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Copeia, Vol. 1996, No. 4. (Dec. 27, 1996), pp. 875-894.

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Fish Community Patterns of Lagoons and Associated Tributaries in the Ecuadorian Amazon

KATERINA GALACATOS, DONALD J. STEWART, AND MYRIAM IBARRA

We analyzed fish distribution patterns of 10 lagoons and six of their tributaries between 200 m and 295 m altitude along two parallel headwater tributaries of the upper Amazon, within the Napo River basin of eastern Ecuador. Multivariate methods of Detrended Correspondence Analysis (DCA) and Two-Way Indicator Species Analysis (TWINSPAN) revealed community patterns that corresponded primarily to altitude and secondarily to habitat. We identified two altitudinal regions, the lowland between 200 m and 220 m and the piedmont between 235 m and 295 m. We recognized four community types associated with lowland lagoon, lowland tributary, piedmont lagoon, and piedmont tributary habitats. Tributary faunas were more closely associated with lagoon faunas within the same region, than with tributary faunas of differing regions. Lagoons and associated tributaries had high species diversity and evenness. Lowland sites showed higher species richness and had more characteristic species than piedmont sites, resulting in a pattern of species addition and species replacement along the altitudinal gradient. Decreased species richness in higher altitudes, coupled with unchanging diversity and evenness, is similar to published findings for riverine sandy beach assemblages of the Napo River basin. Faunal turnover between lowland and piedmont regions was greater for tributaries than for lagoons. Faunal turnover between tributary and lagoon habitats was greater in the lowland region than in the piedmont region. In contrast to observations for riverine sandy beach assemblages of the Napo basin and floodplain lagoons of the Orinoco River basin, separation of lagoon communities based on water type (clearwater vs blackwater) was not well supported. Comparisons among lagoon, tributary, and riverine sandy beach communities of the Napo River basin and Rio Negro (Brazil) communities revealed low similarity. Comparison of numerically dominant characiforms of the Napo, Negro, and Apure River (Venezuela) drainages revealed few shared species but approximately 50% shared genera.

Analizamos patrones de distribución de peces en 10 lagunas y 6 tributarios de estas lagunas entre 200 m y 295 m de altitud a lo largo de dos tributarios paralelos del Alto Amazonas en la cuenca del río Napo al Este del Ecuador. Métodos multivariados de "Detrended Correspondence Analysis (DCA)" y "Two-Way Indicator Species Analysis (TWINSPAN)" revelaron patrones comunitarios relacionados primariamente con altitud y secundariamente con hábitat. Identificamos dos regiones altitudinales, las tierras bajas a 200 m y 220 m y el piedemonte a 235 m y 295 m. Reconocemos cuatro tipos de comunidades asociadas con lagunas de tierras bajas, tributarios de tierras bajas, lagunas de piedemonte y tributarios de piedemonte. Las faunas de los tributarios tienen asociaciones más estrechas con las faunas de las lagunas en la misma región altitudinal que con las faunas de tributarios en diferente región. Las lagunas y sus tributarios tienen alta diversidad e igualdad específica. Los sitios en tierras bajas tienen riqueza específica más alta y tienen más especies características que los sitios en el piedemonte, resultando en un patrón de adición y remplazo de especies a lo largo de la gradiente altitudinal. Reducida riqueza específica a mayores alturas acompañada con inalterada diversidad e igualdad fue similar a los hallazgos publicados acerca de los ensamblajes de playas arenosas de la cuenca del río Napo. Remplazo faunístico entre tierras bajas y piedemonte fue mayor en los tributarios que en las lagunas. Remplazo faunístico entre los hábitates de tributarios y de lagunas fue mayor en tierras bajas que en el piedemonte. Nuestros datos no soportaron bien la separación de comunidades lacustres basadas en tipo de agua (agua clara o agua negra), en contraste con observaciones de ensamblajes de las playas arenosas riverinas y las lagunas del río Orinoco. Comparaciones entre comunidades de lagunas, tributarios y playas arenosas riverinas en las cuencas del río Napo y rio Negro (Brasil) revelaron pocas similaridades. Comparación de Characiformes que son dominantes numéricos en las cuencas del Napo, Negro y Apure (Venezuela) reveló pocas especies compartidas, pero aproximademente 50% de géneros compartidos.

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m COLOGICAL}$ studies focusing on patterns of biodiversity are a vital foundation for natural resource management and conservation in tropical regions. Until now, management and conservation in many parts of the tropics have been based on terrestrial plants and animals because baseline data on aquatic systems are scarce (Stewart et al., 1987). Studies documenting distributional patterns (e.g., Pearson, 1924; Eigenmann and Allen, 1942; Ortega and Vari, 1986) and ecological patterns (e.g., Machado-Allison, 1987; Goulding et al., 1988; Winemiller, 1989) within major river drainages contribute to future management plans by providing a basis for identifying distinct aquatic habitats and associated faunas that might constitute management units. Within the Napo basin of eastern Ecuador, over 470 species of fishes have been reported (Stewart et al., 1987), and further study has increased that number to over 500. Ecuador's Amazon region is characterized by "exceptionally high levels of endemism" within tropical South America (Prance, 1982).

This study examines the fish communities of the Ecuadorian Amazon on a regional scale spanning an area of approximately 20,000 km². To date, no published studies have compared lagoon community patterns within the Amazon basin. Preserved fishes that form the basis for this study were collected for the Field Museum of Natural History, Chicago, Illinois, during 1981 and 1983 expeditions to the eastern region, the Oriente of Ecuador (Stewart et al., 1987). This singular collection (over 120,000 specimens representing over 500 species) provides a good opportunity for describing fish distributional patterns within lagoon habitats. The objectives of this study are to identify, describe, and compare communities of fishes in lagoons and associated tributaries; characterize underlying patterns of community structure; and evaluate the higher taxonomic level of genus as an alternative to the species level for assessing diversity patterns (Schluter and Ricklefs, 1993; Williams and Gaston, 1994).

STUDY AREA

The study lagoons are located in the western Amazon River basin in the Napo Province of eastern Ecuador (Fig. 1). This region sustains a moist tropical forest with a mean annual precipitation from 3000-4000 mm and mean annual temperature greater than 23 C with a 10 C daily fluctuation (Hicks et al., 1990). Precipitation near the equator follows an annual bimodal seasonality with rainy seasons in March and Sept. Saul (1975) reported a primary rainy season of heavy precipitation between March and June, a secondary rainy period in Oct. and Nov., and a dry season between Dec. and Jan.

The steep relief of the western slope of the Andes limits the area for lagoon formation, and therefore, most lagoons occur from the western edge of the piedmont (between 235 m and 295 m in altitude) and eastward where there is very little elevational grade. Core samples from the piedmont lagoons of Lago Agrio, Añangucocha, and Limoncocha suggest that these lagoons have been isolated from river flow through for the past 800 years (Colinvaux et al., 1985). These lagoons are presently fed by small streams and have outflows that connect to the main rivers. No comparable studies of sedimentary history have been done on the lowland lagoons studied here; however, during the wet season, these lagoons flood laterally expanding out into the forest and incorporating tributaries and outflows.



Fig. 1. Study sites in Napo River basin of eastern Ecuador. Site numbers correspond to the following localities: (1) Lago Agrio; (2) Lago Agrio, Tributary I; (3) Lago Agrio, Tributary II; (4) Mandurococha; (5) Limoncocha; (6) Limoncocha, Tributary; (7) Añangucocha; (8) Grande de Cuyabeno; (9) Grande de Cuyabeno, Tributary; (10) Aucacocha I; (11) Aucacocha II; (12) Canangueno; (13) Zancudococha I; (14) Zancudococha II; (15) Lagartacocha; (16) Jatuncocha; (17) Jatuncocha, Tributary I; and (18) Jatuncocha, Tributary II.

