



BIODIVERSITY AND PHYTOGEOGRAPHY OF
BOLIVIA'S WETLAND FLORA

BY

NUR P. RITTER
B.S. University of New Hampshire, 1992

DISSERTATION

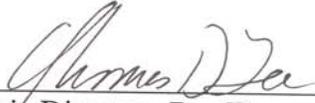
Submitted to the University of New Hampshire
in Partial Fulfillment of
the Requirements for the Degree of

Doctor of Philosophy
in Natural Resources

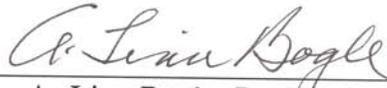
December, 2000

ALL RIGHTS RESERVED
2000
Nur P. Ritter

This dissertation has been examined and approved.



Thesis Director, Dr. Thomas Lee, Associate
Professor of Plant Biology



Dr. A. Linn Bogle, Professor Emeritus of Plant
Biology



Dr. Robert T. Eckert, Professor of Natural
Resources



Dr. Arthur C. Mathieson, Professor of Plant
Biology



Dr. Janet R. Sullivan, Adjunct Associate Professor
of Plant Biology

8 December 2000

Date

DEDICATION

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

And to my wife, Martha Ritter.

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

Acknowledgements

In many ways, this dissertation has become the archetype of those experiences which I internally categorize as “things that I would never have undertaken if I had known what was entailed”. That I survived the process and amassed a store of good memories along the way is due in large part to the assistance, patience, and support of numerous individuals. While the following individuals have all contributed to the completion of the dissertation, all errors or omissions rest firmly with the author.

Tom Lee deserves all manner of praise for his support and guidance as a member of my thesis committee since the inception of the project, and for his willingness to take on the burden of becoming my thesis advisor during the final year of my doctoral program. As the research unfolded, it took many unforeseen turns and Tom, through his engagement and unconquerable good humor, managed to extricate me from all manner of quagmires. I couldn't have hoped for a better friend and mentor.

I am also indebted to the other members of my thesis committee, Janet Sullivan, Art Mathieson, Robert Eckert, and Linn Bogle, for adding their invaluable guidance and expertise to the project. Janet Sullivan is to be particularly commended for her unceasing determination to turn me into a thoughtful writer. Robert Eckert deserves special thanks for first introducing me to plant identification and, thus, for having put up with me for many more years than most people would ever consider. Linn Bogle and Art Mathieson both deserve particular thanks for their willingness to join my thesis committee at a time when the greatest effort was required. Thanks are also due to the three individuals, Garrett Crow, Tim Killeen, and Dan Zarin, who also served on the committee at various times, but who were unable to participate in the final stages. Garrett is to be particularly commended for his contributions to the project from its inception. Likewise, Tim Killeen deserves special thanks for his friendship, for facilitating all manners of work in Bolivia, and for never letting me rest on my laurels, on those rare occasions when I managed to accrue a laurel or two.

I thank all those feckless individuals who assisted at various times during the field work (presented here alphabetically): Poul Andersen, Susana Arázola, Vicky Arázola, Saúl

Arias, Anna Maria Carrion, Richard Brummitt, Garrett Crow, Charlyn Crow, Jason Crow, Bill Cullina, Tracy Cullina, Milton Fernández, Paul Foster, Marisol Garvizu Prado, Tom Grimwood, Carlos Guardia, Jesús Guerrero, Jaime Guillén, Rene Guillén, Edelberto Guzmán Almendras, Brett Hartman, Aleida Justiniano de Angulo, Timothy Killeen, Sjoerd Mayer, Michael Mancuso, Sjoerd Mayer, Jeanette Mercado U., Maria Esther Montano, Daniel Nash, Christopher Oldcorn, Martha Ritter, Raymond Sabella, Pastor Solíz, Juan Surubí, Paul Treadwell, Dieter Wasshausen, John R. Wood, Alberto Zabala Alvarado, and Modesto Zárate.

I express my particular appreciation to John Wood, who participated in, frequently organized, and provided transportation for numerous field trips. Additionally, John brought both Laguna Volcan and the Siberia Marsh to my attention and made possible my initial visits to these sites. I wish to express my gratitude to Daniel Nash (BOLFOR) for his friendship, and thank him for his honesty, his good nature, and his aid in navigating through the complexities of life in Comunidad Nido de Grillos. Saúl Arias also deserves particular thanks for his assistance in the field and for his willingness to join me in facing the wrath of the citizenry of Comunidad Larati.

