CHAPTER 8

Congruence of Diversity Patterns among Fishes, Invertebrates, and Aquatic Plants within the Río Paraguay Basin, Paraguay

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Abstract

Null hypotheses concerning random distributions of species with respect to subregions and macro-habitats within the Río Paraguay are tested with data from 131 species of macro-crustaceans and benthic invertebrates and 186 species of aquatic plants. The patterns are compared to the results for the distributions of fishes presented by Chernoff et al. (2001). The invertebrate data demonstrate the identical pattern among subregions as evident in the fish distributions. The results support the recognition of two zones: (i) the Río Paraguay zone containing the Upper and Lower Río Paraguay and the Río Negro; and (ii) the Río Apa zone containing the Río Apa and the Riacho La Paz. For all data sets, the Río Paraguay zone has higher species richness than the Río Apa zone. The boundary between the two zones is abrupt, which is also supported by the plant data. Only 11 of 186 species of plants were found in both zones. There is no congruence of pattern among macro-habitats. Both invertebrate and plant data sets contain many values that are not different from mean random similarities. The fish data set provides an unambiguous pattern of habitats within the Río Paraguay zone tied together in relation to inundation of habitats during the flood cycle. The invertebrate set provides one cluster that is consistent with the general principal. The plant data set demonstrates a relationship among shore and sand habitats, which experience greater currents than other macro-habitats. The plants found in backwater habitats had little similarity to other macro-habitats. Based on these observations, it is concluded that significant habitat within each of zone needs to be preserved to maintain a large portion of the biodiversity.

Introduction

In previous chapters, Mereles (2001), Barbosa et al. (2001), Magalhães (2001) and Toledo-Piza et al. (2001) have discussed general patterns of the distribution of aquatic and riparian plants, plankton and benthos, macro-crustaceans, and fishes in relation to subregions and macro-habitats within the Río Paraguay basin. Chernoff et al. (2001) tested null hypotheses about the homogeneity of fish distributions with respect to subregions and macro-habitats. They rejected both null hypotheses that the fish distributional data were obtained at random. The distributions of fishes indicate that there are two broad subregional associations: (i) the Upper and Lower Río Paraguay and the Río Negro and (ii) the Río Apa and the Riacho La Paz. The patterns of distribution associated with macro-habitats is congruent with the subregional analysis. Within the Río Paraguay proper, the similarity among macro-habitats is a function of the flooding cycle. In the Río Apa and the Riacho La Paz, the association among macro-habitats is associated with terra firme, headwater conditions. These results were then used to construct a conservation plan relative to fishes and to evaluate the potential effects of threats.

In this chapter, we examine the generality of the patterns discovered by Chernoff et al. (2001) by co-examining patterns found in benthos, plankton, macro-crustaceans and "aquatic" plants. We will then use the commonality or distinctiveness of the patterns to develop a conservation plan that would protect the majority of the aquatic biodiversity within the region that we surveyed.

Methods

The data sets used for these analyses are found in Appendices 5,6, 8–11. Two sets of analyses were performed, including one for invertebrates and one for aquatic plants. The invertebrate data set was obtained by combining the macro-crustacean data of Magalhães (2001) with the plankton and benthos data from Barbosa et al. (2001). Together these data sets comprise 131 species of invertebrates for which presence-absence information was available for all species for the five subregions: Río Negro, Upper Río Paraguay, Lower Río Paraguay, Río Apa and Riacho La Paz (Appendices 8-10). This is referred to as the full invertebrate data set.

Presence-absence information was available for 23 species of shrimps, crabs and molluscs for nine macro-habitats: Río Paraguay beaches, Río Apa beaches, backwaters, flooded forests, floating vegetation, lagoons, rapids, cryptic (crevices in rocks, logs, etc.), and clear waters (Appendix 11). Because the latter three macro-habitats had only 5 or fewer species, they were not analyzed. Furthermore, three species (*Macrobrachium borellii, M. brasiliense,* and *Sylviocarcinus australis*) were eliminated from the dataset because of ambiguity in assigning their macro-habitat for the Río Apa collections. The analysis of macro-habitats, thus, included 20 species of invertebrates and six macro-habitats—the reduced invertebrate data set.

