

Niche partitioning among frugivorous fishes in response to fluctuating resources in the Amazonian floodplain forest

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Abstract. In response to temporal changes in the quality and availability of food resources, consumers should adjust their foraging behavior in a manner that maximizes energy and nutrient intake and, when resources are limiting, minimizes dietary overlap with other consumers. Floodplains of the Amazon and its lowland tributaries are characterized by strong, yet predictable, hydrological seasonality, seasonal availability of fruits, seeds, and other food resources of terrestrial origin, and diverse assemblages of frugivorous fishes, including morphologically similar species of several characiform families. Here, we investigated how diets of frugivorous fishes in the Amazon change in response to fluctuations in food availability, and how this influences patterns of interspecific dietary overlap. We tested predictions from classical theories of foraging and resource competition by estimating changes in diet breadth and overlap across seasons. We monitored fruiting phenology to assess food availability, and surveyed local fish populations during three hydrological seasons in an oligotrophic river and an adjacent oxbow lake in the Colombian Amazon. We analyzed stomach contents and stable isotope data to evaluate temporal and interspecific relationships for dietary composition, breadth, and overlap. Diets of six species of characiform fishes representing three genera changed according to seasonal fluctuations in food availability, and patterns of diet breadth and interspecific overlap during the peak flood pulse were consistent with predictions of optimal foraging theory. During times of high fruit abundance, fishes consumed items to which their functional morphological traits seemed best adapted, potentially enhancing net energy and nutritional gains. As the annual flood pulse subsided and availability of forest food resources in aquatic habitats changed, there was not a consistent pattern of diet breadth expansion or compression. Nonetheless, shifts in both diet composition and stable isotope ratios of consumer tissues during this period resulted in trophic niche segregation in a pattern consistent with competition theory.

Key words: *Amazon River; Apaporis River, Colombia; Characidae; flooded forest; frugivory; fruiting phenology; hydrology; Serrasalminidae; species coexistence; switching; trophic ecology.*

INTRODUCTION

In seasonal environments, consumers have to cope with periodic fluctuations in resource availability that influence not only individual growth and survival, but also interactions with other species (e.g., Carnicer et al. 2008, Venner et al. 2011, Barger and Kitaysky 2012, O'Callaghan et al. 2013). How organisms respond to resource pulses has important implications not only for understanding the manner in which organisms cope with fluctuating environments, but also for predicting how populations and communities respond to larger-scale environmental changes in climate and landscapes (Chesson et al. 2004, McCluney et al. 2012). As resource quality and availability fluctuate, adaptive foragers should adjust their foraging activities to maximize

energy and nutritional gains relative to costs (Abrams 1991). According to predictions of optimal foraging theory, foragers are expected to have more specialized diets when preferred resources are abundant, and to broaden their diets during periods of food scarcity (Stephens and Krebs 1986, Perry and Pianka 1997). Such changes in foraging behavior are, however, likely to affect interactions with other consumer species via increased niche overlap and potential for competition. When demand for resources exceeds supply, competition increases and tolerance of interspecific niche overlap declines (Pianka 1974, 1976). Classical competition theory, i.e., limiting similarity (sensu Hutchinson 1959, MacArthur and Levins 1967, Abrams 1983), and niche partitioning (sensu MacArthur 1958, Pianka 1974, 1976, Schoener 1974) predict that stable coexistence of competing species is achieved through niche differentiation that reduces overlap among competitors. Thus, during periods of relative food scarcity, animals are expected to adjust feeding to reduce niche overlap with competitors. This can be achieved by narrowing diet

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breadth through selective feeding (i.e., trophic niche contraction).

Tropical river–floodplain ecosystems undergo regular changes in water levels and food resource availability, and provide excellent opportunities for testing predictions of classical foraging and niche theories regarding changes in diet breadth and overlap in response to fluctuating resources. Floodplains of the Amazon River and its lowland tributaries have a strong seasonal hydrology (annual water level fluctuates over 10 m) that drastically changes the landscape, affecting not only physical and chemical conditions, but also habitat and food resources available to fish. During the flood season, floodplains are mosaics of interconnected channels, lakes, inundated forests, and savannas (Melack et al. 2009, Junk and Piedade 2010), all of which provide important habitat for diverse fish assemblages (Goulding et al. 1988, Saint-Paul et al. 2000, Petry et al. 2003, Correa et al. 2008). Abundant fruits, seeds, insects, and other food resources of terrestrial origin are available to fishes that move into flooded areas (Goulding 1980, Junk et al. 1997). These allochthonous foods are particularly important sources of energy in aquatic food webs of tropical rivers with low autochthonous primary production due to nutrient limitation (Goulding et al. 1988, Melack and Forsberg 2001). As waters recede from the forest, the availability of habitat and allochthonous foods for fish declines. During this phase of the annual hydrological cycle, competition for limited resources should be stronger and might be expected to induce niche segregation among consumer species.

Fruit consumption is widespread among Amazonian floodplain fishes, with ~120 species consuming variable amounts of fruits and seeds (Horn et al. 2011). Among these, medium- to large-sized frugivorous characid (tetras and their relatives) and serrasalmid (piranhas and pacus) fishes are particularly abundant in local assemblages that include multiple congeneric species (Goulding et al. 1988, Saint-Paul et al. 2000, Correa 2008). While foraging in the flooded forest, these fishes' diets are dominated by fruits and seeds (Goulding 1980, Pizango-Paima et al. 2001, Anderson et al. 2009). How diets are affected by the annual hydrological cycle and implications of possible changes in foraging behavior on interspecific dietary overlap, however, are unknown.

In the Colombian Amazon, several species of frugivorous serrasalmids (*Myloplus asterias*, *M. rubripinnis*, *M. schomburgkii*, *M. torquatus*, *Myloplus* sp., and *Pristobrycon* sp.) and characids (*Brycon amazonicus*, *B. falcatus*, *B. melanopterus*) co-occur in the same floodplain habitats (Correa 2008). To better understand the mechanisms that facilitate coexistence of closely related species of consumers inhabiting seasonal environments, we investigated temporal variation in diets of frugivorous fishes in relation to fluctuations in food availability, and determined how diets and interspecific dietary overlap change in response to the seasonal fruit subsidy.

Specifically, we tested the following hypotheses: (1) seasonal changes in dietary niche breadth and overlap are consistent with predictions of optimal foraging theory; (2) seasonal changes in dietary niche breadth and overlap are consistent with predictions of classical competition theory; and (3) dietary niche breadth and overlap change little across seasons due to dietary inflexibility (see predictions of each hypothesis in Fig. 1). To address these questions, we monitored fruiting phenology to establish changes in food availability and conducted a quantitative analysis of diets of sympatric frugivorous fishes inhabiting an undisturbed flooded forest in the Colombian Amazon across three hydrological seasons.