The members of “Equipo Mula”, Anna Maria Carrion, Carlos Guardia, Rene Guillen, Marisol Garvizu Prado, Pastor Solíz and Juan Surubí, have a special place in my heart for their constant effort and good cheer during our protracted fieldwork on the Serranía de Huanchaca. Marisol Garvizu deserves particular mention for her hard work and unassailably positive outlook during many taxing field expeditions. Likewise, Rob Wallace and Lillian Painter R. deserve endless thanks for all of their assistance at Lago Caiman. Paul Foster, Tom Grimwood, and Jaime Guillén are also deserving of special thanks for their good fellowship and hard work during fieldwork in La Toledo.

I expresses my appreciation to the following individuals for determining specimens and for reviewing and correcting my determinations: Dr. Ihsan Al-Shehbaz (MO), Brassicaceae; Dr. Frank Almeda (CAS), Melastomataceae; Dr. Henrik Balslev (AAU), Juncaceae; Dr. Howard Crum (MICH) *Sphagnum*; Dr. Shirley Graham (KE), Lythraceae; Dr. Robert R. Haynes (UNA), Alismatidae; Dr. Nancy Hensold (F),

Eriocaulaceae; Dr. R. J. Hickey (MU), Dr. Charles Horn NBYC), Pontederiaceae; Isoëtaceae; Dr. Elias J. Landolt (ZT) Lemnaceae; Lucia G. Lohmann (MO), Bignoniaceae; Dr. Michael Nee (NY), Cucurbitaceae and Solanaceae; Dr. Alejandro Novelo R. (MEXU), Podostemaceae; Dr. Rosa Ortiz (MO), Menispermaceae; Dr. Anton Reznicek (MICH) *Carex*; Dr. Harold Robinson (US) Asteraceae; Pr. Hector Rodríguez (MY) *Paspalum*; Dr. Rolf Rutishauser (Z), Podostemaceae; Dr. Zulma Rúgolo de Agrasar (SI) *Deschampsia*; Dr. Charlotte M. Taylor (MO), Rubiaceae; Dr. Galen Smith (WIS), *Schoenoplectus*; Dr. W. D. Stevens (MO), Asclepiadaceae; Dr. C. Thomas Philbrick (WCSU), *Callitriche*; Dr. Henk van der Werff (MO), Lauraceae; Dr. Bruno Wallnöfer (W), Ebenaceae; Dr. Dieter Wasshausen (US), Acanthaceae; John H. Wiersema (BARC), Nymphaeaceae and Cabombaceae; John R. I. Wood, Acanthaceae and Asclepiadaceae; George Yatskievych (MO), Pteridophytes; Dr. Elsa Zardini (MO), *Ludwigia*; and, Dr. Fernando Zuloaga (SI), *Paspalum*. Ron L. Liesner (MO) and Anthony Jardim (USZ) were both invaluable in identifying particularly troubling specimens.

I wish to thank individuals and institutions who contributed data to the project, in particular Tom Hollowell (Smithsonian Institute), George Yatskievych and Peter Jørgensen (Missouri Botanical Garden), Barry Hammel (Missouri Botanical Garden and INBio, Costa Rica), Profesor Udo Schmidt-Munn, Manuel Nique, and María Judith Sanabria. I also wish to thank individuals who sent me literature, particularly Poul Andersen, Garrett Crow, Linda Fahey, Elias Landolt, Lenny Lord, Alejandro Novelo R., and Bruno Wallnöfer. Linda Fahey deserves special thanks for instructing me in the mysteries of plant taxonomy and for her great sacrifice in sending me her copy of Alwyn Gentry's Field Guide to Woody Plants of Northwest South America.

At many stages throughout this project I was reliant upon the good graces of the staffs at numerous herbaria. Particular thanks are due: Monica Moraes and Stephan Beck, of the Herbario Nacional (LPB), Susana Arázola and Gonzalo Navarro of the Herbario Forestal Martín Cardenas (BOLV), Anthony Jardim, Tim Killeen, Rene Guillen, Fabiana Mamani, Maria Esther Montano, and Israel Vargas of the Museo Noel Kempff Mercado (USZ),

James Solomon, Ron L. Liesner of the Missouri Botanical Garden (MO), and Emily Wood of Harvard's Gray Herbarium (GH).