Amazonian waters are characterized by color-whitewater, clearwater, and blackwater. Whitewater systems have a muddy color caused by drainage which carries heavy sediment loads from eroding uplands like the Andes. Clearwater systems drain Amazonian lowlands within the high terra firme forest and carry light sediment loads (Sioli, 1984). Blackwater systems are found in close proximity to clearwater systems but have a dark color associated with humic acids because, in many cases, they originate in lowland swamps and flooded forests. Blackwater is formed when the rate of carbon fixation (photosynthesis) and partial decay (oxidation) to soluble organic acids exceeds the rate of complete decay to carbon dioxide (Goulding et al., 1988).

Blackwaters have been described as systems of low productivity and low faunal diversity relative to whitewater systems (Lowe-McConnell, 1987). However, recent studies (Goulding et al., 1988; Henderson and Walker, 1990; Ibarra and Stewart, 1989) have found blackwater to contain high fish diversity. Allochthonous food sources and seasonal flooding of the forest provide food resources within blackwater habitats (Goulding et al., 1988).

MATERIALS AND METHODS

Sampling.—Sampling and habitat observations were conducted from Sept. through Nov. 1981 and from Sept. through Dec. 1983 (Stewart et al., 1987). Lagoons were sampled using a variety of gears including rotenone, seine nets, gill nets, hook and line, and fine-mesh dipnets. Tributary sites were sampled by blocking off approximately 20-80 m with bag seines and then applying rotenone; typically the downstream seine was near the stream mouth. A primary objective of the 1981 and 1983 field expeditions was to survey the ichthyofauna of the Napo River basin within as many habitats as possible. Therefore, most study sites were sampled only once, but this study includes four sites where two replicate samples were taken in close proximity to each other-the tributaries of Jatuncocha and Lago Agrio and the lagoons Aucacocha and Zancudococha.

Except for some large individuals that were preserved as dried skeletons, all specimens were preserved in formalin (10-12%) and later transferred to ethanol (75%) for permanent museum storage. Specimens were deposited in the Field Museum of Natural History, (FMNH), Chicago, Illinois, and the Museo de la Escuela Politécnica Nacional, (MEPN), Quito. Specimens were sorted to species level, but many of the fishes corresponded to new distribution records or were undescribed taxa that were designated with the generic name and a letter (e.g., Otocinclus sp. A). Additional visits to the FMNH allowed identification of several species in light of recently published generic revisions and species descriptions. Field notes and published data (Stewart et al., 1987) were reviewed to select study sites with intensive collecting efforts using multiple gears. A subset of 10 lagoons and six tributaries was selected for this analysis (Table 1; Appendix). Field numbers for these sites are given in the Appendix and correspond to locality data in Stewart et al. (1987). Sampling efforts were not standardized, with area sampled and sampling effort differing among sites. However, the use of rotenone enabled high catches within both lagoon and tributary habitats, especially for the small characiform fishes that are numerically dominant in these communities. Rotenone was used to sample all six tributaries and all lagoons except Lago Agrio, a drinking water source for the area, where seine nets and gill nets were employed. Because sampling efforts were not standardized, species richness comparisons were conducted with normalized data using the rarefaction method (Simberloff, 1972). Normalization of species richness is essential in comparative studies with inconsistent sampling (Magurran, 1988; Schluter and Ricklefs, 1993). Diversity was measured with Simpson's index which allows comparison between communities with different sample sizes (Rotenberry, 1978).

The 10 lagoons chosen for the analysis (Table 1) varied in altitude, water quality, and surrounding habitat. Lago Agrio, Grande de Cuyabeno, Aucacocha, and Canangueno are clearwater lagoons of the Aguarico River drainage. Grande de Cuyabeno, Aucacocha and Canangueno are in the Cuyabeno subsystem. Zancudococha and Lagartococha are blackwater lagoons of the lower Aguarico River drainage. Mandurococha, of the Napo River drainage, and Jatuncocha, of the lower Napo River drainage, are blackwater lagoons. Limoncocha and Añangucocha are turbid lagoons within the Napo River drainage. Six tributaries were chosen for the analysis, including the western and northern inflows of Lago Agrio and an inflow to Limoncocha. The tributary of Grande de Cuyabeno was a tributary to the Cuyabeno River, 3 km upriver from the lagoon. The two tributary sites for Jatuncocha were located 1 km and 2 km upriver from the lagoon and were tributaries of Jatuncocha River.

Analysis of community patterns.—A sites-by-species abundance matrix was analyzed using the

	Site	Site description	Shoreline	Sampling method	Altitude (m)	Sample depth (m)	Sample length (m)	Temp. (C)	Sampling month/year
Piedr	nont Region								
1.	Lago Agrio	clearwater	forest	12m seine, gill nets	295	3.0		26.5	11/83
2.	Lago Agrio, Tributary I	clearwater	swamp forest	rotenone	295	1.5	20	23.7	11/83
3.	Lago Agrio, Tributary II	clearwater	forest	frame net, 4m seine	295	1.0	100	23.7	11/83
4.	Mandurococha	blackwater	forest	rotenone	260	1.8	_	26.0	9/81
5.	Limoncocha	turbid	forest	rotenone	240	3.0	_	28-32.5	10/81
6.	Limoncocha Tributary	clearwater	forest	rotenone	240	0.5	100	24.3	10/81
7.	Añangucocha	dark	swamp forest	rotenone, frame net, hook and line	235	1.0	—	27.4	10/81
Lowl	and Region								
8.	Grande de Cuyabeno	clearwater	swamp forest	rotenone, 12m seine, trawl, hook and line	220	1.5		28.5	9/83
9.	Grande de Cuyabeno, Tributary	clearwater	swamp forest	rotenone	220	1.0	60	25.2	9/83
10.	Aucacocha I	clearwater	swamp forest	rotenone	220	1.5	_	26.0	9/83
11.	Aucacocha II	clearwater	swamp forest	12m seine	220	1.5	30	26.0	9/83
12.	Canangueno	clearwater	swamp forest	rotenone	220	1.5		-	9/83
13.	Zancudococha I	blackwater	forest	rotenone, 4m seine, gillnets	200	1.5	_	30.7	10/83
14.	Zancudococha II	blackwater	forest	rotenone, 4m seine, gillnets	200	1.5		30.7	10/83
15.	Lagartacocha	blackwater	swamp forest	rotenone	200	1.5		28.5	11/83
16.	Jatuncocha	blackwater	swamp forest	rotenone, 4m seine, hook and line	210	5.0		30.0	10/81
17.	Jatuncocha, Tributary I	blackwater	swamp forest	rotenone	210	1.5	80	27.0	10/81
18.	Jatuncocha, Tributary II	blackwater	swamp forest	rotenone	210	1.5	40	24.7	10/81

TABLE 1.	ENVIRONMENTAL AND ECOLOGICAL CHARACTERISTICS OF COLLECTION SITES IN LAGOONS OF EASTERN ECUADOR. In most cases, sampling extended
	from the shoreline or fringing vegetation to the depth indicated. Sampling length for tributaries refers to linear distance.

multivariate techniques of ordination (Detrended Correspondence Analysis, DCA) and hierarchical classification (Two-Way Indicator Species Analysis, TWINSPAN). DCA is an indirect gradient ordination method in which environmental gradients are inferred from the species composition data. DCA was developed as a modification of Correspondence Analysis (CA) and did not produce the "arch effect" of CA and Principal Components Analysis (PCA) (Hill and Gauch, 1980). The "arch effect" is a spurious second axis, a curvilinear function of the first axis, which can obscure a gradient or indicate one that does not exist (Gauch, 1982; Digby and Kempton, 1987). DCA reduces this curvilinearity; however, DCA may not show an arch even if an arch exists. Although some authors have discouraged using DCA (e.g., Wartenberg et al., 1987; van Groenewoud, 1992), the advantages of simultaneous ordering of sites and species and better ordering of long gradients than PCA make DCA a useful and widely used ordination technique (Digby and Kempton, 1987; Peet et al., 1988; Palmer, 1993). In addition, the DCA axis units and standard deviations (SD) represent species turnover along a gradient (Gauch, 1982). For example, half turnover of species occurs at approximately 1 SD, and a full turnover of species occurs in 4 SD.

