	CQ	GP	AS	TB	GC
	Costus scaber Ruiz & Pavón	H	-	-	-	+	+	+	+	-	+	-	-
Cyclanthaceae	*Carludovica palmata* Ruiz & Pavón	H	-	-	-	-	-	-	-	-	-	-	-
Cyperaceae	*Ascolepis brasiliensis* (Kunth) Benth ex C. B. Clarke	H	-	-	-	-	+	-	-	-	-	-	-
	Bulbostylis capillaris C. B. Clarke	H	-	-	-	-	+	+	+	-	-	-	-
	Calyptrocarya glomerulata (Brogn.) Urban	HP	-	-	-	+	-	-	+	-	-	-	-
	Calyptrocarya luzuliformis L. Koyama	H	-	-	-	-	-	-	+	-	-	-	-
	Carex acutata Boott	H	+	-	-	-	-	-	-	-	-	-	-
	Carex bonplandii Kunth	H	-	+	-	-	-	-	-	-	-	-	-
	Carex lemanniana Boott	H	-	+	-	-	-	-	-	-	-	-	-
	Carex purdiei Boott	H	-	+	-	-	-	-	-	-	-	-	-
	Carex. sp.	H	-	-	-	-	-	-	+	-	-	+	-
	Cladium jamaicense Crantz	H	-	-	-	-	-	-	-	-	-	-	-
	Cyperus articulatus L.	H	-	-	-	-	-	-	-	-	-	+	-
	Cyperus cayennensis (Lam.) Britton	H	-	-	-	-	-	-	+	-	-	-	-
	Cyperus chalaranthus Presl.	H	-	-	-	-	-	-	+	-	+	-	-
	Cyperus compressus L.	H	-	-	-	-	-	+	-	-	-	-	-
	Cyperus digitatus Roxburgh	HP	-	-	-	-	-	-	+	-	-	-	-
	Cyperus distans L.	H	-	-	-	-	-	+	-	-	-	-	-
	Cyperus eragrostis Lam.	H	-	-	+	-	+	-	-	-	-	-	-
	Cyperus esculentus L.	HP	-	-	+	-	-	-	-	-	-	-	-
	Cyperus flavus Boeck.	H	-	-	-	-	-	+	-	-	-	-	-
	Cyperus gardneri Nees ex. Mart.	H	-	-	-	-	-	-	+	+	-	-	-
	Cyperus giganteus Vahl.	H	-	-	-	-	-	+	+	+	-	-	-
	Cyperus haspan L.	HP	-	-	-	+	+	+	+	+	-	-	+
	Cyperus hermaphroditus (Jacq.) Standley	H	-	+	-	-	-	-	-	-	-	-	-
	Cyperus imbricatus Retz.	HP	-	-	-	-	-	+	-	-	-	-	-
	Cyperus iria L.	H	-	-	-	-	-	-	-	-	+	-	-
	Cyperus laetus Presl.	H	-	-	+	-	-	+	-	-	-	-	-
	Cyperus laevigatus L.	H	-	-	+	-	-	-	-	-	-	-	-
	Cyperus ligularis L.	H	-	-	-	-	-	-	-	-	-	-	-

Family	Species	Habit	HA	CF	VS	CP	AP	WW	CQ	GP	AS	TB	GC
	Cyperus luzulae (L.) Retz	HP	-	-	+	+	-	+	+	-	+	-	-
	Cyperus meyenianus Kunth	H	-	-	-	+	-	+	+	-	-	-	-
	Cyperus mutisii (Kunth) Griseb.	H	-	-	-	-	-	+	-	-	-	-	-
	Cyperus ochraceus Vahl.	H	-	-	-	-	-	-	-	+	-	-	-
	Cyperus papyrus L.	H	-	-	-	-	-	-	-	-	-	-	+
	Cyperus prolixus Kunth	HP	-	-	-	-	-	+	-	-	+	-	-
	Cyperus rotundus L.	H	-	-	-	-	+	-	-	+	-	-	-
	Cyperus sphacelatus Rottb.	HA	-	-	-	-	-	+	-	-	-	-	-
	Cyperus surinamensis Rottb.	HA/P	-	-	-	+	-	+	+	-	-	-	+
	Cyperus tabina Steudel ex Boeckeler	H	-	+	-	-	-	-	-	-	-	-	-
	Cyperus virens Michx.	HP	-	-	-	-	-	-	+	-	-	-	-
	Diplacrum longifolium (Griseb.) C. B. Clarke	HP	-	-	-	+	+	-	-	-	-	-	-
	Diplasia karatifolia L. C. Rich.	HP	-	-	-	+	-	+	+	-	-	-	-
	Eleocharis acicularis (L.) Roemer et Schultes	H	+	+	+	-	-	-	-	-	-	-	-
	Eleocharis acutangula (Roxb.) Schultes	FM-F	-	-	-	+	+	+	+	+	-	-	-
	Eleocharis albibracteata Nees et Meyer ex Kunth	H	+	+	+	-	-	-	-	-	-	-	-
	Eleocharis atropurpurea (Retz.) Kunth	H	-	-	-	-	-	+	-	-	-	-	-
	Eleocharis dombeyana Kunth	H	-	-	+	-	-	-	-	-	-	-	-
	Eleocharis eglerioides S. González & Reznicek	HP	-	-	-	-	-	+	-	-	-	-	-
	Eleocharis elegans (Kunth) Roemer et Schultes	HP	-	-	-	+	+	+	+	+	-	-	-
	Eleocharis filiculmis Kunth	H	-	-	-	-	+	+	+	-	-	-	-
	Eleocharis flavescens (Poiret) Urban	H	-	-	+	-	+	-	-	-	-	-	-
	Eleocharis geniculata (L.) Ruiz & Pavón	H	-	+	-	-	+	-	-	-	-	-	-
	Eleocharis interstincta (Vahl.) Roemer et Schultes	HP	-	-	-	+	+	+	+	-	-	-	-
	Eleocharis jelskiana Boeck.	H	-	-	-	-	-	+	-	-	-	-	-
	Eleocharis macrostachya Britton	H	-	-	-	-	+	-	-	-	-	+	-
	Eleocharis maculosa (Vahl) Roemer et Schultes	H	-	-	-	-	-	-	-	-	-	-	-
	Eleocharis minima Kunth	H	-	-	-	-	+	+	-	+	-	-	+
	Eleocharis mitrata C. B. Clarke	H	-	-	-	-	-	-	+	-	-	-	-
	Eleocharis montana (Kunth) Roemer et Schultes	H	-	+	+	-	+	-	-	-	+	-	-

Family	Species	Habit	HA	CF	VS	CP	AP	WW	CQ	GP	AS	TB	GC
	Eleocharis mutata (L.) Roemer et Schultes	H	-	-	-	-	-	-	+	-	-	-	-
	Eleocharis plicarhachis Svenson	H	-	-	-	-	-	+	-	-	-	-	-
	Eleocharis radicans (Poir.) Kunth	H	-	-	-	-	-	-	-	-	-	-	-
	Eleocharis retroflexa (Poir.) Ur	H	-	-	-	-	-	+	-	-	-	-	-
	Eleocharis sellowiana Kunth	H	-	-	-	-	+	-	-	-	-	-	-
	Fimbristylis complanata (Retz.) Link.	H	-	-	-	-	+	-	-	-	-	-	-
	Fimbristylis dichotoma (L.) Vahl.	HA/P	-	-	+	+	+	+	+	-	+	-	-
	Fimbristylis littoralis Gaudich.	HA	-	-	-	+	+	-	-	-	-	-	-
	Fimbristylis spadicea (L.) Vahl	HP	-	-	-	-	-	-	+	-	-	-	-
	Fuirena robusta Kunth	FM-F	-	-	-	-	+	+	+	+	-	-	-
	Fuirena umbellata Rottb.	FM-F	-	-	-	-	+	+	+	+	-	-	-
	Hypolytrum longifolium (L. C. Rich) Nees	H	-	-	-	-	-	+	-	-	-	-	-
	Isolepis cernua (Vahl) Roem. & Schult.	H	+	-	-	-	-	-	-	-	-	-	-
	Isolepis inundata R. Br.	H	+	+	-	-	-	-	-	-	-	-	-
	Kyllinga brevifolia Rottb.	H	-	+	-	-	+	+	-	-	-	-	-
	Kyllinga odorata Vahl.	H	-	-	+	-	+	+	-	-	+	-	-
	Kyllinga pumila Michaux	H	-	-	+	-	-	+	-	-	+	-	+
	Lipocarpha humboldtiana Nees	H	-	-	-	-	+	+	+	-	-	-	-
	Lipocarpha micrantha (Vahl) G. Tucker	H	-	-	-	-	+	-	-	-	-	-	-
	Lipocarpha sphacelata (Vahl.) Kunth	H	-	-	-	-	-	+	-	-	-	-	-
	Oxycaryum cubense (Poepp. & Kunth) Lye	FM-F	-	-	-	+	+	+	+	+	-	-	-
	Pycreus bipartitus (Torey) C. B. Clarke	HA	-	-	+	-	+	-	-	-	-	-	-
	Pycreus flavicomus (Michaux) C. Adams	H	-	-	+	-	+	-	-	-	-	-	-
	Pycreus grammicus Kunth	H	-	-	-	-	-	-	-	-	+	-	-
	Pycreus lanceolatus (Poir. ex Lam.) C. B. Clarke	H	-	-	-	-	+	-	+	-	-	-	-
	Pycreus macrostachyos (Lam.) J. Raynal	H	-	-	-	-	-	+	-	-	-	-	-
	Pycreus niger (R. & P.) Cuf.	HP	+	+	+	-	+	-	-	-	-	-	-
	Pycreus unioloides (R. Br.) Urban	H	-	-	-	-	-	-	+	-	-	-	-
	Rhynchospora albescens (Miq.) Kuek.	H	-	-	-	-	-	+	-	-	-	-	-
	Rhynchospora amazonica Poepp. & Kunth	H	-	-	-	-	-	+	-	-	-	-	-

Family	**Species**	**Habit**	**HA**	**CF**	**VS**	**CP**	**AP**	**WW**	**CQ**	**GP**	**AS**	**TB**	**GC**
	Rhynchospora aristata Boeckeler	H	-	-	-	-	-	-	-	-	-	-	-
	Rhynchospora barbata (Vahl) Kunth	H	-	-	-	-	-	+	+	-	-	-	-
	Rhynchospora brevirostris Griseb.	H	-	-	-	-	-	-	+	-	-	-	-
	Rhynchospora brownii Roem. & Schult.	H	-	+	-	-	-	-	-	-	-	-	-
	Rhynchospora candida (Nees) Boeck.	H	-	-	-	-	-	+	-	-	-	-	-
	Rhynchospora cephalotes (L.) Vahl	H	-	-	-	-	-	+	+	-	-	-	-
	Rhynchospora corymbosa (L.) Britton	H	-	-	-	-	+	+	+	-	-	-	-
	Rhynchospora dissitiflora Steudel ex Boeck.	HP	-	-	-	-	-	-	-	-	-	-	-
	Rhynchospora exaltata Kunth	H	-	-	-	-	-	-	+	-	-	-	-
	Rhynchospora eximia (Nees) Boeckel	HA	-	-	-	-	-	-	+	-	-	-	-
	Rhynchospora filiformis Vahl	HP	-	-	-	-	-	-	+	-	-	-	-
	Rhynchospora gigantea Link.	H	-	-	-	-	-	+	-	+	-	-	+
	Rhynchospora globosa (Kunth) Roem. & Schult.	H	-	-	-	-	+	+	+	-	-	-	-
	Rhynchospora hassleri C.B. Clarke	H	-	-	-	-	-	+	-	-	-	-	-
	Rhynchospora hirta (Nees) Boeck.	H	-	-	-	-	-	+	+	-	-	-	-
	Rhynchospora holoschoenoides (L. C. Rich) Hert	H	-	-	-	-	+	+	+	-	-	-	-
	Rhynchospora pubera (Vahl.) Boeckeler	H	-	-	-	-	-	+	-	-	-	-	-
	Rhynchospora robusta (Kunth) Boeck.	H	-	-	-	-	+	+	-	-	-	-	-
	Rhynchospora rugosa (Vahl.) Gale	H	-	-	-	-	-	+	+	-	-	-	-
	Rhynchospora ruiziana Boeck.	H	-	-	-	-	-	-	-	-	-	-	-
	Rhynchospora scutellata Griseb.	H	-	-	-	-	-	-	+	-	-	-	-
	Rhynchospora tenerrima Nees ex Spreng.	HA/P	-	-	-	-	-	-	-	-	-	-	-
	Rhynchospora tenuis Link	H	-	-	-	-	+	+	+	-	-	-	-
	Rhynchospora trichodes C. B. Clarke	H	-	-	-	-	-	-	+	-	-	-	-
	Rhynchospora trispicata (Nees) Schrad. ex Steud.	H	-	-	-	-	-	+	+	+	-	-	-
	Rhynchospora velutina (Kunth) Boeck.	H	-	-	-	-	+	+	+	-	-	-	-
	Rhynchospora vulcani Boeck.	H	+	-	-	-	-	-	-	-	-	-	-
	Schoenoplectus americanus (Pers.) Volkhart	H	-	-	+	-	-	-	-	-	-	-	-
	Schoenoplectus californicus (C.A. Mey.) Sojak	H	+	-	+	-	-	-	-	-	-	-	+
	Scleria cyperinoides Clark	HP	-	-	-	+	-	+	+	-	-	-	-

Family	Species	Habit	HA	CF	VS	CP	AP	WW	CQ	GP	AS	TB	GC
	Scleria distans Poir.	H	-	-	-	-	-	+	+	-	-	-	-
	Scleria eggersiana Boeck.	H	-	-	-	-	-	+	-	-	-	-	-
	Scleria flagellum-nigrorum P. Bergius	H	-	-	-	-	-	+	+	+	-	-	-
	Scleria hirtella Sw.	H	-	-	-	-	+	+	+	-	-	-	-
	Scleria macrophylla J. S. Presl. & C. Presl	HP	-	-	-	+	+	-	+	-	-	-	-
	Scleria melaleuca Rchb. Schltdl. & Cham.	H	-	-	-	-	+	+	+	-	-	-	-
	Scleria microcarpa Nees ex. Kunth	HP	-	-	-	+	-	+	+	-	-	-	-
	Scleria mitis P. Bergius	H	-	-	-	-	+	-	+	-	-	-	-
	Scleria reticularis Michaux	H	-	-	-	-	+	-	+	-	-	-	-
	Scleria secans (L.) Urb.	H	-	-	-	-	+	+	+	-	-	-	-
	Scleria setuloso-ciliata Boeckeler	H	-	-	-	-	+	-	-	-	-	-	-
	Torulinium odoratum (L.) Hooper	H	-	-	-	-	+	+	+	+	-	-	+
	Websteria confervoides (Poir.) S.S. Hooper	HS	-	-	-	-	-	+	+	-	-	-	-
Eriocaulaceae	*Eriocaulon* aff. *dictyophyllum* Koern. (sensu Moldenke)	H	-	-	-	-	-	-	+	-	-	-	-
	Eriocaulon humboldtii Kunth	H	-	-	-	-	-	-	+	-	-	-	-
	Eriocaulon melanocephalum Kunth	H	-	-	-	-	-	+	+	-	-	-	-
	Eriocaulon sp. nov. "A" (cf. "Bolivia checklist" of N. Hensold, F)	H	-	-	-	-	-	-	+	-	-	-	-
	Eriocaulon steryermarkii Moldenke	H	-	-	-	-	-	-	-	-	-	-	-
	Paepalanthus lamarckii Kunth	H	-	-	-	-	+	-	-	-	-	-	-
	Paepalanthus saxicola Körn.	H	-	-	-	-	-	-	+	-	-	-	-
	Philodice hoffmannseggii Mart.	H	-	-	-	-	-	-	+	-	-	-	-
	Syngonanthus anomalus (Körn. in C. Mart.) Ruhland	HS	-	-	-	-	-	+	-	-	-	-	-
	Syngonanthus bellus Moldenke	H	-	-	-	-	-	-	+	-	-	-	-
	Syngonanthus biformis (N. E. Br.) Gleason	H	-	-	-	-	-	-	+	-	-	-	-
	Syngonanthus caulescens (Poir.) Ruhl.	H	-	-	-	-	+	+	+	-	-	-	-
	Syngonanthus densiflorus Ruhland	H	-	-	-	-	-	+	+	-	-	-	-
	Syngonanthus gracilis (Bong.) Ruhland	H	-	-	-	-	-	+	+	-	-	-	-
	Syngonanthus nitens (Bong.) Ruhl.	H	-	-	-	-	-	-	+	-	-	-	-
	Syngonanthus simplex (Koërn ex C. Mart) Ruhland	H	-	-	-	-	-	-	+	-	-	-	-
	Syngonanthus xeranthemoides (Bong.) Ruhland	H	-	-	-	-	-	-	+	-	-	-	-

