
**DISTRIBUTIONAL CONGRUENCE AMONG AQUATIC PLANTS,
INVERTEBRATES AND FISHES WITHIN THE RÍO PARAGUAY
BASIN, PARAGUAY**

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SUMMARY

Null hypotheses concerning random distributions of species with respect to subregions and macrohabitats within the Río Paraguay are tested with data from 131 species of macrocrustaceans 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. (2004). 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 portions of Río Paraguay and Río Negro, and ii) the Río Apa zone containing Río Apa and 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 macrohabitats. The invertebrate and plant similarity matrices contain many values that are not different from mean random similarities among macrohabitats. The plant data set demonstrates a relationship among shore and sand habitats that experience greater currents than do other macrohabitats. The plants found in backwater habitats had little similarity to other macrohabitats. Based on these observations, we conclude that significant habitat within each of the zones must be preserved to maintain a large portion of the biodiversity.

Introduction

Freshwater ecosystems are home to tens of thousands of species and provide food and critical services for the health of humans and for the planet. Yet freshwater ecosystems

are highly threatened and the organisms that live there are highly vulnerable to ecosystem modification (Naiman *et al.*, 1995; Abramovitz, 1996; Stiassny, 1996; Folkerts, 1997; Pringle *et al.*, 2000; Saunders *et al.* 2002). Water

use, pollution, channelization, deforestation and dams are only a few of the threats facing aquatic habitats and their associated wetlands worldwide (Petts, 1990; Allan and Flecker, 1993; Boon *et al.*, 2000). Our ability to manage

these ecosystems requires knowledge of the organisms, their distributions, and their biotic and abiotic interactions. Integrated-use management or conservation strategies must take into account the patterns of spatial distri-

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RESUMEN

Hipótesis nulas concernientes a distribuciones de especies al azar con respecto a subregiones y macrohábitats dentro del Río Paraguay son examinadas con datos provenientes de 131 especies de macrocrustáceos e invertebrados bénticos y 186 especies de plantas acuáticas. Los patrones son comparados con el resultado de distribuciones de peces presentados por Chernoff et al. (2004). Los datos provenientes de invertebrados mostraron un patrón idéntico entre subregiones, como es evidente en las distribuciones de peces. Los resultados apoyan el reconocimiento de dos zonas: i) la zona del Río Paraguay incluyendo las regiones superiores e inferiores y el Río Negro, y ii) la zona del Río Apa incluyendo el Río Apa y el Riacho La Paz. Para todos los grupos de datos, la zona del Río Paraguay posee una mayor riqueza de especies que

RESUMO

Hipóteses nulas concernientes a distribuições de espécies ao azar com respeito a sub-regiões e macro-hábitats dentro do Rio Paraguai são examinadas com dados provenientes de 131 espécies de macro-crustáceos e invertebrados bénticos e 186 espécies de plantas aquáticas. Os padrões são comparados com o resultado de distribuições de peixes apresentados por Chernoff et al. (2004). Os dados provenientes de invertebrados mostraram um padrão idêntico entre sub-regiões, como é evidente nas distribuições de peixes. Os resultados apoiam o reconhecimento de duas zonas: i) a zona do Rio Paraguai incluindo as regiões superiores e inferiores e o Rio Negro, e ii) a zona do Rio Apa incluindo o Rio Apa e o Riacho La Paz. Para todos os grupos de dados, a zona do Rio Paraguai possui uma maior riqueza de espécies que

la zona del Río Apa. La frontera entre las dos zonas es abrupta, lo cual es también apoyado por los datos provenientes de las plantas. Solo 11 de 186 especies de plantas fueron encontradas en ambas zonas. No existen patrones de congruencia entre macrohábitats. Datos de plantas e invertebrados contienen muchos valores que no son diferentes de las medias de similaridades al azar. Los datos provenientes de las plantas demuestran una relación entre hábitats de orilla y arena, los cuales están más sometidos a grandes corrientes que los otros hábitats. Las plantas encontradas en hábitats de aguas negras poseen poca similaridad con otros macrohábitats. Basado en estas observaciones, se concluye que hábitats significantes dentro de cada zona deben ser preservados para mantener una gran porción de la biodiversidad.

