

# Neotropical fish–fruit interactions: eco-evolutionary dynamics and conservation

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## ABSTRACT

Frugivorous fish play a prominent role in seed dispersal and reproductive dynamics of plant communities in riparian and floodplain habitats of tropical regions worldwide. In Neotropical wetlands, many plant species have fleshy fruits and synchronize their fruiting with the flood season, when fruit-eating fish forage in forest and savannahs for periods of up to 7 months. We conducted a comprehensive analysis to examine the evolutionary origin of fish–fruit interactions, describe fruit traits associated with seed dispersal and seed predation, and assess the influence of fish size on the effectiveness of seed dispersal by fish (ichthyochory). To date, 62 studies have documented 566 species of fruits and seeds from 82 plant families in the diets of 69 Neotropical fish species. Fish interactions with flowering plants are likely to be as old as 70 million years in the Neotropics, pre-dating most modern bird–fruit and mammal–fruit interactions, and contributing to long-distance seed dispersal and possibly the radiation of early angiosperms. Ichthyochory occurs across the angiosperm phylogeny, and is more frequent among advanced eudicots. Numerous fish species are capable of dispersing small seeds, but only a limited number of species can disperse large seeds. The size of dispersed seeds and the probability of seed dispersal both increase with fish size. Large-bodied species are the most effective seed dispersal agents and remain the primary target of fishing activities in the Neotropics. Thus, conservation efforts should focus on these species to ensure continuity of plant recruitment dynamics and maintenance of plant diversity in riparian and floodplain ecosystems.

*Key words:* fruit-eating fish, frugivory, ichthyochory, seed dispersal, seed predation, wetlands, riparian forests, floodplain, Amazon, overfishing.

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## I. INTRODUCTION

Frugivory is a key plant–animal interaction that contributes to the maintenance of biological and functional diversity in tropical and temperate plant communities (Stevenson, 2011; Aslan *et al.*, 2013; Harrison *et al.*, 2013). Through their roles as seed dispersers and predators, frugivorous vertebrates influence plant recruitment dynamics (Wang & Smith, 2002; Howe & Miriti, 2004), distribution patterns and genetic variability (Godoy & Jordano, 2001; Godinez-Alvarez & Jordano, 2007). Frugivores can exert significant natural selection on fruit morphology, colour, and nutrient composition, and on the magnitude of covariation among fruit traits (Valido, Schaefer & Jordano, 2011). In response to selection mediated by frugivores, angiosperm lineages have evolved substantial variation in the phenotypes of fruits (Lomascolo *et al.*, 2010; Valido *et al.*, 2011).

Until recently, the evolutionary origin and ecological relevance of frugivory and seed dispersal by fish received only minimal consideration (Correa *et al.*, 2007), as these processes are classically associated with birds and mammals (Herrera, 2002; Fleming & Kress, 2013). Fishes evolved prior to birds and mammals (Helfman *et al.*, 2009) and likely were the first vertebrates to disperse seeds. Indeed, the diversity and distribution patterns of Carboniferous plants with large diaspores suggest that dispersal by fish could have evolved in ancient lowland swamps and rivers (Tiffney, 1984, 1986), well before the origin of flowering plants in the Late Cretaceous (Berendse & Scheffer, 2009). Recent evolutionary analyses of frugivorous birds and mammals and fleshy-fruited angiosperm families point to a later origin for these major groups of seed dispersers (Fleming & Kress, 2011, 2013). Did fish interactions with fruits evolve before bird–fruit and mammal–fruit interactions? Could fish have contributed to the radiation of angiosperms and current distribution patterns in wetland communities? An early hypothesis focusing on Neotropical wetlands proposed that fish disperse seeds of basal angiosperms and depredate seeds of the most derived lineages (van der Pijl, 1969). If so, the evolutionary and ecological consequences of fish interactions

with fruits will affect basal *versus* derived plant lineages differently.

Frugivory occurs in all major extant freshwater fish orders (i.e. Cypriniformes, Siluriformes and Characiformes; Horn *et al.*, 2011). We now know that at least 276 species of fish consume fruits at some point in their life histories (Horn *et al.*, 2011; Beaune *et al.*, 2013). Most of these species inhabit floodplain forests and savannas in tropical regions, foraging on fruits and seeds that fall into floodwaters (Horn *et al.*, 2011). In the Neotropics alone, there are approximately 150 fruit-eating fish from 17 families and six orders (Horn *et al.*, 2011), which consume fruits and seeds of at least 170 plant species from 55 families (Correa *et al.*, 2007). These Neotropical species represent >60% of the known frugivorous fish worldwide (Horn *et al.*, 2011). Some of these fish exhibit apparent physiological, morphological, and complex behavioural adaptations for the efficient consumption of fruit and seeds, such as molar-like teeth (Goulding, 1980), long intestines (Correa *et al.*, 2007), enzymes associated with digestion of carbohydrates (Drewe *et al.*, 2004), patrolling and defence of trees dropping ripe fruits (Goulding, 1980; Costa-Pereira *et al.*, 2010), and drift compensation manoeuvres in fast-flowing waters (Krupczynski & Schuster, 2008).

In their roles as seed dispersers, fruit-eating fish swallow intact seeds, enhance germination success (Kubitzki & Ziburski, 1994; Pollux *et al.*, 2006; Anderson, Saldaña-Rojas & Flecker, 2009) and disperse viable seeds long distances (i.e. several kilometers) to appropriate habitats (e.g. upstream and seasonally flooded habitats; Horn, 1997; Anderson *et al.*, 2011). Frugivorous fish masticate the seeds of other plant species, especially those with non-fleshy fruits (Goulding, 1980; Lucas, 2008; Anderson *et al.*, 2009). By destroying seeds, fish likely have the same ecological effects as other seed predators: reduced seed and seedling density, resulting in enhanced plant diversity through mechanisms such as competition–colonization trade-offs (Paine & Beck, 2007; Terborgh, 2012; Velho, Isvaran & Datta, 2012). However, we know little about the eco-evolutionary consequences of seed dispersal by fish, and even less about seed predation by fish.

Extensive wetland habitats occupy >250000 km<sup>2</sup> in South America (Eva *et al.*, 2004; Junk & Piedade, 2010). Many plant species in Neotropical floodplain and riparian communities are adapted to flooded conditions and seed dispersal by water (i.e. hydrochory) or fish (i.e. ichthyochory) (Kubitzki & Ziburski, 1994; Lopez, 2001; Parolin, Wittmann & Ferreira, 2013). Most plant species fruit during the first few months of the annual floods, which increases the likelihood that seeds will be transported by water and/or consumed by fish (Kubitzki & Ziburski, 1994; Waldhoff & Maia, 2000; Correa & Winemiller, 2014). Diaspores in these systems generally float (e.g. Kubitzki & Ziburski, 1994) and buoyancy is a key adaptation for seed dispersal in Amazonian flooded forest communities (Goulding, 1980). Traits clearly related to hydrochory include hair-like fibres, wings, low-density sponge- or cork-like tissues, air space between the cotyledons or inside indehiscent diaspores, low seed specific-mass, and water-repellent seed coats (van der Pijl, 1969; Kubitzki & Ziburski, 1994; Lopez, 2001). Floating facilitates hydrochory and increases seed germination success by reducing seed exposure to underwater hypoxia (Lopez, 2001; Mora, Smith-Ramirez & Zuñiga-Feest, 2013; but see Barnett *et al.*, 2012). Fleshy fruits also are common in Neotropical wetlands and may be directly linked to seed dispersal by fish (van der Pijl, 1969; Kubitzki & Ziburski, 1994; Parolin *et al.*, 2013). Whether traits of Neotropical floodplain fruits have evolved in response to selection by fish remains an open question, as little is known about the traits that attract frugivorous fishes (e.g. Goulding, 1980; Correa *et al.*, 2007).