Likewise, a number of individuals associated with various organizations in Bolivia played important roles in facilitating the fieldwork. Special thanks are due Óscar Quiroga (Asociación Hombre y Naturaleza), Marithza del Castillo Antezana and Saúl Arias of CUEMAD (Cochabamba), Gonzalo Peña Bello of F.A.N., and Óscar Barrenachea of PROMETA (Tarija). I would like to recognize the Bolivian Armada for their logistical support during fieldwork in the Gran Pantanal, with particular thanks extended to Teniente Jhonny Muñoz Soliz. Gratitude is also expressed for logistic support provided by the Estación Piscícola Pirahibo (Valle de Sajta, the Chapare).

I would like to recognize the contributions of the staff at the University of New Hampshire's Biological Sciences Library, in particular David M. Lane and Francis R. Hallahan. The staff of the Reference Department at the University's Dimond Library, Louise Buckley, Peter Crosby, Valerie Harper, David Severn, Debbie Watson, Deanna Wood and Geli Zhang, were a constant help and are to be lauded for never backing down from a reference, no matter how obscure or poorly cited. I would also like to thank Vinny Cirasole of Vinny's Coffee Wagon whose coffee fueled many late nights of research and writing and whose positive outlook occasionally induced me to shift out of my dissertation induced melancholia.

Gratitude is due to the Department of Plant Biology, the Natural Resources Doctoral Program, and all individuals and institutions that provided funding: New Hampshire Agricultural Experiment Station, University of New Hampshire Graduate School, Museo de Historia Natural Noel Kempff Mercado, National Geographic Society, Tote Le Monde, and Proyecto Zoé.

I want to offer my sincere gratitude to my family and friends for their continued support and their unflinching ability to withstand the frequent and altogether monothematic diatribes engendered by the dissertation process. Particular thanks are due Johanna Gurland and Mark Kaminsky, Whitney, Susan, and Isaac Scott, Paul Treadwell, and my partners in crime in Cochabamba, Carlos and Anna Aliaga, Kathy Meruvia, Janet

Wellington, and Lee Cridland. Despite constant inducements to respond otherwise, the members of my family have given their unflagging support, and I'm happy to have this opportunity to express my gratitude for their love. Finally, I'd like to express my special love and thanks to my son, Pasha, and to my wife, Martha, from whom all blessings flow.

Table of Contents

Acknowledgements.....	iv
Table of Contents.....	ix
List of Tables.....	xiv
List of Figures.....	xvii
Abstract.....	xxii
Chapter 1. Introduction.....	1
Bolivia.....	1
General Botanical Research In Bolivia.....	4
Research In Bolivian Wetlands.....	6
The Current Study.....	7
Objectives.....	9
Chapter 2. Materials and Methods.....	10
Study Site Selection.....	10
Vegetation Sampling.....	14
Specimen Collection and Preparation.....	16
Specimen Identification.....	18
Wetland Species Database.....	18
Phytogeographic Analysis.....	22
Regions Within Bolivia.....	22
Extra-Bolivian Regions.....	25
Analytical Methods.....	27
Similarity Indices.....	27
Ordination.....	28
Cluster Analyses.....	29
Frequency Analyses.....	30
Chapter 3. Cloud Forest.....	32
Introduction.....	32
Materials and Methods.....	36
Results.....	38
Vegetation Description.....	38
Biodiversity.....	38
Floristic Similarities.....	40
Discussion.....	42
Vegetation Description.....	42
Biodiversity.....	44
Diversity at the Regional Scale.....	47
Floristic Similarities.....	48
Regional Similarities.....	48
Chapter 4. The Chapare.....	50
Introduction.....	50
Materials and Methods.....	53
The Study Area.....	53
Vegetation Sampling.....	53
Floristic Comparisons.....	55