We will refer to the aquatic and riparian plants as aquatic plants for the purpose of this chapter. The aquatic plant data set (Appendices 5,6) contains 185 species. The data do not allow a full sub-regional analysis but rather only a comparison of the flora of the Río Paraguay (upper and lower subregions) with that of the Río Apa. Presence-absence data were collected for the following macro-habitats: shores, flooded banks, semilotic, swamps, and sandy banks. Based upon the definitions provided by Mereles (2001) we will call flooded banks - backwaters, semilotic - flooded forests, and swamps - lagoons in order to use the same language as that for the fish and the invertebrate data. For the fishes and for invertebrates, beach habitats do not specify the type of soils. Whereas, for aquatic plants the presence of sandy soils is significant. Aquatic plants were collected along and on shorelines whether or not a beach was present. Thus, there is not complete congruence between the aquatic plant and the fish plus invertebrate data sets. However, if we make an assumption that aquatic plant shoreline habitats function in the same way as invertebrates and fishes beach habitats (e.g., the zone between deeper waters and areas exposed seasonally), then we can easily estimate the congruence among the data sets.

The patterns constructed within data sets will be compared by inspection and with matrix correlation. Because the presence or absence of any species is used multiple times in the calculation of similarities in a similarity matrix, the matrix correlation coefficient cannot be tested using the distribution of the product moment correlation. To test the significance of a matrix correlation coefficient, a random permutation test was performed with 10,000 iterations. The random permutation tests rewrites the rows and columns of each matrix in each iteration. The proportion of the simulated correlation coefficients greater than the absolute value of the observed matrix correlation coefficient approximates the probability of obtaining the results at random.

Results

I. Subregions

The invertebrate data base shows that the species richness of invertebrates was not distributed equally among all five subregions (Table 8.1). That the fewest number of species was found in the Riacho La Paz is partly an effect of effort because the fewest collections were taken in that tributary. By far the richest subregion was the Upper Río Paraguay where we collected 71 species, 54.2% of all the invertebrates collected. With the exception of the Riacho La Paz, the other subregions were moderately diverse with the Lower Río Paraguay and the Río Apa being slightly more than 50% richer than the samples from the Río Negro (Table 8.1).

The means of Simpson's Similarity Indices are highly variable among subregions (Table 8.1), ranging from 10% to almost 80% similarity. All indices are significantly different ($P<0.01$) from a random distribution among subregions. The low values (e.g., Riacho La Paz and Río Negro or Upper Río Paraguay and Río Apa) are actually less than that expected at random, indicating that species are actively partitioning the basin into distinctive regions. This would also be consistent with a strong faunal turnover between subregions.

The pattern of similarities plotted on the Gabriel network of subregions (Fig. 8.1) reveals the existence of two subregional zones of high similarity. One among the subregions of

Table 8.1. Mean Simpson's Index of Similiarity, S' among macro-crustaceans and benthic invertebrates found living in five subregions of the Río Paraguay basin. Larger samples were rarefied 200 times to the size of the smaller samples. Index values reported as percentages. Abbreviations: APA–Río Apa, LP–Lower Río Paraguay, RLP–Riacho La Paz, RN–Río Negro, UP–Upper Río Paraguay, n–number of species present, u–number of unique species, %u–percentage of unique species.

	RN	UP	LP	APA	RLP
RN					
UP	77.14				
LP	54.29	64.29			
APA	37.14	40.35	37.50		
RLP	10.00	40.00	30.00	75.00	
n	35	71	56	57	20
u	7	21	15	21	4
%*u*	20.00	29.58	26.79	36.84	20.00

the Río Paraguay and the Río Negro and the other between the Río Apa and Riacho La Paz. The high similarities within each of these subregional zones is due to shared taxa within the zone and not due to uniquely shared taxa (Table 8.2). For example, notice that the Upper Río Paraguay shares 27 of 35 and 36 of 56 species with the Río Negro and the Lower Río Paraguay, respectively. However, only six species were found in the Río Negro and the Upper Río Paraguay exclusively; and none were shared exclusively between the latter two subregions (Table 8.2). Thus, within the subregional zones there are no boundaries.