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butions and habitat utilization within watersheds by various groups of organisms (Ward, 1998; Chernoff *et al.*, 1999).

South American aquatic ecosystems are among the richest on the planet (Lundberg *et al.*, 2000). However, information about species identities, phylogenetic relationships, natural histories and ecologies is vastly incomplete. For example, many benthic macroinvertebrates are immature semi-aquatic insects of unknown species (e.g. chironomids, mayflies, caddisflies), a situation that often limits taxonomic resolution of aquatic surveys to the genus or family level (Barbosa and Callisto, 2001).

A number of important studies are elucidating aquatic and riparian community structures (Ibarra and Stewart, 1989; Agostinho and Zalewski, 1995; Cox Fernandes, 1999; Marques and Barbosa, 2001; March *et al.*, 2002; Rosales *et al.*, 2002). Importantly,

researchers are seeking to uncover the determinants of organismal distributions based upon biotic and abiotic parameters (Mérigoux *et al.*, 1999; Lake *et al.*, 2000; Pringle *et al.*, 2000; Rosales *et al.*, 2002).

From the standpoint of ecology and conservation, it is critical to understand the determinants of individual species distributions as well as correlated distributions among species or taxa. Chernoff *et al.* (2001, 2003) and Willink *et al.* (2000), and chapters therein, discussed general distributional patterns among aquatic and riparian plants (termed aquatic plants), plankton, benthos, macrocrustaceans, and fishes from four South American watersheds. For fishes, Chernoff and Willink (2000) established that fish distributions were significantly patterned, exhibiting either sharp faunal turnovers between adjacent regions or macrohabitats (e.g. Río

Orthon), or nested subset relationships (e.g. Pantanal). In contrast, the analyses of Takeda *et al.* (2000) did not reveal obvious spatial trends among benthic invertebrate communities in the middle and lower Río Negro of the Pantanal. Because of inadequate sampling designs it was not always possible to quantitatively co-analyze the distributions among biological groups in the Orthon and Pantanal watersheds (Chernoff *et al.*, 1999, 2001).

In a study of the northern Río Paraguay watershed, Chernoff *et al.* (2004) rejected null hypotheses that the fishes were distributed either randomly or homogeneously with respect to sub-regions and macrohabitats. They discovered two broad sub-regions within which there is high faunistic similarity: i) the Río Paraguay and the Río Negro, and ii) the Río Apa and the Riacho La Paz. The patterns of distribution associated with

macrohabitats are congruent with those of the sub-regional analysis. Their results further indicate that the patterns are linked to the flooding cycle. In the Río Apa and Riacho La Paz, the association among macrohabitats is due to terra firme, headwater conditions. These results were then used to construct a conservation plan to protect fishes and to evaluate the potential effects of environmental threats, such as Hidrovia (Chernoff *et al.*, 2004).

Here the generality of the patterns discovered by Chernoff *et al.* (2004) is examined by analyzing distributions of benthos, plankton, macrocrustaceans and aquatic plants. The commonality or distinctiveness of the patterns is then used to propose a conservation plan that would protect the majority of the aquatic biodiversity within the portion of the Paraguay River watershed that was surveyed.