For three characiform fruit-eating species that have been extensively studied (*Colossoma macropomum*, *Piaractus brachipomus* and *P. mesopotamicus*), seed dispersal effectiveness increases with individual fish size; larger fish generally consume a greater number of fruits (Galetti *et al.*, 2008; Anderson *et al.*, 2009), swallow intact seeds of fleshy fruits at higher frequency (Kubitzki & Ziburski, 1994; Galetti *et al.*, 2008; Anderson *et al.*, 2009), disperse seeds farther (Anderson *et al.*, 2011), and even augment seed germination success of some species (Anderson *et al.*, 2009). Nevertheless, we do not know whether the patterns observed in these three species scale to the entire community of fruit-eating fish. We predict that the quality of seed dispersal should increase with fish size both within and across fish species. Specifically, relative to juveniles and small-bodied fish species, we expect adults of the largest-bodied fish species to disperse more seeds of a greater diversity of plants and range of seed sizes, and to effect longer distance dispersal. These predictions are timely, as large-bodied frugivorous fishes (>35 cm in standard length when mature) are a major component of fisheries throughout tropical South America (Barthem & Goulding, 2007; Junk, Soares & Bayley, 2007; Quirós, Bechara & Resende, 2007;

Rodriguez, *et al.* 2007), and some species have experienced significant recent declines owing to overexploitation [e.g. *Colossoma macropomum* (Isaac & Ruffino, 1996; Reinert & Winter, 2002; Batista & Petrere, 2003; Santos, Ruffino & Farias, 2007), *Piaractus mesopotamicus* (Peixer, Catella & Petrere-Júnior, 2007), *Brycon amazonicus* (Filho & Batista, 2009)]. Overfishing, therefore, could eliminate the most effective seed dispersers from floodplain ecosystems, with negative consequences for plant regeneration dynamics, species diversity, and gene flow among plant populations (Correa *et al.*, 2007; Galetti *et al.*, 2008; Anderson *et al.*, 2009; Harrison *et al.*, 2013; Kurten, 2013).

In this review, we examine fish–fruit interactions, focusing on the evolutionary timing of ichthyochory, fruit traits that enhance the probability of seed dispersal, and the influence of fish size on the likelihood of seed dispersal. Our review concentrates on the Neotropics because this region has the largest contemporary diversity of fruit-producing species (Fleming & Kress, 2013) and specialized fruit-eating fishes (Goulding, 1980; Correa *et al.*, 2007; Horn *et al.*, 2011), and provides unique palaeontological evidence of frugivory in a fish lineage (Characiformes) that has inhabited flooded savannas and forests since the Late Cretaceous (Hoorn *et al.*, 2010; Crampton, 2011; López-Fernández & Albert, 2011). We hypothesize that: (i) in Neotropical wetlands, fish–fruit interactions evolved prior to most bird–fruit, bat–fruit, and primate–fruit interactions; (ii) fish disperse seeds of plant families in all major angiosperm lineages; (iii) fruit traits including fleshiness, dehiscence, colour and seed size influence the likelihood of seed dispersal *versus* seed predation by fish; and (iv) across species, large fruit-eating fish disperse large-seeded species and are more likely to disperse seeds than smaller fish. Our comprehensive approach contributes to a better understanding of the evolutionary timing and ecology of fish–fruit interactions, and provides further evidence for the unique ecological role of large-bodied frugivorous fishes. Given the current overexploitation of large frugivorous fishes across South America, we advocate the conservation of these species to preserve ecosystem function and biodiversity.

## II. METHODS

### (1) Database

We conducted a literature search for records of fruit consumption by fishes in the Neotropical region. We used the key words: ‘fruit-eating fish’, ‘ichthyochory’, ‘fish frugivory’, ‘fruit fish diet’, ‘seed fish diet’, and ‘floodplain fish diet’, in English, Portuguese, and Spanish. We conducted the review in *ISI Web of Science* and *Google Scholar* because these databases reference

articles published in a wide range of journals, including those with local impact, as many of the reports on fruit-eating fish are found in regional journals published in Portuguese or Spanish. The resulting database includes records in which consumed fruits and fruit-eating fish were identified at least to the level of the genus. We also included our unpublished data (see online Appendix S1). Plant nomenclature was validated according to Tropicos (<http://www.tropicos.org>) and fish nomenclature was validated using FishBase (Froese & Pauly, 2013). A comprehensive list of Neotropical frugivorous fishes is provided in Horn *et al.* (2011).

We collected data on fruit traits including fruit type, presence of flesh (tissues including sarcotesta, arile, mesocarp, and endocarp; Fleming & Kress, 2011), dehiscence (fleshy and dry fruits that open at maturity), colour at ripeness, seed size (length and width averaged over at least three seeds per species when possible), and seed roundness (width:length ratio; spherical seeds have a ratio of 1, whereas elongated seeds have lower values). We retrieved trait data from Neotropical floras (Pott & Pott, 1994; Henderson, Galeano & Bernal, 1995; Gentry, 1996; Vasquez, 1997; Ribeiro *et al.*, 1999), fruit guides (Roosmalen, 1985; Stevenson, Castellanos & Quiñones, 2000; Cornejo & Janovec, 2010), herbarium specimens, and online image databases (see online Appendix S2).

We recorded how each fish species interacted with each species of seed in categories modified from Jordano & Schupp (2000): (i) 'seed dispersal' (intact seeds found in fish digestive tracts), (ii) 'seed predation' (masticated seeds found in fish digestive tracts), (iii) 'seed dispersal and predation' (both intact and masticated seeds of the same plant species found in fish digestive tracts), and (iv) 'pulp consumption' (fish consumes pieces of fruit, but does not ingest or disperse seeds). The presence of intact seeds in the digestive system indicates that fish are likely effective vectors of seed dispersal (Galetti *et al.*, 2008; Anderson *et al.*, 2009, 2011; Donatti *et al.*, 2011).

Finally, we compiled data on fish size from Reis, Kullander & Ferraris (2003) and FishBase (Froese & Pauly, 2013). We recorded maximum standard length (SL), measured from the tip of the snout to the base of the tail. When total length (TL: tip of the snout to the end of the tail) was reported, we converted values to SL (see online Appendix S3).

We excluded records of fruits and seeds of exotic and domesticated plants, introduced fish (e.g. the common carp *Cyprinus carpio*), and native fish that consume fruits only accidentally, such as carnivores (i.e. *Sorubim lima*, *Zungaro zungaro*, *Pygocentrus* spp. and *Osteoglossum bicirrhosum*) and detritivores (i.e. *Oxydoras niger* and *Semiprochilodus* spp.) (M. Goulding & S. B. Correa, personal observations). In the Neotropics, frugivorous fish consume fruits intentionally (Horn *et al.*, 2011;

Pollux, 2011); therefore, their behaviour could have ecological and evolutionary consequences for plants.

## (2) Evolutionary context of fish–fruit interactions

To compare the evolutionary origins of frugivory in fish, birds, bats, and primates, we examined the evolutionary ages of the frugivores and the fruit they consume. We plotted the age of the major family of Neotropical fruit-eating fishes (Serrasalminidae; Correa *et al.*, 2007), and major families of Neotropical frugivorous birds (Steatornithidae, Trogonidae, Cotingidae, Ramphastidae, Pipridae, Thraupinae), bats (Phyllostomidae), and primates (Atelidae, Cebidae) against the ages of 18 of their core fruit food families (see online Appendix S4). Core food families for particular frugivore taxa are represented by multiple genera and/or species whose fruits occur in the diets of several species in a wide range of geographical areas (Fleming & Kress, 2013). For serrasalminid fishes, core food families include: Arecaceae, Sapotaceae, Annonaceae, Lauraceae, Fabaceae, Rubiaceae, Euphorbiaceae, Myrtaceae, Urticaceae, and Moraceae. We obtained core food families for birds, bats, and primates from Fleming & Kress (2013, table 3.9) and include those consumed by fish plus: Araliaceae, Burseraceae, Clusiaceae, Loranthaceae, Melastomataceae, Myristicaceae, Piperaceae, Salicaceae and Solanaceae. The ages of bird, bat, primate, and plant families were estimated based on time-calibrated molecular phylogenies (Hedges & Kumar, 2009), and extracted from Fleming & Kress (2013, tables 1.1, 1.3). The origin of the family Serrasalminidae was estimated as 70 Ma based on the fossil record (Gayet & Meunier, 1998; Lundberg, 1998; Dahdul, 2007) and a time-calibrated molecular phylogeny (Thompson *et al.*, 2014).

