Chapter 6. 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 preceding 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-Nielsen 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 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

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	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
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

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.; $\bar{x}$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 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.

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.			

A graphical illustration (Figure 6.1) of the importance of considering system area is presented using three "rich" study sites: 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, the actual relative differences in species richness are not so apparent.

From Figure 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.
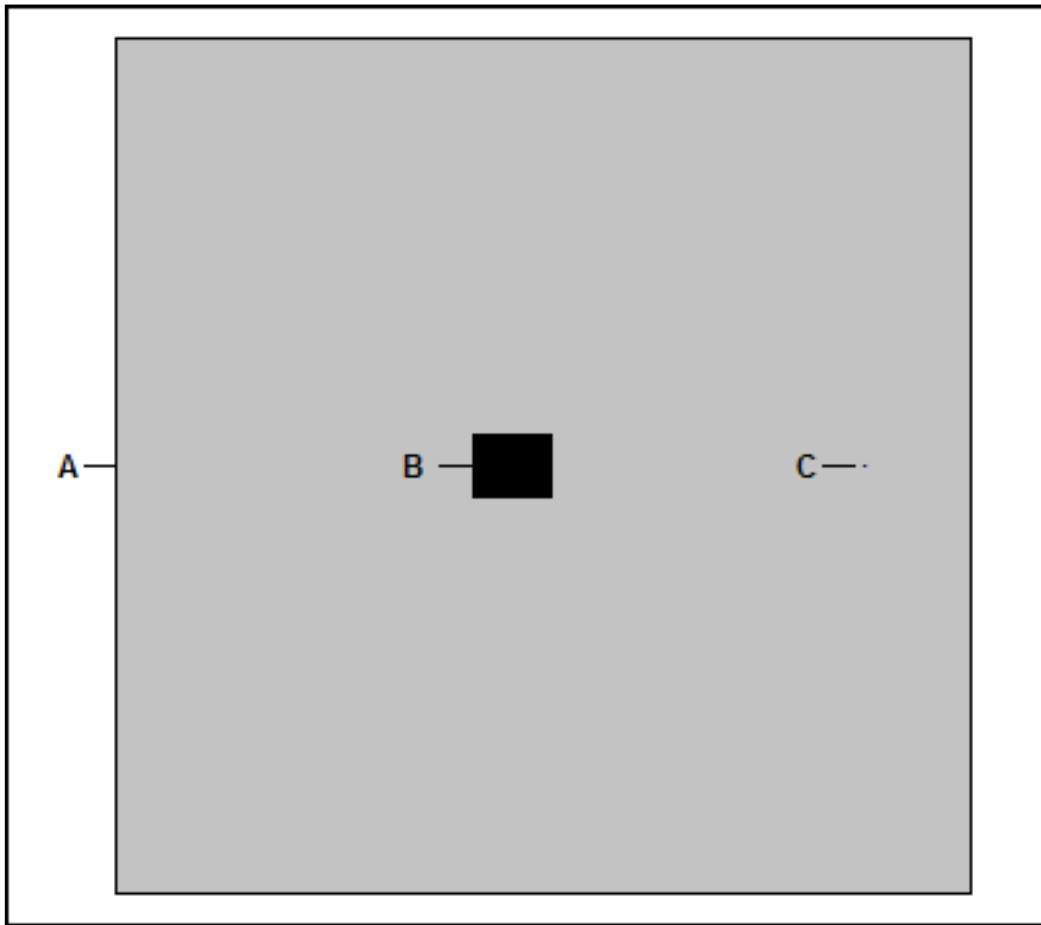

Figure 6-1. Comparison of three systems. **A**: Laguna Cáceres. **B**: Viru Viru Wetland. **C**: The Huanchaca Arroyo. All areas drawn approximately to scale.

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.		

