

Chapter 7. Regional Scale Biodiversity

The species-area curve may be the first diversity pattern described by ecology, but the latitudinal gradient is the most famous. The Tropics, if not the seat of life, are the center of its richest display.

- M. Rosenzweig, *Species Diversity in Space and Time*

Diversity Within Bolivia

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

The number of species noted for the eight Bolivian regions considered in this study varied by nearly an order of magnitude (Table 7-1). Based solely on number of species (Table 7-1), the Cloud Forest was the most species-poor region (57 species), and the Chiquitanía the most species-rich (541 species). Differences in regional area, however, were even greater than differences in number of species, varying by close to two orders of magnitude (e.g., 4.0×10^3 km² in the Chapare to 3.25×10^5 km² in the White-water Floodplain; Table 7.1). Hence, as with the estimates of site-level diversity, accurate estimates of regional diversity were necessarily based on the number of species per unit area.

In a study involving wetland habitats, it seems that the most accurate approximation of species-richness would be calculated from the area of inundated habitat. A few estimates of the extent of wetlands in Bolivia were available, but these varied to such a degree as to render them unserviceable. For example, Flores (1986) estimated that only 5,812 km² of wetlands were present in all of the Bolivian lowlands, whereas Allenby

(1988) estimated that the Beni basin alone (i.e., the White-water Floodplain region, excluding the Pando) contained roughly 250,000 km² of wetlands. Eventually, it seemed best to formulate my own estimates of regional wetland areas based on information from maps, Landsat images, various published sources, and from my impressions from fieldwork and travel. Estimates were restricted solely to the five Bolivian lowland regions considered in this study, as I was unable to confidently estimate wetland areas for the three montane regions. Estimated wetland areas for the lowland regions are presented in Table 7-2.

Table 7-1. The eight Bolivian regions utilized in floristic comparisons, with estimated regional area, elevation range of the study sites, and total wetland species noted for each region.

Region	Approximate Area (km ²)	Elevational Range ^A (m)	No. Spp.
High Andean	210,000	3100-4500	117
Cloud Forest	33,000	2400-2920	57
Valles Secos	83,000	1800-2550	107
Chapare	4000	200-230	113
Andean Piedmont	5000	400-430	244
Whitewater Floodplain	325,000	200-220	463
Chiquitania	190,000	200-750	541
Gran Pantanal	14,000	90-100	174

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

Table 7-2. Area, estimated wetland area, number of wetland species, and the cumulative totals of these three parameters for the five regions and one regional sub-sample used in plotting species-area curves for the Bolivian lowlands. OGU abbreviations: CM - Chimoré; CH - Chapare; AP - Andean Piedmont; WW - White-water Floodplain; CQ - Chiquitania; GP - Gran Pantanal.

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

A species-area curve was constructed for Bolivia with cumulative wetland species plotted against both cumulative estimated wetland area and cumulative total area (Figure 7-1). The curve was constructed commencing with a localized area (an approximately 20 km² area around the town of Chimoré, in the Chapare) and continuing through the addition of

successively larger, contiguous areas (cf. Rosenzweig 1995), as indicated in Table 7-2. A linear regression was fitted to the data, and interaction between area and data source (i.e., total regional area, regional wetland area) was evaluated by an Analysis of Variance (ANOVA) test. Results indicated that interaction between area and area type (regional versus wetland) was insignificant. Thus, as slopes of the regression lines were not different, total regional area was deemed to be an acceptable surrogate for regional wetland area.