Van der Pijl (1969) hypothesized that fish primarily disperse seeds of basal angiosperms. To assess the distribution of fish-mediated seed dispersal and seed predation across the angiosperm phylogeny, we tested whether each type of fish–fruit interaction is equally likely to occur in all major lineages (i.e. basal angiosperms, monocots, basal eudicots, asterids, rosids; APG III, 2009). We first coded each seed species as 'dispersed', 'masticated', or 'dispersed and masticated' (consumed intact by some fish, but masticated by others of the same or different species). We then fitted separate logistic regression models for each type of interaction (i.e. seed dispersal, predation, dispersal and predation) using seed lineage as an ordered predictor with equal distances among lineages (Agresti, 2013; function `glm`, R 3.0.1). Occurrence of each interaction was calculated as the number of families in which an interaction was recorded divided by the number of families known for that lineage. Total number of families per lineage was extracted from Fleming & Kress (2013, table 6.2), excluding seven families absent from the Neotropics

(monocots: two families; asterids: two families; rosids: three families).

### (3) Fruit traits associated with seed dispersal by fish

As a first step to evaluate if frugivorous fish could impose selection on fruit morphology, we tested if fruit traits affect whether fish disperse or masticate seeds. We examined whether the presence of flesh, dehiscence, colour, seed length and roundness influence the probability of seed dispersal *versus* seed predation by fish *via* logistic regression (Proc Glimmix, SAS ver. 9.3). Each seed species was coded as either ‘dispersed’ or ‘masticated’. This analysis excluded seeds that were consumed intact by some fish but masticated by others of the same or different species. To control for phylogenetic effects, plant genus was nested within family and modelled as a random effect.

Next, we classified fruits in five functional types according to Fleming & Kress (2011): (i) berry and berry-like fruits including syconia, (ii) drupes and syncarps, (iii) arillate seeds, (iv) dry fruits (i.e. capsules, legumes, follicles, loment, schizocarps, and nuts), and (v) mixed fleshy fruits (i.e. single and aggregated achenes surrounded by a fleshy perianth, hard-shelled berries, and indehiscent pods with internal pulp). This fruit-type classification encompasses fleshiness and dehiscence as well as other traits such as the number of seeds and extent of seed protection. We tested whether fruit type affects the probability of seed dispersal *versus* predation by fish in a logistic regression model (Proc Glimmix, SAS ver. 9.3) that included seed length and roundness as covariates and plant genus nested within family as a random effect.

### (4) The importance of fish for the dispersal of large-seeded plants

We assessed the influence of seed size on the number of potential fish seed dispersers and functional overlap among small-, medium- and large-bodied fish species. First, we quantified the number of fish species dispersing seeds for different size classes of seeds (i.e. from 0.1 to 9 cm, with intervals of 0.05 cm) and the number of plant species in each class. Using negative binomial regression (Proc Glimmix, SAS ver. 9.3, plotted with package ggplot2, R 3.0.1), we modelled the number of fish species dispersing seeds as a function of seed size. Model fit of the negative binomial was better than that of Poisson regression due to data overdispersion. We controlled for possible effects of plant richness by including the number of plant species per seed size-class as a covariate.

We hypothesize that a wide range of fish can disperse small-seeded plant species, but that large fish serve a unique role as dispersers of large-seeded species. We tested this hypothesis using a generalized linear mixed model (Proc Glimmix, SAS ver. 9.3). Maximum fish sizes

were categorized in four size classes: (1) 4.0–14.9 cm, (2) 15.0–29.9 cm, (3) 30.0–59.9 cm, and (4)  $\geq 60.0$  cm. These size classes follow the range distribution of body sizes in our database. We used size classes because most studies sampled fish spanning a range of sizes and do not report individual sizes of fish consuming a particular fruit species. Moreover, due to overfishing, individuals close to the maximum historical size of their species are uncommon in local populations in contemporary landscapes. This is particularly true for large-bodied characiforms such as *C. macropomum*, *P. brachyponus*, *P. mesopotamicus*, and several *Brycon* species (Reinert & Winter, 2002; Barthem & Goulding, 2007). Thus, it would be inappropriate to model seed size as a function of maximum body size for each fish species. We analysed seed size as a function of fish size class with random effects for the genus and family of plants and fish. We log-transformed seed size to improve homoscedasticity. Only three fish in size class 1 dispersed seeds. Since models failed to converge when we included these small fish species, we focused this analysis on size classes 2–4.

### (5) Fish size and probability of seed dispersal

To assess whether the probability of seed dispersal increases with fish size, we conducted logistic regressions using individual-level data on presence of intact *versus* masticated seeds in stomach contents of three species of *Brycon* (Bryconinae, Characiformes) from the Apaporis River, Colombian Amazon (S. B. Correa, unpublished data; see online Appendix S1). During the flooded season (May to July) of 2009, S.B. Correa sampled  $N = 16$  *B. amazonicus*,  $N = 87$  *B. falcatus*, and  $N = 57$  *B. melanopterus* using fruit-baited hooks. She dissected the digestive contents and quantified seeds as intact (dispersed) or masticated.

## III. RESULTS

We found 344 plant species in 853 records of fruit and seed consumption by 69 fish species in 62 studies in Neotropical wetlands between 1910 and 2013 (see online Appendix S5). Field observations by M. Goulding add another 222 species of fruits and seeds eaten by fish in Central Amazonian floodplain forests (see online Appendix S6). Thus, overall, Neotropical fish consume fruits and seeds of at least 566 plant species from 295 genera and 82 families. Goulding’s observations (see online Appendix S6) do not include data on the identity of the fish consuming fruits and seeds or whether seeds were dispersed or destroyed; therefore, we do not consider these 222 plant species further.

All studies were conducted in South America except for one in Costa Rica (Horn, 1997). Most studies focused on riparian forests and floodplain forests and savannas in the Amazon, Orinoco and Paraná-Paraguay river

basins. Seeds of 234 plant species were found intact in fish stomachs and/or intestines (probable seed dispersal) and seeds of 65 plant species were masticated (seed predation) (Table 1). For some plant species (69 species) one or multiple fish species can serve both as seed dispersers and predators (see online Appendix S5).

### (1) Evolutionary context of fish–fruit interactions

In the Neotropics, fish–fruit interactions appear older than most frugivore–fruit interactions involving bird and mammal families (Fig. 1). Contemporary accounts of seed dispersal and seed predation by fish span from ancient to derived angiosperm clades (Fig. 2). The probability of seed dispersal increased from basal to more derived lineages ( $z = 2.91$ ,  $P = 0.0036$ ). The same was true for seed dispersal and predation on single plant species (SD-SP:  $z = 2.14$ ,  $P = 0.0325$ ), but there was no difference in probability of seed predation among lineages ( $z = 1.47$ ,  $P = 0.14$ ).

