Chapter 3. 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 disproportionately 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 (Figure 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).

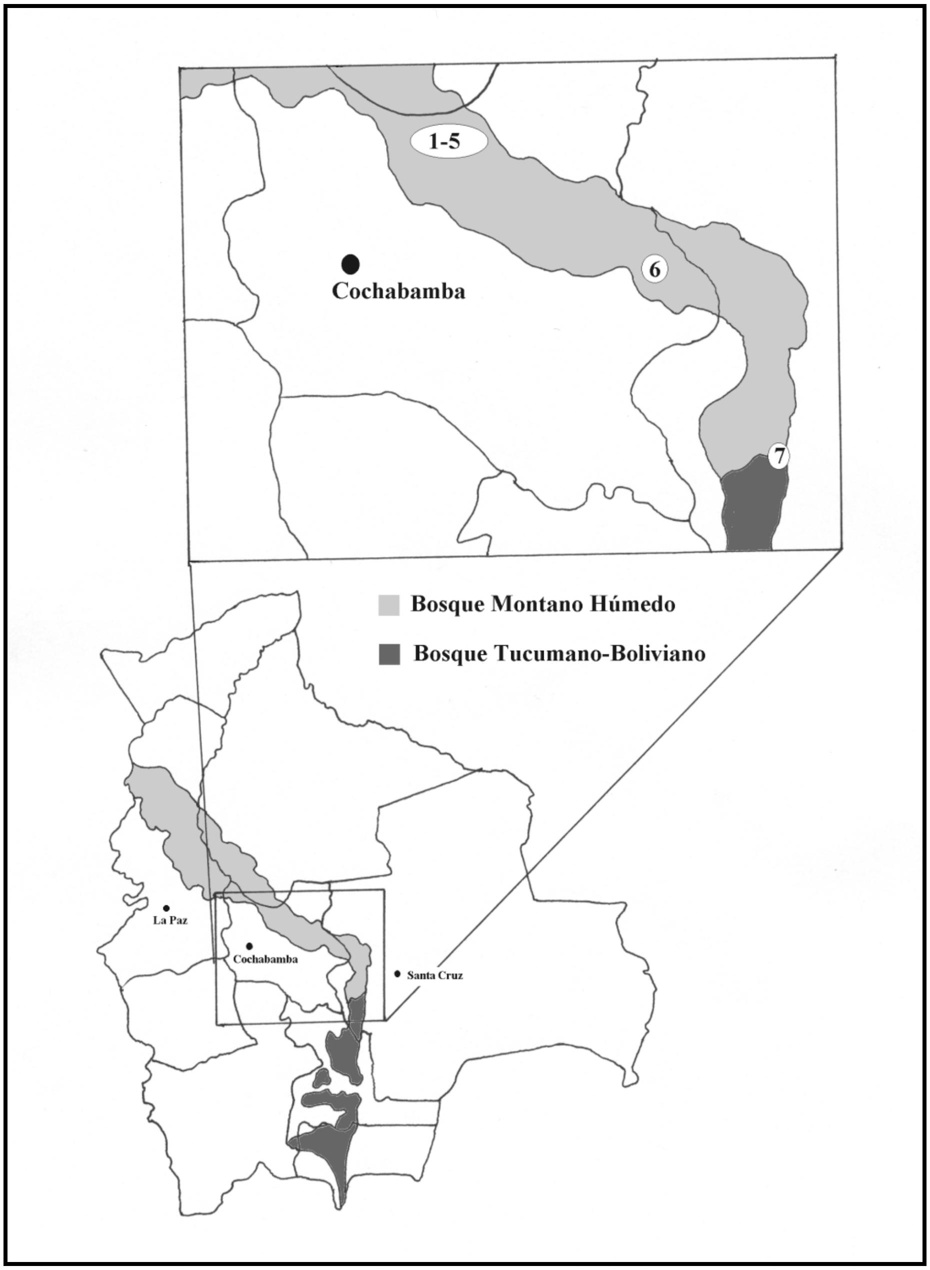

Figure 3-1. The Bolivian Cloud Forest study sites. 1-5. Chimpa Huata Bog, Lagunas Khonchu East and West; Corani Pampa Marsh, and Incachaca Pond. 6. Serranía de Siberia Marsh. 7. Laguna Volcan.