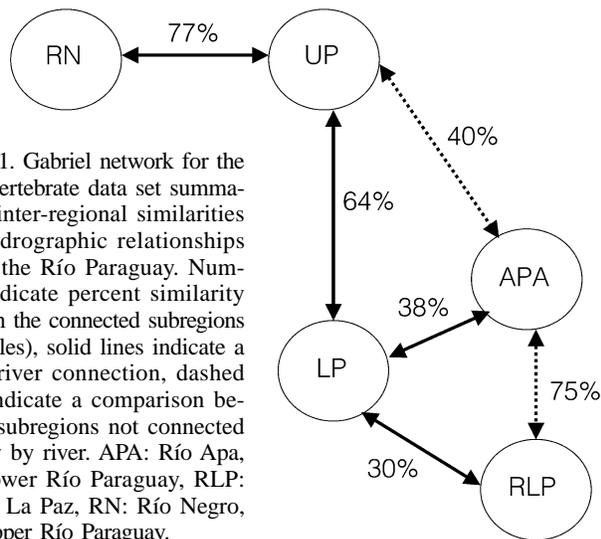


Figure 1. Gabriel network for the full invertebrate data set summarizing inter-regional similarities and hydrographic relationships within the Río Paraguay. Numbers indicate percent similarity between the connected subregions (in circles), solid lines indicate a direct river connection, dashed lines indicate a comparison between subregions not connected directly by river. APA: Río Apa, LP: Lower Río Paraguay, RLP: Riacho La Paz, RN: Río Negro, UP: Upper Río Paraguay.

Methods

Regions

The collecting expedition took place in Sept 4 to 18, 1997, when the Río Paraguay basin was surveyed between Río Negro to the north and Río Aquidabán to the south (see Figure 1 in Chernoff *et al.*, 2004). The survey included portions of Río Apa and Riacho La Paz, independent tributaries of Río Paraguay. To standardize comparisons, the area was divided into five subregions as follows: i) Río Negro; ii) Upper Río Paraguay, upstream from Cerritos Pão de Açúcar, 21°26'S, 57°55'W; iii) Lower Río Paraguay, downstream from Cerritos Pão de Açúcar to the mouth of the Río Aquidabán, 23°04'S, 57°32'W; iv) Río Apa; and v) Riacho La Paz. Table I shows the number of collection or study sites within each of these subregions for plants, invertebrates and fishes. Plants were not collected or observed in Río Negro or Riacho La Paz (discussed below).

A general description of the characteristics of the Río Paraguay, Río Negro and Río Apa is given in the corresponding section in Chernoff *et al.*, 2004.

Data sets

The data sets used for these analyses are found in appen-

dices 5,6, 8-11 of Chernoff *et al.* (2001). Data sets for plants and for invertebrates were constructed and analyzed separately.

Two invertebrate data sets were obtained by combining the macrocrustacean data of Magalhães (2001) with the plankton and benthos data from Barbosa *et al.* (2001). For subregional analyses, the full invertebrate data set was used. This contained presence-absence information for 131 species in the five subregions.

For the macrohabitat analyses it was necessary to use the reduced invertebrate data set. Presence-absence information was only available for 23 species of shrimps, crabs and molluscs for six macrohabitats with sufficient sampling to be quantified: Río Paraguay beaches, Río Apa beaches, backwaters, flooded forests, floating vegetation, and lagoons. We distinguish Río Paraguay beaches from Río Apa beaches because the former are comprised of firm to soft muds; whereas the latter are firm sand. Lagoons are seasonal ponds caused by cycles of inundation. Backwaters are habitats connected to the main river, formed during seasonal flooding and lack current. Because only ≤ 5 species were collected in the latter three macrohabitats, they were removed from the data

TABLE I
NUMBER OF SAMPLING STATIONS WITHIN EACH OF THE FIVE SUBREGIONS OF THE RÍO PARAGUAY FOR THE INVERTEBRATES, PLANTS AND FISHES DATA SETS

	Río Negro	Upper Río Paraguay	Lower Río Paraguay	Río Apa	Riacho La Paz
Invertebrates	5	15	12	7	3
Plants	0	16	14	7	0
Fishes	8	57	26	15	4

set. Furthermore, three species (*Macrobrachium borellii*, *M. brasiliense*, and *Sylviocarcinus australis*) were eliminated from the macrohabitat dataset because their assignment to macrohabitat for the Río Apa collections was ambiguous. The reduced invertebrate data set included 20 species of invertebrates and six macrohabitats.

