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# Viability of Seeds Consumed by Fishes in a Lowland Forest in the Brazilian Central Amazon

Bianca Weiss<sup>1</sup>, Jansen A. S. Zuanon<sup>2</sup>, and Maria T. F. Piedade<sup>2</sup>

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## Abstract

Várzeas are forest areas seasonally flooded by white-water rivers and have a variety of tree species, which bear fruit during the filling or flood and in the beginning of low water periods. During those periods of inundation, fruits and seeds are important resources for different fish species. In this study, the viability of whole seeds removed from the stomach and intestine of fishes was analyzed. Fishes were collected with gillnets installed during 24-hr cycles along the flooded forest, during the filling, flood, and in the beginning of low water periods of the Year 2014 in the Catalão lake, Brazilian Central Amazon. In total, 1,915 specimens of fish were captured, and 148 specimens (8% from the total) contained seeds in their digestive tracts. Some fishes that consumed seeds are species commercially important and have migratory habits. Fishes consumed 3,092 seeds. All whole seeds removed from the digestive tracts of fishes were seeded in várzea soil and maintained in a greenhouse. Seeds of 16 plant species (89%) germinated. Our conclusion is that fish species can play an important role in the ecology of várzea forests by dispersing seeds, contributing to the colonization of new areas, and allowing genetic flow between subpopulations distributed along the rivers.

## Keywords

frugivory, seed germination, ichthyochory, overfishing

## Introduction

Seeds are responsible for the success of plant species propagation in time and space. In general, the process of seed dispersal far from the mother plant is important because this reduces intraspecific competition and increases the chances of establishment in new areas opened to colonization (Janzen, 1971; Willson & Traveset, 2000). However, the success of seedling establishment depends on morphological and chemical characteristics of fruits and seeds and a series of events determined by biotic interactions (Harper, 1977). During the flood period of large Amazonian rivers, lowland areas flooded by rivers with muddy and nutrient-rich waters, called as várzeas, become a mosaic of interconnected lakes, channels, and forested areas (Junk & Piedade, 2010). In these environments, the fruiting period of tree species is closely related to the increase of water level (Ferreira, Almeida, & Parolin, 2010; Kubitzki & Ziburski, 1994; Piedade, Parolin, & Junk, 2006; Schöngart, Piedade, Ludwigshausen, Horna, & Worbes, 2002; Waldhoff & Maia, 2002; Waldhoff, Sant-Paul, & Furch, 1996). For the fishes, flooded forests provide

shelter from predators and food resources, as fruits, seeds, and invertebrates, and are therefore an important habitat for survival of several fish species (Gerking, 1994; Goulding, 1980; Lowe-McConnell, 1987).

Some studies highlight the importance of Amazonian flooded forests for the fish communities (Claro-Jr, Ferreira, Zuanon, & Araujo-Lima, 2004; Lobón-Cerviá, Hess, Melack, & Araujo-Lima, 2015) and record higher fish species richness in vegetated areas compared with nonvegetated areas (Petry, Bayle, & Markle, 2003). In flooded forests, fruits containing nutritional reserves are