METHODS

Study site

The study was conducted in the lower Apaporis River and an adjacent oxbow lake (Taraira Lake) that is connected to the river year-round. The Apaporis is a large (1200 km long, 420 m wide) blackwater river (darkly stained with dissolved humic compounds) that drains a vast extension of the Vaupes region of southern Colombia (47 000 km², PAT 1997; Fig. 2). The Apaporis has low conductivity (5.7–7.5 μ S), turbidity (Secchi 0.61–1.25 m), and pH (5.2–6.5), and concentrations of dissolved nutrients are assumed to be very low as in other blackwater rivers of the region (Sioli 1984). Precipitation follows a bimodal pattern (annual rainfall is 3836 \pm 486 mm/yr, mean \pm SD; Deffler and Deffler 1996) and the annual hydrological cycle causes fluctuations in water level of ~9 m (Appendix A). Margins of the river and oxbow lake are covered by undisturbed evergreen forest with high species diversity. Subsistence fishing by a sparse indigenous population appears to minimally impact local fish populations, as evidenced by the large sizes of the most valuable fish species (e.g., *Arapaima gigas*) compared to those observed in other areas of the Colombian Amazon where villages are larger and more numerous.

Data collection

We monitored fruiting phenology and conducted fish surveys 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 of 2009 (Appendix A). To monitor temporal changes in availability of fruits, seeds, and flowers falling into the water, we placed litter traps at 20 sampling points (10 in the lake and 10 in the river) along areas where fish were sampled. Following a systematic sampling protocol, we choose an initial point at random (using a compass bearing) and selected nine subsequent sampling points every 1000 m along the lake and every 500 m along the river. The greater distance between sampling points within the lake was to provide complete coverage of this larger area compared to the area sampled in the river,

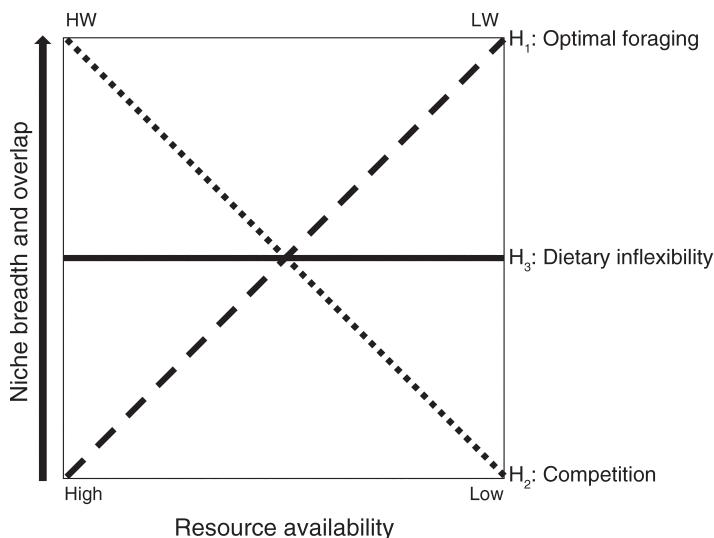


FIG. 1. Divergent predictions for changes in dietary niche breadth and interspecific overlap by fish in response to seasonal reduction in food availability according to three hypotheses. The high-water season (HW) has high allochthonous food abundance; the low-water season (LW) has low allochthonous food abundance. Hypothesis 1 (H_1 , dashed line) is the optimal foraging theory: during HW, fish are expected to consume the most profitable food resources and have relatively narrow diet breadth; during LW, fish are expected to expand diet breadth to include less profitable food items yielding higher trophic niche overlap. Hypothesis 2 (H_2 , dotted line) represents competition theory: during HW, fish are expected to consume a wide variety of foods and have relatively broad diet breadth; during LW, higher fish densities and reduced availability of preferred foods induce reduction in diet breadth and niche overlap to limit interspecific competition. Hypothesis 3 (H_3 , solid line) represents dietary inflexibility: fish are behaviorally or morphologically incapable of adjusting diet, in which case there would be minimal change in diet breadth and niche overlap in response to seasonal changes in food availability.

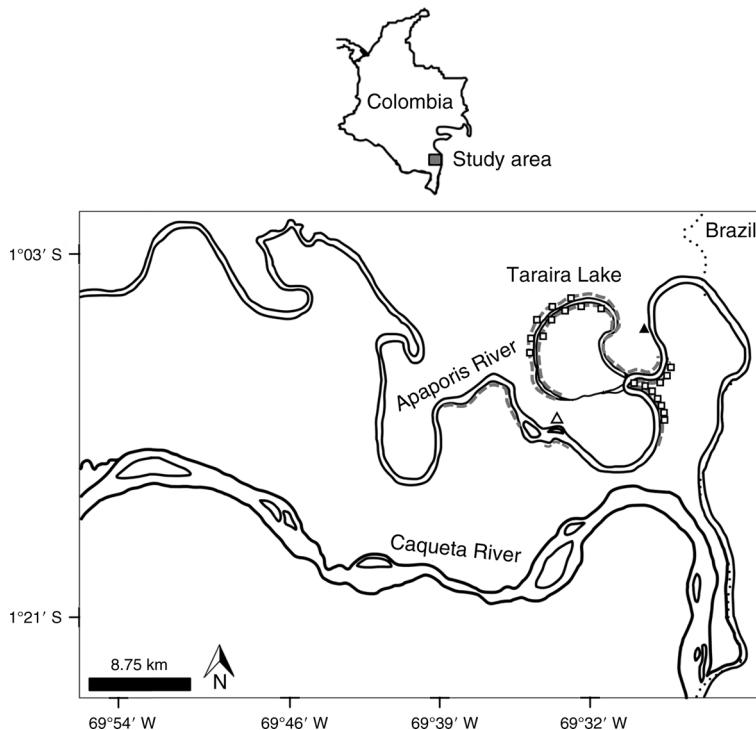


FIG. 2. Map of the study area in the lower Apaporis River, Colombian Amazon. The gray dashed line outlines study reaches along the shoreline of the river and lake. Small open squares represent sampling points where traps to monitor plant phenology were located. Locations of two indigenous communities are shown (solid triangle, Bocas de Taraira; open triangle, Puerto Ñumi).

but with the same number of traps (Fig. 2). At each sampling point, we placed three hanging traps inside the flooded forest, at 25-m intervals, along a transect running parallel to the shore (Fig. 3A). These square traps, covering an area of 0.64 m², were constructed of mosquito-net fabric (mesh size < 0.1 mm) (Stevenson and Vargas 2008). Each corner of the trap was tied to the trunk of the nearest tree in order to suspend it ~1–2 m from the surface of the water (Fig. 3B). We monitored traps in the river every three weeks after installation for the first six weeks, and then every two weeks thereafter. Traps in the oxbow lake were monitored every two weeks. During October, all traps were monitored at a one-month interval. During LW, we moved the traps to the edge of the forest to monitor the fruiting phenology of the riparian vegetation. We placed and monitored traps using a canoe and relocated them as necessary to maintain their position over the water during the study. Fruits, seeds, and flowers collected in the traps were separated from the rest of the litter. Samples were dried in a solar oven or under direct sunlight until constant mass was achieved, and then dry mass was recorded.

During the days of trap monitoring, we conducted a visual census of fruiting plants 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). We recorded the species identity and abundance of plants with ripe fruits, immature fruits, and flowers. A similar census was conducted inside the flooded forest near the location of traps, and data were pooled with those from the forest edge. We conducted visual censuses along six transects in the lake only once during the HW season, following the methodology just described. Throughout the field research period, we collected samples of all plants bearing fruit across the area where fishes were surveyed. Vouchers were deposited at the Colombian Amazon Herbarium (COAH), Instituto Amazónico de Investigaciones Científicas-Sinchi, Bogotá, Colombia.

