TROPHIC ECOLOGY OF FRUGIVOROUS FISHES IN FLOODPLAIN FORESTS OF THE COLOMBIAN AMAZON

A Dissertation

by

SANDRA BIBIANA CORREA VALENCIA

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

August 2012

Major Subject: Wildlife and Fisheries Sciences

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Approved by:

Chair of Committee,	Kirk Winemiller
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ABSTRACT

Trophic Ecology of Frugivorous Fishes in Floodplain Forests of the Colombian Amazon. (August 2012)

Sandra Bibiana Correa Valencia, B.S., Universidad del Valle; M.S., University of Florida

Chair of Advisory Committee: Dr. Kirk Winemiller

Diverse fish species consume fruits and seeds in the Neotropics, in particular in the lowland reaches of large rivers, such as the Amazon, Orinoco, and Paraná in South America. Floodplains of the Amazon River and its lowland tributaries are characterized by marked hydrological seasonality and diverse assemblages of frugivorous fishes, including closely related and morphologically similar species of several characiform families. Here, I investigated whether or not these fishes are capable of detecting fluctuations in food availability and if they are, how they adjust their feeding strategies. I tested predictions of optimal foraging, limiting similarity and resource partitioning theories with regard to expansion or compression of niche breadth and reduction in trophic niche overlap among species in relation with fluctuations in the availability of alternative food resources. I monitored fruiting phenology patterns to assess food availability and conducted intensive fishing during the high-, falling-, and low-water seasons in an oligotrophic river and an adjacent oxbow lake in the Colombian Amazon. I combined analysis of stomach contents and stable isotope ratios to evaluate dietary patterns, niche breadth, and niche overlap.

Diets of six characiform fish species (*Brycon falcatus, B. melanopterus, Myloplus asterias, M. rubripinnis,* and *M. torquatus*) changed in a manner that indicated responses to fluctuations in food availability. Feeding strategies during the peak of the flood pulse were consistent with predictions of optimal foraging theory. During times of high fruit abundance, fish preferentially consumed items to which their phenotype is best adapted, maximizing net energy gain and enhancing fitness. As the flood pulse subsided and the availability of forest food resources was reduced in aquatic habitats, there was not a consistent pattern of diet breadth expansion or compression, even though diet shifts occurred, suggesting interspecific differences in foraging efficiencies. Analyses of diets and isotopic ratios revealed a general pattern of increased dietary segregation as the water level receded. Although there never was complete niche segregation among these fishes, these dietary changes effectively reduced interspecific niche overlap. Implications of these results and contribution of allochthonous food resources to diversity maintenance of floodplain fishes are discussed.

DEDICATION

To my parents Rosalba Valencia and Alvaro Correa, and to my sister Dr. Maritza Correa Valencia, whose unconditional support has helped me achieve my dreams, even though they cannot explain why I choose to chase after fish in the depths of the Amazon forest for a career. To Dr. Michael Goulding, whose dedication to the conservation of Amazon flooded forests has been an inspiration for my career choice.

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I am extremely thankful to volunteer field assistants who helped me sample fishes and plants, and collect data in the Colombian Amazon: Jed Macdonald, Gaby Tamez, Jhon Patarroyo, Lyda Cruz, Ivan Lopez, and Laura Bravo. I would also like to thank the indigenous field assistants: Diomedes Silva, Jeriel Ahue, Ciro, Edgar Tanimuka, Benjamin Mejia, Luis Tanimuka, Alipio Carevilla Tanimuka, Fabio Yucuna, and Angel Yucuna for their help. Without their hard work and commitment, I would not have been able to accomplish all of what is presented in this manuscript.

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CHAPTER I

INTRODUCTION:

AQUATIC FRUGIVORES, THE CONSUMPTION OF FRUITS BY NEOTROPICAL FISHES*

Neotropical frugivorous fishes are distributed from Central America to Southern Brazil (Appendix 1). The Amazon holds the largest diversity of freshwater fishes in the world (Reis et al. 2003), and thus it is no coincidence that the vast majority of records of fruit-eating fishes come from this river basin alone. To date, and based on published stomach or intestine contents analyses, 147–150 fish species belonging to 76 genera have been reported to consume fruits and seeds in the Neotropics (Appendix 1). These figures only account for studies where analysis of stomach contents has been performed and that have been published in peer-reviewed journals and books; thus, it is likely that many more species have been documented in unpublished theses and technical reports. Lack of taxonomic resolution increases the difficulty of getting accurate estimates of the number of fruit-eating fish species. Goulding (1980), for instance, argued that at least 200 fish species in the Amazon Basin feed on seasonally available fruits and seeds. Neotropical fruit-eating fishes range from small- and medium-sized characids and cichlids that mainly feed on aquatic and terrestrial invertebrates and occasionally consume fruits and seeds from riparian

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This dissertation follows the style of Ecology.

*Excerpts of this introduction are reprinted with permission from Horn, M. H., S. B. Correa, P. Parolin, B. J. A. Pollux, J. T. Anderson, C. Lucas, P. Widmann, A. Tiju, M. Galetti, and M. Goulding. 2011. Seed dispersal by fishes in tropical and temperate fresh waters: the growing evidence. Acta Oecologia 37: 561–577, Copyright 2011 by M. H. Horn.

vegetation and wetlands, to large omnivorous catfishes (Doradidae, Pimelodidae) and herbivorous serrasalmids that consume considerable amounts of fruit.

Fishes inhabiting forest streams and small- to medium-sized rivers that run through forested areas gain access to fruits that fall in the water from the riparian vegetation and potentially contribute to upstream seed dispersal. This is the case for the 10 species of fruit-eating fishes that are known from Central America (Appendix 1). A noteworthy case is that of herbivorous *Brycon guatemalensis* in the Rio Viejo, Costa Rica, which consumes large amounts of *Ficus insipida* and presumably contributes to upstream dispersal as the fish enters riparian zones during frequent flooding periods, depositing the seeds in suitable areas for establishment (Horn 1997, Banack et al. 2002).

Another source of fruits and seeds for fishes comes from the large diversity of trees, shrubs and vines distributed in seasonally flooded savannas and forests of the Orinoco, Amazon and Paraguay River basins. Reports of fruit-eating fishes from the Orinoco Basin are surprisingly limited (i.e., five species, Appendix 1) despite the vast extent of seasonally flooded savannas and riparian forests. Herbivorous *Piaractus brachypomus*, for instance, feeds on fruits of nearly 40 species of plants in the Orinoco (Canestri 1970, Knab-Vispo et al. 2003), and its efficiency as a seed disperser has been proven in the Amazon Basin, where the species is also distributed (Anderson et al. 2009). Thus, the species likely plays an important role in seed dispersal in the Orinoco region as well. Five fish species from rivers in French Guiana have been reported to consume fruits and seeds (Appendix 1). Seeds of *Passiflora laurifolia* were found intact in the stomach of frugivorous *Myleus rhomboidalis* from the Approuague and Sinnamary Rivers, but the viability of those seeds was not assessed (Boujard et al. 1990). Seven species have been reported to feed on fruits and seeds in rivers and wetlands of the Paraná-Paraguay basin (Appendix 1). In the Pantanal, a seasonally flooded wetland of the Paraguay River that largely resembles the wetlands of the Orinoco Basin, adult individuals of *Piaractus mesopotamicus* eat large amounts of fruits of the palm *Bactris glaucescens* and are likely to be the most important dispersers of these non-buoyant seeds (Galetti et al. 2008). Omnivorous *Brycon hilarii* consume considerable amounts of fruit and potentially disperse seeds of eight species with small or hard seeds in the riparian forest of Rio Formoso in the Pantanal region. Omnivorous *Pterodoras granulosus* consume fruits in forested areas of the Paraná River, potentially dispersing the seeds of multiple species, especially those with protected seeds, such as species in the genera *Ficus*, *Cecropia* and *Polygonum* (de Souza-Stevaux et al. 1994). None of the studies in the Paraná-Paraguay Basin, however, evaluated the effect of gut passage on seed germination; thus viability of seed dispersal remains to be demonstrated.

In the Amazon River basin, consumption of fruits and seeds is widespread throughout the basin and has been reported for 93 species (Appendix 1). Significant amounts of fruits and seeds that are seasonally available in Amazonian floodplains, are consistently consumed by large herbivorous serrasalmids such as *Colossoma macropomum*, *P. brachypomus* and several species of the genera *Mylossoma*, *Myleus*, *Myloplus*, *Metynnis, Pristobrycon* and *Serrasalmus*; by omnivorous characid species of the genera *Triportheus*, *Brycon*, and *Astyanax;* by anostomids of the genera *Leporinus;* and by catfishes of the families Auchenipteridae, Doradidae and Pimelodidae (Appendix 1). These fishes are likely to be the most relevant for ichthyochory (seed dispersal by fish) in the region.

Several serrasalmid species exhibit morphological adaptations for frugivory, and numerous catfish species attain large body sizes, which, in addition to their benthic habits, probably enhance their potential to be important dispersers of plants with large non-buoyant seeds (Correa et al. 2007). Many of these fish species feed on a large variety of fruits and seeds reflecting the large plant diversity of Amazonian flooded forests. Numerous plant species in these wetlands have their fruiting phenology tightly synchronized with the annual flood pulse, releasing large amounts of fruits and seeds that fall into the water and become available to fish (Kubitzki and Ziburski 1994, Parolin et al. 2004). Waldhoff and Maia (2000), for instance, presented a list of 79 species of fruits that are consumed by Amazonian fishes and da Silva et al. (2003) compiled a list of 133 species of fruits and seeds that are consumed by *C. macropomum*. However, their effectiveness as seed dispersers (e.g., effects of passage through the fish digestive system on seed viability and germination rates) has been evaluated for only a handful of species (Kubitzki and Ziburski 1994, Mannheimer et al. 2003, Lopes de Souza 2005, Maia et al. 2007, Anderson et al. 2009).

The large number of fish species that consume fruits and seeds in the Neotropics, in particular in South American drainages, is not surprising given the extensive lowland watersheds that have existed in the western portion of today's Amazon and upper Orinoco River basins since the beginning of the Cenozoic period (~65.5 Ma) (Lundberg et al. 1998, Hoorn et al. 2010). Moreover, the marine incursions in these basins ended in the late Miocene (10.9 Ma), and since then the landscape has been dominated by these large freshwater drainages (Lundberg et al. 1998). Fossil records of wood and pollen, as well as casts of large seeds and fruits, of important present-day forest families suggest the existence of a lowland closed-canopy rain forests by the Late Cretaceous (~70–65.5 Ma) (Morley 2000). These rainforests appear to have persisted through the global cooling events of the terminal Eocene and, unlike in tropical Africa, no conclusive evidence exists for Pleistocene reductions of tropical South American forests into refuges (Nelson et al. 1990). Instead, the moist conditions that continued through the Quaternary facilitated the maintenance of highly diverse rainforests (Morley 2000). On the other hand, fossil evidence of serrasalmid fishes has been recorded for the late Cretaceous and the entire Cenozoic, suggesting an early origin of the family (i.e., by the Maastrichian, ~70 Ma), with generic-level diversification by 13.5 Ma in the middle Miocene (Lundberg et al. 1986, Lundberg 1998). More recently, fossil teeth of herbivorous *Mylossoma* spp. and *Colossoma macropomum* (Serrasalmidae) fishes have been recovered from the Lower Miocene (approximately 20–15 Ma), providing evidence of morphological stasis in these taxa with highly specialized dentition for fruit and seed consumption (Dahdul 2004). The early and middle Miocene fossils of *C. macropomum* and *Phractocephalus hemiliopterus*, a large pimelodid catfish, confirm the historical longevity of these two highly frugivorous species (Lundberg et al. 1986, Dahdul 2004).

In conclusion, such a scenario of large drainages with old forested wetlands and old fishes adapted to fruit and seed consumption suggest an ancient and tight interaction between fishes and riparian- and wetland-fruits in South America. Given this long and parallel evolutionary history, the South American floodplain and gallery forests, in particular those in the Amazon and Orinoco river basins, are perhaps the primary areas for the development of ichthyochorous species. Thus, South America stands as a prime location where more exhaustive studies can be focused to better understand the evolution and ecological implications of fish frugivory and ichthyochory.

CHAPTER II

CHANGES IN FEEDING STRATEGIES IN RESPONSE TO FLUCTUATING FOOD RESOURCES AMONG AMAZONIAN FLOODPLAIN-FOREST FISHES

Introduction

Because it provides the energy and nutrients that support vital functions, food is perhaps the most essential resource for heterotrophic organisms. Feeding strategies are constrained by an organism's morphology, physiology, behavior, and nutritional demands as well as the characteristics, abundance, and distribution of preferred and alternative food resources (Stephens and Krebs 1986, Cuthill and Houston 1997). Classical foraging theory assumes that maximizing net energy gain ultimately enhances fitness, thus there is great adaptive value in optimal strategies for locating, acquiring, and handling food (MacArthur and Pianka 1966, Schoener 1971, Stephens and Krebs 1986). Food resources can become limiting either in response to environmental fluctuations or consumption, which then affects feeding strategies as well as interactions among consumers. As resources become scarce, increased searching time and movement can increase predation risk in addition to competitive interactions among consumers. Long term coexistence of species is then achieved through a balance between the difference in competitive abilities to use limiting resources and species tolerance to overlap in resource use (MacArthur and Levins 1967, Pianka 1972, Abrams 1983, Meszéna et al. 2006). Competition among ecologically similar species leads to niche differentiation which can be achieved permanently through trait divergence (Taper and Case 1992, Ackerly and Cornwell 2007, Kraft et al. 2007) or temporarily by resource partitioning (Schoener 1974b, Abrams 1984, Chesson 2000, Behmer and Joern 2008, Barger and Kitaysky 2012). Niche compression (Schoener 1974b, a) or niche shifts (Werner and Hall 1976, Gerking 1994) are some of the mechanism by which species partition limiting resources. Thus, in systems with fluctuating resources, consumers are likely to respond to reductions in resource availability by adjusting their feeding strategies. Such responses can be assessed by comparisons of species niche breadth and niche overlap through time. Temporal environmental fluctuations of tropical floodplain ecosystems provide excellent opportunities for testing predictions derived from optimal foraging, limiting similarity, and resource partitioning theories.

Floodplains of the Amazon River and tributaries are characterized by marked hydrological seasonality (i.e., fluctuations in water level of up to 14 m within a year) that drastically changes the landscape, affecting not only physical and chemical conditions, but also habitat and food resources available to fishes. During the flooding season, floodplains are mosaics of interconnected lakes, streams, and seasonally inundated forests and savannas (Junk 1997, Melack et al. 2009). All of these are important habitats for a large diversity of fish species (Goulding et al. 1988, Junk et al. 1997, Petry et al. 2003). Allochthonous food resources of terrestrial origin are highly abundant and readily available to fishes as they disperse into newly inundated areas (Goulding 1980, Junk et al. 1997). As the waters recede, some habitats shrink, while others disappear, diminishing the availability of allochthonous foods to fishes.

Flooded forests in particular support diverse fish assemblages (Saint-Paul et al. 2000, Correa et al. 2008). By way of example, herbivorous serrasalmids and characids of the genera *Brycon* and *Triportheus* are particularly abundant in flooded forests and widely distributed throughout the Amazon basin. Species of these taxa form local assemblages containing multiple congeneric species with seemingly similar body size and morphology. Previous descriptions of the diet of species in these groups revealed a diet largely composed of forest-derived food resources, such as fruits, seeds, flowers, leaves, and insects (Goulding 1980, Goulding 1985). At first look, species within the same genera seem to consume much of the same food resources and trophic partitioning is only apparent at the genus level (Goulding 1980, Goulding et al. 1988). There is, however, no quantitative data to allow evaluating trophic resource partitioning among these seemingly ecologically similar species. Neither is there quantification on how the hydrological seasonality that characterizes the Amazon floodplain influences food availability for fishes and their feeding strategies.

In this study, I present a quantitative analysis of diets of sympatric frugivorous fishes inhabiting undisturbed flooded forests in the Colombian Amazon across three hydrological seasons. I combined analysis of stomach contents and stable isotope ratios to evaluate dietary patterns. In addition, I monitored fruiting phenology patterns to establish changes in food availability. Two fundamental questions that this research seeks to answer are whether fishes are capable of detecting fluctuations in food availability and if they are, how they adjust their feeding strategies. If feeding strategies are consistent with a hypothesis of maximizing energy gain, in accordance with the predictions of optimal foraging theory (MacArthur and Pianka 1966, Stephens and Krebs 1986, Perry and Pianka 1997), then fishes in the flooded forest should consume preferred most profitable food resources during periods of high resource abundance. During periods of food resource scarcity, fishes should expand their diet breadth to include less desirable items. If feeding strategies are consistent with a hypothesis of minimizing niche overlap and competition, in accordance with the limiting similarity theory (MacArthur and Levins 1967, Abrams 1983) and the predictions of Pianka's

(1972) niche overlap hypothesis, during periods of high resource abundance, fishes in the flooded forest could have greatly overlapping niches, because interspecific competition is minimized by the high supply/demand ratio. During periods of food resource scarcity, fishes should narrow their niche breadth or shift their diet, reducing trophic niche overlap, in response to increased competition. However, if fishes are unable to detect fluctuations in food availability, then no seasonal differences in feeding strategies would be expected, even if it is the case that resource availability shows strong seasonal patterns. Patterns of food consumption influence fitness, population growth, and ultimately the structure of the local species assemblage. A better understanding of foraging patterns among frugivorous Amazon fishes therefore has important implications in light of current threats to floodplain forest conservation across the Amazon Basin.

Materials and methods

Study site

This study was conducted in the lower Apaporis River and in an adjacent oxbow lake (Taraira Lake). The Apaporis is a large-black water river (1200 km long (PAT 1997) and 420 m wide) with a drainage (47000 km^2, PAT 1997) covering a vast extension of the Vaupes region of Southern Colombia. Located in the Northwestern part of the Amazon Basin, the Apaporis drains the southwestern portion of the ancient Guyana Shield (Fig. 1). The Apaporis region is characterized by Miocene sand deposits over a Precambrian basement, with regular granitic outcrops, some of which form rapids along the river (Hoorn 2006). Like many black-water rivers in the Amazon, the Apaporis is characterized by low nutrient concentration, low turbidity, and relatively acidic waters (Table 1). Precipitation follows a bimodal pattern with a mean of 3832 mm rainfall per year (n = 11 years, Defler 1996). The annual hydrological cycle fluctuates approximately 9 m, with maximum levels from May to July and minimum levels from December to January (Fig. 2). Taraira Lake is the largest oxbow lake in the Colombian Amazon (approximately 24 km long, Palacios et al. 2009), and it is connected to the Apaporis River year-round. Detailed information on geology and hydrology of the Lower Apaporis is provided elsewhere (PAT 1997, Hoorn 2006). Subsistence fishing by a sparse indigenous population (Tanimuka, Yucuna, Makuna, and Tuyuco ethnic groups) is believed to exert little pressure on local fish populations, although this remains to be quantified. An undisturbed evergreen floodplain forest covers the margins of the river and oxbow lake. The floristic composition of the Lower Apaporis is transitional between Guyana and Western Amazon floras (Clavijo et al. 2009). Species richness in the floodplain forest is estimated at 215 species, 65% of which are not shared with other forest types in the area (Clavijo et al. 2009).

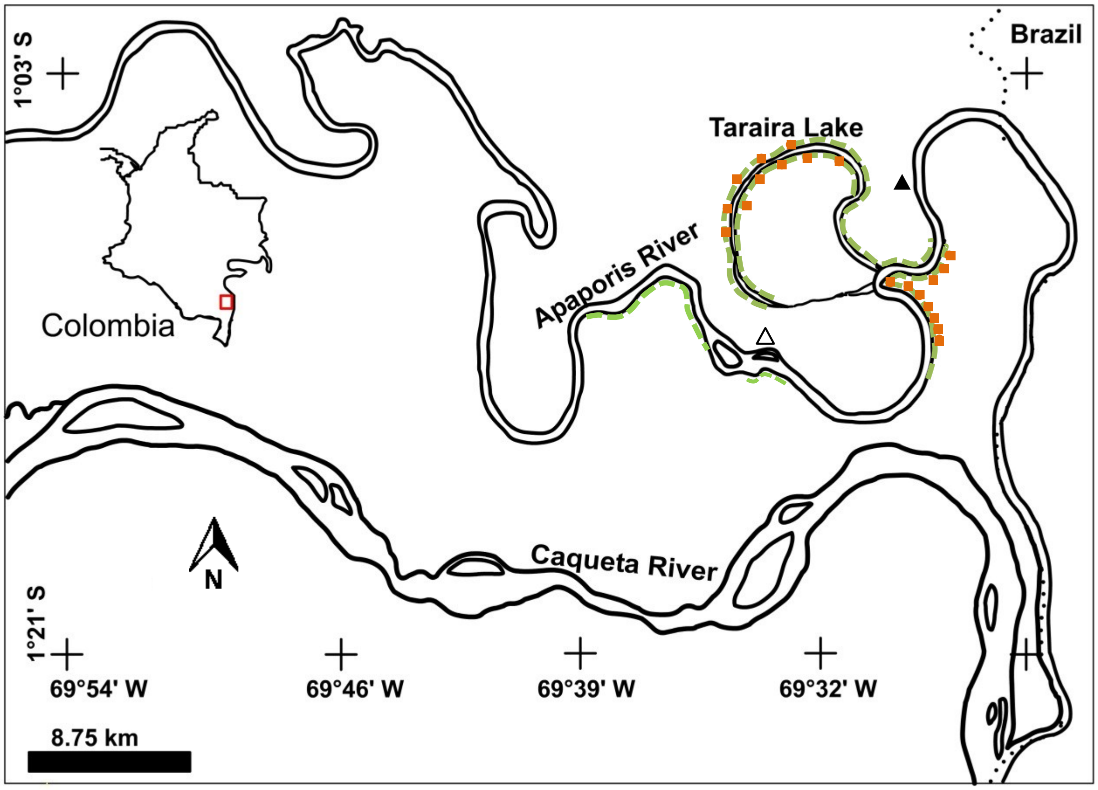


FIG. 1. Map of the study area in the lower Apaporis River, Colombian Amazon. Dashed green line represents the reach along the river and lake where fishing was conducted. Orange boxes represent sampling points where traps to monitor plant phenology were located. Triangles represent the location of two indigenous communities (filled symbol: Bocas de Taraira, empty symbol: Ňumi).

TABLE 1. Site and seasonal variability in water physicochemical characteristics at the two study locations during three hydrological seasons. HW: high waters, FW: falling waters, LW: low waters.

Site	Season	Secchi (cm)	Surface Temp (ºC)	1m depth Temp (ºC)	2m depth Temp (ºC)	3m depth Temp (ºC)	DO (mg/l)	Conductivity (us)	pH
Apaporis River	HW	79.4 ± 10.2 (69.0–100.0)	26.0 ± 0.1 (25.8–26.1)	-	-	-	6.8 ± 0.4 (6.1–7.4)	7.1 ± 0.3 (6.8–7.4)	5.6 ± 0.2 (5.2–6.0)
	FW	77.8 ± 15.0 (61.0–125.0)	27.1 ± 0.5 (26.4–27.9)	-	-	-	7.2 ± 0.3 (6.1–7.6)	6.1 ± 0.2 (5.9–6.5)	5.7 ± 0.4 (5.4–6.5)
	LW	89.3 ± 21.6 (74.0–104.0)	29.9 ± 0.5 (29.1–30.5)	-	-	-	5.5 ± 0.7 (4.5–6.7)	6.3 ± 0.6 (5.7–7.5)	5.6 ± 0.1 (5.4–5.7)
Taraira Lake	HW	158.7 ± 25.2 (114.0–210.0)	27.4 ± 0.8 (26.1–28.6)	27.0 ± 0.4 (26.2–27.6)	26.6 ± 0.4 (26.0–27.0)	26.1 ± 0.2 (25.9–26.3)	4.0 ± 0.8 (2.4–6.0)	6.4 ± 0.4 (5.7–7.1)	5.6 ± 0.2 (5.3–6.5)
	FW	162.8 ± 24.1 (118.0–206.0)	29.4 ± 0.8 (27.9–30.5)	29.4 ± 0.5 (28.6–29.9)	28.6 ± 1.0 (26.8–29.6)	27.6 ± 1.2 (26.2–29.5)	4.0 ± 0.9 (1.8–5.7)	5.4 ± 0.7 (4.0–6.6)	5.5 ± 0.2 (5.3–5.9)
	LW	107.0	32.2	30.9	30.1	28.8	6.3	4.5	5.5

Sample and data collection

Fishing was conducted five days per week throughout the high water (HW, from May to July), falling water (FW, from August to middle October), and low water (LW, from November to early December) seasons (Fig. 2). During the HW and FW seasons, fishing was conducted with hooks. Each fishing day, between 20 to 30 hooks were baited with ripe fruits of *Genipa americana* (Rubiaceae), *Byrsonima japurensis* (Malpigiaceae), or *Nectandra* sp. (Lauraceae). Earthworms were occasionally used toward the end of the FW season when ripe fruits were scarce. Each hook was attached to a 1m green multifilament fishing line suspended from vegetation inside the flooded forest, or along the edge of the river.

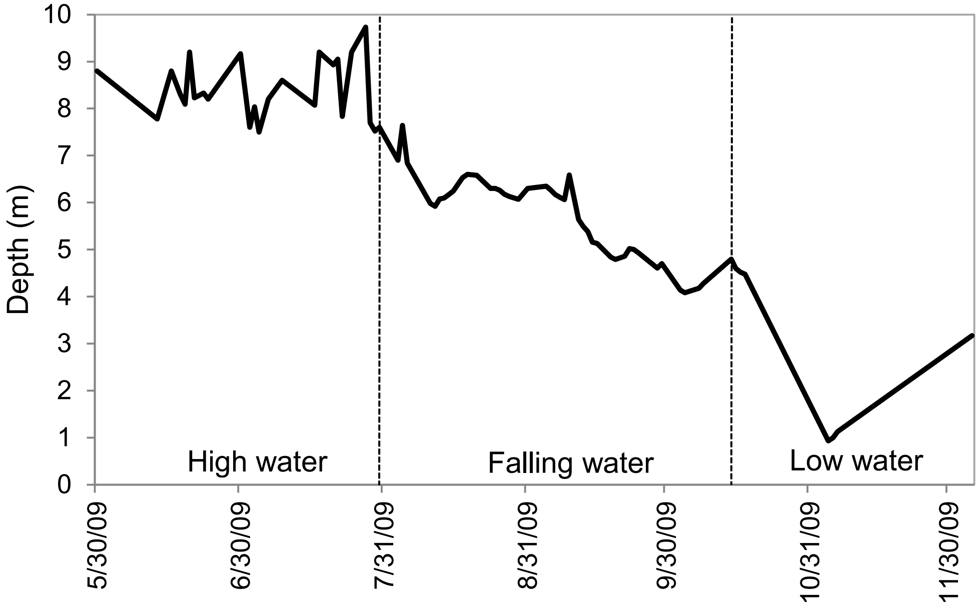


FIG. 2. Hydrological seasonality in Taraira Lake, Lower Apaporis River, during 2009.

Based on the expertise of local fishermen who assisted with fishing, hooks were attached to low branches of the vegetation that were in contact with the water, trapping floating debris which helped to disguise the hooks. During the LW season, all water had drained from the forest. Fishing was conducted during the day with earthworm baited hook and line along the edge of river. During the night, fish were captured from the middle of the river channel using an experimental monofilament gill net (100 m length, 2.5 m wide, 8, 10 and 15 cm stretched mesh size). The gill net was deployed in the middle of the river channel and trolled down river by slowly paddling toward the shore over shallow sandy beaches. The water level in the oxbow lake decreased rapidly during this season, and the lake became a shallow mudflat with a narrow (approximately 5 m wide) wetted channel. These conditions limited access to the lake, therefore surveys only could be done in the river during the LW season. The location of survey sites and the distance between the first and the last hanging hook, or the distance covered while fishing with hook and line, and the distance covered while trolling the gillnet, were recorded using a Garmin 76CS GPS unit. This instrument provides 5-m accuracy under a closed canopy cover. Water physicochemical characteristics were measured daily at each fishing site using a handheld probe (YSI 85; YSI Inc.), a digital pH meter (Oakton Instruments), and a Secchi disk. Species identification, standard length, body weight, time, and site of capture were recorded for each fish specimen. After euthanasia, each specimen was dissected within an hour after capture and the stomach was removed and preserved in 70% ethanol for subsequent analysis. Voucher specimens were deposited at the ichthyological collection of the University of Tolima, Colombia.

Stomach contents were removed from ethanol-preserved stomachs and observed under a dissecting microscope. Individual food items were separated and identified to the lowest feasible taxon. Items were placed on paper towels and left to dry for approximately 10 minutes. The volume of each food item was then estimated as the volume displaced by the item when submerged in a graduated cylinder containing a known volume of water. The volume of small items was estimated using a graduated Eppendorf vial. Items with volumes under 0.1 ml were placed on a petri dish and squeezed to a height of 1 mm. The area covered by the item, and therefore the volume, was measured using a millimetric grid (Hyslop 1980). Identification of fruits retrieved from stomachs was based on characteristics of the husk and seeds. Fruits and seeds retrieved from stomachs were compared against a reference collection of fresh fruits from botanical samples collected in the area during this study. Taxonomic keys were used for identifications (van Roosmalen 1985, Henderson et al. 1995, Stevenson et al. 2000, Cornejo and Janovec 2010) that were later confirmed by experts at the Colombian Amazon Herbarium (N. Castaňo and D. Cardenas) and at the Universidad de los Andes, Colombia (P. Stevenson and I. Vargas). When seeds were highly fragmented or when no seeds were present in the sample, the item was recorded as “fruit and seed fragments”.

Samples for analysis of stable isotope ratios of C ($\delta^{13}C$) and N ($\delta^{15}N$) were collected from fish specimens immediately after euthanasia. A sample of muscle tissue of approximately 2 cm^2 was taken from the dorsum below the dorsal fin. After removal of scales and skin, tissue samples were preserved in table salt. In the lab, samples were rinsed with deionized water and soaked for 24 h, after which water was changed and the samples were soaked for another 24 h. Samples were then rinsed and placed in a drying oven at 60°C. Samples of muscle tissue were dried for 24 h, and plant samples were dried for 48 h. Dried muscle samples were ground to a fine powder with a mortar and pestle. Fibrous plant samples were processed in an electric grinder (Wing-L-Bug by Pike Technologies) for 1 to 5 min until the sample was converted to a fine powder. Samples were weighed to the nearest

0.01 mg and placed into ultra-pure tin capsules. Sealed samples were sent to the Analytical Chemistry Laboratory, Institute of Ecology, University of Georgia, for analysis of carbon and nitrogen percentage composition and stable isotope ratios. Carbon and nitrogen isotope values represent the deviation from the isotopic ratios of Pee Dee Belemnite limestone, and atmospheric nitrogen, respectively, in delta notation: $\delta^{13}C$ or $\delta^{15}N$ = ((Rsample / R standard)-1) x 1000. Precision of the analysis was ≤ 0.11‰ measured as the standard deviation among bovine blood reference samples. Turnover rate of muscle tissue of an herbivorous tropical catfish was estimated at 18.2 days (McIntyre and Flecker 2006). Assuming a similar turnover rate for the species sampled in this study, it is expected that the isotopic signature of the fish will reflect the isotopic composition of food sources during a particular hydrological season, given that samples were taken in the middle of each season.

Litter traps were placed at 20 sampling points, 10 in the lake and 10 in the river, where fishing was conducted to monitor temporal changes in availability of fruits, seeds, and flowers falling to the water. The sampling points were selected following a systematic sampling protocol (Kent and Coker 1992). An initial point was randomly chosen, using a compass bearing, at the most upstream zone of each fishing area. In the lake, nine subsequent sampling points were selected every 1000 m, on both margins of the flooded forest, in an alternating manner. In the river, nine subsequent sampling points were selected every 500 m along one bank of the river. The greater distance between sampling points and their alternating placement in the lake reflects the larger fishing area covered there. At each sampling point, three hanging traps were placed inside the flooded forest, at 25-m intervals along a transect running parallel to the shore (Fig. 3A). Following the design of Stevenson and Vargas (2008), square traps with a concave bottom were constructed of mosquito-net fabric, with a mesh size of less than 0.1 mm and covering an area of 0.64 m^2. Each corner of the trap was tied to the trunk of the nearest tree in order to suspend the trap approximately 1–2 m from the surface of the water (Fig. 3B). Traps in the river were monitored every 3 weeks after installation for the first 6 weeks and every 2 weeks thereafter. Traps in the oxbow lake were monitored every 2 weeks. During October, all traps were monitored at a 1 month interval. The elevation and position inside the forest with respect to the water level and shoreline were adjusted as the water level decreased. During LW, traps were moved to the edge of the forest to monitor the fruiting phenology of the riparian vegetation. Traps were placed and monitored using a canoe. Fruits, seeds, and flowers collected in the traps were separated from the rest of the litter and identified to the lowest feasible taxonomic level. Wet materials were dried in a solar oven or under direct sunlight until a constant weight was reached and dry weight biomass was recorded.

During the days of trap monitoring, a visual census of fruiting plants was conducted along the river at each site where traps were placed. Censuses were conducted over a 100-m line transect parallel to the forest edge by two observers, one with binoculars and one without (a third person maneuvered the boat). The species identity and abundance of plants with ripe fruits, immature fruits, and flowers were recorded. A similar census was conducted inside the flooded forest near the locations of traps, and data were pooled with those from the forest edge. Visual censuses in the lake were only conducted once during the HW season along six transects following the methodology described above. Throughout the field research period, samples of all plants bearing fruit were collected throughout the area where fishes were surveyed. Vouchers were deposited at the Colombian Amazon Herbarium (COAH), Instituto Amazónico de Investigaciones Científicas–Sinchi, Colombia.

FIG. 3. Traps to monitor fruiting phenology. A. Even placement of three traps at a sampling point during the low water season to monitor the fruiting phenology of the riparian vegetation. B. Placement of a trap within the flooded forest during the high and falling water seasons.

Data analysis

*Stomach contents analysis.—*The proportional contribution of each food item to the total volume of all of the foods found in the stomach (excluding the volume of the bait) was estimated for each fish specimen. Highly digested unidentified materials and arthropod fragments of unknown origin were excluded from the total volume. The diverse food types within stomach contents were aggregated into 13 broad functional food categories for statistical analyses (Appendix 2). To assess how seasonality influenced dietary composition irrespective of species identity, mean proportional volumetric contribution (%Vol) and frequency of occurrence (%FO) of each food category were calculated after pooling all species caught in each season.

