

Evolutionary Perspectives on Seed Consumption and Dispersal by Fishes

SANDRA BIBIANA CORREA, KIRK O. WINEMILLER, HERNÁN LÓPEZ-FERNÁNDEZ, AND MAURO GALETTI

Fishes probably were the first vertebrate seed dispersers, yet little research has examined this phenomenon. We review evidence of fruit and seed consumption by fishes, and analyze the evolution of frugivory and granivory using South American serrasalmids as a model. Frugivory and granivory are observed among diverse fish taxa worldwide, although most reports are from the Neotropics. Frugivory and granivory among serrasalmids apparently are derived from omnivory, with powerful jaws and specialized dentition appearing as major adaptations. No particular fruit traits seem to be associated with seed dispersal by fishes (ichthyochory). Recent experimental evidence of ichthyochory suggests that fishes can influence riparian vegetation dynamics. Because of deleterious human impacts on aquatic ecosystems worldwide, many critical interactions between plants and fishes have been disrupted before they could be studied. Exotic frugivorous fishes have recently become established on foreign continents, with unknown ecological consequences.

Keywords: ichthyochory, evolutionary ecology, flooded forests, seed predation, Serrasalminidae

Seed dispersal and seed predation by vertebrates are widespread and complex ecological processes that influence the recruitment, spatial distribution, and diversity of plants (Herrera 2002, Hulme and Benkman 2002). Vertebrate seed dispersers are mainly birds and mammals, but also include fish and reptiles. Although seed dispersal by fishes (ichthyochory) was reported nearly 100 years ago (Huber 1910), little research has been conducted on this subject. The fossil record of cordaitalean seeds (Coniferophyta) distributed along lowland swamps and rivers of the Carboniferous period gave rise to the hypothesis that fishes were the first vertebrate seed dispersers (Tiffney 1986). Although numerous fish species have been reported to consume fruits and seeds in all six of Wallace's biogeographical regions (table 1), direct evidence supporting seed dispersal has been provided only quite recently, and only from locations in the Western Hemisphere (Kubitzki and Ziburski 1994, Horn 1997, Chick et al. 2003, Mannheimer et al. 2003, Pollux et al. 2006).

Fleshy fruits attract animals that consume their nutritious flesh and, in the process, transport undamaged seeds away from the parental plant (e.g., Herrera 2002). Seed dispersal can also be carried out by seed predators, which normally consume and digest seeds, but may occasionally transport and release viable seeds that escape damage (Norconk et al. 1998). Some animals are both seed dispersers and seed predators (e.g., Neotropical monkeys [Norconk et al. 1998] and scatterhoarding rodents and birds [Hulme and Benkman 2002]). Two evolutionary strategies are observed among plants for

dealing with animals that consume seeds. One strategy is to attract seed dispersers by surrounding seeds with nutritious flesh, whereas the other strategy is to protect seeds from predators by encapsulating them (Hulme and Benkman 2002).

To understand the role of fishes as seed dispersers, we reviewed the literature on fish feeding ecology to evaluate the incidence of frugivory and granivory, the degree of dietary specialization, and the evolution of these feeding habits, using South American characiforms as a model. We also summarize recent evidence of ichthyochory and its relevance for vegetation dynamics and fruit traits, and propose some avenues for future studies on ichthyochory.

Fruit and seed eating by fishes

Consumption of fruits and seeds has been documented in approximately 182 species belonging to 32 families of freshwater fishes (table 1). These include fishes that also consume other plant parts, such as leaves and flowers, as well

Sandra Bibiana Correa (e-mail: scorrea@neo.tamu.edu) is a PhD candidate, Kirk O. Winemiller is a professor, and Hernán López-Fernández is a research associate in the section of Ecology and Evolutionary Biology, Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843. Mauro Galetti is an associate professor in the Laboratório de Biologia da Conservação, Departamento de Ecologia, Universidade Estadual Paulista, CP 199, 13506-900 Rio Claro, Brazil. © 2007 American Institute of Biological Sciences.

as omnivores that consume terrestrial and aquatic invertebrates. The importance of fruits and seeds in the diet is strongly associated with their availability. In virtually all ecosystems, fruits and seeds are patchily distributed and seasonally available. In Amazon flooded forests, the fruiting phenology of many tree species is synchronized with the annual flood cycle (Kubitzki and Ziburski 1994). Fruit production within an Amazon floodplain forest near Manaus was estimated at between 9 and 30 metric tons per hectare per year (Waldhoff et al. 1996). The tropical rainforest in the lower Mekong River is subject to a major annual flood lasting at least three months, and several species of large cyprinids and pangasiid catfishes feed on fruits (Rainboth 1996). In Central Africa (Guinean and Congo Basin ichthyological provinces), extensive rainforests surround streams and large rivers; however, reports of frugivory among fishes are rare. Several species of alestids (Characiformes) from the Niger, Chad, and Nile river basins, and the African bonytongue (*Heterotis niloticus* [Osteoglossidae]) in the Sô River, have been reported to consume the seeds of grasses within flooded savannas (e.g., Matthes 1977, Adite et al. 2005).