The aquatic plant data set (Mereles, 2001) contains 186 species. The data do not allow a full sub-regional analysis but rather only a comparison of the flora of Río Paraguay (upper and lower subregions) with that of Río Apa. Presence-absence data were collected for the following macrohabitats: shores, flooded banks, semilotic, swamps, and sandy banks. The macrohabitat terminology of Mereles (2001) corresponds to that used for invertebrates and fishes as follows: flooded banks are referred to as backwaters, semilotic environments as flooded forests, and swamps as lagoons. Aquatic plants were collected along shorelines whether or not a beach (or clear area) was present. Thus, there is not complete concordance between the shoreline collections of aquatic plants with the beach collections of fishes and invertebrates. However, it is assumed that shoreline habitats for the aquatic plants function in the same way as the beach habitats for the invertebrates and fishes (e.g. the zone between deeper waters and areas exposed seasonally), and this assumption is used to estimate the congruence among the data sets.

Statistical methods

The methods of Chernoff *et al.* (2004) are used to test the null hypotheses that distributions of invertebrates and aquatic plants are randomly distributed with respect to subregions or with respect to macrohabitats. The methods compare observed similarities against similarities generated at random for communities containing the same numbers of species. Simpson's Similarity Index is used because similarity reflects the co-occurrence species not from joint absence. Our sampling methods cannot distinguish true absence from not present in sample. Samples containing different numbers of species are compared at the size of the smaller sample by rarefying the larger sample to the size of the smaller. Rarefaction is iterated 200 times and the mean similarity is used as the observed similarity.

If the null hypotheses are rejected, then branching diagrams are constructed as follows. For the subregional data, a Gabriel Network (Gabriel and Sokal, 1969) is used to represent the hydrological pattern of connectivity upon which the pattern of similarities are displayed. A dendrogram is also constructed using Camin-Sokal parsimony (CSp), which does not allow reversals. CSp only permits independent acquisitions. Thus, clustering summarizes similarities due to the shared presence of species, not the shared absence of species. PAUP* 4.0b was used to calculate CSp cluster analyses.

A Mantel's test was used to determine if the similarities among subregions or among macrohabitats for the different data sets were correlated. The similarity matrices with mean, rarefied Simpson coefficients (S'_s of Chernoff *et al.*, 2004) were converted to dissimilarity matrices by subtracting the values from 1.0 (Sneath and Sokal, 1973). The standardized Mantel coefficient, which is equal to the product-moment correlation between two dissimilarity matrices (Sokal and Rohlf, 1995) was calculated for each pair of matrices. The standardized Mantel coefficient was tested for significance using a random permutation test (Sokal and Rohlf, 1995) with 10000 iterations. The proportion of the permuted Mantel coefficients greater than the absolute value of the observed Mantel coefficient approximates the probability of obtaining the results at random (Sokal and Rohlf, 1995).

Results

Subregions

The invertebrate data base shows that the species richness of invertebrates was not distributed equally among all five subregions (Table II). That the fewest number of species was found in Riacho La Paz is partly an effect of effort, because the fewest collections were taken in that tributary (Table I). By far the richest subregion was the Upper Río Paraguay with 71 species. This region contained 54.2% of all the invertebrates collected.

The means of Simpson's Similarity Indices are highly variable among subregions (Table II), ranging from 10% to almost 80% similarity. All indices among subregions differ significantly ($P < 0.01$) from random distribution of similarities. The similarities of Río Apa or Riacho La Paz with Río Paraguay or Río Negro subregions are signifi-