In some cases, only few individuals of a species were caught or a given species was caught during only one season. Because of this, only data from the most abundant species caught in all three hydrological seasons were analyzed. To assess dietary similarity among species, a matrix of proportional volumes of consumed food categories was compiled, with individuals of each species in the rows and food categories in the columns. Volumetric proportions were transformed with arcsine square-root (McCune and Grace 2002). This data matrix was then used to calculate a pairwise dietary similarity matrix using Bray-Curtis distance. Because food availability changes between hydrological seasons, a separate diet matrix was constructed for each season. Zooplankton were not included in the matrix, since this food category was not found in stomachs of the most abundant species. Furthermore, terrestrial vertebrates and nematodes were excluded since these food categories were found in stomachs of only one and two individuals, respectively.

Principal coordinates analysis (PCoA) was used to visually represent dietary similarity among species within seasons. PCoA is a multidimensional scaling technique that uses a measure of distance among objects, in this case individual fish, to approximate the position of such objects in a low-dimensional Euclidean space defined by a set of variables, in this case consumed food categories. This ordination technique was chosen because, unlike most other ordinations, it allows the use of non-Euclidean measures to evaluate similarity among objects. Bray-Curtis is highly recommended in cases when there is a large number of zero values, which was the case in the food consumption matrices analyzed here. Distances were squared prior to PCoA ordination to avoid negative eigenvalues (Legendre and Legendre 1998). Because PCoA is based on a distance matrix, the ordination plot directly represents the similarity among individual fish, with closest individuals having a more similar diet.

A test of homogeneity of multivariate dispersion (PERMDISP) was used to assess differences in dispersion in food space among species within seasons. PERMDISP measures the distance of each individual to its group multivariate median (i.e., similar to the centroid) and assesses differences in distance to the spatial median among groups (Anderson 2006). In this particular case, the prediction is that if there is complete dietary overlap among species, there should be no differences in dispersion among species. If, on the other hand, there are differences in dispersion among species, this would indicate that some species have more restricted diets than others, suggesting a narrower niche breadth and thus reduced dietary overlap. The test was conducted on the dietary similarity matrices described above and, as implemented in Vegan 2.0-2 (Oksanen et al. 2012), it accounts for unequal number of observations per group. This test is robust for analyzing data sets with large numbers of variables that depart from multivariate normality and contain many zero values (Anderson 2006). Probability values for significant differences in dispersion in diet space among species were calculated by permutation of residuals (999 permutations). Post-hoc pairwise comparisons were performed by permutation tests based on a t-test on pairwise group dispersion (9999 permutations). Significance of permutated *P* values was determined after correcting for multiple comparisons using the Benjamin and Hochberg (1995) approach.

Seasonal differences in mean trophic niche breadth and pairwise dietary niche overlap also were assessed. The trophic niche breadth of each species was calculated using Levins' (1968) index, $ß = (\sum p_i^2)^{-1}$, where p_i is the proportional volumetric consumption of food category *i*. The index was calculated in two ways. First, niche breadth was calculated for each individual fish and average niche breadth was computed for each species during a given season. Second, niche breadth was calculated for each species based on the proportional total volume of each food category consumed by the species during a given season. Niche overlap among species pairs during every season was quantified using Pianka's (1973) niche overlap index $O_{jk} = O_{kj} = \Sigma p_{ij} p_{ik} / \sqrt{} \Sigma p_{ij}^2 p_{ik}^2$, where O_{jk} and O_{kj} represent the overlap between a species pair, with possible values ranging from 0 (no overlap) to 1 (complete overlap), and p_{ij} and p_{ik} represent the proportions of the i^{th} resource used by the j^{th} and k^{th} species, respectively.

Pianka's index was calculated two ways for comparison. The first method used the mean volumetric proportional consumption values based on proportions obtained from individual specimens, and the second method used the proportional total volumes of food categories consumed by each species. The significance of the observed mean overlap among species was determined by comparison against a null model of expected niche overlap when resources are randomly consumed. Simulated diets were generated with a randomization algorithm in which niche breadths were preserved, zero values were reshuffled and all resources had the same probability of been consumed (Lawlor 1980, Gotelli and Graves 1996). The null hypothesis stating that the observed niche overlap is not different than that expected under random consumption of resources was rejected if the observed overlap was lower than 2.5% or greater than 97.5% of the expected overlap values. Following the approach of Kleynhans and colleagues (2011), separate Friedman tests were used to assess seasonal differences in niche breadth and niche overlap by comparing matching niche breadth values per species and pairwise niche overlap across seasons, respectively. When significant differences were detected, a series of one-tailed Wilcoxon signed rank tests were conducted to assess a significant increase in niche breadth or a significant decrease in niche overlap during FW and LW seasons relative to the HW season, and between the FW and LW seasons (Corder and Foreman 2009). The significance of P values was adjusted using the Bonferroni correction for multiple comparisons.

The contribution of particular food categories to discriminate diet among species was assessed by a similarity percentages procedure (SIMPER). In SIMPER, foods that are consistently abundant in the diet of a species but are not abundant in multiple species will discriminate its diet (Clarke 1993).

Several broad functional food categories were composed of numerous food types; for instance the category “fruits and seeds” contained over 60 different taxa and the category “terrestrial insects” contained over 20 different taxa (Appendix 2). To achieve higher dietary resolution, within-season analyses were repeated using dietary similarity matrices based on these “food types”, excluding unidentifiable fruit and seed fragments, a category likely to contain more than one fruit taxon. *Pristobrycon* sp. was excluded from these finer resolution comparisons because unlike other species, most fruit and seeds consumed, which represent most of the diet of this piranha, were reduced to unidentifiable fragments.

To evaluate the influence of spatial patterns in food availability on dietary similarity, a Mantel test was conducted to assess the correlation between dietary and geographical distance matrices during each season. Geographic distance matrices were calculated using the Euclidean metric based on the geographical coordinates (decimal degrees) where individual fish were caught. Dietary distance matrices (based on food types) were calculated as described above, including only individuals for which geographical coordinates for capture location were available. PCoA, Friedman tests, and Wilcoxon signed ranks tests were conducted with the package STATS; PERMDISP was conducted with the package VEGAN (Oksanen et al. 2012); Levins' index of niche breadth was calculated with the package SPAA in R (R Foundation for Statistical Computing). Pianka's niche overlap index and Monte Carlo simulations were performed in EcoSim (Gotelli and Entsminger 2010). SIMPER and Mantel tests were conducted using PAST software (Hammer et al. 2001).

Stable isotope analysis.—To adjust for a possible negative bias in $\delta^{13}C$ -values induced by lipid accumulation in fish muscle, the arithmetic correction $\delta^{13}C = -3.32 + 0.99(C:N)$ was used, in which C:N is the elemental ratio (Post et al. 2007). Such bias can be caused by the ^{13}C-depleted signatures characteristic of lipid that result from fractionation during the oxidation of pyruvate to acetyl-Co-A (DeNiro and Epstein 1977). As suggested by Post et al. (2007), the correction was only applied to samples with $C:N > 3.5$. Post and colleagues reported $\delta^{13}C$ values from two serrasalmid species obtained after lipid extraction that were identical or nearly identical to $\delta^{13}C$ values adjusted with the equation above (i.e., *Serrasalmus manuelli* (carnivore): -28.7 vs. -28.7, *Metynnis hypsauchen* (herbivore): -22.4 vs. -22.3), thus the correction seems appropriate for serrasalmids.

To test for differences in isotopic composition among species and across seasons, two-way analysis of variance was performed for δ^{13}C and δ^{15}N values. When significant differences were detected, one-way ANOVA and post-hoc Tukey HSD analyses were performed to determine differences in mean isotopic ratios between species pairs within seasons. The significance of *P* values was adjusted for multiple comparisons. To meet test assumptions, δ^{13}C data were transformed using Box-Cox transformation after adding +34 to each value to make all values positive. Data transformations (package MASS, function "boxcox") and statistical analyses were performed in R (R Foundation for Statistical Computing).

Trophic position (TP) for each species was estimated using the equation TP = $(\delta^{15}N_{fish} – \delta^{15}N_{base}) + 1/\Delta N$, where $\delta^{15}N_{base}$ is the mean δ^{15}N of basal sources, 1 is the TP for primary consumers, and ΔN represents δ^{15}N trophic enrichment caused by the accumulation of $\delta\ ^{15}$N in the consumer as N is transferred up the food chain (Post 2002). A value of 4.08‰ was used to account for ^{15}N enrichment, which was generated from laboratory experiments with a tropical catfish feeding on an algae-based diet (analysis of fin tissue, German and Miles 2010). The estimated $\delta^{15}N_{base}$ value was the mean δ^{15}N of samples of basal production source collected during each season (HW: mean = 3.95, based on 13 species of ripe fruits, leaves from one species of vine with leaves submerged or near the water, and phytomicrobenthos; FW: mean = 4.52, based on five species of ripe fruits, leaves from 11 species of vines and shrubs with leaves in or near the water, flowers from nine species, and leaves and seeds from one species of C3 grass; LW: mean = 5.72, based on three species of ripe fruits, leaves from five species of vines and shrubs with leaves in or near the water, flowers from four species, leaves from one species of C3 grass, and phytomicrobenthos; total samples = 110. PMB were not sampled during FW and therefore the average from samples taken during the HW and LW season was used).

Plant phenology.—For each of the 10 sampling points in which fruit-fall traps were placed to monitor fruiting phenology, the average dry weight of fruits (including ripe, immature, naked seeds, and fruit fragments) and flowers was calculated based on the materials collected by the three traps at each point. These values were then used to calculate average production for each interval of time between one monitoring episode and the next. Some of the traps along the Apaporis River were vandalized or stolen, thus the number of sampling points was smaller during some intervals (mean = 8). Average production was calculated over the number of sampling points from which at least one sample was retrieved. Likewise, the average number of plants bearing ripe fruits, immature fruits, and flowers was calculated for each day in which visual censuses were conducted. In order to estimate the relative abundance of each of the plant species that was observed with ripe fruits, frequency was calculated as the number of individuals of each plant species bearing ripe fruits over the total number of individual plants with ripe fruits recorded at all of the sampling points.

Results

Dietary composition from stomach contents analysis

Stomach contents of 892 individuals (SL 100–370 mm) representing 17 species were analyzed, of which 60 individuals had empty stomachs. The proportion of empty stomachs was larger during the LW (15%) than during the HW or FW seasons (4% and 5%, respectively). The relative contribution of 13 functional food categories to the diets of the 17 fish species changed across seasons (Fig. 4). During the HW season, fruits and seeds were the most important food resource, both in terms of volume (mean ± S.E., 68.75 ± 1.90%) and frequency of occurrence (88%). Fruits and seeds of 73 plant species were recorded in stomach contents during the HW season, and 37% of all fishes had unidentified fruit and seed fragments in their stomachs (Appendix 2). During the FW season, the importance of fruits and seeds decreased (37.60 ± 2.70% Vol, 52.43% FO) and other foods, such as flowers and terrestrial invertebrates, became important, both in terms of volume (20.05 ± 2.13 and 17.59 ± 1.15%, respectively) and FO (30.34 and 35.21%, respectively) (Fig. 4). Fruits and seeds of 21 plant species were recorded among stomach contents during this season, and 28.5% of individuals had unidentified fruit and seed fragments in their stomachs (Appendix 2). During the LW season, leaves became the main food source (35.05 ± 3.25% Vol, 54.09% FO). Other plant materials, fruits and seeds, and terrestrial invertebrates were frequently encountered among stomach contents during this season (29.60, 27.04, and 25.79% FO, respectively), but in small amounts (13.72 ± 2.32, 19.61 ± 2.84, and 13.91 ± 2.48% Vol, respectively) (Fig. 4). Fruits and seeds of only three plant species were recorded in stomach contents during the LW season (Appendix 2), although 24% of individuals had unidentified fruit and seed fragments in their stomachs.

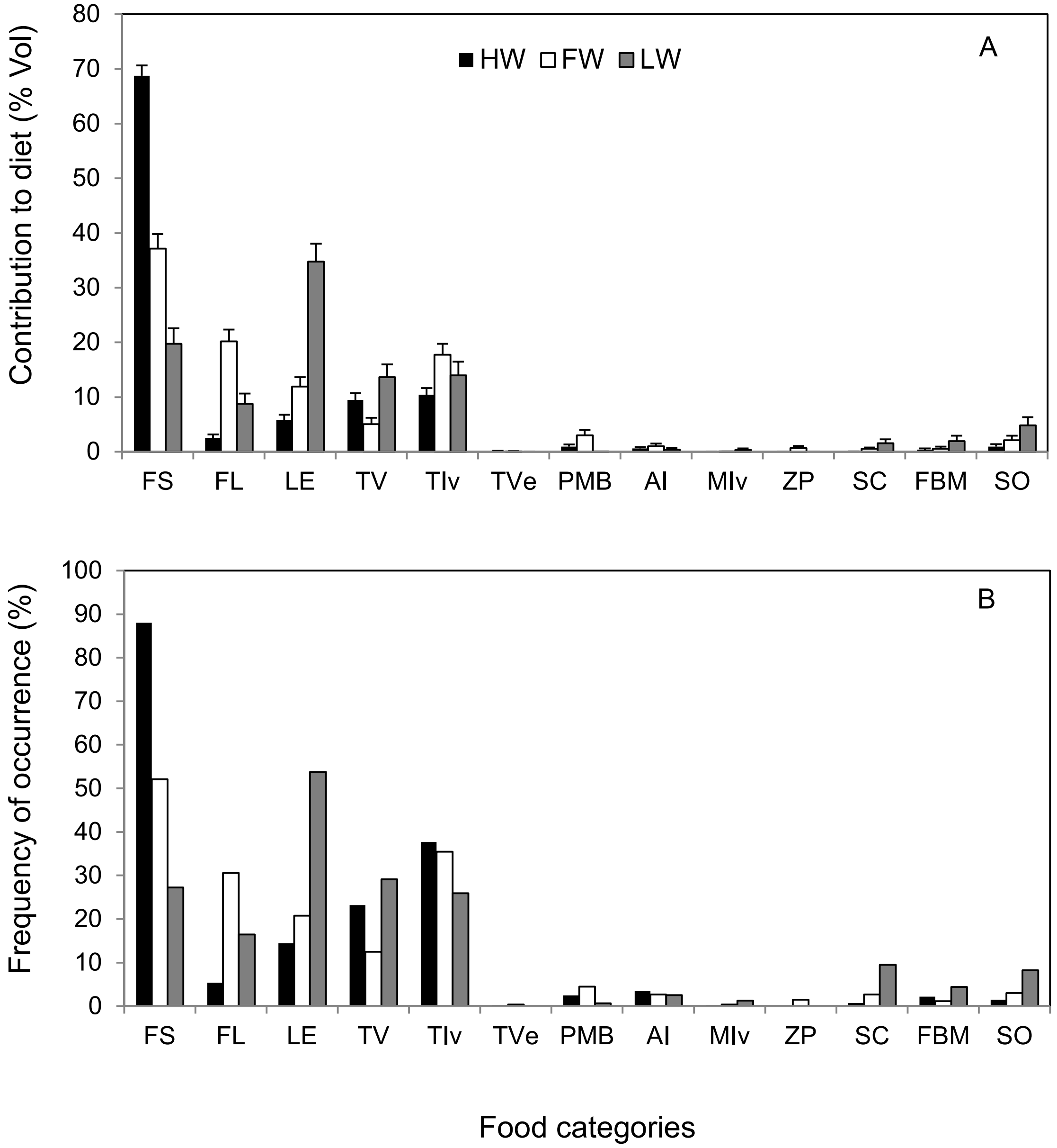


FIG. 4. Relative contribution of 13 broad food categories to diets of 17 fish species in an Amazonian floodplain throughout three hydrological seasons. (A) Mean + S.E. of the percentage volume of each food category estimated across all individuals examined; (B) frequency of occurrence of each food category in stomachs. Food categories: FS–fruits and seeds, FL–flowers, LE–leaves, TV–other terrestrial vegetation, TIv–terrestrial invertebrates, TVe–terrestrial vertebrates, PMB–phytomicrobenthos, AI–aquatic insects, MIv–other aquatic macro-invertebrates, ZP–zooplankton, SC–fish scales, FBM–fish remains, SO–soil and organic debris. Seasons: HW–high water, FW–falling water, LW–low water.

The most abundant fish species were *Brycon falcatus, B. melanopterus, Myloplus asterias, M. rubripinnis, M. torquatus,* and *Pristobrycon* sp.; subsequent results pertain to only these species. A total of 110 different food types were found among the stomach contents of 703 specimens. Stomach fullness was higher during the HW and lowest during the LW season (99% confidence intervals for volume of stomach contents of pooled species, HW: 3.99–5.04 ml, FW: 1.93–2.77 ml, LW: 0.51–0.81 ml). During the HW season, over 85% of *Brycon falcatus, B. melanopterus, Myloplus asterias, M. rubripinnis,* and *Pristobrycon* sp. individuals consumed fruits and seeds (Appendix 3). This food category made the highest volumetric contribution to the diet of these species (Fig. 5). A large percentage of *Brycon falcatus* and *B. melanopterus* (> 60%FO) consumed terrestrial invertebrates, the second-most important food type for these species (~20% Vol). *Myloplus rubripinnis* consumed large amounts of leaves (44% FO, 19% Vol), and fruits and seeds were not as dominant in their diet compared to other species (Fig. 5, Appendix 3).

During the FW season, the importance of fruits and seeds decreased in diets, both in terms of frequency of consumption and also in terms of volumetric contribution for all species except for *Pristobrycon* sp. (85% FO and 83% Vol). During this season, most diets were less dominated by a single food type and instead were comprised of a variety of food categories. A large percentage of individuals of *Brycon melanopterus* consumed terrestrial invertebrates (>80% FO), which represented a significant volumetric proportion of the diet of this species (over 50%). In contrast, a congener, *B. falcatus,* consumed terrestrial invertebrates in smaller amounts, and fruits, seeds, and flowers were frequently consumed and in relatively large amounts (Fig. 5, Appendix 3). A large percentage of individuals of *Myloplus asterias* consumed fruits and seeds, but flowers and leaves were also consumed in

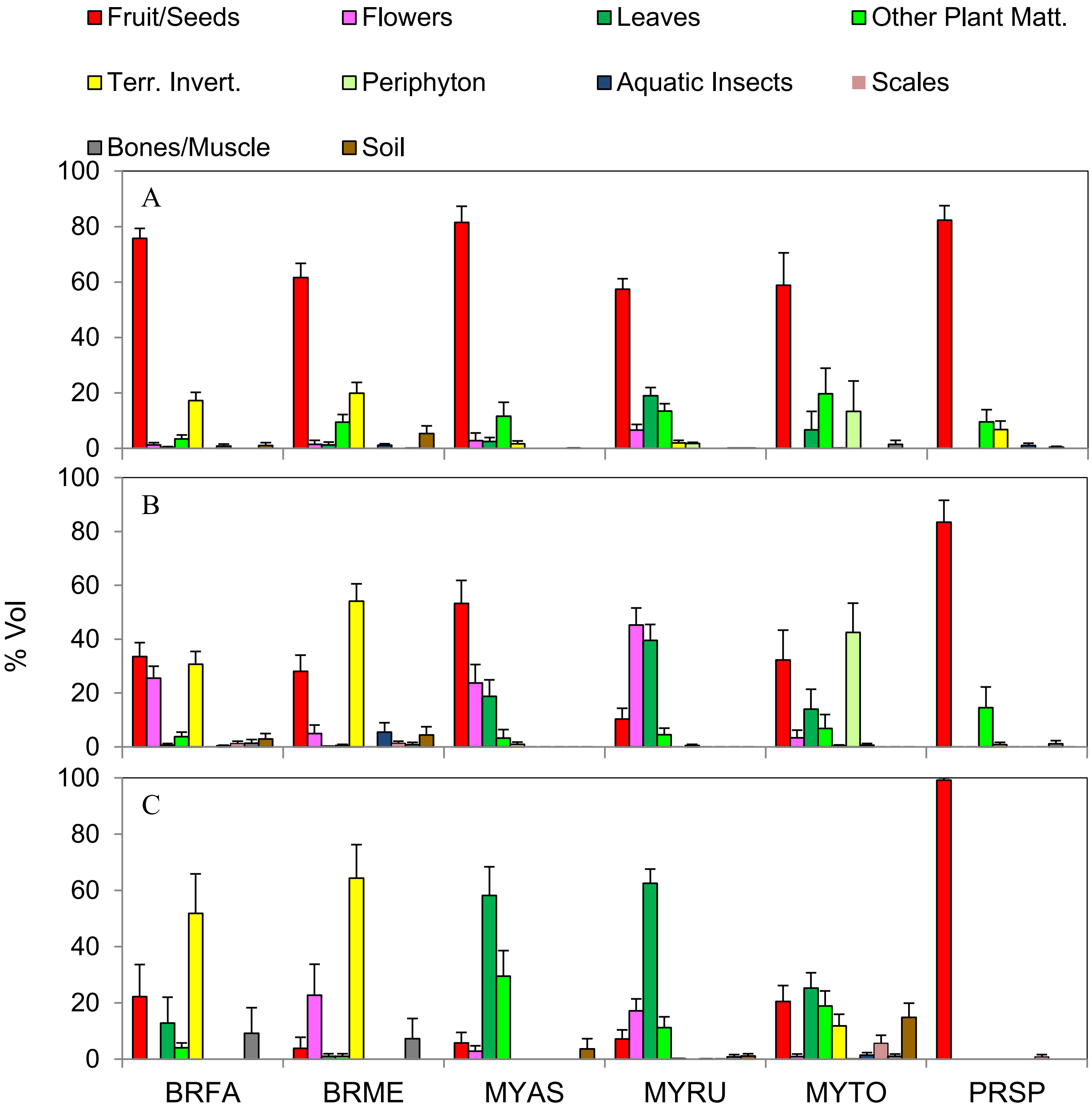


FIG. 5. Average volumetric percentage (% Vol ± S.E.) contributed by 10 broad functional food categories to diets of six frugivorous fish species during three hydrological seasons. (A) high waters, (B) falling waters, and (C) low waters. A complete list of the food items included in each category is presented in Appendix 2

high frequency, although in smaller amounts. The diet of *M. rubripinnis* was largely comprised of flowers and leaves that were consumed by over 60% of the individuals. Individuals of *M. torquatus* frequently consumed large amounts of filamentous algae; fruits, seeds, and leaves were frequently consumed but in small amounts.

During the LW season, similar to the HW season, there were several instances in which a single food type dominated the diet of a species. Individuals of both *Brycon falcatus* and *B. melanopterus* frequently consumed terrestrial invertebrates. Some *B. falcatus* also consumed fruits, seeds, and leaves, whereas some *melanopterus* consumed flowers. As with the other hydrological seasons, *Myloplus rubripinnis* frequently consumed leaves and occasionally fed on flowers and other plant materials during the LW season. Many *M. asterias* also consumed leaves, which contributed the largest volume to their diet, and other plant materials were also important. The diet of *M. torquatus* was diverse during this season, and no single food type dominated its diet. Only four *Pristobrycon* sp. were caught during the LW season, and each individual had consumed fruits and seeds; one individual also had small amounts of fish bones and muscle.

Overall, the number of individual food types consumed was higher during the HW season than in any other season, and mostly consisted of fruits and seeds (64%, Table 2). *Brycon falcatus*, *B. melanopterus,* and *Myloplus rubripinnis* consumed the largest number of fruit and seed taxa during the HW season, when diverse fruits and seeds were available. *Myloplus asterias* and *M. torquatus* consumed fewer fruit and seed taxa during this season. *Pristobrycon* sp. consumed large amounts of fruit and seeds during every season (Fig. 5, Appendix 3), but this material was recovered from their stomachs as unidentifiable fragments. Fewer non-fruit food types and fruits and seed taxa were recorded from stomachs during the LW season (Table 2). Despite the large number of food types recorded across all species and seasons, the average number of food types consumed by individual fish was low, especially for non-fruit categories (Table 2).

Food availability and food consumption

Despite differences in plant species composition, phenological patterns of fruit and flower production were similar in the river and oxbow lake. Greatest fruit production was recorded during June and July. This was followed by an increase in flower production during August with a peak in September (Figs. 6 and 7). Fruit production started again in November when immature fruits were recorded during visual censuses (Fig. 7). These phenological patterns were reflected in the food consumption patterns of fishes (Figs. 4, 8, and 9). More fruits and seeds were consumed during the HW season, followed by an increase in consumption of flowers, leaves and terrestrial invertebrates during the FW season, and greater consumption of leaves, other plant materials (e.g., stems, wood, and grasses), and terrestrial invertebrates during the LW season. Similar patterns of food consumption were observed in the oxbow lake (Fig. 8) and river (Fig. 9).

TABLE 2. Variability in the number of food types consumed by six frugivorous fish species during three hydrological seasons. N represents the number of individuals analyzed per species. Numbers in parenthesis represent average per individual ± S.E. A complete list of food types is presented in Appendix 2. Unidentifiable fruit and seed fragments are not included under "No. Fruit & Seeds Species" although fragments were found in the stomachs of all or most individuals (†).

Season	Species	Spp Codes	*n*	No. All Food Types	No. Fruit & Seed Taxa	No. Non-fruit Food Types
High Waters (HW)	*Brycon falcatus*	BRFA	87	60 (3.22 ± 0.20)	39 (1.45 ± 0.13)	20 (1.45 ± 0.16)
	Brycon melanopterus	BRME	57	59 (3.72 ± 0.28)	36 (1.67 ± 0.14)	22 (1.84 ± 0.23)
	Myloplus asterias	MYAS	35	24 (1.94 ± 0.20)	15 (0.91 ± 0.17)	8 (0.49 ± 0.16)
	Myloplus rupripinnis	MYRU	109	33 (2.47 ± 0.13)	20 (1.15 ± 0.09)	12 (1.07 ± 0.09)
	Myloplus torquatus	MYTO	15	17 (2.07 ± 0.55)	10 (1.00 ± 0.37)	6 (0.73 ± 0.21)
	Pristobrycon sp.	PRSP	43	13 (1.44 ± 0.11)	1 (0.02 ± 0.02)†	11 (0.53 ± 0.12)
		Total	347	95 (2.66 ± 0.10)	61 (1.14 ± 0.06)	32 (1.15 ± 0.07)
Falling Waters (FW)	*Brycon falcatus*	BRFA	66	28 (2.03 ± 0.13)	9 (0.41 ± 0.07)	18 (1.45 ± 0.14)
	Brycon melanopterus	BRME	41	27 (2.51 ± 0.22)	7 (0.37 ± 0.10)	19 (1.95 ± 0.21)
	Myloplus asterias	MYAS	31	15 (1.68 ± 0.18)	9 (0.42 ± 0.13)	5 (0.74 ± 0.14)
	Myloplus rupripinnis	MYRU	44	11 (1.80 ± 0.14)	4 (0.27 ± 0.08)	6 (1.50 ± 0.13)
	Myloplus torquatus	MYTO	18	12 (1.83 ± 0.35)	0	11 (1.44 ± 0.37)
	Pristobrycon sp.	PRSP	20	8 (1.25 ± 0.12)	2 (0.10 ± 0.07)†	5 (0.35 ± 0.15)
		Total	220	48 (1.94 ± 0.08)	23 (0.31 ± 0.04)	24 (1.35 ± 0.08)
Low Waters (LW)	*Brycon falcatus*	BRFA	11	13 (2.45 ± 0.53)	2 (0.18 ± 0.18)	10 (2.09 ± 0.41)
	Brycon melanopterus	BRME	13	10 (2.31 ± 0.31)	0†	9 (2.23 ± 0.30)
	Myloplus asterias	MYAS	23	8 (1.43 ± 0.21)	0†	7 (1.30 ± 0.16)
	Myloplus rupripinnis	MYRU	46	11 (1.83 ± 0.11)	0†	10 (1.70 ± 0.12)
	Myloplus torquatus	MYTO	40	17 (2.10 ± 0.12)	1 (0.03 ± 0.03)	15 (1.78 ± 0.14)
	Pristobrycon sp.	PRSP	4	2 (1.25 ± 0.25)	0†	1 (0.25 ± 0.25)
		Total	137	24 (1.92 ± 0.08)	2 (0.02 ± 0.02)	21 (1.70 ± 0.08)

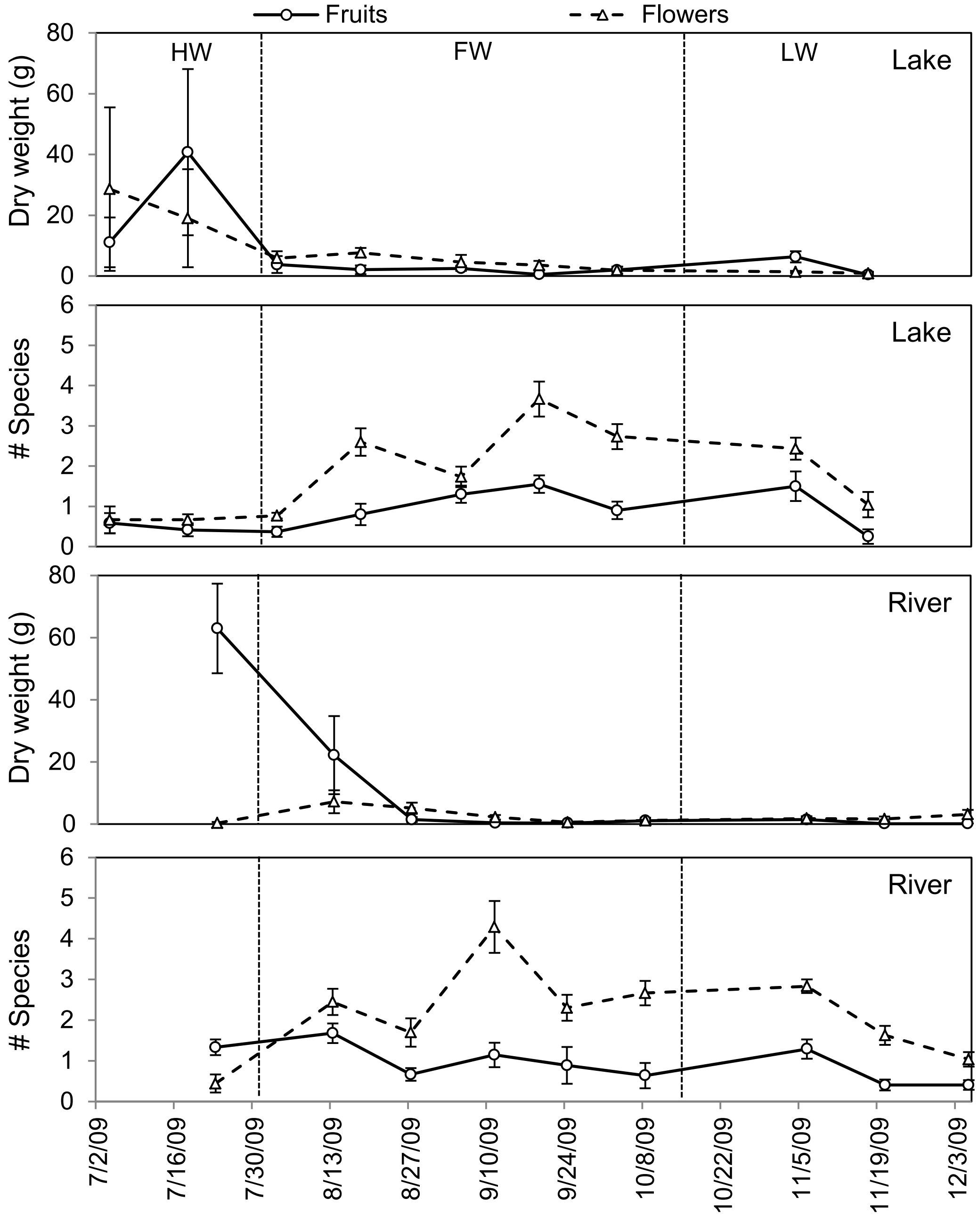


FIG. 6. Biweekly fruit and flower production assessed by collection traps. Each point represents average dry weight and average number of species of ripe fruits and flowers collected under the flooded forest during the high (HW) and falling water (FW) seasons, and under the riparian forest during the low water (LW) season in the Taraira Lake and Apaporis River. Dates represent the end of a two-week collecting period (e.g., 6/19/09 to 7/2/09). Error bars represent S.E. Dotted vertical lines mark the extent of hydrological seasons.

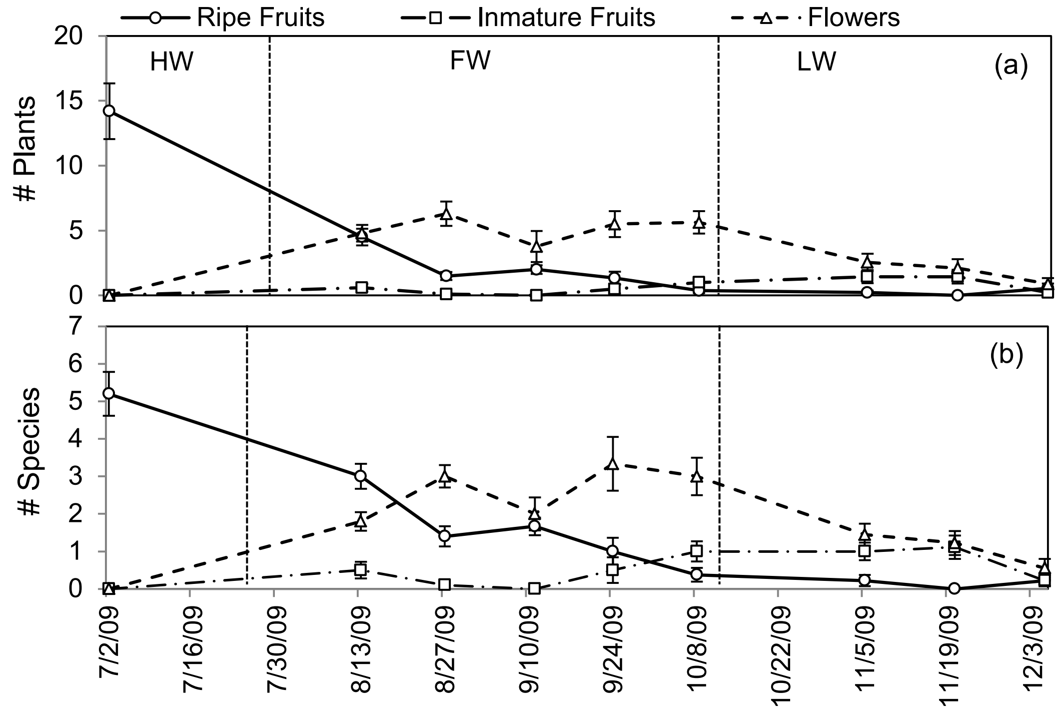


FIG. 7. Fruit and flower production in the flooded forest along the Apaporis River assessed during visual censuses. Each point represents (a) the mean number of individual plants recorded that were bearing fruits or flowers and (b) the mean number of species with fruits or flowers. Error bars represent S.E. Dotted vertical lines mark the extent of hydrological seasons (HW–high water, FW–falling water, and LW–low water).