Data Analysis	55
Results	56
Vegetation Description	56
Biodiversity	56
Floristic Similarities	56
Discussion	61
Vegetation Description	61
Biodiversity	64
Floristic Similarities	71
Chapter 5. The Gran Pantanal	75
Introduction	75
Materials and Methods	79
The Study Area	79
Vegetation Sampling	81
Floristic Comparisons	81
Data Analysis	81
Results	82
Vegetation Description	82
Biodiversity	82
Floristic Similarities	83
Discussion	87
Vegetation Description	87
Biodiversity	91
Floristic Similarities	95
Chapter 6. Site Level Biodiversity	98
Introduction	98
Methodological Considerations	100
Site-Level Diversity	103
Comparison of Species-Richness With Neotropical Terrestrial Habitats	113
Comparison With Temperate Wetlands	115
Chapter 7. Regional Scale Biodiversity	120
Diversity Within Bolivia	120
Macroregional Diversity	124
Literature Cited	138
Appendix A. The Study Sites	161
High Andean	161
Laguna Toro	162
Huayalmarca Pond	163
Laguna Saythu Khocha	163
Laguna Totora Khocha	164
Laguna Larati	165
Laguna Juntutuyo	167
Río Candelaria	168
Chulichuncani Laguna	169
Valles Secos	171
Laguna Alalay	171

Río Mizque Wetland.....	173
Río Guadalquivir Wetland.....	174
Irrigation Canal at Tiquipaya.....	176
Cloud Forest.....	176
Chimpa Huata Bog.....	177
Incachaca Pond.....	178
Lagunas Khonchu East and West.....	178
Corani Pampa Marsh.....	179
Serranía de Siberia Marsh.....	179
The Chapare.....	180
Mariposa Wetland.....	181
Ivirgarsama Marsh.....	181
Senda F Marsh.....	182
Villa Tunari Pond.....	182
Sinahota Pond.....	183
Valle de Sajta Curichi.....	183
Puerto Villarroel Laguna.....	183
Andean Piedmont.....	184
Bermudez Curichi.....	184
Viru Viru Wetland.....	186
White-water Floodplain.....	188
Riberalta Ciénaga.....	188
Laguna Tumi Chuqua.....	191
Laguna Suarez.....	192
Chiquitanía.....	195
Concepción Wetland.....	196
Huanchaca Arroyo.....	198
La Toledo Curichi.....	199
Bahía Toledo.....	201
Río Paraguá.....	204
Cuatro Vientos Palm Swamp.....	206
Lago Caimán.....	209
Gran Pantanal.....	212
Laguna Uberaba.....	212
Laguna La Gaiba.....	213
Laguna Mandioré.....	213
Laguna Cáceres.....	214
Puesto Gonzalo.....	215
Outlying Sites.....	216
Laguna Volcan.....	216
Yolosa Wetland.....	218
Laguna Yaguacua.....	219
Cristalmayu Wetland.....	220
Appendix B. Extra-Bolivian Regional and National Wetland Floras.....	222
Argentina.....	222
Río Paraná Delta Region.....	222

Brazil.....	223
Central Amazonia	223
Gran Pantanal de Mato Grosso	224
Other Brazil.....	225
Colombia.....	226
Costa Rica.....	226
Ecuador	227
El Salvador.....	228
The Guianas	228
Mexico	229
Panama.....	230
Paraguay.....	231
Peru	231
United States and Associated Territories.....	232
Venezuela.....	233
Appendix C. The Bolivian Regions	235
High Andean.....	235
Cloud Forest.....	237
Valles Secos	237
Chapare	238
Andean Piedmont.....	238
White-water Floodplain	239
Chiquitanía.....	241
Gran Pantanal.....	242
Additional Sources Incorporated Into The Bolivian Wetland Species Database	242
Appendix D. Species Associated with Bolivian Wetlands.....	243
Appendix E. Noteworthy Species	275
High Andean.....	275
Laguna Toro.....	275
Laguna Larati	275
Río Candelaria	275
Chulichuncani Laguna	276
Valles Secos.....	276
Laguna Alalay.....	276
Río Guadalquivir Wetland	276
Río Mizque Wetland.....	277
Irrigation Canal at Tiquipaya.....	277
Cloud Forest.....	277
Chapare	277
Andean Piedmont.....	277
Bermudez Curichi	277
Virus Viru Wetland	277
White-water Floodplain	277
Riberalta Ciénaga.....	277
Laguna Tumi Chuqua	278
Laguna Suarez.....	278