Between the Río Paraguay and Río Apa subregional zones there is a strong faunal turnover. This boundary is evident whether it is calculated at the confluence of the Lower Río Paraguay or between the Upper Río Paraguay and the Río Apa (Fig. 8.1). That is, from the Lower Río Paraguay into the Río Apa there is a turnover of more than 35 species (≈62.5%).

Table 8.2. Numbers of species of macro-crustaceans and benthic invertebrates shared (lower triangle) and shared exclusively (upper triangle) among subregions of the Río Paraguay. Abbreviations: APA–Río Apa, LP–Lower Río Paraguay, RLP–Riacho La Paz, RN–Río Negro, UP–Upper Río Paraguay.

	RN	UP	LP	APA	RLP
		6	0	4	0
UP	27		11	0	0
LP	19	36		4	0
APA	13	23	21		7
RLP	2	8	6	15	

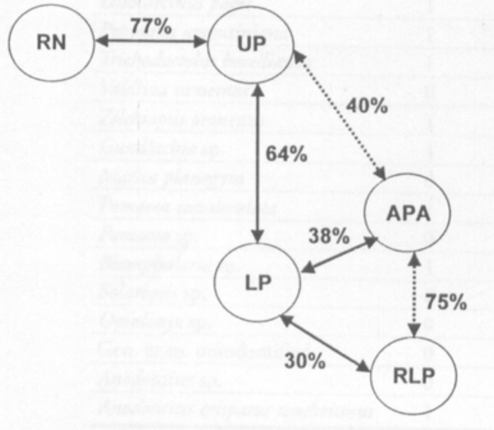

Figure 8.1. Gabriel network summarizing hydrographic relationships within the Río Paraguay. The numbers indicate percent similarity between the connected subregions (in circles). Solid lines indicate a direct river connection. Dashed lines indicate a comparison between subregions not connected directly by river. Abbreviations: APA –Río Apa; LP–lower Río Paraguay; RLP–Riacho de la Paz; RN–Río Negro; and UP–upper Río Paraguay.

The existence of the two groups of subregions results from the cluster analysis using Camin-Sokal parsimony (Fig. 8.2). Notice that the order of joining within the Río Paraguay group reflects the hydrological connections. It is also important to note that the pattern (Figs. 8.1–2) is not due to a particular group of invertebrates, but rather the signal is distributed across phyla and demonstrates the importance of broad taxonomic sampling.

These results are identical to those from the analysis of fish distributions (Chernoff et al., 2001). The identical results are manifest in the highly significant matrix correlation coefficient between the fish and the invertebrate similarity matrices ($r=0.923$, $P<0.001$). The results indicate the following for both aquatic invertebrates and fishes: (i) the Río Negro - Río Paraguay zone contains taxa associated with a flood-zone ecosystem; and (ii) the Río Apa - Riacho La Paz zone contains taxa associated with terra firme, headwater habitats. Furthermore, the rate of faunal turnover between the zones is rather sharp. For both the invertebrates and the fishes, there is a 60% turnover between the zones.

Species of plants were recorded from the Río Paraguay (Upper and Lower) and the Río Apa. A total of 186 species were encountered from which 147 were found in the Río Paraguay and 50 in the Río Negro (Appendices 5,6). Of the 50 species in the Río Apa, 39 were not found in habitats along the Río Paraguay. The remaining 11 species that are shared between these regions are displayed in Table 8.3. This would appear to support the results based upon the invertebrate and fishes.

Despite the low number of species shared between these two areas, however, the observed Simpson's similarity

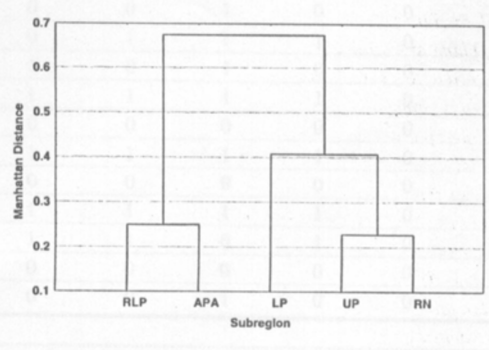

Figure 8.2. Camin-Sokal parsimony cluster analysis of subregions within the Río Paraguay based upon the full invertebrate dataset. Abbreviations: APA – Río Apa; LP–lower Río Paraguay; RLP–Riacho de la Paz; RN–Río Negro; and UP–upper Río Paraguay.