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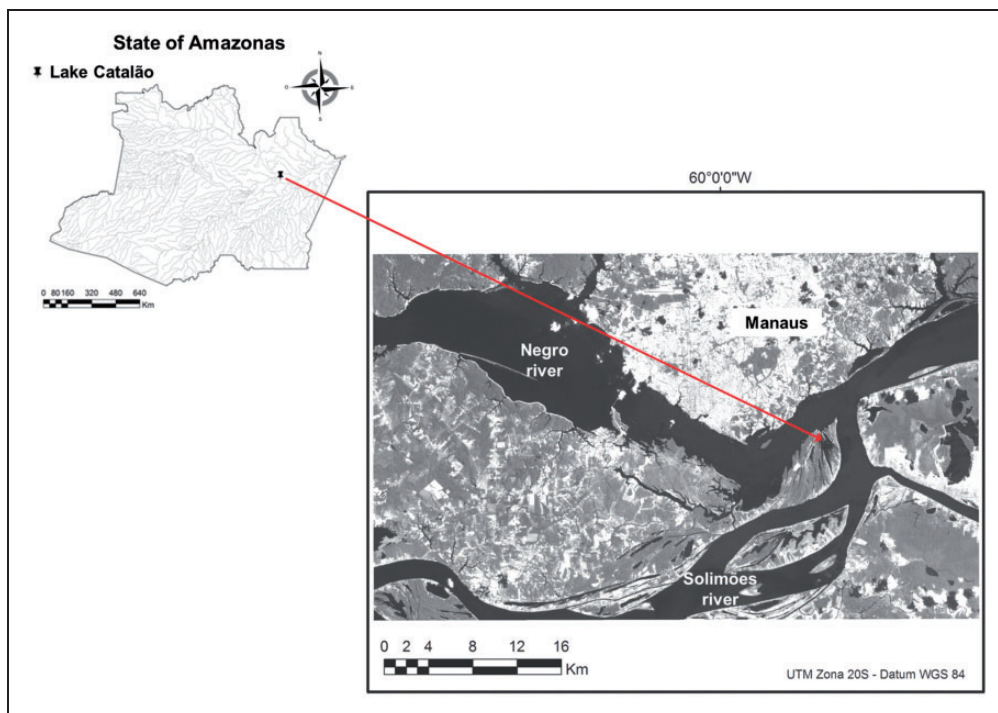
highly important in fish diet (Claro-Jr et al., 2004; Pizango-Paima, 2001). These medium-to-large-sized fruits make noise when fall in the water and are usually immediately consumed by fish, together with their seeds (Van der Pijl, 1972). Horn et al. (2011) highlight that in the Neotropics, it is possible to find about 150 fish species that eat fruits in at least one stage of their lives, representing about 60% of the total of 276 species of frugivorous fish known so far in the world. Besides, 62 studies conducted in tropical areas from 1990 to 2013 showed that fruits and seeds from at least 344 tree species are consumed by 69 fish species (Correa, Costa-Pereira, Fleming, Goulding, & Anderson, 2015).

For the flooded forest trees, ichthyochory is a very important mechanism for the dispersal of diaspores (Gottsberger, 1978). Several studies have shown the occurrence of substantial quantities of intact seeds in fish digestive tracts (Anderson, Saldanã Rojas, & Flecker, 2009; Correa et al., 2015, 2016; Galetti, Donatti, Pizo, & Giacomini, 2008; Horn, 1997; Lucas, 2008; Piedade et al., 2006; Pollux, 2010; Souza-Stevaux, Negrelle, & Citadini-Zanette, 1994). This suggests a high potential of ichthyochory as a means of seed dispersal in Amazonian flooded areas (Ericson, 1979; Gottsberger, 1978; Goulding, 1980). Nevertheless, knowledge about the interaction between fishes and vegetation in these environments is still scarce. Besides the importance for the fish communities, an understanding of the dynamics of tree seed dispersal by fishes may help to understand the colonization processes of plant species in new

environments, such as the process of regeneration of disturbed areas or the colonization of lowland areas recently established. This study aimed to evaluate the viability of intact seeds removed from the stomach and intestine of fishes captured during the flood period of a várzea area in the Brazilian Central Amazon.

## Methods

This study was carried out in the Catalão lake (03°10'04" S and 59°54'45" W), in Iranduba municipality, near Manaus city, Amazonas state, Brazil. The lake covers an area of approximately 20 km<sup>2</sup> and is located at the confluence of Negro and Solimões rivers (Figure 1). Fish specimens were collected from January to August 2014. In a period of 4 days in each month, a set of nine gillnets ranging from 40 to 120 mm between opposite knots (each net with 10 m of length and height between 1.5 and 3.5 m) was employed. Gillnets were installed inside the flooded forest and close to trees with ripe fruits. Gillnets were inspected at intervals of 6 hr and then moved to another local every 24 hr. Additional fish specimens were obtained from samplings conducted under the projects: "Structure and Dynamics of the Catalão Ecotone" and "Composition and trophic structure of fish assemblages in a lowland area in the central Amazon," developed by researchers of the National Institute of Amazonian Research (INPA) in the same area. In those cases, fishes were also captured with similar sets of gillnets positioned close to the flooded forest during 24 hr for each month, also from January to August 2014. After



**Figure 1.** Geographic location of Catalão lake at the confluence of Negro and Solimões rivers, Iranduba municipality, Amazonas state, Brazil.