Other Systems in the White-water Floodplain.....	278
Chiquitanía.....	279
Concepción Wetland.....	279
Huanchaca Arroyo.....	279
La Toledo Curichi.....	279
Bahía Toledo.....	280
Río Paraguá.....	280
Cuatro Vientos.....	280
Lago Caimán.....	281
Additional Systems in Parque Noel Kempff Mercado.....	282
Gran Pantanal.....	282
Outlying Sites.....	283
Laguna Volcan.....	283
Yolosa Wetland.....	283
Cristalmayu Wetland.....	283
Laguna Yaguacua.....	283
Appendix F. Annotated Checklist of Species Associated with Wetlands in the Bolivian Cloud Forest Region.....	284
Bryophytes.....	284
Pteridophytes.....	284
Angiosperms.....	285
Appendix G. Species Associated with Wetlands in the Chapare Region.....	294
Habit.....	294
Appendix H. Species Associated with the Study Sites of the Bolivian Pantanal.....	301
Appendix I. Phytogeography.....	307
Introduction.....	307
Site-level Phytogeographic Patterns.....	307
Regional-Scale Phytogeographic Patterns.....	309

List of Tables

Table 2.1. Forty six study sites selected to represent Bolivian wetlands, with region, elevation, estimated area, Departamento (the 1st major political division), Provincia (the 2nd level political division), and major watershed. Key to Regions: AP, Andean Piedmont; CF, Cloud Forest; CH, Chapare; CQ, Chiquitanía; GC, Gran Chaco; HA, High Andean; LM, Lower Montane; T, Transition Zone; VS, Valles Secos; WW, Whitewater Floodplain.....	12
Table 2.2. The Bolivian regions, with estimated area, elevation range of the study sites, and major watersheds present in each region.	25
Table 2.3. Countries and extra-Bolivian regions utilized in biodiversity and floristic comparisons, with estimated area, total species and total wetland species noted for each OGU. Sources used in compiling the Bolivian flora are given in Appendix B. Sources used in compiling the floras of extra-Bolivian OGUs are given in Appendix C.....	26
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.	37
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.	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.....	40
Table 4-1. Study sites of the Chapare region, Bolivia, with province, elevation, approximate area, and approximate location.	54
Table 4-2. OGU's utilized in floristic comparisons, with estimated area, number of wetland species and estimated mean annual precipitation.....	55
Table 4-3. Comparison of richness and floristic similarity (Sørensen's Index) between study sites in the Chapare, Bolivia. Figures in bold along the main diagonal indicate the number of wetland species noted for each site. Numbers above the main diagonal indicate the number of wetland species shared by both areas. Numbers below the main diagonal indicate the percent floristic similarity between sites.....	57
Table 4-4. Comparison of richness and floristic similarity (Sørensen's Index) among selected OGUs. Figures in bold along the main diagonal indicate the number of wetland species noted for each region. The numbers above the main diagonal	

indicate the number of wetland species shared by both regions. Numbers below the main diagonal indicate the percent floristic similarity between regions..... 58

Table 4-5. Presence of the Alismatidae and the Alismataceae in selected OGUs. Note: the Río Paraná Delta region was excluded from these comparisons because it is situated far outside of the limits of Amazonia. 74

Table 5-1. Study sites in the Bolivian Gran Pantanal region, with elevation, approximate area of the system, and approximate location. 80

Table 5-2. Comparison of richness and floristic similarity (Sørensen's Index) between study sites. Numbers in bold along the main diagonal indicate the number of wetland species noted for each OGU. The numbers above the main diagonal indicate the number of wetland species shared by both OGUs. Numbers below the main diagonal indicate the percent floristic similarity between OGUs. 83

Table 5-3. Comparison of richness and floristic similarity (Sørensen's Index) among the OGUs. Numbers in bold along the main diagonal indicate the number of wetland species noted for each OGU. The numbers above the main diagonal indicate the number of wetland species shared by both OGUs. Numbers below the main diagonal indicate the percent floristic similarity between OGUs. OGUs: GP - Gran Pantanal (combined Bolivian and Brazilian portions); CQ - Chiquitanía; WW - White-water Floodplain; RP - Río Paraná Delta; CA - Central Amazonia; LP - Lowland Amazonian Peru..... 83

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..... 104

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. 106

Table 6-3. Distribution of wetland types in the Bolivian study sites, with number of systems pertaining to each type, etc..... 106

Table 6-4. Comparison of area and species richness among three Bolivian wetland systems..... 107

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..... 113

Table 6-6. Species richness and area of selected Neotropical forests utilized in comparisons of diversity with Neotropical wetlands..... 114