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

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	Elev. (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	64º45"W 17°51'S	7
Laguna Volcan	1150	3.0	63°39'W 18°08'S	39

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 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).

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 below the diagonal 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 below the diagonal 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**

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 (Figure 3-2). Laguna Volcan, however, occupied a fairly disjunct position relative to the Cloud Forest study sites (Figure 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).

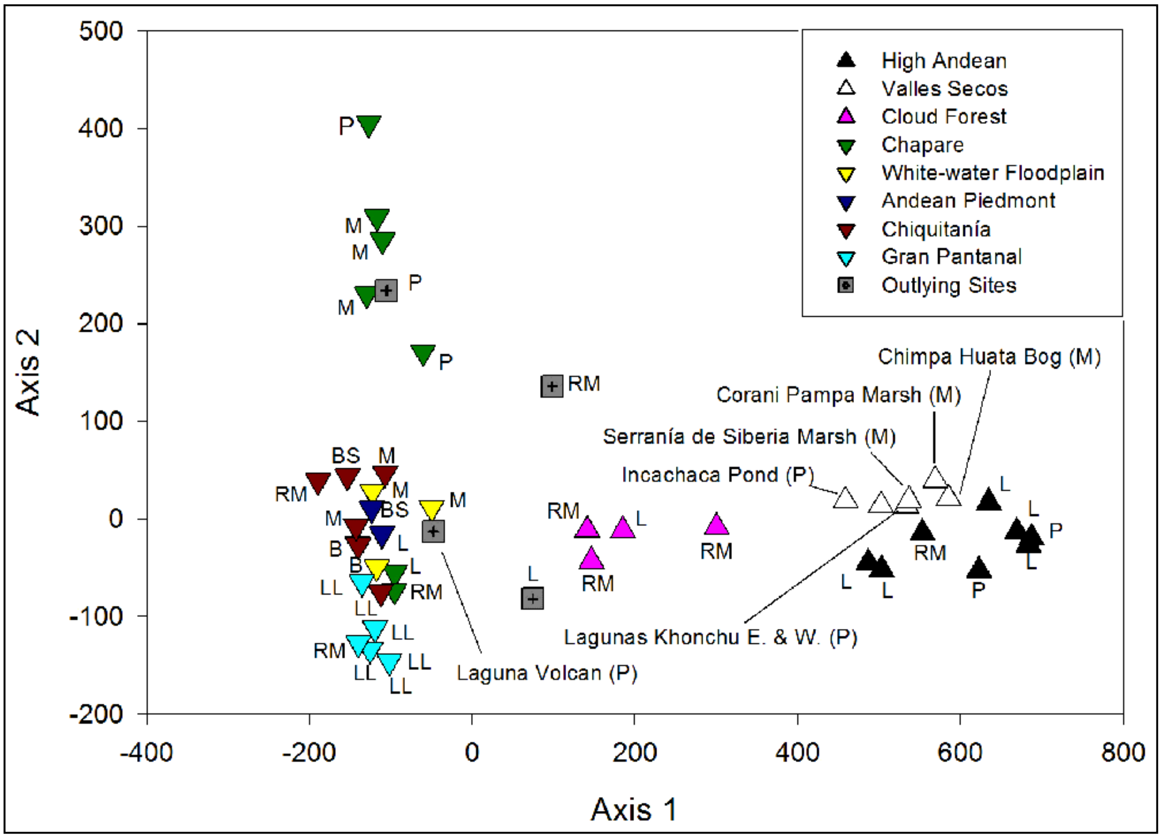

Figure 3-2. Ordination by Detrended Correspondence Analysis (DCA) of the 46 Bolivian study sites. The six Cloud Forest study sites and one outlying montane system (Laguna Volcan) are identified by name. Key to wetland types: B- bahía; BS - basin swamp; L - small lake (< 500 ha); LL - large lake (> 500 ha); M - marsh; P - pond; RM - riparian marsh.