We conducted fish surveys five days per week throughout the three hydrological seasons. During the HW and FW seasons, surveys were conducted with hooks. On each fishing day, we baited between 20 and 30 hooks 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. These baits are commonly used by local people. Each hook was attached to a 1-m green multifilament fishing line suspended from vegetation inside the flooded forest or along the edge of the river. Based on the expertise of local fishermen who assisted us with the surveys, hooks were attached to low branches of the vegetation that were in contact with the water, trapping floating debris that helped to disguise the hooks. During the LW season, we conducted diurnal fish surveys along

the river's edge with earthworm-baited hook and line. During the night, fish were captured from the middle of the river channel using an experimental monofilament gill net (100 m long, 2.5 m wide, 8-, 10-, and 15-cm stretched mesh). 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. During the LW season, the lake became a shallow mudflat with limited access. Therefore, we restricted fish surveys to the river during this season and compensated by expanding the survey area upstream in places with similar conditions. We identified each specimen and recorded basic measurements (standard length, body mass, and time and site of capture). After euthanasia, each specimen was dissected within an hour after capture; the stomach was removed and preserved in 70% ethanol for subsequent analysis. Voucher specimens were deposited at the fish collection of Universidad del Tolima, Tolima, Colombia.

Stomach contents were observed under a dissecting microscope and analyzed using volumetric methods described by Hyslop (1980) and Winemiller (1989). The volume of each food item was estimated to the nearest 0.001 mL. We used characteristics of the husk and seeds to identify fruits retrieved from stomachs by comparison against the reference plant collection and with the aid of taxonomic keys. Identifications were later confirmed by experts at COAH (N. Castaño and D. Cárdenas) 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.”

During every season, we collected samples for analysis of stable isotope ratios of C ($\delta^{13}\text{C}$) and N ($\delta^{15}\text{N}$) from fish specimens and basal production sources (See Appendix B for details of sample collection and preparation). Analyses of carbon and nitrogen percentage composition and stable isotope ratios were conducted by the Analytical Chemistry Laboratory, Institute of Ecology, University of Georgia, Athens, Georgia, USA. 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 reflect the isotopic composition of food sources during the same hydrological season (samples were taken in the middle of each season).

Numerical analysis

Plant phenology.—For each of the 20 sampling points in which fruit-fall traps were placed, we calculated average dry mass of fruits (including ripe and immature fruits, fruit fragments, and naked seeds) and flowers. These values were then used to calculate average production for each interval of time between successive monitoring episodes. Some of the traps along the Apaporis River were stolen, which reduced the number

of sampling points for some time intervals in that habitat (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 that visual censuses were conducted.

Stomach contents analysis.—We assessed diets of the most abundant floodplain forest fish species that were captured during all three seasons (*Brycon falcatus*, *B. melanopterus*, *Myloplus asterias*, *M. rubripinnis*, *M. torquatus*, and *Pristobrycon* sp.) based on 703 stomachs (standard length 101–286 mm). For each individual fish, we estimated the proportional volumetric contribution of each food type (excluding the volume of any bait material that was ingested). Partially digested unidentified material and arthropod fragments of unknown origin were excluded from the total. These unidentified materials comprised a very small fraction (<2%) of the total volume of material extracted from fish guts, and thus were uninformative in terms of dietary trends. To facilitate statistical analyses, we aggregated the 110 different food types found within stomach contents (including fruits and seeds of 73 species of trees, shrubs and lianas) into 12 broad functional food categories (Appendix C). Terrestrial vertebrates and nematodes were excluded from analyses because these food categories were found in stomachs of only one and two individuals, respectively.

We used a two-way contingency table for each species to test for independence between frequencies of food consumption and hydrological seasons. Some food categories with small frequencies of consumption were combined to increase the expected frequencies (Legendre and Legendre 2012). A 3 × 5 contingency table of season vs. food category was analyzed with three levels for seasons (HW, FW, and LW) and five levels for food categories (1, fruits and seeds; 2, other terrestrial plant material; 3, terrestrial invertebrates; 4, algae and soil; 5, aquatic insect and fish remains). A 2 × 4 contingency table was analyzed for *Pristobrycon* sp. due to small sample size during the LW season and the absence of algae and soil from its diet. Probability values were calculated from the chi-squared distribution and from a permutation test (9999 replicates).

A test of homogeneity of multivariate dispersion (PERMDISP) was used to assess within-season differences in diet breadth, measured as dispersion in diet space, among species. 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, our assumption is that differences in dispersion among species indicate that some species have more restricted diets than others. The test was conducted on the dietary similarity matrix previously described (species × proportional volume of 10 food categories), and, as implemented in Vegan 2.0-2

(Oksanen et al. 2012), it accounts for unequal number of observations per group. Volumetric proportions were arcsine square-root-transformed prior to analyses (McCune and Grace 2002). 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 pairwise *t* test of dispersion of combinations of groups (9999 permutations). Significance of permuted *P* values was determined after correcting for multiple comparisons using the Benjamin and Hochberg (1995) approach. We also conducted PERMDISP on dietary similarity matrices (one matrix per season) that included all food types present in each broad food category. Because general patterns of diet breadth were not influenced by scale of resolution, tests results are not shown.

We used the Friedman test to assess seasonal differences in diet breadth and overlap by comparing matching diet breadth values per species and pairwise niche overlap across seasons, respectively. When significant differences were detected, the test was followed by Wilcoxon signed rank tests. The average diet breadth of each species during every season was calculated as the average distance to the centroid in diet space using PERMDISP (i.e., greater distance indicates broader niche). Niche overlap among species pairs during every season was quantified using Pianka's (1973) niche overlap index $O_{jk} = O_{kj} = \frac{\sum p_{ij}p_{ik}}{\sqrt{\sum p_{ij}^2 \sum p_{ik}^2}}$, 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 in two ways for comparison (i.e., using the mean volumetric proportional consumption values based on proportions obtained from individual specimens, and using the proportional total volumes of food categories consumed by the entire population). The first measure reflects individual variation in food consumption, whereas the second measure represents overall food consumption at the population level. 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 diet breadths were preserved, zero values were reshuffled, and all resources had the same probability of being consumed (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.

Two-way contingency tables were analyzed in PAST (Hammer et al. 2001), and Friedman, Wilcoxon signed ranks tests, and PERMDISP were conducted in R 2.11.1 (R Development Core Team 2010). Pianka's niche



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 (high-water and falling-water seasons). Photo credits: S. B. Correa.

overlap index and Monte Carlo simulations were performed in EcoSim 7.72 (Gotelli and Entsminger 2010).

Stable isotope analysis.—To adjust for a possible negative bias in $\delta^{13}\text{C}$ values induced by lipid accumulation in fish muscle, we used the arithmetic correction $\delta^{13}\text{C} = -3.32 + 0.99(\text{C:N})$, 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), we only applied the correction to samples with C:N > 3.5 (i.e., values ranging from 3.51 to 4.78). Post and colleagues reported $\delta^{13}\text{C}$ values from two serrasalmid species obtained after lipid extraction that were identical or nearly identical to $\delta^{13}\text{C}$ values adjusted with this equation (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.