between the two rivers is 22.5%, a value that was not found to differ significantly from the mean random similarity (s=26.5%, std. deviation = 5.38, P>0.05). This indicates that without more information on plant distributions, the low similarity of the Río Apa with respect to the Río Paraguay cannot be interpreted unambiguously. If, however, future studies were to show that the 39 species of Río Apa plants not found in the Río Paraguay were consistent or even larger, then we would conclude that the low similarity is real and not due to the effects of rapid inventory. Nonetheless, the plant information does not contradict the zoological results, it only provides weak or ambiguous support.

Table 8.3. Aquatic and riparian plant species found along the Río Paraguay and the Río Apa (n=11).

Combretum lanceolatum
Crataeva tapia
Genipa americana
Hydrocotyle ranunculoides
Polygonum punctatum
Salix humboldtiana var. *martiana*
Sapindus saponaria
Senna scabriuscula
Solanum sp.
Triplaris cfr. *guaranitica*
Vitex megapotamica

II. Macro-habitats

Only 20 of the 131 species of aquatic invertebrates had reliable information about the macro-habitats in which they were collected (Table 8.4). Of the nine macro-habitats that were identified, three contained five or fewer species (rapids, cryptic and clear water) and were not analyzed further. The six remaining habitats were Río Paraguay beach, Río Apa beach, backwaters, flooded forest, floating vegetation and lagoons that contained between 7 and 12 species (Table 8.4). Only six of the 20 species were found in a single macro-habitat, while the number of species shared between habitats varied from four to eight (Table 8.5).

The similarity matrix (Table 8.5) demonstrates a two fold difference in mean similarities from just above 44% to almost 89%. Two hundred simulations for a universe with 20 species total with 7 to 12 species present per macro-habitat indicate that the observed similarities of 50% or less could not be distinguished from random. The remaining

Table 8.4. Distribution of aquatic invertebrates (n=20) among nine macro-habitats in the Río Paraguay drainage. Abbreviations: BA–Río Apa beach, BP–Río Paraguay beach, BW–backwaters, CR–cryptic, CW–clear waters, FF–flooded forests, FV–floating vegetation, LG–lagoons, RD–rapids.

	BP	BA	BW	FF	FV	LG	RD	CR	CW
Macrobrachium amazonicum	1	1	1	1	1	1	0	0	0
Macrobrachium jelskii	1	0	0	0	0	0	0	0	0
Palaemonetes ivonicus	0	0	0	0	1	1	0	0	0
Pseudopalaemon sp.	0	1	0	0	0	0	0	0	0
Acetes paraguayensis	1	0	0	0	0	1	0	0	0
Dilocarcinus pagei	1	0	1	0	1	1	0	0	0
Poppiana argentiniana	1	0	0	0	0	0	0	0	0
Trichodactylus borellianus	1	1	1	1	1	0	1	1	1
Valdivia camerani	0	0	1	0	1	0	0	0	0
Zilchiopsis oronensis	1	0	0	0	1	0	0	0	0
Gundlachia sp.	1	0	0	1	1	1	0	0	0
Marisa planogyra	0	0	1	0	1	0	0	0	0
Pomacea canaliculata	1	1	1	1	1	1	0	0	0
Pomacea sp.	0	1	0	0	0	0	0	0	0
Biomphalaria sp.	1	1	1	1	1	1	0	0	0
Solaropsis sp.	0	1	0	0	0	0	0	0	0
Omalonyx sp.	0	0	1	1	1	1	0	0	0
Gen. et sp. unindentified	0	1	1	1	0	1	0	0	0
Anodontites sp.	0	1	0	0	0	0	0	1	0
Anodontites crispatus tenebricosus	1	1	0	0	1	0	0	1	0

similarities are significantly different from those expected at random (P<0.01) and reject the null hypotheses.