Documented interactions of fishes with fruits and seeds can be divided into two main categories: frugivory and granivory. Frugivores consume fleshy fruits, normally without destroying the seeds during ingestion or passage through the digestive tract. Species in this category are mainly catfish (Siluriformes) with large mouth gapes that permit fruits and seeds to be swallowed whole (e.g., Mannheimer et al. 2003; figure 1d). Other frugivores target both fleshy fruits and dry fruits, and these may or may not damage seeds. These include many Neotropical characiforms, some of which (e.g., *Colossoma*, *Piaractus*) have multicuspid, molariform teeth that facilitate crushing fruits and hard-coated seeds (Goulding 1980). Other characiform genera (e.g., *Brycon*, *Pristobrycon*, *Serrasalmus*) have sharp-edged multicuspid teeth that can cut seeds (Goulding 1980). Large cyprinids (Cypriniformes) from the Oriental and Palearctic regions lack jaw teeth but possess strong pharyngeal jaws with crushing pads armed with molariform teeth that are used to masticate plant material, including seeds.

Among the piranhas (Characiformes: Serrasalmidae), the intestine length is greater in species that feed heavily on fruits than in those that feed mostly on animal flesh (Nico 1991), a pattern consistent with that described among frugivorous

birds (Herrera 2002). The intestinal length of the fruit-eating Amazonian tambaqui (*Colossoma macropomum* [Serrasalmidae]) (figure 1b), for example, is about five times its body length (Araujo-Lima and Goulding 1997). There also are behavioral adaptations exhibited by these frugivores, such as leaping and snatching, or gathering beneath fruiting trees to capture fruits almost as soon as they hit the water (figure 1a; Goulding 1980, 1983, Horn 1997). Individual tambaqui have been reported to defend areas underneath trees with ripe fruits (Araujo-Lima and Goulding 1997).

Granivores feed on the seeds of dry fruits (including grains) and generally damage the seeds in the process of digestion. Granivorous species usually have morphological adaptations (Norconk et al. 1998) to gain access to highly protected, nutrient-rich seeds (Hulme and Benkman 2002). African alestids have multicuspid teeth used for crushing grass seeds, and the African bonytongue has a muscular gizzard used for grinding grass seeds, which comprise more than 30% of the diet of individuals from floodplain habitats (Adite et al. 2005). In the Neotropics, species of two genera (*Crossoloricaria* and *Loricaria*) from the family Loricariidae (armored suckermouth catfish) possess enlarged pharyngeal jaws with strong molariform teeth used to crush small seeds (Armbruster 2004). In addition to morphological adaptations, specialized behaviors for granivory have been documented. In the inland delta of the Niger River, *Alestes* species (Characiformes: Alestiidae) have been observed to jump out of the water to dislodge dehiscent panicles of wild rice (Matthes 1977). Since many semiaquatic grasses have dehiscent seeds, Matthes (1977) interpreted this behavior as an adaptation.

What are the benefits of frugivory and granivory for fishes? First, the pericarp of fruits contains large fractions of carbohydrates (Herrera 2002). Specialized frugivores tend to have high rates of consumption and fast gut passage in order to maximize energy intake (Stanley and Lill 2002). Second, in most plant species, fruits have lower toxicity than leaves (Janzen 1975). Interestingly, however, the Mekong cyprinids *Leptobarbus hoevenii* and *Tor tambra* sometimes eat the poisonous fruits of *Hydnocarpus anthelminthica* (Flacourtiaceae) and *Quassia harmandiana* (Simaroubaceae) from the flooded forest, which renders their flesh toxic for human consumption (Roberts 1993). Finally, seeds are rich in crude protein and fat (Waldhoff et al. 1996). An analysis of the nutrient contents of 19 fruits eaten by fishes in the Amazon Basin

Table 1. Number of families, genera, and species within each major freshwater fish order that are reported to feed on fruits or seeds, by biogeographical region.