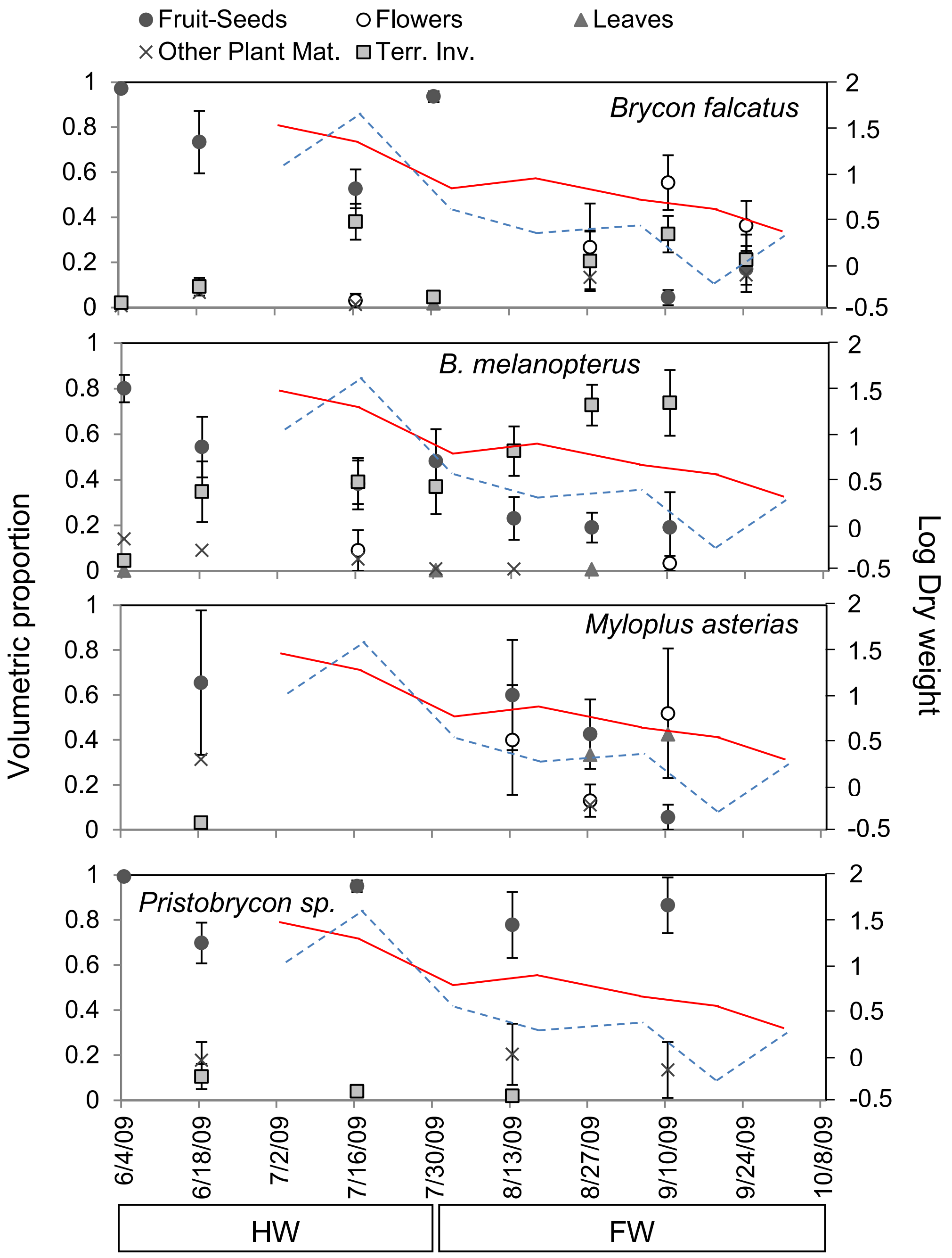
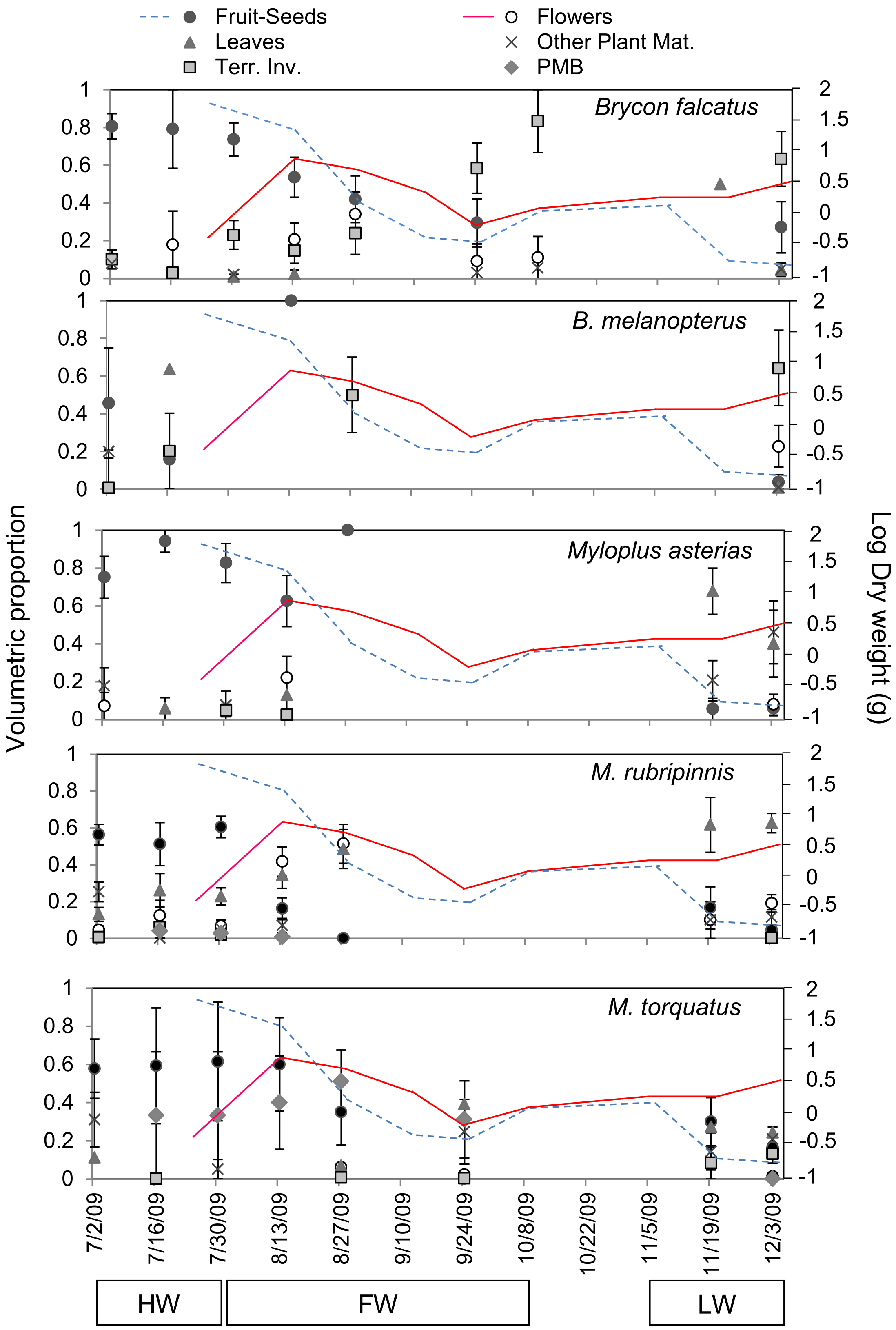


FIG. 8. Biweekly average food consumption by four frugivorous fish species and food availability in Taraira Lake during two hydrological seasons (HW–high water and FW–falling water). The dotted line represents fruit availability; the continuous line represents flower availability. Error bars represent S.E. Dates represent the end of a two-week sampling period (e.g., 5/21/09 to 6/4/09).

FIG. 9. Biweekly average food consumption by five frugivorous fish species and food availability in the Apaporis River during three hydrological seasons (HW–high water, FW–falling water, and LW–low water). The dotted line represents fruit availability; the continuous line represents flower availability. Error bars represent S.E. Dates represent the end of a two-week sampling period (e.g., 6/19/09 to 7/2/09).


Fruit-Seeds
Leaves
Terr. Inv.
Flowers
Other Plant Mat.
PMB
Brycon falcatus
B. melanopterus
Myloplus asterias
M. rubripinnis
M. torquatus
Volumetric proportion
Log Dry weight (g)
0
0.2
0.4
0.6
0.8
1
-1
-0.5
0
0.5
1
1.5
2
7/2/09
7/16/09
7/30/09
8/13/09
8/27/09
9/10/09
9/24/09
10/8/09
10/22/09
11/5/09
11/19/09
12/3/09
HW
FW
LW

Forty three species of trees, shrubs, and vines with ripe fruits were recorded during visual censuses along the Taraira Lake and Apaporis River (Fig. 10). A botanical inventory of plants with ripe fruits conducted in the fishing area throughout the duration of the study yielded 47 additional species (Appendix 4). Fruits of only 24 plant species recorded in the area were found in fish stomachs. During the HW season, *Quiina amazonica* was by far the most abundant shrub with ripe fruits in Taraira Lake. Other abundant species with ripe fruits were the shrub *Ilex* sp. (Aquifoliaceae) and the tree *Macrolobium acaciifolium* (Caesalpinaceae) (Fig. 10). Individuals of the palm tree *Astrocarium javari* (Arecaceae), the tree *Inga* sp. 2 (Mimosacea), and the vine *Marsdenia rubrofusca* (Asclepidaceae) bearing ripe fruits were abundant in the flooded forest along the Apaporis River (Fig. 10). *Quiina amazonica* and *A. javari* have fleshy fruits that were among the most frequently consumed by fishes (Figs. 11A, B). No evidence of consumption of *Ilex* sp. by any fish species was found, even though this plant has abundant fleshy fruits that float and a wide distribution in the area. *Marsdenia rubrofusca* was an abundant vine at the edge of the forest along both the river and lake. This vine produces a large capsule with winged seeds that are most likely dispersed by water. No evidence of consumption by fish was found, although local fisherman mentioned that fishes commonly nip on young leaves of this vine. Fruits of *Cecropia distachyla* (Cecropiaceae), *Genipa americana*, *Bothriospora corymbosa* (Rubiaceae), and *Psychotria* sp. 1 (Rubiaceae) were frequently consumed by fishes in the river (Fig. 11B). Although these species were not particularly abundant in the places where the visual censuses were performed (Fig. 10), they were commonly observed along the river in the areas where fishing was conducted. Likewise, fruits of *Byrsonima japurensis* and *Alchornea discolor* were frequently consumed by fishes in Taraira Lake during the HW season (Fig. 11A),

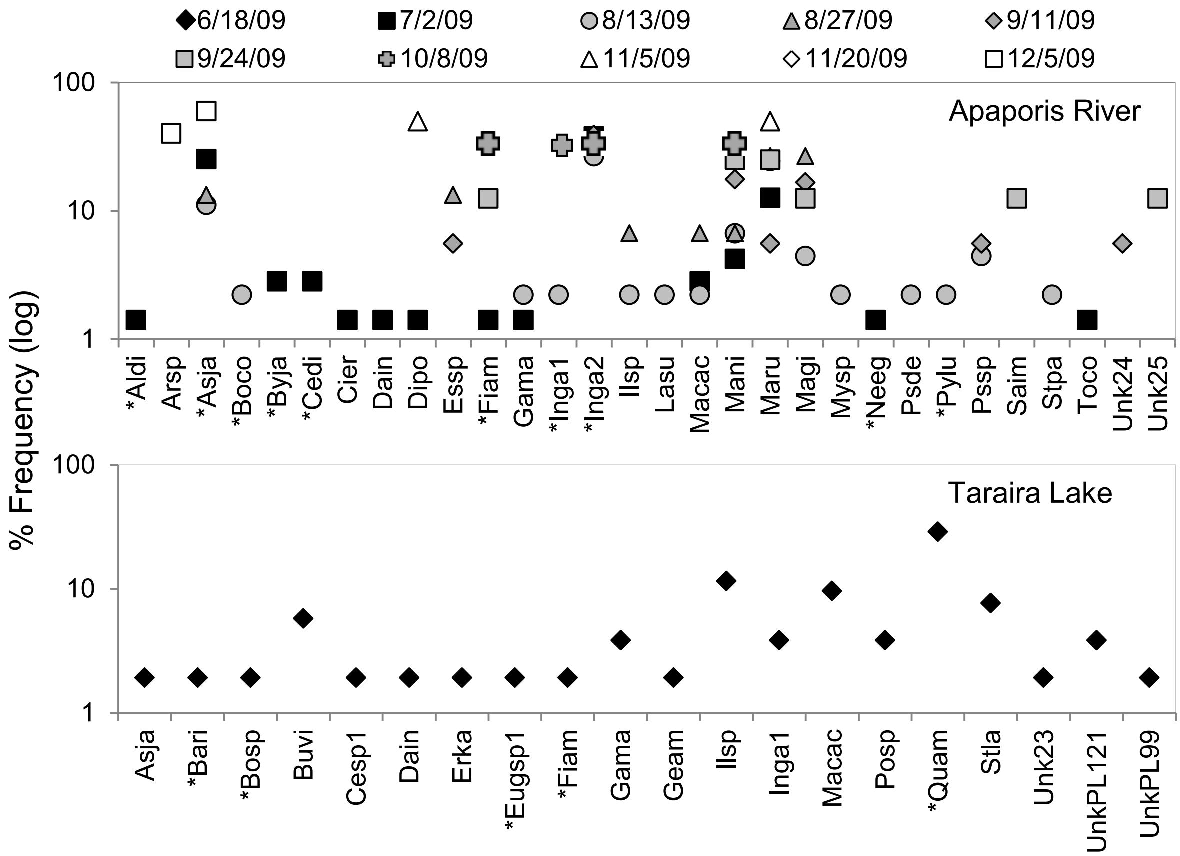
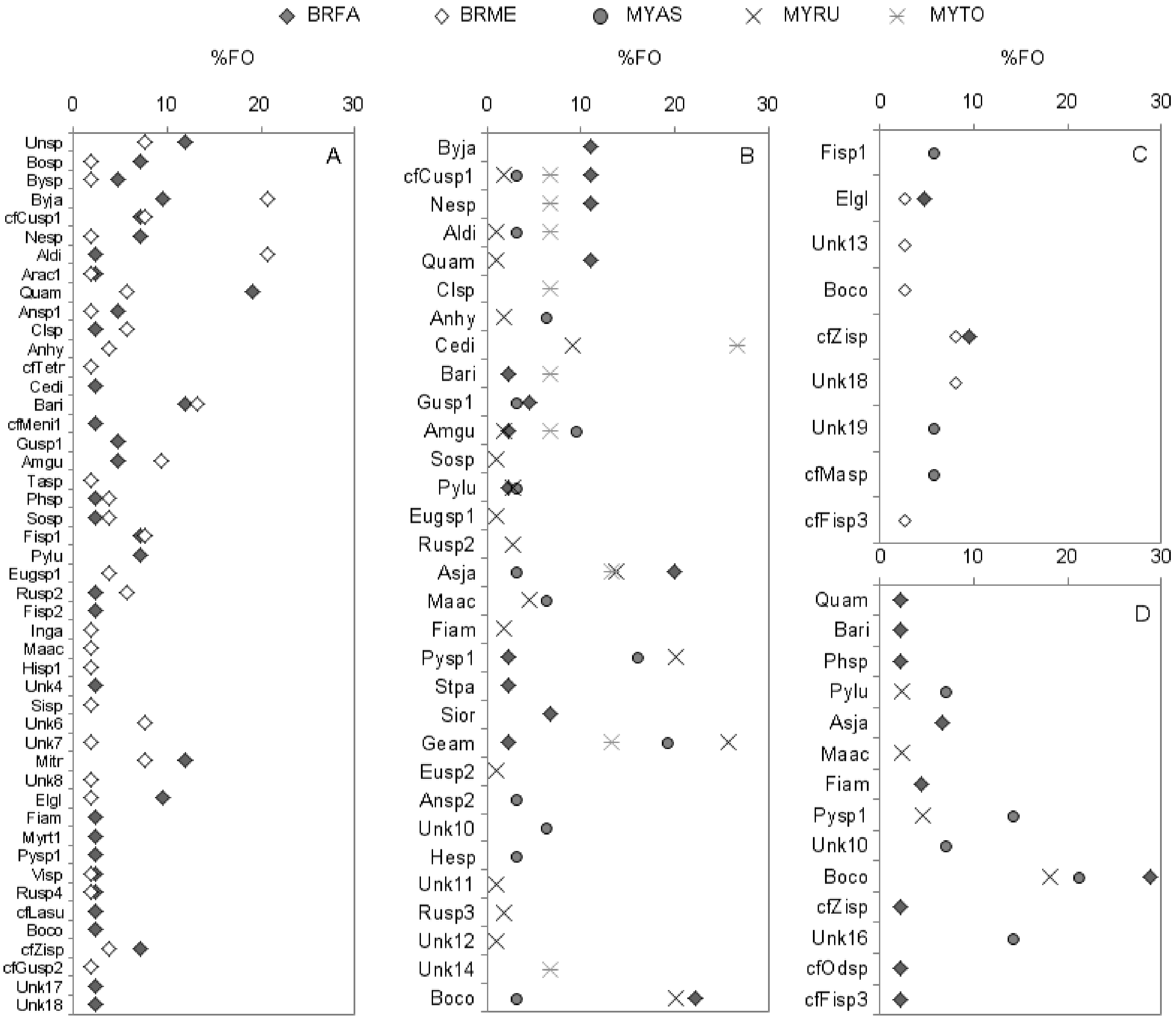


FIG. 10. Plant species with ripe fruits (n = 43) recorded during biweekly visual censuses along the Apaporis River and Taraira Lake. Species marked with asterisks were also found in fish stomachs. Fragments of *Genipa americana* (Geam) fruits were commonly found in stomachs of fish caught in the river but not in the lake. High water: black symbols, falling water: grey symbols, low water: white symbols. Species codes follow Appendix 4.

but were not recorded at the sites where visual censuses were performed despite being observed in the lake.

The number of fruit and seed taxa retrieved from stomachs during the HW season was larger among fish caught in the lake than among fish caught in the river (47 and 35, respectively). In the lake, nearly 50% of fruit and seed taxa retrieved from stomach contents were shared by the two *Brycon* species that ingested approximately the same number of fruit taxa (*B. falcatus*: 35 and *B. melanopterus*: 34, Fig. 11A). Only five individuals of *Myloplus asterias* were caught in the lake during the HW season, and fruits of only two species were recorded in the stomachs of these specimens. In the river, only 7% of fruit and seed taxa retrieved from stomach contents were shared by four fish species, 48% were shared among two or more fish species, and 52% were consumed by only one fish species (Fig. 11B). Only four individuals of *B. melanopterus* were caught in the river during the HW season, and fruits of five taxa were recorded in their stomachs, four of which were not consumed by any other species. Frequency of consumption per fruit taxon was low, suggesting low specificity and instead that fish species were consuming a wide variety of fruits during the HW season (Figs. 11A, B). During the FW season, fewer fruit taxa were consumed (lake: 9, river: 14), which reflects lower diversity of fruit available during this season (Fig. 6). No particular fruit taxon was consumed in high frequency in the lake (Fig. 11C). Fruits of *B. corymbosa* were the most frequently consumed by fishes in the river (Fig. 11D), including *B. melanopterus* of which only four individuals were caught. Ripe fruits of *B. corymbosa* were abundant during August (Fig. 10), although the spatial distribution of this species was strongly aggregated.

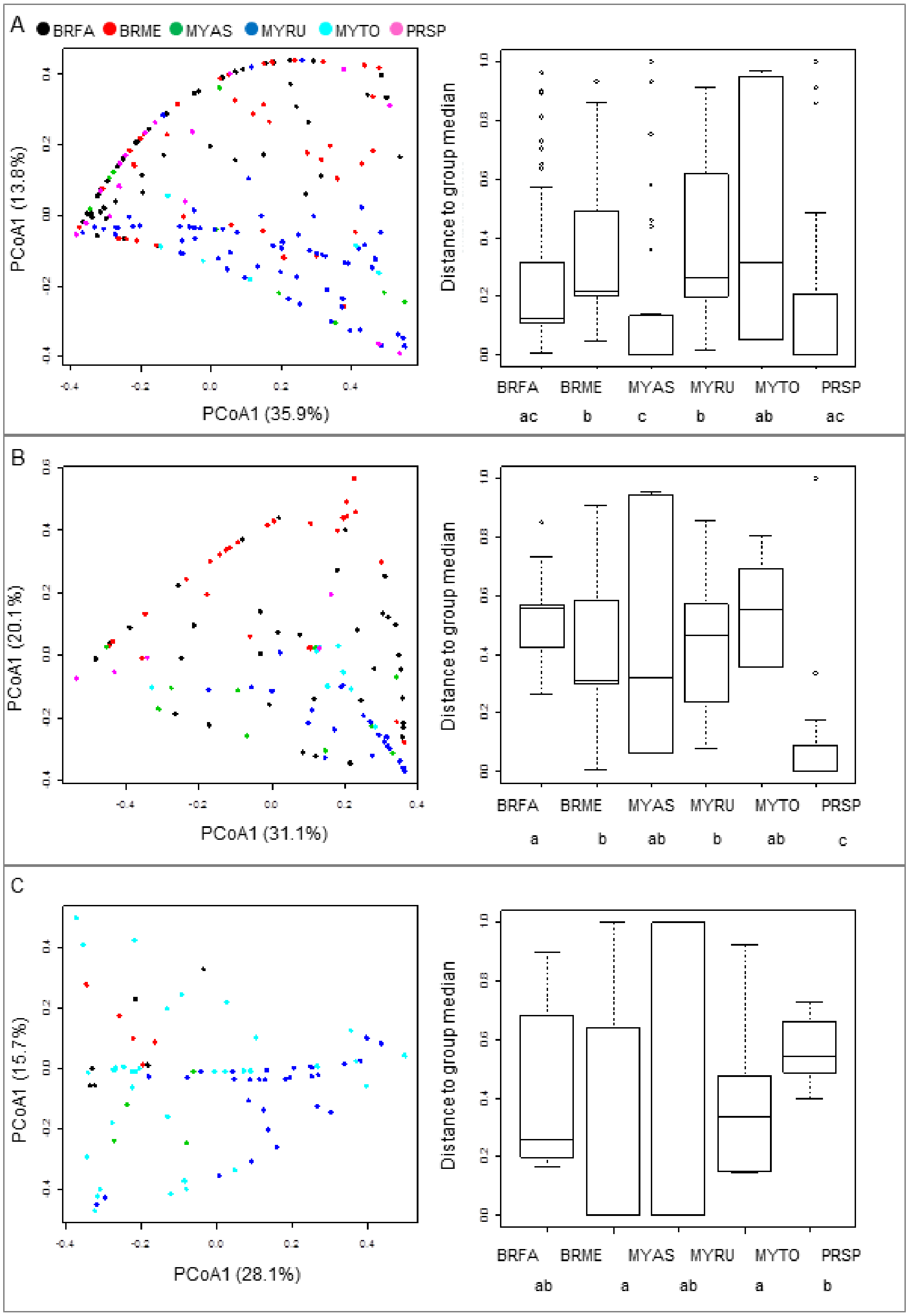
FIG. 11. Relative frequency of consumption of fruit and seed taxa by fishes during the high (HW) and falling water (FW) seasons in the Taraira Lake (A: HW, C: FW) and Apaporis River (B: HW, D: FW). Fish species codes follow Table 2, plant species codes follow Appendix 2.


BRFA
BRME
MYAS
MYRU
MYTO
%FO
0
10
20
30
A
Unsp
Bosp
Bysp
Byja
cfCusp1
Nesp
Aldi
Arac1
Quam
Ansp1
Clsp
Anhy
cfTetr
Cedi
Bari
cfMeni1
Gusp1
Amgu
Tasp
Phsp
Sosp
Fisp1
Pylu
Eugsp1
Rusp2
Fisp2
Inga
Maac
Hisp1
Unk4
Sisp
Unk6
Unk7
Mitr
Unk8
Elgl
Fiam
Myrt1
Pysp1
Visp
Rusp4
cfLasu
Boco
cfZisp
cfGusp2
Unk17
Unk18
B
Byja
cfCusp1
Nesp
Aldi
Quam
Clsp
Anhy
Cedi
Bari
Gusp1
Amgu
Sosp
Pylu
Eugsp1
Rusp2
Asja
Maac
Fiam
Pysp1
Stpa
Sior
Geam
Eusp2
Ansp2
Unk10
Hesp
Unk11
Rusp3
Unk12
Unk14
Boco
C
Fisp1
Elgl
Unk13
Boco
cfZisp
Unk18
Unk19
cfMasp
cfFisp3
D
Quam
Bari
Phsp
Pylu
Asja
Maac
Fiam
Pysp1
Unk10
Boco
cfZisp
Unk16
cfOdsp
cfFisp3

Dietary similarity based on stomach contents

At a coarse scale of resolution (i.e., functional food categories) used for computation of species dietary similarity, diet breadth, and niche overlap, a pattern of high dietary similarity among species emerged during the HW season, with similarity decreasing during the FW and LW seasons as the availability of high-quality foods diminished. Differences in diet breadth between some species, however, were observed during every season, as indicated by differences in distance to group median in multivariate diet space among species. During the HW season, fishes of all species were spread more evenly within diet space and no pattern of clustering was observed in the PCoA ordination plot (Fig. 12A). There were, however, differences in diet breadth among species (PERMDISP, $F_{m\ (5,340)} = 6.81$, $P < 0.001$) during the HW season. *Brycon falcatus, Myloplus asterias* and *Pristobrycon* sp. had a significantly narrower diet breadth than *M. rubripinnis* ($P < 0.01$ in all pairwise comparisons). *Brycon falcatus, M. asterias* and *Pristobrycon* sp. also had significantly narrower diet breadth than *B. melanopterus* ($P < 0.05$ in both pairwise comparisons). These results indicate that *M. rubripinnis* and *B. melanopterus* consumed a wider variety of foods and thus had relatively more generalized diets during the HW season (Fig. 12A). No evidence of differences in diet breadth was found between *M. torquatus* and any of the other species analyzed, except *M. asterias,* which had a significantly narrower diet breadth ($P < 0.05$). *Myloplus torquatus* consumed a wide variety of foods and was one of two species (*M. rubripinnis* was the other) that consumed filamentous algae (Fig. 5, Appendix 3). The wider box in the *M. torquatus* box-plot, however, reveals large intraspecific variability in diet (Fig. 12A) that, given the small sample size ($n = 15$), suggests that a larger sample size may be necessary to evaluate interspecific dietary segregation.

FIG. 12. Variation in the diet of six frugivorous fish species based on 10 functional food categories, assessed by PCoA ordination (left) and PERMDISP (right), during the (A) high water, (B) falling water, and (C) low water seasons. Ordinations show the relative position of individuals of each species in diet space. Proportion of total dietary variance represented by each axis is shown in parenthesis. Box plots represent species dispersion in diet space (i.e., greater distance to spatial median indicates larger dispersion). Species not sharing the same letters have significantly different dispersion ($P < 0.05$). Species codes and number of individuals per species are reported in Table 2.


A
● BRFA ● BRME ● MYAS ● MYRU ● MYTO ● PRSP
PCoA1 (35.9%)
PCoA1 (13.8%)
Distance to group median
BRFA BRME MYAS MYRU MYTO PRSP
ac b c b ab ac
B
PCoA1 (31.1%)
PCoA1 (20.1%)
Distance to group median
BRFA BRME MYAS MYRU MYTO PRSP
a b ab b ab c
C
PCoA1 (28.1%)
PCoA1 (15.7%)
Distance to group median
BRFA BRME MYAS MYRU MYTO PRSP
ab a ab a b

Dietary similarity among species decreased during the FW season, as depicted by clustering patterns in the PCoA ordination plot. The three *Myloplus* species clustered in the lower portion of the plot, *Pristobrycon sp*. clustered in the middle, and the two *Brycon* species overlapped with all other species (Fig. 12B). Patterns of diet breadth differed among species during this season (PERMDISP, $F_{m\ (5,214)} = 6.10$, $P < 0.0001$). *Pristobrycon sp*. had the narrowest diet breadth ($P < 0.05$ for all pairwise comparisons), indicating a restricted diet (Fig. 12B). Indeed 85% of these individuals fed on fruits and seeds, and very few individuals consumed any other food categories (Appendix 3). Contrary to the patterns observed in the HW season, *B. falcatus* had wider diet breadth than both *Brycon melanopterus and M. rubripinnis* (Fig. 12B). This suggests a switch in feeding strategy in which *B. falcatus* became a more generalist feeder. Most *B. falcatus* consumed terrestrial invertebrates, fruits and seeds, and flowers in high frequencies, plus many other food types in lower frequencies, while *M. rubripinnis* consumed leaves and flowers and the diet of *B. melanopterus* was dominated by terrestrial invertebrates during the FW season (Appendix 3). No differences in diet breadth were found between *M. torquatus* and its congener, or between *M. torquatus* and the two *Brycon* species. *Myloplus torquatus* was the only species that consumed significant amounts of filamentous algae during the FW season; fruits, seeds and leaves also were frequent in its diet. A greater mean distance to the group median suggests that *M. torquatus* was a more generalized feeder than *M. rubripinnis* and *B. melanopterus* (Fig. 12B), but P values for pairwise comparisons were only marginally significant after correction for multiple comparisons ($P = 0.084$ and $P = 0.088$, respectively). During the previous season, *M. torquatus* revealed high between-individual dietary variation, as depicted by the box plot, and a larger sample size (n > 18) may be necessary to assess dietary segregation. No differences in diet breadth were found between *M. asterias* and its congener, or between *M. asterias* and the two *Brycon* species. Fruits, seeds, flowers, and leaves dominated *M. asterias* diet (Fig. 5), although high between-individual dietary variation was observed during the FW season, as depicted by the box-plot (Fig. 12B).

During the LW season, dietary similarity among species declined further. *Myloplus rubripinnis* and *M. asterias* clustered in the lower portion of the PCoA ordination plot, while *B. falcatus* and *B. melanopterus* clustered in the upper portion of the plot, and *Myloplus torquatus* overlapped with all other species (Fig. 12C). Patterns of diet breadth differed among species (PERMDISP, $F_{m\ (4,128)} = 2.92$, $P < 0.05$). In this season, *M. torquatus* had wider diet breadth than both *M. rubripinnis and Brycon melanopterus*, suggesting a switch in feeding strategy in which *M. torquatus* became a more generalist feeder. Indeed, *M. torquatus* consumed a wide diversity of foods and no single category dominated. There was no evidence of significant differences in diet breadth between *B. falcatus* and *B. melanopterus* or between *M. asterias* and *M. rubrippinnis* (Fig. 12C). *Myloplus asterias* displayed high between-individual dietary variation during the LW, as depicted by the box-plot, which also was the case in the previous season (Fig. 12C). *Pristobrycon sp*. was not included in this comparison because of low sample size.

As depicted by SIMPER, most of the dietary dissimilarity among species in all three seasons could be attributed to differential contributions of fruits, seeds, flowers, leaves, other plant material (i.e., stems, wood, bark and grasses), terrestrial invertebrates, and periphyton; cumulative contribution of these categories to overall dissimilarity was nearly 90% during each season (Table 3). During the HW season, fruits, seeds, terrestrial invertebrates, and other plant material contributed the most to pairwise dietary dissimilarities, while flowers and leaves became an important contributor to pairwise dietary dissimilarities during the FW and LW seasons, respectively.

Overall trophic niche breadth, as assessed by Levins' index, was similar across seasons (Friedman chi-squared = 1.0, df = 2, $P = 0.61$; median niche breadth = 1.23, 1.28, and 1.27 for HW, FW and LW seasons, respectively, based on the average proportional consumption of each food category. Friedman chi-squared = 2.33, df = 2, $P = 0.31$; median niche breadth = 1.85, 2.83, and 2.36 for HW, FW and LW seasons, respectively, based on the total proportional consumption of each food category; Fig 13). Patterns of niche breadth did not change with the exclusion of *Pristobrycon sp*. due to low sample size during the LW season (results not shown). Among the six species, there was no consistent pattern of niche breadth expansion or niche breadth contraction across seasons. Half of the species (the two *Brycon* species and *Myloplus asterias*) revealed a pattern of narrower niche breadth during the HW season, which expanded during the FW season and contracted again during the LW season (Fig. 13B). The other three species revealed different patterns. *Myloplus torquatus* expanded its niche breadth during the LW season relative to the two previous seasons, whereas *Myloplus rubripinnis* and *Pristobrycon* sp. maintained relatively constant niche breadths across seasons (Fig. 13B). The small sample size obtained for *Pristobrycon* sp. during the LW season, however, prevents an accurate estimation of its niche breadth during this season.