Species abundances were standardized by a $\log_{10}(n + 1)$ transformation, and all species that occurred as single specimens at only one location were removed. This standardization reduced the influence of both very abundant and very rare species. The use of DCA and TWIN-SPAN facilitated comparisons among lagoons, tributaries and published results for riverine sandy beach community patterns (Ibarra and Stewart, 1989).

Classification techniques describe the structure and relationship of groups of similar entities. For example, in a sites-by-species matrix, similar sites are placed together in groups, and similar groups are placed together, progressively incorporating all groups into a branched hierarchy. TWINSPAN is based on reciprocal averaging, and its advantages include classification of both samples and species, an arranged matrix and indicator species (Gauch, 1982). Jackknifing was employed to test the consistency of the TWINSPAN results. The jackknifing procedure involved the sequential deletion of a site from TWINSPAN classifications and the calculation of percent persistence of clusters present at each node of the original dendrogram. Percent persistence of clusters from the jackknifing procedure may also be defined as degree of consistency of the community groups.

Estimation of diversity patterns.—Simpson's index of diversity was used to measure alpha diversity. Simpson's index is an arithmetic mean of proportional abundances (Hill, 1973) which sums the probability that two randomly chosen individuals are conspecific with respect to each species in the sample (Kikkawa and Anderson, 1986). Equitability was calculated as the proportional abundance of each species to the total site diversity (Hill, 1973). Because richness expressed as a simple count of the number of species at each site may be strongly influenced by the number of individuals collected, we employed the rarefaction method (Simberloff, 1972). Rarefaction normalizes species counts down to the smallest sample size of all study sites. Alpha diversity, species evenness, and richness were calculated as follows:

Simpson's Diversity =
$$N_2 = 1 / \sum_{i}^{s} (p_i^2)$$
,
Evenness = N_2 / N_1 .
 $N_1 = \exp\left(-\sum_{i}^{s} p_i \log_e p_i\right)$

where p_i is the proportional abundance of the ith species in a sample, and exp is the base of natural logarithms (Hill, 1973).

Species Richness = $E(S_n)$

$$= \mathbf{S} - \begin{bmatrix} \mathbf{N} \\ \mathbf{n} \end{bmatrix}^{-1} \sum_{i}^{s} \begin{bmatrix} \mathbf{N} - \mathbf{N}_{i} \\ \mathbf{n} \end{bmatrix},$$

where $E(S_n)$ is the expected number of species in a sample of (n) individuals selected at random from a collection containing (N) individuals, (S) species, and (N_i) individuals of the ith species (Hurlbert, 1971). Employing the above formulas provides a basis for comparison of lagoon, tributary, and riverine sandy beach communities (Ibarra and Stewart, 1989). Faunal turnover, the extent of species replacement along environmental gradients (Whittaker, 1972), was calculated using percent similarity:

Percent Similarity = 200
$$\Sigma \min\left(\frac{X_j}{Z}, \frac{Y_j}{Z}\right)$$

where Z is the total number of individuals in both sites, and X_j and Y_j are the number of individuals of species j in samples X and Y. Percent similarities were calculated for lagoon and tributary habitats separately.

Sorensen's Coefficient of Community (CC) (Magurran, 1988) was used for comparisons between lagoon, tributary, and sandy beach com-



Fig. 2. Detrended Correspondence Analysis (DCA) ordination of fish communities in the Napo River basin. The first DCA axis representing the altitudinal gradient had an Eigenvalue of 0.58 whereas the second DCA axis had an Eigenvalue of 0.32. (Numbers in the graph are site numbers, Fig. 1.)

munities (Ibarra and Stewart, 1989) of the Napo River basin as well as with communities of the Rio Negro in Brazil (Goulding et al., 1988) and Apure River in Venezuela (Taphorn, 1992).

$$CC = \frac{2(\text{no. of shared species})}{\text{no. of spp. for community 1}} + \text{no. of spp. for community 2}$$

Sorensen's similarity coefficient measures the number of shared species and is a qualitative index measuring beta diversity (Magurran, 1988). Therefore, communities that are identical will have a CC equal to 1.

RESULTS

Community patterns.—A total of 223 species within 123 genera was collected, of which 14% or 31 species were single individuals occurring at one site (Appendix). Results from the multivariate analyses and hierarchical classification demonstrate community patterns that corresponded with altitude and habitat. DCA ordination (Fig. 2) revealed two primary clusters corresponding to the piedmont region, 235– 295 m elevation, and the lowland region, 200– 220 m. Ordination also revealed two subgroups within each lowland and piedmont cluster that corresponded to lagoon and tributary habitats. Tributary samples for the lowland lagoons Grande de Cuyabeno and Jatuncocha grouped



Fig. 3. Classification of study sites into community types based on Two-Way Indicator Species Analysis (TWINSPAN). TWINSPAN dendrogram scaled by the average Euclidean distance in SD from DCA ordination. (Numbers in parentheses are site numbers, Fig. 1.)

together at extreme low values on DCA axis 1 and the piedmont tributaries for lagoons Lago Agrio and Limoncocha clustered at the opposite end of the axis. The DCA axis 2 separated the piedmont tributary and lagoon habitats but not the lowland tributary and lagoon habitats. DCA axis 3 did not produce an easily interpreted pattern.

The classification of community types by TWINSPAN (Fig. 3; Appendix) revealed patterns similar to the DCA ordination-a primary dichotomy between lowland and piedmont regions and a secondary dichotomy between habitat type, tributary, and lagoon. Four community types were present: (1) the lowland tributary group; (2) the lowland lagoon group; (3) the piedmont tributary group; and (4) the piedmont lagoon group. Within the lowland lagoon group, two subgroups were present-the clearwater lagoons of the Cuyabeno system (Aucacocha, Canangueno, and Grande de Cuyabeno) and the blackwater lagoons of the Aguarico River (Lagartococha and Zancudococha). The inversion at the piedmont lagoon node reflects a lower faunal similarity within the piedmont lagoon subgroup than within the undivided piedmont group. Inversions commonly occur because TWINSPAN scales data subgroups separately and reflect the multidimensionality of data sets (Gauch and Whittaker, 1981; Gauch, 1982).

Jackknifing analysis showed a high degree of consistency for the community groups with 100% consistency of the piedmont and lowland altitudinal groupings. Within the altitudinal



Fig. 4. Species richness and expected number of species using rarefaction method of Simberloff (1972). Expected number of species was calculated using the smallest sample size (137 individuals). Number in parenthesis is total individuals collected at each site, and site numbers correspond to those in Figure 1.

groups, lowland tributaries, piedmont tributaries, and lowland lagoons had 72% consistency of community groupings whereas the piedmont lagoons had 61%. The separation of clear- and blackwater lowland lagoon subgroups was also suggested by a 61% integrity from the jackknifing procedure.

In addition, jackknifing results allowed examination of consistency of sampling pairs for the tributaries to Jatuncocha and Lago Agrio and within lagoons Aucacocha and Zancudococha. Consistency for sampling pairs for Jatuncocha and Lago Agrio tributaries and Lagoon Zancudococha was 100%. The 75% consistency of the Lagoon Aucacocha sample pair can be explained by the first Aucacocha sample being taken at the outflow of the lagoon and not entirely within the lagoon proper as was the case with the second Aucacocha sample.

Characterization of community types.—Lowland sites had a greater species richness than piedmont sites, even with rarefaction down to the smallest sample size (Fig. 4), although species diversity and evenness were similar (Fig. 5). For example, a species-rich site such as the first Jatuncocha Tributary sample, with 20,037 individuals and 72 species, was predicted to have only 20 species at the smallest sample size (137 individuals).

Overall a total of 35 families was collected, but more families were found in the lowland sites. Lowland tributaries had 25 and lowland lagoons 28 families, whereas piedmont tribu-



Fig. 5. Simpson's diversity and evenness for tributary and lagoon study sites; site numbers correspond to those in Figure 1.

taries had 18 and piedmont lagoons 17 families. Characidae was the dominant family of all four community types based on percent abundance calculated either as percent total individuals or percent total species per community type (Table 2). Curimatids and cichlids composed the second or third most dominant families, depending on whether percent abundance was calculated from total individuals or total species. Collection of field data did not include measurement of body mass; however, it is probable that the larger bodied curimatid and cichlid fishes would dominate biomass estimates for these lagoons.