taxonomic identification, each fish had its stomach and intestine removed for the identification of seeds. The seeds were counted and separated by source (fish species and organ of the digestive tract: stomach or intestine). Seeds found with pulp were carefully pulped before sowing, which was done in individual pots in soil taken from the study site. The experiments were carried out under ambient temperature, humidity, solar radiation, and precipitation in a greenhouse of the research group of Ecology, Monitoring, and Sustainable Use of Wetlands (MAUA/INPA). Those environmental factors were monitored in Manaus city by the National Institute of Meteorology (1st DISME/AM/AC/RR-Manaus-AM). From March to September, during the germination experiment in the greenhouse, a daily monitoring from 06:00 to 18:00 hr (local time) showed that temperature varied between 23°C and 36°C, relative humidity ranged from 50% to 86%, precipitation was up to 110 mm, and mean photosynthetic active radiation was  $492.66 \mu\text{mol}\cdot\text{s}^{-1}\text{m}^{-2}$ , which takes into account a reduction of 25% of photosynthetic active radiation due to light interception by the greenhouse. Daily watering of seeds was done with water from an artesian well at INPA (conductivity  $15.60 \mu\text{S}\cdot\text{cm}^{-1}$  and pH 4.45; Environmental Chemistry Laboratory—INPA). The criteria established for seed germination was the observation of radicle protrusion of the embryo, through daily monitoring. For all plant species, seed planting occurred between 24 hr and 72 hr after seeds being removed from the fish digestive tract. The experiment was conducted over the course of 210 days.

The frequency of occurrence of plant species in the fish digestive tracts was calculated with the equation  $\text{FOi}\% = (\text{N}_i/\text{N}_{\text{wf}}) \times 100$  (Hyslop, 1980), where  $\text{FOi}\%$  is the frequency of occurrence of the item  $i$ ;  $\text{N}_i$  is the number of digestive tracts (stomach or intestine) where the item  $i$  were present; and  $\text{N}_{\text{wf}}$  is the total number of digestive tracts (stomach or intestine) with food. The percentage of seed germination was calculated with the equation  $\text{PG} = (\text{SG} \times 100)/\text{AM}$  (Ferreira, 2004), where  $\text{PG}$  is the percentage of germination;  $\text{SG}$  is number of germinated seeds; and  $\text{AM}$  is the total of seeds in the sample.

The Committee of Ethics of Research with the Use of Animals—CEUA (protocol number 031/2013) of the National Institute of Amazonian Research (INPA) approved this study.

## Results

The 1,915 fish individuals captured were distributed in 6 orders, 22 families, 78 genera, and 136 species. The highest number of species was for the Characiformes (69 species; 51%), followed by Siluriformes (30 species; 28%). Whole seeds were found in 148 fish individuals (8% of total), belonging to 14 species, 2 orders, and 5 families. See appendix plant species that were found in the digestive

tract of the studied fish species. *Triportheus albus* was the most abundant species of the samples and presented the highest number of individuals that consumed seeds. *Triportheus auritus*, *Triportheus angulatus*, and *Colossoma macropomum* were also represented by high quantities of individuals in the samples, with high percentages of individuals with seeds in their digestive tracts. The mean percentage of nonempty digestive tracts that contained seeds was  $39.5 \pm 24.8\%$  standard deviation ( $SD$ ). Table 1 shows a list of fish species that consumed seeds, including the total of individuals captured for each species, the percentage found with nonempty guts, and, from those, the percentage that consumed seeds.

During January and February 2014—corresponding to várzea rising water and flood periods—many fishes were found with a variety of food items of animal and plant sources in their guts. However, the consumption of seeds in these 2 months was recorded only for individuals *Triportheus* spp. Seeds consumed during this period belonged to the Poaceae family (wild rice, *Oryza* spp. and “membra” grass, *Paspalum repens*) and were not used for the germination tests. From March on, a modest consumption of seeds of other plant species began, which lasted until August 2014.

Even though *C. macropomum* was the species that consumed the highest number of seeds, *Brycon amazonicus* was responsible for the highest number of plant species consumed. The catfishes *Ageneiosus dentatus*, *Auchenipterus nuchalis*, and *Calophysus macropterus* consumed a lower number of seeds of a few plant species (Figure 2). Chewed seeds were found only in the digestive tract of individuals of *C. macropomum* and *Chalceus erythrus*.

In total, 3,092 whole seeds, belonging to 15 families, 17 genera, and 18 plant species were removed from digestive tracts, with 44.7% obtained from the stomachs and 55.2% from the intestines of the fishes. *Cecropia* spp. ( $n = 1,492$ ) showed the highest number of ingested seeds and the highest frequency of occurrence in the fishes digestive tracts ( $\text{FO} = 28.3\%$ ). *Laetia corymbulosa* ( $n = 259$ ) was the second in frequency of occurrence ( $\text{FO} = 23.4\%$ ), although it represented fewer ingested seeds than *Ficus insipida* ( $n = 893$ ,  $\text{FO} = 17.2\%$ ) and *Tococa cordata* ( $n = 277$ ,  $\text{FO} = 2.1\%$ ; Table 2).