Using data from the study sites (Table 6-1) log number of species was plotted versus log area and a linear regression was fitted to the data. In the resulting plot (Figure 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.
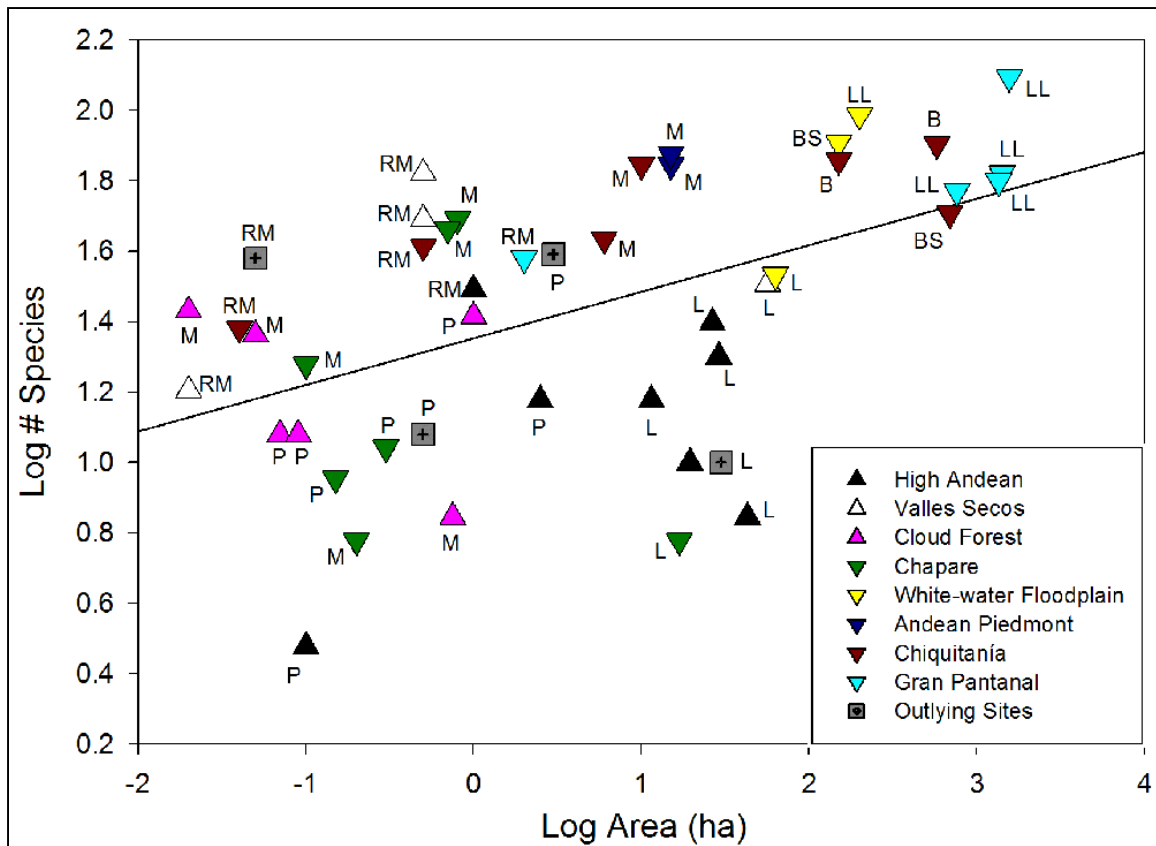

Figure 6-2. Species-area curve for the 46 Bolivian study sites. Wetland types: **B**- bahía; **BS** - basin swamp; **L** - small lake; **LL** - large lake (> 500 ha); **M** - marsh; **P** - pond; **RM** - riparian marsh. Linear regression: log S = 1.35 + 0.13 log A; r² = 0.24.

Ponds were almost always species-poor, regardless of where they occurred (Figure 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.