Order	Number of families (genera, species)					
	African	Palearctic	Oriental	Australian	Nearctic	Neotropical
Characiformes	3 (6, 17)	–	–	–	–	5 (25, 66)
Siluriformes	3 (5, 10)	–	3 (4, 12)	–	1 (1, 1)	6 (22, 22)
Cypriniformes	1 (3, 9)	1 (2, 2)	1 (8, 12)	–	–	2 (2, 2)
Perciformes	1 (2, 2)	1 (1, 1)	2 (2, 3)	2 (2, 2)	–	1 (11, 14)
Osteoglossiformes	2 (2, 2)	–	1 (1, 1)	–	–	1 (1, 1)
Gymnotiformes	–	–	–	–	–	2 (2, 2)
Polypteriformes	1 (1, 1)	–	–	–	–	–



Figure 1. (a) *Brycon hilarii* (Characidae) taking a fruit from the surface of the water at Baía Bonita Spring, Paraguay River Basin, Brazil. Photograph courtesy of José Sabino. (b) *Tambaqui* (*Colossoma macropomum*). Photograph courtesy of Will Crampton. (c) Fish stomach containing seeds of *Cecropia* species (Cecropiaceae) from a floodplain forest in the Pacaya Samiria National Reserve, Peru. Photograph: Sandra Bibiana Correa. (d) Frugivore *Megalodoras uranoscopus* (Doradidae), Apure River, Venezuela. Photograph: Aniello Barbarino. (e) Specimens of the frugivorous Neotropical fish *Piaractus brachipomus*, captured from the Sepik River, Papua New Guinea. This exotic population now supports a fishery. Photograph courtesy of Marie Prchalova and Jiri Hulcr.

revealed that the seeds of *Hevea brasiliensis* (Euphorbiaceae) had the highest energy concentration ever reported for a seed (32.3 kilojoules per gram), and the seeds of *Annona montana* (Sapotaceae) and *Astrocaryum jauari* (Arecaceae) ranked among those with the highest energy (Waldhoff et al. 1996). In Amazonian floodplains, fishes accumulate fat, which is later converted into reproductive tissue, from feeding on fruits and seeds during the floods.

Evolution of fruit and seed eating in fishes: The Neotropical characiforms

Investigation of evolutionary trends in fruit and seed eating by fishes is limited largely by the lack of understanding of phylogenetic relationships within this diverse group of vertebrates. Fortunately, detailed and well-supported phylogenetic hypotheses are available for the order Characiformes, including the Neotropical family Serrasalminidae, which includes fruit- and seed-eating (tambaqui) and carnivorous

(piranha) species. Here we report findings from an analysis of evolutionary patterns of fruit and seed eating in this clade.

To assess how frequently frugivory and granivory have evolved within the Characiformes, we mapped the presence or absence of fruits and seeds in the diets of each taxon as a binary categorical character in the phylogeny of Calcagnotto and colleagues (2005). (The references used for diet are available on request from the authors.) We reconstructed the diet of ancestral nodes by applying stochastic likelihood methods for categorical data (Huelsenbeck et al. 2003), using the software package Mesquite (Maddison and Maddison 2006). Following the method of Espinoza and colleagues (2004), we tallied the number of independent origins of frugivory and granivory within the Characiformes. Within this order, frugivory and granivory seem to have evolved independently in at least five families—the Neotropical Anostomidae, Serrasalminidae, and Characidae (which feed on both fruits and seeds) and the African Alestiidae and Distichodontidae (which are solely granivorous)—and to have been lost and regained

repeatedly within these clades. With the exception of a subclade within the Serrasalminae (figure 2), no characiform lineage has retained frugivory or granivory as its exclusive diet. Some genera contain species that feed heavily on seeds (e.g., *Brycinus*, *Bryconaethiops*, and *Alestes* among the Alestiidae) or on fruits and seeds (e.g., *Brycon* among the Characidae), and these are closely related to other genera that are essentially insectivorous or even piscivorous (e.g., *Hydrocynus* among the Alestiidae, *Salminus* among the Characidae).

Evolutionary patterns at this scale are consistent with the idea that frugivory and granivory are derived from omnivorous diets dominated by insects and other invertebrates, and imply that frugivory and granivory in fishes are strategies that take advantage of highly nutritious resources that are available on a seasonal basis (Howe 1993).