Family	Species	Habit	HA	CF	VS	CP	AP	WW	CQ	GP	AS	TB	GC
	Tonina fluviatilis Aublet	HP	-	-	-	+	-	-	+	-	-	-	-
Heliconiaceae	*Heliconia marginata* (Griggs.) Pitt	HP	-	-	-	+	-	+	+	-	-	-	-
	Heliconia psittacorum L.f.	H	-	-	-	-	-	+	+	-	-	-	-
	Heliconia subulata Ruiz & Pavón	H	-	-	-	-	-	-	+	-	-	-	-
Hydrocharitaceae	*Apalanthe granatensis* (H. & B.) J. E. Planchon	HS	-	-	-	+	+	+	+	-	-	-	-
	Egeria densa Planchon	HS	-	-	-	-	-	-	-	-	-	-	-
	Egeria najas Planchon	HS	-	-	-	-	-	-	+	+	-	-	-
	Elodea potamogeton (Bert.) Espinosa	HS	+	-	-	-	+	-	-	-	-	-	-
	Limnobium laevigatum (H. & B. ex Willd.) Heine	HF-F	-	-	-	+	+	+	+	+	-	-	+
Iridaceae	*Cipura paludosa* Aubl.	H	-	-	-	-	-	+	+	-	-	-	-
	Cypella linearis (H.B.K.) Baker	H	-	-	-	-	-	-	+	-	-	-	-
	Sisyrinchium iridifolium Kunth	H	-	-	-	-	-	-	-	-	-	-	-
Juncaceae	*Distichia filamentosa* Buchenau	CF	+	-	-	-	-	-	-	-	-	-	-
	Distichia muscoides Nees & Meyen	CF	+	-	-	-	-	-	-	-	-	-	-
	Juncus acutus L.	HP	-	-	-	-	-	-	-	-	-	-	-
	Juncus arcticus Willd.	H	+	-	-	-	-	-	-	-	-	-	-
	Juncus bufonius L.	HA	+	-	+	-	-	-	-	-	-	-	-
	Juncus cyperoides Laharpe	H	-	-	-	-	-	-	-	-	-	-	-
	Juncus ebracteatus E. Meyer	H	+	+	+	-	-	-	-	-	-	-	-
	Juncus effusus L.	H	-	+	-	-	-	-	-	-	-	-	-
	Juncus fuscocapitatus Balslev	H	+	+	-	-	-	-	-	-	-	-	-
	Juncus microcephalus Kunth	H	+	+	+	-	-	-	-	-	+	-	-
	Juncus pallescens Lam.	H	-	+	-	-	-	-	-	-	-	-	-
	Juncus stipulatus Nees & Meyen	H	+	+	-	-	-	-	-	-	-	-	-
	Juncus subulitepalus Balslev	H	-	-	+	-	-	-	-	-	-	-	-
	Juncus tenuis Willd.	HP	-	-	+	-	-	-	-	-	-	-	-
	Luzula racemosa Desvaux	H	+	-	+	-	-	-	-	-	-	-	-
	Luzula vulcanica Liebm.	H	-	-	-	-	-	-	-	-	-	-	-
	Oxychloe andina Phil.	CF	+	-	-	-	-	-	-	-	-	-	-
	Patosia clandestina (Philippi) Buchenau	CF	+	-	-	-	-	-	-	-	-	-	-

Family	Species	Habit	HA	CF	VS	CP	AP	WW	CQ	GP	AS	TB	GC
Juncaginaceae	*Lilaea scilloides* (Poiret) Hauman	HS	+	-	+	-	-	-	-	-	-	-	-
Lemnaceae	*Lemna aequinoctialis* Welw.	HF-F	-	-	-	-	+	+	+	+	-	+	-
	Lemna gibba L.	HF-F	+	-	+	-	-	-	-	-	-	-	-
	Lemna minuta Kunth	HF-F	-	-	+	-	-	-	-	-	-	-	-
	Lemna valdiviana Phil.	H	+	+	-	-	+	+	+	+	-	-	+
	Lemna yungensis Landolt	LR	-	-	-	-	-	-	-	-	-	-	-
	Spirodela intermedia W. Kohl	HF-F	-	-	-	-	+	-	+	-	-	-	+
	Wolffia brasiliensis Wedd.	HF-F	-	-	-	-	-	-	+	-	-	+	-
	Wolffia columbiana Karsten	HF-F	-	-	+	-	-	-	-	+	-	+	-
	Wolffiella caudata Landolt	HF-F	-	-	-	-	-	+	-	-	-	-	-
	Wolffiella lingulata (Hegelm.) Hegelm.	HF-F	-	-	-	-	-	+	+	+	-	-	-
	Wolffiella oblonga (Phil.) Hegelm.	HF-F	-	-	+	-	-	-	-	+	-	-	-
	Wolffiella welwitschii (Hegelm.) Monod	HF-F	-	-	-	-	-	-	-	-	-	-	-
Limnocharitaceae	*Hydrocleys mattogrossensis* (Kuntze) Holm-Nielsen & Haynes	RFL	-	-	-	-	-	-	-	-	-	-	-
	Hydrocleys nymphoides (Willd.) Buch.	RFL	-	-	-	-	+	-	+	+	-	-	-
	Hydrocleys parviflora Seubert in Martius	RFL	-	-	-	-	+	+	+	-	-	-	-
	Limnocharis flava (L.) Buchenau	HA/P	-	-	-	+	+	+	+	+	-	-	-
	Limnocharis laforestii Duchassaing ex. Griseb	HA/P	-	-	-	-	-	-	+	-	-	-	-
Marantaceae	*Thalia geniculata* L.	H	-	-	-	-	+	+	+	+	-	-	-
Mayacaceae	*Mayaca fluviatilis* Aublet	HS	-	-	-	-	+	+	+	-	-	-	-
	Mayaca longipes Mart. ex Seubert	HS	-	-	-	-	+	+	+	-	-	-	-
	Mayaca sellowiana Kunth	HS	-	-	-	-	-	-	+	-	-	-	-
Najadaceae	*Najas arguta* H.B.K.	HS	-	-	-	-	+	+	+	-	-	-	-
	Najas guadalupensis (Spreng.) Magnus	HS	-	-	-	-	-	-	-	-	-	-	+
	Najas podostemon Magnus	HS	-	-	-	-	-	-	-	+	-	-	-
Orchidaceae	*Cyrtopodium paludicolum* Hoehne	H	-	-	-	-	-	-	+	-	-	-	-
	Eltroplectris calcarata (Sw.) Garay & H.R. Sweet	NK	-	-	-	-	-	-	+	-	-	-	-
	Eulophia alta (L.) Fawe & Rendl.	H	-	-	-	-	-	-	+	-	-	-	-
	Habenaria alata Hooker	H	-	-	-	-	-	-	-	-	-	-	-
	Habenaria leprieuri Reichb.f.	H	-	-	-	-	-	-	+	-	-	-	-

Family	Species	Habit	HA	CF	VS	CP	AP	WW	CQ	GP	AS	TB	GC
	Habenaria repens Nutt.	H	-	-	-	-	-	+	+	-	-	-	-
	Habenaria sartor Lindl.	H	-	-	-	-	-	+	-	-	-	-	-
	Liparis nervosa (Thunb.) Lindl.	H	-	-	-	-	-	-	+	-	-	-	-
Poaceae	*Acroceras zizanioides* (H.B.K.) Dandy	HA/P	-	-	-	+	-	+	+	-	-	-	-
	Agrostis perennans (Walt.) Tuck	H	+	+	+	-	-	-	-	-	-	-	-
	Agrostis stolonifera L.	H	+	-	+	-	-	-	-	-	-	-	-
	Alopecurus aequalis Sobol.	H	+	-	-	-	-	-	-	-	-	-	-
	Alopecurus magellanicus Lam.	H	+	-	-	-	-	-	-	-	-	-	-
	Amphibromus scabrivalvis (Trin.) Swallen	H	+	-	-	-	-	-	-	-	-	-	-
	Andropogon bicornis (L.) Forsk.	HP	-	-	-	+	+	+	+	+	-	-	-
	Andropogon glaziovii Hackel in Mart.	H	-	-	-	-	-	-	-	-	-	-	-
	Andropogon lateralis Nees	S	-	-	-	-	+	+	+	-	-	-	-
	Andropogon leucostachyus H.B.K.	H	-	-	-	-	+	+	+	-	-	-	-
	Andropogon selloanus (Hackel) Hackel	HP	-	-	-	+	+	+	+	-	-	-	-
	Andropogon virgatus Desv.	H	-	-	-	-	+	-	+	-	-	-	-
	Arundinella hispida (Willd.) Kuntze	H	-	-	-	-	+	+	+	-	-	-	-
	Arundo donax L.	H	-	-	-	-	-	-	+	-	-	-	-
	Axonopus fissifolius (Raddi) Kuhlm.	HP	-	-	-	+	+	+	+	-	-	-	-
	Axonopus leptostachyus (Flüggé) Hitchc.	H	-	-	-	-	-	-	+	-	-	-	-
	Calamagrostis effusa Steud.	H	+	-	-	-	-	-	-	-	-	-	-
	Calamagrostis eminens (Presl.) Steud.	H	+	-	-	-	-	-	-	-	-	-	-
	Coelorachis aurita (Steud.) A. Camus	H	-	-	-	-	+	+	+	-	-	-	-
	Coelorachis balansae (Hack.) Camus	H	-	-	-	-	-	+	-	-	-	-	-
	Coix lacryma-jobi L.	H	-	-	-	+	-	-	-	-	-	-	-
	Cynodon dactylon (L.) Pers.	H	-	-	+	-	+	+	+	+	-	-	-
	Deschampsia caespitosa P. Beauv.	H	-	+	-	-	-	-	-	-	-	-	-
	Deyeuxia chrysantha J. Presl.	H	+	-	-	-	-	-	-	-	-	-	-
	Deyeuxia minima (Pilg.) Rúgolo	H	+	-	-	-	-	-	-	-	-	-	-
	Deyeuxia ovata J. Presl.	H	+	-	-	-	-	-	-	-	-	-	-
	Deyeuxia rigescens (J. Presl) Türpe	H	+	-	-	-	-	-	-	-	-	-	-

Family	Species	Habit	HA	CF	VS	CP	AP	WW	CQ	GP	AS	TB	GC
	Digitaria ciliaris (Retz.) Koel.	H	-	-	-	-	+	+	+	-	+	-	-
	Echinochloa colona (L.) Link	HA	-	-	-	+	+	-	+	-	+	-	-
	Echinochloa crus-galli (L.) Pal. de Beavois	H	-	-	-	-	-	-	-	-	-	-	-
	Echinochloa crus-pavonis (H.B.K.) Schultes	H	-	-	+	-	+	+	-	-	-	-	-
	Echinochloa polystachya (Kunth) Hitchc.	H	-	-	-	-	-	+	+	+	-	-	-
	Echinolaena gracilis Swallen	H	-	-	-	-	-	+	+	-	-	-	-
	Eleusine indica (L.) Gaertn.	H	-	-	-	-	+	+	+	-	+	-	-
	Eragrostis acutiflora (Kunth) Nees	H	-	-	-	-	-	+	-	-	-	-	-
	Eragrostis glomerata (Walt.) L. H. Dewey	H	-	-	+	-	+	-	+	-	-	-	-
	Eragrostis hypnoides (Lam.) Britton, Sterns & Poggenb.	H	-	-	-	-	+	+	-	-	-	-	-
	Eragrostis maypurensis (Kunth) Steud.	S-S	-	-	-	-	-	+	+	-	-	-	-
	Eriochloa distachya H.B.K.	H	-	-	-	-	+	-	+	-	-	-	-
	Eriochloa punctata (L.) Desv.	H	-	-	-	-	+	+	+	+	-	-	-
	Eriochrysis cayennensis Beauv.	H	-	-	-	-	+	+	+	-	-	-	-
	Eriochrysis warmingiana (Hack.) Kuhlm.	H	-	-	-	-	+	+	-	-	-	-	-
	Festuca dolichophylla J. Presl.	H	+	-	-	-	-	-	-	-	-	-	-
	Gymnopogon fastigiatus Nees	H	-	-	-	-	-	+	+	-	-	-	-
	Gynerium sagittatum (Aubl.) Beauv.	HP	-	-	-	+	-	+	+	-	-	-	-
	Hackelochloa granularis (L.) Kuntzey	H	-	-	-	-	-	-	+	-	-	-	-
	Hemarthria altissima (Poir.) Stapf & C.E. Hubb.	HP	-	-	-	+	-	+	+	-	-	-	-
	Holcus lanatus L.	H	-	-	-	-	-	-	-	-	-	-	-
	Homolepis aturensis (H.B.K.) Chase	HP	-	-	-	+	+	+	+	-	-	-	-
	Hymenachne amplexicaulis (Rudge.) Nees	HP	-	-	-	+	-	+	+	+	-	-	-
	Hymenachne donacifolia (Raddi) Chase	HP	-	-	-	+	+	+	+	+	-	-	-
	Hyparrhenia bracteata (Willd.) Stapf	H	-	-	-	-	-	+	+	-	-	-	-
	Ichnanthus pallens (Swartz.) Munro ex Benth.	H	-	-	-	-	+	-	+	-	-	-	-
	Ichnanthus procurrens (Nees) Swallen	H	-	-	-	-	+	+	+	-	-	-	-
	Imperata brasiliensis Trin.	H	-	-	-	-	+	+	+	+	+	-	-
	Imperata contracta (H.B.K.) Hitch.	H	-	-	-	-	+	-	-	-	-	-	-
	Imperata minutiflora Hack.	H	-	-	-	-	+	-	-	-	-	-	-

Family	Species	Habit	HA	CF	VS	CP	AP	WW	CQ	GP	AS	TB	GC
	Imperata tenuis Hack	H	-	-	+	-	+	+	+	+	-	-	-
	Isachne polygonoides (Lam.) Doell	H	-	-	-	-	-	+	+	-	-	-	-
	Leersia hexandra L.	FM-F	-	-	-	-	+	+	+	+	-	-	+
	Leptochloa fascicularis (Lam.) A. Gray	H	-	-	+	-	-	-	-	-	-	-	-
	Leptochloa mucronata (Michx.) Kunth	H	-	-	-	-	-	-	-	-	-	-	-
	Leptochloa panicoides (J. Presl) Hitchc.	H	-	-	-	-	-	-	-	+	-	-	-
	Leptochloa scabra Nees.	H	-	-	-	-	+	+	+	-	-	-	-
	Leptochloa uninervia (J.S. Presl) A. Hitch. et Chase	H	-	-	+	-	-	+	+	-	-	-	-
	Loudetia flammida (Trin.) C. E. Hubbard	H	-	-	-	-	+	+	+	-	-	-	-
	Luziola bahiensis (Steudl.) A. Hitchc.	HP	-	-	-	+	-	-	+	-	-	-	-
	Luziola fragilis Swallen	H	-	-	-	-	-	-	-	-	-	-	-
	Luziola peruviana Juss. ex J.F. Gmel.	H	-	-	+	-	+	+	+	-	-	-	-
	Luziola subintegra Swallen	H	-	-	-	-	-	-	+	+	-	-	-
	Oplismenopsis najada (Hack. & Arechav.) Parodi	H	-	-	-	-	-	-	+	-	-	-	-
	Oryza alta Swallen	H	-	-	-	-	-	-	-	+	-	-	-
	Oryza grandiglumis (Döell) Prodoehl	H	-	-	-	-	-	-	+	-	-	-	-
	Oryza latifolia Desv.	H	-	-	-	-	-	+	+	+	-	+	-
	Oryza rufipogon Griffiths	H	-	-	-	-	+	-	+	+	-	-	-
	Oryza sativa L.	H	-	-	-	-	-	-	+	-	-	-	-
	Otachyrium versicolor (Döll) Henrard	H	-	-	-	-	+	+	+	-	-	-	-
	Panicum caricoides Nees ex Trin.	H	-	-	-	-	-	+	+	-	-	-	-
	Panicum cayennense Lam.	H	-	-	-	-	+	+	+	-	-	-	-
	Panicum dichotomiflorum Michx.	HP	-	-	-	+	+	+	+	+	-	-	-
	Panicum elephantipes Nees ex Trin.	FM-F	-	-	-	-	-	+	-	+	-	-	-
	Panicum grande Hitchcock & Chase	HP	-	-	-	+	-	+	-	-	-	-	-
	Panicum hylaeicum Mez.	HP	-	-	-	+	-	+	+	-	-	-	-
	Panicum laxum Sw.	HP	-	-	-	+	+	+	+	+	-	-	-
	Panicum mertensii Roth	HP	-	-	-	+	-	+	+	-	-	-	-
	Panicum parvifolium Lam.	H	-	-	-	-	+	+	-	-	-	-	-
	Panicum pilosum Sw.	HP	-	-	-	+	-	+	+	-	-	-	-

Family	Species	Habit	HA	CF	VS	CP	AP	WW	CQ	GP	AS	TB	GC
	Panicum polygonatum Schrader	HP	-	-	-	+	+	+	+	-	+	-	-
	Panicum repens Berg.	H	-	-	-	-	-	-	+	-	-	-	-
	Panicum scabridum Döll	S-S	-	-	-	-	-	+	+	-	-	-	-
	Panicum schwackeanum Mez.	HP	-	-	-	+	+	-	+	-	-	-	-
	Panicum stenodes Griseb.	H	-	-	-	-	-	-	+	-	-	-	-
	Panicum stoloniferum Poir.	HP	-	-	-	+	+	+	+	+	-	-	-
	Panicum stramineum Hitchc. & Chase	H	-	-	-	-	+	+	+	-	-	-	-
	Panicum trichoides Sw.	H	-	-	-	-	-	-	+	-	-	-	-
	Paratheria prostrata Griseb.	H	-	-	-	-	-	+	-	-	-	-	-
	Parodiolyra lateralis (J. Presl ex Nees) Soderstr. & Zuloaga	H	-	-	-	-	-	-	-	-	-	-	-
	Paspalidium geminatum (Forssk.) Stapf.	H	-	-	-	-	-	-	+	-	-	-	-
	Paspalum acuminatum Raddi	H	-	-	-	-	-	+	+	-	-	-	-
	Paspalum boscianum Flüggé	H	-	-	-	-	+	+	-	-	-	-	-
	Paspalum carinatum Humb. & Bonpl.	H	-	-	-	-	-	+	+	-	-	-	-
	Paspalum conjugatum Bergius	H	-	-	-	+	+	+	+	-	+	-	-
	Paspalum conspersum Schrader ex Schultes	H	-	-	-	-	-	-	+	-	-	-	-
	Paspalum densum Poir.	H	-	-	-	-	+	+	+	-	-	-	-
	Paspalum distichum L.	H	-	-	+	-	+	-	-	-	-	-	-
	Paspalum fasciculatum Willd. ex Flüggé	H	-	-	-	-	+	+	-	-	-	-	-
	Paspalum intermedium Munro	H	-	-	-	-	-	-	+	-	-	-	-
	Paspalum lividum Trin. in Schlecht.	H	-	-	-	-	-	-	+	-	-	+	-
	Paspalum maculosum Trin.	H	-	-	-	-	-	-	+	-	-	-	-
	Paspalum multicaule Poir.	H	-	-	-	-	-	-	+	-	-	-	-
	Paspalum nudatum Luces	H	-	-	-	-	-	-	-	-	-	-	-
	Paspalum orbiculatum Poir.	H	-	-	-	-	-	+	-	-	-	-	-
	Paspalum pallens Swallen	H	-	-	-	-	-	-	+	-	-	-	-
	Paspalum paniculatum L.	H	-	-	-	-	-	-	+	-	+	-	-
	Paspalum plicatulum Michx.	H	-	-	-	-	+	+	+	-	-	-	-
	Paspalum pygmaeum Hackel	H	+	+	-	-	-	-	-	-	-	-	-
	Paspalum repens Bergius	H	-	-	-	+	-	+	+	+	-	-	-