### (2) Fruit traits associated with seed dispersal by fish

Fish disperse seeds of variable size and elongation (mean  $\pm$  S.D., maximum length =  $1.39 \pm 1.22$  cm,  $N = 135$  species; mean roundness =  $0.67 \pm 0.21$  cm width/cm length,  $N = 129$  species), from the small seeds of *Ficus americana* (Moraceae, length = 0.6 mm) to the large seeds of *Mora paraensis* (Fabaceae, length = 8.96 cm). Seeds of fleshy fruits are significantly more likely to be dispersed by fish than those of non-fleshy fruits (odds ratio: 14.55; 95% C.I. of odds ratio: 1.43, 148.18; Table 2). This higher probability of dispersal of fleshy fruits is not influenced by dehiscence, fruit colour, seed size, or seed roundness (Table 2). Furthermore, fruit type influences the probability of seed dispersal, independent of seed size and roundness (Table 2). Berry-like and drupaceous fruits are more likely to be dispersed by fish than dry fruits, whose seeds are more likely to be destroyed during consumption (berries *versus* dry fruit:  $t = 3.53$ ,  $P = 0.0098$ ; drupes *versus* dry fruit:  $t = 3.60$ ,  $P = 0.0081$ ). All other contrasts among fruit types were non-significant (results not shown).

### (3) The importance of fish for the dispersal of large-seeded plants

Seed size negatively influences the number of fish species dispersing seeds, such that only a few species disperse the largest seeds ( $F_{1,54} = 19.8$ ,  $P < 0.0001$ , Fig. 3). Similarly, large fish species disperse larger seeds ( $F_{2,246} = 5.03$ ,  $P = 0.0072$ ; Fig. 4). Fish in the largest size classes (30.0–59.9 and  $\geq 60.0$  cm, classes 3 and 4, respectively) dispersed significantly larger seeds than fish in the 15.0–29.9 cm class (size class 2 *versus* 3:  $P$  adjusted for multiple tests = 0.0081; size class 2 *versus* 4: adjusted  $P = 0.036$ ). We found no differences in average seed

size between fish in the largest two size classes (class 3 *versus* 4: adjusted  $P = 0.91$ ). Fish in the largest size class, however, appear to disperse seeds with a larger variation in size (i.e. the upper 50% of dispersed seeds are between 1.3 and 4.5 cm long), than fish in size class 3 (i.e. the upper 50% of seeds are between 0.8 and 3.5 cm long; Fig. 4).

### (4) Are large individual fish more likely to disperse seeds than small fish?

The probability of seed dispersal increases with fish body size at the individual level within three species of *Brycon* (Fig. 5). In the joint analysis of *Brycon melanopterus*, *B. falcatus* and *B. amazonicus*, a 1 mm increase in individual fish size augmented the probability of seed dispersal by 4.2% (odds ratio: 1.042; 95% C.I.: 1.003, 1.082;  $F_{1,141} = 4.62$ ,  $P < 0.03$ ; Fig. 5), but species identification did not influence seed dispersal probability ( $F_{2,141} = 0.12$ ,  $P = 0.89$ ).

## IV. DISCUSSION

### (1) Evolutionary context of fish–fruit interactions

Fish may have been the first vertebrate seed dispersers (Tiffney, 1984, 1986). Even today, fish disperse seeds of the gymnosperm genus *Gnetum* in Amazonian flooded forests (Kubitzki, 1985). Several lines of evidence suggest that in South American lowland forests, fish–fruit interactions likely preceded most other vertebrate–fruit interactions, contributing to long-distance seed dispersal and possibly the radiation of early angiosperms.

An ample and widely distributed fossil record demonstrates an early Palaeogene origin for many families and genera of South American freshwater fishes and species-level diversification by the Miocene (Lundberg *et al.*, 2010; López-Fernández & Albert, 2011). The Neotropical family Serrasalminidae (Characiformes) contains two clades of fruit-eating fishes that exhibit specialized dentition for efficient consumption of fruits and seeds (Correa *et al.*, 2007). Fossil records of the most basal of these clades date to the Late Cretaceous of Bolivia (~70 Ma), while fossils of extant *C. macropomum* have been recovered from the Late Eocene of Peru (~35 Ma) (Gayet & Meunier, 1998; Lundberg, 1998; Dahdul, 2007; Lundberg *et al.*, 2010). Aside from serrasalminids, fossil Bryconinae (Characiformes), a monogeneric subfamily containing several frugivorous species (e.g. Fig. 5), have been recovered from the Eocene–Oligocene of Brazil (Malabarba, 2004). Fossilized teeth that resemble those of contemporary frugivorous species demonstrate morphological stasis in these ecologically specialized fish (Dahdul, 2004) and suggest ancient phenotypic–environmental correlations that pre-date modern watershed arrangements (Crampton, 2011; López-Fernández & Albert, 2011).

Table 1. Seed dispersal and seed predation by fish. This table is organized by fish genus, and summarizes data presented in Appendix S5. We categorized fish–seed interactions as ‘seed dispersal’ (seeds found intact in the digestive contents of fish) and ‘seed predation’ (seeds found masticated in the digestive contents of fish). For each category, we indicated the number of fish species per genus that interact with seeds and the number of seed species dispersed or destroyed. When only the fish genus was reported, we added the symbol ‘≥’ to the total number of species. For some fish genera, there was no record of dispersal or predation, in which case we indicated 0 for number of fish species and plant species and NA (not applicable) for source. For a full list of fish and plant species identities and data on fish size, refer to Appendix S5

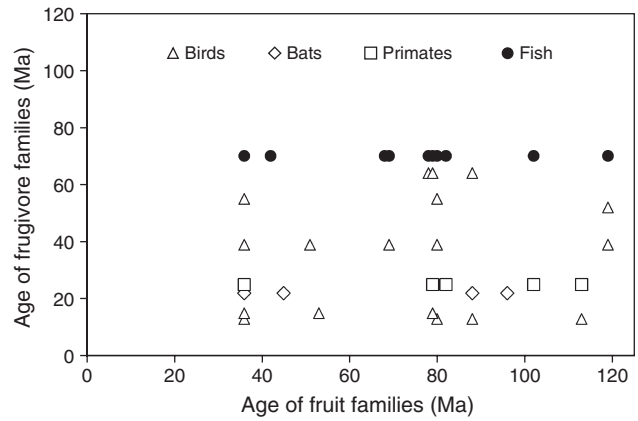
Fish genus	Seed dispersal			Seed predation		
	Number of fish species per genus	Number of plant species	Source	Number of fish species per genus	Number of plant species	Source
<i>Astyanax</i>	5	7	R. Costa-Pereira (unpublished data); Vilella, Becker & Hartz (2002) and Wolff <i>et al.</i> (2009)	1	1	Ortiz (1992)
<i>Auchenipterichthys</i>	1	1	Freitas <i>et al.</i> (2011)	0	NA	NA
<i>Auchenipterus</i>	1	11	Mannheimer <i>et al.</i> (2003)	0	NA	NA
<i>Brycon</i>	≥7	69	Gottsberger (1978), Goulding (1980), Horn (1997), Pizango-Paima, Pereira Filho & Oliveira-Pereira (2001), Banack <i>et al.</i> (2002), Piedade <i>et al.</i> (2006), Anderson <i>et al.</i> (2009), Reys, Sabino & Galetti (2009), Costa-Pereira <i>et al.</i> (2010) and Correa (2012)	≥3	15	Gottsberger (1978), Goulding (1980), Reys <i>et al.</i> (2009) and Correa (2012)
<i>Calophysus</i>	1	3	Goulding (1980)	0	0	NA
<i>Colossoma</i>	1	76	Gottsberger (1978), Goulding (1980), Goulding & Carvalho (1982), Kubitzki & Ziburski (1994), da Silva, Pereira-Filho & Oliveira-Pereira (2003), Lopes de Souza (2005), Lucas (2008) and Anderson <i>et al.</i> (2009)	1	23	Gottsberger (1978), Goulding (1980), Goulding & Carvalho (1982), Saint-Paul (1982), Kubitzki & Ziburski (1994), da Silva <i>et al.</i> (2003) and Lopes de Souza (2005)
<i>Creagrutus</i>	0	0	NA	1	1	Ortiz (1992)
<i>Electrophorus</i>	1	1	Moegenburg (2002)	0	0	NA
<i>Hemibrycon</i>	1	1	Ortiz (1992)	1	1	Ortiz (1992)
<i>Hemiodus</i>	1	2	Lopes de Souza (2005)	0	0	NA
<i>Leiarius</i>	1	1	Correa (1999)	0	0	NA
<i>Leporinus</i>	≥2	6	Gottsberger (1978) and Goulding (1980)	≥1	7	Gottsberger (1978) and Boujard <i>et al.</i> (1990)
<i>Lithodoras</i>	1	12	Cavalcante (1978) cited in Kubitzki (1985), Goulding (1980), Kubitzki & Ziburski (1994) and Piedade <i>et al.</i> (2006)	0	0	NA
<i>Megalechis</i>	1	1	Moegenburg (2002)	0	0	NA
<i>Megalodoras</i>	1	1	Goulding (1980) and Piedade <i>et al.</i> (2006)	0	0	NA
<i>Myleus</i>	1	2	Boujard <i>et al.</i> (1990)	2	17	Goulding (1980), Boujard <i>et al.</i> (1990) and Planquette, Keith & Le Bail (1996)
<i>Myloplus</i>	≥4	19	Correa (2012)	3	5	Correa (2012)
<i>Mylossoma</i>	≥2	3	Goulding (1980) and Costa-Pereira <i>et al.</i> (2010)	1	10	Goulding (1980)
<i>Phractocephalus</i>	1	3	Goulding (1980) and Kubitzki (1985)	0	0	NA
<i>Piaractus</i>	2	104	Honda (1974) and Silva <i>et al.</i> (1977) cited in Gottsberger (1978), Gottsberger (1978), Goulding (1980), Paula <i>et al.</i> (1989), Knab-Vispo <i>et al.</i> (2003), Galetti <i>et al.</i> (2008), Lucas (2008) and Anderson <i>et al.</i> (2009)	2	21	Honda (1974), Gottsberger (1978), Goulding (1980), Paula <i>et al.</i> (1989) and Knab-Vispo <i>et al.</i> (2003)