Community types were further characterized by the taxa that strongly influenced the TWIN-SPAN (Table 3; Appendix). Ubiquitous species such as Hemigrammus cf. lunatus, H. ocellifer, Gymnocorymbus thayeri, Aquidens tetramerus, and Crenicichla proteus, were excluded from Table 3 because they did not contribute to the differentiation of community types. The TWIN-SPAN rankings of species per site demonstrated shifts in the dominant species along the altitudinal gradient. In addition, some species overlapped among geographic regions and among habitats. Lowland tributaries were characterized by Gasteropelecus sternicla, Carnegiella strigata, Hemigrammus microstomus, and H. bellotti. The species Apistogramma cruzi, Amblydoras hancockii, Curimatopsis macrolepis, and Cyphocharax spiluropsis were common in both lowland tributaries and lowland lagoons. Lowland lagoons were characterized by seven species—Heros appendiculatus, Satanoperca jurupari, Chilodus punctatus, Hemigrammus cupreus, Megalamphodus sweglesi, Hyphessobrycon copelandi, and Moenkhausia dichroura.

	Char	acidae	Curin	natidae	Cicl	nlidae
Community type	% indiv.	% species	% indiv.	% species	% indiv.	% species
Lowland Tributaries	74.4	42.9	12.2	6.3	2.6	11.6
Lowland Lagoons	59.8	42.8	17.7	11.0	12.5	9.7
Piedmont Tributaries	55.4	44.8	3.6	1.7	22.4	12.1
Piedmont Lagoons	68.3	46.8	14.6	11.3	11.4	8.1

TABLE 2. PERCENT ABUNDANCE OF THE THREE MOST DOMINANT FAMILIES WITHIN COMMUNITY GROUPS DEFINED BY MULTIVARIATE ANALYSES. Percent abundances were calculated using total individuals and total number of species collected in community types.

Lowland lagoon subgroups, the clearwater Cuyabeno and the blackwater Aguarico lagoons, were not characterized by TWINSPAN high ranking species. However, Megalamphodus sweglesi and Hyphessobrycon copelandi were dominant in the Cuyabeno lagoons and the tributary to lagoon Grande de Cuyabeno. Moenkhausia dichroura was characteristic of the lowland Aguarico and Napo River lagoons but was not found in any of the Cuyabeno system lagoons or tributaries. Other differentiating species within the Cuyabeno lagoons such as Apistogramma cruzi and Characidium boehlkei, and Hemigrammus microstomus were absent or rare from Lagartococha and Zancudococha.

Compared to the large number of species that characterized lowland lagoons, few species characterized piedmont lagoons. Odontostilbe sp. A, Leporinus cf. granti, Steindachnerina guentheri, Ctenobrycon hauxwellianus, Aequidens tetramerus, and Crenicichla proteus characterized both piedmont lagoons and tributaries. Tyttocharax sp. B and Gymnotus carapo characterized piedmont tributaries.

Faunal turnover.—Species turnover was interpreted by several methods. First, the length of the first axis of the DCA ordination which represents the longest environmental gradient also estimates faunal turnover. Second, the TWIN-SPAN dendrogram was scaled according to the mean standard deviations of the first DCA axis, estimating faunal turnover within and among community types. Finally, turnover rates were directly calculated as percent similarity among sites and community types.

The 3.3 SD of first DCA axis (Fig. 2) represents approximately a 90% faunal turnover among all the study sites. The scaled TWIN-SPAN dendrogram (Fig. 3) revealed 50% faunal turnover among sites within each primary group (lowland and piedmont groupings) and an overall 79% turnover among all community types.

The lowest percent similarity occurred between lowland and piedmont lagoon sites within both Aguarico and Napo river drainages. Aguarico River lagoons Grande de Cuyabeno and Lago Agrio had a 3.5% faunal similarity and Napo River lagoons Jatuncocha and Añangucocha had 5.2% faunal similarity. Percent similarity between lowland and piedmont tributaries was also low, 0.4–1.1% for the lagoon tributaries of Lago Agrio and Grande de Cuyabeno, and percent similarity was 1.2–3.3% for the lagoon tributaries of Jatuncocha and Limoncocha.

Degree of faunal overlap (Table 3; Appendix) was further examined as the degree of faunal similarity among all four community types. Faunal similarity between lagoon and tributary habitats was greater within the piedmont region than the lowland region. The piedmont tributaries and lagoons had a 30.2% faunal similarity, whereas the lowland tributaries and lagoons had 21.8% similarity. Within habitat types, lagoons had greater faunal similarity than tributaries. Piedmont and lowland lagoons had 23.5% similarity, whereas piedmont and lowland tributaries had only 5.9% similarity.

Generic analysis.-The generic level DCA ordination and TWINSPAN dendrogram produced the same groups as did the species level analysis. However, the generic analysis revealed less separation among community groups and lower faunal turnover. In the DCA ordination, the first axis was only 2.7 SD, representing only an 83% faunal turnover compared to the 90% faunal turnover for the species level analyses. Few genera characterized community groups because most genera had widespread distributions throughout the study area; however, broad generalities of generic distributions are possible. The percent abundance of genera changes from lowland to piedmont regions in a similar pattern as did the ranked dominant species in Table 3. Lowland sites had more characteristic genera because of the addition of genera from the piedmont to lowland sites. The characid genera Hemigrammus, Hyphessobrycon, and

	Piedn	ont trib	utaries		Piedmor	nt lagoon	IS				Lowland	d lagoon	5			Lowl	and tribu	itaries	Tetal
Species	2	3	6	1	4	5	7	8	10	11	12	13	14	15	16	9	17	18	Indiv.
Gasteropelecus sternicla	*															87	7	4	142
Carnegiella strigata	*															29	61	8	426
Hemigrammus microstomus								*	*	*				*		18	77	3	3706
Hemigrammus bellotti	*								*					*		3	93	3	10,465
Apistogramma cruzi	*								4	2	5				7	25	43	11	583
Amblydoras hancockii								4	1		*	*	*	*	30		49	14	633
Moenkhausia sp. F								8		1				2	*		37	49	687
Curimatopsis macrolepis								1	1	2		*	*	1	1	13	77	1	1798
Cyphocharax spiluropsis							7	4	1	14	*	*		*	19	4	35	12	2989
Heros appendiculatus								11	*	*	18	45	12	4	3		1	1	277
Satanoperca jurupari								1	*	*	14	21	2	26	33		*	*	565
Chilodus punctatus			3					1	3	43	*	17	5	2	1	1	4	13	223
Hemigrammus cupreus								16	6	8	2	5	*	*	39		19	1	626
Megalamphodus sweglesi								19	23	3	2			5		47			509
Hyphessobrycon copelandi								53	1	22	*			1		21			894
Moenkausia dichroura						5						71	1	1	20				832
Odonstostilbe sp. A	*		*	1	73	21	2								*				263
Leporinus cf. granti		3	17	31	3	9	5				*	*					4	23	113
Steindachnerina guentheri		18	3		51	*	25		*										203
Ctenobrycon hauxwellianus	4	14		14	48	13	*	*		*				2	2		*		995
Gymnotus carapo		93	3				*				*		2						841
Tyttocharax sp. B	24	37	38																214

Table 3.	Ranked Dominant	Species from TWINS	'AN SHOWN AS PERCEN	TOTAL INDIVIDUALS FOR	R EACH SPECIES; '	* Indicates Li	ess than 1% Abundanc	CE.
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Sites: 1. Lago Agrio; 2. Lago Agrio, Tributary I; 3. Lago Agrio, Tributary II; 4. Mandurococha; 5. Limoncocha; 6. Limoncocha; 7. Janagucocha; 8. Grande de Cuyabeno; 9. Grande de Cuyabeno, Tributary; 10. Aucacocha I; 11. Aucacocha II; 12. Canangueno; 13. Zancudococha I; 14. Zancudococha II; 15. Lagartacocha; 16. Jatuncocha; 17. Jatuncocha, Tributary I; 18. Jatuncocha, Tributary II.