Family	**Species**	**Habit**	**HA**	**CF**	**VS**	**CP**	**AP**	**WW**	**CQ**	**GP**	**AS**	**TB**	**GC**
	Paspalum urvillei Steudel	H	-	-	+	-	+	-	-	-	-	-	-
	Paspalum vaginatum Swartz	H	-	-	-	-	+	-	+	-	-	-	-
	Paspalum virgatum L.	H	-	-	-	-	-	+	+	-	-	-	-
	Paspalum wrightii Hitchc. & Chase	H	-	-	-	-	-	-	+	+	-	-	-
	Pennisetum clandestinum Hochst. ex Chiov.	H	-	-	-	-	-	-	-	-	-	-	-
	Phalaris angusta Nees ex Trin.	H	-	-	-	-	-	-	-	-	-	-	-
	Poa annua L.	H	+	+	-	-	-	-	-	-	-	-	-
	Poa gymnantha Pilg.	H	+	-	-	-	-	-	-	-	-	-	-
	Poa perligulata Pilg.	H	+	-	-	-	-	-	-	-	-	-	-
	Polypogon elongatus Kunth ex. Humb.	H	+	-	+	-	-	-	-	-	-	-	-
	Polypogon interruptus Kunth	H	+	-	+	-	-	-	-	-	-	-	-
	Polypogon monspeliensis (L.) Desf.	H	+	-	-	-	-	-	-	-	-	-	-
	Polypogon viridis (Gouan) Breistr.	H	+	-	+	-	-	-	-	-	-	-	-
	Reimarochloa aberrans (Döll) Chase	H	-	-	-	-	-	+	-	-	-	-	-
	Reimarochloa acuta (Flügge) Hitchcock	H	-	-	-	-	-	-	+	-	-	-	-
	Saccharum trinii (Hack.) Renvoize	H	-	-	-	-	-	+	+	-	-	-	-
	Sacciolepis angustissima (Hochst.) Kuhlm	H	-	-	-	-	-	+	+	-	-	-	-
	Sacciolepis myuros (Lam.) Chase	H	-	-	-	-	+	+	+	-	-	-	-
	Sacciolepis vilvoides (Trin.) Chase	H	-	-	-	-	-	+	-	-	-	-	-
	Schizachyrium sulcatum (Ekman) S.T. Blake	H	-	-	-	-	-	+	+	-	-	-	-
	Setaria parviflora (Poir.) Kerguélen	H	-	-	+	-	+	+	+	+	-	-	-
	Setaria sphacelata (Schumach.) M. B. Moss ex Stapf & C.E. Hubb.	H	-	-	-	-	+	-	-	-	-	-	-
	Sorghastrum nutans (L.) Nash	H	-	-	-	-	+	-	-	-	-	-	-
	Sorghastrum setosum (Griseb.) Hitchc.	H	-	-	-	-	+	-	+	-	-	-	-
	Sporobolus indicus (L.) R. Br.	H	-	-	-	-	-	+	-	-	-	-	-
	Steinchisma hians (Elliot) Nash ex Small	HP	-	-	+	+	+	+	-	-	-	-	-
	Stenotaphrum secundatum (Walter) Kuntze	H	-	-	-	-	+	-	-	-	-	-	-
	Urochloa fasciculata (Sw.) R. Webster	H	-	-	-	-	+	+	-	-	-	-	-
	Urochloa mutica (Forssk.) T. Q. Nguyen	H	-	-	-	-	+	-	-	-	+	-	-
Pontederiaceae	*Eichhornia azurea* (Sw.) Kunth	HF-S	-	-	-	-	+	+	+	+	-	-	-

Family	**Species**	**Habit**	**HA**	**CF**	**VS**	**CP**	**AP**	**WW**	**CQ**	**GP**	**AS**	**TB**	**GC**
	Eichhornia crassipes (Mart.) Solms-Laubach	HF-S	-	-	-	+	-	+	+	+	-	-	-
	Eichhornia diversifolia (Vahl.) Urban	HS	-	-	-	+	-	+	+	-	-	-	-
	Heteranthera limosa (Sw.) Willd.	H	-	-	+	-	-	+	+	-	-	-	-
	Heteranthera reniformis C. Presl.	H	-	+	-	-	+	+	-	-	+	-	-
	Heteranthera spicata C. Presl.	H	-	-	-	-	-	-	-	-	-	-	-
	Heteranthera zosterifolia Mart.	HS	-	-	-	-	-	-	-	-	-	+	-
	Pontederia cordata L.	H	-	-	-	-	-	+	+	+	-	-	-
	Pontederia rotundifolia L.f	HF-S	-	-	-	+	+	+	+	+	-	-	-
	Pontederia subovata (Seubert in Martius) Lowden	H	-	-	-	-	+	+	+	-	-	-	-
	Pontederia triflora (Endl. ex Seub.) Agost. & Velásquez	HF-S	-	-	-	-	-	-	-	+	-	-	-
Potamogetonaceae	*Potamogeton gayii* A. Bennett	HS	-	-	-	-	-	-	-	-	-	-	+
	Potamogeton illinoensis Morong	HS	+	-	-	-	+	-	-	-	-	-	+
	Potamogeton pusillus L.	HS	+	-	+	-	-	+	-	-	-	-	-
	Stuckenia filiformis (Persoon) Börner	HS	+	-	+	-	-	-	-	-	-	-	-
	Stuckenia pectinata (L.) Börner	HS	+	-	+	-	-	-	-	-	-	-	-
	Stuckenia striata (Ruiz & Pavón) Holub	HS	+	-	-	-	-	-	-	-	-	+	-
Ruppiaceae	*Ruppia filifolia* (Phil.) Skottsb.	HS	+	-	-	-	-	-	-	-	-	-	-
Typhaceae	*Typha domingensis* Pers.	HP	-	-	+	-	+	-	+	+	-	-	+
Xyridaceae	*Abolboda grandis* Griseb.	H	-	-	-	-	-	-	+	-	-	-	-
	Abolboda pulchella Bonpl.	H	-	-	-	-	-	-	-	-	-	-	-
	Xyris aquatica Idrobo & L. B. Smith	H	-	-	-	-	-	-	+	-	-	-	-
	Xyris atriceps Malme.	H	-	-	-	-	-	-	+	-	-	-	-
	Xyris jupicai L.	H	-	-	-	-	+	-	+	-	-	-	-
	Xyris lacerata Pohl ex Seub.	H	-	-	-	-	-	+	+	-	-	-	-
	Xyris laxifolia Mart. var. laxifolia	H	-	-	-	-	+	+	+	-	-	-	-
	Xyris savanensis Miq.	H	-	-	-	-	+	+	+	-	-	-	-
Zannichelliaceae	*Zannichellia palustris* L.	HS	+	-	-	-	-	-	-	-	-	-	-
Zingiberaceae	*Hedychium coronarium* J. König	H	-	-	-	-	-	-	-	-	-	-	-
	Renealmia alpinia (Rottb.) Maas	H	-	-	-	-	-	+	+	-	-	-	-
	Renealmia aromatica (Aubl.) Griseb.	H	-	-	-	-	-	-	+	-	-	-	-

APPENDIX E. NOTEWORTHY SPECIES

High Andean

Laguna Toro. No rare species were observed at Laguna Toro, but, the population of *Myriophyllum quitense* (Haloragaceae) at this site was noteworthy for possessing some unusual characteristics. Numerous individuals (ca. 5-10% of the population) of *M. quitense* were noted with leaves arrayed in 5-merous whorls. By contrast, *M. quitense* typically possesses leaves in 4-merous (occasionally 3-merous) whorls (Orchard 1981). *M. quitense* is extremely common in Andean aquatic habitats, and has a very broad distribution, ranging along the Andes from Tierra del Fuego to Venezuela, with disjunct populations in Mexico, the Northwestern United States, and British Columbia (Ritter and Crow 1998). Nevertheless, leaves in 5-merous whorls have only been reported for the species from a single herbarium specimen from North America (Orchard 1981), and, more recently, from Cochabamba's Laguna Alalay (Ritter and Crow 1998).

Laguna Larati. Two species at Laguna Larati, *Ludwigia peploides* (Onagraceae) and *Potamogeton illinoensis* (Potamogetonaceae), were noteworthy for their presence in a high altitude habitat. *Ludwigia peploides*, an extremely widespread species (Raven 1963), is fairly common in wetlands in the Valles Secos and at lower elevations. The population at Laguna Larati represented the highest elevation at which this species was encountered in Bolivia. *Potamogeton illinoensis* is also widely distributed, ranging from Canada to Argentina (Novelo R. and Lot H. 1994b), but this species apparently has only been reported for Bolivia from three populations: Laguna Larati, Laguna Volcan, and a wetland in the Santa Cruz area.

Río Candelaria. The sole noteworthy species noted at Río Candelaria was the cosmopolitan weed *Sagina procumbens* (Caryophyllaceae). A small population of *S. procumbens* was observed growing on a sand bars in the river channel at Río Candelaria. Although this species is extremely widespread (Gleason and Cronquist 1991), its presence in the Río Candelaria apparently constitutes a new record for Bolivian, albeit not a terribly interesting one.

Chulichuncani Laguna. The sole species of note at the Chulichuncani Laguna was *Amphibromus scabrivalvis* (Poaceae), an aquatic grass with lax semi-floating culms. *A scabrivalvis* was common in the shallow end of the system, growing in depths of up to ca. 0.5 m. Although this species has a fairly broad distribution in high elevation areas in the southern half of South American (Renvoize 1998), this was the sole system in which *A. scabrivalvis* was encountered during fieldwork in Bolivia.

Valles Secos

Laguna Alalay. No rare species were observed at Laguna Alalay, but a few species were noteworthy. The populations of two semi-aquatic grasses, *Leptochloa uninervia* (Poaceae) and *L. fascicularis* (Poaceae) represented the highest elevation known for these species (Neil Snow, pers. com.). Additionally, the population of *Myriophyllum quitense* was noteworthy for possessing an unusual semi-terrestrial growth form. Although semi-terrestrial forms are known for various species of *Myriophyllum,* this was apparently the first record of this growth-form for *M. quitense* (Ritter and Crow 1998). As with the population at Laguna Toro, the *M. quitense* at Laguna Larati was also noteworthy for possessing leaves in 5-merous whorls and for the presence of 5-merous flowers and fruits (Ritter and Crow 1998).

Río Guadalquivir Wetland. Two species at the Río Guadalquivir wetland were noteworthy. The watermilfoil, *Myriophyllum aquaticum* (Haloragaceae), a widespread aquatic weed previously unknown for Bolivia, was abundant in small pools and on seasonally inundated sediment bars (see Ritter and Crow 1999). A second noteworthy species, *Oenothera tarijensis* (Onagraceae), an herb endemic to this region, was present along the transition from wetland to upland.

Río Mizque Wetland. Although this system possessed the richest flora of the Valles Secos sites, no rare or noteworthy species were observed.

Irrigation Canal at Tiquipaya. No rare or noteworthy species were observed.

Cloud Forest

See Chapter 3.

Chapare

See Chapter 4.

Andean Piedmont

Bermudez Curichi. A number of noteworthy species were encountered in the Bermudez Curichi. The shrub *Ludwigia martii* (Onagraceae), which was abundant in the transition between basin and upland, constituted a new country record. Three submersed macrophytes, *Apalanthe granatensis, Mayaca longipes,* and *Bacopa aquatica*, were also of interest as they have rarely been reported for Bolivia.

Viru Viru Wetland. Despite this system's rich flora, the only species of note encountered at the Viru Viru Wetland was the robust emergent fern *Acrostichum danaeifolium* (Pteridaceae). This species is generally associated with mangrove communities in brackish water (Tryon and Tryon 1982), but is occasionally known to occupy freshwater sites in central and upper Amazonia. Although *A. danaeifolium* was previously known for Bolivia, Tryon and Tryon (1982) listed only a single population for the country.

White-water Floodplain

Riberalta Ciénaga. Two noteworthy species were encountered at this system, *Diospyros nur* (Ebenaceae) and *Tetralocularia pennellii* (Convolvulaceae). The voucher specimen of *Diospyros nur*, an arborescent species that was common in various parts of the Riberalta Ciénaga, was designated as the holotype for the species (Wallnöfer 1999). The genus *Tetralocularia* is said to be endemic to the swamps of Colombia's Magdalena Valley (Gentry 1993), but this species was collected at the Riberalta Ciénaga and at various wetlands in Parque Noel Kempff Mercado (see the Chiquitanía, below).

Laguna Tumi Chuqua. Although Laguna Tumi Chuqua possessed a relatively small flora (34 sp.) two noteworthy species were observed. *Potamogeton pusillus* (Potamogetonaceae) has a cosmopolitan distribution (Novelo R. and Lot H. 1994b), but in Bolivia this species was typically encountered in High Andean systems. The population at Laguna Tumi Chuqua represented the sole population of *P. pusillus* encountered in the Amazonian lowlands. The second noteworthy species *Ludwigia hyssopifolia* (Onagraceae) possesses a pantropical distribution (Zardini and Raven 1991); however, in the New World it appears to be more typical of Central America and northern South America. The population of *L. hyssopifolia* at Laguna Tumi-Chuqua apparently represented one of only a few collections of this species from Bolivia.

Laguna Suarez. Despite the rich flora at Laguna Suarez, no rare or particularly uncommon species were encountered.

Other Areas in the White-water Floodplain. The submersed macrophyte *Syngonanthus anomalus* (Eriocaulaceae) was collected from a stream in the area around Guayaramerin. This represented just the second known locality for this species in Bolivia. Two species of Podostemaceae were collected from the Río Iténez at Guayaramerin. One, a putative *Mourera* species, would represent a new genus for Bolivia, if confirmed. At the time of this writing, the identity of the second species has yet to be determined.

Chiquitanía

Concepción Wetland. Three species at this system were noteworthy, *Ludwigia martii* and *Ludwigia torulosa* (Onagraceae), and an unidentified species of *Carex* (Cyperaceae). *L. martii* was previously known only from one other site in Bolivia (the Curichi at Bermudez). *L. torulosa* is broadly distributed in the Neotropics, ranging from Mexico to Brazil (Zardini and Raven 1991), but this species has only been reported for a few systems in Bolivia (including two other study sites, the Cuatro Vientos Palm Swamp and the La Toledo Curichi). The species of *Carex* collected at the Concepción wetland represented the lowest elevation at which I encountered this genus in Bolivia.

Huanchaca Arroyo. A number of species from the Huanchaca Arroyo were noteworthy. Two bladderworts, *Genlisea guianensis* and *Utricularia nana* (Lentibulariaceae), represented new country records, with the former the first record for the genus in Bolivia (Ritter and Crow 2000). The diminutive herb *Siphanthera foliosa* (Melastomataceae), which was previously known for Bolivia from only two other populations (F. Almeda, CAS, pers. com.), was collected here and at a stream at the base of the Serranía de Huanchaca. One of the species of *Xyris* collected at this site was not completely identified at the time of this writing. I was unable to match it to specimens, nor did it appear to match any descriptions in the literature. Most likely, it corresponds to one of the six undescribed species of *Xyris* listed for Parque Nacional Noel Kempff Mercado by Killeen and Schulenberg (1999).

La Toledo Curichi. Species of note at the La Toledo Curichi were *Cyrtopodium paludicolum* (Orchidaceae), *Ludwigia torulosa* (see notes for the Concepción Wetland), and *Tetralocularia pennellii* (Convolvulaceae). *Cyrtopodium paludicolum* was noteworthy for being a wetland representative of a genus that is normally associated with rock outcroppings and other xeric habitats. Although *C. paludicolum* was common on floating mats in the wetlands of Parque Nacional Noel Kempff Mercado, this species does not appear to have been collected elsewhere in Bolivia. The genus *Tetralocularia* is said to be endemic to the swamps of Colombia's Magdalena Valley (Gentry 1993). Nevertheless, this species was common on floating mats at the La Toledo Curichi, Bahia Toledo, and in other wetlands in the El Refugio/La Toledo area.

Bahía Toledo. This system contained three species of note: *Operculina hamiltonii* and *Tetralocularia pennellii* (see notes for the La Toledo Curichi), and *Cyrtopodium paludicolum* (see notes for the La Toledo Curichi). All three species were noteworthy for having rarely been collected in Bolivia.

Río Paraguá. Rare or noteworthy species encountered at the Río Paraguá study areas were: *Egeria najas* (Hydrocharitaceae), *Nymphaea oxypetala* (Nymphaeaceae), and *Websteria confervoides* (Cyperaceae). *Egeria najas*, a submersed macrophyte, is endemic to South America, with a distribution ranging from Brazil southwards to Argentina and Paraguay (Cook 1984). This species appears to have rarely been collected in Bolivia, as Cook did not cite any Bolivian specimens of *E. najas* in his monograph of the genus. Frey (1995), however, did list this species for Laguna Cáceres in the Bolivian Gran Pantanal.