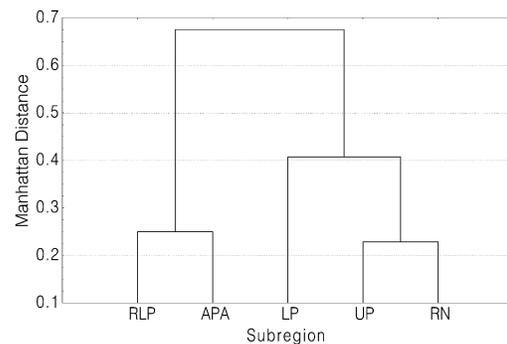


Figure 2. Camin-Sokal parsimony cluster analysis of subregions within the Río Paraguay based upon the full invertebrate dataset. APA: Río Apa, LP: Lower Río Paraguay, RLP: Riacho La Paz, RN: Río Negro, UP: Upper Río Paraguay.

cantly lower than that expected at random. This indicates zones of marked faunal turnover; species are actively partitioning the basin into distinctive regions.

The pattern of similarities plotted on the Gabriel network of subregions (Figure 1) reveals two subregional zones of high similarity. The Río Paraguay subregional zone contains the Upper and Lower subregions of the Río Paraguay and the Río Negro. The Río Apa subregional zone contains Río Apa and Riacho La Paz. The high similarities within each of these subregional zones is due to large numbers of shared taxa within the zone but not due to uniquely shared taxa. For example, 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 11 and 6 species were found exclusively in the Upper Río Paraguay and the Lower Río Paraguay or Río Negro, respectively. Thus, each of the subregional zones is internally homogeneous and represents a different faunal assemblage with respect to the other subregional zone.

Between the Río Paraguay and Río Apa subregional zones there is a strong faunal turnover (Figure 1). From the Lower Río Paraguay into Río Apa there is a turnover of

more than 35 species (62.5%).

The existence of the two groups of subregions is evident in the CSp cluster analysis (Figure 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 (Figures 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 almost identical to those from the analysis of fish distributions (see Figure 6 in Chernoff *et al.*, 2004). The similarity of

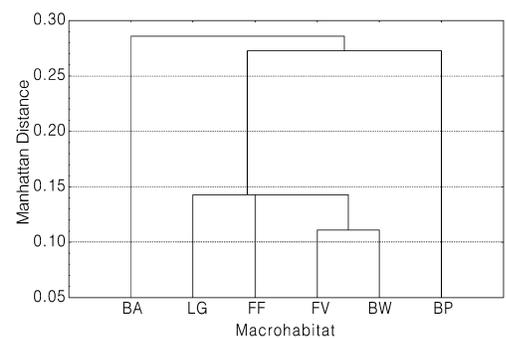


Figure 3. Camin-Sokal parsimony cluster analysis of macrohabitats within the Río Paraguay based upon the reduced invertebrate dataset. BA: beach Río Apa, BP: beach Río Paraguay, BW: backwater, FF: flooded forest, FV: floating vegetation, LG: lagoon.

pattern found in the invertebrate and fish data sets is manifest in the highly significant standardized Mantel coefficient ($r = 0.923$, $P < 0.0001$). 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 at least 60% turnover between the zones.

A total of 186 plant species was encountered from

TABLE II
MEAN SIMPSON'S INDEX OF SIMILARITY, S'_s ,
AMONG MACROCRUSTACEANS AND BENTHIC
INVERTEBRATES FOUND LIVING IN FIVE SUBREGIONS
OF THE RÍO PARAGUAY BASIN

	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

Larger samples were rarefied 200 times to the size of the smaller samples. Index values reported as percentages. All indices among subregions differ significantly ($P < 0.01$).

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.

which 147 were found in Río Paraguay and 50 in Río Negro (appendices 5 and 6 in Mereles, 2001); plants were not surveyed in Río Negro or Riacho La Paz. Of the 50 species noted in Río Apa, 39 were not found along Río Paraguay. Only the following 11 species were found in common between Río Apa and Río Paraguay: *Combrethum lanceolatum*, *Crataeva tapia*, *Genipa americana*, *Hydrocotyle ranunculoides*, *Polygonum punctatum*, *Salix humboldtiana* var. *martiana*, *Sapindus saponaria*, *Senna scabriuscula*, *Solanum* sp., *Triplaris* cfr. *guaranitica*, and *Vitex megapota*. This result would appear to be congruent with the strong faunal turnover in invertebrates and fishes between the Río Paraguay and Río Apa subregional zones.