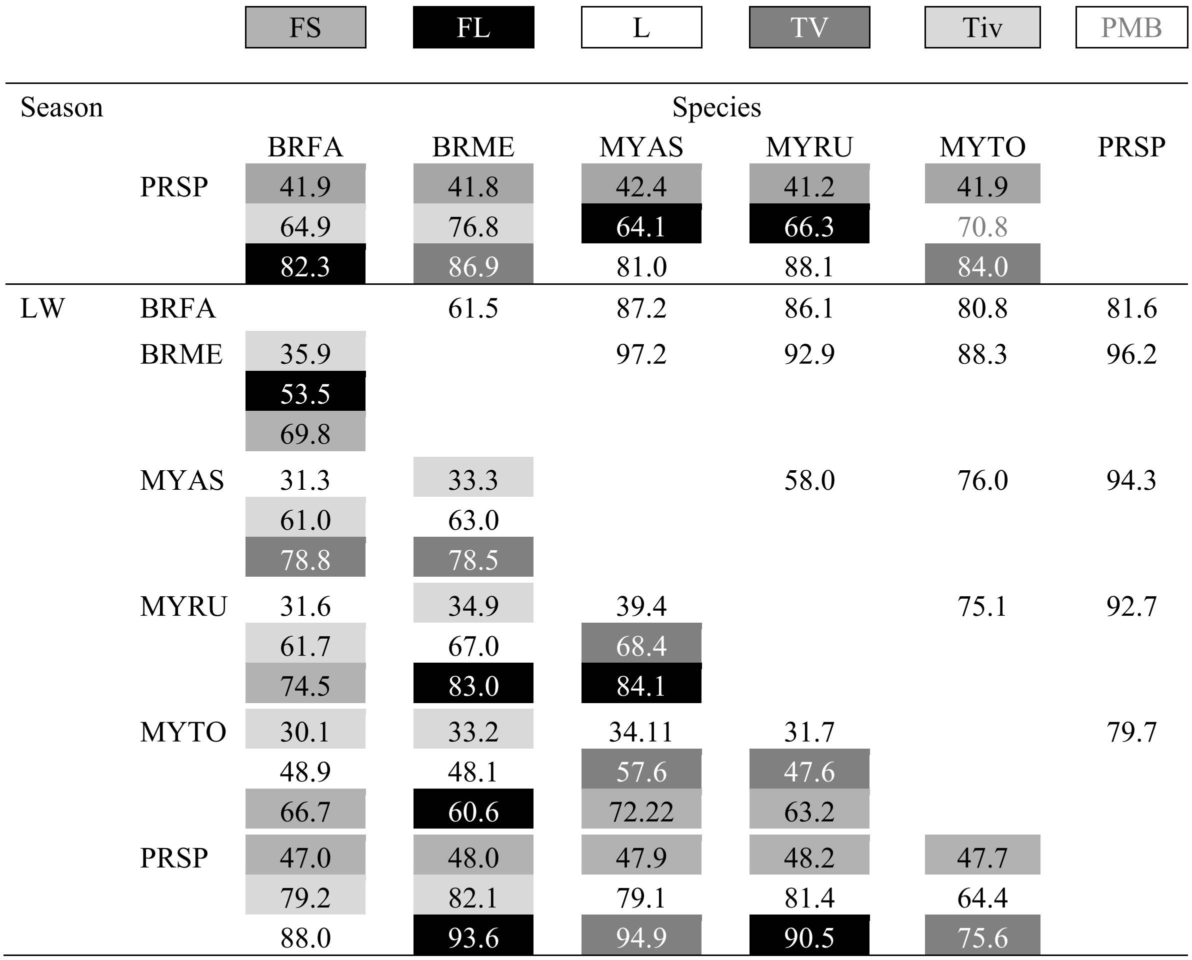
During every season, mean dietary overlap among species, as assessed using Pianka's index, was significantly greater than expected under a null model of random consumption of resources ($P < 0.05$ for all seasons). The degree of dietary overlap among species, however,

TABLE 3. Cumulative percentage contribution (below diagonal) of six functional food categories to pairwise dissimilarities between six frugivorous fish species computed by SIMPER. Values above the diagonal represent Bray-Curtis dissimilarities. Species and season codes follow those in Table 2. FS: fruits and seeds, FL: flowers, L: leaves, TV: other terrestrial plant material, TIv: terrestrial invertebrates, PMB: phytomicrobenthos.

FS FL L TV Tiv PMB

Season		Species					
		BRFA	BRME	MYAS	MYRU	MYTO	PRSP
HW	BRFA		44.2	36.0	53.1	55.1	36.4
	BRME	41.2 (FS) 71.2 (Tiv) 85.6 (TV)		45.7	58.4	60.5	45.8
	MYAS	42.8 (FS) 69.1 (Tiv) 87.3 (TV)	41.6 (FS) 65.1 (Tiv) 85.1 (TV)		48.4	49.6	30.9
	MYRU	36.6 (FS) 55.3 (Tiv) 73.9 (L)	33.6 (FS) 52.6 (Tiv) 69.6 (L)	42.2 (FS) 63.0 (L) 83.5 (TV)		60.6	51.0
	MYTO	38.4 (FS) 58.9 (TV) 76.7 (Tiv)	35.8 (FS) 56.3 (TV) 74.5 (Tiv)	43.5 (FS) 69.7 (TV) 82.9 (PMB)	36.5 (FS) 58.8 (TV) 78.4 (L)		51.1
	PRSP	43.6 (FS) 73.5 (Tiv) 91.2 (TV)	42.3 (FS) 68.2 (Tiv) 87.2 (TV)	45.0 (FS) 72.5 (TV) 86.8 (Tiv)	40.6 (FS) 60.2 (TV) 79.6 (L)	42.6 (FS) 68.2 (TV) 81.2 (PMB)	
FW	BRFA		67.2	73.4	81.7	86.2	70.4
	BRME	33.6 (Tiv) 62.7 (FS) 82.2 (FL)		81.7	93.0	89.1	75.1
	MYAS	33.1 (FS) 56.6 (FL) 78.7 (Tiv)	32.0 (Tiv) 62.0 (FS) 77.9 (FL)		72.5	78.2	55.6
	MYRU	26.3 (FL) 49.8 (L) 71.5 (FS)	28.3 (Tiv) 52.1 (FL) 72.9 (L)	35.0 (FS) 65.7 (FL) 93.3 (L)		86.3	89.3
	MYTO	24.8 (FS) 48.98 (PMB) 67.5 (Tiv)	29.2 (Tiv) 52.5 (PMB) 75.5 (FS)	32.0 (FS) 58.6 (PMB) 75.4 (L)	25.2 (FL) 49.2 (PMB) 71.9 (L)		72.3

TABLE 3. Continued



FS FL L TV Tiv PMB

Season		Species					
		BRFA	BRME	MYAS	MYRU	MYTO	PRSP
	PRSP	41.9 64.9 82.3	41.8 76.8 86.9	42.4 64.1 81.0	41.2 66.3 88.1	41.9 70.8 84.0	
LW	BRFA		61.5	87.2	86.1	80.8	81.6
	BRME	35.9 53.5 69.8		97.2	92.9	88.3	96.2
	MYAS	31.3 61.0 78.8	33.3 63.0 78.5		58.0	76.0	94.3
	MYRU	31.6 61.7 74.5	34.9 67.0 83.0	39.4 68.4 84.1		75.1	92.7
	MYTO	30.1 48.9 66.7	33.2 48.1 60.6	34.11 57.6 72.22	31.7 47.6 63.2		79.7
	PRSP	47.0 79.2 88.0	48.0 82.1 93.6	47.9 79.1 94.9	48.2 81.4 90.5	47.7 64.4 75.6	

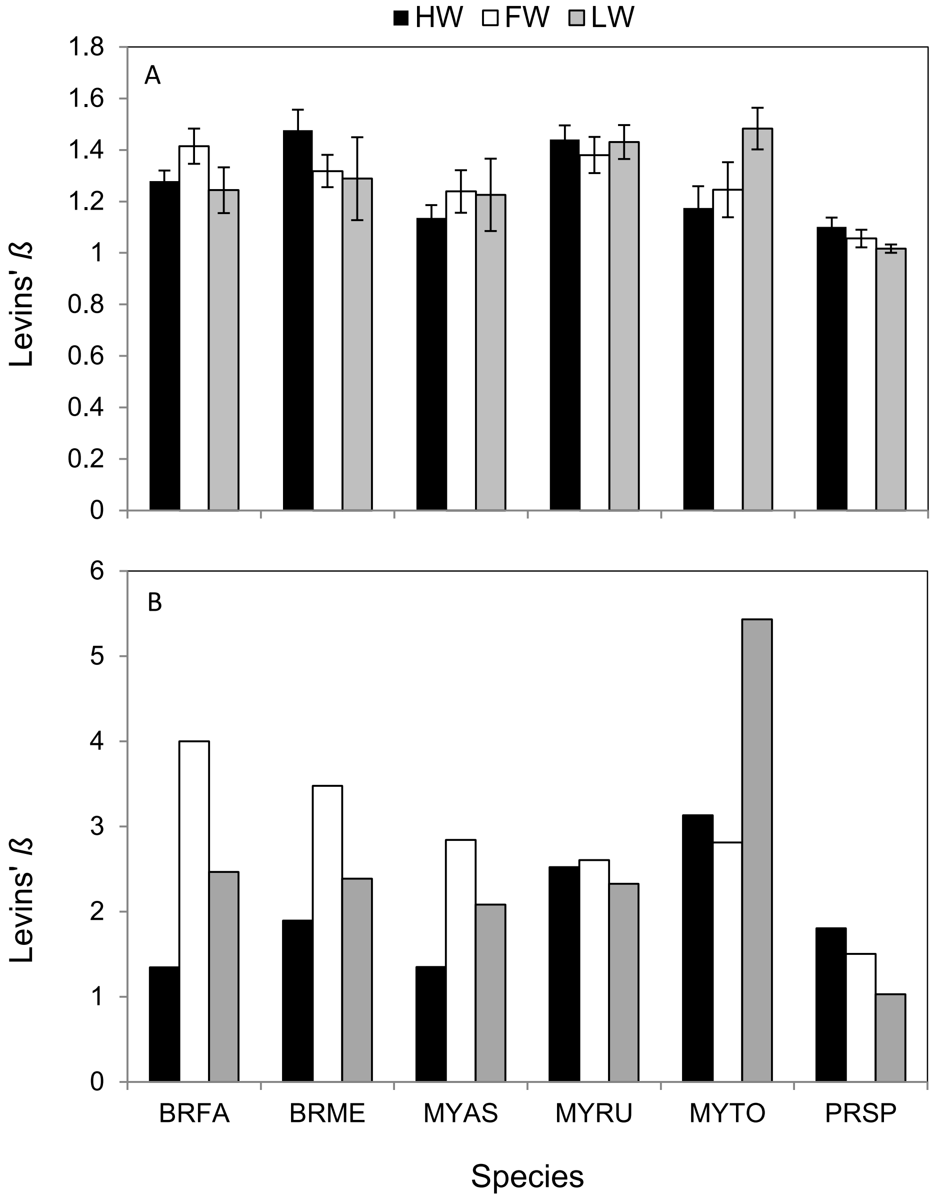


FIG. 13. Trophic niche breadth (Levins' *ß*) of six frugivorous fish species during three hydrological seasons. (A) based on the average proportional consumption of 10 food categories, and (B) on the total proportional consumption of 10 food categories. Season and species codes follow those in Table 2.

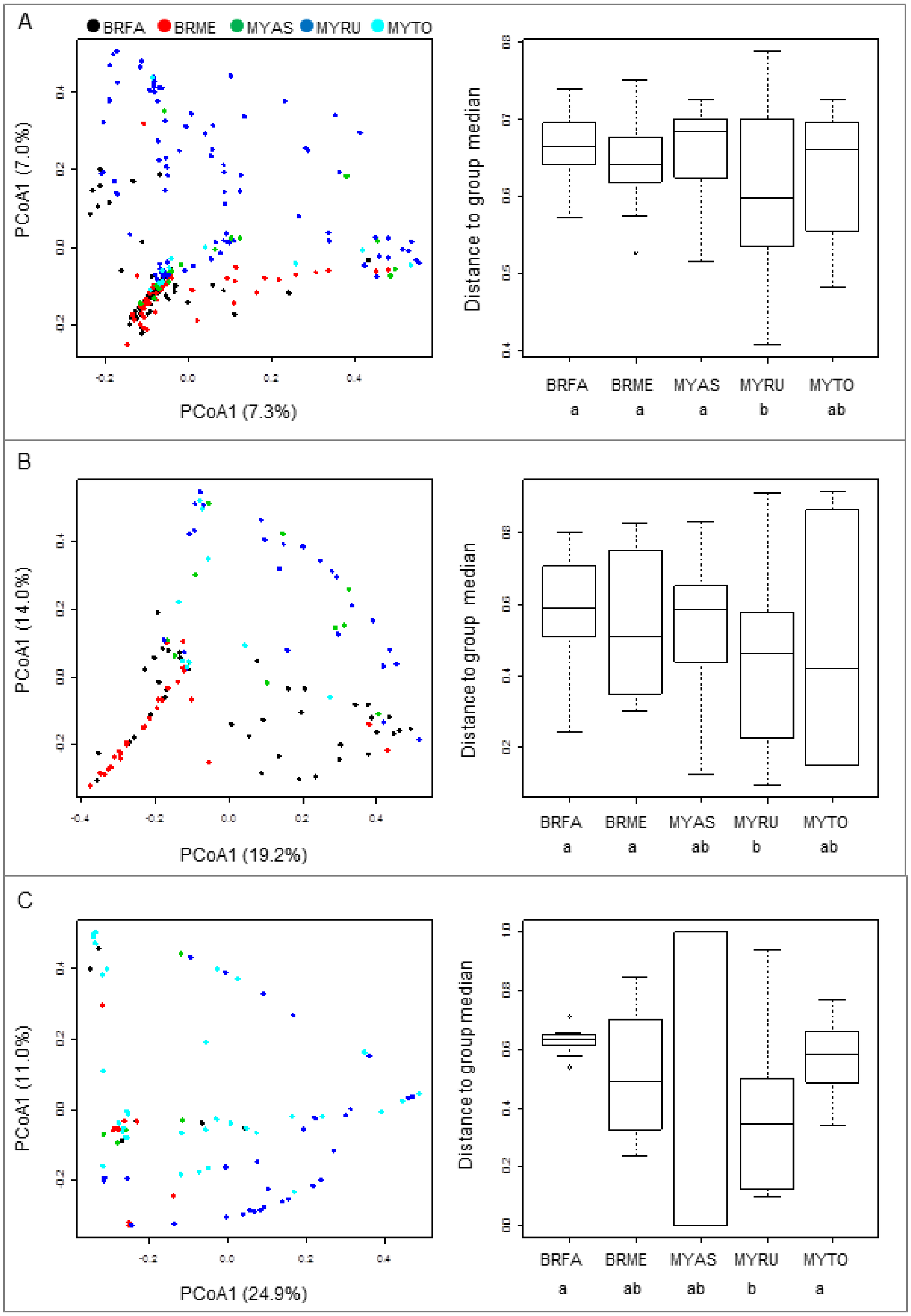
was significantly different across seasons (Friedman chi-squared = 22.8, df = 2, $P < 0.0001$; median overlap = 0.95, 0.58, and 0.28 for HW, FW and LW seasons, respectively; based on the total proportional consumption of each food category). Greater dietary overlap occurred during the HW season (Wilcoxon signed ranks test, HW vs. FW: W = 120, $P < 0.001$, $n = 15$ and HW vs. LW: W = 120, $P < 0.001$, $n = 15$). No significant reduction in dietary overlap was detected from the FW to the LW season (Wilcoxon signed ranks test, W = 88, $P = 0.18$, $n = 15$). Similar patterns were observed when niche overlap was calculated based on the average proportional consumption of food categories computed from volumetric proportions consumed by individual fish (results not shown). Likewise, patterns of niche overlap did not change with the exclusion of *Pristobrycon sp.* due to low sample size during the LW season (results not shown).

In general, interspecific and seasonal differences in dietary similarity and diet breadth were not significantly influenced by scale of resolution. Differences in diet breadth among species, as calculated at the fine scale of resolution (i.e., food types), were observed during every hydrological season (PERMDISP, HW: $F_{m\ (4,285)} = 4.81$, $P < 0.005$; FW: $F_{m\ (4,175)} = 6.97$, $P < 0.005$; LW: $F_{m\ (4,125)} = 4.694$, $P < 0.005$; Fig. 14). Except for a few cases, pairwise differences in diet breadth were the same as those observed when diet was analyzed at the coarse scale of resolution. *Myloplus rubripinnis,* for instance, had a narrower diet breadth than *B. falcatus* and *M. asterias* ($P < 0.001$ and $P < 0.05$, respectively) during the HW season, which is opposite to the pattern derived from the analysis of functional food categories. While *M. rubripinnis* consumed more food types during this season, it consumed relatively fewer fruit and seed taxa. This category, however, comprised most of the food types consumed during the HW season by all species combined (~65%, Table 2). Likewise, *M. rubripinnis* also had narrower diet breadth than *B. melanopterus* ($P < 0.05$). Like *B. falcatus, B. melanopterus* also consumed diverse fruit, seed, and terrestrial invertebrate taxa during the HW season (Table 2, Appendix 2). This was also the case during the FW season (*B. falcatus,* $P < 0.001$; *B. melanopterus*, $P < 0.02$, Fig. 14B). During the LW season, *M. rubripinnis* had relatively narrower diet breadth than *B. falcatus* ($P < 0.02$, Fig. 14C) which was due to *B. falcatus* consumption of diverse terrestrial invertebrate taxa (Appendix 2).

As depicted by SIMPER, the food types segregating species diets were different during different seasons, and this reflected differences in food availability. During the HW season, 31 food types, most of them various fruit and seed taxa, contributed in small individual percentages up to 90% of the dietary dissimilarity among fish species. During the FW season, 18 food types contributed nearly 90% of dietary dissimilarity among fish species, and flowers made the highest contribution. During the LW season, 90% of dietary dissimilarity was contributed by nine food types. Leaves made the highest contribution to interspecific differences (Appendix 5).

During each hydrological season, dietary differences among individual fish were weakly correlated with distances between their capture locations (Mantel Test, HW: $n = 278$, $r = 0.18$, $P < 0.0001$; FW: $n = 201$, $r = 0.09$, $P < 0.005$; LW: $n = 134$, $r = 0.06$, $P < 0.05$).

FIG. 14. Variation in the diet of five frugivorous fish species based on food types consumed (excluding fruit and seed fragments), assessed by PCoA ordination (left) and PERMDISP (right) during the (A) high water, (B) falling water, and (C) low water seasons. Ordinations show the relative position of individuals of each species on diet space. Proportion of total dietary variance represented by each axis is shown in parenthesis. Box plots represent species dispersion in diet space (i.e., greater distance to spatial median indicates larger dispersion). Species not sharing the same letters have significantly different dispersion ($\alpha = 0.05$). Species codes and number of individuals per species is reported in Table 2.


A
● BRFA ● BRME ● MYAS ● MYRU ● MYTO
PCoA1 (7.0%)
0.4
0.2
0.0
-0.2
-0.2
0.0
0.2
0.4
PCoA1 (7.3%)
Distance to group median
0.8
0.7
0.6
0.5
0.4
BRFA
a
BRME
a
MYAS
a
MYRU
b
MYTO
ab
B
PCoA1 (14.0%)
0.4
0.2
0.0
-0.2
-0.4
-0.2
0.0
0.2
0.4
PCoA1 (19.2%)
Distance to group median
0.8
0.6
0.4
0.2
BRFA
a
BRME
a
MYAS
ab
MYRU
b
MYTO
ab
C
PCoA1 (11.0%)
0.4
0.2
0.0
-0.2
-0.2
0.0
0.2
0.4
PCoA1 (24.9%)
Distance to group median
1.0
0.8
0.6
0.4
0.2
0.0
BRFA
a
BRME
ab
MYAS
ab
MYRU
b
MYTO
a

Dietary similarity based on stable isotopes

Analysis of $\delta^{13}C$ and $\delta^{15}N$ revealed significant seasonal and interspecific variation in the isotopic composition of frugivorous fishes. Muscle samples from 138 individuals (HW = 58, FW = 39, LW = 41) of six species were analyzed. Significant differences in mean $\delta^{13}C$ were detected across seasons (2-Way ANOVA, $F_{2,120} = 3.02$, $P < 0.05$) and among species ($F_{5,120} = 35.42$, $P < 0.0001$) with a significant interaction effect of seasons and species ($F_{10,120} = 3.01$, $P < 0.01$). Mean $\delta^{15}N$ was only marginally different across seasons (2 Way-ANOVA, $F_{5,120} = 2.68$, $P = 0.07$), but significantly different among species ($F_{5,120} = 16.31$, $P < 0.0001$), and the interaction effect of seasons and species was significant (and $F_{10,120} = 2.24$, $P < 0.02$). One-way ANOVA detected significant differences in isotopic signatures among species during every season for both $\delta^{13}C$ (ANOVA, HW: $F_{5,52} = 15.52$, $P < 0.0001$; FW: $F_{5,33} = 25.58$, $P < 0.0001$; LW: $F_{5,35} = 8.67$, $P < 0.0001$) and $\delta^{15}N$ (ANOVA, HW: $F_{5,52} = 4.24$, $P < 0.01$; FW: $F_{5,33} = 5.22$, $P < 0.001$; LW: $F_{5,35} = 10.91$, $P < 0.0001$). Post-hoc Tukey HSD analyses revealed significant within season differences in $\delta^{13}C$ and $\delta^{15}N$ isotopes between some pairs of species but not others (Table 4). In general, species spanned a narrow range of $\delta^{13}C$ signatures (-27 to -25‰), except for *Myloplus torquatus*, which had extremely depleted $\delta^{13}C$ signatures during both FW and LW seasons (Fig. 15). Species also tended to span a narrow range of $\delta^{15}N$ signatures (7 to 9‰), except for *Brycon falcatus* which had largely ^{15}N-enriched signatures during the LW season. During each season, *Myloplus rubripinnis* had relatively ^{15}N-enriched signatures, while *M. torquatus* had ^{15}N-depleted signatures (Fig. 15). Due to small sample sizes, the isotopic signatures of *B. melanopterus* and *M. rubripinnis* during FW were not statistically compared with those of

TABLE 4. Stable isotope ratios of C and N of six frugivorous fish species during three hydrological seasons. $\delta^{13}C$ values were arithmetically corrected for lipid content. Values are mean ± S.E.; means not sharing the same letter are significantly different from each other (post-hoc Tukey HSD, $P < 0.05$ after correction for multiple comparisons). Species with $n < 5$ were not considered in post-hoc comparisons. Season and species codes follow those in Table 2.

Season	Species	SL (mm)	*n*	δC^{13}	δN^{15}
HW	BRFA	201 – 265	8	-25.68 ± 0.10^{A}	8.35 ± 0.17^{A}
	BRME	170 – 255	14	-25.44 ± 0.12^{A}	8.04 ± 0.12^{AB}
	MYAS	156 – 202	7	-25.50 ± 0.11^{A}	7.99 ± 0.16^{AB}
	MYRU	147 – 212	16	-26.24 ± 0.11^{B}	8.38 ± 0.14^{A}
	MYTO	202 – 248	8	-26.67 ± 0.13^{B}	7.45 ± 0.15^{B}
	PRSP	164 – 175	5	-26.69 ± 0.36^{B}	7.79 ± 0.38^{AB}
FW	BRFA	193 – 278	14	-25.84 ± 0.09^{A}	8.33 ± 0.15^{A}
	BRME	218 – 227	3	-25.69 ± 0.06	7.89 ± 0.16
	MYAS	168 – 185	7	-25.70 ± 0.11^{A}	7.40 ± 0.14^{B}
	MYRU	178 – 200	3	-26.27 ± 0.15	8.77 ± 0.12
	MYTO	145 – 211	5	-29.33 ± 1.13^{B}	7.49 ± 0.29^{B}
	PRSP	157 – 198	7	-25.86 ± 0.09^{A}	8.12 ± 0.23^{AB}
LW	BRFA	229 – 253	5	-25.25 ± 0.17^{A}	9.52 ± 0.17^{A}
	BRME	198 – 231	5	-25.57 ± 0.24^{AB}	7.88 ± 0.29^{B}
	MYAS	152 – 174	6	-25.76 ± 0.18^{AB}	7.73 ± 0.18^{BC}
	MYRU	101 – 199	12	-26.19 ± 0.17^{B}	8.65 ± 0.16^{D}
	MYTO	102 – 234	10	-28.20 ± 0.71^{C}	7.64 ± 0.19^{BC}
	PRSP	167 – 175	3	-26.16 ± 0.41	8.51 ± 0.30

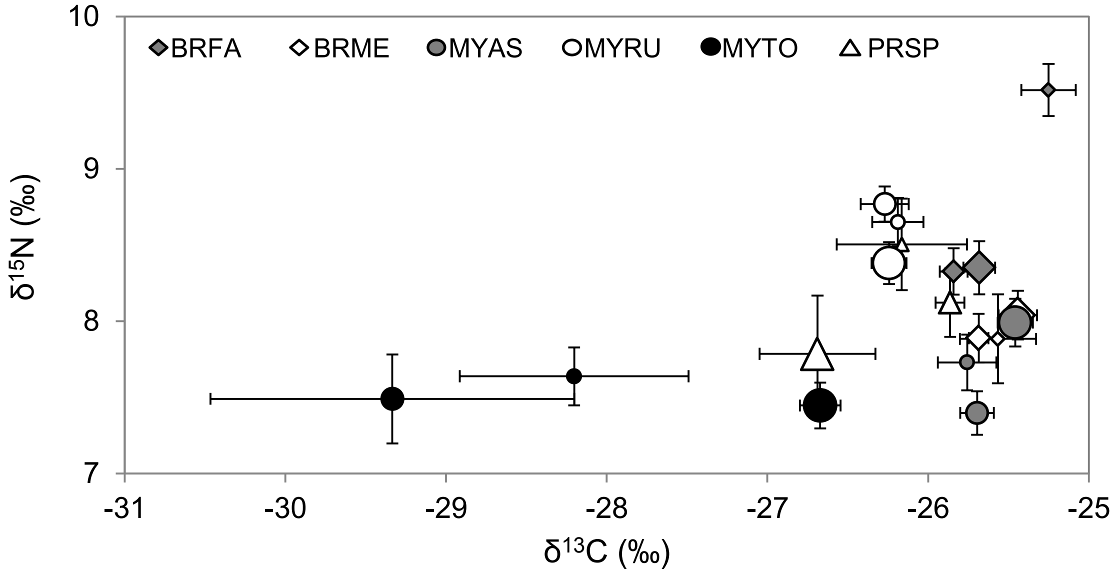


FIG. 15. Carbon and nitrogen isotope ratio biplots (mean ± S.E.) for six frugivorous fish species during three hydrological seasons. Species codes follow Table 2. Large symbols represent high water, medium symbols falling water, and small symbols low water.

the other species. The $\delta^{13}C$ signature of *B. melanopterus* appears to overlap those of all species except *M. rubripinnis* and *M. torquatus,* both of which had more ^{13}C-depleted signatures. The $\delta^{15}N$ signature of *B. melanopterus* appeared to overlap that of *Pristobrycon* sp. and to be intermediate to those of all other species. *Myloplus rubripinnis* had a ^{13}C-depleted signature compared to other species, except for *M. torquatus,* and a ^{15}N-enriched signature in comparison to all other species in the dataset (Fig. 15).

The narrow range of $\delta^{15}N$ signatures was reflected in the low variation in trophic positions (TP) estimated across all three seasons. No fish species had a TP > 2.5 and most species had TP ≈ 2, indicating that all species are primary consumers. The average TP during the HW season was 2.0, and there was a difference of only 0.23 TP units between the lowest (*M. torquatus*) and the highest consumer (*Myloplus rubripinnis*). During the FW season, the average TP was 2.0, with a difference of 0.33 TP units between the lowest (*M. asterias*) and the highest consumer (*Myloplus rubripinnis*). The average TP during the LW season was 2.1 with a difference of 0.46 TP units between the lowest (*M. torquatus*) and the highest consumer (*B. falcatus*) (Fig. 16).

Discussion

Fish consumption of seasonally available allochthonous food resources

In the lower Apaporis River, fishes consumed food resources derived from the floodplain forest during every hydrological season, and in proportions largely concordant with availability. Fruit and seeds made the strongest contribution (in terms of volume) to the diet of all of the species analyzed and were the most frequently consumed food type during the HW season. As demonstrated here, and in previous studies of the fruiting phenology in the Amazon, many plants in floodplain forest are synchronized with the annual flood (Kubitzki and Ziburski 1994, Parolin et al. 2004, Vargas and Stevenson 2009). This is a strategy that facilitates passive seed dispersal by water (i.e., hydrochory) and active seed dispersal by fishes (i.e., ichthiochory; Goulding 1983b, Kubitzki and Ziburski 1994, Correa et al. 2007, Horn et al. 2011). The large diversity, volume, and frequency of consumption of fruit and seeds during the HW season suggest that the fishes studied here would be best characterized as seasonal frugivores. The ability to feed on fruits is the result of morphological, physiological and behavioral adaptations possessed by certain Neotropical characiform lineages (Correa et al. 2007). Moreover, this is a derived feeding strategy that, at least among characiform fishes, appears to have evolved from omnivory and takes advantage of a seasonal but rich food resource (Correa et al. 2007).

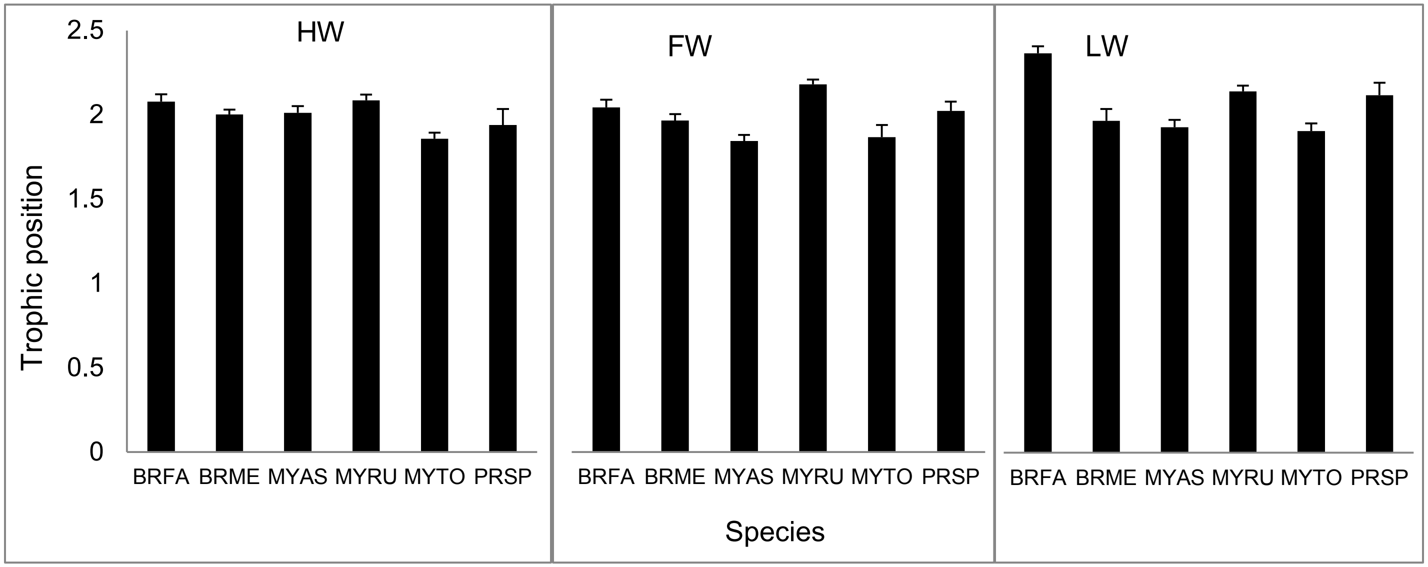


FIG. 16. Trophic position of six frugivorous fish species during three hydrological seasons. Values are mean +S.E. Season and species codes follow those in Table 2.

Frugivorous diets during floods are consistent with earlier findings for other species within the genera studied here. *Myloplus rhomboidales* from French Guiana consumed large amounts of seeds during the rainy season (Boujard et al. 1990), and two *Myloplus* species (referred to as *Myleus* sp. A and B) from the Machado River in Central Brazil also consumed large amounts of fruit and seeds during the HW season (Goulding 1980). Several piranha species are known to consume variable amounts of fruits and seeds on a seasonal basis (Goulding 1980, Nico and Taphorn 1988, Nico 1991). Goulding (1980) analyzed a few individuals of an unidentified piranha species (*Serrasalmus* sp. B) from the Central Amazon which, based on a photograph included in his publication, largely resembles the species identified as *Pristobrycon* sp. in this study (most likely an undescribed species). The species found in this study, like the species examined by Goulding, has a diet that in every season was dominated by fruit and seeds. Furthermore, analysis of $\delta^{15}N$ isotopic ratios placed *Pristobrycon* sp. at the same trophic position as *Myloplus* and *Brycon* species, confirming that *Pristobrycon* sp. is a primary consumer. *Brycon* species are usually considered omnivores because terrestrial insects and also small vertebrates (including fish) are frequently consumed (Goulding 1980, Albrecht et al. 2009). Results of the current study revealed a strong pattern of frugivory for both *B. falcatus* and *B. melanopterus* during the HW season. During the FW and LW seasons, both *Brycon* species consumed greater volumes of terrestrial invertebrates.

As the flood pulse subsided in the lower Apaporis River, fruiting was followed by renewed flowering. Fishes responded to this change in food availability by supplementing their diet with flowers floating on the surface and by nipping on leaves. It is important to clarify that although the extent of the flooded forest gradually decreased with lower water levels, fishes still had access to the forest during the FW season. By the middle of the FW season (beginning of September) for instance, the width of the flooded forest in the Taraira Lake ranged from 10 – 100 m, depending on the elevation gradient and forest composition at a particular site. Dense shrub patches (e.g., *Q. amazonica*, *Psidium densicomum* (Myrtaceae), *Symmeria paniculata* (Polygonaceae)) that remained partially or completely submerged during the FW season, were fairly common along the edge of the lake. The forest was not completely drained until the end of October, and therefore fishes could enter the flooded forest more than 6 months during the year. The low-water season is interrupted by 1–2 weeks of locally heavy rainfall in November, which increases the water level nearly 3 m (Correa 1999). Fish sampling was conducted at the beginning of the LW season. During this season, the average volume of stomach contents was lower and there was a higher frequency of empty stomachs than during the two previous seasons. Most of the fishes caught during this season, however, had ingested significant amounts of food of terrestrial origin. Similar results were reported in a two-year study in Lago do Prato, a black-water lake of the Rio Negro, that showed that fish species consistently fed on forest resources across seasons (Junk et al. 1997). During the LW season, fishes fed on forest resources along the edge of the Apaporis River. Even though fishes cannot enter the forest during this season, they take advantage of plant materials and terrestrial insects that fall from vegetation that extends over the water, as well as plant material that rolls down the bank or blows into the water.