Nymphaea oxypetala, another South American endemic, was previously known from only a few sites (Wiersema 1987). The population at the Río Paraguá represented the first record of this rare species in Bolivia, although, additional populations have since been encountered in both the Parque Nacional Noel Kempff Mercado area and in the Bolivian Pantanal (Ritter *et al.* 2000).

Websteria confervoides, an aquatic sedge with an unusual, submersed habit, is broadly distributed throughout the Tropics and Subtropics (Adams 1994e). Nevertheless, there appear to have been few other collections of this species from Bolivia.

Cuatro Vientos. Cuatro Vientos possessed a number of rare or noteworthy species: *Calyptrocarya luzuliformis* (Cyperaceae), *Cyrtopodium paludicolum* (see notes for the La Toledo Curichi), *Diospyros yomomo* (Ebenaceae), *Isoëtes panamensis* (Isoëtaceae), and *Ludwigia torulosa* (see notes for the Concepción Wetland).

Calyptrocarya luzuliformis is widely distributed, ranging from Costa Rica to Brazil (Gómez-Laurito 1994). Nevertheless, the population at Cuatro Vientos appeared to be the first record for *C. luzuliformis* in Bolivia. *Diospyros yomomo* (Ebenaceae), is a recently-described arborescent species (Wallnöfer 1999) known only from this system. *Isoëtes panamensis* is another widely distributed species, ranging from Central America to Brazil and Paraguay (Hickey 1995), however, there appear to have been few collections from Bolivia. *I. panamensis* was also noteworthy as the sole representative of this genus collected in the lowlands.

Lago Caimán. Noteworthy species were *Cyrtopodium paludicolum* (see notes for the La Toledo Curichi), *Egeria najas* (see notes for the Río Paraguá), *Floscopa glabrata* (Commelinaceae), *Limnophila* sp. nov. (Scrophulariaceae), *Nymphaea jamesoniana* (Nymphaeaceae), *Operculina hamiltonii* (see notes for Bahía Toledo), and *Websteria confervoides* (see notes for the Río Paraguá).

Floscopa glabrata possesses a fairly broad distribution, ranging from Costa Rica to Brazil and Paraguay (Hunt 1994). Nevertheless, the population at Lago Caimán constituted one of the few records of this species in Bolivia. *Nymphaea jamesoniana* is another widespread species (Wiersema 1987), nevertheless, the population at Lago Caimán represented the first record for this species in Bolivia (Ritter *et al.* 2000).

The population of the undescribed species of *Limnophila* was particularly interesting, as it represented the second record for this genus in South America. The first record for this species was from collections I made from the Río Iténez, approximately 20 km south of Lago Caimán). When this species is eventually described, however, the material from Lago Caimán will most likely be designated as the holotype, as both flowers and fruits were present (only fruits were present at the Río Iténez site).

Additional Areas in Parque Noel Kempff Mercado. A number of additional noteworthy species were present in this national park.. Two noteworthy species of *Utricularia* were collected in the inundated savannas surrounding Flor de Oro. One of these, *U. simulans*, represented a new country record. The second species, *Utricularia* cf. *guyanensis*, putatively represented another country record, but more work needs to be done to confirm this determination. A few other species collected in these savannas, *e.g.*, *Acisanthera limnobios* (Melastomataceae), *Bacopa myriophylloides* (Scrophulariaceae), *Limnosipanea spruceana* (Rubiaceae), and *Philodice hoffmannseggii* (Eriocaulaceae), were known from only a few other collections from Bolivia.

The inundated savannas around La Toledo also supported a number of noteworthy species. Three species, *Eriocaulon melanocephalum* (Eriocaulaceae) and *Benjaminia reflexa* and *Lindernia brachyphylla* (Scrophulariaceae) had apparently only been known for Bolivia from one or two additional localities. Another species of note was an aquatic species of *Bacopa*, which apparently represents a heretofore undescribed species.

Parque Nacional Noel Kempff Mercado was also rich in species of Podostemaceae. Two species, *Tristicha trifaria* and cf. *Podostemum*, were collected in the Río Iténez. The former represented a new genus record for Bolivia. If the putative *Podostemum* is indeed a member of that genus, it would also represent a new genus record for the county. A third species in the Podostemaceae, *Apinagia pilgeri*, was collected in the waterfall Arco Iris, at the base of the Serranía de Huanchaca. This represented a new species record for Bolivia. Large numbers of rheophytes were observed growing on rocks in the Río Paucerna during overflights of the Serranla de Huanchaca. Many of these were undoubtedly members of the Podostemaceae, a family which has been particularly poorly collected in Bolivia. Regrettably, it was not possible to gain access to these areas from the ground.

Gran Pantanal

See Chapter 5.

Outlying Sites

Laguna Volcan. A number of noteworthy species were encountered at Laguna Volcan. The population of *Nymphaea lingulata* (Nymphaceae), which was abundant at this system, represented the first record for this species in Bolivia (Ritter *et al.* 2000). The submersed macrophyte *Potamogeton gayii* (Potamogetonaceae) was abundant at Laguna Volcan. Its presence at this system also represented a new country record (R. R. Haynes, UNA, pers. com.). A small population of *Nymphoides verrucosa* (Menyanthaceae) were also noted. This species was previously known for Bolivia from just two other sites (Galán de Mera and Navarro 1989), and the population at Laguna Volcan apparently represented the northernmost known limit of its distribution.

Two common wetland herbs *Echinodorus bolivianus* and *E. paniculatus* (Alismataceae), which were present in low abundance along the edges of the basin, were noteworthy for their presence at such a high elevation site. The herb *Hydrocotyle verticillata* (Apiaceae), which was common in one part of the system, has apparently only been collected a few other times in Bolivia.

Yolosa Wetland. No species of note were encountered at the Yolosa wetland. Nevertheless, a population of the "rockweed", *Apinagia boliviana* (Podostemaceae), was encountered in the Río Coroico, a few kilometers below the point where the Río San Juan enters this system. A second population of *A. boliviana* was collected in the Río

Huarinilla, a few kilometers above its juncture with the Río Coroico. This species is endemic to Bolivia (Van Royen 1951).

Cristalmayu Wetland. No rare or noteworthy species were encountered.

Laguna Yaguacua. No rare or noteworthy species were encountered.

APPENDIX F. ANNOTATED CHECKLIST OF SPECIES ASSOCIATED WITH WETLANDS IN THE BOLIVIAN CLOUD FOREST REGION

An annotated checklist of species encountered in wetlands in the Bolivian Cloud Forest, including life-form, abundance, habitat, specimen citations, and distribution. Site abbreviations are as follows: CHB - Chimpa Huata Bog, INC - Incachaca Pond, LKE - Laguna Khonchu East, LKW - Laguna Khonchu West, CP - Corani Pampa Marsh, SSM - Serranía de Siberia Marsh, GC - auxiliary collections from other Cloud Forest wetland habitats. Voucher specimens: NHA and LPB, with additional duplicates (when available) at BOLV and MO. Two wetland bryophytes were also observed in the Cloud Forest systems. These are listed here, but were not included in the calculations of floristic similarity (Chapter 3), as only vascular species were considered in these calculations.

BRYOPHYTES

Ricciaceae

Riccia fluitans* L. .*sl. Free-floating aquatic liverwort. LKE, LKW (Occasional). *Ritter 1570, Ritter & Crow 2206.* Nearly cosmopolitan. Said to characteristically occur in eutrophic water (Cook 1974). In Bolivia, we have encountered *R. fluitans* only in the Cloud Forest.

Sphagnaceae

***Sphagnum costa-ricense* Crum & Crosby.** Floating, mat-forming macrophyte. CHB, GC (common to abundant). *Ritter & Oldcorn 2677, 2683, 2688.* Common in pools, stream and river edges and in damp areas along trails.

PTERIDOPHYTES

Azollaceae

***Azolla* cf. *caroliniana* Willd.** Free-floating macrophyte. INC (occasional to abundant). *Ritter 1554.* Encountered in wetlands throughout Bolivia, ranging from elevations of <100 to >3300 m. Abundance fluctuated significantly seasonally, with the greatest abundance observed during wetter portions of the year.

Equisetaceae

***Equisetum bogotense* Kunth.** Emergent herb. INC, CP (occasional to common). *Ritter 1848, Ritter & Crow 2286.* Widely distributed in the Neotropics (Hauke 1995). In Bolivia, *E. bogotense* is common along the edges of rivers and streams and in marshes in the high elevation zones (Valles Secos, Puna, and Bosque Nublado).

Isoëtaceae

***Isoëtes herzogii* U. Weber**. Submerged herb. LKE, LKW, GC (abundant). *Ritter et al. 1274, Ritter & Crow 2201, 2209.* Often forming very dense populations.

ANGIOSPERMS

DICOTS

Apiaceae

***Eryngium ebracteatum* Lam.** Emergent herb. GC (locally abundant). *Ritter & Wood 2868.* Generally, more characteristic of lowland systems. A single population was observed in the Cloud Forest, where it was growing in a sedge-dominated marsh.

***Hydrocotyle leucocephala* Cham. & Schltdl.** GC (locally abundant). *Ritter & Hartman 2730.* Trailing emergent herb. Generally restricted to system edges and shallow water. Also collected at a lower elevation pond in the transition between the lower montane and piedmont zones.

***Hydrocotyle pusilla* A. Rich.** Trailing, emergent herb. CHB, INC, CP (rare to locally abundant). *Ritter 1290, Ritter & Wood 1717, Ritter & Ritter 1851, Ritter & Oldcorn 2689.* In Bolivia, characteristically encountered in relatively high elevation systems. Along system edges or on *Sphagnum* mats.

***Hydrocotyle ranunculoides* L.f.** Trailing, emergent herb, at times forming weak floating mats. INC (abundant in shallow water). *Ritter & Nash 1329.* Widespread, ranging from the United States to southern South America (Kahn *et al.* 1993). In Bolivia, *H. ranunculoides* occurs in aquatic habitats at elevations ranging from the lowlands to >3500 m.

Asteraceae

***Acmella repens* (Walt) L. C. Rich var. *beccabunga* (DC.) R. K. Jansen**. Herb. INC (common). *Ritter 1552, 2123.* A weedy species, more characteristic of terrestrial habitats. Occasionally observed along the edges of wetlands in both the wet montane and dry-valley regions.

***Adenostemma brasiliense* Cass.** Herb. CP, GC (common to frequent) *Ritter 1849, Ritter & Wood 3383.* Distributed throughout the Neotropics, generally growing in wet, shaded habitats (Cabrera 1974).

***Ageratum conyzoides* L.** Herb. GC (common). *Ritter 923.* A common weedy species, originally from tropical America, now spread to all the warm regions of the globe (Cabrera 1977). Commonly grows in waste ground, in wet, disturbed habitats, and as a garden weed (Williams 1976). Frequently encountered in systems in the Valles Secos Interandinos.

***Baccharis juncea* (Lehm.) Desv.** Herb. INC (occasional in shallow water along the edge of the system). *Ritter 1556.* Characteristic of disturbed soil along the edges of wetlands in drier habitats (*e.g.*, the Valles Secos) where it can dominate large areas.

***Baccharis trimera* (Less) DC.** Perennial. CHB, LKE (occasional, on the bog mat at CHB; on hummocks and in standing water in depths up to about 0.3 m at LKE). *Ritter & Crow 2197, 2203.* Generally characteristic of terrestrial habitats in somewhat drier, high elevation habitats.

***Conyza bonariensis* (L.) Cronquist.** Herb. CP (locally common on sand bars in the stream that ran through the marsh). *Ritter & Ritter 1850.* Pantropical weed (Williams 1976), originally from South America, now distributed throughout the world (Cabrera 1974).

***Cotula australis* (Sieb. ex Spreng) Hook. f.** Trailing, emergent herb. GC (along the edge of one river, growing in shallow water in quiet water, directly downstream from a boulder). *Ritter 1374.* A widespread species, naturalized in many parts of the world (Dillon 1980). In Bolivia, commonly associated with high elevation marshes.

***Cotula mexicana* (DC.) Cabr.** Diminutive, creeping herb. LKE, occasional in shallow water, and in formerly inundated areas. *Ritter 1251, Ritter et al. 1275.* Widely distributed in the Neotropics, from Mexico to Costa Rica and from Colombia to Costa Rica (Dillon 1980). As with, *Cotula australis, C. mexicana* is more commonly associated with high elevation marshes.

***Erechtites valerianaefolia* (Wolf.) DC.** Herb. Coarse, weedy species. CP (a few individuals in saturated soil along the edge of the system). *Ritter & Ritter 1846.* Widespread in montane habitats throughout northern South American. Apparently well-adapted to disturbed habitats.

***Galinsoga quadriradiata* Ruiz & Pavón**. Emergent herb. CP, GC (stream edges and marshy habitats). *Ritter & Ritter 1852.* Weedy species, with a nearly cosmopolitan distribution (Mabberly 1997).

***Gamochaeta americana* (Miller) Wedd.** Emergent herb. CP, GC (occasional). *Ritter & Ritter 1837, 1856.* Widespread (the Antilles to Tierra del Fuego) in the Americas (Cabrera 1977). More characteristic of terrestrial habitats, occurring both in disturbed and undisturbed soils (Williams 1976).

Brassicaceae

***Cardamine bonariensis* Juss. ex Pers.** Emergent herb. INK, LKE, CP (rare to common). *Ritter & Crow 1102, 2097, Ritter et al. 1276, Ritter 1370.* Cosmopolitan weed. Frequently observed in wetland habitats in the Cloud Forest, Valles Secos and Puna

Callitrichaceae

***Callitriche albomarginata* Fassett.** Submerged macrophyte with floating upper leaves. INC, LKE, CP, GC (generally abundant, growing in shallow water. *Ritter & Crow 1094, 2098, 2204, Ritter 1283, 1372, 1566*. Also occasionally encountered in high elevation (Puna) aquatic habitats, and in trailside streams and pools.

***Callitriche heteropoda* Engelm. ex Hegelm.** Submerged macrophyte with floating upper leaves. CHB, LKW, GC (fairly abundant, in shallow water). *Ritter 1220, Ritter & Ritter 1458, Ritter & Crow 2215, Ritter & Oldcorn 2685*. More characteristic of higher elevation (Puna) aquatic habitats.

Caryophyllaceae

***Cerastium nutans* Raf.** Trailing, emergent herb. CP (locally abundant along the edges of the system). *Ritter 1289, 1862.*

Crassulaceae

***Crassula venezuelensis* (Steyer.) Bywater & Wilkins.** Diminutive, submerged macrophyte. CHB, INC, LKW (in shallow water, and in pockets of open water along the edge of the *Sphagnum* mat at CHB). *Ritter 1260, 1373, 1551, Ritter & Wood 1720, Ritter & Crow 2218, Ritter & Oldcorn 2676*. An interesting aquatic member of a genus generally associated with harsh terrestrial environments. Very common in high elevation (Puna) aquatic habitats.

Cucurbitaceae

***Cyclanthera cordifolia* Cogn.** Climber. CP (occasional). *Ritter 1736, 1861*. Also noted growing in drier habitats (road cuts) in the same general area as CP. Apparently most commonly associated with forested montane habitats.

Elatinaceae

***Elatine* aff. *peruviana* Baehni & Macbr.** Diminutive, submerged macrophyte. LKW (abundant in shallow water). *Ritter & Crow 2217*. Distribution limited to Peru and Bolivia (Schmidt-Mumm and Bernal 1995).

***Elatine triandra* var. *andina* Fassett.** Diminutive submerged macrophyte. INC. Abundant in shallow water. *Ritter & D. Nash 1325, Ritter 1547, Ritter & Wood 1719*. A very widely distributed species, occurring in Eurasia, North America and South America (Gleason and Cronquist 1991). In South America, known from Bolivia, Peru (Macbride 1941), Chile, and Argentina (Bacigalupa 1970). Variety *andina* was originally described from Sorata, Bolivia.

Lamiaceae

***Stachys petiolosa* Briq.** Herb. INC (a small number of individuals grew in saturated sediment in the center of the outflow channel, in the midst of a large population of

Heteranthera reniformis, Pontederiaceae). *Ritter 1369.* Widely distributed in South America (Crespo and Burkart 1978).

Lentibulariaceae
***Utricularia gibba* L.** Free-swimming macrophyte (*sensu* Cook 1990). CHB, LKE, LKW (locally abundant to common). *Ritter 1261, 1561,1565, Ritter & Crow 2195, 2202, 2216.* Very widely distributed, from southern New England to the Antilles, Central America and South America and in the Old World. Ubiquitous in aquatic habitats in the Bolivian lowlands.

Lythraceae
***Cuphea setosa* Koehne.** Herb. GC (a streamside marsh in saturated soil alongside the channel. Locally abundant, forming a dense community). *Ritter & Hartman 2729.*

Nyctaginaceae
***Colignonia rufopilosa* Kuntze**. Arching, suffrutescent semi-climber. CP (in saturated soil alongside the stream, with a few individuals rooted in the channel). *Ritter & Ritter 1844.* An Andean genus (Bohlin 1988), whose members are characteristically found in terrestrial habitats.

Onagraceae
Fuchsia sp. Arching, semi-climbing shrub. CP (locally abundant). *Ritter & Ritter 1847.* A terrestrial species that was observed in a single wetland (CP).

***Ludwigia peruviana* (L.) Hara.** Emergent shrub. GC (common in a small streamside marsh; also occasionally noted growing in wet roadside ditches in the area). *Ritter & Hartman 2728.* A weedy, fairly ubiquitous species. Frequently encountered in wetland habitats over a wide range of elevations (in Bolivia, ca. 100-2200 m).

Oxalidaceae
***Oxalis spiralis* Ruiz & Pavón ex G. Don**. Decumbent herb. CHB, LKW, CP, GC (occasional to common; system edges, alongside streams, and on *Sphagnum* mats). *Ritter & Crow 1096, 2211, Ritter 1858, Ritter & Oldcorn 2686.* Common in the cloud forest habitats of Central America and northern South America (Lourteig 1980). *Oxalis spiralis* is said to be favored as a cultivar in these areas and is frequently grown in hanging pots (Burger 1980; Lourteig 1980).