The Serrasalminae (*sensu* Calcagnotto et al. 2005) appear to be unusual among Neotropical characiforms in having diverged into tropically specialized clades that range from

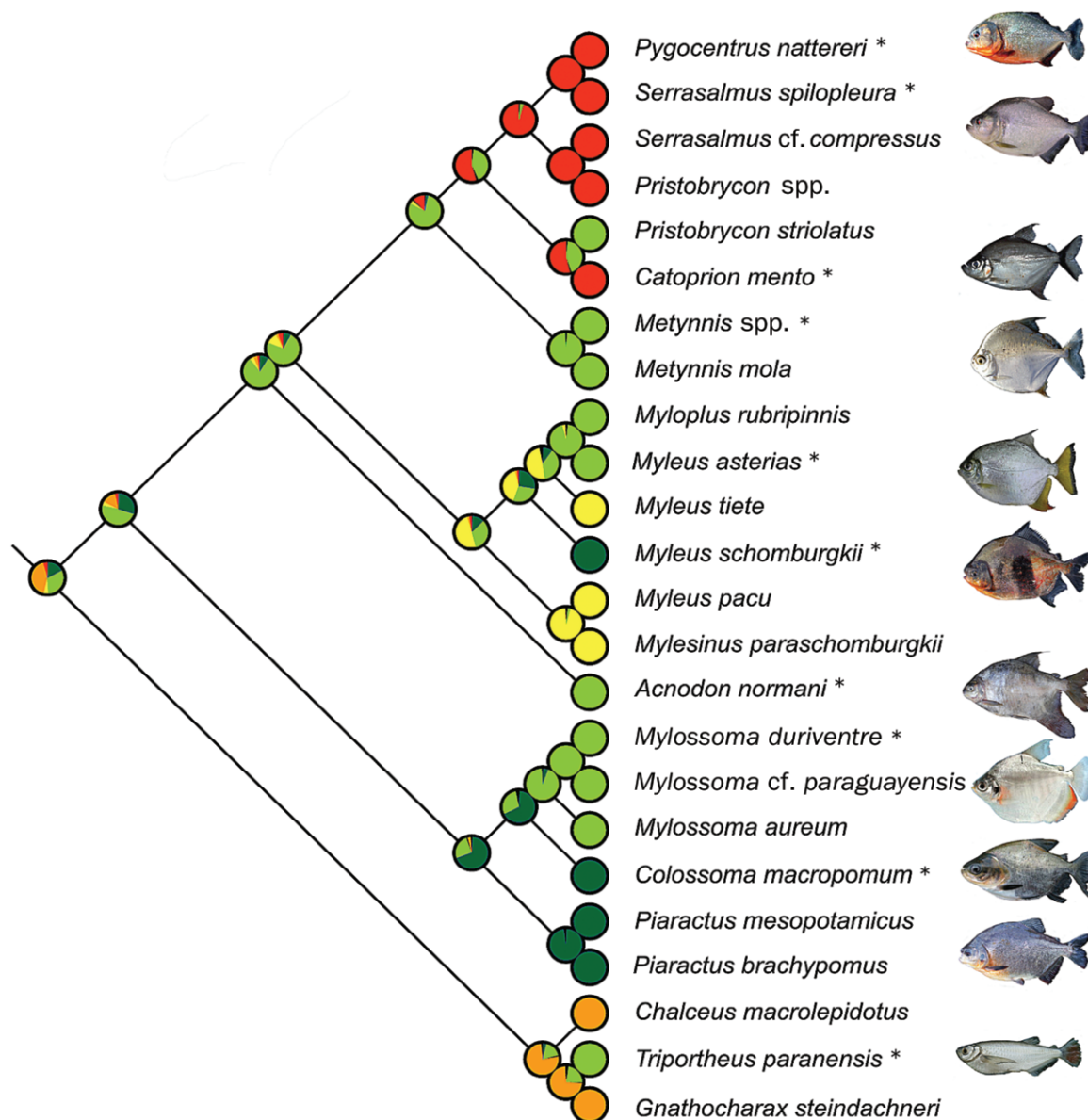


Figure 2. Phylogeny of the characiform family Serrasalminae (Ortí et al. 1996) with maximum-likelihood ancestral character reconstructions for diet. Colored pie charts illustrate diets of each terminal taxon and ancestral node. Pie charts for ancestral nodes show estimated probabilities for diet categories: Red = fish only; orange = invertebrates only; yellow = algae, leaves, and invertebrates; light green = fruit or seeds, other plant material (stems, leaves, flowers), and invertebrates; dark green = fruit or seeds and other plant material. Genera marked with an asterisk are illustrated. Flesh-eating piranhas (e.g., *Pygocentrus*, *Serrasalmus*) have sharp, incisor-like teeth, and the scale-scraping specialist *Catoprion mento* has highly modified dentition. Generalized herbivores (e.g., *Metynnis*, *Myleus*) and fruit-eating taxa (e.g., *Mylossoma*, *Colossoma*) have molariform teeth. Photographs: Kirk O. Winemiller, Hernán López-Fernández, and William R. Crampton.