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. 117

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 118

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. 121

Table 7-2. Area, estimated wetland area, number of wetland species, and the cumulative totals of these three parameters for the five regions and one regional sub-sample used in plotting species-area curves for the Bolivian lowlands. OGU abbreviations: CM - Chimoré; CH - Chapare; AP - Andean Piedmont; WW - White-water Floodplain; CQ - Chiquitanía; GP - Gran Pantanal. 121

Table 7-3. Comparison of area and flora size for three Bolivian OGUs. 124

Table 7-4. United States OGUs used in plotting a species-area curve for the wetland flora of the coterminous United States, with cumulative total area, cumulative wetland area, and cumulative wetland species noted for each OGU..... 126

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. 129

Table 7-6. Evolution of the Wetland Species Database..... 135

Table 7-7. OGUs used in plotting a species-area curve for the Neotropics (South America, Central America, and Mexico), with cumulative OGU area, cumulative wetland species, cumulative wetland and provisional wetland species, and percent increase resulting from the inclusion of provisional wetland species..... 136

List of Figures

Figure 1-1. Bolivia, including major population centers and regionally important towns, primary roads, major water bodies, and political divisions (reproduced from the World Factbook, Central Intelligence Agency 2000). Uppercase names indicate the country's nine Departamentos (the highest level political division). 2

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

Figure 2-1. The forty-six Bolivian study sites. Letters in circles correspond to study sites as indicated in Table 2.1. 13

Figure 2-2. A record from the Wetland Species database. Fields along the left hand edge indicate whether references to the species were encountered in the TROPICOS database, in herbarium specimens, or in the literature. The large field in the center of the image stores information on synonymy and other taxonomic notes. The large field in the lower right hand corner contains information on species' habitats..... 20

Figure 2-3. The same record from the Wetland Species database as in Figure 2.3. In this layout, the presence of the species in various countries and regions is displayed. Fields indicate the source of the species' references (e.g., various published accounts, the TROPICOS and Flora Mesoamericana databases, herbarium specimens, etc.). Note: Only a small subset of the sources used in compiling species list for each OGU are presented in this layout..... 21

Figure 2-4. Bolivian Regions (modified from Killeen et al. 1993): 1) High Andean; 2) Valles Secos; 3) Cloud Forest; 4) White-water Floodplain; 5) Chiquitanía; 6) Chapare; 7) Andean Piedmont of Santa Cruz; 8) Gran Pantanal; 9) Bosque Tucumano-Boliviano; 10) Gran Chaco..... 24

Figure 2-5. Sample of the binary matrix of species versus OGUs. The top row indicates OGUs. The left-hand column lists the species, with species names abbreviated to eight characters in or to accommodate the restrictions of the analysis program (PC-Ord). The remaining columns contain presence/absence data for each species. 29

Figure 2-6. Frequency of species shared between a subset of hypothetical OGUs. Figures below the OGU names indicate the number of species shared between that OGU and OGU #1, followed by percent floristic similarity (Sørensen's Index) of the two floras. The boxes correspond to species classes (i.e., number of OGUs in which the species was present), as indicated by the key along the bottom edge of the figure. The vertical dimension of each box is proportional to the number of species that it represents. Figures associated with the boxes indicate the number of species that occurred in both the OGU and OGU #1, followed by the percentage that this portion of the flora contributed to the total species shared between the OGU and OGU #1. For example, considering the relationship between OGU #1 OGU #2, the initial (lefthand-most) box represents the 5 species that were present in all seven OGUs. These accounted for 12.8% of the species shared between these two OGUs. Continuing from left to right, the second box represents the 13 species that were present in both OGU #1 and OGU #2 and that occurred in exactly 6 OGUs. These

accounted for 33.3 % of the species shared between these two OGUs. Note: due to rounding off, the percentages may not add up to exactly 100%..... 30

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. 34

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..... 41

Figure 3-3. Ordination by Detrended Correspondence Analysis of the Bolivian Cloud Forest wetland flora and the wetland floras of selected regions. 42

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: $\text{Log } S = 1.35 + 0.13 \text{ Log } A$. $r^2 = 0.24$, $p = 0.00005$ 46

Figure 4-1. Location of the Chapare (Bolivia) study sites. 1. Villa Tunari Pond. 2. Sinahota Pond. 3. Senda F Wetland. 4. Mariposa Wetland. 5. Ivirgarsama Wetland. 6. Puerto Villarroel Laguna. 7. Valle de Sajta Curichi. 54