Table 1. continued

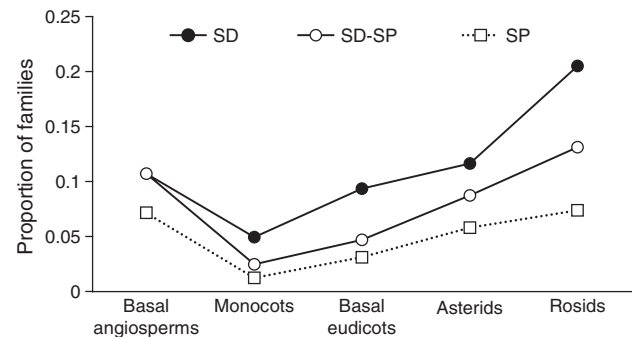
Fish genus	Seed dispersal		Seed predation	
	Number of fish species per genus	Number of plant species	Number of fish species per genus	Number of plant species
<i>Pimelodella</i>	1	6	1	1
<i>Pimelodus</i>	≥2	3	0	0
<i>Poecilia</i>	0	0	1	1
<i>Pterodoras</i>	1	16	0	0
<i>Rhamdia</i>	1	3	1	1
<i>Serrasalmus</i>	1	2	≥2	5
<i>Tocantinsia</i>	1	3	0	NA
<i>Trachycorystes</i>	≥2	5	0	NA
<i>Triportheus</i>	≥6	29	≥1	7

	Source
Gottberger (1978)	Gottberger (1978)
Goulding (1980); R. Costa-Pereira (unpublished data)	NA
NA	Ortiz (1992)
Goulding (1981), de Souza-Stevaux <i>et al.</i> (1994), Pilaui <i>et al.</i> (1999) and Agostinho <i>et al.</i> (2009)	NA
Gottberger (1978) and Piedade <i>et al.</i> (2006)	Gottberger (1978)
Nico (1991)	Goulding (1980)
Carvalho & Kawakami-Resende (1984)	NA
Goulding (1980) and Exponent (2011)	NA
Gottberger (1978), Goulding (1980), Maia, Santos & Parolin (2007), Costa-Pereira <i>et al.</i> (2010) and Correa (2012)	Gottberger (1978) and Goulding (1980)



**Fig. 1.** Ages of origin of angiosperm and Neotropical frugivore families. Each symbol represents the age of a family of frugivores and one of the most important fruit-producing families consumed by that lineage. The two oldest bird families (Tinamidae and Cracidae, ages 97 and 89 Ma) cannot be included due to uncertainty about their diets, but pre-date the origin of the fish family plotted. Ma = millions of years. Based on Fleming & Kress (2013). The ages of each vertebrate and plant family are listed in Appendix S4.



**Fig. 2.** Occurrence of fish-fruit interactions across angiosperm lineages, calculated as the number of families in which frugivory is reported divided by the number of families known for that group. SD, seed dispersal; SP, seed predation; SD-SP, seed dispersal and seed predation upon a single plant species by Neotropical fish.

Despite an earlier origin of their stem groups, many modern frugivorous birds, primates, and bats evolved in the Oligocene/Miocene (between 34 and 10 Ma; Fleming & Kress, 2011), much later than the origin of frugivorous serrasalmids and diversification of modern Neotropical fishes (Fig. 1) (Lundberg *et al.*, 2010; López-Fernández & Albert, 2011). Tinamous and guans (Tinamidae: 97 Ma, Cracidae: 89 Ma, respectively) are the two oldest lineages of Neotropical frugivorous birds. Thus, it is possible that taxa in these lineages could have interacted with fruits before serrasalmid fishes. However, the ground-dwelling habits of tinamous and guans limit their abilities to move seeds long distances relative to fish.



Lowland rainforests, with similar family-level composition and physiognomy of modern forests, were already established across South America by the Early Palaeocene (~60 Ma) and reached maximum diversity during the Early Eocene (~50 Ma; Jaramillo *et al.*, 2010). Some of the ‘core’ plant families in the diet of frugivorous fishes originated in South America (i.e. western Gondwana) in the Cretaceous (e.g. *Arecaceae*, *Euphorbiaceae*, and some *Sapotaceae*; Pennington & Dick, 2004). However, other important families for fish (e.g. *Fabaceae*, *Melastomataceae*, *Moraceae*, *Rubiaceae* and clades of *Annonaceae* and *Lauraceae*) did not reach South America until later in the Early/Middle Eocene (between 50 and 40 Ma) when high global temperatures and incipient emergence of island chains allowed expansion and migration of tropical taxa from North America (Morley, 2003; Pennington & Dick, 2004; Antonelli *et al.*, 2009; Pennington & Dick, 2010).