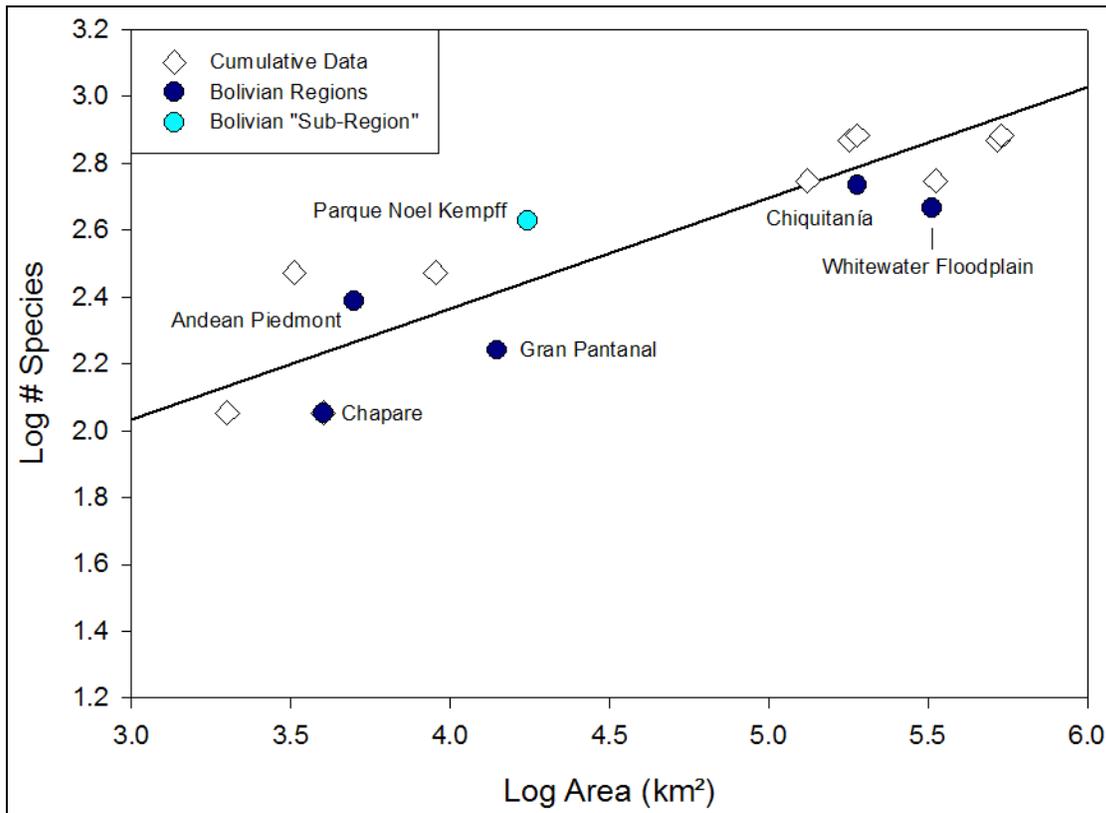


Figure 7-1. Species-area curves plotted from cumulative totals from the five Bolivian lowland regions considered in this study. Linear regression: $\text{Log } S = 1.04 + 0.33 \text{ log } A$, $r^2 = 0.97$.

Discrete (i.e., non-cumulative) regional species-area data were plotted for each lowland region, gray circles). As with the species-area curves for site-level data, regions above the regression line were considered as relatively species-rich and those below as relatively species-poor.

Figure 7-1 was previously referenced in Chapters 4 (the Chapare) and 5 (the Gran Pantanal), where it was used to establish the species-poor character of these two regions. It can also be seen that the White-water Floodplain regions, despite possessing a large flora (463 spp., Table 7-1), was somewhat species-poor, when considered in terms of overall regional area. The Chiquitanía, the region with the largest wetland flora (541 spp., Table 7-1), was also somewhat species-poor in terms of its position to the regression line. The Andean Piedmont was seemingly the most species-rich region (i.e., furthest above the regression line) of the Bolivian lowlands.

The preceding characterizations should be accepted provisionally, as regional checklists were undoubtedly influenced by differences in density of botanical collecting. Solomon (1989) identified the areas of highest collection density as the vicinity of La Paz (habitats in both the Altiplano and the upper slopes of the Yungas), the Cochabamba Valley, the vicinity of Lago Titicaca, and to a lesser extent, the areas around the cities of Santa Cruz and Tarija. Since the time of Solomon's report, the focus of botanical collecting has shifted to the lowlands, with the Departamento of Santa Cruz receiving a disproportionately large amount of the lowland research. Thus, the region with the most wetland species, the Chiquitanía (Table 7-1), and the most species-rich Bolivian lowland region, the Andean Piedmont (Figure 7-1) were both within one of the most heavily investigated (botanically) Departamentos. The Bolivian Gran Pantanal was also situated within the Departamento of Santa Cruz. As noted in Chapter 5, however, the Gran Pantanal has received relatively little botanical investigation in comparison with the Departamento's more heavily researched areas (e.g., Parque Nacional Noel Kempff Mercado and the Andean Piedmont region).

The White-water Floodplain region has also been the site for a significant portion of the botanical research conducted in the Bolivian lowlands, and a number of the published floristic accounts from this region were from wetlands (e.g., Beck 1984; Haase 1989, 1990; Haase and Beck 1989; Hanagarth 1993). Botanical investigations in the White-water Floodplain, however, have seemingly been restricted to fewer areas than in the Departamento of Santa Cruz, with most studies located either in a few parts of the Llanos

de Moxos and, to a lesser extent, in the area around the town of Riberalta, and in the Pando. Hence, it appears probable that the White-water Floodplain flora was somewhat under-represented relative to the number of botanical collections made from this region.

Although differences in collection density make these regional comparisons somewhat qualified, nevertheless, their utility is undeniable. To illustrate, the relative diversity of Parque Nacional Noel Kempff Mercado (PNNK), a particularly speciose “sub-region” of the Chiquitanía was examined (Table 7-3)

Table 7-3. Comparison of area and flora size for three Bolivian OGUs.

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

Four hundred and twenty four wetland species were noted for PNNK (Table 7-3); thus, this area possessed approximately 41% of Bolivia’s wetland flora (1026 species, Table 7.3) in an area equivalent to just 1.6% of the national territory. Within the regional context, PNNK possessed nearly four fifths (78.3%) of the Chiquitanía’s wetland species (541 species) in less than a tenth (9.2%) of the region’s area. As the diminutive (by comparison) PNNK contained such a large portion of the regional and national wetland floras, it seemed likely that it would prove to be an extremely high diversity area (i.e., that it would occupy a position well above the regression line of the Bolivian lowlands species-area curve). Locating the datum from PNNK on Figure 7-1 demonstrated that this area was indeed species-rich, but not nearly as much as might be expected, based on the magnitude of the areal differences.

Macroregional Diversity

In order to undertake macroregional-scale comparisons of diversity in the Neotropical wetland flora, the next logical step was to construct a species-area curve using national data. A number of publications were encountered that offered partial or complete estimates of wetland area for various Neotropical countries and regions (e.g., Aselman and Crutzen 1989; Junk 1993; Olmsted 1993; Olson et al. 1998; Naranjo 1995; Scott and

Jones 1995). Regrettably, there was a large amount of variance among these estimates, and data were incomplete for most countries, and entirely lacking for some. Hence, it was necessary to rely on a country's total area as a surrogate for wetland area. In the preceding inter-Bolivian regional-scale comparison total regional area was found to be an acceptable surrogate for regional wetland area. Before proceeding with the Neotropical comparisons, the correlation between these two elements was first analyzed in another data set, the North American data.