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 (Figure 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).
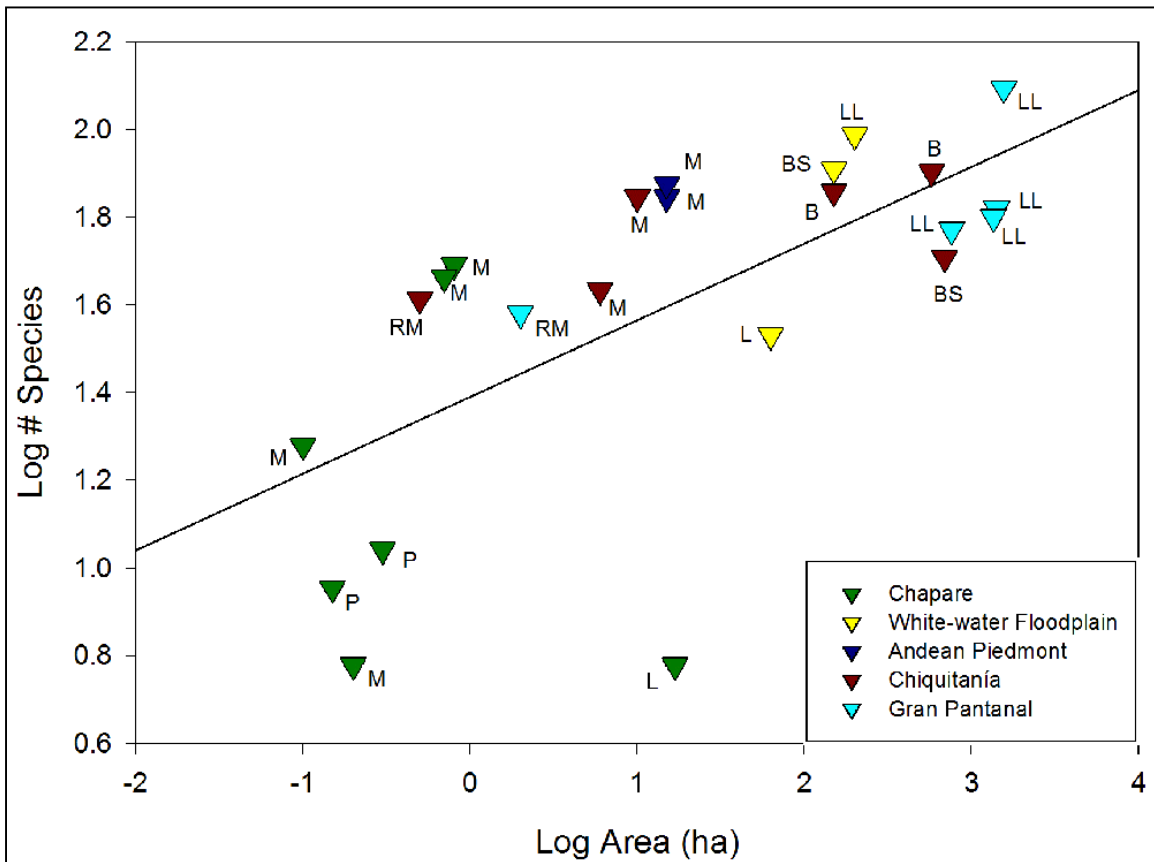

Figure 6-3. Species-area curve for the 23 lowland Bolivian study sites. Wetland types: B- bahía; BS - basin swamp; L - small lake; LL - large lake (> 500 ha); M - marsh; P - pond; RM - riparian marsh.   Linear regression: Log S = 1.39 + 0.17 Log A. r² = 0.44.