piscivores to fruit and seed eaters. On the basis of a compilation of literature reports (e.g., Goulding 1980, Nico 1991; a complete list of references is available from the authors on request), we classified the diet of adult size classes for each taxon into five categories (fish only; invertebrates only; algae, leaves, and invertebrates; fruit, seeds, other plant material [stems, leaves, flowers], and invertebrates; fruit, seeds, and other plant material), and mapped these as unordered character states on the serrasalmid phylogeny proposed by Ortí and colleagues (1996), which has a larger number of taxa than Calcagnotto and colleagues' (2005) order-level phylogeny. We estimated the diet at each ancestral node (figure 2) using maximum-likelihood ancestral character reconstruction, following the algorithm of Pagel (1999), under an Mk1 optimization model (Lewis 2001) as implemented in Mesquite (Maddison and Maddison 2006). Diet categories on the serrasalmid tree coincide with the major clades within the family. The most basal lineage includes the almost exclusively fruit- and seed-eating genera *Colossoma*, *Mylossoma*, and *Piaractus* (figure 2). There are two additional major lineages, one with the piscivorous piranhas and another with *Myleus* and other herbivorous genera. The herbivorous *Metynnis* and omnivorous *Acnodon* are positioned between the three major clades, the former apparently closer to piranhas and the latter closer to *Myleus* (figure 2). Serrasalmid outgroup taxa represent

every diet category, and ancestral nodes for both the family and each of its clades are reconstructed as omnivorous. Thus it appears that trophic specialization in each serrasalmid clade is derived from an originally omnivorous condition.

This prompts questions about the ecological conditions that select for trophic diversification among clades. Interestingly, all taxa in the family share certain morphological attributes that appear to be associated with their dietary specializations. All have discoid bodies and strong jaws, but they possess multicuspid teeth that range from broad molariform teeth in several herbivorous taxa to sharp triangular incisors in fin-nipping and flesh-biting piranhas. Specialized dentition may have allowed the former group to use fruits and seeds that fall into the water, where they are inaccessible to other frugivores, such as birds and primates. Further analyses in an expanded phylogenetic context are needed to test this evolutionary hypothesis. The current phylogeny of serrasalmids is based on two mitochondrial genes and lacks several taxa within the clade. Our comparative analysis included dietary data for every species in Ortí and colleagues' phylogeny (1996), but these were gleaned from diverse sources in the literature and thus are fairly crude. Better-resolved phylogenies and ecological data will improve researchers' understanding of the evolution of frugivory and granivory in fishes.

Table 2. Effects of gut passage on the germination of seeds ingested by fish.

Reference	Site	Fish species ingesting seeds or fruits	Plant species with seeds or fruits ingested by fish	Physical damage to seeds found in fish guts	Percentage of seeds germinating after removal from fish guts	Germination rate (number of days to germination)
Agami and Waisel 1988	Artificial reservoir, Israel	3	2	0% to 60% undamaged	6% to 16%	NA
Kubitzki and Ziburski 1994	Amazon River, Brazil	2	12	0% to 100% undamaged	0% to 100%	Faster than control (3 spp.); slower than control (4 spp.)
Horn 1997	Puerto Viejo River, Costa Rica	1	1	Not reported; assumed near to 100% undamaged because of small seed size	70% (not statistically different from control)	Slower than control
Banack et al. 2002	Puerto Viejo River, Costa Rica	1	1	Same as in Horn 1997	NA	High (authors used a ranking system)
Mannheimer et al. 2003	Amazon River Basin, Brazil	1	20	100% undamaged	0% to 66%	NA
Chick et al. 2003	Mississippi River, USA	1	2	Same as in Horn 1997	60% to 80% (significantly higher than control)	NA
Lopes de Souza 2005	Amazon River Basin, Brazil	8	–	0% to 39% (seeds removed from stomach), 0% to 57% (seeds removed from intestine)	8% to 96%	NA
Pollux et al. 2006	Artificial reservoir, Netherlands	1	2	NA	71% to 83% (significantly lower than control for one plant species)	Faster than control for hard-coated seeds

NA, not available.