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

Data (regional area, regional wetland area, and number of species) were tabulated for the ten regional groupings utilized by Reed (1996) for the coterminous United States. Not all species listed by Reed were used in the comparisons; rather, species were adjudged as wetland species based on various criteria (see Appendix C). A species-area curve was constructed commencing with a single state (Maine) and continuing through the stepwise addition of successively larger, contiguous areas (cf. Rosenzweig 1995). Initial additions involved 2-3 states, until all states in the initial region (New England) were added. Subsequent additions generally consisted of a single region; however, in two instances adjacent regions were combined as each contained a portion of the same state (see Table 7-4). OGUs, their stepwise order, cumulative area, cumulative wetland area, and cumulative wetland species are given in Table 7-4. A linear regression was fitted to the data and interaction between area and area type (i.e., total regional versus regional wetland) was evaluated by an Analysis of Variance (ANOVA) test. Results indicated that the interaction between data sources was significant; thus, it was uncertain that total

regional area could function as a suitable surrogate for regional wetland area in North America.

Table 7-4. United States OGU's used in plotting a species-area curve for the wetland flora of the coterminous United States, with cumulative total area, cumulative wetland area, and cumulative wetland species noted for each OGU.

OGUs	Cumulative Area (km ²)	Cumulative Wetland Area (km ²)	Cumulative Wetland Spp.
ME	80,170	20,068	601
ME & NH & VT	127,474	23,598	667
ME & NH & VT & MA & RI & CT	163,091	29,316	782
ME & NH & VT & MA & RI & CT & NY & PA	402,110	40,664	908
N-E	826,183	56,765	1201
N-E & S-E	1,936,421	252,391	1736
N-E & S-E & N-C	2,991,606	325,960	1772
N-E & S-E & N-C & S-P	3,848,011	360,360	1857
N-E & S-E & N-C & S-P & C-P & I-M	5,023,802	378,456	2108
N-E & S-E & N-C & S-P & C-P & I-M & N-W & N-P	6,662,543	416,050	2312
N-E & S-E & N-C & S-P & C-P & I-M & N-W & N-P & CA	7,067,337	417,887	2516
N-E & S-E & N-C & S-P & C-P & I-M & N-W & N-P & CA & S-W	7,657,565	422,777	2543
Regions:			
N-E (Northeast):	CT, DE, KY, MA, MD, ME, NH, NJ, NY, OH, PA, RI, VA, VT, WV		
S-E (Southeast):	AL, AR, FL, GA, LA, MS, NC, SC, TN		
N-C (North Central):	IA, IL, IN, MI, MO, MN, WI		
N-P (North Plains):	ND, MT (Eastern), SD, WY (Eastern)		
C-P (Central Plains):	CO (Eastern), KS, NE		
S-P (South Plains):	OK, TX		
S-W (Southwest):	AZ, NM		
I-M (Intermountain):	CO (Western), NV, UT		
N-W: (Northwest):	ID, MT (Western), OR, WA, WY (Western)		
CA (California):	CA		

To examine the differences between the two measures of area, separate species-area curves were plotted and regression lines fitted to each set of data (Figure 7-2). The line fitted to the wetland area data (Figure 7-2-A) possessed a lower y-intercept (1.07) than that for the total area data (Figure 7-2-B) and the slope was somewhat greater (0.41, A; 0.31 B). Still, the slopes of the two lines seemed to be sufficiently similar for total regional area to serve as a reasonable surrogate for regional wetland area.