These relationships were generally reflected in the ordination of the 8 OGUs (Figure 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 (Figure 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 (Figure 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 (Figure 3-3).

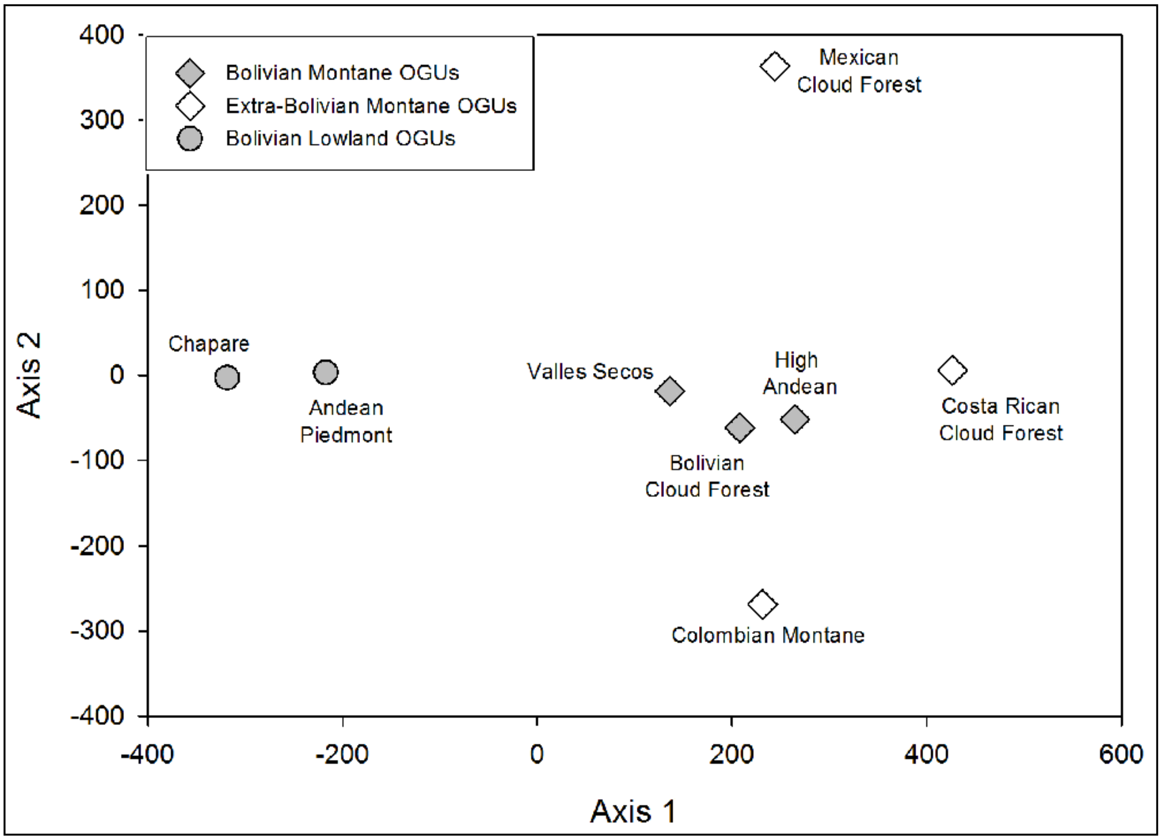

Figure 3-3. Ordination by Detrended Correspondence Analysis of the Bolivian Cloud Forest wetland flora and the wetland floras of selected regions.

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 (see Chapter 6). 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). 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 (see Chapter 6). 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 (see Chapter 6). 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 (Figure 3-4).

When interpreting Figure 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, 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). 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.