Fishes as seed dispersers

Despite the numerous accounts of fruits and seeds in fishes' diets, almost all of the research testing ichthyochory has been done within the last 10 years. With three exceptions, all of these studies are from the Neotropics (table 2). The effectiveness of a seed disperser can be predicted from variables such as the amount of seeds ingested, the mechanics of ingestion, the effects of gut passage on germination, and the disperser's patterns of movement (Schupp 1993). The amount of fruit eaten by fishes under natural conditions is difficult to assess from the literature, because frugivory is usually inferred from the presence of fruit fragments and seeds in gut contents (as opposed to direct observation of foraging activities, which is commonly reported in studies of seed dispersal by birds and mammals). Banack and colleagues (2002) observed fruiting fig trees (*Ficus insipida*) for 77 hours and found that 83% of the figs that fell into the water were consumed by *Brycon guatemalensis* (Characidae).

Another problem in quantifying the importance of fruits in fish diets is that most studies report the frequency of occurrence in the diet of a species, but not the quantity consumed (e.g., Goulding 1980, de Souza-Stevaux et al. 1994, Mannheimer et al. 2003). Boujard and colleagues (1990) examined the stomach contents of the characid *Myleus rhomboidalis* from Guyana and reported the percentage of the total weight accounted for by the seeds of 13 plant species. The relative weight represented by seeds varied among seasons and plant species; for instance, palm seeds (*Euterpe oleracea*) accounted for 59% of total food mass during the dry season, whereas during the wet season they accounted for only 2% of the mass in gut contents. Using data on fruit traits reported by van Roosmalen (1985), we determined from Boujard and colleagues' data (1990) that smaller seeds made a greater contribution than larger seeds, in terms of percentage of biomass, to the diet of *M. rhomboidalis* during the wet season (Pearson's correlation, $r = -0.83$, $p < 0.05$), but not during the dry season ($r = 0.11$ [not statistically significant]). Fruit size and the percentage of total fruit biomass in the diet were uncorrelated during both seasons.

The damage to seeds during their ingestion by fishes is variable (table 2). Most frugivorous catfishes swallow entire fruits, and most of the seeds seem to pass undamaged through the gut. As mentioned earlier, most characids and cyprinids have the ability to destroy seeds, but even among fruit crushers, such as the tambaqui and *Brycon* species, some seeds can pass through the gut intact (Goulding 1980, 1983). The proportion of seeds destroyed by the tambaqui actually decreases with body size (Kubitzki and Ziburski 1994). For fruits with small seeds, the pericarp may be well masticated while the seeds are swallowed whole (e.g., Cucurbitaceae, *Ficus* spp., *Cecropia* spp., *Genipa* spp., *Luffa* spp.; figure 1c, Goulding 1980). Fruit and seed morphology also influences the probability that seeds pass through the alimentary canal undamaged; for instance, hard-coated seeds ingested by common carp (Cyprinidae) are more likely to pass undigested with improved germination rates than soft-coated seeds (Pollux et al. 2006). Thus, like gen-

eralist frugivorous mammals and birds (Norconk et al. 1998), fishes may destroy the seeds of some plant species and disperse the seeds of others.

Studies evaluating the effects on seed germination of passage through fish guts have reported variable results (table 2). In most cases, a large proportion of seeds were viable after the passage through fish guts. Some of the ingested seeds actually germinated faster. An earlier break in seed dormancy, yielding a faster germination, is commonly assumed to be a positive effect of vertebrate dispersal. Germination in Amazon floodplain forests, however, does not occur until the emergence of dry land (Kubitzki and Ziburski 1994). Earlier germination is exacerbated by anoxic conditions as floodwaters recede from the forest floor (Kubitzki and Ziburski 1994). Therefore, an earlier break in seed dormancy may not be universally advantageous in floodplain forests.

Seed retention time and distance of animal movement are important predictors of seed dispersal (Schupp 1993). Seed retention time in fishes is long compared with that of other vertebrate dispersers. For instance, Pollux and colleagues (2006) found that 50% of the seeds consumed by common carp were excreted approximately 7 hours later; Agami and Waisel (1988) found that the same proportion of seeds were excreted approximately 40 hours after ingestion by tilapia and grass carp; and Horn (1997) reported that approximately 30% of seeds were excreted at 24 hours, 84% at 36 hours, and 88% at 48 hours by *B. guatemalensis*. In contrast, seed retention time is generally less than one hour in bats (Shilton et al. 1999) and passerine birds (Levey 1986). Many, if not most, tropical fishes have lateral migrations between river channels and seasonal floodplain habitats. In addition, migrating characiforms in the Amazon Basin move between 20 and 30 kilometers (km) per day (Goulding 1983), and *B. guatemalensis* in the Río Puerto Viejo, Costa Rica, were observed to travel distances from 0.1 to 10 km in a single week (Horn 1997). Fishes that undergo annual spawning migrations could disperse seeds along the longitudinal fluvial gradient over much greater distances than monkeys, rodents, and even many birds. Moreover, these patterns of movement among frugivorous fishes could yield long-distance dispersal of seeds, with major consequences for plant spatial distributions (Cain et al. 2000).