In a previous study of fish assemblage structure in Taraira Lake, Correa (2008) documented habitat affinities during periods of the annual hydrological cycle. During the LW season, species from the flooded forest moved into habitats with dense vegetation cover, such as the lower portions of lagoon channels and streams and isolated patches of shrubs, where they had access to allochthonous food resources. The lower Apaporis River has a continuous and diverse forest that produces allochthonous food resources throughout the year. Because black-water ecosystems in the Amazon (e.g., Rio Negro and Apaporis watersheds) have extremely low autochthonous primary production (Melack and Forsberg 2001 provide a comparative review of Amazon floodplain lakes), allochthonous forest resources are particularly important sources of energy for their aquatic food webs (Goulding et al. 1988). It would be interesting to compare trophic ecology of fishes from the relatively pristine Apaporis with that of fishes from areas that have been deforested, and also with intact forested areas from other regions of the Amazon that have clay-rich alluvial sediments and higher inorganic nutrient concentrations. The relative nutritional value of food resources is a key factor in models of optimal foraging (Stephens and Krebs 1986) as well as the nutritional ecology paradigm (Clements et al. 2009, Raubenheimer et al. 2009). Waldhoff and colleagues (1996) analyzed the nutrient composition of 19 fruit species consumed by fishes from a flooded forest near Manaus, Brazil. Most fruits were rich in soluble carbohydrates (mean 67.3% of fruit flesh dry mass), with variable amounts of crude protein (ranging from 43% to 3% dry mass) and crude fat (ranging from 59.9 to 0.6 % dry mass). Feeding trials with fruits and seeds collected in the floodplain forests resulted in positive growth rates for juveniles of the frugivorous serrasalmid *Colossoma macropomum*, although growth was correlated with protein content of the fruits (Roubach and Saint-Paul 1994). Digestibility and energy assimilation by fish also was variable across fruit taxa (da Silva et al. 1999). How differences in nutritional value of fruits and other plant matter influence patterns of consumption by fishes in natural settings, however, is unknown. The consumption of a large diversity of fruits and other plant material by these fishes may be related to food complementarity. Complementary food consumption has been shown to be an efficient strategy to obtain balanced nutrition (Raubenheimer et al. 2005, Raubenheimer and Jones 2006) and to minimize toxic effects of plant defense compounds (Provenza et al. 2007). Compare to the advances in the study of the feeding biology of herbivorous marine fishes (Clements et al. 2009), the study of frugivory in freshwater fishes remains in its infancy. A better understanding of physiological traits associated with fish frugivory, nutritional requirements, capability to regulate macronutrient intake (Simpson and Raubenheimer 2001), and the extent in which fruits meet nutrient requirements would greatly add to the development of predictive models of foraging.

By consuming large amounts of allochthonous foods derived from flooded forests, frugivorous fishes are an important part of the nutrient cycle in floodplains, not only by transferring energy from the forest into the aquatic food web, but also by accelerating nutrient cycling. Fruits, seeds, flowers, leaves and other plant material that fall into the water accumulate on the substrate as forest litter. Decomposition in floodplain forests is a slow process; in part because of hypoxic conditions associated with submerged sediments prevent shredding by aquatic invertebrates (Furch and Junk 1997). Moreover, forest litter inundated by acidic black waters may take twice the time to decompose as litter in floodplain forests inundated by more neutral waters (Furch and Junk 1997, Piedade et al. 2001). By assimilating material from terrestrial vegetation that falls into the water, fishes not only incorporate this material into the aquatic food web as biomass that can be transferred to upper trophic levels, but they also reduce the amount of biomass that otherwise would accumulate as detritus that moves through the microbial loop. Frugivorous fishes can play important roles in seed dispersal and forest regeneration in Amazonian floodplains (Kubitzki and Ziburski 1994, Correa et al. 2007, Anderson et al. 2009, Horn et al. 2011), and the seed dispersal activities of migratory frugivores, in particular, can yield food web subsidies in these ecosystems (Flecker et al. 2010).

This study appears to be the first to quantify seasonal changes in food availability while simultaneously analyzing food consumption and dietary overlap among Amazon floodplain fishes. Fruits of several plant species consumed by fish were not collected in traps or recorded during visual censuses. *Quiina amazonica* and *B. corymbosa,* for instance, were the most abundant shrubs that produced fruits in the lake during the HW season and the river during the FW season. Because shrub branches were positioned close to the water, their fruits were not collected in the traps in proportions that accurately reflect their availability in the habitat. Fruits from these shrubs were consumed in large amounts by fishes. Given the high floristic diversity in the floodplain forest of the lower Apaporis and the observed patchy distribution of many plant species, it is difficult to obtain an accurate estimate of fruit and flower production, and large samples are needed. Visual censuses were useful in finding fruits that were not collected in the traps, and the combination of the two methods improves estimates of availability (Vargas and Stevenson 2009).

Seasonal diet shift and food partitioning

The first question this study attempted to answer was whether or not fishes respond to fluctuations in food availability. I predicted that if fishes were unable to detect fluctuations in food availability, no seasonal differences in feeding strategies would be observed; even if, as in the case in the lower Apaporis River, resource availability showed strong seasonal patterns. This study, indeed, detected changes in patterns of food consumption for six floodplain fish species across seasons. The second question was related to the manner in which feeding strategies change in response to fluctuations in food availability. If frugivory primarily serves to maximize net energy gain, then fishes should preferentially feed on items to which their phenotype is best adapted (e.g., strong multicuspide teeth and a long intestine, reviewed by Correa et al. 2007) during times of high fruit abundance. This was the case during the HW season when all of the species consumed a large diversity and volume of fruits. Specialization on fruits during the HW season, when fishes are able to forage throughout the flooded forest, represents an optimal feeding strategy facilitated by both food availability and environmental connectivity (Table 1 in MacArthur and Pianka 1966). In the context of optimal foraging theory, I predicted that species would expand their diet breadth to include less desirable foods as preferred foods become scarcer. There was not a consistent pattern of diet breadth expansion in relation to decreased food availability (Fig. 13). Instead, the response was variable among species, which suggests interspecific differences in foraging efficiencies. Only three species, *Brycon falcatus, B. melanopterus,* and *Myloplus asterias* expanded their trophic niche breadth as the availability of fruits decreased. They, however, compressed their diet again during the LW season when the availability of terrestrial food resources was even lower. Unlike these species, *Myloplus torquatus* did not expand its diet breadth until the LW season, whereas *Myloplus rubripinnis* and *Pristobrycon* sp. maintained a relatively constant diet breadth across seasons.

The alternative response to reduction in food availability is a reduction in niche breadth, which is consistent with the theory of limiting similarity and the niche overlap hypothesis, in which increased interspecific competition should induce niche segregation and reduction in niche overlap. Analyses of diets at coarse and fine scales of resolution and stable isotopes all revealed a general pattern of increased dietary segregation among species as the water level receded (FW and LW seasons) and terrestrial food resources were less available for fishes. Although there was more dietary segregation during the FW season relative to the HW season, mean niche breadth was not statistically significantly different across seasons. This suggests that in this fish assemblage, dietary segregation among species was not associated with seasonal niche compression even though diet shifts were involved.

During the HW season, diets of all species were dominated, to various degrees, by fruits and seeds. Species that specialized on fruits and seeds had relatively narrow diet breadths (e.g., *Brycon falcatus* and *Pristobrycon* sp.), whereas those species that consumed significant amounts of other food categories had broader diet breadths (e.g., *Myloplus rubripinnis* and *M. torquatus*). During the FW season, when fruits were less available, all species except for *Pristobrycon* sp. switched their diets. Some species expanded their trophic niche breadth by adding a variety of alternative foods to their diets (e.g., *Brycon falcatus*, *B. melanopterus*, and *M asterias*), while other species maintained a relatively constant niche breadth by replacing fruits and seeds with other dominant food categories (e.g., flowers and leaves in the case of *M. rubripinnis,* and periphyton in the case of *M. torquatus*). During the LW season, as water completely receded from the forest and the availability of forest food resources to fish was reduced, some species reduced their diet breadth by feeding heavily on one or a few food categories (e.g., insects by *Brycon falcatus* and *B. melanopterus*; leaves by *M asterias*). However, other species either maintained a relatively constant diet breadth by replacing one or more dominant food types with others (e.g., *Myloplus rubripinnis*) or expanded their diet breadth by adding several alternative foods to their diets (e.g., *Myloplus torquatus*). These changes in feeding strategies are consistent with the concept of diet switching, which according to Gerking (1994) "is not an all-or-none proposition, but instead it is a change in the relative proportions" of food in the diet. Although there never was complete niche segregation among these fishes, these dietary changes effectively reduce interspecific niche overlap. In a three species model, Abrams and Rueffler (2009) found that coexistence was favorable under moderate niche segregation when species were efficient consumers. Under these circumstances, ecological separation among species does not need to be symmetrical. This was the case among the fishes studied here; during the LW season both *Brycon falcatus* and *B. melanopterus* had become largely insectivores, and both *Myloplus asterias* and *M. rubripinnis* had become primarily leaf eaters. Fat storage, which was commonly observed in these fishes during the LW season, could buffer the negative effects of food scarcity on fitness and thereby increase tolerance of niche overlap under competition.

Although food resource partitioning appears to be ubiquitous among fishes (Ross 1986, Gerking 1994), few studies have analyzed its occurrence among Neotropical fish assemblages and no consensus exists on how seasonality influences dietary niche overlap among species. Seasonal patterns of community-wide resource partitioning were observed in four Neotropical fish assemblages (Winemiller and Pianka 1990) in which significantly lower dietary overlap occurred during low-water periods in the most species-rich assemblages. A community-wide study of trophic resource partitioning among fishes in a floodplain lake in Central Amazonia found no seasonal differences in overlap among trophic guilds (Mérona and Rankin-de-Mérona 2004). Research on piscivorous Neotropical fishes has found variable patterns of dietary segregation in relation to season. Some studies report ranges of dietary overlap values among species throughout the year (Nico and Taphorn 1988, Barbarino-Duque and Winemiller 2003). Winemiller (1989) reported lower interspecific dietary overlap among juvenile piscivores in the llanos region of Venezuela during the falling-water season when availability of invertebrate prey was reduced. Seasonal habitat partitioning among piscivorous *Cichla* species in a llanos river was reported by Jepsen et al. (1997). Studies on trophic resources partitioning among herbivorous fishes are more limited. Diets of two *Myleus* species and *Leporinus friderici* (omnivore) in two French Guianan rivers were broad during the rainy season; diet breadth declined and interspecific dietary overlap was essentially nil during the dry season (Boujard et al. 1990). In contrast, two herbivorous characids, *Astyanax shubarti* and *Cheirodon stenodon*, in a floodplain lake in the Paraná River basin had broadly overlapping diets during the dry season and lower dietary overlap during the wet season (Eichbaum Esteves and Galetti 1995).

An important finding of the approach followed here to estimate niche breadth is that the patterns of niche breath revealed by PERMDISP (Fig. 12) were consistent with those revealed by Levins' index (Fig. 13). This suggests that PERMDISP can be a useful alternative method to estimate trophic niche breadth, with the advantage that PERMDISP allows statistical quantification of the significance of variation in niche breadth between species pairs.

Contribution of allochthonous food resources to fish diversity maintenance

Fruit production of importance to fishes as a food resource in Amazon floodplain forests is estimated between 1'600,000 to 5'300,000 t/y/ha (wet weight). This estimate is conservative and represents only 10% of the estimated total annual fruit production in this region (Waldhoff et al. 1996). Ample evidence has been accumulated supporting the significant contribution of fruit production to fish biomass in floodplain forests in the Amazon Basin (Goulding 1980, Goulding 1983a, Saint-Paul et al. 2000, Barthem and Goulding 2007). High fish diversity in the Amazon often is associated with high biomass (Goulding et al. 1988). How is this diversity and biomass maintained? In a synthesis of the ecological dynamics of fishes in Amazon floodplains, Junk et al. (1997) argued that high fish species richness in Amazonian white-water and black-water floodplain forests is maintained by habitat diversity. The high floristic diversity of the lower Apaporis River yields a diverse resource base for frugivores. Fishes in the lower Apaporis River consumed these diverse fruits and seeds and had broadly overlapping diets. During the flood, the high abundance and diversity of fruits and seeds probably facilitates coexistence of frugivorous fishes. These highly nutritious food resources allow fishes to store energy that can be utilized during periods of food scarcity.

Accumulation of lipids during periods of high food abundance is commonly observed among fishes of floodplain rivers in South America (Junk 1985, Arrington et al. 2006). Visceral fat deposits were frequently observed in fishes of the Apaporis River, especially during the LW season. Junk et al. (1997) argued that interspecific competition among floodplain fishes is reduced when populations are reduced during the annual LW season, with local extirpation prevented by dispersal and recolonization. Chesson and Huntly (1997) countered the view that species diversity is promoted by environmental fluctuations through a reduction in competition. They demonstrated that reductions in population size *per se* do not diminish competition, and instead lower the tolerance of species to competition. They further argued that “niche differences are essential to species coexistence” and species coexist (in the long term) only when responding differently to environmental fluctuations, i.e., temporal niche segregation. Under these circumstances, environmental fluctuations promote the maintenance of species diversity (Chesson and Huntly 1997, Chesson 2000). In the lower Apaporis, falling-water levels shrink flooded areas which, in combination with phenological cycles, alter food availability; fishes in turn, adjust their feeding strategies in response to changes in food availability. Thus, under reduced food availability, during low water conditions, coexistence appears to be facilitated by trophic niche partitioning.

CHAPTER III

INTERSPECIFIC AND WITHIN-PLANT $\delta^{13}C$ AND $\delta^{15}N$ ISOTOPIC VARIABILITY AMONG FLOODPLAIN FORESTS WOODY PLANTS IN THE WESTERN AMAZON BASIN

Introduction

The use of stable isotopes in ecology has increased steadily during the past three decades, and ecological applications are diverse in scope and scale (Dawson et al. 2002, Fry 2006, West et al. 2006). Stable isotopes have been used to reconstruct paleo-climate, model global biogeochemical cycles, understand patterns of migration, depict food sources for consumers, and elucidate physiological processes at the organismal level. All of these applications rely on natural variation in the abundance of stable isotopes in the environment (Peterson and Fry 1987, Fry 2006). Patterns of variation in the ratio of carbon stable isotopes ($^{13}C/^{12}C$ and indicated by $\delta^{13}C$) in plants, for instance, are commonly used to trace the origin of food assimilated by animals. $\delta^{13}C$ variation among plants originates from the discrimination against the heavy ^{13}C isotope during photosynthesis, resulting in plants having $\delta^{13}C$-depleted tissues relative to atmospheric CO_2. Local abiotic factors, such as irradiance, atmospheric humidity, soil moisture, salinity and N availability, as well as traits related to plant morphology, physiological processes and genotype, influence ^{13}C discrimination to various degrees (reviewed by Dawson et al. 2002 and Bowling et al. 2008). Thus, plants have distinctive $\delta^{13}C$ signatures that are transferred to herbivores and other consumers at higher levels in the food web (DeNiro and Epstein 1978, Fry and Sherr 1984, McCutchan et al. 2003). Nitrogen isotopes ($^{15}N/^{14}N$ as indicated by $\delta^{15}N$) are commonly used to estimate trophic positions of consumers in food webs. $\delta^{15}N$ accumulates incrementally from the base to the top of a food chain (Post 2002). With the exception of some species (e.g., N-fixing legumes), plants do not uptake N_2 from the atmosphere, but instead N is absorbed directly from the soil by the roots or indirectly through mycorrhizal associations. Spatial and temporal variation in N sources, as well as mycorrhizal associations and physiological mechanisms of N assimilation and allocation, cause variation in plant $\delta^{15}N$ isotopic signatures (reviewed by Evans 2001 and Dawson et al. 2002). Even among N-fixing legumes, unequal rates of N fixation across taxa and differences in N soil concentration yield different plant $\delta^{15}N$ isotopic signatures (West et al. 2005).

Given that abiotic factors as well as individual physiological processes and genotype can influence isotopic variation, how much isotopic variation is expected among species within a local plant community or between tissues at the individual level? In a mixed temperate forest, shaded leaves in a single crown had $\delta^{13}C$-depleted signatures relative to leaves directly exposed to sunlight; interestingly, no interspecific differences were found in the forest (Chevillat et al. 2005). In tropical forests, leaves from understory plants usually have more negative $\delta^{13}C$ signatures relative to leaves at the canopy top where light is more available (Medina and Minchin 1980, Martinelli et al. 1998). Within-plant $\delta^{13}C$ variation appears to be common, at least for roots and woody tissues which generally have more enriched signatures than leaves (mean enrichment = 2.3 and 3.2‰, respectively; Bowling et al. 2008). In terms of $\delta^{15}N$, differences among co-occurring species usually range from 0 to 10‰ (Evans 2001), with differences of ≈1‰ being considered biologically significant (Handley and Raven 1992). Within-plant variation in $\delta^{15}N$ is usually < 3‰ between leaves and roots from plants in temperate deciduous forests and tall-grass prairies, and desert plants can have up to 7‰ individual variation (Evans 2001). Most of these examples come from studies attempting to quantify isotopic discrimination between plants and global C and N pools, and usually were conducted under controlled conditions or measured natural isotopic variation of only a few species in the field. Most of these studies only analyzed vegetative tissues and therefore it is not known if reproductive tissues follow similar patterns of interspecific and within-plant isotopic variability. Given that fruits are major food resources for a large suite of vertebrate consumers, especially in tropical forests, it is important to investigate whether fruits follow the same patterns of variation as leaf tissues. In seasonally flooded forests in the Amazon Basin, for instance, a large diversity of frugivorous mammals (Haugaasen and Peres 2005, Haugaasen and Peres 2007), birds (Borges and Carvalhaes 2000, Naka et al. 2007), and fishes (Goulding 1980, Goulding et al. 1988) feed within the forest during annual flood, the period when the majority of plants produce fruits and seeds (Parolin et al. 2004).

The current study investigates natural variation in C and N stable isotopes among leave, wood and fruit tissues of plant species in two Amazonian floodplain forests. Results from this study will contribute to a better understanding of natural isotopic variation in plants and how such variation could influence the interpretation of isotopic signatures and the establishment of trophic links between plants and consumers.

Materials and methods

Study sites

Floodplain forests in two areas of the western Amazon (southern Colombia) with distinct biogeochemistry were sampled. The first forest (várzea, which refers to a forest inundated by whitewater) is located on the floodplain between the Amazon and Loreto-Yacu rivers, at an elevation of ≈50 m.a.s.l. The mean annual rainfall is 3,325.2 mm, mean monthly rainfall is 277.4 mm (1974–2004), and mean monthly temperature ranges from 23 to 28ºC (Duque et al. 1997). Like most lowland regions of the Amazon Basin, this area has an annual flooding regime, with a difference of 12 m between maximum (May to June) and minimum (September) water levels (Duque et al. 1997). Sampling was conducted during the mid-rising-water season (February to March, 2007) in the evergreen flooded forest surrounding three interconnected lakes within the floodplain (these will be referred to as the "Tarapoto Lakes complex" here after). Sampled lakes included Lago Shaman (3°46' 93" S, 70°24' 42" W), Lago Tarapoto (sampled at Poza de Soraida 3° 49' 13" S, 70° 28' 29" W), and Cocha Larga (3° 49' 36" S, 70° 28' 23" W). These lakes have physicochemical properties similar to those of other upper whitewater Amazonian floodplain lakes (Sioli 1984), with conductivity ranging from 78.1 to 95.2 μS cm^{-1}, pH from 6.2 to 6.9, Secchi disk transparency from 0.4 to 0.8 m, and temperature from 26.2 to 29.4 ºC. The vegetation corresponds to a seasonally flooded medium-height forest over alluvial deposits of Andean origin (Botero 1999).

The second forest (igapó, which refers to a forest inundated by blackwater) is located in the lower Apaporis River, a large blackwater river that drains the southwestern portion of the ancient Guyana Shield. Elevation in the lower Apaporis region is ≈100 m.a.s.l., with a mean annual rainfall of 3,832.5 mm, mean monthly rainfall ranging from 270 to 391 mm

(1984–1995), and mean annual temperature of 25.1ºC (Defler 1996). The annual flooding regime causes a 9-m fluctuation between maximum (May to July) and minimum (December to January) water levels, flooding the forest for up to 7–8 mo every year. Sampling was conducted during the high-and falling-water seasons (from late May to early October 2009) in the evergreen flooded forest along the river and in an adjacent oxbow lake (Lago Taraira, 1°08'46.3" S, 69°29' 14.4" W). Physicochemical properties of the river are similar to those of other blackwater rivers in the Amazon Basin (Sioli 1984), with conductivity ranging from 5.9 to 7.4 µS cm^{-1}, pH from 5.2 to 6.5 pH, Secchi disk transparency from 0.6 to 1.3 m, and temperature from 25.8 to 27.9 ºC. Species richness in the flooded forest is estimated in 215 species, 65% of which are not shared with other forest types in the area (Clavijo et al. 2009), and the soil is characterized as infertile white clay (Defler 1996).

Samples collection

Samples for analysis of C and N stable isotope ratios were collected from 20 to 30 species of woody plants, at each site. Species included trees, shrubs, vines, and hemi-epiphytes that were common at each site, most of which were bearing fruits at the time when sampling was conducted. Sampling was conducted inside the flooded forest and along the forest edge using a canoe; samples from the canopy were obtained by climbing. In the Tarapoto Lakes, samples of fruits, leaves, and trunk wood (which included bark and sapwood) were collected from individual plants in order to assess within-plant and interspecific variation. Samples of fruits and leaves were also collected in the lower Apaporis River to assess interspecific variation. Except for one shrub species (*Symmeria paniculata*), no species were common between sites. Botanical samples of all species were collected and deposited in the Colombian Amazon Herbarium (COAH), Instituto Amazónico de Investigaciones Científicas–Sinchi, Colombia. Taxonomic identifications were conducted at the COAH by the herbarium curator (D. Cárdenas).

Samples were preserved in NaCl immediately after collection. In the lab, samples were rinsed with deionized water and soaked for 24 h, after which water was changed and the samples were soaked for another 24 h. Samples were then rinsed and placed in a drying oven at 60°C for 48 h. Dried samples were processed in an electric grinder (Wing-L-Bug by Pike Technologies) for 1 to 5 min until the sample was converted to a fine powder. Samples were weighed to the nearest 0.01 mg and placed into ultra-pure tin capsules. Sealed samples were sent to the Analytical Chemistry Laboratory, Institute of Ecology, University of Georgia, for analysis of carbon and nitrogen percentage composition and stable isotope ratios. Carbon and nitrogen isotope values represent the deviation from the isotopic ratios of Pee Dee Belemnite limestone and atmospheric nitrogen, respectively, in delta notation: $\delta^{13}C$ or $\delta^{15}N$ = ((R sample / R standard) -1) x 1000. Precision of the analysis was $\leq 0.11‰$ measured as the standard deviation among bovine reference samples. Because all samples were taken while the forest was flooded, isotopic variation due to seasonality is not expected. Likewise, no within-site spatial variation is expected because sampling was done within a continuous floodplain forest.

Mean values of $\delta^{13}C$ and $\delta^{15}N$ of leaves and fruits were compared within and between sites using t-tests, for which, assumptions of data distribution normality and homoscedasticity were met. Paired tissue samples taken from a single individual plant were compared with non-parametric Wilcoxon signed rank tests in order to test the null hypothesis that isotopic signatures ($\delta^{13}C$, $\delta^{15}N$) are equal between tissues. In the occurrence of tied ranks, *P*-values were calculated from the exact null distribution using the Package "COIN" in R (Hothorn et al. 2012). Spearman's rank correlation was conducted to determine correlations between variables (δ^{13}C, δ^{15}N) measured from the same tissue samples. Statistical analyses were conducted in R (R Foundation for Statistical Computing).

Results

Interspecific isotopic variation

Within each site, δ^{13}C and N δ^{15}N of both leaves and fruits of flooded forest plant species showed a wide range of variation. In the Tarapoto Lakes complex, δ^{13}C of leaves of 28 species ranged from -35.4 to -27.03‰ (absolute difference = 8.38‰, mean ± SD = -32.05 ± 2.10‰) while δ^{15}N ranged from -0.33 to 4.73‰ (absolute difference = 5.06‰, mean ± SD = 1.64 ± 1.41‰; Table 5, Fig. 17A). δ^{13}C signatures of fruits of 22 species had a wider range of variation than those of leaves (-36.17 to -24.97‰, absolute difference = 11.2‰), but a similar mean (δ^{13}C mean ± SD = -31.14 ± 2.45‰, t-test = 1.40, df = 48, *P* = 0.17). δ^{15}N signatures of fruits had a slightly narrower range of variation than those of leaves (0.29 to 4.40‰, absolute difference = 4.11‰) and a marginally more enriched mean (δ^{15}N mean ± SD = 2.33 ± 1.27‰, t-test = 1.80, df = 48, *P* = 0.08; Table 5, Fig. 18A).

TABLE 5. Isotopic and elemental composition of leaves and fruits of woody plants (*n* = 28 and 22 species, respectively) in the flooded forest (várzea) of the Tarapoto Lakes complex, western Amazon Basin. Abbreviations – Species: indet. = indeterminate. Growth habit: Pl = palm, S = shrub, T = tree, V = vine. Tissue: L = leaf, F = fruit (pulp and seed/s), S = seed only, P = pulp only. Maturity: M = mature, R = ripe, I = immature

Family	Species	Code	Growth habit	Tissue	Maturity	δ^{13}C	δ^{15}N	C:N Ratio	Total %C	Total %N
Annonaceae	Annonaceae indet.	Anin	T	L	M	-29.52	1.64	27.46	53.81	1.96
	Guatteria sp.	Gusp	T	L	M	-32.97	0.46	24.90	47.11	1.89
Apocynaceae	*Tabernaemontana* sp.	Tasp	S	L	M	-29.73	1.16	18.37	44.39	2.42
Arecaceae	*Bactris* sp.1	Basp1	Pl	L	M	-34.08	0.34	36.96	40.36	1.09
	Bactris sp.2	Basp2	Pl	L	M	-33.90	0.85	28.64	44.83	1.56
Asclepiadaceae	*Blepharodon* sp.	Blsp	V	L	M	-32.21	4.73	14.19	43.13	3.04
Cecropiaceae	*Cecropia sp.*	Cesp	T	L	M	-28.70	1.44	18.23	44.35	2.43
Clusiaceae	*Garcinia macrophylla*	*Gama*	T	L	M	-30.57	1.21	31.17	48.92	1.32
	Vismia macrophylla	Vima	T	L	M	-32.96	1.04	33.59	41.46	1.23
Euphorbiaceae	*Amanoa oblongifolia*	Amob	T	L	M	-30.19	-0.28	30.72	47.14	1.53
	Phyllanthus sp.	Physp	S	L	M	-32.64	1.21	22.59	48.05	2.13
Melastomataceae	*Mouriri grandiflora*	Mogr	T	L	M	-34.31	2.47	30.63	36.66	1.20
	Tococa guianensis	Togu	S	L	M	-31.47	2.71	24.52	34.35	1.40
Myristicaceae	*Iryanthera* sp.	Irsp	T	L	M	-33.47	0.82	27.78	50.89	1.83
Myrtaceae	Myrtaceae indet. 1	Myrt1	T	L	M	-34.61	2.52	34.35	41.38	1.20
	Myrtaceae indet. 2	Myrt2	T	L	M	-35.41	-0.33	34.69	44.74	1.29
	Myrtaceae indet. 3	Myrt3	T	L	M	-33.01	2.18	42.51	46.77	1.10
Ochnaceae	*Ouratea* sp.	Ousp	S	L	M	-27.03	3.32	36.02	55.51	1.54
Olacaceae	*Dulacia* sp.	Dusp	T	L	M	-33.69	-0.11	32.21	43.99	1.37
Polygonaceae	*Symmeria paniculata*	Sypa	S	L	M	-29.84	2.56	36.45	48.77	1.34
Rubiaceae	*Alibertia* sp.	Alsp	T	L	M	-32.12	4.65	15.98	46.06	2.88
	Faramea sp.	Fasp	S	L	M	-33.21	2.88	26.70	34.18	1.28
	Psychotria sp.	Pssp	S	L	M	-30.89	4.21	15.00	41.30	2.75

TABLE 5. Continued

Family	Species	Code	Growth habit	Tissue	Maturity	$\delta^{13}C$	$\delta^{15}N$	C:N Ratio	Total %C	Total %N
Sapindaceae	*Paullinia* sp.	Pasp	V	L	M	-32.07	0.19	33.89	40.74	1.20
Sapotaceae	*Micropholis* cf. *venulosa*	Micfve	T	L	M	-31.39	1.42	38.85	49.72	1.28
	Micropholis sp.	Misp	T	L	M	-35.22	1.24	27.23	39.27	1.44
	Pouteria sp.	Posp	T	L	M	-32.82	0.67	29.62	47.54	1.61
Vitaceae	*Cissus* sp.	Cisp	V	L	M	-29.48	0.75	15.63	41.56	2.66
Annonaceae	Annonaceae indet.	Anin	T	P	I	-28.62	3.35	50.80	45.18	0.89
	Guatteria sp.	Gusp	T	F	I	-32.70	1.87	44.95	43.64	1.05
Apocynaceae	*Tabernaemontana* sp.	Tasp	S	F	I	-29.55	3.76	23.41	42.97	1.84
Arecaceae	*Bactris* sp.2	Basp2	Pl	F	R	-32.65	3.40	58.16	40.66	0.70
	Bactris sp.3	Basp3	Pl	F	I	-30.76	1.60	44.30	30.05	0.68
	Bactris sp.1	Basp1	Pl	S	n/a	-33.61	3.40	74.68	43.32	0.58
Cecropiaceae	*Cecropia* sp.	Cesp	T	F	I	-29.01	0.88	22.84	37.27	1.63
Clusiaceae	*Vismia macrophylla*	Vima	T	F	n/a	-35.33	2.68	28.56	80.29	2.81
Euphorbiaceae	*Croton bilocularis*	Crbi	T	F	I	-29.25	1.15	18.66	38.17	2.05
Melastomataceae	*Mouriri grandiflora*	Mogr	T	F	R	-32.53	4.23	75.48	45.29	0.71
Myristicaceae	*Iryanthera* sp.	Irsp	T	F	I	-32.01	1.91	39.80	60.89	1.53
Myrtaceae	Myrtaceae indet. 2	Myrt2	T	F	R	-32.62	1.13	41.10	38.77	1.25
	Myrtaceae indet. 3	Myrt3	T	F	I	-31.06	2.68	46.04	41.66	0.90
Ochnaceae	*Ouratea* sp.	Ousp	S	F	R	-24.97	4.40	30.93	39.64	1.28
Olacaceae	*Dulacia* sp.	Dusp	T	F	R	-33.30	2.63	31.01	52.86	1.75
Polygonaceae	*Symmeria paniculata*	Sypa	S	S	I	-29.60	4.18	43.34	37.53	0.87
Rubiaceae	*Faramea* sp.	Fasp	S	F	I	-36.17	1.39	21.54	44.26	2.05
	Psychotria sp.	Pssp	S	F	R	-29.83	3.08	20.18	47.49	2.35
Sapindaceae	*Paullinia* sp.	Pasp	V	F	I	-30.53	1.62	46.97	52.56	1.46
Sapotaceae	*Micropholis* cf. *venulosa*	Micfve	T	P	I	-29.93	1.01	43.52	36.16	0.83
	Pouteria sp.	Posp	T	F	I	-30.96	0.52	22.72	43.47	1.91
Vitaceae	*Cissus* sp.	Cisp	V	F	I	-30.00	0.29	19.10	36.91	2.03

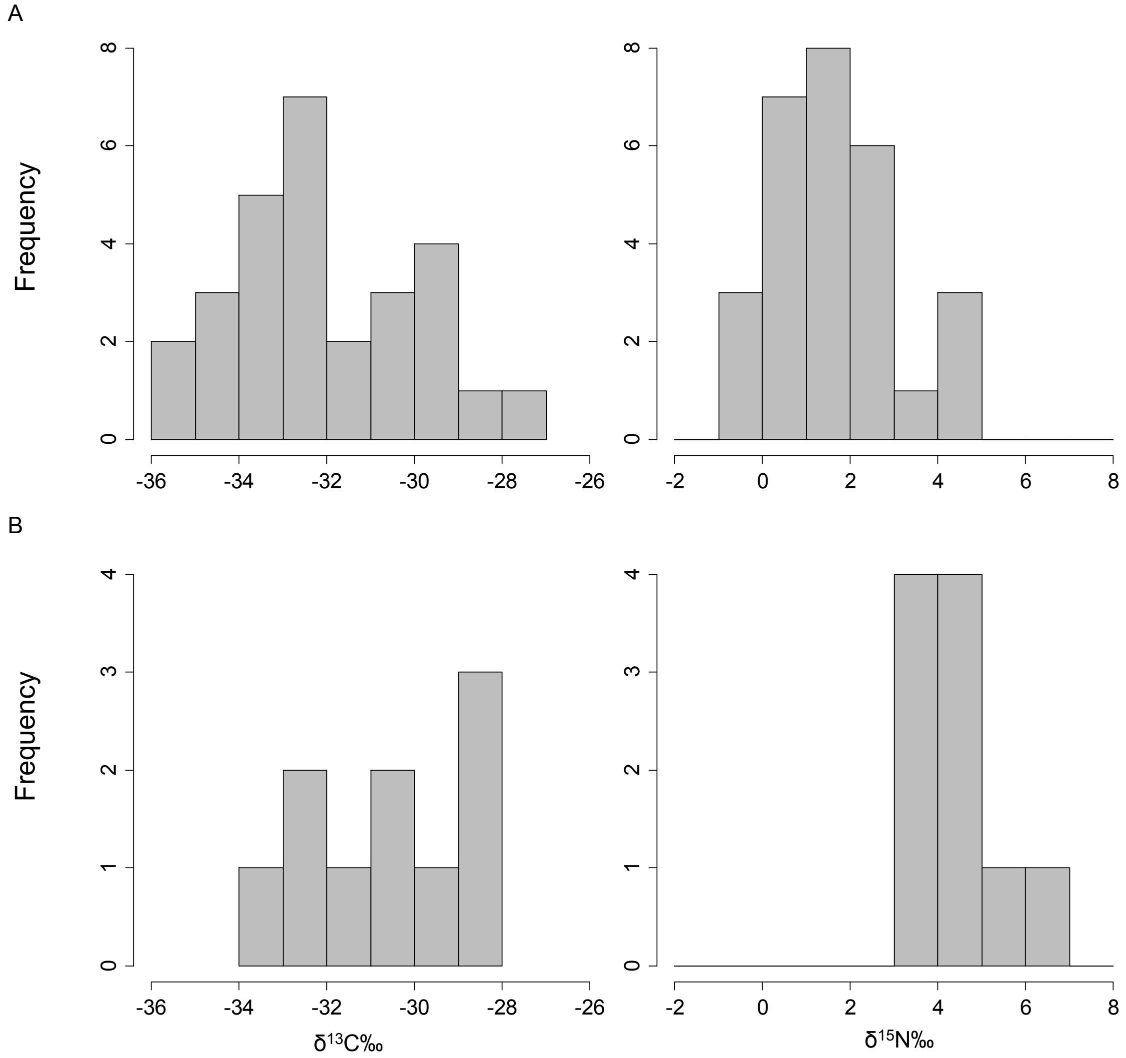


FIG. 17. Frequency distributions of foliar $\delta^{13}C$ and $\delta^{15}N$ of co-occurring plant species from two western Amazonian flooded forest sites with different biogeochemistry. (A) Tarapoto Lakes complex (várzea, 28 species) and (B) lower Apaporis River (igapó, 10 species).