Long-distance seed dispersal mediated by water currents and frugivorous fish could have facilitated dispersal of early angiosperms across South America, contributing to the low phylogenetic geographical structure and broad geographical distribution observed in today’s highly diverse Amazonian lowland forests (Henderson, Hamilton & Crampton, 1998; Normand *et al.*, 2006; Pennington & Dick, 2010; Wittmann *et al.*, 2013; but see Eiserhardt *et al.*, 2013 for palms). For instance, 9 of the 10 plant families here considered as ‘core’ food for frugivorous fish are widely distributed and ecologically dominant in lowland and floodplain forests throughout South America (Wittmann *et al.*, 2013). Initial establishment along rivers could have promoted radiation of early angiosperms as edaphic conditions in gallery forests are relatively stable (Morley, 2003). In addition, long-distance seed dispersal along rivers in the deep past could have contributed to plant colonization of regions across South America over long timescales (Levin, 2006; Fleming & Kress, 2013). Such a scenario could have been possible, given that currently isolated lowland watersheds were interconnected over extensive periods of time throughout

the Palaeogene (i.e. proto-Amazonas-Orinoco and proto-Paraná-Paraguay systems; Lundberg *et al.*, 1998; López-Fernández & Albert, 2011) and extensive wetlands developed in the Early Miocene and persisted over millions of years (Hoorn *et al.*, 2010). Moreover, the palaeo-distribution of frugivorous *Colossoma macropomum* ranged beyond the current Amazon and Orinoco basins to the currently isolated Magdalena Basin in Northern Colombia (Lundberg, Machado-Allison & Kay, 1986). In contemporary landscapes, *C. macropomum* comprises a panmictic population that occupies a 2200 km stretch in the Amazon river (Santos *et al.*, 2007) and produces long-distance seed dispersal *via* extensive daily feeding movements within floodplain forests (e.g. 0.13–2.7 km) combined with long retention time of seeds in the digestive system (e.g. up to 212 h) (Anderson *et al.*, 2011). Thus, independent of exactly when fish–fruit interactions originated, the available evidence suggests that frugivorous fish likely contributed to the maintenance of tree diversity in South American lowland forests over tens of millions of years.

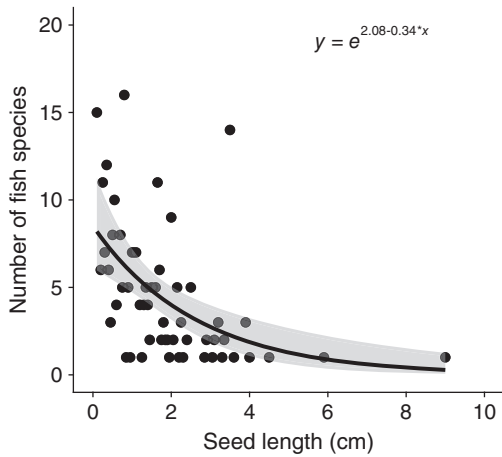
Lastly, our analyses revealed that in Neotropical wetlands, fish frugivory ranges from basal angiosperms to advanced eudicots, and that seed dispersal is proportionally higher among advanced eudicots (i.e. rosids). These findings contrast with an earlier hypothesis suggesting that seed dispersal by fish is mostly relevant for basal angiosperm families (van der Pijl, 1969). Taken together, our results demonstrate the relevance of fish as seed dispersers of angiosperms in a broader evolutionary context than initially presumed (van der Pijl, 1969; Gottsberger, 1978).

## (2) Fruit traits associated with seed dispersal by fish

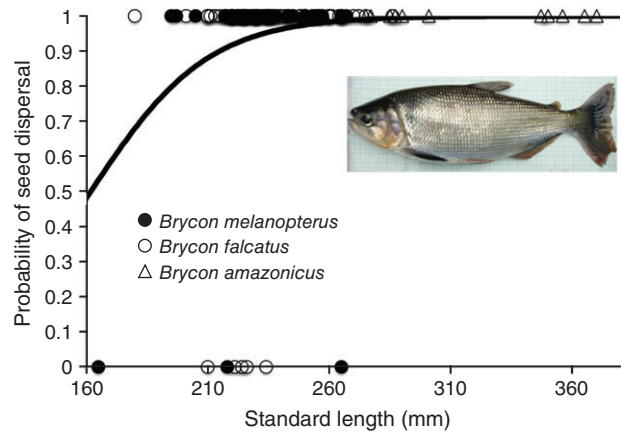
Fish consume fruits of a large number of plant species distributed in riparian and floodplain communities across the Neotropics. Our results demonstrate that seeds of fleshy fruits are more likely to be dispersed by fish than seeds of dry fruits, independent of seed size. This finding contradicts a previous hypothesis that small

Table 2. The probability of seed dispersal *versus* mastication as a function of several key fruit characteristics. We conducted two separate logistic regressions to examine whether seed dispersal is associated with specific traits (analysis 1) or fruit types (analysis 2). For analysis 1 we did not include fruit type (coded as NA, for not applicable), and for analysis 2 we did not include specific fruit characteristics because traits and fruit type are confounded with each other. Significant p-values are highlighted in bold.

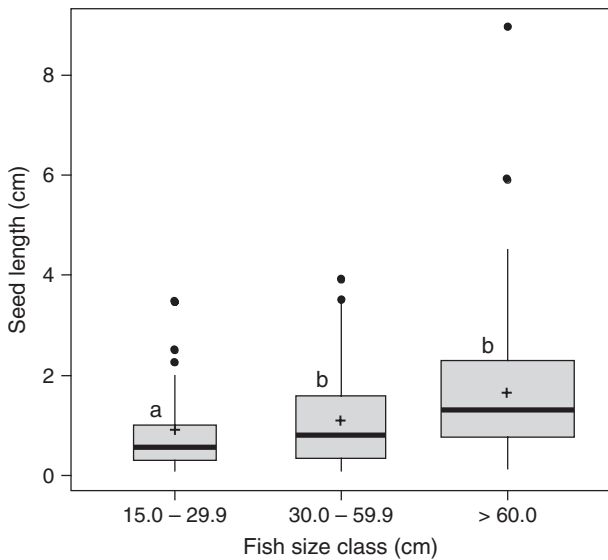
	Analysis 1: traits		Analysis 2: fruit type	
	$F_{1,17}$	$P$	$F_{1,35}$	$P$
Fleshy	5.93	<b>0.026</b>	NA	—
Dehiscence	0.62	0.44	NA	—
Colour	0.00	0.99	NA	—
Seed length	0.39	0.54	0.08	0.77
Seed roundness	0.01	0.94	0.72	0.40
Fruit type	NA	—	$F_{4,35} = 4.22$	<b>0.0068</b>
Plant genus (family)	$\chi^2 = 0.33$	0.28	$\chi^2 = 0.12$	0.37



**Fig. 3.** Negative binomial regression modelling the number of fish species dispersing seeds in Neotropical wetland and riparian plant communities as a function of seed size (longest length).



**Fig. 5.** Logistic regression modelling the probability of seed dispersal as a function of fish size based on individual-level data on presence of intact *versus* masticated seeds in stomach contents of *Brycon amazonicus* (photograph inset), *B. falcatus* and *B. melanopterus* (Bryconinae, Characiformes), in flooded forests of the Apaporis River, Colombian Amazon (standard length: 16.5–37.0 cm).



**Fig. 4.** Size distribution of seeds dispersed per fish size class. Size classes with different lower case letters are significantly different at  $\alpha = 0.05$  after Tukey’s correction for multiple comparisons. Box lower and upper endpoints represent the 25th and 75th quartiles. Horizontal bars inside the box represent median seed size; plus symbols represent mean values. Whiskers represent the location of the lower and upper 25% of the data, respectively, excluding outliers which are represented by dots. Box width is proportional to the square root of the number of samples per size class (class 2,  $N = 80$ ; class 3,  $N = 94$ , class 4,  $N = 208$ ).

seeds are an adaptation of fish-dispersed Amazonian fruits to reduce destruction by seed predators (Goulding, 1980). The presence of flesh likely protects seeds, thereby reducing the probability of seed damage during consumption by fish. Although not

surprising, this is an important finding for understanding fish–fruit interactions, considering that fleshy fruits are assumed to be animal dispersed by default (Gautier-Hion *et al.*, 1985).

Fleshy tissues have high carbohydrate and/or lipid contents and represent the base for mutualistic frugivore–fruit interactions (Herrera, 2002). If fleshy fruit facilitates high-quality endozoochory, and particularly ichthyochory in wetlands, this trait will be favoured by natural selection and will be frequent among plants in these communities. In a floodplain forest of the Central Amazon, for instance, 80% of fruits ( $N = 144$  species in a 2 ha plot) have fleshy tissues (e.g. pulp, arile; Ayres, 1993). Alternatively, fleshy tissues may confer floating capability to diaspores. A thin, low-density, lipid-rich tissue surrounding the seed is associated with short-term flotation in *Virola surinamensis* (i.e. <10 days; Lopez, 2001), while a spongy mesocarp allows moderate flotation in *Vitex cymosa* (12 days; Kubitzki & Ziburski, 1994). Unfortunately, to the best of our knowledge, no study has quantified the relative importance of hydrochory *versus* endozoochory in the evolution of fleshy fruits among wetland plants (Parolin *et al.*, 2013).