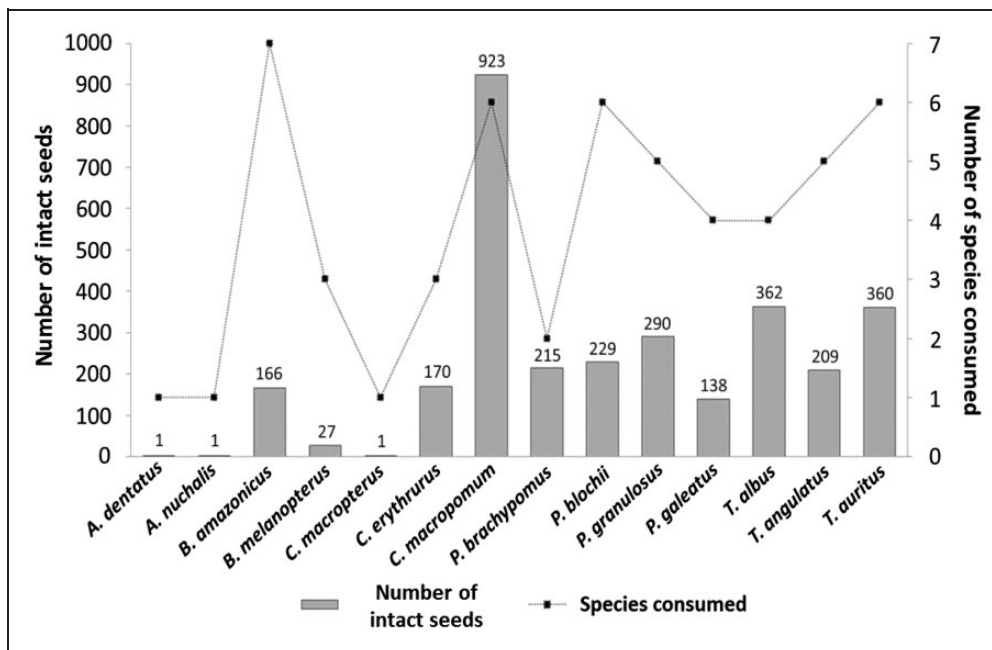
For the experiment in the greenhouse, seeds of three species showed 100% of germination (*Psychotria ernestii*, *Ficus trigona*, and *Cissampelos andromorpha*); eight species had germination rates above 50% (*Cecropia* spp., *Doliocarpus* sp., *Lophantera longifolia*, *Allophyllus amazonicus*, *Alchornea discolor*, *Endlicheria anomala*, *Vitex cymosa*, and *Ficus insipida*); five species showed a percentage of germination below 50% (*Crataeva tapia*, *Macrolobium* sp., *Tococa cordata*, *Nectandra amazonum*, and *Laetia corymbulosa*); and seeds of two species did not germinate during the conduction of the experiment (*Bactris riparia* and *Senna alata*; Figure 3).



**Table 1.** Captured Fish Species That Consumed Seeds.

Order	Family	Fish species	Common name	± SL (mm)	Total	PF (%)	PS (%)
Characiformes	Alestidae	<i>Chalceus erythrus</i> (Cope, 1870)	Arari	203	8	100	37
	Characidae	<i>Brycon amazonicus</i> (Spix & Agassiz, 1829)	Matrinxã	230	25	80	80
		<i>Brycon melanopterus</i> (Cope, 1872)	Jatuarana	220	11	100	36
		<i>Triportheus albus</i> (Cope, 1872)	Sardinha rabo-de-fogo	126	230	86	16
		<i>Triportheus angulatus</i> (Spix & Agassiz, 1829)	Sardinha papuda	139	47	85	37
		<i>Triportheus auritus</i> (Günther, 1864)	Sardinha comprida	145	110	67	36
	Serrasalminidae	<i>Colossoma macropomum</i> (Cuvier, 1818)	Tambaqui	155	62	81	38
		<i>Piaractus brachypomus</i> (Cuvier, 1818)	Pirapitinga	116	4	100	100
Siluriformes	Auchenipteridae	<i>Ageneiosus dentatus</i> (Kner, 1858)	Mandubé	199	28	43	8
		<i>Auchenipterus nuchalis</i> (Spix & Agassiz, 1829)	Mandi-peruano	167	15	60	11
		<i>Trachelyopterus galeatus</i> (Linnaeus, 1766)	Cangati	143	20	70	36
	Doradidae	<i>Pterodoras granulosus</i> (Valenciennes 1821)	Bacu	197	13	100	54
	Pimelodidae	<i>Calophysus macropterus</i> (Lichtenstein, 1819)	Piracatinga	263	3	100	33
		<i>Pimelodus blochii</i> (Valenciennes, 1840)	Mandi	137	45	87	31