Plantaginaceae
***Plantago australis* Lam.** Herb. CP, GC (occasional to common; in saturated soil along system edges at CP, and under similar conditions in a riverside marsh in the same general area). *Ritter 924, 1857.* Typically a terrestrial, weedy species. Widely distributed, ranging from the southern United States to the Patagonia region of Argentina (Tolaba and Fabbroni 1998).

***Plantago rigida* Kunth.** Cushion-forming, perennial herb. CHB (occasional; growing on small hummocks along the edge of the system). *Ritter 1222.* Frequently can be a dominant in high elevation bogs and swamps (Rahn 1984). Based on site descriptions from specimens at the Missouri Botanical Garden, *P. rigida* has been most often encountered in much higher (4000-4500 m) habitats in Bolivia.

Polygonaceae

***Polygonum hydropiperoides* Michx.** Emergent herb. INC, CP, GC (common to frequent). *Ritter & D. Nash 1334, Ritter 1859, Ritter & Wood 2702.* Fairly widespread, with a distribution from southern Canada (Gleason and Cronquist 1991) to central Argentina (Cialdella 1989). In Bolivia, *P. hydropiperoides* is most often encountered in lowland aquatic systems.

***Polygonum punctatum* Elliot.** Emergent herb. LKW (locally abundant in shallow water). *Ritter 2219.* Widespread, reaching from southern Canada to South America (Gleason and Cronquist 1991), and common in the tropical and subtropical regions of South America (Cialdella 1989). In Bolivia, *P. punctatum* is frequently encountered in lowland wetland habitats and in wetlands in the Valles Secos Interandinos.

Ranunculaceae

***Ranunculus flagelliformis* Smith.** Creeping herb. CHB, INC, LKW, CP, GC. (occasional to abundant). *Ritter 920, 1287,1853, Ritter & Crow 2192, 2220, Ritter & D. Nash 1333. Ritter & Ritter 1459.* Fairly widespread in South America, from Brazil and Bolivia south to the northern half of Argentina (Lourteig 1951). Characteristic of river and stream edges and seasonally inundated habitats (Molero 1985).

***Ranunculus psychrophilus* Wedd.** Trailing, emergent herb. CHB, LKE, LKW (occasional to abundant; on bog mats and in shallow water, up to ca. 20 cm). *Ritter 1219, 1254, 1258, 1571, Ritter et al. 1271, Ritter & Crow 2194, 2205.* Distribution limited to Bolivia and northern Argentina, at elevations greater than 2000 m (Lourteig 1951).

***Ranunculus sarmentosus* Griseb.** Trailing, emergent herb. CHB, CP, GC (occasional to locally abundant). *Ritter & Crow 1099, Ritter 1286, 1854, Ritter & Oldcorn 2691.* Distribution restricted to high elevation sites in Bolivia and Argentina (Lourteig 1951).

Rubiaceae

Coccosypselum sp. Trailing herb. LKW (locally abundant; growing on *Sphagnum* and on the marshy area around the inlet of the stream that feeds this system; only sterile individuals were encountered). *Ritter & Crow 2210.* Occasionally observed along trails and in low areas in the Cloud Forest.

Scrophulariaceae

***Calceolaria aquatica* A. Br. & Bouché.** Emergent herb. INC, CP, GC (occasional). *Ritter 1281, 1544, 1281, 1860, Ritter & Ritter 1457.* Endemic to the Departamento of

Cochabamba, where it occurs along stream beds and in other wet sites, in montane habitats between 2000-3700 m (Molau 1988).

Limosella cf. ***aquatica*** **L.** Diminutive emergent herb. INC (occasional in shallow water; all individuals were sterile). *Ritter & D. Nash 1330.* In Bolivia, more typical of higher elevation wetlands.

Mimulus glabratus **Kunth**. Trailing perennial, at times more or less erect and emergent. INC, GC (occasional in shallow water). *Ritter 1553.* In Bolivia, more typical of higher elevation wetlands. Distributed from the southern United States to Bolivia (Grant 1924).

Veronica peregrina **L. var. *xaladensis* (H.B.K.) Pennell**. Herb. INC (common in shallow water and in formerly inundated areas). *Ritter 1371.* Widely distributed in the western hemisphere and cultivated worldwide (Edwin 1971).

Veronica serpyllifolia **L**. Herb. INC, GC (low abundance). *Ritter & Crow 1100, Ritter 1555.* A high-altitude species, well adapted to alpine meadows (Edwin 1971).

Urticaceae

Pilea dauciodora **(R. & P.) Wedd**. Trailing herb. GC (locally abundant wherever encountered). *Ritter 1456.* Growing alongside streams and waterfalls and in wet soil alongside trails. In this study, only encountered in the Yungas below La Paz.

MONOCOTS

Commelinaceae

Commelina sp. Emergent herb. INC (growing in shallow water along on edge of the system). *Ritter & Wood 1718.* Possibly *C. diffusa*, a fairly common species in Bolivian wetlands, however, only sterile individuals were present.

Cyperaceae

Carex bonplandii **Kunth**. Emergent herb. CHB, LKE, SSM (occasional; growing on the bog mat and in partially submerged conditions). *Ritter 1259, 1264, 1569, Ritter et al. 1273, Ritter & Crow 2198, Ritter & Wood 2898.* A widespread species, from Arizona to Bolivia, characteristically found in cloud forests, thorn scrub and swamps (Chater 1994).

Carex lemanniana **Boott**. Emergent herb. CHB, CP, SSM (common to abundant; growing on the bog mat and in partially inundated conditions). *Ritter 1282, Ritter & Oldcorn 2678, Ritter & Wood 2900.* Distributed from Mesoamerica to Bolivia, and characteristically occurring in wetlands and páramos (Chater 1994).

Carex purdiei **Boott.** Emergent herb. CHB, CP (occasional to abundant). *Ritter 1221, 1284, Ritter & Ritter 1845.* Distributed from southern Mesoamerica to Bolivia, and characteristically occurring in cloud forests, páramos, and inundated areas (Chater 1994).

***Cyperus hermaphroditus* (Jacq.) Standley.** Herb. CP, GC (generally present in low abundance). *Ritter 1285.* Widespread species (Mexico to Costa Rica), generally characteristic of well-drained, disturbed or undisturbed soils (Adams 1994a).

***Cyperus tabina* Steudel ex Boeckeler.** Emergent herb. SSM, GC (low abundance in shallow water at the former; encountered during general collecting in roadside habitats in the Cloud Forest, growing under a variety of soil and moisture conditions). *Ritter & Wood 2897.* Fairly widely distributed in the Neotropics, where it is adapted to terrestrial and wetland habitats (Adams 1994a).

***Eleocharis acicularis* (L.) Roemer et Schultes.** Emergent herb. CHB, INC, LKE, CP, GC (generally abundant). *Ritter 1292, Ritter & D. Nash 1332, Ritter & Crow 2200, Ritter & Oldcorn 2684.* Extremely widespread (North America to South America, Europe), characteristically found in wet montane habitats (Socorro González E. 1994).

***Eleocharis albibracteata* Nees et Meyer ex Kunth**. Emergent herb. CHB (growing sparsely on the bog mat). *Ritter & Oldcorn 2680.* Fairly widely distributed in the Neotropics, characteristic of subalpine meadows (Socorro González E. 1994).

Eleocharis cf. ***geniculata* (L.) Roemer et Schultes**. Emergent herb. INC (common in shallow water and in seasonally inundated areas). *Ritter 1550.* Widespread in the tropics and subtropics.

***Eleocharis montana* (Kunth) Roemer et Schultes**. Emergent herb. SSM (fairly abundant in shallow water). *Ritter & Wood 2870, 2899.* Widespread: United States and the Antilles to South America (Socorro González E. 1994). Known to occur in a variety of forested and unforested semiaquatic and wetland habitats (Socorro González E. 1994). In Bolivia, *E. montana* characteristically occurs in wetlands in the Valles Secos.

***Isolepis inundata* R. Br.** Emergent herb, at times viviparous. CHB, LKE, LKW (common to locally abundant; growing on *Sphagnum*, in shallow water and along the edges of streams). *Ritter et al. 1270, Ritter 1216, 1563, 1568, Ritter & Crow 2191, 2213.* Widespread in the Neotropics, and also occurring in Australia, New Zealand, and Indonesia, at elevations from 2200-3200 m (Adams 1994b).

***Kyllinga brevifolia* Rottb.** Herb. INC (common, in shallow water and in formerly inundated areas). *Ritter 1548.* Widespread, more or less terrestrial, weedy species, commonly found in disturbed soil in grass dominated habitats (Adams 1994c).

***Pycreus niger* (Ruiz & Pavón) Cuf**. Herb. CHB, INC, SSM. (rare to common; growing on *Sphagnum* or in shallow water). *Ritter 1549, 1562, Ritter & Wood 2901.* Widespread semi-aquatic species. In the new world, distributed from the southern United States to Argentina (Adams 1994d).

Juncaceae

***Juncus ebracteatus* E. Meyer.** Herb. CHB (abundant, on the bog mat). *Ritter 1559.* Widely distributed in the Neotropics, at elevations of 1800-4000 m (Balslev 1996). Well-adapted to wetland habitats.

***Juncus effusis* L.** Herb. CP, GC (locally abundant; along river edges and in riverine marshes). *Ritter 1291, 1843, Ritter & Ritter 1835.* A cosmopolitan species, often growing in disturbed sites (Balslev 1996).

***Juncus fuscocapitatus* Balslev.** Herb. SSM (common; growing along the edges of the pond). *Ritter 2896.* Known only from Bolivia and Peru, where it grows in wet seepages and swampy soils at elevations of 2650-4000 m (Balslev 1996).

***Juncus microcephalus* H.B.K.** Herb. CHB, INC, LKE, LKW, CP, GC (occasional to abundant). *Ritter 1215, 1255, 1262, 1288, 1564, Ritter et al. 1272, Ritter & Crow 2099, 2196, 2212, 2214, Ritter & Wood 2871.* An extremely polymorphic species (Balslev 1996), *J. microcephala* is widely distributed throughout the highland habitats of the Neotropics.

***Juncus pallescens* Lamarck** Herb. GC (locally abundant in a small, stream-fed marsh). *Ritter 928,* (Balslev 1996). Distributed along the Andes from central Ecuador to Chile, and in eastern South America from Rio Grande do Sul (Brazil) to Buenos Aries (Argentina) (Balslev 1996).

***Juncus stipulatus* Nees & Meyen ex Meyen.** Herb. CHB, SSM (present in low abundance in shallow water and in marshy, edge habitats). *Ritter 1545, Ritter & Wood 2902.* Distributed along the Andes from Colombia to Tierra del Fuego (Moore 1983). *Juncus stipulatus* is said to grow in a variety of habitats, ranging from roadsides to bogs (Balslev 1996).

Lemnaceae

***Lemna valdiviana* Phil.** Diminutive, free-floating herb. LKE (locally abundant). Ritter 1567, 4081. Distributed throughout the tropical, subtropical, and warm temperate regions of the New World (Landolt 1996). Common in Bolivian lowland aquatic habitats, *L. valdiviana* was the sole species of Lemnaceae that I encountered in the Cloud Forest.

Poaceae

***Agrostis* cf. *lenis* Roseng., B. R. Arill. & Izag.** Herb. CHB, GC, (only a few individuals present wherever encountered). *Ritter & Ritter 1836, Ritter & Oldcorn 2681.* Said to favor wet, shaded sites (Renvoize 1998).

***Agrostis perennans* (Walt.) Tuck.** Herb. CHB, LKW (occasional to common). *Ritter 1217, 1256, 1257, 1572, Ritter & Crow 2193.* According to Renvoize (1998), in Bolivia this species characteristically occurs in páramos and humid sites, on rocky, forested slopes.

***Deschampsia caespitosa* P. Beauv.** Herb. CHB (locally abundant, forming hummocks on the bog mat). *Ritter 1218,1263, 1560, Ritter & Crow 2199, Ritter & Oldcorn 2679.* A European species. Introduced in South America (Renvoize 1998). Based on label data from the Harvard Herbaria, in South America this species appears to be frequently associated with wet habitats.

***Poa annua* L.** Herb. INC, CP (occasional in shallowly inundated areas). *Ritter & D. Nash 1331, Ritter 1855.* Cosmopolitan, primarily terrestrial, introduced weedy species that characteristically occurs on disturbed sites (Renvoize 1998).

Pontederiaceae

***Heteranthera reniformis* C. Presl.** Emergent herb, at times the stems becoming more or less floating. INC (abundant in shallow water, and in the inflow channel). *Ritter 1546* Ritter & D. Nash 1335. A widely distributed species, from Connecticut to the Antilles, Central America and South America. In Bolivia, generally associated with lowland and lower montane aquatic habitats.

APPENDIX G: SPECIES ASSOCIATED WITH WETLANDS IN THE CHAPARE REGION

Study sites: MW, Mariposa Wetland; IM, Ivirgarsama Marsh; SC, Senda F Curichi; VT, Villa Tunari Pond; SP, Sinahota Pond; PV, Puerto Villarroel Laguna; SC, Valle de Sajta Curichi; GC, General Collecting. **Species Abundances**: A, Abundant; F, Frequent; C, Common; O, Occasional; R, Rare; L.A., Locally Abundant. **Habit**: H, Herb; HE, Epiphytic Herb; HT, Trailing Herb; HA, Annual Herb; HP, Perennial Herb; HA/P, Annual or Perennial Herb; HF-F, Free-Floating Herb; HS, Submersed herb; HSA, Suspended Aquatic Herb; HF-S, Herb with floating stems and/or petioles; FM-F, Floating Mat-forming Herb; RFL, Rooted macrophyte with floating leaves; S, Shrub; TU, Understory Tree; T, Tree; C, Climber. Life-forms wereas could be determined from descriptions in the literature, live material, and herbarium speciemens.

Family	**Species**	**Life-form**	**MW**	**IM**	**SC**	**VT**	**SP**	**SC**	**PV**	**GC**
Pteridophytes										
Lycopodiaceae	*Lycopodium clavatum* L.	HT	O	L.A.	—	—	—	—	—	—
Hymenophyllaceae	*Trichomanes rigidum* Sw.	H	—	—	—	—	—	—	—	N.N.
Marattiaceae	*Danaea elliptica* J. E. Smith	H	—	—	—	—	—	—	—	N.N.
Pteridaceae	*Ceratopteris pteridoides* (Hook.) Hieron	HF-F	—	—	—	—	—	F	—	A
	Pityrogramma calomelanos (L.) Link	H	—	O	—	—	—	—	—	—
Salviniaceae	*Salvinia minima* Baker	HF-F	—	—	—	—	—	F	—	—
Thelypteridaceae	*Thelypteris interrupta* (Willd.) Iwatsuki	H	—	C	—	—	—	—	—	—
	Thelypteris serrata (Cav.) Alston	H	C	C	—	R	—	—	—	—
	Thelypteris sp.	HP	—	L.A.	—	—	—	—	—	—
Dicotyledons										
Acanthaceae	*Hygrophila costata* Nees	HA/P	—	—	—	—	—	—	—	L.A.
	Justicia comata (L.) Sw.	H	—	—	—	A	—	—	—	L.A.
Anacardiaceae	*Tapirira guianensis* Aubl.	T	—	—	—	—	—	—	—	N.N.
Apocynaceae	*Mandevilla hirsuta* (Rich.) K. Schum.	C	O	—	—	—	—	—	—	—
	Odontadenia geminata (Hoffmanns. ex Roem. & Schult.) Müll. Arg.	C	R	—	—	—	—	—	—	—
	Prestonia aff. *acutifolia* (Benth. ex Müll. Arg.) K. Schum.	C	—	—	O	—	—	—	—	—
	Rhabdadenia macrostoma (Benth.) Müell. Arg.	C	—	—	—	—	—	O	—	—
Asclepiadaceae	*Cynanchum montevidense* Spreng.	C	—	—	—	—	—	—	—	N.N.