Despite this limitation, ichthyochory likely is the main dispersal mode for heavy non-floating seeds that sink immediately after falling into the water (Kubitzki & Ziburski, 1994). Furthermore, water only disperses seeds downstream, whereas fish likely disperse seeds downstream, upstream and laterally within the floodplain (Horn, 1997; Anderson *et al.*, 2011). Thus, the eco-evolutionary consequences of ichthyochory and hydrochory are probably quite different.

Fruit traits such as dehiscence, colour, and seed size and shape do not appear to influence the outcome of

fish interactions with seeds (i.e. seed dispersal *versus* predation). These findings, added to the large taxonomic diversity of fruits consumed by some fish species (e.g. *C. macropomum* and *P. brachypomus*) suggest that frugivorous fish may not impose much selection on morphological fruit traits. However, under some circumstances, fish might selectively consume fruits with certain traits. Contrasting colours could enhance detection and influence consumption of ripe fruits falling into transparent water bodies (e.g. Krupczynski & Schuster, 2008). Additionally, fish might impose selection on non-morphological fruit traits, such as water-soluble organic compounds, which could facilitate the localization of ripe fruits in extensive floodplain forests (e.g. Rodriguez, Alquezar & Pena, 2013). Nutrient composition greatly influences food selection by animals, including fish (Raubenheimer *et al.*, 2005; Ruohonen, Simpson & Raubenheimer, 2007), but its influence on feeding choices of frugivorous fishes is unknown. The nutritional ecology (*sensu* Raubenheimer, Simpson & Mayntz, 2009) of frugivorous fishes is a promising field that could greatly benefit from developments in the study of the role of nutrients on food selection by marine herbivorous fishes (Clements, Raubenheimer & Choat, 2009) and other vertebrate frugivores (Ganzhorn *et al.*, 2009; Felton *et al.*, 2009*a,b*; Corlett, 2011).

### (3) Seed predation by fishes

Many frugivore species, including birds, mammals, and fish, serve crucial roles as both seed dispersers and seed predators of the same plant species or of other species (e.g. Poulsen, Clark & Smith, 2002; Stevenson, 2007; Lucas, 2008; Anderson *et al.*, 2009; Albrecht, Neuschulz & Farwig, 2012). Even species traditionally regarded as specialized seed predators can contribute significant seed dispersal services (Donatti, Guimaraes & Galetti, 2009; Guerrero & Tye, 2009; Heleno *et al.*, 2011; Barnett *et al.*, 2012; Young, Kelly & Nelson, 2012). Nevertheless, most empirical studies focus on one or the other role, rarely considering the importance of both dispersal and predation in structuring plant communities (Hulme, 2002; Heleno *et al.*, 2011). Our analyses revealed that dry fruits are more likely to be masticated by fish than fleshy fruits and that small- and medium-sized fish tend to masticate seeds more often than large-sized fish. In a non-flooded lowland Amazonian rainforest, selective seed predation on common and large-seeded species by small mammals (i.e. mice and spiny rats) increases species richness by reducing the recruitment success of such species (Paine & Beck, 2007). In fragments of Brazilian Atlantic forest, seed removal and scatter hoarding by small mammals fail to compensate for decreased abundance of the agouti (*Dasyprocta* spp.), a medium-sized mammal affected by hunting and the main disperser of an endemic large-seeded palm tree (Donatti *et al.*, 2009). How the seed predation activities of frugivorous fish compare with those of other animals

is virtually unknown. After floodwaters recede, wetland habitats are accessible to terrestrial animals, including a diversity of seed predators from beetles to rodents and peccaries. Do fish act synergistically with these other seed predators, e.g. reducing the density of common seeds? Or do fish and other seed predators consume different species of seeds, such that the non-fish seed predators could not replace frugivorous fish if overfishing continues unabated? These questions remain unanswered.

### (4) Functional redundancy and seed size

Seed size is highly variable within angiosperms, even among coexisting species (Muller-Landau, 2010). Large seeds first evolved as an adaptation to closed canopy habitats where light is very limited at ground level (Eriksson, 2008; Bolmgren & Eriksson, 2010). In harsh environments, such as dry or flooded systems, a larger seed mass increases tolerance to stressful conditions and enhances seedling survival (Leishman *et al.*, 2000; Lopez, 2001; Muller-Landau, 2010). In oligotrophic environments, such as forests inundated by black water rivers, plants produce large seeds to compensate for limited soil nutrients (Parolin, 2000). Yet larger and heavier seeds often depend on animals for their dispersal.

In turn, many frugivores are constrained by gape size, which imposes a limit on the size of fruits and seeds that they can swallow (Wheelwright, 1985). As a result, there is a significant reduction in the number of species of dispersers as seed size increases [e.g. in birds (Wheelwright, 1985), primates (Peres & van Roosmalen, 2002), and fish (this study)]. Large-bodied primates and birds are key dispersers of large-seeded species (e.g. Holbrook & Loiselle, 2007; Kitamura, 2011; Stevenson, 2011; Levi & Peres, 2013). Our analyses demonstrated that large-bodied fish species disperse seeds with a broad range of sizes, including both small- and large-seeded species (i.e.  $\geq 2.0$  cm length) and, on average, disperse larger seeds than medium-sized fish species (Fig. 4). These results suggest that large-bodied frugivorous fish likely are key dispersers of large-seeded species in wetland communities, much as large-bodied primates and birds are in these and non-flooded forests. Functional redundancy, especially among unrelated mutualistic species, can help mitigate negative impacts of losing one player (e.g. Sethi & Howe, 2009).

Ichthyochory appears to be the main dispersal mode for heavy fleshy fruits (e.g. large-seeded palm trees such as *Astrocaryum jauari*; Goulding, 1980; Kubitzki & Ziburski, 1994; Piedade, Parolin & Junk, 2006). The relevance of ichthyochory for non-floating seeds resides in the relative high diversity and abundance of families with large heavy seeds in Neotropical floodplain forests [e.g. Annonaceae, Arecaceae, Chrysobalanaceae, Clusiaceae, Lauraceae, Sapotaceae (Peres & van Roosmalen, 2002; Haugaasen & Peres, 2006; Wittmann *et al.*, 2006)]. If large-bodied fish species are exterminated from these

ecosystems, medium- and small-sized fish species will not replace their seed dispersal services, limiting the dispersal capabilities of numerous plant species.

##### (5) Fish size and the probability of seed dispersal

Our individual-level analysis of seed consumption for three species of *Brycon* adds to a growing body of evidence demonstrating that among fleshy fruits, seed destruction by mastication decreases with frugivore body size; a pattern previously observed at the individual level in three large-bodied species of serrasalmid fishes: *C. macropomum* (Kubitzki & Ziburski, 1994; Anderson *et al.*, 2009), *P. brachypomus* (Anderson *et al.*, 2009) and *P. mesopotamicus* (Galetti *et al.*, 2008). In general, large-bodied frugivores consume greater amounts of fruits, have longer seed-retention times, and disperse seeds further than small species (Kitamura, 2011; Wotton & Kelly, 2012). The positive association between fish size and different aspects of seed dispersal effectiveness highlights the disproportionate importance of large fish on the reproductive dynamics of tropical riparian and floodplain plant communities.