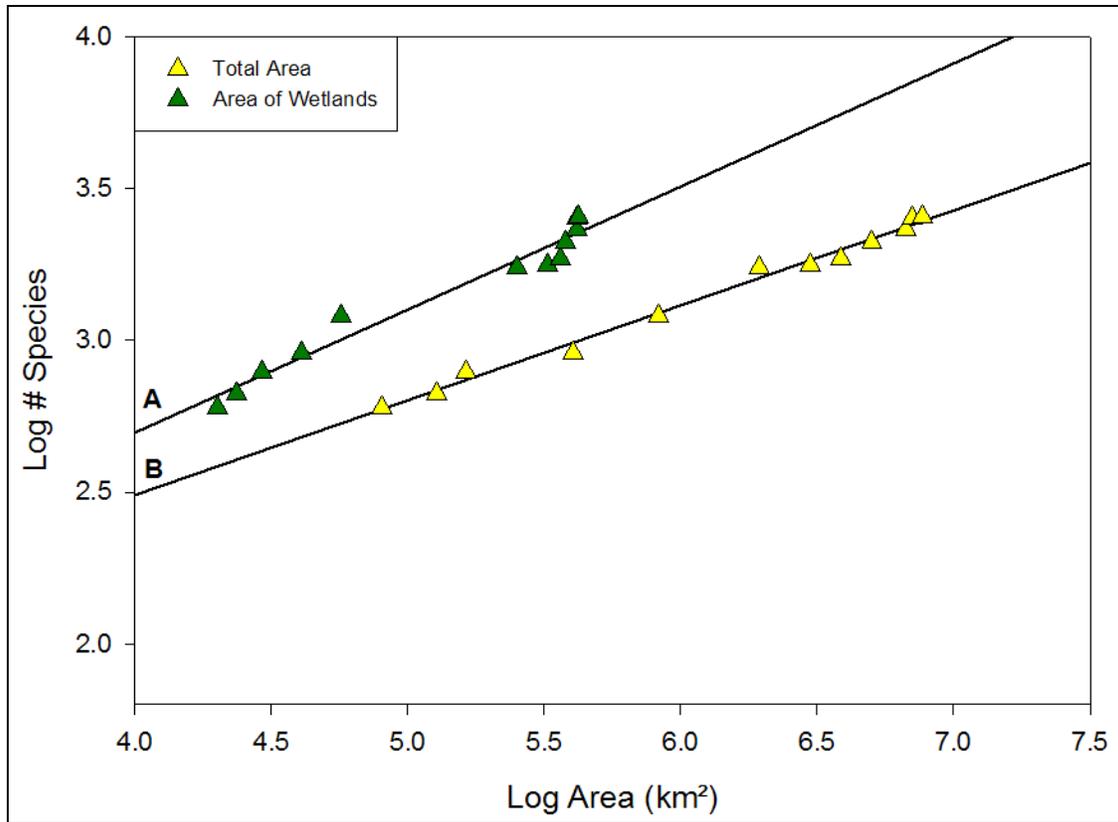


Figure 7-2. Species-area curves for the wetland flora of the coterminous United States. Species-area curves generated from cumulative data (Table 7-4). A. Area of wetlands within each region. Linear regression: $\text{Log } S = 1.07 + 0.41 \log A$, $r^2 = 0.96$. B. Total regional area. Linear regression: $\text{Log } S = 1.24 + 0.31 \log A$, $r^2 = 0.99$.

The congruence of the two areal measures was further investigated by adding plots of discrete (i.e., non-cumulative) regional species-area data to the plots of the cumulative data (Figure 7-3). It seemed that if total regional area were indeed a reasonable surrogate for regional wetland area, then regions (as represented by plotted discrete data) would consistently be either species-rich or species-poor relative to both sets of data. Although this relationship held true for some regions, more often than not regions varied considerably in their position relative to both the regression lines. The most radical discrepancies were with the Californian and Southwest regions. When referenced to the curve generated from cumulative wetland area (Figure 7-3-A), California and the Southwest both appeared to be species-rich (i.e., above the regression line), with California by far the most species-rich of all the regions. When referenced to the curve generated from total regional area (Figure 7-3-B), however, California was of average

richness (i.e., situated on the regression line), whereas the Southwest was the most species-poor region. The large differences in relative species-richness in California was perhaps partially attributable to its having lost about 90% of its original wetlands (Dahl 1990). It seems probable that at the regional scale the rate of species loss must lag behind wetland loss, as it seems unlikely that California once supported ten times as many wetland species as at present. Thus, the position of California far above the regression line for the species-area curve generated from regional wetland area (Figure 7-3-A) is most likely an exaggeration of its relative diversity.