Moenkhausia were dominant throughout the lowland tributaries, lowland lagoons, and piedmont tributaries. The greatest species richness occurred in the characid genera *Hemigrammus* (9 spp.) and *Moenkhausia* (12 spp.) and the curimatid genus *Cyphocharax* (7 spp.; Appendix).

Comparisons with other communities.--Comparison of Napo basin sandy beach fishes with all lagoon plus tributary faunas combined revealed 70 shared species (within 55 genera) out of 431 species, corresponding to an intermediate Sorensen's Coefficient of Community, CC = 0.40. Sandy beaches shared a greater number of species with lowland tributary and lagoon communities (CC = 0.22 for both) than with piedmont tributary and lagoon communities (CC = 0.16 for both). Characins dominated sandy beaches, lagoons, and tributary communities with a total of 36 shared characid species. Most of the shared species were numerically dominant either in the lagoons or the sandy beaches. For example, the genera Knodus and Creagrutus dominated the riverine sandy beaches (Ibarra and Stewart, 1989), whereas the characins Astyanax abramis and A. asymmetricus and the loricariid Otocinclus sp. A were found primarily in lagoon tributary samples.

Other differences between the sandy beach and lagoon communities were the dominance of siluriforms within the sandy beaches, whereas curimatids and cichlids dominated within lagoons. Only six curimatid species were collected in the sandy beaches; of these, *Steindachnerina* guentheri and S. dobula had broad distributions in both white- and blackwater sandy beaches (Ibarra and Stewart, 1989; reported as S. robustula and nasa, respectively).

Comparison between the Napo basin lagoon fauna and the Rio Negro fauna listed by Goulding et al. (1988) revealed 82 shared genera and approximately 44 shared species out of 643. The Napo and Negro had a generic CC = 0.55and a specific CC = 0.14. Results were equivalent when comparing the numerically dominant characiforms: generic CC = 0.57 and specific CC = 0.15 out of 172 species. Similarity of characiforms between the Napo and the Apure River fauna listed by Taphorn (1992) was comparable to the Napo and Negro contrasts: 44 shared genera and 28 shared species out of 138 species, corresponding to a generic CC = 0.63and specific CC = 0.21.

Although some of the shared characiform species such as *Hoplias malabaricus*, *Pyrrhulina* semifasciata, Chilodus punctatus, and Iguanodectes spilurus are broadly distributed throughout the Amazon basin, many of the shared species appear to have patchy distributions. For example, Pyrrhulina semifasciata occurs predominantly in lowland tributaries of the Napo River but was also found in piedmont lagoons and lowland lagoons. Within the Rio Negro basin, Pyrrhulina semifasciata was found in flooded forest and island lake habitats. Slightly over 50% (54%) of the shared characiform genera of the Rio Negro, Apure River and Napo River drainages occur in all three regions. Many of these shared genera are widely distributed (e.g., Curimata and Potamorhina) and speciose (e.g., Astyanax, Hemigrammus, Hyphessobrycon, and Moenkhausia).

DISCUSSION

Community types.—Results from the multivariate analyses of ordination and classification suggest four community types defined by altitude (piedmont vs lowland) and habitat (lagoon vs tributary). Each of the four community types (lowland tributaries, lowland lagoons, piedmont tributaries, piedmont lagoons) was characterized by a suite of dominant species.

The four community types were further supported by the high consistency values of the jackknifing procedure applied to the TWIN-SPAN. In addition, the high consistency of the three sample pairs provided initial evidence that sampling methods were comparable between sites. In the fourth pair, the evidence was less clear. The first Aucacocha sample was an outflow sample and during the jackknifing analysis would sometimes switch to the lowland tributary cluster. Although some variability in sampling gear existed between sites, the use of rotenone yielded consistent results for paired study sites.

The TWINSPAN further separated the lowland lagoon community into three subgroups: the clearwater Cuyabeno lagoons, the blackwater lower Aguarico lagoons, and Laguna Jatuncocha. The separation of Lagoon Jatuncocha within the lowland lagoons was due to the large number of species collected and may reflect, in part, the increased sampling effort for that site. Although the Cuyabeno clearwater and Aguarico blackwater lagoon subgroups had high persistence in the jackknifing analysis due to some differentiating species, the subgroups had approximately 50% faunal similarity. That level of faunal similarity is comparable to between-site differences within our other community groupings. Overall, clearwater and blackwater lowland lagoons seem to represent a single community type in contrast to studies of sandy beach assemblages of the Napo and floodplain lagoons of the Orinoco River basin studied by Rodríquez and Lewis (1990, 1994).

Sandy beach faunal assemblages were differentiated by water type (e.g., clear-, white-, and blackwater), rock substrata, and degree of slope (Ibarra and Stewart 1989). Orinoco floodplain lagoon assemblages were differentiated by water clarity: lagoons flooded by turbid whitewater vs lagoons flooded by blackwater (Rodríguez and Lewis, 1990). Therefore, it is possible that the differences in water clarity between whitewater and blackwater lagoons of the Orinoco were more pronounced than between clearwater and blackwater lowland lagoons of the Napo. However, Rodríguez and Lewis (1990, 1994) did not include common small characids in their analysis. When the numerically dominant characids (the genera Hemigrammus, Hyphessobrycon, and Moenkhausia) were removed from the TWINSPAN, a clear division of lowland clearwater and lowland blackwater lagoons emerged. Therefore, differences between the Napo and Orinoco lagoon analyses may, in part, be due to the many characid species found in both clearwater and blackwater lagoons. Differences in sampling and analysis methods between this study and that of Rodríguez and Lewis (1990, 1994) also make comparison of results difficult.

Community patterns.-Lowland lagoons had greater species richness than piedmont lagoons, however, species diversity and evenness were similar between both habitat types. The pattern of decreased species richness at higher altitude but unchanged diversity and evenness is similar to findings for riverine sandy beach communities (Ibarra and Stewart, 1989). A number of factors may allow for higher species richness among the lowland habitats such as overall surface area, lagoon age, and flooding intensity. It is possible that the lowland lagoons experience greater flooding that increases their habitat area and diversity, whereas environmental characteristics of the piedmont habitats may be barriers for the dispersal of lowland species. Winemiller (1990) attributed higher diversity in the Venezuelan llanos vs piedmont streams to the greater seasonal variability and high primary productivity during the wet season in the llanos.

It is also important to discern the influence of local vs regional factors. For example, Jackson and Harvey (1989) found that, for lakes within the Laurentian Great Lakes region, geologic history and thermal regimes may be important in regional patterns of fish assemblages, but physical factors such as lake depth and pH may influence species composition within individual lakes. In addition, the degree to which species interactions influence community structure should be investigated. As Hinch (1992) demonstrated for central Ontario lakes, variation in predation pressure and food base may have the most influence on patterns of abundance.

Faunal turnover.—The faunal turnover between lagoons along the altitudinal gradient was of comparable magnitude to that for riverine sandy beach faunas (Ibarra and Stewart, 1989). However, the sandy beach study sites extended over approximately a 400 km gradient whereas the lagoon sites only extended over approximately a 300 km gradient. The greatest turnover for the lagoons, measured from the distance of the confluence of the Napo and Aguarico rivers, occurred between 100 km and 175 km for the Napo River lagoons and between 190 km and 250 km for the Aguarico basin lagoons. For the sandy beaches, the greatest change occurred further upriver between 250 km and 280 km in both rivers, suggesting that different environmental factors may be influencing the community structure of sandy beach and lagoon ichthyofaunas.

Overall, faunal turnover among lagoon and tributary habitats corresponded with differences in altitude. Faunal turnover among tributaries should be considered preliminary because only three piedmont and three lowland sites were analyzed. Sampling more sites along this gradient would improve resolution of where changes occur and environmental correlates of those changes.

Comparisons with other communities.—The greatest community similarity occurred between sandy beaches of the main rivers and lowland tributary communities. However, many shared species tended to be numerically dominant in only one habitat type, suggesting that, within the Napo basin, many species have habitat specialization with irregular occurrences in other habitats.