Sample size for leaves was lower for Apaporis than for Tarapoto. $\delta^{13}C$ of leaves of 10 species ranged from -33.69 to -28.57‰ (absolute difference = 5.12‰, mean ± SD = -30.63 ± 1.86‰) while $\delta^{15}N$ ranged from 3.41 to 6.59‰ (absolute difference = 3.18‰, mean ± SD = 4.43 ± 1.02‰; Table 6, Fig. 17B). $\delta^{13}C$ varied greatly among fruits of 22 species, ranging from -33.32 to -26.88‰ (absolute difference = 6.44‰). Fruits had a mean $\delta^{13}C$ similar to that of leaves ($\delta^{13}C$ mean ± SD = -30.18 ± 1.91‰, t-test = 0.63, df = 30, $P = 0.54$). $\delta^{15}N$ signatures of fruits were varied, ranging from 0.60 to 6.35‰ (absolute difference = 5.75‰) and had a mean value similar to that of leaves ($\delta^{15}N$ mean ± SD = 3.92 ± 1.53‰, t-test = -1.11, df = 30, $P = 0.28$; Table 6, Fig. 18B).

Despite differences in biogeochemistry and floristic composition, both sites showed similar mean $\delta^{13}C$ values, as depicted by both leaves and fruits. Mean $\delta^{13}C$ of leaves in the Tarapoto Lakes complex was only marginally more depleted than that in the Lower Apaporis River (t-test = -2.00, df = 36, $P = 0.06$). Fruits in both sites had similar mean $\delta^{13}C$ values (t-test = -1.44, df = 42, $P = 0.16$), although fruits in the Tarapoto Lakes complex had a much wider range of variation (absolute difference = 11.2 vs. 6.44‰, respectively; Fig 18). In contrast, mean $\delta^{15}N$ signatures of leaves and fruits were more depleted in the Tarapoto Lakes complex than in the Apaporis (leaves-t-test = -6.67, df = 36, $p < 0.0001$; fruits-t-test = -3.77, df = 42, $P < 0.0001$; respectively). Fruits from the Tarapoto Lakes complex revealed less variation in $\delta^{15}N$ relative to those from the Apaporis River (absolute difference = 4.11 vs. 5.75‰, respectively; Fig 18).

TABLE 6. Isotopic and elemental composition of leaves and fruits of woody plants (n = 10 and 22 species, respectively) in the flooded forest (igapó) of the lower Apaporis River, western Amazon Basin. Values represent mean ± SD. Abbreviations – Species: indet. = indeterminate. Growth habit: H = hemi- epiphyte, Pl = palm, S = shrub, T = tree, V = vine. Tissue: L = leaf, F = fruit (pulp and seeds), S = seed only, P = pulp only. Maturity: M = mature, Y = young, R = ripe.

Family	Species	Growth habit	Tissue	Maturity	$\delta^{13}C$	$\delta^{15}N$	C:N Ratio	Total %C	Total %N	*N*
Asclepidaceae	*Marsdenia rubrofusca*	V	L	Y & M	-28.85 ± 0.80	4.76 ± 0.48	17.22 ± 4.55	47.09 ± 6.48	2.88 ± 0.73	4
Caesalpinaceae	*Macrolobium acaciifolium*	T	L	Y	-28.61	5.83	13.72	47.58	3.47	1
Chrysobalanaceae	*Indet.*	T	L	Y	-32.47	6.59	23.66	49.65	2.10	1
Euphorbiaceae	*Mabea nitida*	T	L	M	-33.69	3.93	22.90	45.90	2.00	1
Lauraceae	*Nectandra egensis*	T	L	M	-30.86 ± 0.57	4.11 ± 0.52	26.66 ± 3.37	39.06 ± 6.48	1.48 ± 0.31	3
Mimosaceae	*Inga* sp.1	T	L	Y	-30.14 ± 0.16	3.45 ± 0.41	15.12 ± 1.24	47.02 ± 8.87	3.10 ± 0.33	2
	Inga sp.2	T	L	Y	-31.60	3.41	12.53	50.12	4.00	1
Moraceae	*Ficus americana*	H	L	Y & M	-32.46 ± 0.23	4.07 ± 0.63	24.48 ± 3.43	49.96 ± 5.20	2.05 ± 0.07	2
Myrtaceae	*Psidium densicomum*	S	L	Y & M	-29.07 ± 1.98	4.20 ± 0.82	17.60 ± 5.01	46.75 ± 2.92	2.89 ± 1	6
Polygonaceae	*Symmeria paniculata*	S	L	Y	-28.57 ± 1.26	3.99 ± 1.06	17.69 ± 2.17	47.54 ± 5.21	2.74 ± 0.63	3
Aquifoliaceae	*Ilex* sp.	S	F	R	-31.43 ± 096	4.29 ± 0.39	42.36 ± 10.70	49.27± 1.80	1.22 ± 0.27	5
Arecaceae	*Bactris riparia*	Pl	P	R	-32.83	5.62	47.70	40.59	0.85	1
	Astrocaryum jauari	Pl	P	R	-29.57± 0.28	5.15 ± 0.17	33.89 ± 2.02	45.74 ± 5.53	1.35 ± 0.08	2
Asclepidaceae	*Marsdenia rubrofusca*	V	S	R	-26.97	5.35	18.29	35.67	1.95	1
Caesalpinaceae	*Macrolobium acaciifolium*	T	S	R	-27.89	4.02	29.21	37.90	1.30	1
Ebenaceae	*Diospyros poeppigiana*	T	S	n/a	-31.14	2.67	43.82	42.56	0.97	1

TABLE 6. Continued

Family	Species	Growth habit	Tissue	Maturity	$\delta^{13}C$	$\delta^{15}N$	C:N Ratio	Total %C	Total %N	*n*
Euphorbiaceae	*Alchornea discolor*	T	F	R	-27.60	1.24	19.13	52.48	2.74	1
	Mabea nitida	T	F	R	-30.52	4.26	34.80	45.35	1.30	1
Lauraceae	*Nectandra egensis*	T	F	R	-29.78 ± 1.11	3.82 ± 1.21	65.67 ± 23.03	47.96 ± 5.43	0.79 ± 0.23	3
Malpigiaceae	*Byrsonima japurensis*	T	F	R	-32.60 ± 0.23	3.97 ± 0.91	71.85	48.22	0.67	3
Melastomataceae	*Tococa coronata*	S	F	R	-30.54	6.35	24.09	44.63	1.85	1
	Miconia splendens	T	F	n/a	-29.38	4.14	33.01	56.12	1.70	1
Mimosaceae	*Inga* sp. 1	T	P	R	-30.45 ± 1.14	0.77 ± 0.24	22.43 ± 1.96	41.42 ± 7.94	1.87 ± 0.48	3
Moraceae	*Ficus americana*	H	F	R	-31.86 ± 0.87	4.37 ± 0.46	47.63 ± 7.18	43.92 ± 5.84	0.93 ± 0.10	3
Myrtaceae	*Eugenia* sp.	T	F	R	-33.32	0.60	85.96	58.80	0.68	1
Quiinaceae	*Quiina amazonica*	S	F	R	-26.88	3.22	49.51	47.67	0.96	1
Rubiaceae	*Psychotria* cf. *lupulina*	S	F	R	-31.46 ± 1.67	4.86 ± 0.69	23.86 ± 4.97	45.14 ± 2.94	1.95 ± 0.38	4
	Bothriospora corymbosa	S	F	R	-29.51 ± 0.76	5.45 ± 0.68	22.24 ± 1.14	40.47 ± 11.94	1.84 ± 0.62	4
	Genipa americana	T	F	R	-29.40 ± 0.57	3.59 ± 4.27	43.09 ± 17.53	44.29 ± 4.41	1.21 ± 0.59	2
	Amaioua guianensis	T	F	R	-32.18	3.41	78.12	47.10	0.60	1
Sapindaceae	*Matayba guianensis*	T	F	R	-31.02 ± 1.14	3.72 ± 1.08	44.95 ± 6.41	45.94 ± 4.94	1.04 ± 0.18	4
Simaroubaceae	*Simaba orinocensis*	T	P	R	-27.68	5.46	15.76	36.35	2.31	1

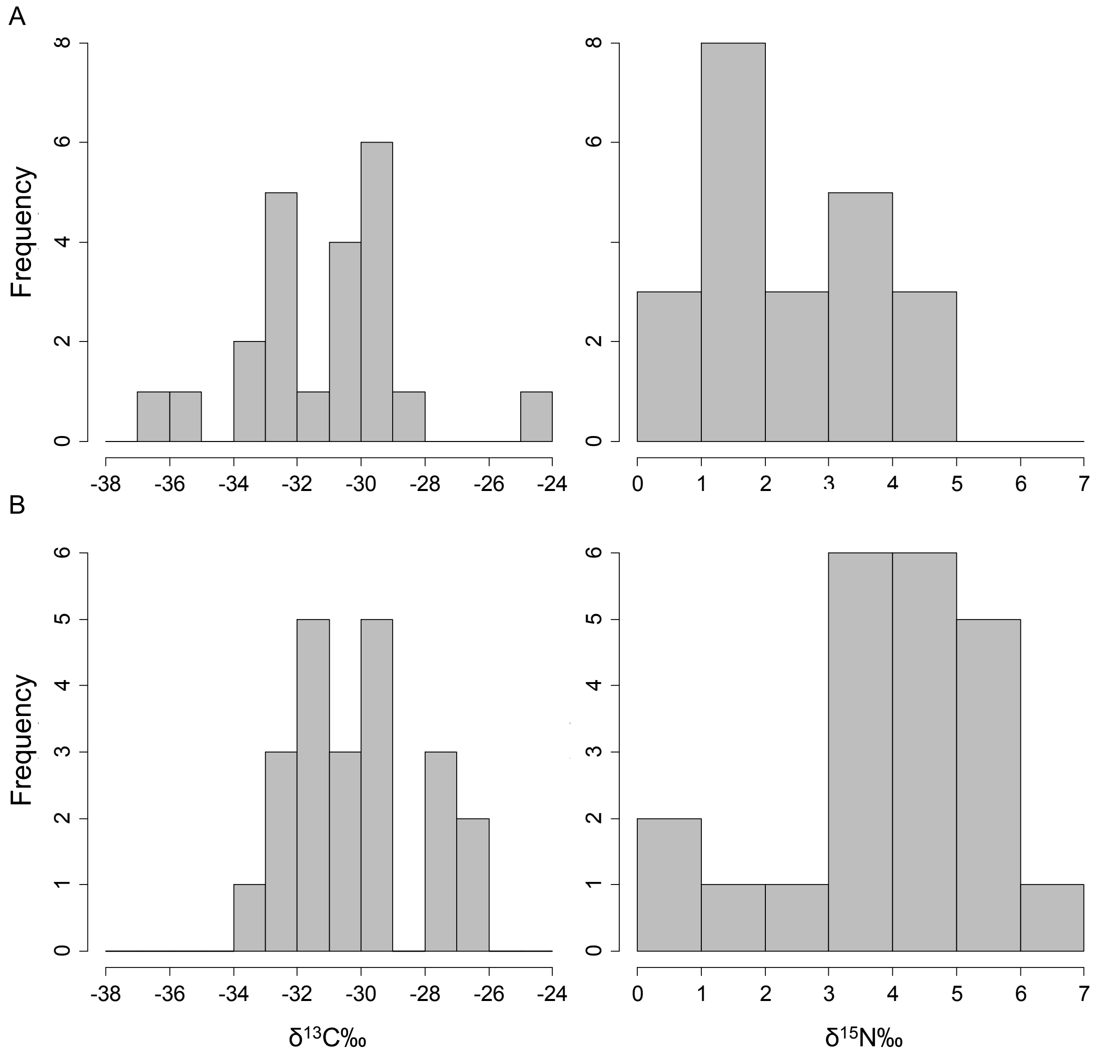


FIG. 18. Frequency distributions of $\delta^{13}C$ and $\delta^{15}N$ fruits of 22 co-occurring plant species in two western Amazonian flooded forest sites with different biogeochemistry. (A) Tarapoto Lakes complex (várzea) and (B) lower Apaporis River (igapó).

Within-plant isotopic variation

Paired comparisons were made for different tissues sampled from individual plants from the Tarapoto Lakes complex. $\delta^{13}C$ isotopic signatures of wood were generally more enriched than those of corresponding leaves (Wilcoxon signed rank test, W = 131, *n* = 18, *P* < 0.05), with a difference of 1.02‰. Few species, however, had wood with more depleted signatures, which, with the exception of one species with wood 1.8‰ lighter than leaves, differed by ≤ 0.5‰ difference (Fig. 19A). δ^{13}C signatures of wood were positively and significantly correlated with those of corresponding leaves (Spearman's rank correlation, rho = 0.66, *P* < 0.05). δ^{15}N isotopic signatures of wood generally were more ^{15}N enriched than those of corresponding leaves; however, the difference was only marginally significant (Wilcoxon signed rank test, W = 126, Z = 1.76, *n* = 18, *P* = 0.08) with an difference of 0.73‰. Only a few species had leaves that were more ^{15}N enriched than wood. In three of these species, leaf signatures were enriched as much as nearly 2‰ (Fig. 19B). δ^{15}N signatures of wood were not correlated with those of corresponding leaves (Spearman's rank correlation, rho = 0.22, *P* = 0.39). Wood C:N ratios were consistently greater than those of leaves across all species (Wilcoxon signed rank test, W = 171, *n* = 18, *P* < 0.0001), with an average difference of 14.7 (1.4–75.3).

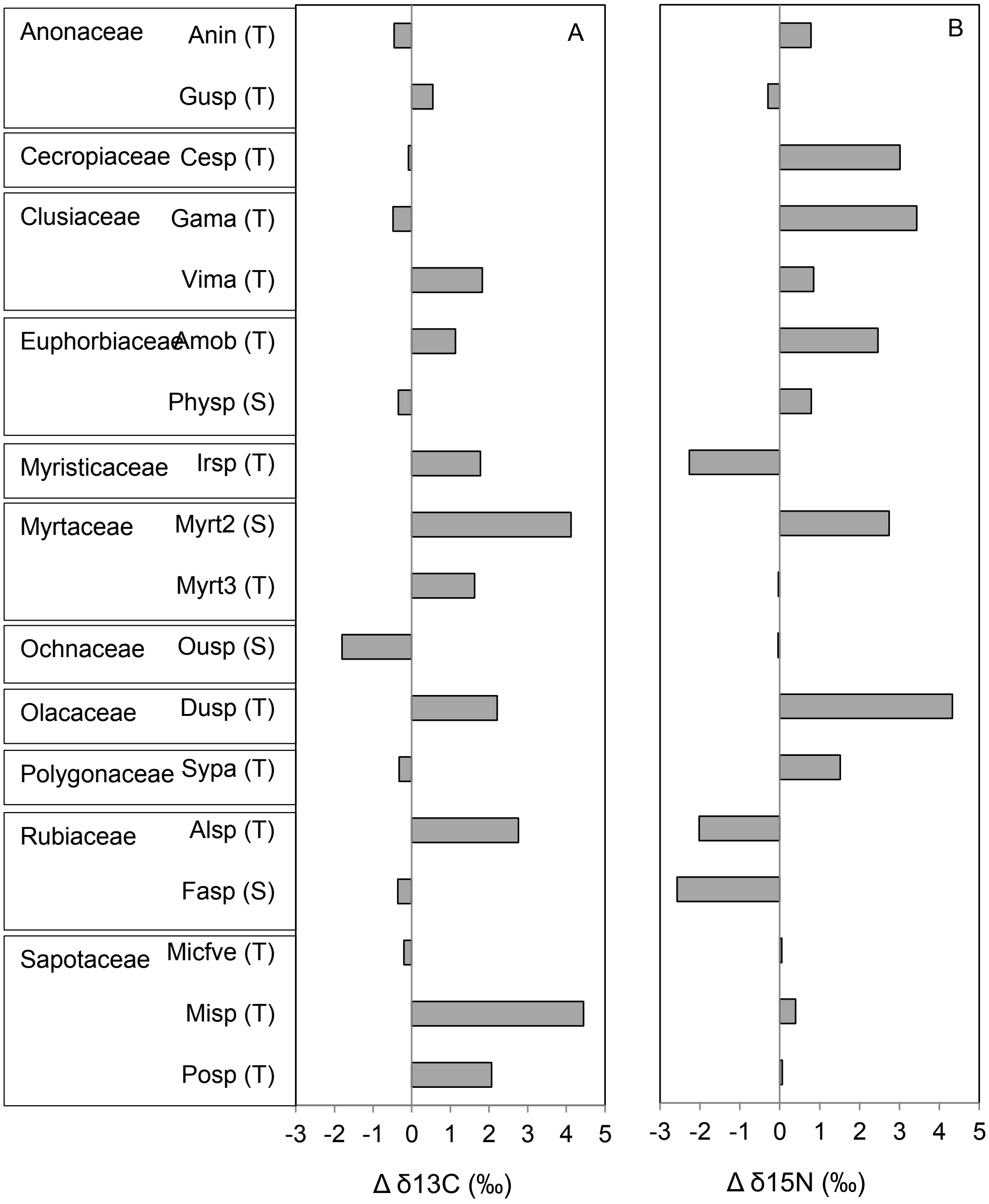


FIG 19. Isotopic variation between trunk wood and leaf tissue of 18 co-occurring plant species from the flooded forest (várzea) of the Tarapoto Lakes complex, western Amazonia. (A) $\Delta\delta^{13}C$ (Wood $\delta^{13}C$ - Leaf $\delta^{13}C$) and (B) $\Delta\delta^{15}N$ (Wood $\delta^{15}N$ - Leaf $\delta^{15}N$). Positive values indicate that wood has heavier isotopic signatures with respect to leaves from the same individual plant. Species codes follow those in Table 5. Plant growth habit is indicated in parenthesis (T=tree, S=shrub).

$\delta^{13}C$ isotopic signatures of fruits were generally more ^{13}C enriched than those of corresponding leaves (Wilcoxon signed rank test, W = 161, $n = 20$, $P < 0.04$), with an average difference of 0.68‰. There were, however, four species in which leaves had more ^{13}C enriched signatures than fruits; in one of them, the difference was as much as nearly 3‰ (Fig. 20A). $\delta^{13}C$ signatures of fruits were positively and significantly correlated with those of corresponding leaves (Spearman's rank correlation, rho = 0.82, $P < 0.0001$). $\delta^{15}N$ isotopic signatures of fruits generally were more ^{15}N enriched than those of corresponding leaves (Wilcoxon signed rank test, W= 179, $n = 20$, $P < 0.005$), with a difference of 1.02‰. There again were few species in which leaves had more ^{15}N enriched signatures than fruits; in two species, the difference was as much as nearly 1.5‰ (Fig. 20B). $\delta^{15}N$ signatures of fruits were weakly correlated with those of corresponding leaves (Spearman's rank correlation, rho = 0.44, $P = 0.055$). Fruit C:N ratios generally were greater than those of leaves (Wilcoxon signed rank test, W = 173, $n = 20$, $P < 0.01$), with an average difference of 9.9 (-6.9 to 44.9). A few species, however, had fruits with lower C:N ratios than leaves; in three species, the difference was nearly 5, and in one species, the difference was nearly 7 (Table 5).

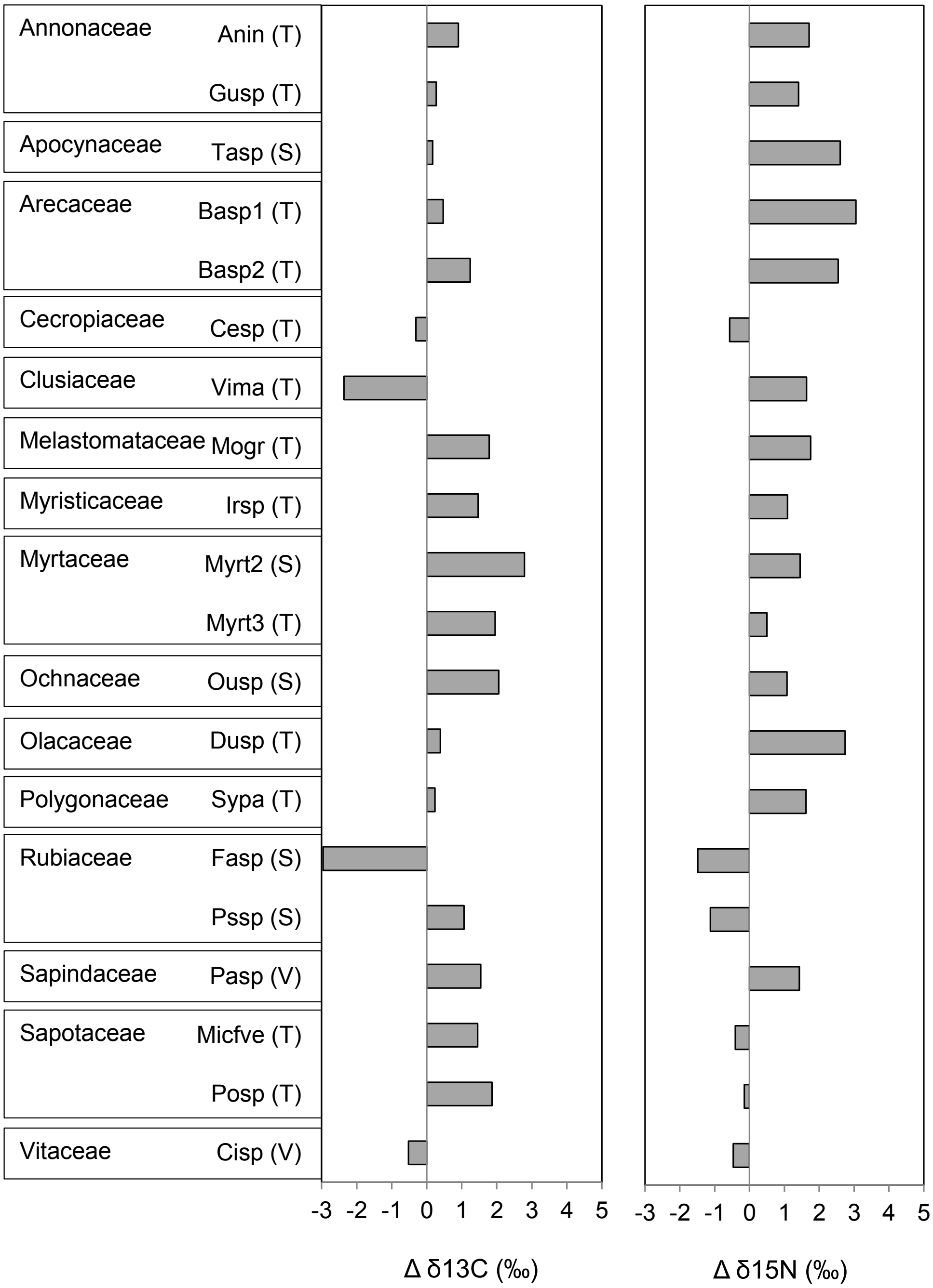


FIG. 20. Isotopic variation between fruits (pulp and seeds) and leaves of 20 co-occurring plant species from the flooded forest (várzea) of the Tarapoto Lakes complex, western Amazonia. (A) $\Delta\delta^{13}C$ (Fruit $\delta^{13}C$ - Leaves $\delta^{13}C$) and (B) $\Delta\delta^{15}N$ (Fruit $\delta^{15}N$ - Leaves $\delta^{15}N$). Positive values indicate that fruits had heavier isotopic signatures with respect to leaves from the same individual plant. Species codes follow those in Table 5. Plant growth habit is indicated in parenthesis (T=tree, S=shrub, V=vine).

Discussion

Interspecific isotopic variation

The isotopic variation found among flooded forest plants at the two western Amazon study sites was comparable to the isotopic variation reported for várzea forests along a 1800 km stretch of the Amazon River (Martinelli et al. 1991, Martinelli et al. 1994). Natural variation in $\delta^{13}C$ among flooded forest plants has seldom been investigated. Hedges and colleagues (1986) reported mean $\delta^{13}C$ differences in foliar (mean ± SD = -30.0 ± 0. 9‰) and wood tissues (-27.6 ± 1.0‰) for 14 tree species distributed in várzea forests along the Amazon River. Their samples were obtained from herbarium specimens and included multiple unspecified locations. A data set containing $\delta^{13}C$ signatures of nearly 500 plant samples collected in várzea forests along a 1,800 km stretch of the central Amazon River revealed patterns in isotopic composition at a regional scale. A west to east gradient of $\delta^{13}C$ was observed in foliar tissue of trees and understory plants (Martinelli et al. 1991, Martinelli et al. 1994). This pattern is hypothesized to be the result of higher recycling of ^{13}C-depleted biogenic CO_2 in the western (inland) portion of the basin. Data from pooled sites showed that tree leaves from open areas had $\delta^{13}C$ signatures about 3‰ greater than leaves from understory plants inside the forest, as well as a smaller difference in $\delta^{13}C$ signatures between canopy and understory leaves, relative to non-flooded forests (Martinelli et al. 1994). This data set also portrays large variation in foliar $\delta^{13}C$ (e.g., canopy trees: -36 to -28‰, understory plants: -37.5 to -29‰, and trees from open areas: -27 to -32‰; see Fig. 2 in Martinelli et al. 1994). The degree to which this variation results from geographical environmental differences in $\delta^{13}C$ is not known.

The large variation in $\delta^{13}C$ among co-occurring species found in this study is comparable to levels of interspecific within-site variation found in other non-flooded forests in the Amazon Basin. A recent study on isotopic composition of vegetation in four non-flooded Amazonian forests revealed within-site variation in foliar $\delta^{13}C$ ranging from 9 to 12‰ (see Fig. 1 in Ometto et al. 2006). Another study of a non-flooded forest in southern Amazonia detected 8‰ variation in foliar $\delta^{13}C$ (Martinelli et al. 1998). One of the explanations for within-site variation in $\delta^{13}C$ is the "canopy effect" in which leaves closer to the forest ground have more depleted $\delta^{13}C$ signatures relative to leaves at the canopy level. Two hypotheses have been postulated to explain this pattern. One idea is that light availability influences CO_2 concentration in intercellular spaces within the leaf (Farquhar et al. 1982), and the other proposes vertical stratification in the isotopic composition of forest CO_2 (Medina and Minchin 1980). Contrary to what is expected in non-flooded forests, some of the most depleted $\delta^{13}C$ values in the two flooded forests examined here came from tree leaves (< -33‰, Table 5 and 6). Martinelli et al. (1994) hypothesized that the proximity to the river may promote better mixing of atmospheric and ^{13}C-depleted biogenic CO_2 which, in conjunction with better light penetration, may prevent the occurrence of a strong "canopy effect" in flooded forests. Since the samples analyzed in this study include species growing at different heights (e.g., small and large trees, shrubs, and vines) and in different light conditions (e.g., inside the forest and along the edge), the variation depicted by these data sets are examples of the natural distribution of $\delta^{13}C$ among vascular plants at a single forest site. Larger sample sizes within each stratum are necessary to test for effects of plant height or distance from the river's edge.

Despite large within-site variation, the two flooded forest sites analyzed in this study had similar mean $\delta^{13}C$ values, as depicted by both leaves and fruits. The two sites have different biogeochemistry, but have similar climatic regimes (precipitation, humidity, temperature, and hydrological cycle) suggesting that, in flooded forests, climate may have a stronger influence on plant $\delta^{13}C$ than soil characteristics (but see Fyllas et al. 2009, for non-flooded forests). The isotopic composition of plants in additional flooded forest sites, however, should be examined before making conclusions. Mean foliar $\delta^{13}C$ values in these two flooded forests are also congruent with those of other non-flooded forests in the Amazon Basin (Table 7), despite the great differences in floristic composition in flooded and non-flooded forests even within a locality (Campbell et al. 1986, Haugaasen and Peres 2006, Clavijo et al. 2009).

The two flooded forest sites analyzed in this study also revealed wide ranges of variation in $\delta^{15}N$ among co-occurring species. Such ranges are similar to those reported for foliar $\delta^{15}N$ among non-N-fixing woody plants in a várzea forest near Manaus, central Amazon Basin (ca. 5.5‰, Fig. 2 in Kreibich et al. 2006) and in a non-flooded forest near Manaus (5.5‰, Ometto et al. 2006). Wider ranges of variation in foliar $\delta^{15}N$ among non-N-fixing woody plants have been reported in other non-flooded forests, including three other terra-firme forests in the Amazon Basin (7–8‰, Ometto et al. 2006). Within-site variation in foliar $\delta^{15}N$ is partially accounted by the presence of N-fixing species. N-fixers have $\delta^{15}N$ signatures slightly more depleted than that of atmospheric N_2 (i.e., from -1 to -2‰, Shearer and Kohl 1991). Samples from the Tarapoto Lakes complex did not include legume species, while only three legume species were sampled in the lower Apaporis. Foliar $\delta^{15}N$ of these

TABLE 7. Foliar isotopic composition (mean ± SD) reported from single forest sites in the Amazon Basin. *N* = number of samples analyzed, followed by the number of species in parenthesis. Source: 1 = Medina & Minchin (1980), 2 = Ometo et al. (2006), 3 = Martinelli et al. (1998).

$\delta^{13}C$	*N*	Forest layer	Forest type	Region	Country	Source
-32.1 ± 2.1‰	28 (28)	canopy and understory	várzea	western Amazonia	Colombia	This study
-30.6 ± 1.9‰	24 (10)	canopy and understory	igapó	western Amazonia	Colombia	This study
-28.7 ± 1.7‰	5 (5)	upper canopy	terra-firme	western Amazonia	Venezuela	1
-34.3 ± 1.5‰	5 (5)	lower canopy	terra-firme	western Amazonia	Venezuela	1
-30.5 ± 1.4‰	4 (4)	upper canopy	caatinga	western Amazonia	Venezuela	1
-33.4 ± 1.5‰	9 (9)	lower canopy	caatinga	western Amazonia	Venezuela	1
-35.2 ± 1.2‰	11 (11)	understory	caatinga	western Amazonia	Venezuela	1
-31.9 ± 2.2‰	40 (n/a)	canopy and understory	terra-firme	central Amazonia (Roraima)	Brazil	2
-32.2 ± 2.5‰	133 (n/a)	canopy and understory	terra-firme	central Amazonia (Amazonas)	Brazil	2
-32.6 ± 2.7‰	42 (n/a)	canopy and understory	terra-firme	central Amazonia (Amazonas)	Brazil	2
-32.8 ± 2.2‰	150 (n/a)	canopy and understory	terra-firme	central Amazonia (Pará)	Brazil	2
-32.1 ± 2.6‰	280 (n/a)	canopy and understory	terra-firme	central Amazonia (Pará)	Brazil	2
-32.1 ± 1.5‰	208 (≈100)	canopy	terra-firme	southern Amazonia (Rondônia)	Brazil	3

species, however, had values >3‰ suggesting that these are most likely non-N-fixers. Access to different N pools due to differential root depth can cause δ^{15}N variation among non-fixing plants (Handley and Raven 1992). Roggy et al. (1999) found longer roots and more depleted δ^{15}N signatures among pioneer species compared with primary-forest species in a non-flooded rainforest site in French Guiana. In flooded forests, root length can reach up to 30 m in some species (Worbes 1997), but the relationship between root length and foliar δ^{15}N remains to be examined in these forests.

The flooded forest in the lower Apaporis River had a more enriched mean δ^{15}N than the flooded forest in the Tarapoto Lakes Complex, as depicted by leaves and fruits. Differences in mean annual rainfall (MAR) have been identified as a main factor contributing to inter-site variation in site-averaged foliar δ^{15}N at a global scale (Handley et al. 1999). The two forest sites analyzed in this study, however, have very high and similar MAR (3.32 m and 3.83 m in the Tarapoto Lakes Complex and lower Apaporis River, respectively), thus it is unlikely that such relatively small differences in precipitation are causing the observed differences in enrichment. Interestingly, mean foliar δ^{15}N from the Tarapoto Lakes Complex is more similar to the mean value obtained from composite samples of young leaves from várzea forest sites along the Madeira River during the high water season (mean ± SD = 1.3 ± 1.4‰) than it is to the mean from várzea forest sites along a 1,800 km stretch of the central Amazon River (mean ± S. D. = 3.8 ± 1.9‰ and 3.1 ± 2.0‰, during the mid-rising and high water seasons respectively; Martinelli et al. 1992), despite the fact that the Tarapoto Lakes complex is also located in the Amazon River floodplain. Dry season samples from a várzea forest near Manaus had a foliar δ^{15}N mean of 4.6‰ for 11 species of non-legume woody plants (Kreibich et al. 2006). Interestingly, the mean foliar δ^{15}N value of this várzea site was nearly as high as the mean foliar $\delta^{15}N$ value from the igapó site in the lower Apaporis River. Influence of floodplain sediments originating at various watersheds was postulated as a possible explanation for differences in foliar $\delta^{15}N$ among várzea forests in the Madeira and the Amazon Rivers (Martinelli et al. 1992). That may also be the reason for the observed differences in mean $\delta^{15}N$ between the two sites analyzed here.