Two-way analysis of variance was used to test for differences in isotopic composition among species and across seasons using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ 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. P values were corrected for multiple comparisons. To meet test assumptions, we transformed $\delta^{13}\text{C}$ data (Box-Cox transformation) after adding $+34$ to each value to make all values positive. Data transformations (package "MASS") and statistical analyses were performed in R 2.11.1 (R Development Core Team 2010).

The trophic position (TP) of each species during each season was estimated using the equation $\text{TP} = 1 + (\delta^{15}\text{N}_{\text{fish}} - \delta^{15}\text{N}_{\text{base}})/\Delta_{\text{N}}$, where $\delta^{15}\text{N}_{\text{base}}$ is the mean $\delta^{15}\text{N}$ of basal sources, 1 is the TP for primary producers, and Δ_{N} represents $\delta^{15}\text{N}$ trophic enrichment caused by the accumulation of $\delta^{15}\text{N}$ in the consumer as N is transferred up the food chain (Post 2002). We used a value of 4.08‰ 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 $\delta^{15}\text{N}_{\text{base}}$ value was the mean $\delta^{15}\text{N}$ of samples of basal production sources collected during each season (Appendix B).

RESULTS

Food availability and food consumption

Despite differences in plant species composition, we found similar phenological patterns of fruit and flower production in forests surrounding 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 (Fig. 4; Appendix D). Fruit production started again in November when immature fruits were recorded during visual censuses (Appendix D). These phenological patterns were reflected in the food consumption patterns of fish (Fig. 4). The null hypothesis of independence between frequencies of food consumption and hydrological seasons was rejected for all species (χ^2 , $df = 8$, $P < 0.01$, for each species), except for *Pristobrycon* sp. (χ^2 , $df = 3$, $P = 0.47$). Similar P values were obtained from permutation tests (results not shown). Most fish consumed different food types in frequencies that are influenced by hydrological seasonality (Appendix E). During the HW season, fruits and seeds were consumed in higher frequency and contributed high volumes to the diet of all fish species. Increased flower production during the FW season was reflected in higher frequency and volume of flowers in fish stomachs. In general, from the HW to the LW season, both *Brycon* species switched from fruits and seeds to terrestrial insects,

Myloplus species switched from fruits and seeds to leaves and phytomicrobenthos (PMB), while *Pristobrycon* sp. maintained a constant diet. Stomach fullness was variable during every season, and lowest fullness was observed 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). Frequency of empty stomachs did not increase from the HW to the FW season (HW, 5.2%; FW: 5.9%; binomial chi-square for proportions = 0.03, $df = 1$, $P = 0.86$). Frequency of empty stomachs increased during the LW season with respect to the previous season (LW, 20.4%; binomial chi-square for proportions = 16.13, $df = 1$, $P < 0.0001$).

Dietary similarity based on stomach contents

We observed widespread interspecific differences in diet breadth, even among congeneric species (PERM-DISP, $F_{m(17,685)} = 7.19$, where subscript m refers to spatial medians; $P < 0.0001$; Fig. 5, Table 1). Across the six species, however, there was no consistent pattern of diet breadth expansion or contraction from one season to the next (Fig. 5, Table 1). Furthermore, average diet breadth was similar across seasons (Friedman chi-square = 4.0, $df = 2$, $P = 0.14$; median diet breadth = 0.30, 0.45, and 0.39 for HW, FW, and LW seasons, respectively). These patterns did not change after exclusion of *Pristobrycon* sp., a species that had low sample size during the LW season (results not shown).

During every season, mean dietary overlap among species was 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, was different among seasons (Friedman chi-square = 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 total proportional consumption of food categories). Greater dietary overlap occurred during the HW season (Wilcoxon signed ranks test: for HW vs. FW, $W = 120$, $P < 0.001$, $N = 15$; for HW vs. LW, $W = 120$, $P < 0.001$, $N = 15$). A marginally significant reduction in dietary overlap was detected from the FW to the LW season (Wilcoxon signed ranks test, $W = 88$, $P = 0.06$, $N = 15$). Similar patterns were observed when dietary overlap was calculated based on average proportional consumption of food categories computed from volumetric proportions consumed by individual fish (results not shown). Likewise, patterns of dietary overlap did not change with the exclusion of *Pristobrycon* sp., the species with low sample size during the LW season (results not shown).

Dietary similarity based on stable isotopes

Analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ revealed significant variation in the isotopic composition of fish muscle among species (Tables 2 and 3). This variation was