Family	Species	Life-form	MW	IM	SC	VT	SP	SC	PV	GC
	Tassadia cf. *grazielae* Fontana	C	A	L.A.	—	—	—	—	—	—
Asteraceae	*Barrosoa confluentis* (B. L. Rob.) R. M. King & H. Rob.	HP	—	R	—	—	—	—	—	—
	Eclipta prostrata (L.) L.	HA/P	—	—	—	—	R	—	—	—
	Erechtites hieracifolia (L.) DC.	HA	—	O	—	—	—	—	—	—
	Mikania congesta DC.	C	—	—	C	—	—	—	—	—
	Mikania psilostachya DC.	C	F	—	—	—	—	—	—	—
	Tessaria integrifolia Ruiz & Pavón	T	—	—	—	—	—	—	—	A
Begoniaceae	*Begonia fischeri* Schrank	H	—	O	—	—	—	—	—	—
Boraginaceae	*Cordia tetrandra* Aubl.	T	—	—	—	—	—	—	—	N.N.
Cabombaceae	*Cabomba furcata* Schultes & Schultes.f	HS	—	—	—	—	—	—	—	A
Campanulaceae	*Centropogon cornutus* (L.) Druce	HP	L.A.	C	—	—	—	—	—	—
Clusiaceae	*Calophyllum brasiliense* Cambess.	T	—	—	—	—	—	—	—	N.N.
	Vismia sp.	T	—	R	—	—	—	—	—	—
Convolvulaceae	*Ipomoea* cf. *phillomega* House	C	—	O	—	—	—	—	—	—
Chrysobalanaceae	*Hirtella triandra* Sw.	T	—	—	—	—	—	—	—	N.N.
Dilleniaceae	*Davilla nitida* (Vahl) Kubitzki	C	—	R	—	—	—	—	—	—
Erythroxylaceae	*Erythroxylum coca* Lam.	S	—	R	—	—	—	—	—	—
Euphorbiaceae	*Caperonia palustris* (L.) St.-Hil.	HA/P	—	—	O	—	—	—	—	C
Fabaceae	*Aeschynomene rudis* Benth.	HP	—	—	—	—	—	—	—	A
	Desmodium adscendens (Sw.) DC.	C	C	C	—	—	—	—	—	—
	Indet.	H	C	—	—	—	—	—	—	—
	Inga umbellifera (Vahl) Steud. ex DC.	T	—	—	—	—	—	—	—	N.N.
	Mimosa pigra L. (= *Mimosa pellita* H. & B. ex Willd.)	S	—	—	—	—	—	—	—	F
	Phaseolus sp.	C	R	C	—	—	—	—	—	—
	Zygia cauliflora (Willd.) Killip ex Record	T	—	—	O	—	—	—	—	—
Haloragaceae	*Myriophyllum mattogrossense* Hoehne	HS	—	—	—	—	—	—	—	L.A.
Lamiaceae	*Hyptis atrorubens* Poir.	H	L.A.	—	—	—	—	—	—	—
	Hyptis brevipes Benth.	HP	—	—	—	—	O	—	—	—

Family	Species	Life-form	MW	IM	SC	VT	SP	SC	PV	GC
	Hyptis lacustris St.-Hil. ex Bentham	HP	—	O	—	—	—	—	—	—
Lentibulariaceae	*Utricularia gibba* L.	HSA	—	O	—	—	—	—	—	—
Loranthaceae	*Phthirusa pyrifolia* (Kunth) Eichler	P	C	O	—	—	—	—	—	—
Lythraceae	*Cuphea melvilla* Lindl.	S	—	—	—	—	—	—	F	—
Malvaceae	*Hibiscus sororius* L.	HP	—	—	—	—	—	—	O	—
	Pavonia fruticosa (Miller) Fawcett & Rendle	HP	—	—	—	O	—	—	—	—
Melastomataceae	*Aciotis acuminifolia* (Mart. ex DC.) Triana	HA	O	L.A.	—	—	—	—	—	L.A.
	Aciotis caulialata (Ruiz & Pavón) Triana	H	O	—	—	—	—	—	—	—
	Clidemia capitellata (Bonpl.) D. Don	S	—	N.N.	—	—	—	—	—	—
	Clidemia cf. *biserrata* DC.	S	C	—	—	—	—	—	—	—
	Miconia ampla Triana	S	A	R	—	—	—	—	—	—
	Miconia tomentosa (L. C. Rich) D. Don	S	—	R	—	—	—	—	—	—
	Miconia sp.	S	O	—	—	—	—	—	—	—
	Tococa aff. *macrophysca* Spruce ex Triana	S	L.A.	—	—	—	—	—	—	—
Myrtaceae	*Eugenia florida* DC.	TU	—	—	—	—	—	—	—	N.N.
	Psidium guajava L.	TU	—	—	—	O	—	—	—	—
Nymphaeaceae	*Nymphaea amazonum* Mart. & Zuccarini subsp. *amazonum*	RFL	—	—	—	—	—	—	—	C
	Nymphaea glandulifera Rodschied	RFL	L.A.	—	—	—	—	—	—	—
Ochnaceae	*Sauvagesia erecta* L.	HA	C	C	—	—	—	—	—	—
Onagraceae	*Ludwigia affinis* (DC.) Hara	H	—	—	—	—	—	—	—	R
	Ludwigia decurrens Walt.	H	—	O	—	—	—	—	—	L.A.
	Ludwigia inclinata (L.f) Gómez	H	—	—	C	—	—	—	—	A
	Ludwigia latifolia (Benth.) Hara	S	—	—	—	—	—	—	—	O
	Ludwigia leptocarpa (Nutt.) Hara	HP	—	—	—	—	—	O	O	C
	Ludwigia nervosa (Poiret) Hara	S	A	A	C	—	—	—	—	—
	Ludwigia octovalvis (Jacq.) Raven	HP	—	—	C	—	C	—	—	—
Piperaceae	*Piper pilirameum* C. DC.	S	C	O	—	—	—	—	—	—
Polygonaceae	*Polygonum ferrugineum* Wedd.	HP	—	—	—	—	—	—	—	L.A.

Family	Species	Life-form	MW	IM	SC	VT	SP	SC	PV	GC
	Polygonum hydropiperoides Michx.	HP	C	O	—	—	F	—	—	A
	Polygonum meisnerianum Cham. et Schltdl.	HP	—	—	—	—	—	—	—	L.A.
	Polygonum punctatum Elliot	HA/P	—	—	—	—	—	A	F	—
	Triplaris americana L.	T	—	—	—	—	—	—	—	N.N.
Rubiaceae	*Borreria ocymifolia* (Willd. ex Roem. & Schult.) Bacig. & E.L. Cabral	HA/P(?)	—	—	—	—	—	—	—	L.A.
	Coccocypselum hirsutum Bartl. ex DC.	H	L.A.	—	—	—	—	—	—	—
	Genipa americana L.	T	—	—	—	—	—	—	—	N.N.
	Oldenlandia lancifolia (Schumach.) DC.	HA/P(?)	O	O	C	C	F	—	—	F
	Palicourea riparea Benth	S	—	—	O	—	—	—	—	—
	Palicourea triphylla DC.	S	—	R	—	—	—	—	—	—
	Psychotria poeppigiana Muell.-Arg.	S	F	—	—	—	—	—	—	—
	Sabicea novogratensis K. Schum.	C	A	O	C	—	—	—	—	0
	Sabicea villosa Willd. ex Roem. & Schult.	C	—	—	—	—	—	—	—	N.N.
	Spermacoce tenuior L.	H	—	—	—	L.A.	—	—	—	—
Sapindaceae	*Paullinia pinnata* L.	L	—	—	O	—	—	—	—	—
Scrophulariaceae	*Lindernia* sp.	HA	—	—	—	—	L.A.	—	—	—
	Torenia thouarsii (Cham. & Schltd.) O. Kuntze	HA	O	R	—	—	—	—	—	C
	Scoparia dulcis L.	H	—	—	—	—	—	—	—	N.N.
Sphenocleaceae	*Sphenoclea zeylanica* Gaetrn.	HA/P	—	—	—	—	—	—	—	R
Vitaceae	*Cissus erosa* L.C. Rich.	CL	—	—	—	—	—	—	—	L.A.

Family	Species	Life-form	MW	IM	SC	VT	SP	SC	PV	GC
Monocotyledons										
Alismataceae	*Echinodorus* cf. *subalatus* (Mart.) Grisebach	HP	—	—	O	—	—	—	—	—
Araceae	*Pistia stratiotes* L.	HF-F	—	—	—	—	—	—	—	N.N.
Commelinaceae	*Commelina* sp.	H	N.N.	—	—	—	—	—	—	—
Costaceae	*Costus arabicus* L.	HP	—	F	—	—	—	—	—	—
	Costus scaber Ruiz & Pavón	H	—	—	—	—	—	—	—	N.N.
Cyperaceae	*Calyptrocarya glomerulata* (Brogn.) Urban	HP	L.A.	—	—	—	—	—	—	—
	Cyperus aggregatus (Willd.) Endl.	HP	—	—	—	—	—	—	—	L.A.
	Cyperus haspan L.	HP	F	R	—	—	—	—	—	—
	Cyperus luzulae (L.) Retz	HP	—	O	C	C	—	—	—	—
	Cyperus meyenianus Kunth	HP(?)	R	C	O	—	—	—	—	—
	Cyperus surinamensis Rottb.	HA/P	—	—	—	—	F	—	—	—
	Diplacrum longifolium (Griseb.) C. B. Clarke	HP	F	—	—	—	—	—	—	—
	Diplasia karatifolia L. C. Rich.	HP	R	—	—	—	—	—	—	—
	Eleocharis acutangula (Roxb.) Schultes	FM-F	—	A	—	—	—	—	—	—
	Eleocharis elegans (Kunth) Roemer et Schultes	HP	—	—	—	—	—	—	—	O
	Eleocharis interstincta (Vahl.) Roemer et Schultes	HP	A	—	—	—	—	—	—	—
	Fimbristylis dichotoma (L.) Vahl.	HA/P	—	L.A.	—	—	—	—	—	C
	Fimbristylis littoralis Gaudich.(= F. miliacea sensu (L.) Vahl)	HA	—	—	—	—	—	—	—	F
	Oxycaryum cubense (Poepp. & Kunth) Lye	FM-F	—	O	—	—	—	—	—	—
	Scleria cyperinoides Clark	HP	C	—	—	—	—	—	—	—
	Scleria macrophylla J. S. Presl. & C. Presl	HP	L.A.	—	C	—	—	—	—	C
	Scleria microcarpa Nees ex. Kunth	HP	—	—	O	A	—	—	—	—
Eriocaulaceae	*Tonina fluviatilis* Aublet	HP	A	—	—	—	—	—	—	—
Heliconiaceae	*Heliconia marginata* (Griggs.) Pitt	HP	—	—	—	—	—	A	—	—
Hydrocharitaceae	*Apalanthe granatensis* (H. & B.) J. E. Planchon	HS	—	—	A	—	—	—	—	—
	Limnobium laevigatum (Humb. & Bonpl. ex Willd.) Heine	HF-F	—	—	—	—	—	—	—	N.N.
Limnocharitaceae	*Limnocharis flava* (L.) Buchenau	HA/P	—	—	—	—	—	—	—	R

Family	Species	Life-form	MW	IM	SC	VT	SP	SC	PV	GC
Orchidaceae	*Campylocentrum minutum* C. Schweinf.	HE	—	O	—	—	—	—	—	—
	Epidendrum schomburgkii Lindl.	HE	R	—	—	—	—	—	—	—
	Trizeuxis falcata Lindl.	HE	—	C	—	—	—	—	—	—
Poaceae	*Acroceras zizanioides* (H.B.K.) Dandy	HA/P	—	—	—	—	—	—	—	A
	Andropogon bicornis (L.) Forsk.	HP	O	O	—	—	—	—	—	—
	Andropogon selloanus (Hackel) Hackel	HP	O	—	—	—	—	—	—	—
	Axonopus fissifolius (Raddi) Kuhlm.	HP	—	—	—	—	R	—	—	—
	Coix lacryma-jobi L.	H	—	—	—	—	—	—	—	L.A.
	Echinochloa colona (L.) Link	HA	—	—	—	—	—	—	—	O
	Gynerium sagittatum (Aubl.) Beauv.	HP	—	—	—	—	—	—	—	A
	Hemarthria altissima (Poir.) Stapf & C.E. Hubb.	HP	—	—	—	—	—	—	—	L.A.
	Homolepis aturensis (H.B.K.) Chase	HP	C	—	—	—	—	—	—	—
	Hymenachne amplexicaulis (Rudge.) Nees	HP	—	—	—	—	—	—	—	A
	Hymenachne donacifolia (Radd.) Chase	HP	—	—	F	—	—	—	—	—
	Hyparrhenia rufa (Nees) Staph.	HP	—	F	—	—	—	—	—	—
	Luziola bahiensis (Steudl.) A. Hitchc.	HP	O	—	—	—	—	—	—	—
	Panicum dichotomiflorum Michx.	HP	—	—	—	—	F	—	—	—
	Panicum grande Hitchcock & Chase	HP	C	—	—	—	—	—	—	—
	Panicum hylaeicum Mez.	HP	L.A.	—	—	—	—	—	—	—
	Panicum laxum Sw.	HP	—	—	—	C	—	—	—	—
	Panicum mertensii Roth	HP	—	—	—	—	—	—	C	—
	Panicum pilosum Sw.	HP	O	—	—	C	—	—	—	L.A.
	Panicum polygonatum Schrader	HP	A	L.A.	—	—	—	—	—	—
	Panicum schwackeanum Mez.	H	F	—	—	—	—	—	—	—
	Panicum stoloniferum Poir.	HP	—	—	—	C	—	—	—	—
	Paspalum repens Bergius	H	—	—	—	—	—	—	—	N.N.
	Paspalum conjugatum Bergius	H	—	—	—	—	—	—	—	N.N.
	Steinchisma hians (Elliot) Nash ex Small	HP	C	—	—	—	—	—	—	—

Family	**Species**	**Life-form**	**MW**	**IM**	**SC**	**VT**	**SP**	**SC**	**PV**	**GC**
Pontederiaceae	*Eichhornia crassipes* (Mart.) Solms-Laubach	HFS	—	—	—	—	—	—	—	N.N.
	Eichhornia diversifolia (Vahl.) Urban	HFS	—	—	—	—	—	—	—	R
	Pontederia rotundifolia L.f	HFS	—	—	A	—	—	—	—	—

APPENDIX II. SPECIES ASSOCIATED WITH THE STUDY SITES OF THE BOLIVIAN PANTANAL

Study Sites: LC, Laguna Cáceres; LU, Laguna Uberaba; LG, Laguna La Gaiba; LM, Laguna Mandioré; PG, Puesto Gonzalo. Specimens without a reference to a study site were from general collecting, from references in the literature, or from herbarium specimens. **Life-form**: H, Herb; HE, Epiphytic Herb; HT, Trailing Herb; HA, Annual Herb; HP, Perennial Herb; HA/P, Annual or Perennial Herb; S-WP, Sub-woody Perennial; HF-F, Free-Floating Herb; HS, Submersed herb; HSA, Suspended Aquatic Herb; HF-S, Herb with floating stems and/or petioles; FM-F, Floating Mat-forming Herb; RFL, Rooted macrophyte with floating leaves; S, Shrub; TU, Understory Tree or "Treelet"; T, Tree; C, Climber. Life-forms wereas could be determined from descriptions in the literature, live material, and herbarium speciemens.

Family	**Species**	**Life-form**	**LC**	**LU**	**LG**	**LM**	**PG**
Pteridophytes							
Marsileaceae	*Marsilea crotophora* D. M. Johnson	RFL	+	–	–	+	–
Pteridaceae	*Ceratopteris pteridoides* (Hook.) Hieron	HF-F	+	–	–	+	–
	Pityrogramma calomelanos (L.) Link	H	+	+	–	–	–
Salviniaceae	*Azolla caroliniana* Willd.	H	–	–	+	–	–
	Azolla mexicana C. Presl.	HF-F	–	–	–	+	–
	Salvinia auriculata Aubl.	HF-F	+	+	+	+	+
	Salvinia minima Baker	HF-F	+	+	–	–	–
Dicotyledons							
Acanthaceae	*Justicia laevilinguis* (Nees) Lindau	H	+	–	+	+	+
Amaranthaceae	*Alternanthera aquatica* (D. Par.) Chodat	H	+	–	–	–	–
	Alternanthera philoxeroides (Mart.) Griseb.	HF-S	+	–	–	–	+
	Pfaffia glomerata Pedersen	H	+	+	–	–	–
Apiaceae	*Hydrocotyle ranunculoides* L.f	H	+	+	+	+	–
Apocynaceae	*Rhabdadenia pohlii* Müell. Arg.	C	+	–	–	–	+
	Thevetia bicornuta Müell. Arg.	S	+	–	–	–	–
Asclepiadaceae	*Cynanchum montevidense* Spreng.	C	+	–	–	+	–
	Sarcostemma clausum (Jacq.) Schult. in Roem. & Schult.	C	–	–	+	–	–
Asteraceae	*Barrosoa candolleana* (Hook. & Arn.) R. M. King & H. Rob.	HP	–	–	–	–	–
	Barrosoa confluentis (B. L. Rob.) R. M. King & H. Rob.	HP	+	+	+	+	–
	Eclipta prostrata (L.) L.	HA/P	+	–	–	–	–
	Enhydra anagallis Gardner	H	+	–	+	+	–
	Erechtites hieraciifolia (L.) Raf. ex DC.	HA	+	–	+	–	+
	Lepidaploa remotiflora (L. C. Rich) H. Rob.	H	–	–	–	+	–
	Melanthera latifolia (Gardner) Cabrera	H	+	–	–	+	–

Family	Species	Life-form	LC	LU	LG	LM	PG
	Mikania cordifolia Willd.	C	–	–	+	–	–
	Mikania micrantha Kunth	C	+	+	+	+	+
	Pacourina edulis Aubl.	H	+	–	–	+	–
	Vernonanthura brasiliana (L.) H. Rob.	S	–	+	+	–	–
	Wedelia aurantiaca (Grisebach) ined.	H	–	+	+	–	–
Bignoniaceae	*Anemopaegma chrysanthum* Dugand	L	+	–	–	–	–
	Tabebuia insignis (Miquel) Sandwith	T	–	+	–	–	–
Cabombaceae	*Cabomba furcata* Schultes & Schultes.f	HS	+	–	–	–	+
Capparaceae	*Cleome spinosa* Jacq.	H	+	–	–	–	–
Chrysobalanaceae	*Couepia uiti* Bentham	T	–	–	–	+	–
Clusiaceae	*Rheedia brasiliensis* (Mart.) Planch. & Triana	T	–	–	+	+	–
Combretaceae	*Combretum lanceolatum* Pohl	S	+	–	+	+	+
Convolvulaceae	*Aniseia martinicensis* (Jacq.) Choisy	C	+	–	+	+	–
	Ipomoea alba L.	C	+	–	–	–	–
	Ipomoea carnea Jacq. subsp. *fistulosa* (Choisy) Austen	PH	+	+	+	+	+
	Ipomoea chiliantha Hallier f.	C	+	+	–	+	–
	Ipomoea rubens Choisy	C	+	–	–	–	–
	Ipomoea subrevoluta Choisy	C	–	+	–	–	–
	Merremia umbellata (L.) Hall f.	C	+	–	–	–	+
	Stictocardia tiliifolia (Desr.) Hallier f.	C	+	–	–	–	–
Cucurbitaceae	*Cayaponia podantha* Cogn.	C	+	–	–	–	–
	Melothria pendula L.	C	+	–	–	–	–
	Indet.	C	+	–	–	–	–
Euphorbiaceae	*Alchornea castaneifolia* (Willd.) A. Juss.	S	+	+	–	+	–
	Caperonia castaneifolia (L.) A. St.-Hil.	HF-S	+	+	+	+	+
	Caperonia palustris (L.) Saint-Hilaire	HA/P	+	–	–	–	–
	Croton argenteus L.	S	+	–	–	–	–
	Phyllanthus fluitans Müell. Arg.	HF-F	+	–	–	+	–
Fabaceae	*Aeschynomene fluminensis* Vell.	S-WP	–	+	–	–	–
	Aeschynomene sensitiva Swartz	H	+	+	+	–	+
	Albizia inundata (Mart.) Barneby & J.W. Grimes	T	+	–	–	–	–
	Bauhinia bauhinioides (Mart.) J.F. Macbr.	T	+	–	–	–	–
	Bauhinia corniculata Bentham	T	+	–	–	–	–
	Bergeronia sericea Micheli	T	+	–	–	+	–
	Calopogonium velutinum (Benth.) Amshoff	C	+	+	–	–	–
	Camptosema paraguariense (Chodat & Hassl.) Hassl.	C	+	–	–	–	–