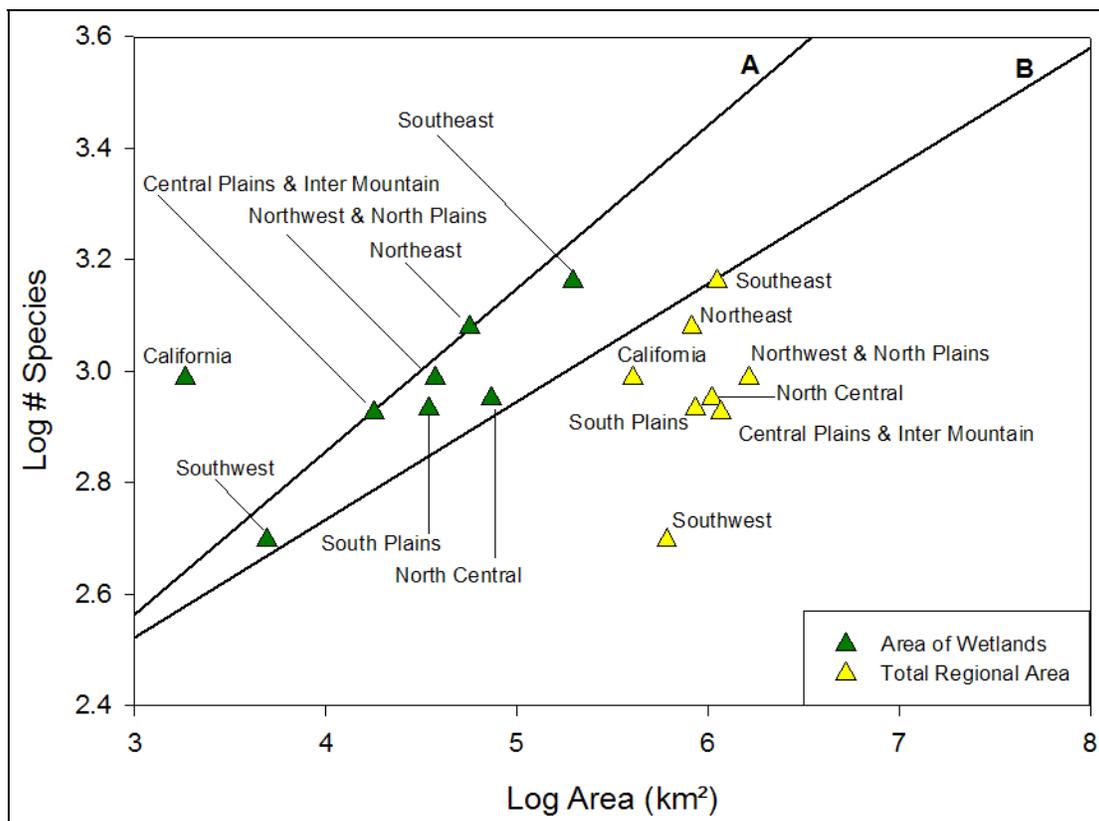


Figure 7-3. Species-area curves for the wetland flora of the coterminous United States, with discrete regional data added to the plots. A. Total regional area. Linear regression: $\text{Log } S = 1.07 + 0.41 \text{ Log } A$, $r^2 = 0.96$. B. Area of wetlands within each region. Linear regression: $\text{Log } S = 1.24 + 0.31 \text{ Log } A$, $r^2 = 0.99$. Regression lines were fitted to species-area curves generated from cumulative data (Table 7-4), but in order to avoid visual clutter data points from the cumulative data are not shown.

Having accepted (with some provisions) total regional area as a valid surrogate for regional wetland area, it was then possible to examine macroregional-scale diversity in

the Neotropics. Data (cumulative species and cumulative total area) were compiled for all Neotropical countries (Table 7-4). Although northern Mexico was not strictly within the Neotropics, species and area data from the entire country were used (Table 7-4). The inclusion of the entire country was necessary because distribution data in sources used in compiling the wetland species database frequently indicated little more than the species presence in the country. The three countries that constituted “the Guianas” (French Guiana, Guyana, and Suriname) were treated as a single OGU (Table 7.5), because references (e.g., literature and herbarium labels) occasionally failed to differentiate between them. Additionally, five Central American countries (Belize, El Salvador, Guatemala, Honduras, and Nicaragua) were considered as a single OGU, designated here by the decidedly inelegant appellation “Mid-Central America” (Table 7-5). These countries were grouped because their checklists were obviously incomplete relative to the other OGUs and I thought it better to have one large, under-represented OGU, rather than five small, contiguous, under-represented OGUs.

Table 7-5. OGUs used in plotting a species-area curve for the Neotropical (South America, Central America, and Mexico) wetland flora, with OGU area, number of wetland species noted for each OGU, cumulative wetland area, and cumulative wetland species.

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

A species-area curve was constructed commencing with a localized area (the Andean Piedmont, Bolivia) and continuing through the addition of successively larger, contiguous areas (cf. Rosenzweig 1995) and a linear regression was fitted to the data (Figure 7-4). The order of additions was as indicated in Table 7-5. Discrete regional species-area data were then plotted for each lowland region (Figure 7-4, green circles). As with the preceding species-area curves, regions above the regression line were considered as relatively species-rich and those below as relatively species-poor.

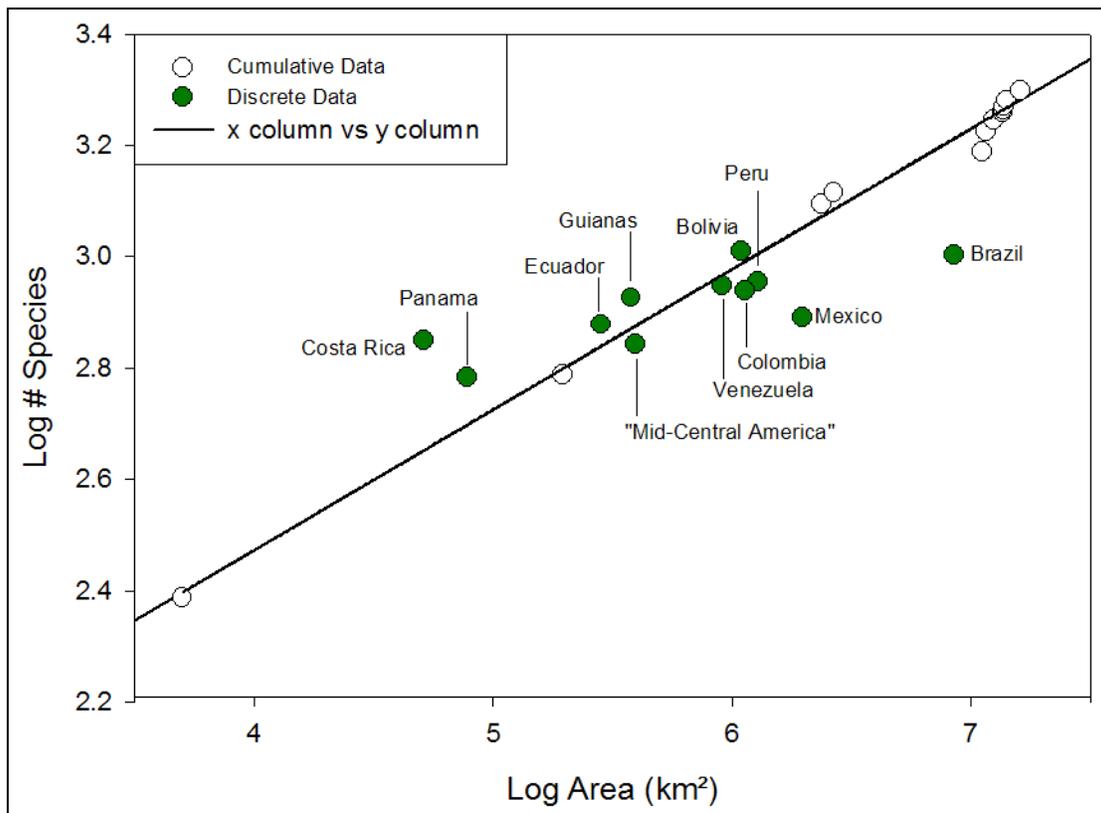


Figure 7-4. Figure 7.4. Species-area curve for the wetland flora of the Neotropics. Linear regression: $\text{Log } S = 1.46 + 0.25 \text{ Log } A$, $r^2 = 0.98$. The linear regression was fitted to the species-area curve generated from cumulative data (Table 7-5).