Camin-Sokal parsimony cannot completely resolve the relationships among the macro-habitats (Fig. 8.3a). The polychotomy is caused by the large number of taxa shared among the flooded forest, floating vegetation, backwater, and lagoon habitats. But apart from the polychotomy, the results of the different clustering methods are congruent (Fig. 8.3). The close relationship between backwater and floating vegetation habitats results from their sharing uniquely two species, *Valdivia camerani* and *Marisa planogyra*.

The major result is that there an intimate relationship among habitats that are seasonally indundated, with the beach habitats being more dissimilar (Fig. 8.3). The group of four inundated habitats share more species in common (6–8) than they do in general with either the Río Apa or Río Paraguay beaches (4–5; Table 8.5). The one exception to this is that eight species were found in common between Río Paraguay beaches and floating vegetation habitats (Tables 8.4, 8.5). This, however, is due to the fact that floating vegetation habitats can extend to the shorelines in proximity to beaches. Nonetheless, the majority of the invertebrate biodiversity is found in less exposed, lentic habitats that are seasonally inundated. The overall pattern based upon shared species or distances emphasizes a Río Paraguay group that communicate vis a vis flooding cycles. The Río Apa beaches are the most distant from the Río Paraguay group.

The pattern of clustering among the macro-habitats, given the invertebrate data, is fairly congruent with the pattern for fishes (compare Fig. 7.11 with Fig. 8.3), in that the inundated habitats form a cluster separated from the Río Apa beach samples. However, in the case of fishes, the Río Paraguay beaches share the most number of species with backwater habitats. Remember that backwater habitats extend inland and communicate, at least seasonally, with the shorelines or beaches. The differences in branching patterns among invertebrates and fishes is reflected in the relatively low matrix correlation among the sample similarity matrices (Tables 7.10, 8.5; r=0.27, P>0.05) that was not significant. Thus, the similarity between the fishes and the invertebrates is due to the association among habitats that are created during the flood zone along the Río Paraguay. Beach habitats experience the effects of currents, and many species of invertebrates may prefer quieter habitats and may not require access to deeper waters, thereby inverting the association among habitats from that demonstrated for fishes.

Table 8.5. Number of species shared (upper triangle) and mean Simpson's Index of Similiarity, S', among macro-crustaceans and benthic invertebrates found living in six macro-habitats within the Río Paraguay basin. Larger samples were rarefied 200 times to the size of the smaller samples. Index values reported as percentages. Coefficients shown in bold are significantly different from random (P<0.001). Abbreviations: BA–Río Apa beach, BP– Río Paraguay beach, BW–backwaters, FF–flooded forest, FV–floating vegetation, LG–lagoon, n–number of species present, u– number of unique species, %u–percentage of unique species.

	BP	BA	BW	FF	FV	LG
BP		5	5	5	8	6
BA	50.00		5	5	5	4
BW	**55.56**	**55.56**		6	8	6
FF	**71.43**	**71.43**	**85.71**		6	6
FV	**72.73**	50.00	**88.89**	**85.71**		7
LG	**66.67**	44.44	**66.67**	**85.71**	**77.78**	
n	11	10	9	7	12	9
u	2	4	0	0	0	0
%u	18.18	40.00	0.00	0.00	0.00	0.00

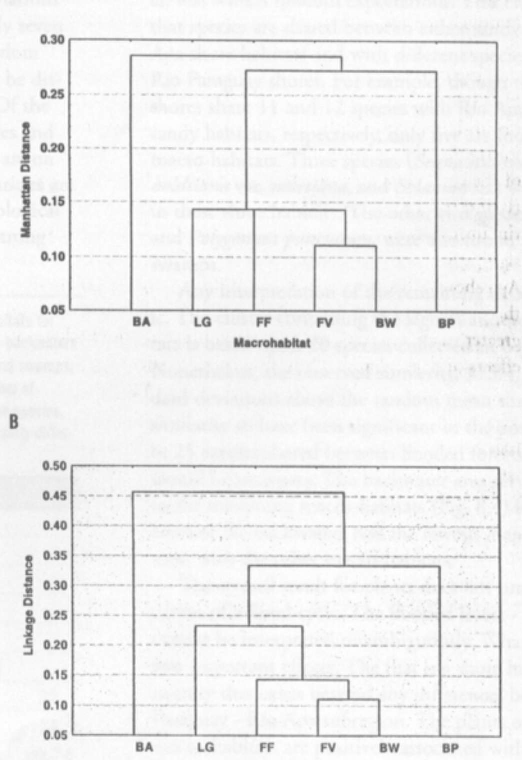

Figure 8.3. Camin-Sokal parsimony (a.) and UPGMA (b.) cluster analyses of macrohabiotats within the Río Paraguay based upon the reduced invertebrate dataset. Abbreviations: BA–beach Rio Apa; BP–beach Río Paraguay; BW–backwater; FF–flooded forest; FV–floating Vegetation; and LG – lagoon.