Figure 4-2. Ordination by Detrended Correspondence Analysis (DCA) of the 46 Bolivian study sites. The seven Chapare study sites are identified by name. Key to wetland types: B- bahía; BS - basin swamp; L - small lake (< 500 ha); LL - large lake (> 500 ha); M - marsh; P - pond; RM - riparian marsh... 57

Figure 4-3. Ordination of the OGUs by Detrended Correspondence Analysis (DCA). OGUs: AP - Andean Piedmont; CA - Central Amazonia; CQ - Chiquitanía; GP - Gran Pantanal; PA - Lowland Amazonian Peru; RP - Río Paraná Delta; WW - White-water Floodplain. Values in parentheses indicate estimated mean annual precipitation (mm). 59

Figure 4-4. Frequency of species shared between the Chapare and the other OGUs. Figures below the OGU name indicate the number of species present in both the OGU and the Chapare, followed by floristic similarity (Sørensen's Index). Boxes correspond to species classes (i.e., the number of OGUs in which the species was present) as indicated by the key along the bottom of the figure. The vertical dimension of each box is proportional to the number of species that it represents. Values associated with the boxes indicate the number of species in that class that occurred in both the OGU and the Chapare, followed by the percentage that this portion of the flora contributed to the total species shared between the OGU and the Chapare. For example, considering the relationship between the Chapare and the Andean Piedmont, the initial (lefthand-most) box represents the 20 species that were present in all seven OGUs. These species accounted for 33.3% of the species shared between these two OGUs. Continuing from left to right, the second box represents the 16 species that were present in both the Chapare and the Andean Piedmont and that occurred in exactly 6 OGUs. These accounted for 28.3% of the species shared between these two OGUs..... 60

Figure 4-5. Species-area curve plotted from the 23 lowland Bolivian study sites with the Chapare study sites identified by name. Wetland types: B – bahia; BS – basin swamp; L – small lake (<500 ha); LL – large lake (> 500 ha); M – marsh; P – pond; RM – riparian marsh. Linear regression: $\text{Log } S = 1.39 + 0.17 \text{ Log } A$. $r^2 = 0.44$, $p = 0.00005$ 64

Figure 4-6. Species diversity of the OGUs considered in comparisons with the Chapare (Bolivia) wetland flora. Diversity is relative to a regression line fitted to a species-area curve plotted from cumulative species-area data from the Neotropical countries, including Mexico (see Chapter 6). Linear regression: $\text{Log } S = 1.46 + 0.25 \text{ Log } A$; $r^2 = 0.99$ 67

Figure 4-7. The relationship between precipitation and species richness. Linear regression: $S = 560.8 - 0.12 P$; $r^2 = 0.48$ 68

Figure 5-1. South America, with an inset of the study sites from the Bolivian Gran Pantanal. Study sites: 1. Laguna Uberaba. 2. Puesto Gonzalo. 3. Laguna La Gaiba. 4. Laguna Mandioré. 5. Laguna Cáceres. Rivers: A. Río Paraguay. B. Río Cuiaba. 80

Figure 5-2. Ordination by Detrended Correspondence Analysis (DCA) of the 46 Bolivian study sites. The five study sites from the Bolivian Gran Pantanal are identified by name. Key to wetland types: B- bahía; BS - basin swamp; L - small lake (< 500 ha); LL - large lake (> 500 ha); M - marsh; P - pond; RM - riparian marsh. 84

Figure 5-3. Ordination of the OGU Detrended Correspondence Analysis (DCA). OGUs are those used in floristic comparisons with the Gran Pantanal. The wetland flora of the Gran Pantanal was compiled from species recorded from the Bolivian and Brazilian portions of this system. 85

Figure 5-4. Frequency of species shared between the Gran Pantanal (Bolivian and Brazilian portions) and the other OGUs utilized in floristic comparisons. Figures below the OGU name indicate the number of species present in both the OGU and the Gran Pantanal, followed by floristic similarity (Sørensen's Index). Boxes correspond to species classes (i.e., the number of OGUs in which the species was present) as indicated by the key along the bottom of the figure. The vertical dimension of each box is proportional to the number of species that it represents. Values associated with the boxes indicate the number of species in that class that occurred in both the OGU and the Gran Pantanal, followed by the percentage that this portion of the flora contributed to the total species shared between the OGU and the Gran Pantanal. 86