Despite the low number of plant species shared between the two subregional zones, the observed similarity, S'_s , between them is 22.5%. This value is not significantly different from mean random similarity ($S^* = 26.5\%$, standard deviation = 5.38, $P > 0.05$). Thus, without more information on plant distributions, the low similarity of Río Apa with respect to Río Paraguay

cannot be interpreted unambiguously. The plant information does not contradict the zoological results, it only provides weak or ambiguous support.

Macrohabitats

The reduced invertebrate data set was used to analyze faunal similarities among six macrohabitats. Only 6 of the 20 species were found in a single macrohabitat, while the number of species shared between habitats varied from 4 to 8 (Table III). There is a two fold difference in S'_s from just above 44% to almost 89%. Based upon simulations, observed similarities $\leq 50\%$ could not be distinguished from random. Those $> 50\%$ are significantly different from random ($P < 0.01$).

The Camin-Sokal parsimony analysis cannot completely resolve relationships among the macrohabitats (Figure 3). The polytomy results because of the relatively large number of taxa shared among flooded forest, floating vegetation, backwater, and lagoon habitats. The close relationship between backwater and floating vegetation habitats results from

their sharing uniquely two species: a crab, *Valdivia camerani* and a gastropod mollusk, *Marisa planogyra*. The overall pattern is that there is high similarity among habitats that are seasonally inundated with the beach habitats being more dissimilar (Figure 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 III). The exception is that 8 species were found in common between the Río Paraguay beaches and floating vegetation (Table III). This may result because floating vegetation habitats can extend to the shorelines. Nonetheless, the majority of the invertebrate biodiversity is found in less exposed, lentic habitats that are seasonally inundated. The overall pattern emphasizes a Río Paraguay group that communicates vis a vis flooding cycles. The Río Apa beaches are the most distant from the Río Paraguay group.

The pattern of clustering among the macrohabitats for the reduced invertebrate data is basically congruent with the pattern found for fishes (compare Figure 3 with Figure 7 in Chernoff *et al.*, 2004): the Río Paraguay beach and 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 species with backwater habitats. The differences in details of branching patterns among the inundated habitats for invertebrates and fishes result in the non-significant standardized Mantel coefficient among the sample similarity matrices ($r = 0.27$, $P > 0.05$). Thus, the similarity between the fishes and the invertebrates is due to the association among habitats that are created during the flood cycle along Río Paraguay. Beach habitats experience the effects of currents and many species of invertebrates may prefer quieter habitats with higher accumulations of decomposing organic matter. The invertebrates may not require access to deeper waters, thereby inverting the association among habitats from that demonstrated for fishes.

Information about six macrohabitats was collected from all 186 species of plants (appendices 5 and 6 in Mereles, 2001). There was more than twice the number of species in the richest macrohabitats (Río Paraguay shores, and lagoons) as in the poorest (Table IV). Although Mereles (2001) noted that there was usually a high negative

TABLE III
NUMBER OF SPECIES SHARED* AND MEAN SIMPSON'S INDEX OF SIMILARITY, S'_s , AMONG MACROCRUSTACEANS AND BENTHIC INVERTEBRATES FOUND LIVING IN SIX MACROHABITATS WITHIN THE RÍO PARAGUAY BASIN

	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

* Upper triangle. * Coefficients significantly different from random ($P < 0.001$).

Larger samples were rarefied 200 times to the size of the smaller samples. Index values reported as percentages.

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.

TABLE IV
MEAN SIMPSON'S INDEX OF SIMILARITY, S'_s , AMONG SIX MACROHABITATS FOR 186 SPECIES OF PLANTS IN THE RÍO PARAGUAY DRAINAGE

	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

* Coefficients significantly different from random ($P < 0.001$).