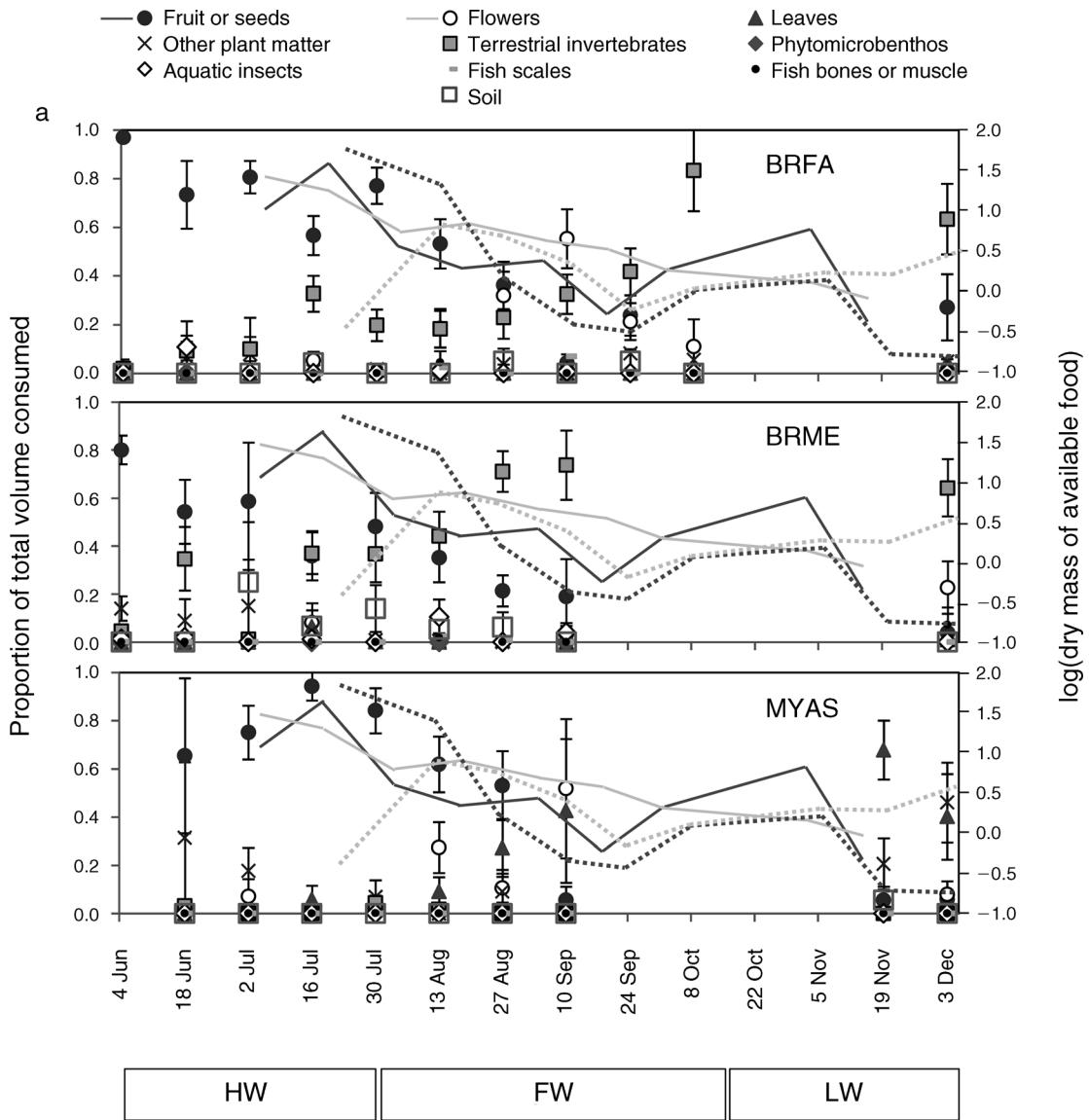


FIG. 4. Average food consumption by six frugivorous fish species (assessed once every two weeks from stomach contents) and food availability (assessed by collection traps) during three hydrological seasons. Food consumption data from the lower Apaporis River and Taraira Lake were combined. Symbols represent the proportional volume (mean \pm SE) of different foods found in stomach contents (left-hand axis; volume was measured in mL). Lines represent fruit (dark gray) and flower (light gray) availability (right-hand axis; log-transformed dry mass, originally measured in grams) at each site (dashed lines, Apaporis River; solid lines, Taraira Lake). Dates represent the end of a two-week sampling period (e.g., from 21 May to 4 June 2009); all sampling shown was in 2009. Species codes are: BRFA, *Brycon falcatus*; BRME, *Brycon melanopterus*; MYAS, *Myloplus asterias*; MYRU, *Myloplus rubripinnis*; MYTO, *Myloplus torquatus*; and PRSP, *Pristobrycon* sp. The diet of PRSP during LW is not presented because of low sample size. Boxes below the x-axis mark the extent of the hydrological seasons: HW, high water; FW, falling water; and LW, low water.

influenced by seasonality, as depicted by the significant interaction effect of season and species, despite marginal seasonality in overall isotopic ratios. Within season, interspecific differences in isotopic composition were detected, even at the genus level (Table 3). In general, species spanned a narrow range of $\delta^{13}\text{C}$ (-27‰ to

-25‰) and $\delta^{15}\text{N}$ ($+7\text{‰}$ to $+9\text{‰}$) signatures, with few exceptions (Appendix F). The narrow range of $\delta^{15}\text{N}$ signatures was reflected in the low variation in trophic positions (TP) estimated across all three seasons. No fish species had $\text{TP} > 2.5$ and most species had $\text{TP} \approx 2$, indicating that all species are primary consumers.

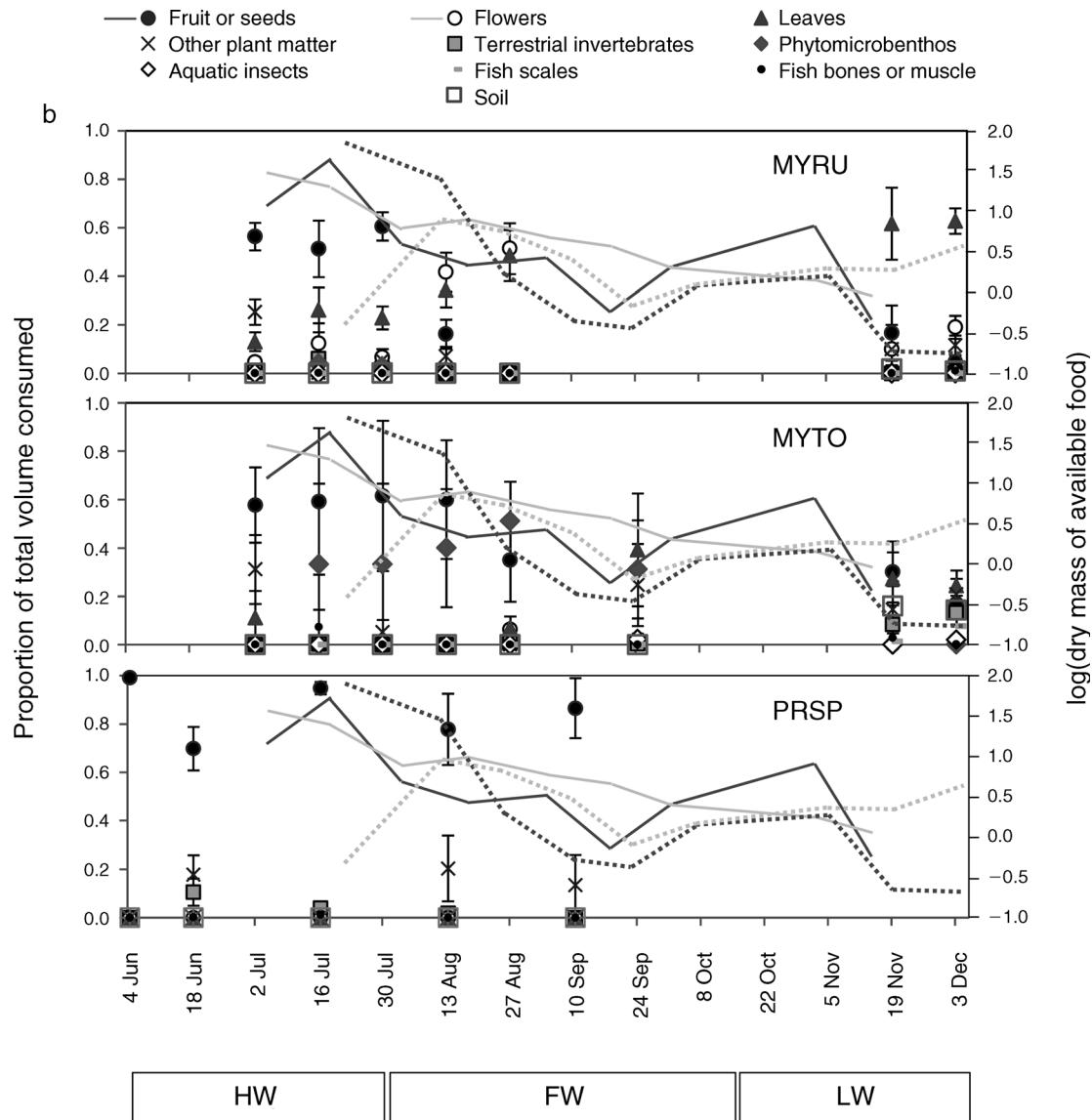


FIG. 4. Continued.