Note. Standard length average (±SL) in millimeters with variance around the mean 174 millimeters; Total captured specimens, percentage of fish captured with nonempty guts (PF%, stomach, or intestine), and, of these, the percentage of fish found with seeds (PS%).



**Figure 2.** Total number of intact seeds consumed by 14 fish species (grey bars) and species richness of plants consumed by each fish species (black dots).

## Discussion

The 14 fish species observed with seeds in their digestive tracts in the Catalão lake represent almost 10% of the 150 species known to consume fruits and seeds in wetlands of South America according to Horn et al. (2011). Moreover, the high percentage of individuals with seeds in their digestive tracts (almost 40% of individuals with

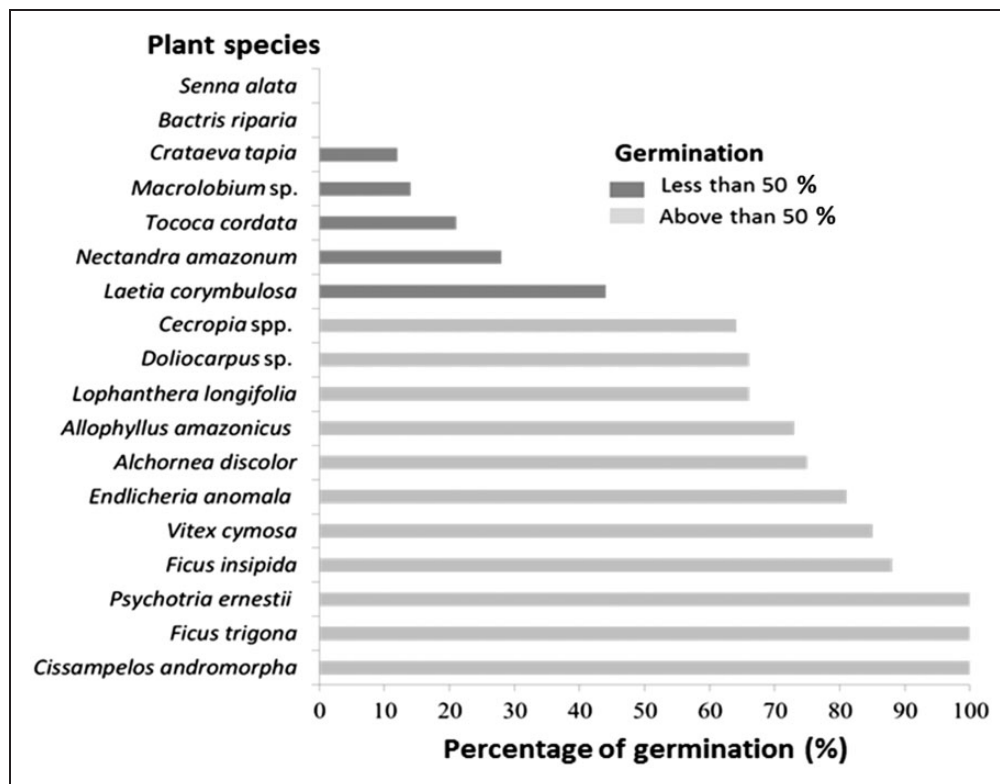
nonempty guts) indicates that fruits and seeds constitute an important portion of the diet of those species during the rising and flood periods. Our results also showed that *T. albus* was the most abundant fish species in the samples and the species that consumed the most seeds, confirming the dominance of this species in experimental fisheries with gillnets in the Catalão lake (Röpke, Amadio, Winemiller, & Zuanon, 2015). This indicates a