The slope of the regression line (0.25, Figure 7-4) was slightly lower than the regression lines for both the inter-Bolivian regional data (0.33, Figure 7-1) and for the regional data from the coterminous United States (0.31, Figure 7-3). I can think of no processes that would affect regional-scale diversity in both Bolivia and the United States without also

operating in the Neotropics, as a whole. Therefore, it seemed reasonable to consider all three slopes as roughly equivalent.

The slopes from the regression lines fitted to the regional data were much steeper than those from the three sets of site-level data (0.13, Southeastern U.S.; 0.13 New England; and, 0.17 Lowland Bolivia; Figure 6-7). These results were striking, as they were the inverse of what was expected. Assuming that individual wetlands are functionally islands (i.e., small areas of a particular habitat isolated by much larger expanses of unsuitable habitat), then the species-area curves generated from the site-level data were expected to possess slopes approximating those known for islands (e.g., 0.25-0.33, Rosenzweig 1995). Instead, the site-level species area curves all fell within the range known for “mainlands” (e.g., 0.13-0.17, Rosenzweig 1995). Conversely, the species-area curves from the macroregional data, rather than corresponding to those known for mainlands, were analogous to those expected for islands. This incongruity was particularly puzzling as the two macroregional data sets (i.e., the Neotropics, and the coterminous United States) both were constructed from sufficiently large areas such that they were expected to possess even steeper slopes than the figures cited for mainlands (Rosenzweig 1995). I am unable to suggest a mechanism that would account for these anomalies.

The discrete regional data formed a tight fit to the regression line of the cumulative data (Figure 7-4). Costa Rica and Panama were found to be the two most diverse countries (i.e., situated furthest above the regression line). In general, Central America appeared to possess a somewhat higher diversity than South America. An exception was Mid-Central America, which was situated just below the regression line, however, the species checklist for this OGU was most likely very incomplete, as relatively little botanical work seems to have taken place in the wetlands of the constituent countries.

The characterization of Central America as more diverse than South America was confounded by indications that the smallest OGUs (and, hence, Central America) were generally represented by more complete floristic accounts. This pattern was evidenced from two trends in the plot of the discrete regional data (Figure 7-4, green circles). First,

diversity was (generally) negatively correlated with area. The most diverse OGU (i.e., OGU situated above the regression line) were generally the smallest, whereas the largest OGU (Mexico and Brazil) were the least diverse (i.e., OGU situated below the regression line, Figure 7-4). It would seem that, rather than representing some heretofore unrecognized facet of biodiversity, this was simply a function of a much greater percentage of the area of the smaller countries having been surveyed. The second pattern was that OGUs represented by putatively complete national checklists (Costa Rica, Ecuador, the Guianas, Panama, and Peru) were generally the most diverse (exception, Peru), whereas those that were represented by checklists that I compiled (Bolivia, Brazil, Colombia, Mexico, Mid-Central America, and Venezuela) were the least diverse. In some cases (e.g., Brazil), I recognized that the wetland flora was most likely significantly incomplete, but in other instances I felt as if a substantial portion of the wetland flora was probably accounted for. For example, the number of wetland species noted for Mexico (778 species, Table 7-5) was of the same order as the 747 species noted for Mexico by Lot et al. (1993). Still, they noted that large gaps remained in the country's floristic inventory. Thus, it may well be that a significant portion of the Mexican wetland flora was not accounted for in the wetland species database.

Although the OGUs varied in how completely their floras were represented in the wetland species database, the characterization of Central America as more diverse than South America appears warranted, if somewhat qualified. Because (the aptly named) Central America occupies a position proximal to two larger land masses and, as wetland plants frequently possess extremely large distributions (Arber 1920), it was not unexpected that this region would possess a diverse wetland flora. Still, it is antithetical to the latitudinal gradient, which predicts a greater diversity for South America. Furthermore, four countries in Meso- and South America (Brazil, Colombia, Mexico, and Peru) have been identified as “megadiversity” countries (Mittermeier and Werner 1990), i.e., countries that possess large numbers of species, high levels of endemism, or both. Based on Figure 7-4, however, none of these could be characterized as possessing a particularly diverse wetland flora.

At this point, it was possible to again address the question that originally kindled my interest in Neotropical wetlands. How does diversity in the Neotropical wetland flora compare with that of the New World Temperate region? The data (cumulative species and cumulative total regional area) that were previously used to generate the species-area curves for these regions were combined and the interaction between area and data source (i.e., Neotropics versus coterminous United States) was evaluated by an ANOVA. Results indicated that the interaction between data sources was significant; thus, separate regression lines were fitted to the data (Figure 7-5). Although the two regression lines varied slightly, the New World Temperate region was the more diverse. The y-intercept of the regression line for the Neotropics (1.46) was higher than that for the New World Temperate region (1.24); thus, below a certain area (ca. 10,000 km²) the regression line for the former was situated above the line for the latter. It did not appear that this represented a difference in regional-scale diversity in smaller areas, as Neotropical wetlands were also determined to be less diverse than New World Temperate at a smaller scale (i.e., the comparison of site-level diversity; Figure 6-7). Rather, it most likely was the result of the “starting point” for the New World Temperate region species-area curve (i.e., Maine) being an order of magnitude or so larger than the smallest unit for the Neotropics, and as such it can be ignored.