Family	Species	Life-form	LC	LU	LG	LM	PG
	Dioclea burkartii Maxwell	C	+	+	+	–	–
	Discolobium pulchellum Benth.	S	+	+	–	–	–
	Macroptilium lathyroides (L.) Urb.	H	+	–	–	–	–
	Mimosa pigra L.	S	–	+	–	–	–
	Mimosa weddelliana Benth.	S	+	–	–	–	–
	Mimosa xanthocentra C. Martius	S	+	+	+	+	–
	Neptunia natans (L.f.) Druce	HF-S	+	–	–	+	+
	Neptunia plena (L.) Benth.	S	–	–	–	+	–
	Senna pendula (H. & B. ex Willd.) H. S. Irwin & Barneby	S	+	+	–	–	–
	Senna splendida (Vogel) H. S. Irwin & Barneby	S	–	–	+	+	–
	Sesbania exasperata Kunth	S	+	–	+	–	–
	Vigna luteola (Jacq.) Benth.	C	+	–	+	+	–
	Vigna peduncularis Fawc. & Rendle	C	+	–	–	–	–
Lamiaceae	*Hyptis recurvata* Poit.	HP	–	+	–	–	–
Lentibulariaceae	*Utricularia breviscapa* Wright ex Grisebach	H	+	–	–	–	–
	Utricularia foliosa L.	HSA	+	–	–	–	+
	Utricularia gibba L.	HSA	+	+	–	–	+
	Utricularia hydrocarpa Vahl	HSA	+	–	–	–	–
Lythraceae	*Cuphea carthagenensis* (Jacq.) J. F. Macbr.	H	+	–	–	–	–
Malvaceae	*Hibiscus furcellatus* Lam.	S-WP	+	+	–	–	–
	Hibiscus sororius L.	S-WP	+	–	–	–	–
	Malachra rudis Benth.	S-WP	+	–	–	–	–
	Pavonia vitifolia Hochr.	S-WP	+	+	–	–	–
Melastomataceae	*Rhynchanthera novemnervia* (Martius) DC.	S	+	+	+	–	–
Myrtaceae	*Calyptranthes paniculata* Ruiz & Pavón	T	–	–	–	+	–
	Myrcia fallax (Rich.) DC.	TU	–	–	+	–	–
	Indet. # 1	TU	+	–	–	–	–
	Indet. # 2	TU	+	–	–	–	–
Nymphaeaceae	*Nymphaea amazonum* Mart. & Zuccarini subsp. *pedersenii* Wiersema	RFL	+	–	–	–	+
	Nymphaea belophylla Trickett	RFL	+	–	–	–	–
	Nymphaea gardneriana Planchon	RFL	+	–	–	–	–
	Nymphaea oxypetala Planchon	H	+	–	–	–	+
	Victoria amazonica (Poepp.) Sower	RFL	+	–	–	+	–
Onagraceae	*Ludwigia affinis* (DC.) Hara	HA/P	+	–	–	–	–
	Ludwigia decurrens Walt.	H	–	–	–	+	–
	Ludwigia grandiflora (Michaux) Greuter & Burdet	S	+	+	+	–	+

Family	**Species**	**Life-form**	**LC**	**LU**	**LG**	**LM**	**PG**
	Ludwigia helminthorrhiza (Mart.) Hara	HF-S	+	+	+	+	+
	Ludwigia leptocarpa (Nutt.) Hara	S-WP	–	–	–	+	+
	Ludwigia nervosa (Poiret) Hara	S	–	+	+	–	–
	Ludwigia sedoides (H. & B.) Hara	HP	–	+	–	–	+
	Ludwigia tomentosa (Cambess.) H. Hara	S	–	+	–	–	–
Passifloraceae	*Passiflora misera* H.B.K.	C	+	–	–	–	–
Piperaceae	*Piper fuligineum* Kunth	S	–	+	–	–	–
Polygonaceae	*Coccoloba ovata* Bentham	S	–	–	–	+	–
	Polygonum acuminatum Kunth	H	+	+	+	+	+
	Polygonum ferrugineum Wedd.	HP	–	–	+	–	+
	Triplaris gardneriana Wedd.	T	+	–	+	+	–
Rubiaceae	*Psychotria carthagenensis* Jacq.	S-WP	–	–	+	–	–
	Rudgea cornifolia (Kunth) Standl.	TU	–	–	+	–	–
	Simira rubescens (Benth.) Bremek. ex Steyerm.	TU	–	–	+	–	–
	Sphinctanthus hasslerianus Chodat	S-WP	+	–	–	–	–
Sapindaceae	*Paullinia pinnata* L.	L	+	+	–	+	–
	Sapindus saponaria L.	TU	–	–	+	–	–
Scrophulariaceae	*Alectra aspera* (Cham. & Schltdl.) L .O. Williams	H	–	–	+	–	–
	Bacopa salzmannii (Benth.) Edwall	H	–	+	–	–	–
	Bacopa stricta (Scrad.) Edwall	H	+	–	–	–	–
Solanaceae	*Solanum americanum* Mill.	HP	+	–	–	–	–
Sphenocleaceae	*Sphenoclea zeylanica* Gaetrn.	HA/P	+	–	–	+	–
Sterculiaceae	*Byttneria filipes* Mart.	S-WP	+	+	+	+	+
	Melochia arenosa Benth.	S-WP	+	+	+	+	–
Verbenaceae	*Lippia alba* (Miller) N.E. Brown	S-WP	+	–	–	–	–
	Phyla nodiflora (L.) Greene	H	+	–	–	–	–
	Stachytarpheta cayennensis (L. C. Rich) Vahl	S	–	–	+	–	–
	Stachytarpheta elatior Schrad. ex Schult.	H	+	–	–	–	–
Vitaceae	*Cissus spinosa* Camb.	C	+	+	+	+	+
	Cissus verticillata (L.) Nicholson & C. E. Jarvis	C	+	–	–	–	–
Monocotyledons							
Alismataceae	*Echinodorus grandiflorus* subsp. *aureus* (Fassett) Haynes & Holm-Niels.	H	–	+	–	–	–
	Echinodorus paniculatus Micheli	H	+	–	–	–	+
	Sagittaria rhombifolia Chamisso	H	–	+	–	–	–
Araceae	*Pistia stratiotes* L.	HF-F	+	–	+	+	–

Family	Species	Life-form	LC	LU	LG	LM	PG
Arecaceae	*Bactris major* Jacq.	T	+	–	–	–	–
	Copernicia alba Mor. ex Mor. & Britt.	T	+	–	+	+	–
Cannaceae	*Canna glauca* L.	H	–	–	–	–	–
Commelinaceae	*Commelina erecta* Chapm.	H	–	–	+	–	–
Cyperaceae	*Cyperus gardneri* Nees ex. Mart.	H	+	–	–	–	–
	Cyperus giganteus Vahl.	H	+	+	–	–	–
	Cyperus haspan L.	HP	+	+	–	–	–
	Cyperus rotundus L.	H	+	–	–	–	–
	Eleocharis acutangula (Roxb.) Schultes	FM-F	–	+	–	–	–
	Eleocharis elegans (Kunth) Roemer et Schultes	HP	–	+	–	–	–
	Eleocharis minima Kunth	H	+	+	–	–	–
	Fuirena umbellata Rottb.	FM-F	–	+	–	–	–
	Oxycaryum cubense (Poepp. & Kunth) Lye	FM-F	+	+	+	+	+
	Rhynchospora gigantea Link.	HP	–	+	+	–	–
	Rhynchospora trispicata (Nees) Schrad. ex Steud.	HP	+	–	–	–	–
	Scleria flagellum-nigrorum P. Bergius	HP	–	–	+	–	–
	Torulinium odoratum (L.) Hooper	H	+	+	–	+	–
Hydrocharitaceae	*Egeria najas* Planchon	HS	+	–	–	–	–
	Limnobium laevigatum (H. & B. ex Willd.) Heine	HF-F	+	+	–	+	–
Lemnaceae	*Lemna aequinoctialis* Welw.	HF-F	–	–	–	+	–
	Lemna valdiviana Phil.	HF-F	–	–	+	+	–
	Wolffia columbiana Karsten	HF-F	–	–	–	+	–
	Wolffiella lingulata (Hegelm.) Hegelm.	HF-F	–	–	+	+	–
	Wolffiella oblonga (Phil.) Hegelm.	HF-F	–	–	–	+	–
Limnocharitaceae	*Limnocharis flava* (L.) Buchenau	HA/P	–	+	–	–	–
Marantaceae	*Thalia geniculata* L.	H	+	+	–	–	+
Najadaceae	*Najas podostemon* Magnus	HS	–	–	–	–	+
Poaceae	*Andropogon bicornis* (L.) Forsk.	HP	+	+	+	–	+
	Cynodon dactylon (L.) Pers.	H	+	–	–	–	–
	Echinochloa polystachya (Kunth) Hitchc.	H	+	+	+	+	–
	Eriochloa punctata (L.) Desv.	H	+	–	–	–	–
	Hymenachne amplexicaulis (Rudge.) Nees	HP	+	+	+	+	+
	Hymenachne donacifolia (Raddi) Chase	HP	+	–	–	–	–
	Imperata tenuis Hack	H	+	+	+	+	+
	Leersia hexandra L.	H	+	+	+	+	+
	Leptochloa panicoides (J. Presl) Hitchc.	H	–	–	–	+	–

Family	Species	Life-form	LC	LU	LG	LM	PG
	Luziola subintegra Swallen	H	+	–	–	–	–
	Oryza alta Swallen	H	–	–	+	+	–
	Oryza rufipogon Griffiths	H	+	+	–	–	–
	Panicum dichotomiflorum Michx.	HP	+	+	–	–	–
	Panicum elephantipes Nees ex Trin.	H	+	–	+	+	–
	Panicum laxum Sw.	HP	–	–	+	–	+
	Paspalum repens Bergius	FM-F	+	–	+	+	+
	Paspalum wrightii Hitchc. & Chase	H	+	–	–	–	–
	Setaria parviflora (Poir.) Kerguélen	H	+	–	–	–	–
Pontederiaceae	*Eichhornia azurea* (Sw.) Kunth	HF-S	+	+	+	+	+
	Eichhornia crassipes (Mart.) Solms-Laubach	HF-S	–	+	+	+	+
	Pontederia cordata L. var. *ovalis* (Mart. in Roemer et Schultes) Solms	H	–	+	+	+	–
	Pontederia rotundifolia L.f	HF-S	+	+	+	+	+
	Pontederia subovata (Seubert in Martius) Lowden	H	+	–	–	–	–
	Pontederia triflora (Endl. ex Seub.) Agost. & Velásquez	HF-S	–	+	–	–	–

APPENDIX I: PHYTOGEOGRAPHY

> "If philosophy is the devil's whore, as Martin Luther once quipped, then biogeography and biological systematics are fast becoming Old Nick's bordello."
> - R. Craw, "Panbiogeography: Methods and Synthesis in Biogeography"

Introduction

During the evolution of this project, it became obvious that the species-distribution data that were being compiled could potentially be used to investigate a range of phytogeographic questions. The work of Crovello (1981) and McLaughlin (1994) was particularly useful in directing this aspect of the research. The wetland species database compiled for this study (Ritter 2000) contained a wealth of information, and could likely have served as the basis for a number of chapters. Time limitations, however, limited the analysis of these data to a few, broadly drawn examples. These examples, along with some brief notes, are presented here.

Site-level Phytogeographic Patterns

Initially, floristic relationships at the site-level were examined using similarity matrices. Results of these analyses were generally unsatisfactory. Many of the study sites were sufficiently depauperate such that calculated indices of similarity gave a poor representation of the actual floristic associations. Furthermore, the Bolivian wetland flora contained a large number of common, widespread species, and in some cases these undoubtedly served to elevate calculated floristic similarities between some sites. Site-level comparisons were limited to study sites within the same region, but had all 46 sites been compared in a single similarity matrix the results would likely have been confounding, if not misleading.

More meaningful results were obtained using Detrended Correspondence Analysis (DCA). In an ordination by DCA of the 46 study sites (Figure I.1), sites from each region were almost always grouped in close proximity in ordination space. The sole exceptions were two sites from the Chapare region which possessed particularly depauperate floras (see Chapter 4 for an elaboration).

As noted in Chapter 6, seasonal fluctuations in floristic composition, which are characteristic of wetlands in the Neotropical lowlands, can affect estimates of site-level biodiversity. Likewise, these fluctuations can also affect calculated floristic similarities. An example of the magnitude of these seasonal differences can be found in the work of Prado *et al.* (1994) in the Brazilian Gran Pantanal. As noted, the authors sampled from a 2500 m^2 study plot during the course of a year, with sampling scheduled during each of the four hydrologic seasons. The data presented by Prado *et al.* (1994) were compiled and analyzed using Sørensen's Index (Table I.1). Floristic similarities within the site varied from 74.0-88.2% during the year (Table I.1). In like manner, calculated floristic similarities from two systems that had been sampled during different hydrologic seasons could vary by 10-25% simply because of seasonal differences in species composition. It should be emphasized, however, that the preceding example should not be interpreted as

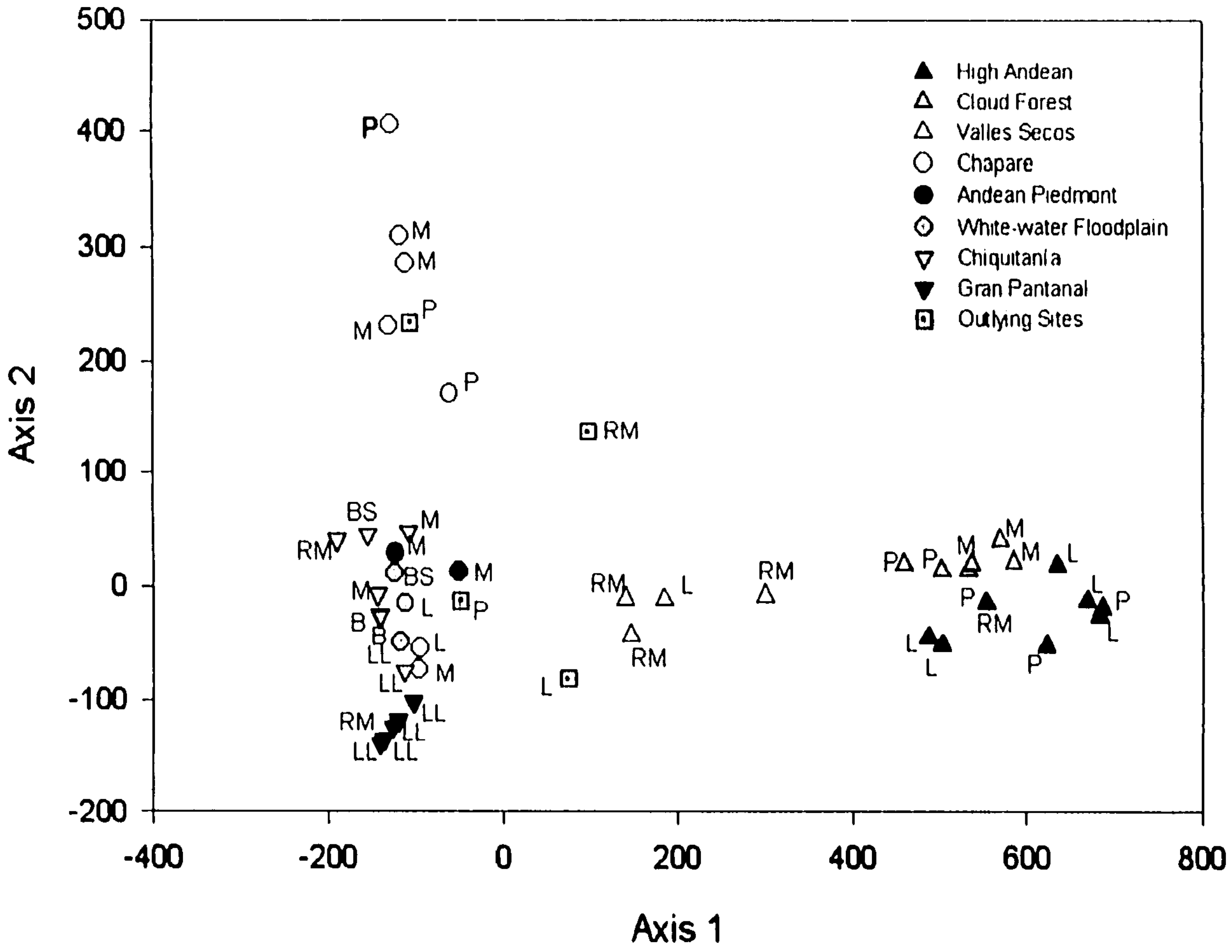

Figure I.1. Ordination of the 46 Bolivian study sites by Detrended Correspondence Analysis (DCA). Key to wetland types: B- bahía; BS - basin swamp; L - small lake (< 500 ha); LL - large lake (> 500 ha); M - marsh; P - pond; RM - riparian marsh.

representing the average magnitude of seasonal changes in floristic composition in Neotropical wetlands, as it was based on a single study.