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 (Figure 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 (Figure 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 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 (Figure 6-2) will be referenced. Both marshes and riparian marshes were characteristically species-rich, with most systems located on or above the regression line (Figure 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, Figure 6-1). It was clear from a plot of the data (Figure 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 (Figure 6-2; Figure 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
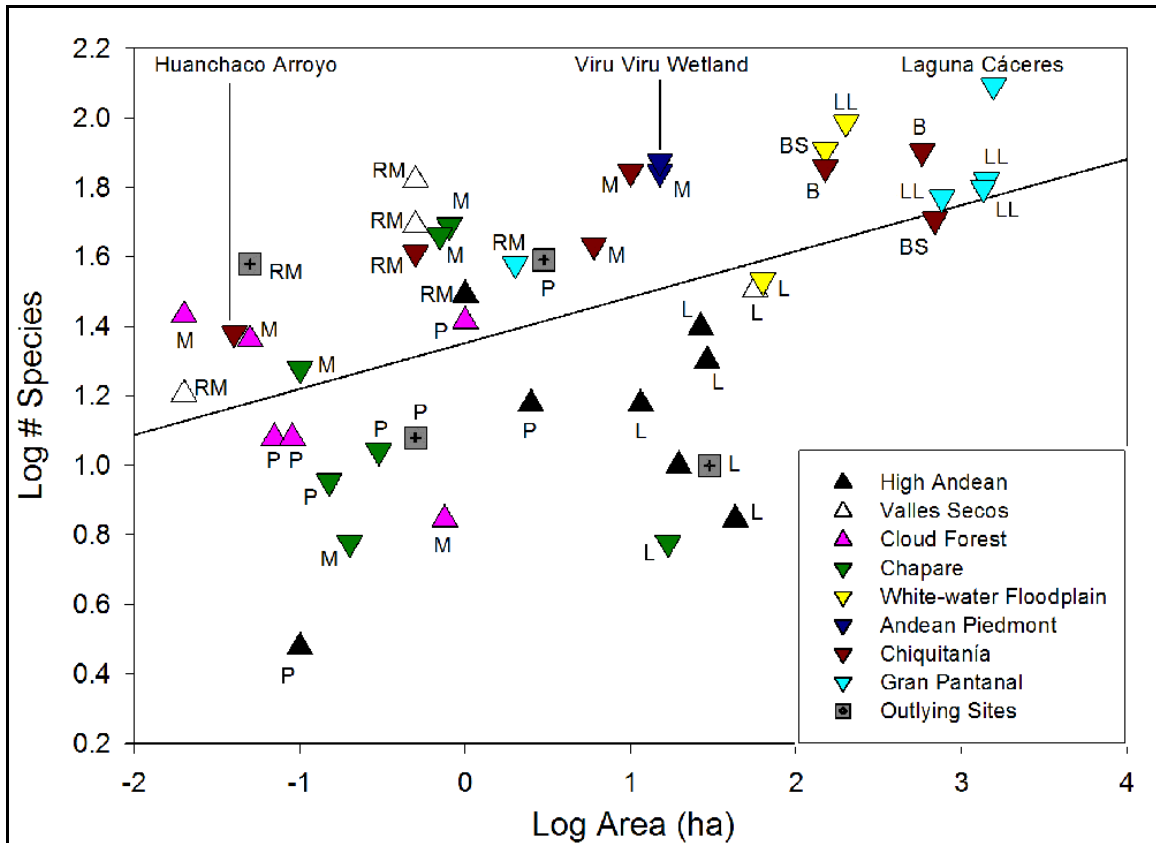
Figure 6-4. Species-area curve for the 46 Bolivian study sites. The three sites which were used in the example of the influence of area on richness are identified. Wetland types: **B**- bahía; **BS** - basin swamp; **L** - small lake; **LL** - large lake (> 500 ha); **M** - marsh; **P** - pond; **RM** - riparian marsh. Linear regression: log S = 1.35 + 0.13 log A; r² = 0.24.