Information about six macro-habitats were collected from all 186 species of plants (Mereles, 2001) (Appendices 5,6). There was more than a doubling of species found among the macro-habitats, and the richest were flooded forests, Río Paraguay shores, and lagoons. Although Mereles (2001) noted that there is usually a high negative correlation between species richness and degree of current, the Río Paraguay shoreline habitats were very rich with 56 species present. The plants exhibited a stronger degree of macro-habitat partitioning than the fishes or invertebrates. For example, the number of unique species (Table 8.6) were exceptionally high ranging from 41% to 86% of the species collected in any habitat. Using the methods of Chernoff et al. (2001), the number of unique species were significantly higher than random expectations (P<0.001). Furthermore, out of 186 species, there were no species found in all five macro-habitats. Only five species (*Pistia stratiotes, Crataeva tapia, Combretum lanceolatum, Polygonum punctatum,* and *Mikania periplocifolia*) were found in four macro-habitats. Fourteen species were found to occupy three macro-habitats.

The matrix of similarity coefficients (Table 8.6) shows that the coefficients range from 0% to 44.4% similarity. However, because of the relatively few taxa found in each macro-habitat out of the large total, the standard deviations for the randomly simulated data are rather high. Only seven of the coefficients are significantly different from random (P<0.001). The remaining eight comparisons cannot be distinguished from a random distribution (Table 8.6). Of the significant coefficients, only two (Ríos Paraguay shores and Apa shores; Río Paraguay shores and sandy habitats) are on the positive tail of the distribution. That is the similarities are greater than expected by chance and illustrate the biological effects of dependence. Thus, even though there is a strong regional effect between the Río Paraguay and Río Apa subregions, the disparity is not a function of the shore macro-habitats.

Table 8.6. Mean Simpson's Index of Similarity, S', among six macro-habitats for 186 species of plants in the Río Paraguay drainage. Abbreviations: BW–backwaters or behind flooded banks, FF–flooded forests or semilotic, LG–lagoons and swamps, SA–Río Apa shore, SN–sandy habitats, SP–Río Paraguay shore, n–number of species present, u–number of unique species, %u–percentage of unique species. Shore habitats include beaches. Coefficients shown in bold are significantly different from random (P<0.001).

	SP	SA	BW	FF	LG	SN
SP						
SA	**44.00**					
BW	11.11	12.00				
FF	**16.67**	**8.00**	**0.00**			
LG	31.48	12.00	**0.00**	37.04		
SN	**44.44**	20.00	0.00	25.93	22.22	
n	56	22	28	62	54	27
u	30	14	24	36	24	11
%u	53.57	63.64	85.71	58.06	44.44	40.74

Interestingly, the remaining five significant coefficients are on the negative tail of the distribution (i.e., more than three standard deviations below the random mean similarity). These lower than expected similarities indicate strong habitat partitioning among the aquatic plants. Extreme cases are found in backwater or flooded bank habitats such that they possess no species in common with flooded forests (semilotic), lagoons (swamps) or sandy habitats. The flooded forest habitats also show fewer than expected species in common with shore macro-habitats.

The branching diagram that results from Camin-Sokal parsimony, Ward's Method or UPGMA are identical (Fig. 8.4). The resulting analysis must be interpreted with caution because of the large number of coefficients that were not significantly different from random. The cluster containing the sandy and the ríos Paraguay and Apa shore habitats is an example. The Río Paraguay shore habitat had similarities that were greater than can be expected at random with both sandy habitats and Río Apa shore environments (Table 8.6). The 20% similarity displayed between the latter two, however, was within random expectations. This cluster indicates that species are shared between either sandy habitat or Río Apa shore habitats and with different species found along Río Paraguay shores. For example, though the Río Paraguay shores share 11 and 12 species with Río Apa shores and sandy habitats, respectively, only five are found in all three macro-habitats. Three species (*Senna scabriuscula, Salix humboldtiana* var. *martiana,* and *Solanum* sp.) were collected only in these three habitats. The other two species, *Crataeva tapia* and *Polygonum punctatum,* were also found in lagoons and swamps.