A more important consideration is what portion of each region’s wetland flora was included in the data. Although the checklist used to represent the wetland flora of the United States (Reed 1996) was considered to be a draft, the United States has unquestionably been subjected to a much more comprehensive floristic investigation than have any of the Neotropical countries. The checklist assembled here to represent the Neotropical wetland flora (Ritter 2000) was compiled from a portion of the floristic accounts from what were, generally, incompletely surveyed countries, and can only be considered as embryonic relative to the checklist of Reed (1996).

In an attempt to assess how completeness of the Neotropical wetland species database may have affected the preceding analysis (Ritter 2000), data regarding the evolution of the database were compiled and tabulated (Table 7-6). Ideally, the condition of the database (e.g., number of wetland species entered, etc.) would have been recorded at

regular intervals throughout the duration of the research. Regrettably, this was not the case. Instead, the data presented in Table 7-6 represents an ex post facto reconstruction based on versions of the database that had been fortuitously archived on various computers. January 23, 1994 (the date of the first botanical collections I made in Bolivia), was designated as the starting date for the compilation of the database.

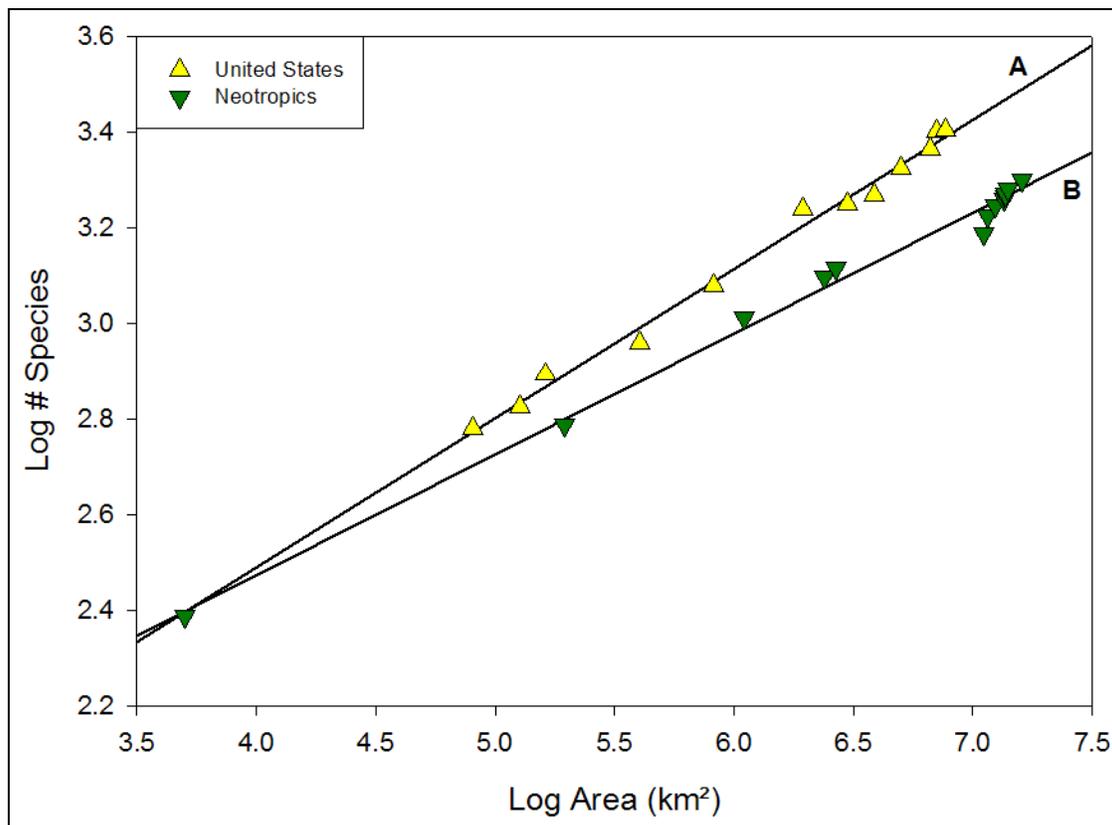


Figure 7-5. Species-area curves for the wetland floras of the coterminous United States and the Neotropics. A. Coterminous United States. Linear regression: $\text{Log } S = 1.24 + 0.31 \text{ Log } A$, $r^2 = 0.99$. B. The Neotropics. Linear regression: $\text{Log } S = 1.46 + 0.25 \text{ Log } A$, $r^2 = 0.99$.

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

the status of the database at the time when I first felt that a reasonable approximation of the number of Neotropical wetland species had been achieved. This perception was primarily based on this estimate (1,111 spp.) corresponding to the number of species noted for South America (ca. 1,100) in a checklist compiled by Conservation International and the Chicago Field Museum (Tyana Wachter, Field Museum, pers. com.). Nevertheless, after two additional years of work on the database the number of wetland species had nearly doubled (2,060 spp., Table 7-6). This suggests a rule of thumb, “when you’ve reached the point where you think the checklist is reasonably complete, you might be halfway there.” In other words, although I feel confident that the levels of diversity presented here for the various Neotropical OGUs are reasonably representative, I have been wrong before.