The Napo and Rio Negro faunas both were characterized by high diversity values and large faunal turnover between sites. Rio Negro fish communities were hypothesized to be random and seasonal (Goulding et al., 1988). Many species seem to be adapted to migrating between a variety of habitats often with different environmental factors (Henderson, 1990; Lowe-McConnell, 1987) and dominant taxa (e.g., Ibarra and Stewart, 1989). Goulding et al. (1988) found only 34% of 450 species captured occurring in only one habitat type, whereas 66% occurred in more than one habitat type.

Implications for conservation, management, and research.—Even though the taxonomy and systematics of neotropical fishes is still in flux, initial assessment of local, regional, and continental diversity patterns is vital for ongoing management, conservation, and research efforts. Differences between the generic- and specieslevel analyses suggest that, for the purpose of rapid, regional comparisons, the generic level may be suitable. However, the species level of analysis is required for studies documenting fish diversity, distributional patterns, and for characterizing the dominant taxa.

As with many ichthyological studies conducted in the Amazon basin, this study and the related sandy beach study (Ibarra and Stewart, 1989) describe fish community structure during the dry season, a period of restricted habitat area. As tributary and lagoon water levels recede, the mobility and dispersal of fishes may decrease whereas competition and predation increase as habitat, food, and cover sites decrease. Seasonal changes in oxygen concentrations may also influence community composition via effects on migration, habitat selection, and other behavior (Saint-Paul and Soares, 1987).

We analyzed the distributions of species within lagoon and tributary habitats on a scale of 20,000 km². Community patterns similar to those reported here should be present along the Andes from Colombia and Venezuela to Bolivia and elsewhere around the margins of the Amazon basin. We hypothesize that similar patterns will be found when other drainages are studied on a comparable scale. The community patterns revealed by our multivariate analyses also need to be examined on finer geographic and temporal scales to identify ecological processes responsible for those patterns.

Future sampling should incorporate more replication of sampling within study sites to assist in interpretation of observed between-site differences. Seasonal sampling would determine not only the mobility of fish species (Henderson and Walker, 1990) but also the variation in community structure and its correlation with water level, chemistry, and flow. Information on life-history characteristics, ecology, and distribution of each species is needed to understand how they have adapted to the dynamic flood regime and influence observed community patterns. In addition, attention should be paid to microhabitats that may serve as spawning sites and nurseries, such as the blackwater litter banks (Henderson and Walker, 1990).

Ecuador's Amazon region with its rich biodiversity and Amerindian populations (between 85,000 and 100,000) is currently experiencing increased environmental stresses from human population growth, immigration from the mountain and coastal regions, deforestation, and oil exploration (Hicks et al., 1989; Kimerling et al., 1993). Because these environmental stresses will impact both terrestrial species (e.g., Myers, 1988) and aquatic species (Henderson, 1990) that feed on the seeds, fruits, and flowers of the rainforest (Goulding, 1980; Smith 1981), the Ecuadorian Amazon deserves immediate attention (Wilson, 1992).

There are two faunal reserves and one national park within the Napo River basin; however, agricultural and industrial activities still affect the biota within these protected areas. Habitat degradation and oil spills associated with the installation of oil wells and pipelines upstream and inside the Yasuni National Park and the Cuyabeno Reserve have negatively impacted the local ecosystem (Kimerling et al., 1993). For example, within the Cuyabeno Reserve, recent changes in avifauna were documented as well as the relative extinction-proneness of insectivorous forest birds in areas of human presence (Canaday, 1991). This study has identified regional patterns of biodiversity that can be applied to management and conservation efforts. Effective management and conservation of the Napo River basin ichthyofauna will facilitate the sustainable uses of these valuable resources.

ACKNOWLEDGMENTS

Exploratory research in the Napo River basin was partially funded by grants to DS from the American Philosophical Society (Grant 8877, Penrose Fund) and National Science Foundation (INT 83-03194), with supplemental support from FMNH and MEPN. R. Barriga-Salazar assisted with all aspects of the fieldwork and sorting of the 1981 collections. We are grateful for logistic and material support from G. Orcés and L. Albuja, MEPN, the Ministerio de Agricultura y Ganadería, Corporación Estadal Petrolera Ecuatoriana, and the Comandancia Militar de la Brigada de la Selva No. 19 "Napo." We also thank R. Timm, B. Clauson, R. Nero, B. Goo, D. Rudaitis, T. Grande, and B. Schmitz for their assistance with various aspects of this research. Recent visits to Field Museum of Natural History in Chicago were supported by the FMNH, Visiting Scholar Award to DS and MI. D. Raynal, N. Ringler, MI, and especially DS provided much appreciated guidance and assistance to KG throughout her thesis work. KG received financial support in the form of teaching assistantships from SUNY-College of Environmental Science and Forestry and a summer traineeship award from the Edna Bailey Sussman Fund.

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APPENDIX. TWINSPAN ORDERED MATRIX OF SPECIES ABUNDANCES PER STUDY SITES. Numbers in parentheses are Field Museum of Natural History Site I.D. Sites: 1. Lago Agrio (DJS83-84); 2. Lago Agrio, Tributary I (DJS83-83); 3. Lago Agrio, Tributary II (DJS83-85); 4. Mandurococha (DJS81-19); 5. Limoncocha (DJS81-38); 6. Limoncocha, Tributary (DJS83-39); 7. Añangucocha (DJS81-49, -52); 8. Grande de Cuyabeno (DJS83-21); 9. Grande de Cuyabeno, Tributary (DJS83-25, -26); 10. Aucacocha I (DJS83-27); 11. Aucacocha II (DJS83-28); 12. Canangueno (DJS83-24); 13. Zancudococha I (DJS83-59); 14. Zancudococha II (DJS83-60); 15. Lagartacocha (DJS83-62, -63); 16. Jatuncocha (DJS81-59); 17. Jatuncocha, Tributary I (DJS81-58); 18. Jatuncocha, Tributary II (DJS81-60).

									Study	sites:								
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Myleus pacu		1						1	5									
Rivulus cf. urophthalmus			1		_				10									
Cyphocharax gouldingi							34			1	3	1		—			50	39
Moralesia tectifera			1			9		2		3		1	1				21	33
Phenacogaster pectinatus					1		9		3	8	40					43		144
Hemigrammus cf. lunatus		1		327				215	18	10	201	1	22	2	55	22	104	407
Erythrinus erythrinus		_		1				1	6	1		_					23	10
Pyrrhulina semifasciata			5					10	396	6				4	1	5	95	11
Crenicichla anthurus				1					26								81	21
Gasteropelecus sternicla						1			124								11	6
Carnegiella strigata		1							127			_					260	38
Symbranchus marmoratus									2									
Bario steindachneri		_							2									
Rhamphichthys sp.									3									
Parauchenipterus cf. galeatus									3							_		
Cyphocharax pantostictos									4									
Ancistrus sp. A																_	3	2
Corydoras leopardus																	6	
Osteoglossum bicirrhosum						_	—										7	
Hoplerythrinus unitaeniatus																_	7	
Gnathocharax steindachneri							_	_					_				10	
Boulengerella maculata						_		1									10	
Potamorrhaphis guianensis	_								3	1			_				1	7
Rhamdia sp. A	_																12	1
Corydoras trilineatus																	15	—
Gymnotus coatesi									2		_		_				13	6
Corydoras arcuatus																	30	—
Nannostomus marginatus									5								25	4

Appendix. Continued.