Any interpretation of the remaining clusters is problematic. The cluster containing the lagoon and flooded forest habitats is based upon 20 species collected in both habitats. Nonetheless, the observed similarity, 37.04, is only 1.34 standard deviations above the random mean similarity. For the similarity to have been significant in the positive tail, a total of 25 species shared between flooded forests and the lagoons would be necessary. The backwater area serving as the outlier to the remaining macro-habitats (Fig. 8.4) is very reasonable because the backwaters had the fewest, if any, species in common with the other macro-habitats.

The overall result for plants does not present strong indication of a flood cycle. The flooded forest - lagoon cluster cannot be interpreted unambiguously. What we do see are two important effects. The first is a shore habitat plant community that exists beyond any differences between the Río Paraguay - Río Apa subregion. The plants of the sandy macro-habitats are positively associated with, and perhaps dependent upon, the Río Paraguay shore habitats. This association does not extend to the Río Apa shore samples. The second effect is that the backwater macro-habitats comprise a unique assemblage of aquatic plant species. No species were found in common between the backwaters and flooded forests, or lagoons and sandy macro-habitats.

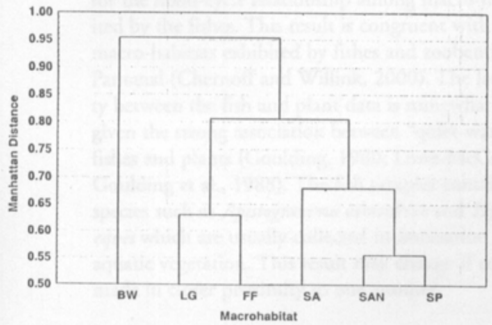

Figure 8.4. Camin-Sokal parsimony cluster analysis of macrohabiotats within the Río Paraguay based upon the planet dataset. Abbreviations: BW—backwater; FF—flooded forest; LG—lagoon; SA—shoreline Río Apa; and SP—shoreline Río Paraguay.

Discussion

The purpose of this chapter has been to compare patterns of distributions of invertebrates, plants and fishes with respect to the subregions of the Río Paraguay basin and with respect to macro-habitats. Integration of patterns among the components of biodiversity will enable us to derive the most effective conservation plan for the Río Paraguay basin between Concepción and the Brazilian border.

In an earlier chapter, Chernoff et al. (2001) were able to reject null hypotheses that the distributions of fishes were random with respect to subregions and with respect to macro-habitats. The subregional analysis demonstrated that there were two main zones: (i) a Río Paraguay zone that contained the Upper and Lower Río Paraguay subregions plus the Río Negro, and (ii) a Río Apa zone that contained the Río Apa and Riacho La Paz subregions. Within each zone species were shared broadly, between zones there was a strong faunal turnover. The macro-habitat analysis demonstrated that within the Río Paraguay zone there was a non-random association of macro-habitats due to seasonal cycles of inundation. The Río Paraguay beach habitats were central, from which most of the other interior habitats (e.g., flooded forests, backwaters, floating vegetation, and lagoons) were basically nested subsets. The deeper waters of the main channel bore the closest faunal similarity to the Río Paraguay beaches but were distant from inland habitats. Another major finding of the macro-habitat analysis was that a different faunal assemblage was present in the habitats that characterize the Río Apa zone: beaches, rapids, and clear water. This zone contains habitats more associated with terra firme and headwater areas than lowland floodplains.