Table 7-6. Evolution of the Wetland Species Database.

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

A. The first species were added to the database on January 23, 1994.

B. Total taxa entered in the database, including accepted taxa, synonyms, invalid names, sub-specific taxa, non-wetland species, etc.

Therefore, it seemed appropriate to augment the number of species listed for the Neotropical OGUs and reexamine the differences in diversity between the Neotropical and New World Temperate regions. The provisional wetland species noted for each OGU were used to augment the checklists (Table 7-7). I originally considered increasing the species list for each OGU by a uniform 50%, but it seemed that the provisional wetland species might better represent actual diversity patterns in the OGUs. As it turned out, both methods would have been more or less equivalent, as the average percent increase in the floras was 47.8%, with relatively little variance (Table 7-7).

Table 7-7. OGU used in plotting a species-area curve for the Neotropics (South America, Central America, and Mexico), with cumulative OGU area, cumulative wetland species, cumulative wetland and provisional wetland species, and percent increase resulting from the inclusion of provisional wetland species.

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

A species-area curve was plotted using the augmented floras for the Neotropical OGUs, a regression line was fitted to the data and the resulting plot added to the existing species-area curves for the Neotropics and the New World Temperate regions (Figure 7-6). Despite the floras of the Neotropical OGUs having been increased by nearly 50%, the level of diversity was no more than equivalent to that of the New World temperate region. The (approximately) 50% increase in species engendered by the addition of the provisional wetland species undoubtedly exceeds the actual diversity of the Neotropical wetland flora. Hence, I am confident in the assessment of the wetland flora of the Neotropical region as not demonstrably richer than that of the New World Temperate region.

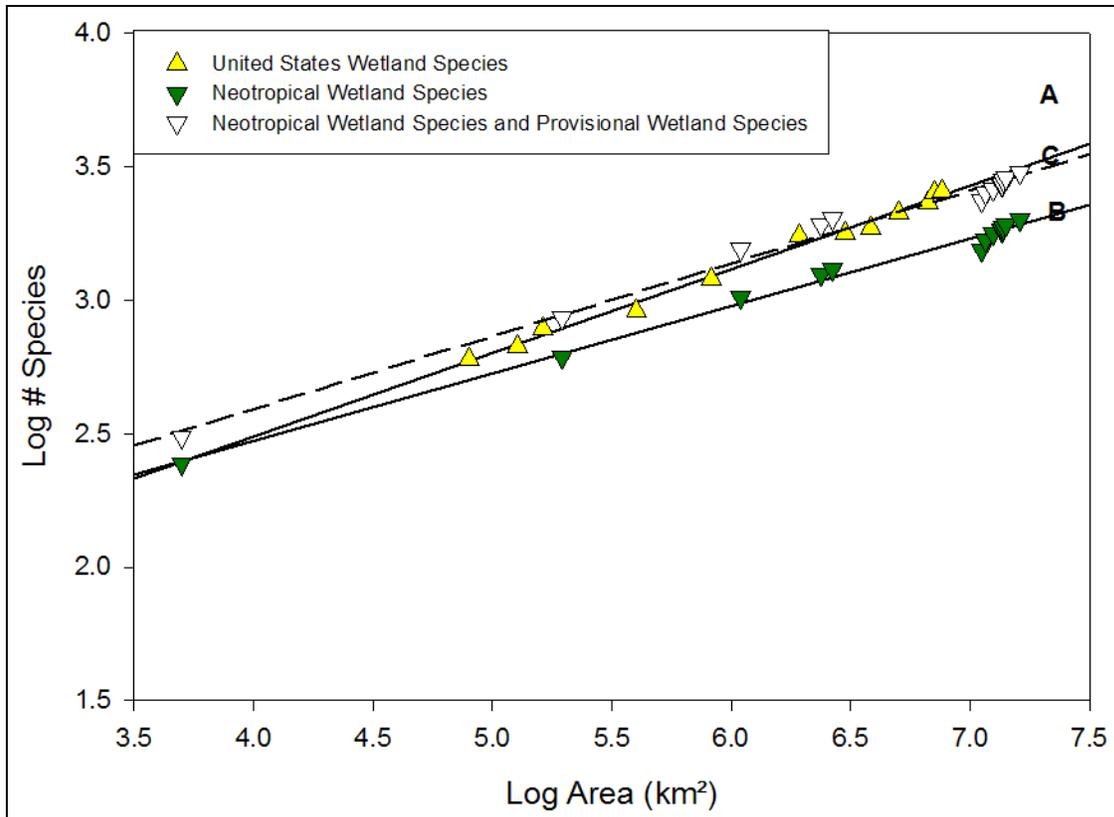


Figure 7-6. Species-area curves for the wetland floras of the coterminous United States and the Neotropics, and for the combined wetland and potentially wetland species of the Neotropics. A. Coterminous United States. Linear regression: $\text{Log } S = 1.24 + 0.31 \text{ Log } A$, $r^2 = 0.99$. The Neotropics: B. Wetland Species. Linear regression: $\text{Log } S = 1.46 + 0.25 \text{ Log } A$, $r^2 = 0.99$. C. Wetland and Provisional Wetland Species. Linear regression: $\text{Log } S = 1.50 + 0.27 \text{ log } A$, $r^2 = 0.99$.