During the HW season (mean TP = 1.99), a difference of 0.23 TP units separated the lowest (*M. torquatus*) and the highest (*M. rubripinnis*) consumer. During the FW season (mean TP = 2.0), a difference of 0.34 TP units separated the lowest (*M. asterias*) and highest (*M. rubripinnis*) consumer. During the LW season (mean TP = 2.1), a difference of 0.46 TP units separated the lowest (*M. torquatus*) and the highest (*B. falcatus*) consumer.

DISCUSSION

This study apparently is the first to quantify seasonal changes in food availability while simultaneously analyzing food consumption and dietary overlap among Amazonian floodplain fishes. In the lower Apaporis River, flowering and fruiting phenology showed strong

seasonal patterns, altering the availability of allochthonous food resources for fishes. We found changes in patterns of food consumption for six species across seasons that closely matched fluctuations in food availability. In general, dietary shifts in response to changes in the availability of preferred foods reduced interspecific niche overlap and may be a mechanism that facilitates coexistence in this species-rich fish assemblage. During the period of greatest fruit production, diets of all six species were dominated, to varying degrees, by fruits and seeds, yielding broadly overlapping trophic niches among species. Analyses of diets at coarse and fine scales of resolution and stable isotopes all revealed a general pattern of decreased trophic niche overlap among species as the water level fell (FW and

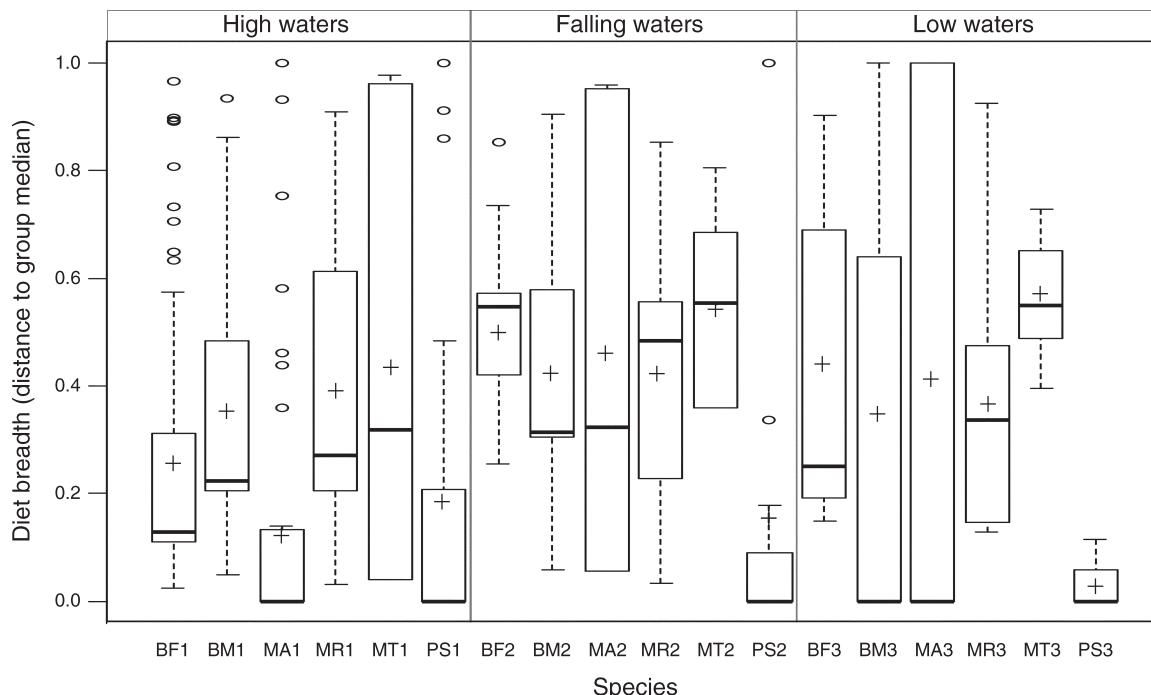


FIG. 5. Variation in diet breadth among six frugivorous fish species based on 10 functional food categories during three hydrological seasons. Diet breadth was assessed as species dispersion in diet space using PERMDISP (i.e., greater distance to spatial median indicates larger dispersion and therefore a broader trophic niche). Box lower and upper endpoints represent the 25th and 75th quartiles, respectively. The horizontal bar and plus symbol inside each box represent median and average diet breadth, respectively, excluding outliers, which are represented by open ovals. See Table 1 for *P* values from species comparisons. Species codes are: BF, *Brycon falcatus*; BM, *Brycon melanopterus*; MA, *Myloplus asterias*; MR, *Myloplus rubripinnis*; MT, *Myloplus torquatus*; and PS, *Pristobrycon* sp. Season codes are: 1, high water; 2, falling water; and 3, low water.

LW seasons) and fruits and other terrestrial food resources were less available for fishes. We presented two opposite predictions as to how species would respond to relative food scarcity. Optimal foraging

theory predicts that the consumer species will broaden their diet (i.e., trophic niche expansion) to include alternative foods in an attempt to meet dietary requirements (Perry and Pianka 1997) and thereby

TABLE 1. Summary of PERMDISP *P* values for comparisons of diet breadth in six frugivorous fish species in southern Colombia during three hydrological seasons (1, high water; 2, falling water; 3, low water).

Species	BM1	MA1	MR1	MT1	PS1	BF2	BM2	MA2	MR2	MT2	PS2	BF3	BM3	MA3	MR3	MT3	PS3
BF1	<i>0.054</i>	<i>0.202</i>	0.003	<i>0.074</i>	<i>0.387</i>	0.001	0.005	0.005	0.002	0.001	0.383	0.045	0.425	0.079	0.045	0.001	0.142
BM1		0.007	<i>0.476</i>	<i>0.510</i>	0.018	0.001	0.317	0.202	0.229	0.010	0.040	0.373	0.937	0.606	0.899	0.001	0.025
MA1			0.001	0.050	<i>0.811</i>	0.001	0.002	0.010	0.001	0.001	0.937	0.033	0.209	0.054	0.009	0.001	0.534
MR1				<i>0.756</i>	0.002	0.007	0.695	0.361	0.610	0.054	0.006	0.610	0.667	0.874	0.640	0.002	0.018
MT1					<i>0.076</i>	0.317	0.937	0.848	0.966	0.427	0.129	0.923	0.695	0.937	0.610	0.115	0.143
PS1						0.001	0.005	0.010	0.002	0.001	0.902	0.054	0.302	0.080	0.025	0.001	0.476
BF2							0.045	<i>0.617</i>	0.033	<i>0.429</i>	0.001	0.431	0.025	0.245	0.001	0.037	0.001
BM2								<i>0.636</i>	<i>0.937</i>	<i>0.103</i>	0.009	0.791	0.566	0.952	0.440	0.004	0.010
MA2									<i>0.667</i>	<i>0.606</i>	0.037	0.937	0.510	0.750	0.294	0.275	0.090
MR2										<i>0.096</i>	0.004	0.827	0.499	0.936	0.353	0.001	0.002
MT2											0.004	0.435	0.143	0.412	0.025	0.667	0.001
PS2												0.091	0.361	0.148	0.045	0.001	0.586
BF3													<i>0.610</i>	<i>0.879</i>	<i>0.451</i>	<i>0.096</i>	0.046
BM3														<i>0.756</i>	0.899	0.009	0.259
MA3															<i>0.686</i>	<i>0.114</i>	0.243
MR3																0.001	0.025
MT3																	0.001

Notes: Values in italics are adjusted *P* values for within-season pairwise species comparisons. Non-italicized values are adjusted *P* values for between-season comparisons of all of the possible pairwise species comparisons. Statistically significant *P* values ($P \leq 0.05$) are highlighted in bold. Species codes are: BF, *Brycon falcatus*; BM, *Brycon melanopterus*; MA, *Myloplus asterias*; MR, *Myloplus rubripinnis*; MT, *Myloplus torquatus*; PS, *Pristobrycon* sp. See Fig. 5 for boxplots showing diet breadth.