This evidence indicates great potential for effective seed dispersal by fishes. Although seeds in riparian and floodplain forests also can be carried by water and by a variety of nonaquatic vertebrates, we argue that fishes should be important seed dispersers when seeds are nonbuoyant or when there are few nonaquatic dispersers. Although many plants that inhabit floodplains have buoyant fruits or seeds that may be dispersed by water, several species have heavy fruits that quickly sink to the bottom. (The latter group includes species-diverse families such as Arecaceae and Lauraceae; Kubitzki and Ziburski 1994.) Nonbuoyant fruits are deposited beneath the parental tree, where survival probability is low (Chapman and Chapman 1996). Kubitzki and Ziburski (1994) found that within the seed shadow of *A. jauari*, a

palm with nonbuoyant fruits that ripen during the peak of the annual flood, a large percentage of the seedlings were located within 20 meters of the parental tree. The authors hypothesized that a doradid catfish, *Lithodoras dorsalis*, probably dispersed these large seeds (Kubitzki and Ziburski 1994).

Seed size constrains potential dispersers, with large seeds expected to have restricted and specialized suites of vertebrate dispersers (Peres 2000). Large seeds generally are dispersed by large monkeys, which are susceptible to hunting and habitat destruction (Peres 2000). In areas where monkeys have been effectively extirpated, catfish may be the most important dispersers of large seeds. This may be the case particularly within the floodplains of nutrient-poor watersheds of South America, where seed mass tends to be larger than that observed in other watersheds (Parolin 2000). Peres and van Roosmalen (2002) identified large-seeded trees and lianas from upland forests of the Amazon and Guiana Shield that are susceptible to low seedling recruitment due to loss of dispersers. Of these large-seeded genera, 28 contain species with seeds consumed by fishes, and of those genera, 17 have seeds that have been reported passing intact through fishes' digestive tracts. The catfishes reported to feed on fruits tend to be large species with large gut volumes. Seven species of Neotropical pimelodid and doradid catfishes reported to consume fruits commonly measure over 50 centimeters (cm), and five frugivorous pangasiid catfishes from the Mekong Basin range in length from 80 cm to 130 cm.

Ichthyochory seems to conform to predictions of the generalized dispersal system proposed for frugivorous birds (Howe 1993). Most frugivorous birds complement an insectivorous diet by consuming almost any fruits that are seasonally available, which yields a high dietary overlap among species of this guild. Despite being trophic generalists that consume fruits on a seasonal basis, and that are likely to have a high dietary overlap with nonaquatic frugivores, fruit- and seed-eating fishes nonetheless could play a significant role in dispersing the seeds of many plants in riparian and floodplain vegetation communities. Thus, ichthyochory is likely to influence local plant distributions and affect regional diversity.

Plant diversity and fruit traits in relation to fruit and seed eating by fishes

Fruits and seeds reported to be consumed by fishes belong to 55 families (149 genera, 170 species) in the Neotropical region, 16 families (17 genera, 18 species) in the Oriental region, 7 families (8 genera, 8 species) in the African region, 4 families (4 genera, 4 species) in the Palearctic region, 4 families (4 genera, 4 species) in the Australian region, and 2 families (2 genera, 2 species) in the Nearctic region. Within the Neotropical region, the 10 families with the highest reported numbers of fish species feeding on their fruits are also among the most important families in terms of abundance and species richness in flooded forests of nutrient-rich white-water (Wittmann et al. 2006) and nutrient-poor black-water basins (Worbes 1997). (The family Malpigiaceae is an exception, with low diversity but high incidence in fish diets.) These

findings suggest that fishes feed on the most abundant fruits. However, although Fabaceae is the most abundant and diverse family in the riparian forests of both white-water (Wittmann et al. 2006) and black-water regions of Amazonia (Worbes 1997), Arecaceae has more reports of fruit consumption by fishes. This indicates a degree of selectivity by fishes. Goulding (1980) presented evidence of selective feeding in large characiforms, such as tambaqui. He found several specimens with their stomachs filled with seeds or seed parts from a single plant species (see also figure 1c).