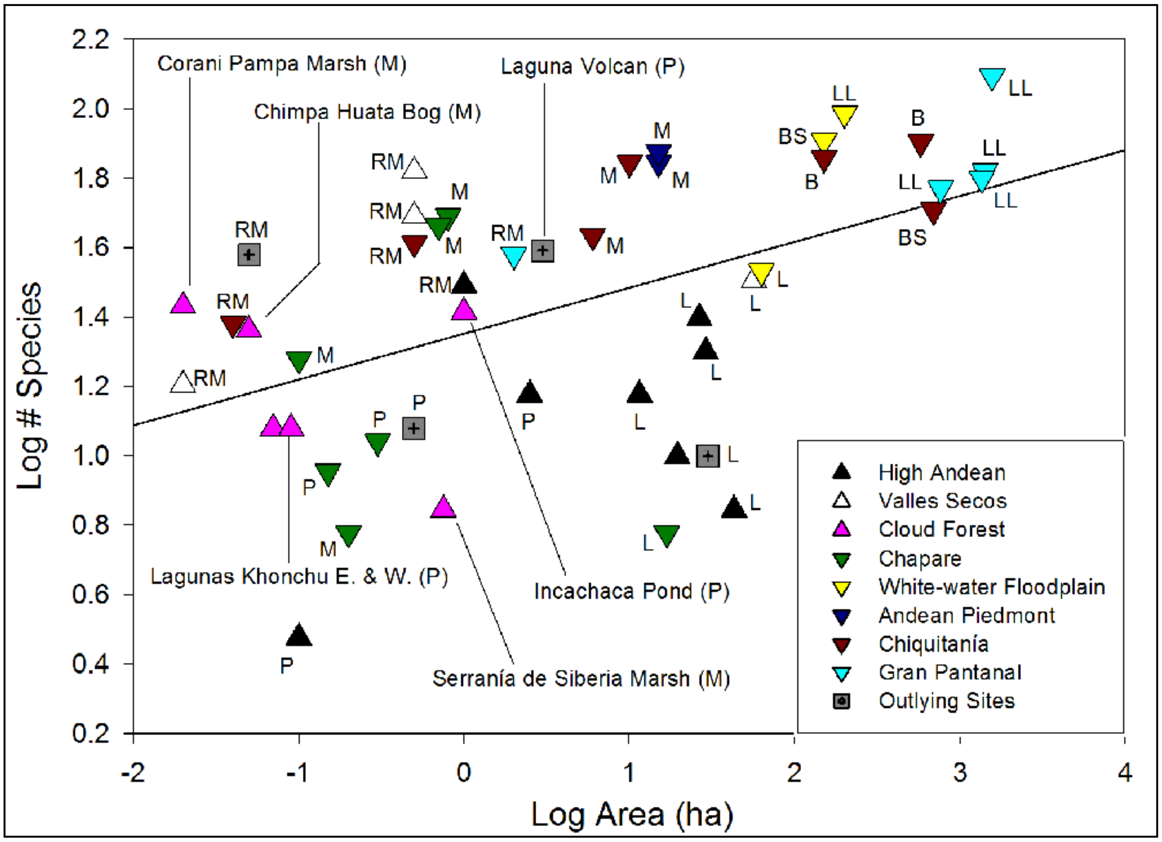

Figure 3-4. Species-area curve plotted from 46 Bolivian wetland study sites. Wetland types: B- bahía; BS - basin swamp; L - small lake; LL - large lake (> 500 ha); M - marsh; P - pond; RM - riparian marsh. Linear regression: Log S = 1.35 + 0.13 Log A. $r^2 = 0.24$, $p = 0.00005$.

The Cloud Forest wetlands were noticeably richer than the High Andean wetlands, all but one of which were below the regression line (Figure 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 (Figure 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 (Figure 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 Figure 3-2, Figure 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 (Figure 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 (Figure 3-2).

A close floristic relationship among the Bolivian montane regions was not surprising, as 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 (Figure 3-3) and study site data (Figure 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 (Figure 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 (Figure 3-3).