**Table 2.** Total Number (*n*) of Plant Species Seeds Removed From the Stomach and Intestine of Fishes.

Family	Plant species	Common name	Digestive tract	
			( <i>n</i> )	FOi (%)
Areaceae	<i>Bactris riparia</i> Mart.	Pupunharana	11	2.8
Caparidaceae	<i>Crataeva tapia</i> L.	Catoré	16	2.1
Dilleniaceae	* <i>Dolioscarpus</i> sp.	Cipó de fogo	3	0.7
Euphorbiaceae	<i>Alchornea discolor</i> Poepp.	Supiarana	4	2.8
Fabaceae	<i>Macrolobium</i> sp.	Arapari	14	0.7
Fabaceae	<i>Senna alata</i> (L.) Roxb.	Mata pasto	3	0.7
Lauraceae	<i>Endlicheria anomala</i> (Nees) Mez	Louro	11	2.1
Lauraceae	<i>Nectandra amazonum</i> Nees	Louro	7	3.4
Malpighiaceae	<i>Lophanthera longifolia</i> (Kunth) Griseb.		3	1.4
Melastomataceae	<i>Tococa cordata</i> Berg ex Triana		277	2.1
Menispermaceae	* <i>Cissampelos andromorpha</i> DC.		2	1.4
Moraceae	<i>Ficus insipida</i> Willdenow	Caxinguba	893	17.2
Moraceae	<i>Ficus trigona</i> L.f.	Apuí	50	0.7
Rubiaceae	<i>Psychotria ernestii</i> K.Krause		2	0.7
Salicaceae	<i>Laetia corymbulosa</i> Spruce ex Benth.	Sardinheira	259	23.4
Sapindaceae	<i>Allophylus amazonicus</i> (Mart.) Radlk.		38	4.8
Urticaceae	<i>Cecropia</i> spp.	Imbaúba	1.492	28.3
Verbenaceae	<i>Vitex cymosa</i> Bertero ex Spreng.	Tarumã	7	4.8

Note. FOi = % frequency of occurrence of plant species in the digestive tracts of fishes with nonempty guts.

\*Vine Species.



**Figure 3.** Percentage of germination for each plant species of seeds obtained from the stomach or intestine of fishes captured in the Catalão lake between March and August 2014.

good representativeness of our sampling during the filling and flood periods of 2014.

The consumption of seeds of woody species and of one species of vine began in the rising water period (March), following the fruit production period of the flooded forest trees. Fruit and seed consumption gradually intensified up to August, and then reduced when the water level started to decrease (Schöngart et al., 2002). In general, the flowering of várzea trees occurs between September and October, when precipitation is less intense in Central Amazon. After this period, in the beginning of subsequent year, precipitation increases and fruits start the growing process. However, the duration of the fructification process during the high water period is possibly related to phenological aspects of each species (Kubitzki & Ziburski, 1994) and can be affected by prolonged periods of flooding or drought (Ferreira et al., 2010).

Seeds of *Cecropia* spp. were the most frequently consumed by fishes. Species of this genus bear fruits during almost the whole aquatic phase of the lowlands and show an infructescence composed of numerous tiny seeds (Parolin, 2002), which could explain the high proportion of consumed seeds (Anderson et al., 2009; Gottsberger, 1978; Pilati, Andrian, & Carneiro, 1999; Reys, Sabino, & Galetti, 2009). The consumption of certain fruits and seeds by fishes is probably influenced by the smell and the sound produced when they drop into the water (Araujo-Lima & Goulding, 1998). Moreover, changes in plant cover can also influence the availability of fruits and seeds for the fishes. Claro-Jr et al. (2004) related a high consumption of *Cecropia* seeds by fishes to the presence of deforested areas and loss of original vegetation cover in eight várzea lakes along the Central Amazon. This is similar to what occurs in other várzea areas, especially in the eastern Amazon and around large cities of the Brazilian Amazon, such as Itacoatiara, Manaus, and Tefé. Deforestation and the selective removal of trees, as well as the extensive exploration of these areas for agricultural purposes are causing a significant reduction in some populations of tree species (Wittmann & de Oliveira Wittmann, 2010). Species of *Cecropia* are considered pioneer species that colonize recently deforested areas; thus, the opening of clearings increases the availability of light and favors the establishment of these plants in great abundance.

The fish species that consumed seeds of the highest number of plant species were *B. amazonicus*, *C. macropomum*, *T. auritus*, and *P. blochii*. Although *B. melanopterus* and *B. amazonicus* have shown only intact seeds in their digestive tracts, an analysis carried out by Correa et al. (2015) recorded seed predation (chewed) by these species and also by *Brycon falcatus* and highlighted smaller seed destruction rates for seeds surrounded by fleshy pulp. According to Souza (2005), *B. amazonicus* may have a more effective role as a seed disperser rather than as

predator, since only 13% of the seeds ingested by the 164 individuals analyzed had been broken, whereas for *C. macropomum*, the percentage was 72% (274 specimens analyzed). However, the size of the specimens used in that study was not stated. Other studies also pointed out species of *Brycon* as important fruit consumers and seed dispersers (Correa & Winemiller, 2014; Piedade et al., 2006; Reys, Sabino, & Galetti, 2009).