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. Shore habitats include beaches.

n: number of species present, u: number of unique species, %u: percentage of unique species.

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 macrohabitat partitioning than the fishes or invertebrates. Out of 186 species, there were no species found in five or six macrohabitats. Only 5 species (*Pistia stratiotes*, *Crataeva tapia*, *C o m b r e t u m lanceolatum*, *Polygonum punctatum* and

Mikania periplocifolia) were found in four macrohabitats. Fourteen species were found to occupy three macrohabitats. Furthermore, the number of unique species (Table IV) were high ranging from 41 to 86% of the species collected in any habitat. The number of unique species were significantly higher than random expectations ($P < 0.001$).

The matrix of similarity coefficients (Table IV) shows that the coefficients range from 0 to 44.4% similarity. Only 7 of the coefficients are significantly different from random ($P < 0.001$) because the standard deviations for the randomly simulated data are rather high. Only 2 of the significant coefficients (Río Paraguay shores vs. Río Apa shores, Río Paraguay shores vs. sandy habitats) are on the positive tail of the distribution. Thus, the strong zonal effect between the Río Paraguay and Río Apa subregions is not due to the shore macrohabitats.

Five significant coefficients are on the negative tail of the distribution indicating 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 for-

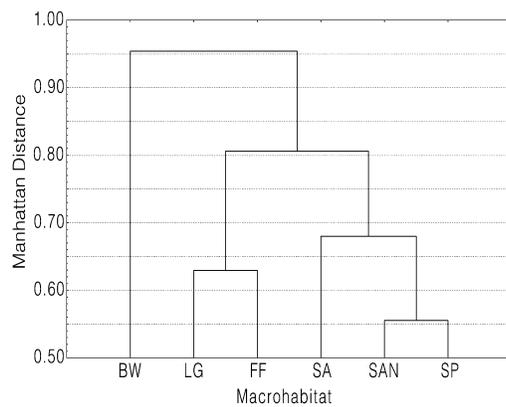


Figure 4. Camin-Sokal parsimony cluster analysis of macrohabitats within the Río Paraguay based upon the plant dataset. BW: backwater, FF: flooded forest, LG: lagoon, SA: shoreline Río Apa, SAN: sandy, SP: shoreline Río Paraguay.

ests (semilotic), lagoons (swamps) or sandy habitats. The flooded forest habitats have fewer than expected species in common with shore macrohabitats.

The CSp branching diagram (Figure 4) must be interpreted with caution due to the large number of coefficients that were not significantly different from random. The cluster joining the Río Apa shore with the cluster containing the Río Paraguay shore and sandy habitats provides a good example. Only two significant similarities generate this cluster of three macrohabitats (Table IV). The 20% similarity observed between the Río Apa shores and sandy habitats falls within random expectations. The clustering is due to the independent, significant similarities of sandy habitat or Río Apa shore habitat with the Río Paraguay shore habitat. The clustering does not, however, indicate a general flora shared by the three. The Río Paraguay shores share 11 and 12 species with the Río Apa shores and sandy habitats, respectively; only 5 are found in all three macrohabitats of which 3 species (*Senna scabriuscula*, *Salix humboldtiana* var. *martiana*, and *Solanum* sp.) were unique to the 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 but the observed similarity, 37.04, is only 1.34 standard deviations above mean random similarity. At least 25 species shared be-

tween flooded forests and the lagoons would have been necessary for the similarity to have been significant in the positive tail of the distribution. The backwater areas serving as the outlier to the remaining macrohabitats (Figure 4) is very reasonable because the backwaters had the fewest, if any, species in common with the other macrohabitats.

The plant dataset does not demonstrate a pattern of similarities that are congruent with the dynamics of the flood cycle. The flooded forest - lagoon cluster cannot be interpreted unambiguously. What is seen are two important effects. The first is a shoreline plant community that exists beyond differences between the Río Paraguay - Río Apa subregions; the plants of the sandy macrohabitats are positively associated with muddy shorelines of Río Paraguay. The second effect is that the backwater macrohabitats comprise a unique assemblage of aquatic plant species. No species were found in common between the backwaters and flooded forests, lagoons and sandy macrohabitats.