Within-plant isotopic variation

Greater $\delta^{13}C$ enrichment of wood relative to leaves from the same individual tree is known to occur in both temperate (Leavitt and Long 1982, Leavitt and Long 1986) and tropical systems, including non-flooded forests in the Amazon Basin (Martinelli et al. 1998, Ometto et al. 2006). Paired wood and leaf samples of trees in a non-flooded forest in the southwestern Amazon, for instance, revealed large variation (range = -0.85 to 9‰, n = 33 trees; Martinelli et al. 1998), larger than that observed in the Tarapoto Lakes complex. Although the pattern of ^{13}C enrichment in wood relative to leaves appear to be widespread across different taxa and ecosystems, the causal mechanisms are still poorly understood (reviewed by Bowling et al. 2008). ^{15}N enriched signatures in trunk wood (i.e., bark and sapwood) relative to leaves were apparent for most species in the Tarapoto Lakes complex, however, this pattern may not be repeated in other ecosystems. Lower $\delta^{15}N$ values in wood relative to leaves were found among a N_2-fixing legume (*Prosopis glandulosa*) in the Sonora Desert (Shearer et al. 1983).

Evidence of isotopic variation between fruits and leaves in woody plants is limited. A detailed investigation of an abandoned agricultural field in Scotland, dominated by three shrub species, did not find consistent patterns of ^{15}N enrichment in fruits relative to leaves

(Handley and Scrimgeour 1997). Fruits of *P. glandulosa* in the Sonora Desert have slightly lower δ^{15}N signatures than leaves (Shearer et al. 1983). A recent study in mangrove forests revealed that fruits of most species had δ^{13}C enriched signatures and lower C:N ratios relative to their leaves (Figs. 3 and 7 in Muzuka and Shunula 2006). Under experimental conditions, higher δ^{13}C signatures in seeds relative to leaves were observed among tanoak (*Lithocarpus densiflorus*) seedlings (>2‰, Kennedy et al. 2004). Among non-woody plants, δ^{13}C signatures of chickpea pods and seeds were enriched by at least 3.1‰ and 4.7‰, respectively, relative to leaves under experimental watered and water-stress conditions (Behboudian et al. 2000). Movement of compounds with differential isotopic composition inside the plant (Kennedy et al. 2004), respiratory differences among tissues and recycling of CO_2 inside the pod (Behboudian et al. 2000) were hypothesized as possible causes for these differences in δ^{13}C ratios. Varied enrichment values among flooded forest species of the Tarapoto Lakes complex suggest that the enrichment in δ^{13}C of fruits relative to leaves may be species specific. Fruit age also could influence isotopic variation, although, Handley and Scrimgeour (1997) found that fruits of one shrub species became slightly more enriched as they matured, whereas fruits of another shrub species in the same field became lighter by nearly 3‰ with age. Sampling fruits and leaves from a larger number of species at different developmental stages and from multiple individuals will help clarifying these relationships.

Implications of isotopic variation

Variation in isotopic composition of plants between and within-sites and between tissues from an individual plant should be considered in the design of sampling protocols and interpretation of isotopic signatures in food web research. Mean foliar δ^{13}C has the potential to change across precipitation regimes (Fyllas et al. 2009, Diefendorf et al. 2010) and mean foliar δ^{15}N values can be affected by precipitation and N sources (Handley et al. 1999, Martinelli et al. 1999, Swap et al. 2004). Requirements for multiple samples from species, individuals and tissues, depend on the research question and spatiotemporal scale of the study. Within a site, samples that include plant taxa with diverse physiological attributes (e.g., fixers- and non-N-fixers), growth forms, and microhabitats (e.g., understory, canopy, inside forest, and edge) may be needed in order to encompass the natural variation of δ^{13}C and δ^{15}N. This is especially true in species-rich ecosystems, such as tropical forests. Because δ^{15}N increases by 2–3‰ per trophic level (Peterson and Fry 1987), establishing a reliable baseline is essential for calculation of consumer trophic positions in a food web. For instance, including only N_2-fixers or only non-N_2-fixers can yield very different mean δ^{15}N values for vegetation at a site (e.g., Roggy et al. 1999, Kreibich et al. 2006). Because δ^{15}N can show between-site interspecific variation, in-situ data are preferred in order to establish the primary production baseline for a local food web. The large within-site variation in both δ^{13}C and δ^{15}N observed at both sites in this study, stresses the need to account for sources of variation in mixing models that estimate contributions of basal production sources to consumer biomass (e.g., MixSIR, Moore and Semmens 2008). Lastly, within-plant variability across tissues and organs needs to be considered because this could also be reflected in the isotopic composition of consumers, such as frugivores and nectarivores that specialize on certain plant tissues.

CHAPTER IV

CONCLUSIONS AND CONSERVATION IMPLICATIONS

Summary

A literature review shows that the consumption of fruits and seeds is not an uncommon feeding habit among Neotropical freshwater fishes as documented in nearly 150 species distributed in Central and South America. Such diversity includes species in a wide range of body sizes and phenotypes and both river and stream dwellers. Access to fruits and seeds is gained from riparian vegetation or inside seasonally flooded savannas and forests that border large lowland rivers of South America. The high frequency and volume of fruit and seed consumption by some of these frugivorous fishes gives them potential to be important seed dispersers. The fact that some of the most specialized frugivorous taxa from South America are old lineages that have experienced little morphological change and have inhabited extensive wetland forests for tens of millions of years suggests that interactions between fishes and fruits is ancient and strong.

Combined analysis of stomach contents and stable isotope ratios of six floodplain fish species revealed that patterns of food consumption changed across seasons, in response to fluctuation in food availability. Feeding strategies during the peak of the flood pulse were consistent with predictions of optimal foraging theory. During times of high fruit abundance, fishes consumed greater proportions of fruits to which their phenotype is best adapted, maximizing net energy gain and enhancing fitness. As the flood pulse subsided and the availability of forest food resources to fish was reduced, there was not a consistent pattern of diet breadth expansion or compression, even though diet shifts occurred, suggesting interspecific differences in foraging efficiencies. Analyses of diets and isotopic ratios revealed a general pattern of increased dietary segregation as the water level receded. Although there never was complete niche segregation among these fishes, these dietary changes effectively reduced interspecific niche overlap. During the flood, coexistence of frugivorous fishes is probably facilitated by the high abundance and diversity of fruits and seeds. Under reduced food availability, coexistence appears to be facilitated by trophic niche partitioning.

The high floristic diversity of floodplain forests in the Amazon Basin is reflected in large within-site variation in stable isotope ratios of C and N observed in two floodplain forests in the Colombian Amazon. Enrichment values in $\delta^{13}C$ of wood relative to leaves from the same individual tree, and enrichment values in $\delta^{13}C$ and $\delta^{15}N$ of fruits relative to leaves from the same individual tree are consistent with findings in plant communities in other ecosystems. Variation in isotopic composition of plants between and within-sites and between tissues from an individual plant should be considered in the design of sampling protocols and interpretation of isotopic signatures in food web research.

Conservation implications and future directions

Fishes usually are left out of the forest conservation debate, even though frugivorous fishes, along with many other vertebrates that inhabit tropical forests, are part of the so-called *forest-dependent biodiversity*. According to Moritz and McDonald (2005), "the overall goal of a conservation strategy should be to protect the processes, both ecological and evolutionary, that sustain diversity at the ecosystem, species, and genetic levels". Several lines of evidence suggest that a significant portion of the fish diversity in Amazonian floodplain forests, in particular forests bordering nutrient-poor, blackwater rivers, is likely to directly or indirectly be sustained by fruits from a diverse plant assemblage. A single frugivorous fish species, for instance, can consume a large biomass and number of fruit and seed taxa at a given site (e.g., 10–39 plant taxa in this study, Table 2; 21–23 plant taxa, *Colossoma macropomum* and *Piaractus brachypomus*, respectively, Anderson et al. (2009); 32 plant taxa, *Brycon bicolor*, Flecker et al. (2010)). This can yield broadly overlapping diets among sympatric species, as was demonstrated in the lower Apaporis River, facilitating coexistence. Fruits constitute an abundant and highly nutritious resource for fishes (Waldhoff et al. 1996, Waldhoff and Maia 2000). Many floodplain fish species are capable of accumulating fat storages that during periods of food scarcity are catabolized to provide energy to support reproduction and migration (Junk 1985, Arrington et al. 2006). Frugivorous fishes provide a relatively stable food resource for predatory fishes in river-floodplain systems. Thus, maintaining functionally diverse flooded forests in a time of increased deforestation and climate change is one of the major challenges to the long term persistence of Amazonian floodplain fishes. The preservation of floodplain forest and meadows is more likely to have positive long-term effects on fish stocks than regulations on fishermen (Barthem and Goulding 2007).

Interviews were conducted with residents of two indigenous communities in the lower Apaporis River, in an effort to assess their perception about fish dependence on flooded forests and effects of sparse fruits on fishing. The interview data revealed deep knowledge of fishes and forest interactions (see Appendix 6 for the interview questionnaire in Spanish). Seventeen people were interviewed in Puerto Ñumi (9 males between 15 and 65 years old, and 8 females between 15 and 50 years old). Fish species belonging to at least 19 genera of the main Neotropical freshwater orders (Characiformes, Siluriformes and Perciformes) were observed by these villagers to consume fruits and seeds of at least 46 plant taxa. Fourteen people were interviewed in Bocas de Taraira (8 males between 15 and 65 years old, and 6 females between 30 and 40 years old). Fish species belonging to at least 17 genera (Characiformes, Siluriformes and Perciformes) were observed consuming fruits and seeds of at least 23 plant taxa. In both communities, over 70% of people responded yes to the question: D*o you think that frugivorous fishes depend on the flooded forest plants?* Of those that responded positively, 75% in Ňumi and 50% in Bocas stated that the flooded forest represented a source of food for fishes. Of these, 36% in Ňumi and 40% in Bocas emphasized that such dependence was particularly important during the rising- and high-water seasons. Of the 30% that answered negatively, 50% in Ňumi and 75% in Bocas stated that fishes do not depend on the forest plants because they consume other foods besides plant material. The other 50% in Ňumi and 25% in Bocas stated that fishes also forage in other areas besides the flooded forest, so they do not depend on the forest plants. Over 80% of the interviewees in both communities responded yes to the question: D*o you think that fish yield is lower in areas with sparse fruits?* Although the results of this survey indicate that people know that many fish species consume diverse fruits, seeds and other plant material (e.g., flowers and leaves), and that when fruits are not available fishes change habitats or diets, there is a disconnection in the understanding of long-term processes. For instance the consumption of alternative foods (e.g., terrestrial insects, earth worms, benthic invertebrates and algae) in times of food scarcity is not seen as complementary. Result of stomach contents analyses of frugivorous fishes in the Lower Apaporis during the low-water season demonstrated a reduction in the average volume of stomach contents and an increase in the frequency of empty stomachs. Significant visceral fat stores were commonly observed during the low water season. Behavioral and physiological changes of herbivores in seasonal habitats are adaptive responses that develop over long time scales (Owen-Smith 2002). Community education initiatives, focused on integrating ecological research results with primary and secondary school curricula, could help clarify the ecological links between fishes and forests and provide greater awareness of the importance of flooded forests for fish conservation. Some of these activities were conducted with local children during the course of this investigation, and easily could be replicated across the Amazon region.

Among the fruit-eating fishes, characiform fishes in the genera *Brycon, Myleus, Myloplus, Leporinus, Schizodon,* and *Triportheus* were reported as being most frequently captured by villagers in both communities (Appendix 7). Except for the sábalo (*Brycon amazonicus*) that can reach up to 60 cm length, all of these are medium-size fishes (~20–30 cm). Some of these species are widely distributed and abundant in Amazonian floodplains. Frugivorous fishes generally are highly valued for the taste of their flesh (Barthem and Goulding 2007). Subsistence fisheries, particularly in remote areas, are seldom included in fisheries statistics, and therefore their impact on local fish stocks is frequently unknown. Subsistence fishing by people in the small and widely dispersed villages of the Lower Apaporis River is unlikely to pose a threat to local fish stocks, especially because most people use hooks instead of gill nets for fishing. Species of these genera, some of which are migratory (e.g., *Brycon, Leporinus, Schizodon*, and *Triportheus*) are, however, heavily exploited in other areas of the Amazon Basin (Barthem and Goulding 2007).

Fruits of *Astrocarium javari*, *Byrsonima japurensis, Genipa americana*, *Cecropia distachyla*, *Alchornea discolor, Ficus americana, Quiina amazonica, Psychotria* sp. 1 and

Bothriospora corymbosa were among the most frequently consumed by fishes in the Lower Apaporis. *Bothriospora corymbosa* is an abundant shrub along the edges of the Lower Apaporis River that can be of particular importance as a food resource for fishes because it produces fruits during the falling-water season, which follows the peak fruiting season of most plant species. Likewise, *Nectandra egensis* and *N. oppositifolia* (Lauraceae) trees produce fruits during the rising-water season, when many plant species are still flowering; these fruits are frequently consumed by fishes. All of the species listed above represent potential candidates for restoration purposes in blackwater regions that have been deforested.

In conclusion, results of this study contribute baseline information demonstrating the need for protection of floodplain forests in the Colombian Amazon for long-term persistence of fish stocks and fish diversity. Given the large mobility and complex lifecycles of many Amazonian fishes, a basin scale management approach, such as the one described by Barthem and Goulding (2007), likely would be most effective to achieve conservation.

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APPENDIX 1

NEOTROPICAL FRESHWATER FISH SPECIES THAT CONSUME FRUITS AND SEEDS*

Order and Family	Species	River Basin	Country	Source
Characiformes				
Anostomidae	*Abramites hypselonotus*	Amazon	Brazil	M. Goulding (Personal Commun.)
	Anostomoides laticeps	Amazon	Brazil	M. Goulding (Personal Commun.)
	Laemolyta taeniata	Amazon	Brazil	M. Goulding (Personal Commun.)
	Laemolyta varia	Amazon	Brazil	M. Goulding (Personal Commun.)
	Leporellus vittatus	Amazon	Brazil	M. Goulding (Personal Commun.)
	Leporinus agassizii	Amazon	Colombia	Blanco-Parra and Bejarano-Rodriguez, 2006
	Leporinus brunneus	Amazon	Brazil, Colombia	Goulding et al., 1988; Blanco-Parra and Bejarano-Rodriguez, 2006
	Leporinus desmotes	Amazon	Brazil	M. Goulding (Personal Commun.)
	Leporinus elongatus	Paraná	Brazil	Duraes et al., 2001
	Leporinus fasciatus	Amazon	Brazil, Colombia	Goulding et al., 1988; Blanco-Parra and Bejarano-Rodriguez, 2006
	Leporinus friderici	Amazon, Paraná, Approuague, Sinnamary	Brazil, French Guiana	Gottsberger, 1978; Goulding, 1980; Boujard, et al., 1990; Duraes et al., 2001, Melo et al., 2004
	Leporinus klausewitzi	Amazon	Colombia	Blanco-Parra and Bejarano-Rodriguez, 2006
	Leporinus maculatus	Amazon	Brazil	M. Goulding (Personal Commun.)
	Leporinus trifasciatus	Amazon	Brazil	M. Goulding (Personal Commun.)
	Leporinus y-ophorus	Amazon	Brazil	M. Goulding (Personal Commun.)
	Schizodon fasciatus	Amazon	Brazil	M. Goulding (Personal Commun.)
	Schizodon vittatum	Amazon	Brazil	M. Goulding (Personal Commun.)

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Order and Family	Species	River Basin	Country	Source
Characidae	*Acnodon normani*	Amazon	Brazil	Leite and Jegu,1990
	Acnodon senai	Amazon	Brazil	Leite and Jegu,1990
	Aphyocharax sp.	Amazon	Brazil	Melo et al., 2004
	Astyanax altiparanae	Paraná, Piracicaba	Brazil	Gomiero and Braga, 2003
	Astyanax bimaculatus	Amazon	Brazil	Melo et al., 2004
	Astyanax cf. *guianensis*	Amazon	Brazil	Goulding et al., 1988
	Astyanax fasciatus	Amazon, Claro, Sirena	Brazil, Costa Rica	Winemiller, 1983; Winemiller and Morales, 1989; Melo et al., 2004
	Astyanax sp.	Orinoco	Venezuela	Prejs and Prejs, 1987
	Brycon amazonicus	Amazon	Brazil	Lopes de Souza, 2005
	Brycon cephalus	Amazon	Brazil, Colombia	Goulding, 1980; S.B. Correa (Unpublished results)
	Brycon chagrensis	Chagres	Panama	Menezes, 1969
	Brycon falcatus	Amazon	Brazil, Colombia	Melo et al., 2004; Blanco-Parra and Bejarano-Rodriguez, 2006
	Brycon guatemalensis	Sarapiqui	Costa Rica	Horn, 1997; Banack et al., 2002
	Brycon hilarii	Amazon, Paraná	Brazil	Gottsberger, 1978; Sabino and Sazima, 1999; Reys et al., 2009
	Brycon melanopterus	Amazon	Brazil, Colombia	Goulding, 1980; Lopes de Souza, 2005; Blanco-Parra and Bejarano-Rodriguez, 2006; S.B. Correa (Unpublished results)
	Brycon petrosus	n/a	Panama, Honduras	Menezes, 1969
	Bryconamericus sp.	Amazon	Brazil	Melo et al., 2004
	Chalceus (2–3 species)	Amazon	Brazil	M. Goulding (Personal Commun.)
	Creagrutus cf. *caucanus*	Amazon	Brazil	Goulding et al., 1988
	Creagrutus hildebrandi	Catatumbo	Colombia	Galvis et al., 1997
	Creagrutus sp.	Amazon	Brazil	Melo et al., 2004
	Ctenobrycon hauxwellianus	Amazon	Brazil	Marlier, 1967
	Hemigrammus levis	Amazon	Brazil	Goulding et al., 1988

Order and Family	Species	River Basin	Country	Source
	Hemigrammus sp.	Amazon	Brazil	Melo et al., 2004
	Hyphessobrycon sp.	Amazon	Brazil	Goulding et al., 1988
	Hyphessobrycon eques	Amazon	Brazil	Marlier, 1967
	Hyphessobrycon savagei	Claro, Sirena	Costa Rica	Winemiller, 1983; Winemiller and Morales, 1989
	Jupiaba zonata	Amazon	Brazil	Goulding et al., 1988
	Moenkhausia collettii	Amazon	Brazil	Goulding et al., 1988
	Moenkhausia oligolepis	Amazon	Brazil	Goulding et al., 1988
	Moenkhausia sanctaefilomenae	Amazon	Brazil	Melo et al., 2004
	Oligosarcus hepsetus	Amazon, Paraná	Brazil, Argentina	Menezes, 1969
	Roeboides dayi	Orinoco	Venezuela	Prejs and Prejs, 1987
	Tetragonopterus argenteus	Amazon, Orinoco	Brazil, Venezuela	Prejs and Prejs, 1987; Melo et al., 2004
	Tetragonopterus chalceus	Amazon	Brazil	Goulding et al., 1988
	Triportheus albus	Amazon	Colombia	Blanco-Parra and Bejarano-Rodriguez, 2006; S.B. Correa (Unpublished results)
	Triportheus angulatus	Amazon	Brazil, Colombia	Goulding, 1980; Almeida, 1984; Melo et al., 2004; Yamamoto et al. 2004; Blanco-Parra and Bejarano-Rodriguez, 2006; Maia et al., 2007; S.B. Correa (Unpublished results)
	Triportheus auritus	Amazon	Colombia	S.B. Correa (Unpublished results)
	Triportheus elongatus	Amazon	Brazil, Colombia	Goulding, 1980; Almeida, 1984; Claro-JR et al., 2004; Lopes de Souza, 2005; Blanco-Parra and Bejarano-Rodriguez, 2006
	Triportheus sp.	Amazon	Brazil	Gottsberger, 1978; Goulding, 1980; Goulding et al., 1988
Hemiodontidae	*Argonectes longiceps*	Amazon	Brazil	Goulding et al., 1988
	Hemiodus immaculatus	Amazon	Brazil	Lopes de Souza, 2005
	Hemiodus unimaculatus	Amazon	Brazil, Colombia	Goulding et al., 1988; Blanco-Parra and Bejarano-Rodriguez, 2006
Serrasalmidae	*Colossoma macropomum*	Amazon	Brazil	Gottsberger, 1978; Goulding, 1980; Goulding and Carvalho, 1982; Kubitzki and Ziburski, 1994; da Silva et al, 2003; Lopes de Souza, 2005
	Metynnis argenteus	Amazon	Brazil	M. Goulding (Personal Commun.)

Order and Family	Species	River Basin	Country	Source
	Metynnis luna	Amazon	Brazil, Colombia	Lopes de Souza, 2005; S.B. Correa (Unpublished results)
	Metynnis sp.	Amazon	Brazil	Goulding et al., 1988
	Myleus pacu	Amazon	Colombia	Blanco-Parra and Bejarano-Rodriguez, 2006
	Myleus rhomboidalis	Approuague, Sinnamary	French Guiana	Boujard et al.,1990; Planquette et al, 1996
	Myleus setiger	Amazon	Brazil	M. Goulding (Personal Commun.)
	Myleus sp.	Amazon	Brazil	Melo et al., 2004
	Myloplus asterias	Amazon	Colombia	S.B. Correa (Unpublished results)
	Myloplus rubripinnis	Amazon	Brazil, Colombia	Lopes de Souza, 2005; Blanco-Parra and Bejarano-Rodriguez, 2006; S.B. Correa (Unpublished results)
	Myloplus schomburgkii	Amazon	Brazil, Colombia	Goulding et al., 1988; S.B. Correa (Unpublished results)
	Myloplus torquatus	Amazon	Brazil, Colombia	Goulding et al., 1988; S.B. Correa (Unpublished results)
	Myloplus sp.	Amazon	Colombia	S.B. Correa (Unpublished results)
	Mylossoma acanthogaster	Catatumbo	Colombia	Galvis et al. 1997
	Mylossoma aureum	Amazon	Brazil, Colombia	Gottsberger, 1978; Goulding, 1980; S.B. Correa (Unpublished results)
	Mylossoma duriventre	Amazon	Brazil, Colombia	Gottsberger, 1978; Goulding, 1980; Claro-JR et al., 2004; Lopes de Souza, 2005; S.B. Correa (Unpublished results)
	Mylossoma sp.	Amazon	Brazil	Goulding, 1980
	Piaractus brachypomus	Amazon, Orinoco	Brazil, Colombia, Venezuela	Marlier, 1967; Canestri, 1970; Honda, 1974 ; Gottsberger, 1978; Goulding, 1980, Knab-Vispo et al., 2003; S.B. Correa (Unpublished results).
	Piaractus mesopotamicus	Paraná	Brazil	Paula et al., 1989; Galetti et al., 2008
	Pristobrycon aureus	Amazon	Colombia	Blanco-Parra and Bejarano-Rodriguez, 2006
	Pristobrycon calmoni	Amazon	Colombia	Blanco-Parra and Bejarano-Rodriguez, 2006
	Pristobrycon striolatus	Amazon	Colombia, French Guiana	Planquette et al, 1996; Blanco-Parra and Bejarano-Rodriguez, 2006
	Pristobrycon sp.	Amazon	Colombia	S.B. Correa (Unpublished results)
	Pygopristis denticulata	Amazon	Brazil	M. Goulding (Personal Commun.)
	Serrasalmus altuvei	Amazon	Brazil	M. Goulding (Personal Commun.)

Order and Family	Species	River Basin	Country	Source
	Serrasalmus gouldingi	Amazon	Brazil	M. Goulding (Personal Commun.)
	Serrasalmus hastatus	Amazon	Brazil	M. Goulding (Personal Commun.)
	Serrasalmus manueli	Amazon	Brazil	M. Goulding (Personal Commun.)
	Serrasalmus spilopleura	Amazon	Brazil, Colombia	M. Goulding (Personal Commun.); S.B. Correa (Unpublished results)
	Serrasalmus rhombeus	Amazon	Brazil	Goulding, 1980
	Serrasalmus sp.	Amazon	Brazil	Goulding, 1980
	Tometes makue	Amazon	Brazil	M. Goulding (Personal Commun.)
Cypriniformes				
Anablepidae	*Oxyzygonectes dovii*	Claro	Costa Rica	Winemiller & Morales, 1989
Poeciilidae	*Brachyrhaphis rhabdophora*	Claro	Costa Rica	Winemiller & Morales, 1989
Gymnotiformes				
Electrophoridae	*Electrophorus electricus*	Amazon	Brazil	Goulding, 1980
Sternopygidae	*Sternopygus macrurus*	Amazon	Brazil	Goulding et al., 1988; Melo et al., 2004
Osteoglossiformes				
Osteoglossidae	*Osteoglossum bicirrhosum*	Amazon	Brazil	De Arango, 1947 (cited in: Van der Pijl, 1972)
Perciformes				
Cichlidae	*Acarichthys heckelii*	Amazon	Brazil	Marlier, 1967
	Amphilophus diquis	Claro	Costa Rica	Winemiller & Morales, 1989
	Apistogramma ramirezi	Orinoco	Venezuela	Prejs and Prejs, 1987
	Archocentrus sajica	Claro	Costa Rica	Winemiller & Morales, 1989
	Astronotus ocellatus	Amazon	Brazil	Goulding et al., 1988
	Biotodoma wavrini	Amazon	Brazil	Goulding et al., 1988
	Dicrossus filamentosus	Amazon	Brazil	Goulding et al., 1988
	Geophagus altifrons	Amazon	Brazil	Goulding et al., 1988
	Geophagus surinamensis	Amazon	Brazil	Melo et al., 2004
	Heros severus	Amazon	Brazil	Goulding et al., 1988
	Satanoperca jurupari	Amazon	Brazil, French Guiana	Goulding et al., 1988; Le Bail et al., 2000
	Retroculus lapidifer	Amazon	Brazil	Melo et al., 2004
	Uaru amphiacanthoides	Amazon	Brazil	Goulding et al., 1988

Order and Family	Species	River Basin	Country	Source
Eleotridae	*Dormitator latifrons*	Claro	Costa Rica	Winemiller & Morales, 1989
	Eleotris picta	Claro, Sirena	Costa Rica	Winemiller,1983
Siluriformes				
Ageneiosidae	*Ageneiosus* sp.	Amazon	Brazil	Goulding et al., 1988
Aspredinidae	*Buconocephalus* sp.	Amazon	Brazil	Melo et al., 2004
Auchenipteridae	*Auchenipterichthys* sp.	Amazon	Brazil	Goulding et al., 1988
	Auchenipterus longimanus	Amazon	Brazil	Mannheimer et al., 2001
	Tocantinsia piresi	Amazon	Brazil	Carvalho and Kawakami, 1984
	Trachelyopterus galeatus	Amazon	Brazil, French Guiana	Le Bail et al., 2000; Claro-JR et al., 2004
	Trachycorystes (4+ species)	Amazon	Brazil	Goulding, 1980; Goulding et al., 1988; M. Goulding (Personal Commun.)
Doradidae	*Astrodoras asterifrons*	Amazon	Brazil	M. Goulding (Personal Commun.)
	Lithodoras dorsalis	Amazon	Brazil	Goulding, 1980, 1993; Kubitzki and Ziburski, 1994
	Megalodoras uranoscopus	Amazon	Brazil	Goulding, 1980; Goulding et al., 1988
	Platydoras armatulus	Amazon	Brazil	M. Goulding (Personal Commun.)
	Platydoras costatus	Amazon	Brazil	Goulding et al., 1988
	Pterodoras granulosus	Amazon, Paraná	Brazil	Goulding, 1981; de Souza-Stevaux et al, 1994
	Scorpiodoras heckelii	Amazon	Brazil	M. Goulding (Personal Commun.)
Loricaridae	*Loricaria* sp.	Amazon	Brazil	Armbruster, 2004; Melo et al., 2004
	Crossoloricaria sp.	n/a	n/a	Armbruster, 2004
	Spatuloricaria sp.	Amazon	Brazil	Melo et al., 2004
Pimelodidae	*Calophysus macropterus*	Amazon	Brazil	Goulding, 1980
	Phractocephalus hemioliopterus	Amazon	Brazil	Goulding, 1980; Kubitzki, 1985; Goulding et al., 1988
	Pimelodella cristata	Amazon	Brazil	Melo et al., 2004
	Pimelodella sp.	Amazon	Brazil	Gottsberger, 1978
	Pimelodus blochii	Amazon	Brazil, Colombia	Goulding, 1980; Melo et al., 2004; Blanco-Parra and Bejarano-Rodriguez, 2006
	Pimelodus (4–5 species)	Amazon	Brazil	M. Goulding (Personal Commun.)
	Platynematichthis notatus	Amazon	Colombia	Blanco-Parra and Bejarano-Rodriguez, 2006

Order and Family	Species	River Basin	Country	Source
	Rhamdia schomburgkii	Amazon	Brazil	Gottsberger, 1978
	Sorubim lima	Amazon	Brazil	Gottsberger, 1978

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APPENDIX 2

FUNCTIONAL FOOD CATEGORIES (CODES ARE IN PARENTHESIS) AND THE FOOD TYPES INCLUDED IN EACH CATEGORY THAT WERE CONSUMED BY 17 FISH SPECIES DURING THREE HYDROLOGICAL SEASONS. VALUES REPRESENT THE NUMBER OF INDIVIDUALS CONSUMING THE ITEM PER SEASON. NUMBERS IN PARENTHESIS ARE SPECIES CODES WHICH FOLLOW FOOTNOTE. NUMBER OF INDIVIDUALS = 832 (HW = 409, FW = 265, LW = 158)

			Season		
Food Category	Food Types	Code	High Waters (HW)	Falling Waters (FW)	Low Waters (LW)
Allochthonous					
Fruits and Seeds (FS)	*Alchornea discolor* (Euphorbiaceae)	Aldi	23 (2–6,8,17)	0	0
	Amaioua guianensis(Rubiaceae)	Amgu	15 (2–6,8)	0	0
	Annona hypoglauca (Annonaceae)	Anhy	6 (3–5)	0	0
	Annonaceae sp. 1	Ansp1	4 (1–3)	0	0
	Annonaceae sp. 2	Ansp2	1 (4)	0	0
	Araceae sp. 1	Arac1	2 (2,3)	0	0
	Astrocaryum jauari (Arecaceae)	Asja	32 (1,2,4–6)	3 (2)	0
	Bactris riparia (Arecaceae)	Bari	21 (1–3,6,17)	1 (2)	2 (13)
	Bocageopsis sp. (Annonaceae)	Bosp	4 (2,3)	0	0
	Bothriospora corymbosa (Rubiaceae)	Boco	35 (1,2,4,5)	34 (1–3,4,5,8,15,17)	0
	Buchenavia viridiflora (Combretaceae)	Buvi	1 (1)	0	0
	Byrsonima japurensis (Malpigiaceae)	Byja	22 (2,3,17)	0	0
	Byrsonima sp. (Malpigiaceae)	Bysp	3 (2,3)	0	0
	Cecropia distachya (Cecropiaceae)	Cedi	17 (2,5,6,8)	0	0
	Clusia sp. (Clusiaceae)	Clsp	10 (2–4,6,17)	0	0
	cf. Cucurbitaceae sp. 1	cfCusp1	18 (1–6,17)	0	0
	cf. Cucurbitaceae sp. 2	cfCusp2	1 (3)	0	0
	Elaeoluma glabrescens (Sapotaceae)	Elgl	1 (1)	0	0
	Eugenia sp. 1 (Myrtaceae)	Eugsp1	4 (1,3,5)	0	0

			Season		
Food Category	Food Types	Code	High Waters (HW)	Falling Waters (FW)	Low Waters (LW)
	Euphorbiaceae sp. 1	Eusp1	1 (2)	0	0
	Euphorbiaceae sp. 2	Eusp2	1 (5)	0	0
	Ficus americana (Moraceae)	Fiam	11 (1–3,5,8,15,17)	5 (1–3)	0
	Ficus sp. 1 (Moraceae)	Fisp1	9 (1–3,17)	1 (4)	0
	Ficus sp. 2 (Moraceae)	Fisp2	2 (1,2)	0	0
	cf. Ficus sp. 3 (Moraceae)	cfFisp3	0	1 (3)	0
	Genipa americana (Rubiaceae)	Geam	40 (2,4–6,8,17)	0	0
	Guateria sp. 1 (Annonaceae)	Gusp1	5 (2,4)	0	0
	cf. *Guatteria* sp. 2 (Annonaceae)	cfGusp2	1 (3)	0	0
	Heliconia sp. (Heliconiaceae)	Hesp	1 (4)	0	0
	Hippocrateaceae sp. 1 (Celastraceae)	Hisp1	2 (1,3)	0	0
	Inga sp. (Mimosaceae)	Inga	2 (3)	0	0
	Lacmellea sp. 1 (Apocynaceae)	Lasp1	1 (3)	0	0
	Lacmellea sp. 2 (Apocynaceae)	Lasp2	1 (1)	0	0
	cf. *Laetia suaveolens* (Flacourtaceae)	cfLasu	1 (2)	0	0
	Lecythidaceae sp. 1	Lecy1	0	0	1 (2)
	cf. *Machaerium* sp. (Fabaceae)	cfMasp	0	1 (4)	0
	Mauritiella aculeata (Arecaceae)	Maac	11 (1,3–5)	1 (5)	0
	Mendoncia sp. (Acanthaceae)	Mesp	1 (1)	0	0
	cf. Menispermaceae sp. 1	cfMeni1	1 (2)	0	0
	Miconia truncata (Melastomataceae)	Mitr	10 (1–3)	0	0
	Myrtaceae sp. 1	Myrt1	1 (2)	0	0
	Nectandra sp. (Lauraceae)	Nesp	12 (2,3,6,16,17)	0	0
	cf. *Odontocaria* sp. (Menispermaceae)	cfOdsp	0	1 (2)	0
	cf. *Parkia* sp. (Mimosoidea)	cfPasp	1 (1)	0	0
	Phyllantus sp. (Euphorbiaceae)	Phsp	3 (2,3)	4 (2,3,15)	0
	Psychotria lupulina (Rubiaceae)	Pylu	10 (1,2,4,5,8)	3 (4,5,8)	0
	Psychotria sp. 1 (Rubiaceae)	Pysp1	31 (2,4,5,8)	5 (4,5,8)	0
	Quiina amazonica (Quiinaceae)	Quam	27 (1–3,5,8,15,17)	1 (2)	0
	Rubiaceae sp.1	Rusp1	1 (15)	0	0
	Rubiaceae sp. 2	Rusp2	10 (2,3,5,8,15,16)	0	0
	Rubiaceae sp. 3	Rusp3	2 (5)	0	0
	Rubiaceae sp. 4	Rusp4	2 (2,3)	0	0