									Study	sites:								
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Astyanax anteroides		_	_	_	_		_	_	_	_		—	—	_	_	_	29	8
cf. Megalamphodus	_		_	—	—	—	_	—	47	—		_	_	—		_	_	_
Moenkhausia chrysargyrea	—	_	_	_	_	_	_	_	_	_	_		_	_	_	_	47	8
Cyphocharax laticlavius	—		_	_	_	_	_	_	_	_	_	_	_	_	_	_	53	6
Gladioglanis conquistador	—		_		_	_	_	—	21	8	_	_	_	_	_		22	26
Thayeria obliqua	_	_	—	_		_	_	—	_	_		_	_	_	_	1	1	78
Astyanax asymmetricus	_	—	_				_	_	15		_	_	_		—	—	33	60
Otocinclus sp. A	—	—	_	_		_	—	_	60	_		_	1	_	_	—		48
Characidium sp. C	_	—	_	_	—	_	—	—	95	_	—	_	—	_	_	_	_	14
Bryconella pallidifrons	_		_	_			_	—	105	—	—	_	—	_	_	_	85	15
characin cf. Knodus	_	_	_	_	_	_	_			—		_	_	_	_	_	252	_
Megalamphodus sp.	_		_	_	_	_	_	_	_	—	_	—	_	_	_	_		353
Tridentopsis sp.	_	_	_	_	—	_	_	—		—	_	—	_	_	_	_	346	567
Hemigrammus microstomus				_		_	_	3	675	3	2	—	_	_	1	_	3103	141
Chaetobranchus flavescens	_	—		—	_	_	_	_	_	—	—	—	_	_	_	1	3	_
Hypopygus lepturus	_	_	_	_	_	_	_	—	1	2	—		_	—	_	1	_	3
Crenicara punctulatum		_	_	_		_	_	—		1	4	—	_	1	_	_	46	5
Hemigrammus unilineatus	_	—		—	_	_	_	—	2	_	_	_	3	—	_	26	220	11
Hemigrammus bellotti	_	1	_	_		_	_	1	345	11	3	—		—	4	_	9788	312
Acanthodoras cataphractus	_	—	_	_		_	_	_	_	1	_	_	_	_	_	—	1	—
Elachocharax pulcher	_		_	_	—	_	—	_	1	1	_	—	_		—	_	—	—
Pseudanos trimaculatus	—	—	_	_	_	_	—	_	_	1	_	—	_	_	1	1	1	5
Laetacara flavilabris	—	—	—	_	—	—	—	_	4	_	—	—	_	6	_	_	—	
Curimatella alburna	_		_		—	_	—	1	_	—	1	—	_	_	8	1	5	1
characin cf. Moenkhausia sp.	—	_	—	_	—	_	—	5	111	1	_	—	_	_	3	_	—	—
Tetragonopterus chalceus	_	—	_		—	_	_	4	_	—	_	—	_	_	_	39	65	17
Apistogramma cruzi	—	1	_		—	—	—	_	151	27	25	32	—	_	—	41	252	64
Amblydoras hancockii	_	_	_	_	_	_	_	26		7		2	3	1	1	190	314	89
Moenkhausia sp. F, lepidura	_	_	_	_	_		_	56	_	_	9	—	_	—	20	4	256	342
Curimatopsis macrolepis	_	—	_	_	_	_	_	22	237	28	47	—	2	14	18	22	1387	21
Ochmacanthus sp. A	_	_	_	_	_	_	_	_	_	_	4	—	_	_	_	20	2	2
Crenicichla johanna	_	_	_	—	_	_	—	—		_	—	—	—	_	—	34	6	1

Appendix. Continued.

									Study s	ites:							<u></u>	
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Heterocharax macrolepis		1		_	_	_	_	6	_	1	_	1	_	_	_	30	26	31
Cyphocharax spiluropsis	_	—					228	144	126	34	424	24	3	_	18	578	1045	365
Charax gibbosus	_		_	_	_	1	_	_	_	_	19	5	_	1	_	25	5	—
Hydrolycus pectoralis	_	_	_	_	_		_	_	_	_	_	_	_		_	3	_	1
Moenkhausia intermedia			_	_	_	_	_	_	_	_	1	_	_	_	_	2		2
Pimelodella sp. F	_			_	_	_	_	5	_	_		1	_	_	_	6		1
Leporinus agassizi	_	_	_	_	_	_	_	_		_	_	_	_	_	2	18		6
Cyphocharax notatus		_	_	_	_	_	_	_	_	_	_	_	_	_	18	162	2	1
Acestrorhynchus heterolepis	_		_	_	_	_	_	_	_	_	_	_	_	_	_	2		_
Triportheus angulatus	_	_	_	_	_	_	_	_	_		_	_	_	_	_	2		_
Anodus elongatus	_		_	_		_	_	_	_	_	_	_	_	_	_	2	_	_
Leporinus cf. muyscorum	_	_	_			_	_	_		_	_	_		_	2	1		_
Psectrogaster essequibensis	_	—	_	_				_	_	_		_		_	_	4	—	—
Moenkhausia sp. A			—	—	_	—	—	—		_	—	_	_	_	2	2		_
Pristobrycon sp.	_	—	—	_		_	_	_		_	_	_	_		_	4		_
Potamotrygon sp.	_	—	—	_		_	_	_	_	_	_	_		_	_	5	_	—
Roeboides cf. thurni	_		—		_	—	_	—	—	_	—	_	_	_	—	6	—	—
Anodus melanopogon	_		_			—	_	_	—	_	—	—	—	_	_	6		_
Leporinus niceforoi	_	—	_		_		—	_		_	_	_		_	_	7	—	—
Steindachnerina dobula	_		_		_		_	—	_	_	—	_			_	10	—	—
Aphyocharax sp. A	_		_			_	_	_	_	—	6		_		_	8		_
Curimata cisandina	_	_	_		_	_	_	_	_	—		_		_	_	15		_
Lycengraulis batesii	_		_		_	—	—	—	_	—	—	_	—		_	16	—	—
Triportheus elongatus	_	_	_		_	_	_	_		_		—	_	_	_	16		_
Triportheus albus	_	—	_		_	_	_	_	_	—		_		—	_	18	_	_
Potamorhina latior	_	_	_		_	_	_	_	_	—	—	—			_	23		_
Acestrorhynchus sp.	_	_	_	_	—	_	_	_	_	—	2	1	3	1	2	21		_
Arapaima gigas	_	—	_			_	_	_	_	_	_	_	_	—	2	_	_	_
Callichthys callichthys	_	_	_	_	_	_	_	2	_	—		—			_	_		_
Myleus cf. rubripinnis	_	_	_	—	_	_	_	2	_	_	_	_	_		_	_	_	_
Moenkhausia sp. E	_	_	_	_	_	_	_	_	_	—	_	—		—	2	_	_	_
Corydoras leucomelas	—	—	—		—	—	—	—	—	—	2	—	—	—	—	—	—	—

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Appendix. Continued.

									Study sit	es:								
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Steatogenys elegans					_					—	5	_				—		_
Eigenmannia cf. limbatus	_			_	_	_	_	3	_	1	_	1	_	—	—	1		_
Eigenmannia cf. virescens	_			_	_	_	—	3	_	1	2	_	_	—	—	1		_
Acestrorhynchus falcirostris	_		_	_	_	_	_	3	_	_	_	_	1	1	1	1		_
Scopaeocharax rhinodus	_	_	_	_	_	_	_		_	—	_	_	_	_	14		—	
Metynnis sp. B	_		_	_	—	_	_	1		1	16	—	_	_		_	—	_
Moenkhausia lepidura			_		·	_	_	1		—		_	14	1	2	_	_	_
Bryconops sp. C	_		_	—	_	_	—		_	_	_	_		_	18		_	_
Tatia cf. intermedia	_	_	_	_	—	_	_	1	_	_		_	24	_	2	_	_	
Mesonauta insignia	_			_	_	_	_	4		1	_	7	7	8	4	_	_	—
Hypselecara temporalis	_	_	_	_	_	_	_	3	_	1		62	6	8	1	_	2	—
Hemigrammus cylindricus	_	_	_	_	—	—	_	45	_	_		_	61	1	6		_	_
Curimata vittata	_	_	_	_	_	_	_	156	_	1		_	_	_		17		—
Heros appendiculatus	_	_	_	_	_	_	_	33	_	2	2	51	127	34	13	9	3	3
Satanoperca jurupari	_	_	_	_	_	_	_	6	_	2	1	83	120	13	148	190	1	1
Cichla monoculus	_		_	_	—	_	_	1	_		_	_	6	3	1	_	4	
Bryconops sp. A	_	_	_	_	_	_	_	35	_	_	26	_	21	—	—	23		11
Chilodus punctatus	_	_	_	_	_	_	_	2	4	8	98	40	12	6	4	7	11	31
Hyphessobrycon cf. serpae	_	_	_		—	_	_	19	59	26	143	6	_	_	_	—	—	2
Hemigrammus cupreus	_	_	_	_	_	_	_	105	_	38	54	18	31	1	5	245	121	8
Axelrodia stigmatias	_	_	_	_		_	—	_	1	2	2	1	_	2	_	—	_	—
Hemiodus unimaculatus	1	_	_	_	—	_	_	5	_	—	_	_	_	—	4	8	—	
Apistogramma sp. A	_	_	_	_	2	22	_	5	_	_	_	_	48	21	19	—		
Moenkhausia dichroura	—		_	_	43	—	_	_	—	—	—	—	594	10	12	173		
Potamotrygon motoro	_	_	_	_	1	—	_	_	_	—	1	—	_	—	—	3	—	
Serrasalmus sp.	2	_	_	_	_	_	_	3	_	—	2	_	—	1	—	—	_	
Serrasalmus cf. rhombeus	—		_	—	8	—	4	8	1	1	9	1	12	—		5	_	
Astronotus ocellatus	—	_	_	—	1	_	_	1	_	_	_	—	—	—	1	2	1	
Characidium boehlkei	_		_	_	4	3	1	2	22	3	12	3	—	—	—	_	_	11
Hemigrammus ocellifer	_	_	_	—	35	—	33	46	553	7	2	—	2	29	16	24	721	36
Hoplias malabaricus	19	_	4	—	33	23	4	111	13	—	8	7	16	23	13	22	20	3
Limatulichthys punctatus	_	2	_	—	—	—	—		_	—		—	1	_	_	_	—	_