Discussion

Conservation strategies for this part of the Río Paraguay basin should ideally be based

upon as many groups of organisms as possible. Congruence 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 above the Río Negro.

Chernoff *et al.* (2004) rejected null hypotheses that the distributions of fishes were random with respect to subregions and with respect to macrohabitats. 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. Species within each zone were shared broadly and there was strong faunal turnover between zones. The subregional analyses of the full invertebrate data set displayed almost identical results to those for fishes (Figures 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 collected in a way to support a full subregional analysis. Nonetheless, the aquatic plants demonstrated a strong floral boundary between the Río Paraguay and Río Apa zones; only 11 out of 186 species were collected in both. Thus, our conservation recommendations, presented below, emphasize that the Río Paraguay and Río Apa zones are highly distinctive and require separate conservation efforts.

The macrohabitat analysis of fishes demonstrated that within the Río Paraguay zone there was a non-random association of macrohabitats due to seasonal cycles of inundation (Chernoff *et al.*, 2004). 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 macrohabitat 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.

Unlike the subregional analyses, there was less congruence among the results for macrohabitats. For the reduced invertebrate data set, the majority of the observed similarities were significantly different from random but the pattern of similarities among macrohabitats was not significantly correlated with those for fishes. 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 (Figure 3 and Figure 7 in Chernoff *et al.*, 2004). Furthermore, for both the invertebrates and for the fishes, the Río Apa beaches are most different with respect to the other macrohabitats. These results must be regarded as preliminary, however, because only 23 species of invertebrates were scored for a subset of the macrohabitats for which the fishes were collected.

The patterns of similarities among macrohabitats are difficult to interpret for the plant data. Less than half of the similarity coefficients were significantly different from random. Given this limitation, two aspects of

the plant data were not ambiguous. The first is that both sandy beaches and the Río Apa shores share a relatively large (>10) number of species with the Río Paraguay beaches. These three 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 results indicate that the distribution of species of riparian plants, aquatic invertebrates and fishes among the subregions is not random. Furthermore, the subregional congruence between the invertebrate and fish data sets was very high. Non-random spatial or subregional patterns within a watershed have been documented for lowland forests in the Río Caura, Venezuela, and the Río Negro, Brazil (Rosales *et al.*, 2002, 2003), for invertebrates (Ramírez and Pringle, 2001; García and Pereira, 2003) and for fishes (e.g., Chernoff *et al.*, 2004). The invertebrates add weak support for the flood-cycle relationship among macrohabitats exhibited by fishes (Chernoff *et al.*, 2004). Similar results were obtained for macrohabitats by fishes and zoobenthos in the Southern Pantanal, Brazil (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; Meschiatti *et al.*, 2000). The fish samples contain many species such as *Apistogramma commbrae* and *Hyphessobrycon eques* that are usually collected in association with rooted aquatic vegetation.

Conclusions and Recommendations

Conservation plans must reflect departures from random distributions of the flora and fauna with respect to geography and macrohabitats. Geographic pattern can be interpreted from the full invertebrate data set and 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 weak confirmation by the reduced invertebrate data set of the flood-cycle relationship among macrohabitats that was displayed by the fishes. Though the plants are incongruent with the fish and invertebrate pattern, the plants have a somewhat non-random distribution that is affected by different underlying causes. These conclusions lead to the following recommendations:

1. The aquatic flora and fauna comprise two major zones within the Río Paraguay basin above Concepción to the Brazilian Border: i) the Río Paraguay zone containing Río Paraguay and Río Negro, and ii) the Río Apa zone containing Río Apa and Riacho 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 macrohabitats but not with aquatic plants. As a result samples of all macrohabitats 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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