Large frugivorous vertebrates are strongly affected by deforestation and hunting (e.g. Bodmer & Pezo-Lozano, 2001; Milner-Gulland & Bennett, 2003). Large vertebrates in general are highly susceptible to even small-scale harvesting operations due to their slow growth and low reproductive rates (Begazo & Bodmer, 1998; Levi & Peres, 2013). In tropical ecosystems across the globe, defaunation is changing forest recruitment dynamics (Beaune *et al.*, 2013; Harrison *et al.*, 2013; Kurten, 2013), especially of large-seeded tree species (e.g. Nunez-Iturri & Howe, 2007; Wang *et al.*, 2007; Wotton & Kelly, 2011), and altering patterns of natural selection on seed traits (Galetti *et al.*, 2013).

Globally, selective harvesting of commercially important fish targets large individuals, and within a few decades induces changes in population structure by favouring the survival of smaller fish that reproduce at an earlier age (Jørgensen *et al.*, 2007; Sharpe & Hendry, 2009). Thus, four decades of overexploitation of Neotropical fruit-eating fish has likely skewed populations to younger and smaller individuals (Isaac & Ruffino, 1996; Reinert & Winter, 2002; Santos *et al.*, 2007). Overharvesting likely eliminates the best dispersers from the system, affecting interactions with plants and functional complementarity with other seed dispersers in different ways. For example, large individuals of larger-bodied fish species disperse large-seeded plant species, which are more likely to be disperser-limited (Peres & van Roosmalen, 2002; Holbrook & Loiselle, 2009; Kurten, 2013). Also, because smaller individuals are more likely to destroy seeds, increased abundance of smaller frugivorous fish will increase the frequency of seed predation relative to

seed dispersal, changing the nature of fish–fruit interactions and potentially altering the structure of riparian and floodplain plant communities.

Here we have focused mostly on large scaled fishes of the family Serrasalminidae. Catfishes, however, are just as important or more important as seed dispersers of fleshy fruits since they lack the type of teeth necessary for mastication (Goulding, 1980; de Souza-Stevaux, Negrelle & Citadini-Zanette, 1994; Kubitzki & Ziburski, 1994; Pilati, Andrian & Carneiro, 1999; Maia & Chalco, 2002; Mannheimer *et al.*, 2003; Piedade *et al.*, 2006), but less is known about them. The largest fruit-eating fish is also a catfish (*Phractocephalus hemiliopterus*, Pimelodidae) and a major seed disperser over a large part of the Amazon and Orinoco basins (M. Goulding, personal observations; see also Piedade *et al.*, 2006). The relative roles of serrasalmids and catfishes in seed dispersal and predation await further study. Additional data on overexploitation of fruit-eating serrasalmids and catfishes will be necessary to evaluate potential impacts of large-scale commercial and recreational fisheries on seed dispersal, seed predation, and regeneration dynamics in flooded forest and savannas.

## V. CONCLUSIONS

(1) We demonstrate that fish were among the first frugivores in the Late Cretaceous (~70 Ma). Furthermore, fish–fruit interactions are widespread among lineages of contemporary Neotropical flowering plants, especially among advanced eudicots. Long-distance ichthyochory likely facilitated dispersal and possibly the radiation of early angiosperms across South America.

(2) Our review has more than tripled the number of species reported in a previous effort to quantify plant diversity related to fish frugivory in the Neotropics (i.e. an increase of 396 species and 27 families over Correa *et al.*, 2007). Despite growing evidence of ichthyochory in the Neotropics in recent decades, we still lack robust quantitative measures of dispersal effectiveness and recruitment effects of ichthyochory.

(3) Fleshy fruits are common in wetland and their seeds are more likely to be dispersed by fish than seeds of dry fruits. We still do not have a clear understanding of the role of ichthyochory in the evolution of fleshy fruits in wetland plants. A phylogenetically controlled comparison of fruit traits in flooded forests and adjacent terra firme forests could distinguish the role of different seed dispersers on trait evolution. Terra firme forests do not flood for extensive periods of time, and frugivorous fish and water do not serve as seed dispersers in those systems. By contrast, water and fish are the primary vectors of seed dispersal in flooded forests. The best comparisons will focus on diverse plant lineages with species in both habitats for which robust phylogenies are available.

(4) Large-bodied species of frugivorous fish masticate seeds of fleshy fruits less frequently than smaller species. These large fish species also disperse seeds with a broad range of sizes, including large-seeded species, which are more likely to be disperser-limited, and non-floating seeds that cannot be dispersed by water. Our analyses highlight the importance of large frugivorous fishes as effective and key seed dispersal agents in wetlands communities. Given the current over-exploitation of large frugivorous fishes across South America, alternative fisheries management strategies that account for the ecological role of these species are crucial to preserve ecosystem function and biodiversity in wetlands.

(5) Fruiting synchrony also attracts birds, mammals, and turtles, to flooded habitats (Barnett *et al.*, 2005; Haugaasen & Peres, 2007; Haugaasen & Peres, 2008). As such, seed dispersal in riparian and floodplain communities is carried out by a diverse suite of vertebrate dispersers. We know very little about the relative contributions of fruit-eating fish *versus* other frugivorous vertebrates to seed dispersal in these systems (Banack, Horn & Gawlicka, 2002; Donatti *et al.*, 2011). If fish disperse the same species of seeds as birds and mammals, ecological redundancy among dispersers might mitigate losses of certain frugivores due to hunting and habitat alteration (Correa *et al.*, 2007). Comprehensive empirical studies simultaneously assessing seed dispersal and predation by suites of co-occurring frugivorous vertebrates at single locations would be necessary to shed light on functional redundancy among groups.

(6) Studies of fish diets do not usually identify seeds and fruit found in stomach contents. An efficient solution is to collect available fruit and seeds in the riparian forest at the time when diet is being investigated, for comparisons with those found in gut contents (e.g. Anderson *et al.*, 2009; Correa & Winemiller, 2014). Recent applications of DNA barcodes (short sequence markers used for taxonomic identification) to diet reconstruction (reviewed by Pompanon *et al.*, 2012) suggest that barcoding of local fruit-producing species and seeds retrieved from fish guts could be a useful tool, particularly in the identification of heavily masticated seeds.

(7) Collaborations between ichthyologists and plant ecologists will further advance our understanding of the relative importance of fruit-eating fish for forest regeneration. To the best of our knowledge, no study has attempted to evaluate recruitment rates of fish-dispersed seeds in nature. Without these data, we cannot unravel the direct effects of ichthyochory on plant regeneration, community structure, and biodiversity in riparian and floodplain ecosystems (Wang & Smith, 2002; Howe & Miriti, 2004; Godinez-Alvarez & Jordano, 2007). Further studies of flooded forest population dynamics, especially on seedling densities of fish-dispersed fruits in various river types, would shed light on the possibility that over-exploitation of large frugivorous fishes is affecting plant

recruitment and ultimately biodiversity in Neotropical wetlands.

(8) South America harbours the largest diversity of fruit-eating fishes (Horn *et al.*, 2011) and some of the most diverse tropical wetland systems on earth (e.g. Amazon, Orinoco, and Pantanal; Junk *et al.*, 2006; Junk & Piedade, 2010; Fleming & Kress, 2013). The diversity of fruits and seeds consumed by fish and the antiquity of fish and fruit interactions revealed by our analyses reinforce the relevance of South American wetlands as focal points for studying the importance of ichthyochory in the early diversification and maintenance of current plant communities.

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## VIII. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

**Appendix S1.** Study site and sampling information for unpublished data.

**Appendix S2.** Sources for fruit traits.

**Appendix S3.** Conversion of fish size data from total length to standard length.

**Appendix S4.** Ages of origin of Neotropical frugivores and fruit-producing families.

**Appendix S5.** Fruits and seeds consumed by Neotropical fish.

**Appendix S6.** Fruits and seeds observed in stomach contents of fish in the Central Amazonian floodplain forests (M. Goulding, unpublished data).

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