regression lines to each curve (Figure 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. Although Figure 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). 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 (Figure 6-2).
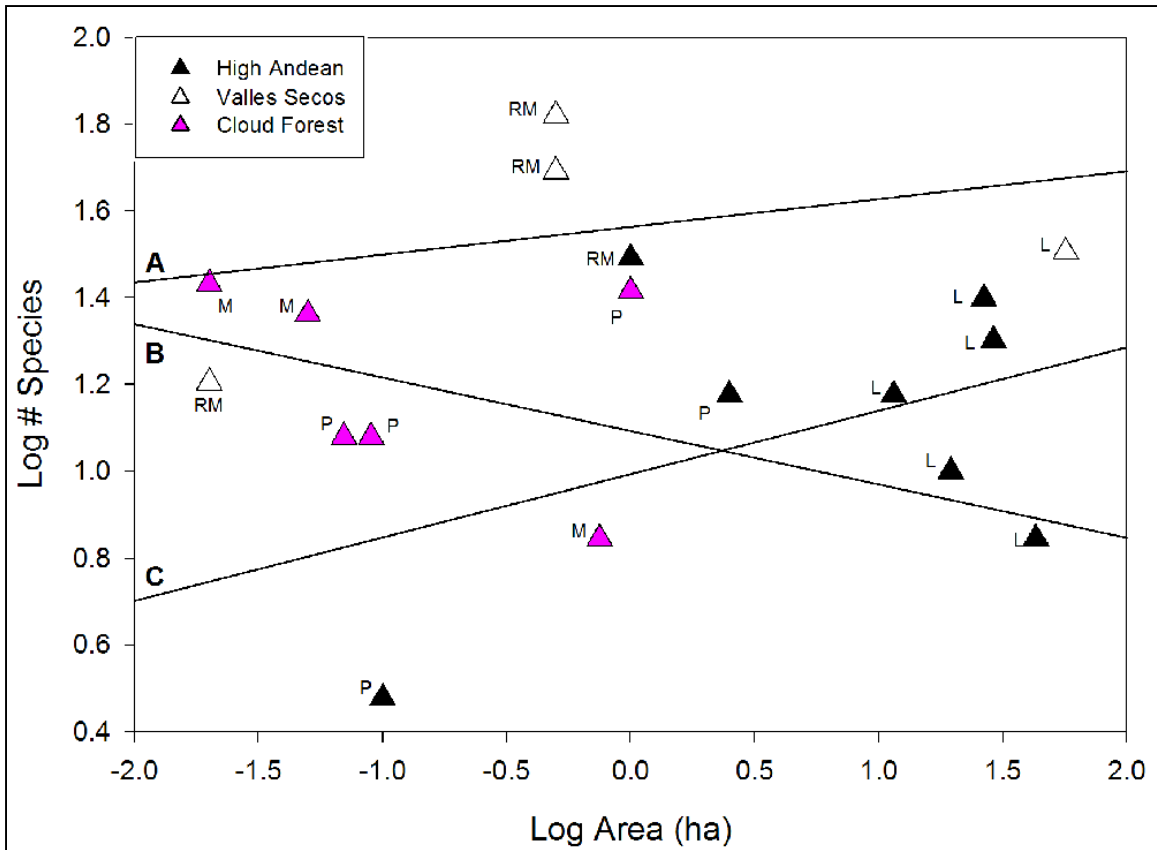
Figure 6-5. Species-area curves for the Bolivian montane study sites. A. Valles Secos. Log S = 1.6 + 0.04 Log A. r^2 = 0.12. B. Cloud Forest. Log S = 1.09 -0.12 Log A. r^2 = 0.12. C. High Andean Region. Log S = 0.99 + 0.15 Log A. r^2 = 0.16. Wetland types: L - small lake; M - marsh; P - pond; RM - riparian marsh.

The High Andean region was clearly species-poor, with all but one system below the regression line and the remaining site on the line (Figure 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. The Cloud Forest sites were characteristically species-poor, with four of the six systems situated below the regression line. 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 (Figure 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

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species richness was shown to decrease with an increase in system area (Figure 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 (Figure 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. 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. The Andean Piedmont sites were both very species-rich, 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. 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. 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. 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., Figure 6-2; Figure 6-3) than from the tables of species counts (Table 6-2; Table 6-3).

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

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; 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) contained only 19 species (Table 6-1). The single 1.0 ha Neotropical forest site (Cuyabeno, in the Ecuadorian 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).