TABLE 2. Summary of two-way ANOVA for stable isotope ratios of C and N of six frugivorous fish species in southern Colombia during three hydrological seasons.

Variable and effect	<i>F</i>	df	<i>P</i>
$\delta^{13}\text{C}$			
Seasons	3.02	2, 120	0.053
Species	35.42	5, 120	<0.0001
Seasons \times Species	3.01	10, 120	0.002
$\delta^{15}\text{N}$			
Seasons	2.68	2, 120	0.073
Species	16.31	5, 120	<0.0001
Seasons \times Species	2.24	10, 120	0.020

increase interspecific dietary overlap. Conversely, resource competition theory predicts that species will specialize and consume fewer alternative resources (i.e., trophic niche contraction), thereby segregating in niche space by reducing interspecific dietary overlap (Pianka 1974, Schoener 1974, Abrams 1983). Neither of these predictions was fully supported, given that we did not observe a consistent pattern of dietary niche expansion or contraction in relation to decreased food availability. Instead, the response was variable among species, which suggests interspecific differences in foraging behavior. As water receded from the forest and the availability of fruits and other allochthonous food was reduced, all species except for *Pristobrycon* sp. changed their diets. Some species initially expanded their trophic niche by adding a variety of alternative foods to their diets during the FW season (e.g., *Brycon falcatus* and *Myloplus asterias*), yet these species maintained a constant diet

breadth later during the LW season by switching from certain dominant food types to others. Other species maintained a relatively constant diet breadth throughout the HW, FW, and LW seasons by replacing fruits and seeds with other food types as they became more prevalent in their environment (e.g., *Brycon melanopterus*, *Myloplus rubripinnis*, and *M. torquatus*).

Our results demonstrate that seasonal decline in the allochthonous subsidy that is provided by fruits and seeds is associated with variation in niche overlap among frugivorous fish species of this Amazonian floodplain forest, but this reduction in overlap was not the result of trophic niche contraction. Although no season was associated with complete niche segregation within this fish assemblage, diet shifts effectively reduced trophic niche overlap during periods when fruits were less available, in a pattern consistent with predictions of competition theory. That is, we observed a reduction in dietary overlap during periods of scarcity (Pianka 1974, 1976). Seasonal resource partitioning in response to environmental fluctuations can be an effective mechanism by which competing species achieve coexistence (Chesson and Huntly 1997, Chesson 2000). In the lower Apaporis, recession of the annual flood pulse reduces the area of flooded forest, which, in combination with plant phenology, alters availability of forest food resources. Frugivorous fishes adjust their diets predictably in response to these seasonal changes in the quality and availability of alternative food resources. Under reduced food availability during low-water conditions, coexistence in the floodplain appears to be facilitated by trophic niche partitioning achieved via dietary shifts.

TABLE 3. Stable isotope ratios of C and N of six frugivorous fish species in southern Colombia during three hydrological seasons.

Season and species	SL (mm)	<i>N</i>	δC^{13}	δN^{15}
High waters				
BRFA	201–265	8	$-25.68^a \pm 0.10$	$8.35^a \pm 0.17$
BRME	170–255	14	$-25.44^a \pm 0.12$	$8.04^{ab} \pm 0.12$
MYAS	156–202	7	$-25.50^a \pm 0.11$	$7.99^{ab} \pm 0.16$
MYRU	147–212	16	$-26.24^b \pm 0.11$	$8.38^a \pm 0.14$
MYTO	202–248	8	$-26.67^b \pm 0.13$	$7.45^b \pm 0.15$
PRSP	164–175	5	$-26.69^b \pm 0.36$	$7.79^{ab} \pm 0.38$
Falling waters				
BRFA	193–278	14	$-25.84^a \pm 0.09$	$8.33^a \pm 0.15$
BRME	218–227	3	-25.69 ± 0.06	7.89 ± 0.16
MYAS	168–185	7	$-25.70^a \pm 0.11$	$7.40^b \pm 0.14$
MYRU	178–200	3	-26.27 ± 0.15	8.77 ± 0.12
MYTO	145–211	5	$-29.33^b \pm 1.13$	$7.49^b \pm 0.29$
PRSP	157–198	7	$-25.86^a \pm 0.09$	$8.12^{ab} \pm 0.23$
Low waters				
BRFA	229–253	5	$-25.25^a \pm 0.17$	$9.52^a \pm 0.17$
BRME	198–231	5	$-25.57^{ab} \pm 0.24$	$7.88^b \pm 0.29$
MYAS	152–174	6	$-25.76^{ab} \pm 0.18$	$7.73^{bc} \pm 0.18$
MYRU	101–199	12	$-26.19^b \pm 0.17$	$8.65^d \pm 0.16$
MYTO	102–234	10	$-28.20^c \pm 0.71$	$7.64^{bc} \pm 0.19$
PRSP	167–175	3	-26.16 ± 0.41	8.51 ± 0.30

Notes: We arithmetically corrected δC^{13} values for lipid content. Values are mean \pm SE; means not sharing the same lowercase 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. Species codes follow Fig. 4.

The ability to switch diets between alternative food resources obviously is adaptive in systems with seasonally fluctuating resources (Abrams 2006, Rueffler et al. 2007, Carnicer et al. 2008). Passerine birds in a diverse Mediterranean scrubland, for instance, switch diets between insects and fleshy fruits in response to asynchronous resource fluctuation (Carnicer et al. 2008); similar to frugivorous fishes in the Amazon, this bird assemblage revealed seasonal reduction in dietary overlap through temporal resource partitioning in a pattern consistent with competition theory. However, there are limits to dietary flexibility, because foraging behavior and digestion are constrained by morphological and physiological traits as well as by phylogeny. In the Mediterranean system, birds with beaks specialized for fruit consumption rapidly increased the consumption of fruits in response to increased fruit availability, whereas species with beaks more efficient for feeding on insects delayed switching to fruits until the fruit production had peaked (Carnicer et al. 2008). In our system, *Myloplus* have morphological traits that clearly are adaptive for frugivory (e.g., strong jaws, multicuspid molariform teeth, and long intestines) and are members of a clade of herbivorous serrasalmids (Correa et al. 2007). Among *Myloplus* species, *M. asterias* had a fruit-dominated diet during the peak of fruit production (Fig. 4; Appendix E), and, although it supplemented its diet with other food items as fruit availability decreased during the FW season, it delayed switching from fruits until the LW season, when it fed heavily on leaves. In contrast, *Myloplus rubripinnis* switched from fruits to leaves as soon as the peak of fruit production came to an end during the FW season (Fig. 4; Appendix E). *Brycon* species have strong jaws with incisor-like multicuspid teeth, which, although less specialized for crushing, can be used for cutting seeds, and they have a larger gape size than *Myloplus* species. Relative intestine length, however, is much shorter than in *Myloplus* species (i.e., about one-third to one-quarter shorter; S. B. Correa, unpublished data). Although largely plastic, intestine length is inversely related to trophic position among fishes (Wagner et al. 2009). Furthermore, *Brycon* is most closely related to taxa that are insectivorous or piscivorous (Calcagnotto et al. 2005). *Brycon falcatus* behaved similarly to *M. asterias* in terms of expanding its diet and delaying switching until the LW period, but the two species contrasted in that insects dominated the former's diet during the LW season. *Brycon melanopterus* also switched to insects, but much earlier during the FW season. It is thus apparent that fishes in this seasonal habitat have evolved divergent feeding behaviors that effectively partition trophic niche space.