Meta-analysis of 431 cases of fruit consumption by Neotropical fishes also supports the idea of selective feeding. The types of fruits consumed by fishes were drupes (mainly from palms; 34.3%), capsules (26.5%), berries (15.3%), syconia (9.5%), legumes (9.3%), caryopses (2.3%), nuts (1.4%), apocarps (0.9%), and samaroid schizocarps (0.5%). In the Oriental region, only berries, capsules, and syconia have been reported in fish diets, whereas in the African region, only caryopses (grains) are reported; however, literature accounts for these regions are scant. Seeds of all of these fruit types have been recovered intact after passing through the digestive system of several fish species. There are also, however, reports of destroyed seeds of each fruit type, with the exception of caryopses and syncarpous fruits, the latter having very small seeds (Goulding 1980, Kubitzki and Ziburski 1994).

Fruit traits such as size, color, and husk thickness have a strong influence on the selection of fleshy fruits by primates and birds (Voigt et al. 2004). Among characiform fishes, tambaqui consume fleshy fruits of variable size, ranging from small capsules of *Alchornea schomburgkii* (Euphorbiaceae, 1.0 × 0.7 cm) containing two to three small seeds (0.6 × 0.4 cm) to large berries of *Crateva benthamii* (Capparidaceae, 5.7 × 11.5 cm) containing multiple seeds (1 × 0.8 cm). *C. benthamii* is also the largest fruit reported to be consumed by fishes (e.g., doradid catfish *L. dorsalis*). *Cecropia latiloba* (Cecropiaceae, 0.4 × 0.1 cm) has the smallest seeds among the fleshy fruits consumed by tambaqui, and the largest are the palm nuts of *A. jauari* (4 × 2.5 cm). These nuts have a thick husk that can be crushed by the tambaqui's strong jaws; however, as mentioned previously, the rate of seed predation is lower for larger fish specimens. *A. jauari* is also consumed by nine species of catfish, which swallow seeds intact. The colors of fleshy fruits (based on human perception) consumed by fishes include black, red, purple, yellow, gray, brown, and green. Araujo-Lima and Goulding (1997) hypothesize that olfaction may play a strong role in the location of fruits by fishes in Amazonian floodplain forests, but vision and the sound of falling fruits are also important.

Prospects for the study of ichthyochory and conservation implications

Aquatic ecosystems and biodiversity are affected by a variety of human actions, including water diversion; pollution; deforestation; overfishing; and dams that eliminate lotic habitats, create barriers to migration, and alter natural hydrology. These problems are global, yet they are likely to

be most serious in tropical regions with high species richness and potential for coevolution, where growing and sometimes impoverished human populations rely heavily on inland fisheries, forest products, and hydroelectricity. In some fish species, larger individuals have been shown to be more effective seed dispersers, which means that fishing practices that selectively harvest large individuals will skew populations toward smaller size classes that are mostly seed predators rather than dispersers.

The influence of exotic frugivorous fishes on native riparian plant populations has not been examined. Exotic fish introductions are a global problem, and, once established, these populations are exceedingly difficult to control. *Piaractus brachypomus* (Serrasalimidae), a specialized frugivore from the Amazon and Orinoco basins, recently became established in the Sepik River in Papua New Guinea (Coates 1997) and now provides an important fishery resource (figure 1e). Grass carp (*Ctenopharyngodon idella* [Cyprinidae]) that were introduced into reservoirs in Israel enhanced the seed germination of two native aquatic plants, *Najas marina* (Najadaceae) and *Ruppia maritima* (Potamogetonaceae); given their longitudinal and lateral migrations in river systems, *Ct. idella* may be able to disperse seeds over long distances (Agami and Waisel 1988).

Our review indicates that knowledge of ichthyochory is fragmentary and derived mostly from Neotropical studies. Research is needed to reveal evolutionary patterns, ecological dynamics, and their implications for the conservation of this threatened plant–animal interaction. Investigations should address dispersal distances, seasonal dynamics, and germination under variable environmental conditions. The nutritional value of fruits has been highlighted as a predictor of the strength of frugivore–plant relationships (Herrera 2002), yet there have been few studies of fish nutrition apart from aquaculture research. Nondestructive techniques for analyzing stomach contents could be used in combination with telemetry to examine dietary variation as fish move through flooded forests or savannas. Methods used to examine terrestrial seed dispersal could be adopted for investigating the dispersal of riparian plants by fishes (e.g., PIT [passive integrated transponder] tags, Surprison and Gómez 1989; genetic markers, Godoy and Jordano 2001; stable isotope analysis, Nathan et al. 2003).

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