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		

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 (Figure 6-6). Viewed in this manner, Neotropical forested ecosystems were (as expected from the tabular data) unequivocally richer than Neotropical wetlands. Although the slopes of the regression lines were extremely close (0.15, forests; 0.17, wetlands), the difference between the y intercepts was 1.21 (log scale). Thus, a Neotropical forest would generally be expected to possess more than ten times the species of a Neotropical wetland of comparable area.
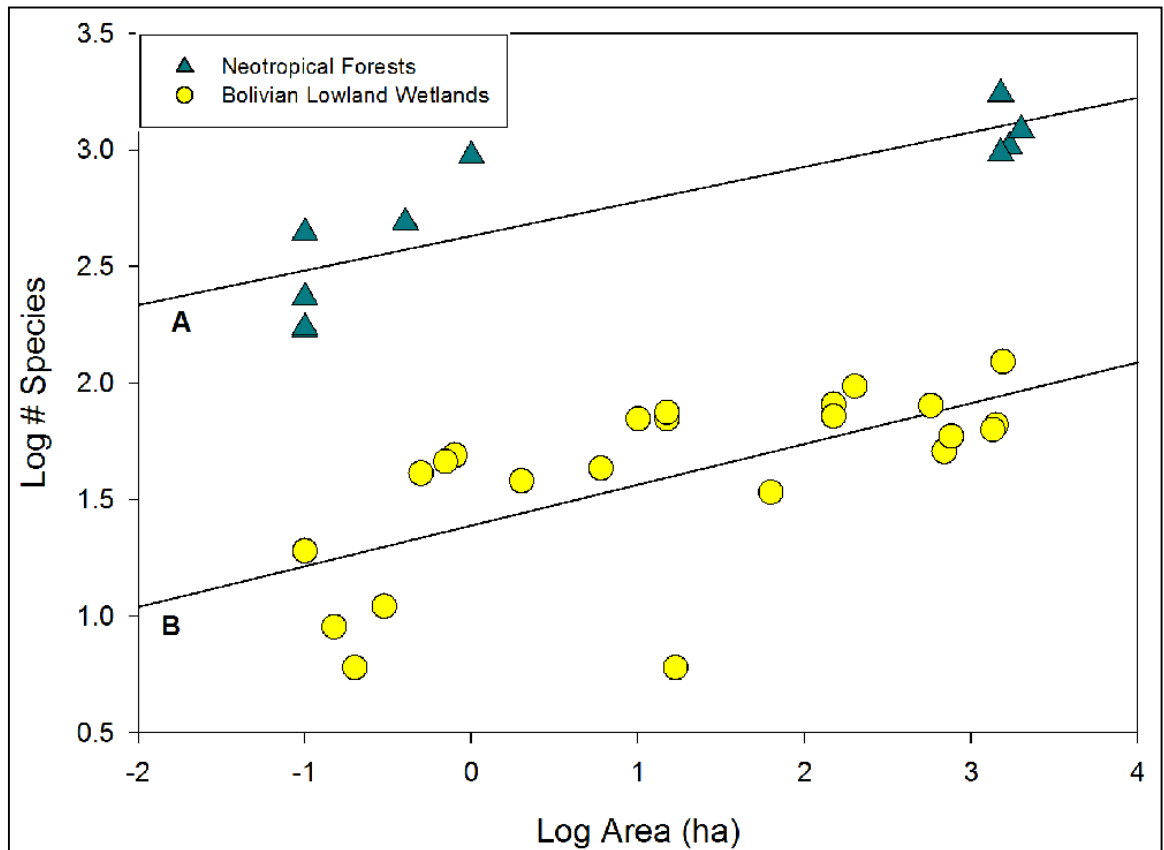
Figure 6-6. Comparison of a species-area curve plotted from 11 Neotropical forest sites with a species-area curve from 23 wetlands in the Bolivian lowlands. A: Linear regression of the forest data. Log S = 2.6 + 0.15 log A; $r^2 = 0.71$. B: Linear regression of the wetland data. Log S = 1.39 + 0.17 log 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

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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 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).