Tropical freshwater fish ecologists have long debated whether ecological specialization is greater during periods when resources are more abundant or during periods of resource scarcity (reviewed by Lowe-McConnell 1987), and new research is beginning to integrate ecological and functional morphology (e.g., Lujan et al.

2011). Some have argued that morphological specializations enable efficient exploitation of alternative low-quality food resources when preferred resources are scarce, therefore reducing competition and increasing the likelihood of survival during bottleneck periods (McKaye and Marsh 1983, Winemiller and Pianka 1990, Robinson and Wilson 1998). The opposite view, which is consistent with predictions of classical optimal foraging theory (Stephens and Krebs 1986), is that when preferred high-quality foods are abundant, consumers use morphological specializations to maximize feeding efficiency and rate of energy intake (Goulding 1980). The fish species examined in our study represent a unique feeding guild with morphological (Correa et al. 2007) and physiological (Drewe et al. 2004) characteristics that enable efficient utilization of fruits and seeds. Because fruiting phenology in Amazonian floodplains is synchronized with the annual flood pulse, fishes gain access to a seasonal, but highly predictable, abundant, and nutritious food resource (Waldhoff and Maia 2000, Parolin et al. 2004) within the expanded aquatic habitat. In our fish assemblage, morphological specializations are associated with intensive exploitation of a seasonally abundant food resource, supporting predictions of optimal foraging theory.

Niche segregation has been observed in tropical fish assemblages during both the dry season, when fish densities are highest, and the wet season, when fish densities are low within expanded aquatic habitats (Lowe-McConnell 1987). Interpretation of seasonal food abundance and scarcity appears to depend on the taxon and ecosystem. Similar to our findings, a study of fish assemblages from four lowland streams in the neotropics found significantly lower dietary overlap during the dry season, when most food resources were less available (Winemiller and Pianka 1990). In contrast, a community-wide study of trophic niche 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 hydrological seasons, with some studies reporting broad ranges of values for pairwise dietary overlap 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 a four-month period of gradual water recession, when availability of invertebrate prey declined but densities of small fishes increased. Studies of trophic niche partitioning among herbivorous fishes are scarce. Diets of two congeneric herbivores and one omnivore in two French Guianan rivers (Boujard et al. 1990) were broad during the rainy season; diet breadth declined and interspecific dietary overlap was essentially nil during the dry season. In contrast, two herbivorous characids 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).

Our results demonstrate not only seasonal dietary shifts consistent with optimal foraging theory and temporal patterns of interspecific niche overlap predicted by classical niche theory, but also the importance of terrestrial resource subsidies to Amazonian fishes. Terrestrial subsidies were in the form not only of fruits and seeds, but also as flowers, leaves, and insects during the FW and LW seasons, respectively. During the LW period, leaves and insects continued to be available for fishes along the land–water interface, and phytomicrobenthos became a more important food resource as dissolved nutrient concentrations peaked in the contracted aquatic habitat. Fishes cannot enter the forest during this period, but they continue to feed on plant material and terrestrial arthropods that fall from vegetation extending over the water as well as wind-blown plant material and flying insects (Goulding et al. 1988). Aquatic primary production in the Apaporis probably increases during the LW season, given higher light irradiance on the benthos in shallow littoral areas and higher concentrations of dissolved nutrients in the water column within the contracted aquatic habitat. This was the finding in a study of the Cinaruco River, an oligotrophic floodplain river in the Orinoco River Basin that has a similar pattern of seasonal hydrology (Cotner et al. 2006, Montoya et al. 2006). In the Apaporis, however, only two of our focal fish species consumed phytomicrobenthos, and this food resource made a significant contribution to the diet of only one (*Myloplus torquatus* consumed more algae and sand particles and had relatively ^{13}C -depleted isotopic signatures, consistent with those of benthic algae; Fig. 4; Appendix F). Taken together, our findings suggest that, with one exception, allochthonous food makes a stronger contribution to the diets of these floodplain fishes than the autochthonous primary production, even during the peak low-water period. The great importance of allochthonous subsidies to aquatic food webs is recognized for oligotrophic streams in temperate regions (e.g., Nakano and Murakami 2001), and the present study adds to the body of evidence (e.g., Goulding et al. 1988, Winemiller and Jepsen 2004, Oliveira et al. 2006) revealing that these subsidies support significant fish biomass in lowland rivers in the tropics.

Our findings advance knowledge of how animals respond to changes in availability of food resources, and patterns were largely consistent with models predicting that temporal dietary shifts facilitate species coexistence in fluctuating environments (Abrams 2010). Findings from this study also will be useful for predicting how species in the Amazon, the most biodiverse region on Earth, will respond to changing climate, land cover, and hydrology. Climate change is predicted to transform current precipitation patterns, human encroachment is altering forest cover, and hydroelectric dams are changing hydrological regimes within the Amazon Basin

(Reis 2013), all of which probably will modify patterns of food availability for frugivorous fishes.

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SUPPLEMENTAL MATERIAL

Appendix A

Hydrological seasonality in Taraira Lake, Lower Apaporis River, Colombia, during 2009 ([Ecological Archives E095-019-A1](#)).

Appendix B

Methods of collection and preparation of samples for analysis of stable isotopes ([Ecological Archives E095-019-A2](#)).

Appendix C

Functional food categories and the food types included in each category that were consumed by six species of frugivorous fishes during three hydrological seasons ([Ecological Archives E095-019-A3](#)).

Appendix D

Biweekly fruit and flower production in the flooded forest along the Apaporis River assessed during visual censuses ([Ecological Archives E095-019-A4](#)).

Appendix E

Percentage frequency of occurrence and average volumetric percentage contributed by 12 broad functional food categories to diets of six frugivorous fish species during three hydrological seasons ([Ecological Archives E095-019-A5](#)).

Appendix F

Carbon and nitrogen isotope ratio biplots for six frugivorous fish species and food sources during three hydrological seasons ([Ecological Archives E095-019-A6](#)).