Table I.1. Seasonal^{A} changes in species-richness and floristic similarities (Sørensen's Index) in a 2500 m^2 study plot in the Northern Brazilian Pantanal. Data compiled from Prado *et al.* (1994).

	Seca	Enchente	Cheia	Vazante
Seca	**36**	27	24	27
Enchente	**76.1**	**35**	29	29
Cheia	**71.6**	**87.9**	**31**	30
Vazante	**74**	**80.6**	**88.2**	**37**

A. Seasons are as follows: 1) *seca*: the dry season; 2) *enchente*: the period of flooding associated with the beginning of the rainy season; 3) *cheia*: the high water period, which begins approximately 3-4 months after the onset of the rainy season and which is maintained by daily rains; and, 4) *vazante*: the transition to the dry season during which water levels drop rapidly and rainfall is diminished, but does not cease completely.

Regional-Scale Phytogeographic Patterns

At the regional scale, similarity matrices were of greater utility than at the study-site scale. Nevertheless, ordination (DCA) was more instructive for representing overall floristic relationships among OGUs. For example, based on calculated floristic similarity (Sørensen's Index) the Andean Piedmont wetland flora was most similar to the Gran Pantanal (61.7%, Table I.2). When viewed within the context of floristic relationships among all regions, however, the Andean Piedmont was seen to be much more strongly associated with the other lowland Bolivian regions (*e.g.*, the Chiquitanía, White-water Floodplain, and the Chapare) than with the Gran Pantanal (Figure I.2).

Table I.2. Comparison of diversity and floristic similarity (Sørensen's Index) between the eight Bolivian regions considered in this study. Figures in bold along the main diagonal indicate the number of species noted for each region. Numbers above the main diagonal indicate the number of species shared by both region. Numbers in the shaded cells indicate the percent floristic similarity between areas. Regions: HA - High Andean; CF - Cloud Forest; VS - Valles Secos; CH - Chapare; AP - Andean Piedmont; WW - White-water Floodplain; CQ - Chiquitanía; GP - Gran Pantanal.

	HA	CF	VS	CH	AP	WW	CQ	GP
HA	**117**	35	45	0	8	6	6	5
CF	**40.2**	**57**	24	3	13	10	8	7
VS	**40.2**	**29.3**	**107**	7	30	22	19	11
CH	**0.0**	**3.5**	**6.4**	**113**	60	91	93	38
AP	**2.1**	**3.9**	**7.7**	**31.6**	**244**	60	324	115
WW	**4.4**	**8.6**	**17.1**	**33.6**	**45.3**	**463**	172	129
CQ	**1.8**	**2.7**	**5.9**	**28.4**	**43.8**	**64.5**	**541**	131
GP	**3.4**	**6.1**	**7.8**	**26.5**	**61.7**	**36.1**	**36.6**	**174**

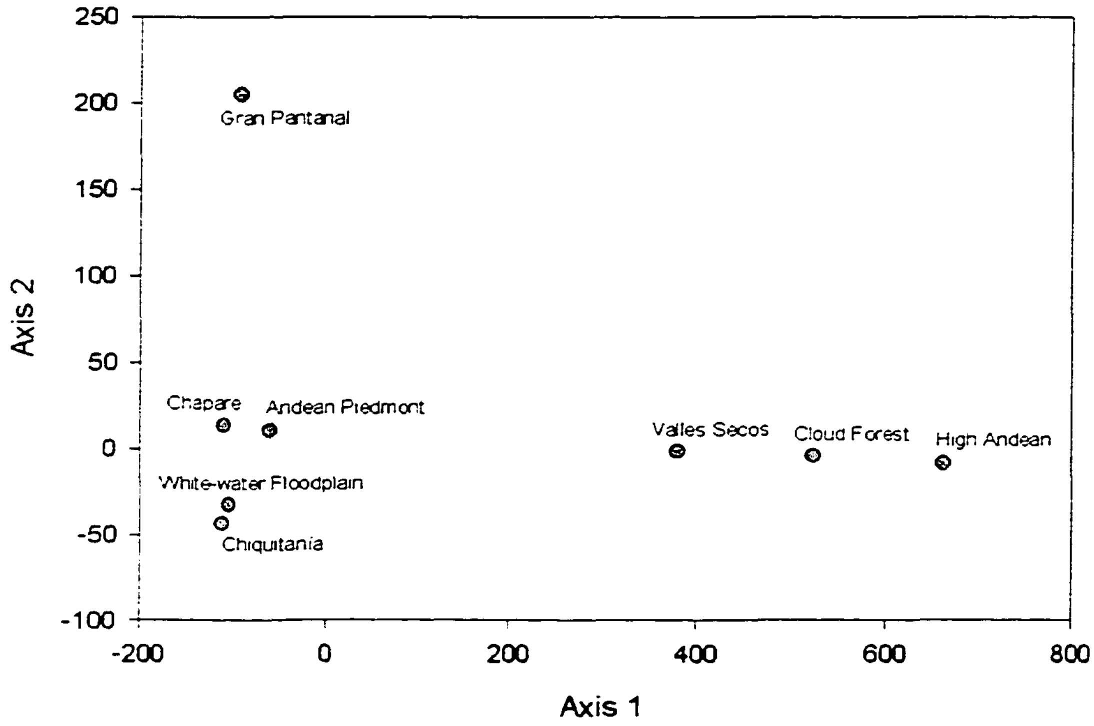

Figure I.2. Ordination of the Bolivian Regions by Detrended Correspondence Analysis (DCA).

The position of the eight Bolivian regions in an ordination by DCA (Figure I.2) was, in most cases, in accordance with the generalization that floristic affinities will be strongest between adjacent regions. An exception was the position of the Gran Pantanal relative to that of the Chiquitanía. Although these regions are geographically contiguous they were disjunct in ordination space, forming the axile endpoints of the second axis (Figure I.2). The distribution of the eight regions along the first axis appeared to be strongly correlated with elevation (Figure I.2), a relationship that was also discernible from the similarity matrix (Table I.2).

At the macroregional scale, floristic similarities (Sørensen's Index) between OGUs were astonishingly high, ranging from 48.9-79.3% (Table I.3), with floristic similarities between the two most geographically disjunct OGUs (Bolivia and Mexico) greater than 50% (51.3%, Table I.3). In order to examine relative differences in floristic similarities calculated from wetland floras versus those calculated from terrestrial floras, indices of similarity (Sørensen's Index) were calculated for five Neotropical OGUs (Costa Rica, Panama, Ecuador, Peru, and the Guianas; Table I.4). These were selected because their species checklists were considered to be relatively complete. The "terrestrial flora" was considered to be all species not listed in the wetland species database. The wetland species data from Table I.3 was compiled for these five OGUs and was re-ordered to match the presentation of the OGUs in Table I.4 (Table I.5). Floristic similarities for the terrestrial floras ranged from 17.2-50.8% (Table I.4), whereas those for the wetland floras ranged from 53.3-78.5% (Table I.5). In all but one instance (Costa Rica and Panama), floristic similarities between OGUs were at least twice as high for the

Table I.3. Comparison of diversity and floristic similarity (Sørensen's Index) between OGU vascular wetland floras. Figures in bold along the main diagonal indicate the number of species noted for each OGU. The numbers above the main diagonal indicate the number of species shared by both OGUs. Numbers in the shaded cells indicate the percent floristic similarity between OGUs.

	Bolivia	Peru	Ecuador	Brazil	The Guianas	Venezuela	Colombia	Panama	Costa Rica	Mid-Central America [B]	Mexico
Bolivia	**1026**	683	565	680	570	580	589	436	498	447	463
Peru	**70.8**	**903**	651	531	513	544	596	459	518	472	488
Ecuador	**63.4**	**78.5**	**756**	438	427	472	542	434	499	444	450
Brazil	**66.9**	**55.6**	**49.7**	**1007**	566	541	524	377	421	400	379
The Guianas	**60.1**	**58.7**	**53.3**	**61.2**	**845**	602	516	419	445	433	397
Venezuela	**60.6**	**60.8**	**57.5**	**57.1**	**69.5**	**887**	587	414	467	436	418
Colombia	**62.1**	**67.2**	**66.7**	**55.8**	**60.1**	**66.8**	**870**	439	490	452	441
Panama	**53.4**	**60.8**	**63.7**	**46.7**	**57.7**	**55.4**	**59.4**	**607**	512	479	434
Costa Rica	**57.4**	**64.3**	**68.2**	**49.1**	**57.3**	**58.6**	**62.1**	**77.9**	**708**	557	514
Mid-Central America	**51.9**	**59.0**	**61.2**	**47.0**	**56.2**	**55.1**	**57.7**	**73.5**	**79.3**	**696**	557
Mexico	**51.3**	**56.9**	**58.7**	**42.5**	**48.9**	**50.2**	**53.5**	**62.7**	**69.2**	**75.6**	**778**

Table I.4. Comparison of diversity and floristic similarity (Sørensen's Index) between "terrestrial" vascular floras (*i.e.*, all species not listed in the wetland species database) of five Neotropical OGUs. Figures in bold along the main diagonal indicate the number of species noted for each OGU. The numbers above the main diagonal indicate the number of species shared by both OGUs. Numbers in the shaded cells indicate the percent floristic similarity between OGUs.

	Costa Rica	Panama	Ecuador	Peru	The Guianas
Costa Rica	**8654**	3967	2871	2313	1665
Panama	**50.8**	**6981**	2197	2088	1500
Ecuador	**23.4**	**19.3**	**15843**	6474	2317
Peru	**17.2**	**16.6**	**38.0**	**18255**	2874
The Guianas	**20.1**	**20.1**	**19.5**	**21.9**	**7950**

Table I.5. Comparison of diversity and floristic similarity (Sørensen's Index) between vascular wetland floras of five Neotropical OGUs. Figures in bold along the main diagonal indicate the number of species noted for each OGU. The numbers above the main diagonal indicate the number of species shared by both OGUs. Numbers in the shaded cells indicate the percent floristic similarity between OGUs.

	Costa Rica	Panama	Ecuador	Peru	The Guianas
Costa Rica	**708**	512	499	518	445
Panama	**77.9**	**607**	434	459	419
Ecuador	**68.2**	**63.7**	**756**	651	427
Peru	**64.3**	**60.8**	**78.5**	**903**	513
The Guianas	**57.3**	**57.7**	**53.3**	**58.7**	**845**

wetland flora as for the terrestrial flora. The elevated floristic similarities of the wetland flora can be attributed to a large portion of the Neotropical wetland species being widely distributed. Additionally, a great many of these species must be sufficiently common throughout their ranges so that their presence has been noted during the relatively small amount of botanical research that has been conducted in Neotropical wetlands.

An ordination by DCA ordered the 11 OGUs into three groups, with Mexico and Ecuador occupying disjunct positions (Figure I.3). Groupings were: 1) Bolivia, Brazil and Peru; 2) Colombia, The Guianas, and Venezuela; and, 3) all Central American countries (Figure I.3). As with the ordination of the Intra-Bolivian regions (Figure I.2), there was a strong tendency for geographically proximal OGUs to be located in close proximity in ordination space.

In the three chapters which focused on biodiversity and phytogeographic affinities of three particular Bolivian regions (Chapters 3, 4, and 5), the utility of Frequency Analysis in mesoregional-scale investigations was demonstrated. This approach also was instructive in macroregional-scale studies. To demonstrate, the relative contributions of species classes to overall similarity were calculated between Bolivia and the other 10 OGUs considered in the preceding macroregional floristic comparisons. Frequencies between Bolivia and four OGUs (Brazil, Colombia, Ecuador, and Peru) were graphed (Figure I.4). These were selected because they showed the strongest floristic similarities (Sørensen's Index., Table I.3) to the Bolivian flora. Floristic similarities between Bolivia and the four OGUs were fairly equitable, ranging from 62.1-70.8% (Table I.3). Of these, the greatest similarity (70.8% Table I.3) was between Bolivia and Peru, although this was

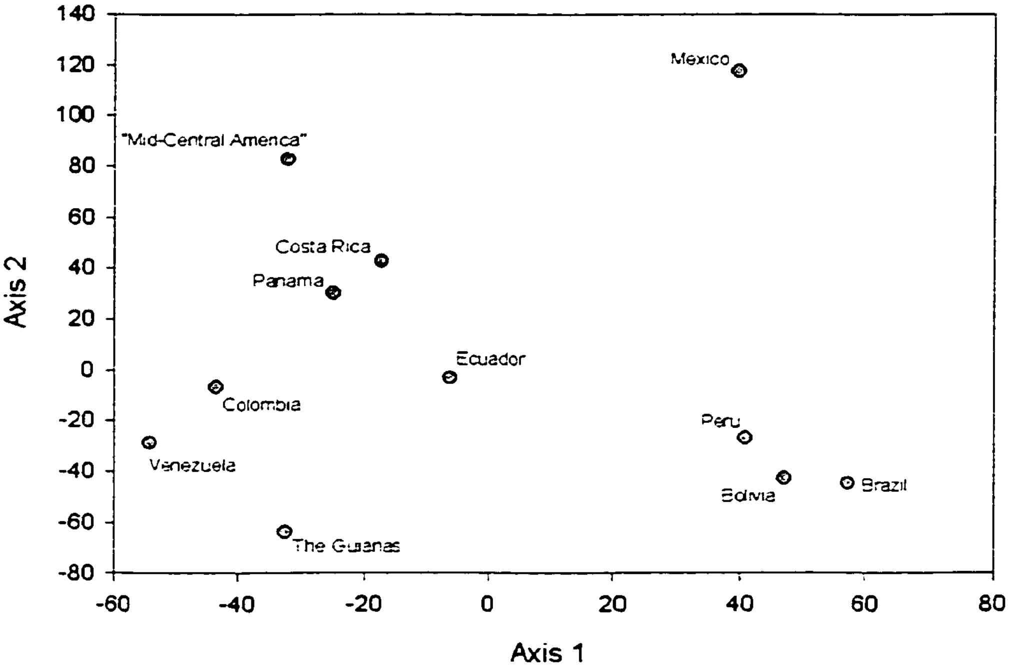

Figure I.3. Ordination of the Neotropical OGUs by Detrended Correspondence Analysis (DCA).

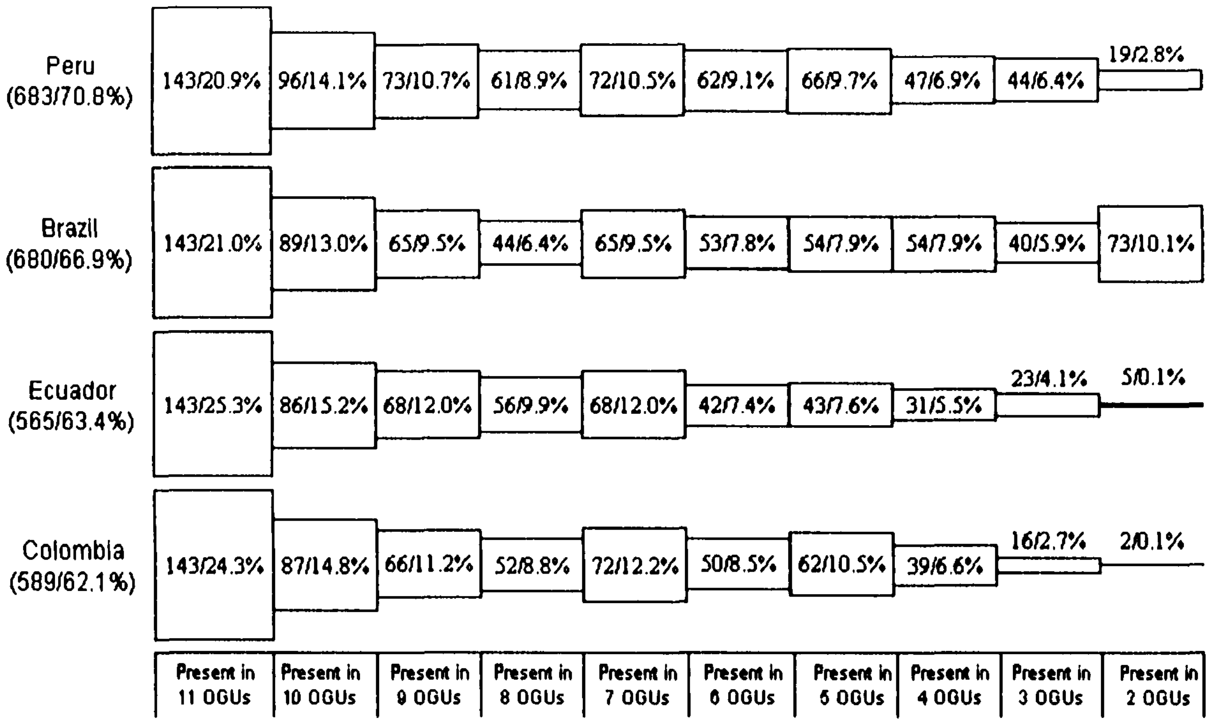

Figure I-4. Frequency of species shared between Bolivia and selected OGUs. Figures below the OGU name indicate the number of species present in both the OGU and Bolivia, followed by floristic similarity (Sørensen's Index). Boxes correspond to species classes (i.e., the number of OGUs in which the species 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 Bolivia, followed by the percentage that this portion of the flora contributed to the total species shared between the OGU and Bolivia.

scarcely higher than that between Bolivia and Brazil (66.9%, Table I.3). Likewise, in the ordination by DCA (Figure I.3), Bolivia occupied a position in ordination space approximately equidistant from Peru and Brazil. It was evident from the Frequency Analysis (Figure I.4), however, that Bolivia and Brazil shared a greater proportion of "rarely shared species" (*i.e.*, species restricted to 2-3 OGUs) than did Bolivia and Peru (Figure I.4).