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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

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 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 (Figure 6-7). From this figure, it was evident that wetlands from the Southeastern United States were markedly richer than those from lowland Bolivia. 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. The New England systems were generally somewhat richer than those of lowland Bolivia, as evidenced by the regression line (Figure 6-7-B) of the former being situated above that of the latter (Figure 6-7-C)

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

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; Figure 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.
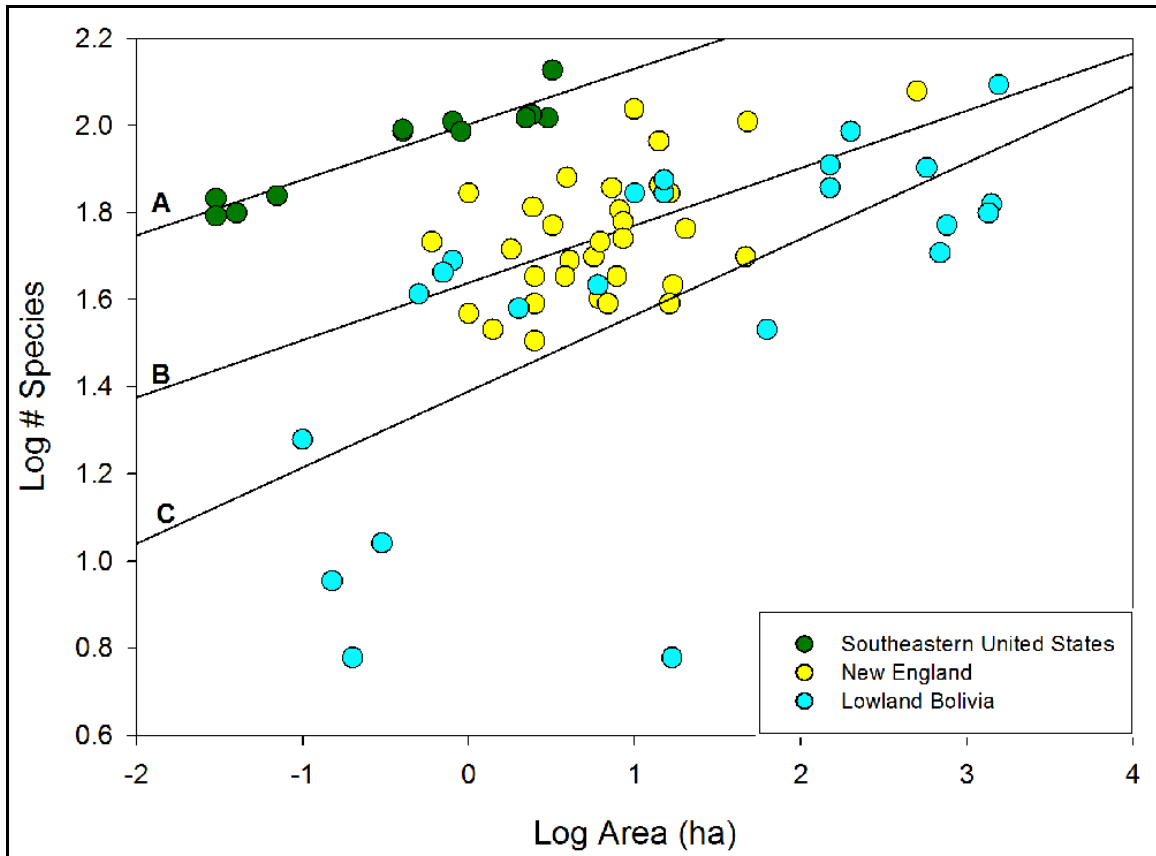
Figure 6-7. Comparison of species-area curves of wetlands from three New World regions. **A**. Linear regression of the Southeastern U.S. wetland data. Log S = 2.00 + 0.13 Log A; r^2 = 0.90. **B**. Linear regression of the New England wetland data. Log S = 1.6 + 0.13 Log A; r^2 = 0.27. **C**. Linear regression of the Lowland Bolivian wetland data. Log S = 1.4 + 0.17 Log A; r^2 = 0.44.