Food Category	Food Types	Code	Season High Waters (HW)	Falling Waters (FW)	Low Waters (LW)
	Simaba orinocensis (Simaroubaceae)	Sior	3 (2)	0	0
	Simaba sp. (Simaroubaceae)	Sisp	1 (3)	0	0
	Sourobea sp. (Marcgraviaceae)	Sosp	4 (2,3,5)	0	0
	Strychnos panurensis (Loganiaceae)	Stpa	1 (2)	0	0
	Tapirira sp. (Anacardiaceae)	Tasp	1 (3)	0	0
	cf. *Tetracera* sp. (Dileneaceae)	cfTetr	1 (3)	0	0
	cf. *Urvillea* sp. (Sapindaceae)	cfUrsp	0	2 (4)	0
	Unonopsis sp. (Annonaceae)	Unsp	9 (2,3)	0	0
	Virola sp. (Myristicaceae)	Visp	4 (1–3)	0	0
	cf. Zigia sp. (Fabaceae)	cfZisp	2 (2)	6 (2,3)	0
	Unknown 1	Unk1	2 (2,6)	0	0
	Unknown 2	Unk2	2 (1)	0	0
	Unknown 3	Unk3	1 (1)	0	0
	Unknown 4	Unk4	1 (2)	0	0
	Unknown 5	Unk5	1 (12)	0	0
	Unknown 6	Unk6	4 (3)	0	0
	Unknown 7	Unk7	1 (3)	0	0
	Unknown 8	Unk8	1 (3)	2 (15,17)	0
	Unknown 9	Unk9	1 (3)	0	0
	Unknown 10	Unk10	2 (4)	1 (4)	0
	Unknown 11	Unk11	1 (5)	0	0
	Unknown 12	Unk12	1 (5)	0	0
	Unknown 13	Unk13	3 (15)	0	0
	Unknown 14	Unk14	1 (6)	0	0
	Unknown 15	Unk15	0	1 (12)	0
	Unknown 16	Unk16	0	1 (9)	0
	Unknown 17	Unk17	1 (2)	0	0
	Unknown 18	Unk18	1 (2)	3 (3)	0
	Unknown 19	Unk19	0	1 (4)	0
	Unknown 20	Unk20	0	2 (8,12)	0
	Unknown 21	Unk21	0	1 (2)	0
	Unknown 22	Unk22	0	0	1 (1)

			Season		
Food Category	Food Types	Code	High Waters (HW)	Falling Waters (FW)	Low Waters (LW)
	Unidentified fruit & seed fragments		150 (1–6,8,10,12,15,17)	76 (2–8,9,12,14,15)	38 (1–7,12)
Flowers (FL)	Flowers and flower fragments		22 (2–5,15)	81 (2–6,8,17)	26 (1,3–6,11,15)
Leaves (LE)	Leaves and leaf fragments		59 (2–6,17)	55 (1–6,8,9,15)	85 (1–7,11,15)
Other Terrestrial Vegetation (TV)	Wood & bark		17 (1–3,5,12)	7 (2,3,5,6,9,12,15)	9 (2,4,6,7,15)
	Stems		2 (4,6)	7 (2,3,6,7)	17 (4–6,11)
	Grasses		0	3 (1,3,6)	4 (1,2,5,6)
	Digested plant matter different from fruits & seeds		78 (1–6,8,12,15–17)	22 (2,4–6,8,9,12)	25 (1–7,15)
Terrestrial Invertebrates (TIv)	Annelida		2 (12)	1 (2)	1 (6)
	Arachnida		15 (1–3,17)	4 (3)	0
	Chilopoda (Centipedes)		1 (3)	0	0
	Diplopoda (Millipedes)		2 (8,17)	0	0
	Blattodea		3 (2,12)	2 (3,15)	0
	Coleoptera (Adult)		7 (2,3)	6 (2,3,15)	2 (3,15)
	Coleoptera (Larvae)		10 (1–3,5)	7 (2,3)	0
	Diptera (Adult & non aquatic larvae)		3 (2,3)	0	0
	Hemiptera		1 (3)	1 (15)	1 (3)
	Hymenoptera (mainly Formicoidea)		74 (1–6,8,12,15–17)	32 (1–4,6,8,9,12,15)	13 (2,3,6,7,15)
	Isoptera		9 (2,3,8)	4 (2,3)	14 (2,3,6,15)
	Lepidoptera (Adult)		1 (8)	0	0
	Lepidoptera (Chrysalid)		4 (4,5,8,15)	0	1 (2)
	Lepidoptera (Larvae)		24 (1–3,5,8,12,15)	4 (1–3)	0
	Odonata (Adult)		1 (3)	0	1 (2)
	Orthoptera		15 (2,3,16,17)	7 (2–4,15)	1 (15)
	Phasmathodea		1 (2)	0	0
	Terrestrial insect fragments		81 (1–5,8,12,15–17)	72 (1–3,6,9,12,15,17)	28 (1–3,5–7,15)
Terrestrial Vertebrates (TVe)	Amphibia, Aves		1 (2)	1 (15)	0

Food Category	Food Types	Code	Season High Waters (HW)	 Falling Waters (FW)	 Low Waters (LW)
Authochthonous					
Phyto-macro-benthos(PMB)	Periphyton		10 (5,6)	10 (5,6)	1 (6)
	Filamentous algae		0	3 (5,6,9)	0
Aquatic Insects (AI)	Coleoptera (Aquatic larvae)		2 (2,3)	0	0
	Diptera (Aquatic larvae)		4 (3,17)	0	0
	Hemiptera-Heteroptera		1 (3)	5 (2,3)	1 (7)
	Megaloptera (Larvae)		1 (12)	0	0
	Odonata (Larvae)		0	2 (2,6)	0
	Plecoptera (Adult & nymph)		0	0	2 (6)
	Unknown aquatic larvae and fragments		6 (2,8,12,17)	1 (3)	1 (5)
Other Aquatic Macro-invertebrates (MIv)	Nematoda		1 (12)	1 (9)	1 (4)
	Decapoda		0	0	1 (7)
Zooplankton (ZP)	Zooplankton		0	4 (9)	0
Fish Scales (SC)	Scales		3 (2,3)	7 (2,3,15)	15 (5–7,12)
Fish Remains (FBM)	Whole fish, bones, muscle		9 (3–6,8,12,17)	3 (2,3,12)	7 (2,3,5,6,11)
Soil and organic debris (SO)	Soil, gravel, debris		6 (2,3,5)	8 (2,3,9)	13 (4–7)

Species Codes: 1-*Brycon amazonicus*, 2-*B. falcatus*, 3-*B. melanopterus*, 4-*Myloplus asterias,* 5-*M. rubripinnis,* 6-*M. torquatus,* 7-*M. schomburgkii,* 8-*Myloplus sp.* , 9-*Metynnis luna,* 10- *Pristobrycon calmoni,* 11-*P. striolatus,* 12-*Pristobrycon sp.* , 13-*Piaractus brachypomus,* 14-*Serrasalmus* cf. *gouldingi,* 15-*Triportheus albus,* 16-*T. angulatus,* 17-*T. culter.*

APPENDIX 3

PERCENTAGE FREQUENCY OF OCCURRENCE (%FO) AND AVERAGE VOLUMETRIC PERCENTAGE (% VOL ± S.E.) CONTRIBUTED BY 12 BROAD FUNCTIONAL FOOD CATEGORIES TO DIETS OF SIX FRUGIVOROUS FISH SPECIES DURING THREE HYDROLOGICAL SEASONS. A COMPLETE LIST OF THE FOOD ITEMS INCLUDED IN EACH CATEGORY IS PRESENTED IN APPENDIX 2

Species/Food Category	*Brycon falcatus*		*B. melanopterus*		*Myloplus asterias*		*M. rubripinnis*		*M. torquatus*		*Pristobrycon sp.*	
	BRFA		BRME		MYAS		MYRU		MYTO		PRSP	
	%FO	%Vol	%FO	%Vol	%FO	%Vol	%FO	%Vol	%FO	%Vol	%FO	%Vol
High Waters (HW)												
n	87		57		35		109		15		43	
Fruit & Seeds	93.1	75.8 ± 3.6	89.5	61.6 ± 5.1	94.3	83.8 ± 5.5	86.2	57.4 ± 3.8	66.7	58.8 ± 11.7	90.7	82.3 ± 5.3
Flowers	2.3	1.2 ± 0.9	1.8	1.4 ± 1.4	2.9	2.9 ± 2.9	15.6	6.5 ± 2.1	-	-	-	-
Leaves	2.3	0.3 ± 0.2	5.3	1.2 ± 1.1	8.6	2.6 ± 1.5	44.0	19.0 ± 2.9	13.3	6.7 ± 6.7	-	-
Other Plant Materials	20.7	3.3 ± 1.5	31.6	9.4 ± 2.8	11.4	9.1 ± 4.4	28.4	13.4 ± 2.7	33.3	19.7 ± 9.2	11.6	9.5 ± 4.5
Terrestrial Invertebrates	62.1	17.2 ± 3.0	61.4	19.9 ± 3.8	17.1	1.60 ± 1.1	9.2	1.9 ± 0.9	6.7	0.03 ± 0.03	23.3	6.7 ± 3.1
Terrestrial Vertebrates	1.1	0.4 ± 0.4	-	-	-	-	-	-	-	-	-	-
Filamentous algae	-	-	-	-	-	-	7.3	1.7 ± 0.8	13.3	13.3 ± 9.1	-	-
Aquatic Insects	2.3	0.8 ± 0.7	7.0	1.1 ± 0.5	-	-	-	-	-	-	9.3	1.0 ± 0.8
Nematoda	-	-	-	-	-	-	-	-	-	-	2.3	0.7 ± 0.1
Fish Scales	2.3	0.1 ± 0.06	1.8	0.1 ± 0.04	-	-	-	-	-	-	-	-
Fish Bones & Muscle	-	-	1.8	0.01 ± 0.01	2.9	0.04 ± 0.04	0.9	0.02 ± 0.02	6.7	1.4 ± 1.4	4.7	0.4 ± 0.3
Soil	1.1	1.0 ± 1.0	7.0	5.4 ± 2.7	-	-	0.9	0.02 ± 0.02	-	-	-	-

Species/Food Category	BRFA		BRME		MYAS		MYRU		MYTO		PRSP	
	%FO	%Vol	%FO	%Vol	%FO	%Vol	%FO	%Vol	%FO	%Vol	%FO	%Vol
Falling Waters (FW)												
n	66	41	31	44	18	20						
Fruit & Seeds	53.0	33.6 ± 5.1	46.3	28.1 ± 5.9	64.5	53.3 ± 8.5	27.3	10.3 ± 4.0	38.9	32.3 ± 11.1	85.0	83.4 ± 8.1
Flowers	39.4	25.5 ± 4.5	9.8	5.0 ± 3.1	35.5	23.8 ± 6.8	65.9	45.2 ± 6.3	11.1	3.4 ± 2.8	0.0	-
Leaves	3.0	0.6 ± 0.6	2.4	0.2 ± 0.2	29.0	18.8 ± 6.2	63.6	39.5 ± 6.0	27.8	14.0 ± 7.4	0.0	-
Other Plant Materials	9.1	3.7 ± 1.8	7.3	0.6 ± 0.4	3.2	3.2 ± 3.2	13.6	4.5 ± 2.5	16.7	6.9 ± 5.1	20.0	14.6 ± 7.7
Terrestrial Invertebrates	63.6	30.7 ± 4.8	82.9	54.1 ± 6.4	6.5	0.9 ± 0.8	-	-	11.1	0.4 ± 0.3	10.0	0.9 ± 0.8
Terrestrial Vertebrates	-	-	-	-	-	-	-	-	-	-		-
Filamentous algae	-	-	-	-	-	-	2.3	0.5 ± 0.5	55.6	42.5 ± 10.9	-	-
Aquatic Insects	3.0	0.3 ± 0.3	9.8	5.5 ± 3.4	-	-	-	-	5.6	0.6 ± 0.6	-	-
Nematoda	-	-	-	-	-	-	-	-	-	-	-	-
Fish Scales	3.0	1.2 ± 0.9	9.8	1.3 ± 0.7	-	-	-	-	-	-	-	-
Fish Bones & Muscle	1.5	1.4 ± 1.4	2.4	0.8 ± 0.8	-	-	-	-	-	-	5.0	1.2 ± 1.2
Soil	3.0	2.9 ± 2.0	4.9	4.4 ± 3.1	-	-	-	-	-	-	-	-
Low Waters (LW)												
n	11		13		23		47		40		4	
Fruit & Seeds	27.3	22.2 ± 11.5	7.7	3.8 ± 3.8	13.0	5.7 ± 3.8	12.8	7.2 ± 3.2	32.5	20.5 ± 5.7	100.0	99.2 ± 0.8
Flowers	.	.	30.8	22.7 ± 11.0	8.7	2.7 ± 2.0	31.9	17.1 ± 4.3	2.5	0.9 ± 0.9	-	-
Leaves	27.3	12.8 ± 9.2	7.7	1.0 ± 1.0	65.2	58.2 ± 10.2	89.4	62.5 ± 5.1	52.5	25.2 ± 5.4	-	-
Other Plant Materials	36.4	4.0 ± 1.8	7.7	1.0 ± 1.1	39.1	29.4 ± 9.2	25.5	11.2 ± 3.8	32.5	18.9 ± 5.3	-	-
Terrestrial Invertebrates	81.8	51.8 ± 14.1	92.3	64.3 ± 11.9	-	-	-	-	-	-	-	-
Terrestrial Vertebrates	-	-	-	-	-	-	4.3	0.1 ± 0.1	27.5	11.7 ± 4.2	-	-
Filamentous algae	-	-	-	-	-	-	-	-	2.5	0.01 ± 0.01	-	-
Aquatic Insects	-	-	-	-	-	-	2.1	0.04 ± 0.04	5.0	1.3 ± 1.0	-	-

Species/Food Category	BRFA		BRME		MYAS		MYRU		MYTO		PRSP	
	%FO	%Vol	%FO	%Vol	%FO	%Vol	%FO	%Vol	%FO	%Vol	%FO	%Vol
Nematoda	-	-	-	-	4.3	0.4 ± 0.4	-	-	-	-	-	-
Fish Scales	-	-	-	-	-	-	2.1	0.02 ± 0.02	20.0	5.7 ± 2.8	25.0	0.8 ± 0.8
Fish Bones & Muscle	18.2	9.1 ± 9.1	7.7	7.2 ± 7.2	-	-	2.1	0.8 ± 0.8	5.0	0.9 ± 0.8	-	-
Soil	-	-	-	-	4.3	3.6 ± 3.6	4.3	1.1 ± 0.8	22.5	14.8 ± 5.1	-	-

APPENDIX 4

SPECIES WITH RIPE FRUITS ($N = 90$) COLLECTED DURING VISUAL CENSUSES AND IN A BOTANICAL INVENTORY CONDUCTED BETWEEN MAY AND DECEMBER 2009 IN THE FLOODPLAIN FOREST OF THE TARAIRA LAKE AND LOWER APAPORIS RIVER, COLOMBIAN AMAZON

Species	Codes	Forest Location		Evidence of Fish Consumption	
		Lake	River	Fruits/Seeds	Flowers
Acosmium nitens (Fabaceae)	Acni	x			
Alchornea discolor (Euphorbiaceae)	Aldi	x		x	
Amaioua guianensis (Rubiaceae)	Amgu		x	x	
Amphirrhox longifolia (Violaceae)	Amlo		x		
Anaxagorea dolichocarpa (Annonaceae)	Ando		x		
Annona hypoglauca (Annonaceae)	Anhy		x	x	
Anturium gracile (Araceae)	Angr		x		
Ardisia sp. (Myrsinaceae)	Arsp		x		
Astrocarium jauari (Arecaceae)	Asja	x	x	x	
Bactris riparia (Arecaceae)	Bari	x		x	
Bocageopsis sp. 1 (Annonaceae)	Bosp	x		x	
Bothriospora corymbosa (Rubiaceae)	Boco	x	x	x	
Buchenavia viridiflora (Combretaceae)	Buvi	x		x	
Byrsonima japurensis (Malpigiaceae)	Byja	x	x	x	
Cecropia distachya (Cecropiaceae)	Cedi		x	x	
Celastraceae (Hippocrateoidea)	Cesp1	x			
Cissus erosa (Vitaceae)	Cier		x		
Couepia cf. *guianensis* (Chrysobalanaceae)	Cocfg	x	x		
Croton bilocularis (Euphorbiaceae)	Crbi	x			
Cupaina sp. (Sapindaceae)	Cupsp	x			
Dalbergia inundata (Fabaceae)	Dain	x	x		
Diospyros poeppigiana (Ebenaceae)	Dipo	x	x		
Dycranostyles ampla (Convolvulaceae)	Dyam		x		
Elaeoluma glabrescens (Sapotaceae)	Elgl	x		x	
Erythroxylum kapplerianum (Erythroxylaceae)	Erka	x			
Eschweilera sp. (Lecythidaceae)	Essp	x	x		x
Eugenia sp. 1 (Myrtaceae)	Eugsp1	x		x	
Eugenia sp. 2 (Myrtaceae)	Eugsp2	x			
Ficus americana (Moraceae)	Fiam	x	x	x	
Ficus sp. 4 (Moraceae)	Fisp4	x			
Garcinia madruno (Clusiaceae)	Gama	x	x		
Genipa americana (Rubiaceae)	Geam	x	x	x	
Gnetum leiboldi (Gnetaceae)	Gnle	x			
Guatteria sp. 3 (Annonaceae)	Gusp3	x			

Species	Codes	Forest Location		Evidence of Fish Consumption	
		Lake	River	Fruits/Seeds	Flowers
Gustavia hexapetala (Lecythidaceae)	Guhe		x		
Heteropterys sp. (Malpigiaceae)	Hesp		x		
Ilex sp. (Aquifoliaceae)	Ilsp	x	x		
Inga sp. 1 (Mimosacea)	*Inga*1	x		x	
Inga sp. 2 (Mimosacea)	Inga2		x	x	
Iranthera cf. juruensis (Myristicaceae)	Ircfju		x	x	
Laetia suaveolens (Flacourtiaceae)	Lasu	x			
Lasistema sp. (Flacourtiaceae)	Lassp		x		
Licania mollis (Chrysobalanaceae)	Limo	x			
Licania sp. (Chrysobalanaceae)	Lisp	x			
Loranthaceae sp. 1	Losp1	x			
Loranthaceae sp. 2	Losp2	x	x		
Mabea nitida (Euphorbiaceae)	Mani	x	x		
Macrolobium acacifolium (Caesalpinaceae)	Maac	x	x		
Maquira coriacea (Moraceae)	Maco	x			
Marsdenia rubrofusca (Asclepidaceae)	Maru	x	x		
Matayba guianensis (Sapindaceae)	Magi	x	x		
Mauritiella aculeata (Arecaceae)	Maac	x		x	
Miconia aplostachya (Melastomataceae)	Miap		x		
Miconia rugosa (Melastomataceae)	Miru	x			
Miconia splendens (Melastomataceae)	Misp		x		
*Miconia truncata (*Melastomataceae)	Mitr	x			
Myrcia sp. (Myrtaceae)	Mysp	x	x		
Nectandra cuspidata (Lauraceae)	Necu	x			
Nectandra egensis (Lauraceae)	Neeg		x	x	x
Nectandra oppositifolia (Lauraceae)	Neop	x		x	
Odontadenia geminata (Apocynaceae)	Odge		x		
Phtirusa sp. (Loranthaceae)	Phtsp	x		x	
Phtirusa stelis (Loranthaceae)	Phtst	x			
Pouteria sp. (Sapotaceae)	Posp	x			
Pseudoxabdra papillosa (Annonaceae)	Pspa	x	x		
Psidium densicomum (Myrtaceae)	Psde	x	x		
Psittacanthus sp. (Loranthaceae)	Pssp	x			
Psychotria lupulina (Rubiaceae)	Pylu		x	x	
Psychotria sp. 2 (Rubiaceae)	Pysp2	x			
Quiina amazonica (Quiinaceae)	Quam	x		x	
Salacia impressifolia (Hyppocrateaceae)	Saim		x		
Simaba orinocensis (Simaroubaceae)	Sior		x	x	
Strichnos panurensis (Loganiaceae)	Stpa	x	x		
Stylogyne laxiflora (Myrsinaceae)	Stla	x			
Symmeria paniculata (Polygonaceae)	Sypa	x			
Passiflora candollei (Passifloraceae)	Pasca		x		
Paullinia carpopoda (Sapindaceae)	Paca	x			
Peperonia macrostachya (Piperaceae)	Pema		x		
Peritassa laevigata (Hyppocrateaceae)	Pela		x		

Species	Codes	Forest Location		Evidence of Fish Consumption	
		Lake	River	Fruits/Seeds	Flowers
Tococa cordata (Melastomataceae)	Tocd	x			
Tococa coronata (Melastomataceae)	Toco		x		
Tontelea sp. (Hyppocrateaceae)	Tosp		x		
Trichilia rubra (Meliaceae)	Trru		x		
Unknown	Unk23	x			
Unknown	Unk24		x		
Unknown	Unk25		x		
Unknown	UnkPL99	x			
Unknown	UnkPL105	x			
Unknown	UnkPL121	x			
Unknown	UnkPL199	x			

APPENDIX 5

CONTRIBUTION OF FOOD ITEMS TO DIETARY DIFFERENCES AMONG FIVE FRUGIVOROUS FISH SPECIES DURING THREE HYDROLOGICAL SEASONS. ONLY FOODS WITHIN 90% OF CUMULATIVE CONTRIBUTION TO THE DIFFERENCE AMONG SPECIES ARE LISTED. THE LAST FIVE COLUMNS SHOW THE MEAN ± S.E. PROPORTION (UN-TRANSFORMED) OF EACH FOOD ITEM PER SPECIES. FRUIT CODES (F-) FOLLOW APPENDIX 2. NUMBER OF STOMACHS ANALYZED PER SPECIES IS REPORTED IN TABLE 3

Season/Taxon	Cumulative Contribution %	BRFA	BRME	MYAS	MYRU	MYTO
High Waters						
Fruit & seed fragments	12.73	0.12 ± 0.03	0.06 ± 0.02	0.43 ± 0.07	0.12 ± 0.03	0.22 ± 0.10
Digested vegetable material	20.92	0.03 ± 0.01	0.08 ± 0.03	0.11 ± 0.05	0.13 ± 0.03	0.19 ± 0.09
Leaves	27.96	0.003 ± 0.002	0.01 ± 0.01	0.02 ± 0.01	0.19 ± 0.03	0.07 ± 0.07
F-Boco	33.66	0.10 ± 0.03	-	0.02 ± 0.02	0.10 ± 0.02	-
F-Byja	38.47	0.07 ± 0.02	0.15 ± 0.04	-	-	-
F-Geam	42.76	0.01 ± 0.01	-	0.04 ± 0.02	0.11 ± 0.02	0.03 ± 0.02
Terrestrial insect fragments	46.83	0.05 ± 0.01	0.08 ± 0.02	0.01 ± 0.01	0.01 ± 0.01	-
F-Asja	50.73	0.04 ± 0.02	-	0.02 ± 0.02	0.06 ± 0.02	0.08 ± 0.07
F-Bari	54.08	0.06 ± 0.02	0.07 ± 0.03	-	-	0.07 ± 0.07
F-Pscflu	57.37	0.002 ± 0.002	-	0.04 ± 0.03	0.07 ± 0.02	-
Flowers	60.39	0.01 ± 0.01	0.01 ± 0.01	0.03 ± 0.03	0.06 ± 0.02	-
Hymenoptera	63.11	0.04 ± 0.02	0.03 ± 0.01	0.003 ± 0.002	0.01 ± 0.01	0.003 ± 0.003
F-cfcucu	65.68	0.06 ± 0.02	0.05 ± 0.03	0.04 ± 0.04	0.001 ± 0.001	0.004 ± 0.004
F-Quam	68.19	0.08 ± 0.02	0.01 ± 0.005	-	0.01 ± 0.01	-
F-Cedi	70.58	0.01 ± 0.01	-	-	0.05 ± 0.02	0.08 ± 0.07

Season/Taxon	Cumulative Contribution %	BRFA	BRME	MYAS	MYRU	MYTO
F-Aldi	72.81	0.002 ± 0.002	0.05 ± 0.02	0.07 ± 0.04	0.0004 ± 0.0004	0.001 ± 0.001
F-Nesp	75.03	0.05 ± 0.02	0.02 ± 0.02	-	-	0.07 ± 0.07
F-Maac	76.66	-	0.0003 ± 0.0003	0.06 ± 0.04	0.03 ± 0.01	-
Lepidoptera (larvae)	78.27	0.04 ± 0.02	0.01 ± 0.01	-	0.01 ± 0.01	-
Periphyton	79.74	-	-	-	0.02 ± 0.01	0.13 ± 0.09
F-Bosp	81.17	0.02 ± 0.01	0.04 ± 0.02	-	-	-
F-Amgu	82.58	0.01 ± 0.01	0.001 ± 0.001	0.06 ± 0.04	0.004 ± 0.003	0.001 ± 0.001
Soil & detritus	83.85	0.01 ± 0.01	0.05 ± 0.03	-	0.0002 ± 0.0002	-
F-Mitr	84.86	0.02 ± 0.01	0.03 ± 0.02	-	-	-
F-Fiam	85.78	0.02 ± 0.01	0.001 ± 0.001	-	0.01 ± 0.01	-
Orthoptera	86.67	0.01 ± 0.01	0.02 ± 0.01	-	-	-
F-Sior	87.50	0.03 ± 0.02	-	-	-	-
F-Clsp	88.28	0.0002 ± 0.0002	0.003 ± 0.002	0.03 ± 0.03	-	0.04 ± 0.04
Wood & bark	89.00	0.01 ± 0.003	0.02 ± 0.01	-	0.0004 ± 0.0004	-
Arachnida	89.68	0.01 ± 0.005	0.02 ± 0.01	-	-	-
Isoptera	90.22	0.01 ± 0.01	0.01 ± 0.005	-	-	-
Falling Waters						
Flowers	18.86	0.26 ± 0.04	0.05 ± 0.03	0.24 ± 0.07	0.45 ± 0.06	0.03 ± 0.03
Fruit & seed fragments	33.61	0.11 ± 0.04	0.08 ± 0.03	0.39 ± 0.08	0.02 ± 0.02	0.32 ± 0.11
Leaves	47.11	0.01 ± 0.01	0.002 ± 0.002	0.19 ± 0.06	0.40 ± 0.06	0.14 ± 0.07
Terrestrial insect fragments	59.98	0.18 ± 0.04	0.35 ± 0.06	-	-	0.003 ± 0.003

Season/Taxon	Cumulative Contribution %	BRFA	BRME	MYAS	MYRU	MYTO
F-Boco	67.10	0.11 ± 0.03	0.09 ± 0.05	0.03 ± 0.02	0.05 ± 0.03	-
Periphyton	71.46	-	-	-	0.004 ± 0.004	0.37 ± 0.11
Hymenoptera	75.58	0.04 ± 0.02	0.10 ± 0.04	0.001 ± 0.001	-	0.001 ± 0.001
Digested vegetable material	78.24	0.01 ± 0.01	-	0.03 ± 0.03	0.04 ± 0.03	0.06 ± 0.05
Soil & detritus	80.04	0.03 ± 0.02	0.04 ± 0.03	-	-	-
F-cfzi	81.27	0.02 ± 0.02	0.02 ± 0.01	-	-	-
F-Asja	82.49	0.04 ± 0.02	-	-	-	-
Coleoptera	83.66	0.03 ± 0.02	0.01 ± 0.01	-	-	-
F-Fiam	84.81	0.02 ± 0.02	0.02 ± 0.02	-	-	-
Hemiptera_Heteroptera	85.93	0.003 ± 0.003	0.04 ± 0.03	-	-	-
Orthoptera	87.02	0.02 ± 0.02	0.005 ± 0.005	0.01 ± 0.01	-	-
F-Unk20	88.01	-	0.05 ± 0.03	-	-	-
Coleoptera (larvae)	89.00	0.02 ± 0.01	0.01 ± 0.01	-	-	-
Arachnida	89.94	-	0.04 ± 0.03	-	-	-
Low Waters						
Leaves	28.51	0.13 ± 0.09	0.01 ± 0.01	0.58 ± 0.10	0.62 ± 0.05	0.25 ± 0.05
Fruit & seed fragments	39.63	0.15 ± 0.10	0.04 ± 0.04	0.06 ± 0.04	0.07 ± 0.03	0.20 ± 0.06
Flowers	49.18	-	0.23 ± 0.11	0.03 ± 0.02	0.17 ± 0.04	0.01 ± 0.01
Digested vegetable material	58.71	0.02 ± 0.01	0.01 ± 0.01	0.20 ± 0.08	0.07 ± 0.03	0.08 ± 0.04
Terrestrial insect fragments	67.19	0.15 ± 0.09	0.22 ± 0.09	-	0.001 ± 0.001	0.10 ± 0.04
Soil & detritus	73.11	-	-	0.04 ± 0.04	0.01 ± 0.01	0.15 ± 0.05

Season/Taxon	Cumulative Contribution %	BRFA	BRME	MYAS	MYRU	MYTO
Isoptera	78.87	0.12 ± 0.09	0.29 ± 0.09	-	-	0.01 ± 0.01
Stems	84.41	-	-	0.07 ± 0.05	0.04 ± 0.02	0.06 ± 0.03
Hymenoptera	88.98	0.18 ± 0.12	0.11 ± 0.08	-	-	0.01 ± 0.01

APPENDIX 6

INTERVIEW QUESTIONNAIRE USED TO ASSESS THE PERCEPTION ABOUT FISHES AND FISHING DEPENDENCE ON FLOODED FORESTS AND VICE-VERSA OF RESIDENTS OF TWO RIVERSIDE INDIGENOUS COMMUNITIES (BOCAS DE TARAIRA AND PUERTO ŇUMI) IN THE LOWER APAPORIS RIVER, COLOMBIAN AMAZON

Fecha: Nombre del Encuestado:____________________________________

Nombre de la Comunidad: _______________________________

Nombre del Encuestador:_________________________________

Encuesta

Objetivo: Evaluar la percepción de la comunidad sobre la dependencia de los peces y la pesca del bosque inundado y viceversa.

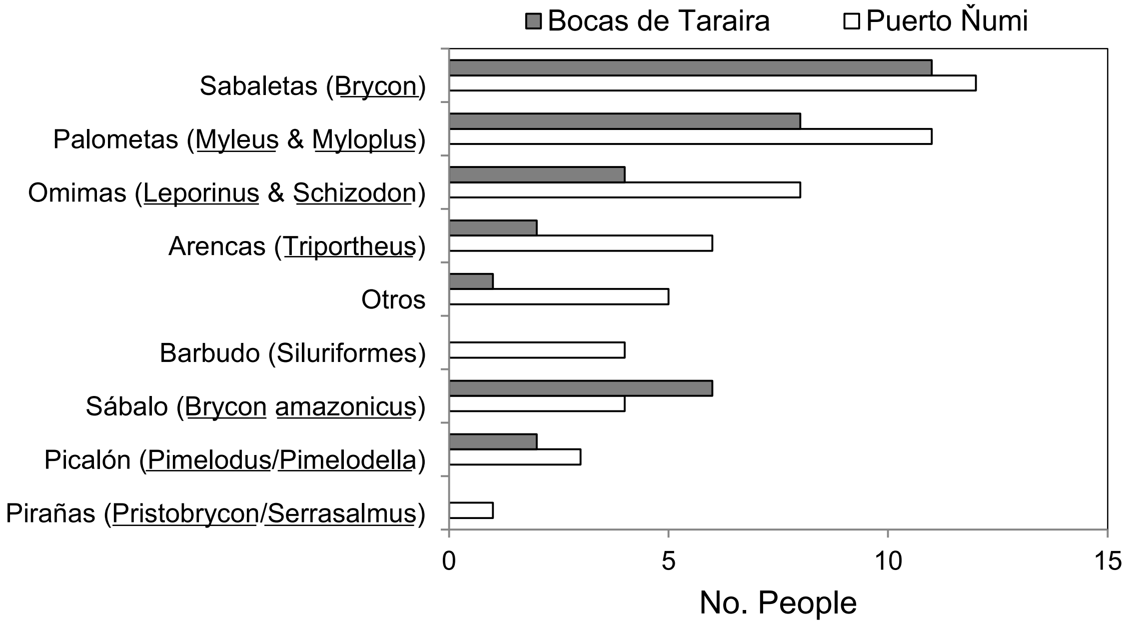
1. Que peces ha observado comiendo pepas?
____
2. Cuales son las pepas que consumen estos peces?
____
3. De las siguientes artes de pesca, cuales son las que mas usa para coger peces peperos?

   Malla____ Vara___ Colgadero____Otros________________________
4. Cuales son las pepas que utiliza para pescar?
____
5. Donde busca las pepas para pescar?
____
6. De los peces peperos: Cuales son los que usted mas pesca?
____
7. Cuando usted sale a pescar, ha observado si los peces peperos comen los frutos que:

   Flotan___ los que están en las ramas cerca al agua___ o los que se hunden__
8. Al desviscerar los peces peperos, usted le observa que pepas hay en el estomago o en el intestino?
Si___ No__ Cuales?: ____
9. Que tamaño de peces ha visto comiendo pepas?
Grandes_____ Medianos___ Pequeños_____
10. Usted cree que los peces peperos dependen de las plantas del rebalse?
Si___ No__ Por qué?: ____
11. Ha visto que donde no hay muchas pepas, se reduce la pesca? Si__ No__

APPENDIX 7

PRINCIPAL FRUIT-EATING FISH TAXA CONSUMED BY RESIDENTS OF TWO RIVERINE INDIGENOUS COMMUNITIES (BOCAS DE TARAIRA AND PUERTO ŇUMI) IN THE LOWER APAPORIS RIVER, COLOMBIAN AMAZON



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