The subregional analyses of macro-crustaceans and benthic invertebrates displayed almost identical results to those for fishes. The correlation of the similarity matrices was 0.92 ($P<0.001$). The results highlighted that there was strong faunal resemblance within the Río Paraguay zone, and that there was a rather sharp boundary to the Río Apa zone (Figs. 8.1–2). Importantly, the invertebrate result was not due to any single taxon, rather the evidence was scattered across a number of families, orders and phyla. The plant data were not presented in a way to support a full subregional analysis. We were able to test for difference between the Río Paraguay and the Río Apa zones. The aquatic plants demonstrated a strong floral boundary between the zones—only 11 out of 186 species were collected in both. Thus, our conservation recommendations, presented below, emphasize that the Río Paraguay and the Río Apa zones are highly distinctive and require separate conservation efforts.

Unlike the subregional analyses, there was less congruence among the results based upon the macro-habitats. For invertebrates, the majority of the observed similarities were significantly different from random. The pattern of similarities among macro-habitats for invertebrates was not significantly correlated with those for fishes (matrix $r<0.27$, $P>0.05$), but this lack of correlation is due to the close association in fishes between the Río Paraguay beaches and backwater habitats. Nevertheless, the clustering order of the nested sequence lagoons, flooded forests, floating vegetation, and backwaters is identical in both fishes and invertebrates (Figs. 7.11, 8.3). Furthermore, the Río Apa beaches are most different with respect to the other macro-habitats for both the invertebrates and the fishes. These results must be viewed only as a preliminary result, however, because only 23 species of invertebrates were scored for a subset of the macro-habitats for which the fishes were collected.

The plant data are difficult to interpret. Less than half of the similarity coefficients were not significantly different from random and the entropy analysis also conveyed that the matrix of species presences by macro-habitats were not significantly more ordered than a random distribution. Given these limitations, there were two aspects of the plant data that were not ambiguous. The first is that both sandy beaches and Río Apa shores share a relatively large (>10) number of species with Río Paraguay beaches. These habitats are subject to relatively stronger currents than are other habitats and may accumulate similar species. The second is that backwater samples were very different from other samples such that no species were found in common with flooded forests, lagoons, and sandy habitats.

The discovery that the invertebrate and plant data are not significantly more ordered than random expectations is due to the large number of idiosyncratic species distributions across subregions and macro-habitats. This is reflected in the relatively high number of similarity coefficients that were not significantly different from random mean similarity. The fish distributions are highly patterned and pass both tests of significance (Chernoff et al., 2001). This means that the invertebrates add weak support for the subregional analysis and for the flood-cycle relationship among macro-habitats exhibited by the fishes. This result is congruent with the results for macro-habitats exhibited by fishes and zoobenthos in the Pantanal (Chernoff and Willink, 2000). The lack of similarity between the fish and plant data is somewhat surprising given the strong association between "quiet-water" species of fishes and plants (Goulding, 1980; Lowe-McConnell, 1987; Goulding et al., 1988). The fish samples contain many species such as *Apistogramma commbrae* and *Hyphessobrycon eques* which are usually collected in association with rooted aquatic vegetation. This result may change if collections were made in closer proximity to one another.

Conclusions and Recommendations

Conservation plans must reflect departures from random distributions of the flora and fauna with respect to geography and macro-habitats. To the extent that pattern can be interpreted from the invertebrate data set, it is congruent with the non-random pattern exhibited by the fishes. The plant data provided a test that the Río Paraguay zone is different from the Río Apa zone—a finding congruent with both invertebrates and fishes. There is no confirmation by invertebrates or plants of the flood-cycle relationship among macro-habitats that was displayed by the fishes. These conclusions lead to the following recommendations:

1. The flora and the fauna comprise two major zones within the Río Paraguay basin above Concepción to the Brazilian Border: (i) the Río Paraguay zone containing the Upper and Lower Río Paraguay and the Río Negro; and (ii) the Río Apa zone containing the Río Apa and the Riachó La Paz.

2. Based upon fishes, invertebrates and plants the Río Paraguay zone contains more species than does the Río Apa zone.

3. Significant habitat within each of these zones needs to be preserved to maintain a large portion of the biodiversity.

4. There is some congruence among the fishes and invertebrates with respect to their distributions among macro-habitats but not with aquatic plants. As a result samples of all macro-habitats must be preserved to maintain the majority of species.

5. Elimination of habitats that require seasonal flooding, such as flooded forests, lagoons, and backwaters, would eliminate almost 50% of the plant species.

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