Figure 5-5. Species-area curve plotted from the 23 lowland Bolivian study sites with the Gran Pantanal study sites identified by name. Wetland types: B – bahia; BS – basin swamp; L – small lake (<500 ha); LL – large lake (> 500 ha); M – marsh; P – pond; RM – riparian marsh. Linear regression: $\text{Log } S = 1.39 + 0.17 \text{ Log } A$. $r^2 = 0.44$, $p = 0.00005$ 92

Figure 5-6. Phytodiversity of the OGUs considered in comparisons with the wetland flora of the Gran Pantanal (Bolivian and Brazilian portions). Diversity is relative to a regression line fitted to a species-area curve plotted from cumulative species-area data from the Neotropical countries, including Mexico (see Chapter 6). Linear regression: $\text{Log } S = 1.19 + 0.29 \text{ Log } A$; $r^2 = 0.90$ 93

Figure 6-1. Comparison of three systems. **A**: Laguna Cáceres. **B**: Viru Viru Wetland. **C**: The Huanchaca Arroyo. All areas drawn approximately to scale. 107

Figure 6-2. Species-area curve for the 46 Bolivian study sites. Wetland types: **B**- bahía; **BS** - basin swamp; **L** - small lake; **LL** - large lake (> 500 ha); **M** - marsh; **P** - pond; **RM** - riparian marsh. Linear regression: $\log S = 1.35 + 0.13 \log A$; $r^2 = 0.24$ 108

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: $\text{Log } S = 1.39 + 0.17 \text{ Log } A$. $r^2 = 0.44$ 109

- Figure 6-4. Species-area curve for the 46 Bolivian study sites. The three sites which were used in the example of the influence of area on richness are identified. Wetland types: **B**- bahía; **BS** - basin swamp; **L** - small lake; **LL** - large lake (> 500 ha); **M** - marsh; **P** - pond; **RM** - riparian marsh. Linear regression: $\log S = 1.35 + 0.13 \log A$; $r^2 = 0.24$. 110
- 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. 111
- 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. 115
- 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. $\log S = 1.4 + 0.17 \log A$; $r^2 = 0.44$. 119
- Figure 7-1. Species-area curves plotted from cumulative totals from the five Bolivian lowland regions considered in this study. Linear regression: $\log S = 1.04 + 0.33 \log A$, $r^2 = 0.97$. 122
- Figure 7-2. Species-area curves for the wetland flora of the coterminous United States. Species-area curves generated from cumulative data (Table 7-4). A. Area of wetlands within each region. Linear regression: $\log S = 1.07 + 0.41 \log A$, $r^2 = 0.96$. B. Total regional area. Linear regression: $\log S = 1.24 + 0.31 \log A$, $r^2 = 0.99$. 127
- Figure 7-3. Species-area curves for the wetland flora of the coterminous United States, with discrete regional data added to the plots. A. Total regional area. Linear regression: $\log S = 1.07 + 0.41 \log A$, $r^2 = 0.96$. B. Area of wetlands within each region. Linear regression: $\log S = 1.24 + 0.31 \log A$, $r^2 = 0.99$. Regression lines were fitted to species-area curves generated from cumulative data (Table 7-4), but in order to avoid visual clutter data points from the cumulative data are not shown. 128
- Figure 7-4. Figure 7.4. Species-area curve for the wetland flora of the Neotropics. Linear regression: $\log S = 1.46 + 0.25 \log A$, $r^2 = 0.98$. The linear regression was fitted to the species-area curve generated from cumulative data (Table 7-5). 130
- Figure 7-5. Species-area curves for the wetland floras of the coterminous United States and the Neotropics. A. Coterminous United States. Linear regression: $\log S = 1.24 + 0.31 \log A$, $r^2 = 0.99$. B. The Neotropics. Linear regression: $\log S = 1.46 + 0.25 \log A$, $r^2 = 0.99$. 134
- Figure 7-6. Species-area curves for the wetland floras of the coterminous United States and the Neotropics, and for the combined wetland and potentially wetland species of the Neotropics. A. Coterminous United States. Linear regression: $\log S = 1.24 + 0.31 \log A$, $r^2 = 0.99$. The Neotropics: B. Wetland Species. Linear regression: $\log S = 1.46 + 0.25 \log A$, $r^2 = 0.98$. 135