*Piaractus brachypomus* was the only species of Characiformes in which all fish captured had seeds in the digestive tract. A study carried out by Correa, Betancur-R, de Mérona, and Armbruster (2014) showed that fruits and seeds are the dominant items in the diet of this species during the flood period, since young and adult specimens are highly adapted to exploit this food source (Lucas, 2008). The contribution to the seed dispersal by *P. brachypomus* and *C. macropomum* was investigated by Anderson et al. (2009) in an area of flooded forest in Peru. They found that, together, these two fish species disperse seeds of tree species such as *Cecropia latiloba* and some species of vines, totaling 35% of the plant species of that area. For this study, two species of vines, *Doliocarpus* sp. and *C. andromorpha* were found in the fish digestive tracts.

Some studies were conducted in order to identify the efficiency of fish as seed dispersers. These studies attribute to young *C. macropomum*, a greater propensity to grind the seeds with its molariform dentition, whereas the adults are able to swallow the seeds whole and intact, possibly due to the larger size of the mouth opening in relation to the size of ingested seeds (Anderson et al., 2009; Kubitzki & Ziburski, 1994; Piedade et al., 2006). In this study, from the 50 specimens of *C. macropomum* captured with nonempty food in their digestive tracts, 10% contained chewed ground seeds. All specimens were young, with a mean standard length around 155 mm (Araujo-Lima & Goulding, 1998). The almost exclusive capture of small-sized specimens of *C. macropomum* possibly reflects the occurrence of historical overfishing in the study area. This process may directly affect the efficiency of *C. macropomum* as a seed disperser, once bigger fish individuals apparently cause less damage to the seeds and are also able to disperse a greater diversity of plant species (Correa et al., 2015). From the eight captured specimens of *C. erythrusus*, 25% also showed damaged seeds in their digestive tracts. This species has three sets of several multicuspidate teeth in the premaxillaries (Queiroz, Torrente-Vilara, Ohara, Pires, Zuanon, & Doria, 2013), which may facilitate breaking the seeds before swallowing.

Goulding (1980) recorded the consumption of seeds of *Paullinia* sp., *Astrocaryum jauari*, and *Cecropia* spp. by the catfish *P. blochii*. Although experiments to test germination and viability of those seeds were not carried out by the author, he considered *P. blochii* as an important seed

disperser of those plant species. Souza-Stevaux et al. (1994) confirmed through germination tests that *Pterodoras granulosus* is able to excrete viable seeds of genera *Ficus*, *Cecropia*, and *Polygonum* in the Paraná River basin. After doing germination tests with seeds taken from the digestive tracts of some specimens of *P. granulosus*, Pilati et al. (1999) also concluded that this species can be an important disperser of *Cecropia pachystachya*.

Overfishing is causing the reduction in size of frugivorous catfishes (Correa et al., 2015). Several species of catfish have large mouths, some of them without teeth, making them more prone to swallow whole seeds that are regurgitated or expelled apparently intact (Piedade et al., 2006). Moreover, they are excellent long-distance migrators (Queiroz et al., 2013), which may allow seed dispersal to long distances from the mother plants. However, some other factors of both species—plant and fish—may play important role in the process (Pollux, 2010). Additionally, the reduction of catfish size may be leading to the exploitation of some other large-sized frugivore fish species (Correa et al., 2015), which may further impair seed dispersal by fish in floodplains.

Finally, the potential role of *P. blochii* and *P. granulosus* as seed dispersers should be noted, since they were able to consume seeds of five and six plant species, respectively. Besides, three other catfishes (*A. dentatus*, *A. nuchalis*, and *C. macropterus*), which are not predominantly frugivores, also consumed a smaller number of seeds. Although they should not be considered as important seed dispersers, they may also help in the distribution of some trees along the floodplains.