CONTINUED.	
APPENDIX.	

									Study	sites:									
Species	-	5	3	4	5	9	7	80	6	10	=	12	13	İ	-	5	16	17	18
Hypopomus cf. beebei		1								1				1	64	1			
Pygocentrus nattereri			I	I	ŝ		60	2	1				1	14			4	I	
Gymnocorymbus thayeri	5	0		210	73		24	40	1	1		31	æ	41	30	380	'		I
Ancistrus sp.	I	I			I	61	I		1	1		Ì	I	I	I		1	I	
Hypostomus sp.	Ι	I					1		1	1		1	I	I	I	I	64		I
Plagioscion squamosissimus	4	Ι			1		I	1	1	1		1	I	I	I	I	9		I
Psectrogaster amazonica	I			æ	I				1	1			I	I	I	I	22	l	ł
Steindachnerina bimaculata	Ι	I		I	25		9		I	1			I	I	I	I	35	l	ł
Hemigrammus sp.	Ι	I			20		166		. 1	1		1	I	I	I	I	593	70	0
Acestrorhynchus falcatus	Ι	I			I	1			1	1		1	I	١	I	I	I	1	I
Trichomycterus sp. B	1	1			I		I			ן א			1	١	I	I	I	I	
Moenkhausia comma		I	I	I		I	I			4	•		1	I		I	ł	l	ł
characin sp.	Ι	I			16		4			ן אס			I	I	I	l			11
Hypopomus sp. C	Ι	I			5		œ			2	_	1	I	I	I	I	I	2	1
Carnegiella schereri	Ι	I	I	I	5				01	0	-		Ι	I	I	ł	ł		ł
Moenkhausia oligolepis	Ι	I	16	3	æ	39	I		Ι	3 0			I	I	I	Ι	ŋ	160	44
Hyphessobrycon sp.	Ι	I	I	I	4	5	159		I	1			1	I	I	Ι	454	925	I
Knodus gamma	ŝ	I		I	Ι		I		I				Ι	I	I	I	I	I	I
Copeina guttata				1	I	0	-	I		-			T	I	Ι			I	
Curimata aspera		I		10	I		I		I	1	ļ		I	I	I		I	I	
Characidium sp. A	Ι	Ι		14	I		I		I	1			I	I	I	I	I	I	I
Liposarcus pardalis	I				6		12		I				T	I	I	I	I	I	
Roeboides cf. affinis	ļ	I	l	16	Ι		I		I	1			1	I	I	I		I	
Roeboides myersi	I	I			20		I		I			1	T	I	Ι	I	I	I	I
Holoshestes sp.	Ι	١	I	22	I				I	1			Ι	I	I	I		l	I
Potamorhina altamazonica	I	I		26	-				I			1	I	I	I		7	I	I
Roeboides sp.	80	I	l	I	28				I			Ì	ł	I	I	I	I		
Pyrrhulina sp. A	I	I		5	35		16		I			· I	T	Ι	I		I		I
Astyanax cf. integer	I	-	0	78	I				I			1	Т	I	I		I	I	I
Odontostilbe sp. A	5 C	1		192	56	2	9	1	I	1		1	T	I		I	1		
Hypoclinemus mentalis	I	I	Ι		I	1	1		I	1		1	I	I	Ι	Ι		I	I
Rhambia sp. B		Ι	l		-	4		1	I			' I	I	I	Ι	Ι	Ι	I	ł

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Appendix. Continued.

									Study si	tes:								
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Pimelodella sp. A			2			2	6			_								
Sternopygus macrurus	_	_	—	—	3	4	—	—	2	_		—	1	I —	. <u> </u>	_	_	
Astyanax fasciatus	7	—	_		—	4			_	_			_			_		_
Astyanax cf. fasciatus		—	2	_	9	3		_	_	_		_	_		·	_		_
Brachychalcinus nummus	_	—	46	_	—	3	20	_	_	_	_	_			·	_		_
Leporinus cf. granti	35	—	4	4	10	19	6	_			_	1	1	ı —	·	_	5	26
Steindachnerina guentheri	_	—	38	105	1	6	52	_	_	—	1	_		- —	· <u> </u>	_		—
Parodon pongoense	_	_	2	_	_	_	_	_	_	—	_	_			· <u> </u>	_		_
Astyanax sp.	_	—	_	_		2	_	_	_		_	_	_		·	_		_
Hypostominae cf. Ancistrus	_	3	1	_	—	_	_	_	_	—	_		_			_		_
Knodus sp. B		—	12	_	_	_	_	_	_	—	_	_			_	_	_	_
Hypostomus sp. A	1	16	2	_	_	_	_	_	1	—	_	_		- —	1	_	_	—
Gymnotus carapo	—	—	106	_	_	3	1	_	_	—	_	1		- 2	_	—	—	—
Astyanax abramis	—			—		121	1	_	_	_		—	_	- —	_	—		—
Tyttocharax sp. B	—	52	80	_	—	82	—	—	_	—		—		- —	_	—	_	—
Electrophorus electricus		1	1	_	_	_	_	_	_	_	—	—		- 1	—	—		—
Aequidens tetramerus	55	4	3	2	85	134	2	12	_	—	1	2	1	. 9	23	2	41	
Crenicichla proteus	116	1	86	8	68	13	62	5	_	1	1	8	5	57	22	6	9	6

The following are rare species, single individuals collected at only one site, included in all analyses except multivariate analyses of DCA ordination and TWINSPAN classification. Numbers in parentheses are study site locations. Laemolyta garmani (16); Prochilodus nigricans (7); Steindachnerina sp. C (13); Steindachnerina sp. D (13); Cynodon gibbus, (16); Acestrocephalus boehlkei (2); Astyanax sp. A (17); Brycon melanopterus (8); characin sp. (17); Creagrutus cf. beni (9); Creagrutus sp. C (2); Knodus beta motatanensis (2); Metynnis sp. A. (16); Moenkhausia megalops (17); Moenkhausia sp. (4); Mylossoma duriventris (16); Serrasalmus elongatus (13); Serrasalmus sp. (16); Tetragonopterus argenteus (15); Centromochlus heckelii (16); Pimelodella sp. G (2); Pimelodus cf. rigidus (16); Corydoras ambiacus (17); Astroblepus sp. (2); Ancistrus sp. B (15); Hypostomus sp. C (13); Hypopomus sp. A (16); Rivulus simoncochae (6); Rivulus sp. (17); Crenicichla sedentaria (6); Semaprochilodus insignis (16).

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