Chapter 1. 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 (Figure 1-1). The country occupies an estimated area of 1,098,581 km2 (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.

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).

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 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 (Figure 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 (Figure 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 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 (Figure 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 (Figure 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.

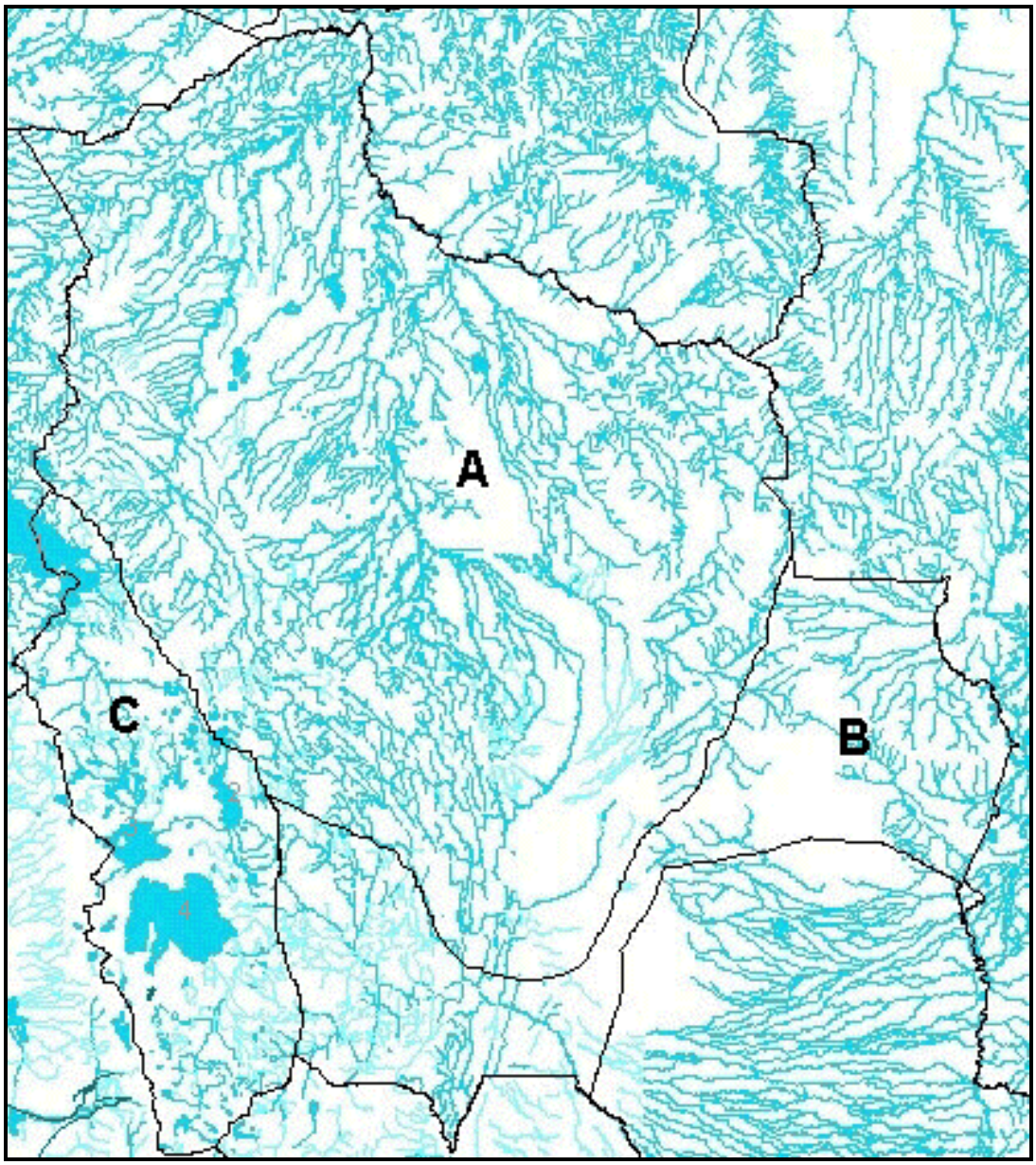

Figure 1-2. Hydrographic map of Bolivia. Watersheds: A. Amazon. B. Paraná. C. Desaguadero. Principal catchments: 1. Lago Titicaca. 2. Lago Poopó 3. Salar de Coipasa. 4. Salar de Uyuni. Map generated with AGIS (1999). Limits of the watersheds drawn as per Nogales et al. (1991).

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).