Our study showed that most of the seeds consumed by the examined fish are able to germinate. From the 18 plant species whose seeds were found in the fishes' digestive tracts, 16 germinated and only 2, *S. alata* and *B. riparia*, did not germinate. *S. alata* is a pioneer species of rapid colonization, requiring a short time for germination (Parolin, 2001). Since seeds of this species did not germinate until the end of the 210 days of this experiment, they probably were not viable. For *B. riparia*, the lack of germination could also indicate that the tested seeds were not viable. However, it is known that *Bactris* species may require varying dormancy periods, which can last from 6 weeks to 14 months, depending on the species (Mora Urpi, 1979). Thus, even after the seed is excreted, seed germination of these palms probably depends on many other factors related to the morphology and physiology of the plant, to the disperser's manipulation of the propagule, and to the environmental conditions of the area where the seed was deposited (Schupp, 1988).

Some of the fish species found in this study exhibit short- to long-distance migratory habits, including *C. macropomum*, *B. amazonicus*, *B. melanopterus*, *P. brachypomus*, *P. granulosus*, *P. blochii*, *T. albus*, *T. angulatus*,

and *T. auritus* (Araujo-Lima & Ruffino, 2003; Menezes & Vazzoler, 1992; Oliveira & Ferreira, 2002). In South American rivers, there is a high number of fish species that perform reproductive or trophic migrations (Araujo-Lima & Ruffino, 2003), including species of Characiformes and Siluriformes. Individuals may migrate over long distances for reproductive purposes, which frequently occur at the beginning of the flood period. They can also move upriver inside the flooded forests, and then move downstream during the low water period after spawning (Goulding, 1980). The consumption of seeds by migratory species and the observed seed viability of most species after passing through the fish digestive tract suggest that fish may play an important role as long-distance disperser vectors, particularly for areas upstream from the mother plant, where hydrochoric dispersal would not be able to conduct the seeds.

## Implications for Conservation

Human populations inhabiting the floodplains of Amazonian rivers were able to adjust their use strategies and management of natural resources between the flood and low water periods (Junk & Piedade, 2010). When the flood reduces the area available for agriculture, fishing usually becomes the most important source of income. In the studied area (Catalão lake), fish stocks have been exploited intensively in the last decades. Between the 1930s and 1950s, this process was accelerated by the introduction of new fishing technologies that facilitated fish capture, such as synthetic fiber gillnets and nylon fishing lines (Lowe-McConnell, 1999). Especially in the last 30 years, pressure on fish stocks in Amazon floodplains has also increased due to the loss of vegetation cover, which is a result of changes in the local economy, the expansion of cattle raising (Castello et al., 2013; McGrath, de Castro, Câmara, & Futemma, 1999), and rapid regional population growth (Junk, 1982). Based on fisheries data, Barthem and Goulding (1997) reported a decrease around 50% in the total capture of fishes that consume fruits and seeds since the 1970s. Other recent studies in floodplains show marked decreases in frugivorous fish population that could cause an imbalance in seed dispersal (Correa, Costa-Pereira, Fleming, Goulding, & Anderson, 2015; Correa et al., 2016; Costa-Pereira & Galetti, 2015). It is important to emphasize that human activity such as deforestation of the floodplains can cause strong impacts on the food habits of fishes that use fruits and seeds as major food resources. Therefore, this can compromise not only fish stocks but also impair seed dispersal by fish that may further decrease the populations of floodplain trees. Taken together, those factors can affect local and regional human populations for whom the consumption of fish constitutes the main source of animal protein in the diet.



## Appendix. Plant species that were found in the digestive tract of the studied fish species

Plant species	Fish species															
	C. erythrurus	B. amazonicus	B. melanopterus	T. albus	T. angulatus	T. auritus	C. macropomum	P. brachypomus	A. dentatus	A. nuchalis	T. galeatus	P. granulosus	C. macropterus	P. blochii		
<i>B. riparia</i>		X									X	X				
<i>C. tapia</i>							X					X				
<i>Doliocarpus</i> sp.						X										
<i>A. discolor</i>					X		X							X		
<i>Macrobium</i> sp.								X								
<i>S. alata</i>			X													
<i>E. anomala</i>				X		X						X				
<i>N. amazonum</i>		X								X				X		
<i>L. longifolia</i>	X	X														
<i>T. cordata</i>					X		X									
<i>C. andromorpha</i>							X									
<i>F. insipida</i>		X		X	X	X	X	X		X	X	X		X		
<i>F. trigona</i>														X		
<i>P. ernestii</i>			X													
<i>L. corymbulosa</i>				X	X	X								X		
<i>A. amazonicus</i>		X				X										
<i>Cecropia</i> spp.	X	X	X	X	X	X	X		X		X			X		
<i>V. cymosa</i>	X	X										X	X			

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