



Fishing-down within populations harms seed dispersal mutualism

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ABSTRACT

Large fish are often the most effective seed dispersers, but they are also the preferred target for fisheries. We recently started to comprehend the detrimental impacts of the extirpation of large frugivorous fish species on natural forest regeneration, but we lack a general understanding of how intraspecific size-selective harvest affects fish–fruit mutualism. Our literature review demonstrated that large individuals within populations positively affect diverse aspects of seed dispersal, from consuming a higher diversity of seeds to enhancing germination. Furthermore, we filled a research gap by studying how individual size variations within two small frugivorous fish species (<16 cm) affect seed dispersal in flooded savannas. Even within small-bodied species, large individuals swallow a higher number of intact seeds, but not necessarily a higher proportion. Overall, our results demonstrate the disproportional role of large-bodied individuals as key seed dispersers in flooded habitats. Consequently, fishing-down within both large- and small-bodied species can negatively affect seed dispersal and natural regeneration in overfished wetlands.

Abstract in Spanish is available with online material.

Key words: body size; downsizing; floodplain; frugivory; ichthyochory; overfishing; Pantanal; size-selective harvesting.

DEFAUNATION, THE LOCAL OR GLOBAL EXTINCTION OF ANIMAL SPECIES (sensu Dirzo *et al.* 2014), POSES A MAJOR THREAT TO BIODIVERSITY (Young *et al.* 2016). Only recently, it became apparent that the functional loss of terrestrial vertebrates (particularly birds and mammals) leads to the disruption of ecological interactions and ecosystem functions in ‘empty forests’ (Anderson *et al.* 2011b, Galetti *et al.* 2013). However, the negative consequences of overharvesting mutualistic animals are not restricted to terrestrial organisms. Commercial and recreational operations remove billions of tons of fish annually from oceans and inland waters worldwide (Allan *et al.* 2005, McCauley *et al.* 2015).

Overfishing is pervasive in Neotropical freshwater ecosystems (Isaac & Ruffino 1996, Castello *et al.* 2013). The overexploitation of large fish leads to changes in population structure and dynamics and ultimately, to local extinctions (Castello *et al.* 2015). As an immediate response to depletion, fishermen expand their targets to small-bodied, abundant species, a process known as fishing-down the food web (Pauly *et al.* 1998). In marine ecosystems, the negative consequences of fishing-down are relatively well-known, resulting in trophic cascades and changes in ecosystem functions (Worm *et al.* 2006). In freshwater ecosystems, however, the lack of long-term data on fish landings and size of fish stocks makes it difficult to quantify and predict the consequences of overfishing (Allan *et al.* 2005).

Although neglected in classic studies of seed dispersal, we now know that freshwater fishes are important seed dispersers, consuming the fruits of ~600 Neotropical plant species (Correa *et al.* 2015a,b). Many trees concentrate their fruiting period during the flooding season, making fruits and seeds available to fish in floodplains (Parolin *et al.* 2004). Interestingly, big fish species are disproportionately more effective seed dispersers than smaller species: they carry numerous, diverse, large-sized intact seeds over long distances (Correa *et al.* 2015b). However, beyond interspecific size variations, intraspecific variations also influence seed dispersal.

Galetti *et al.* (2008) demonstrated that larger size classes within a species of fruit-eating fish are more effective seed dispersers than smaller ones, a hypothesis first proposed by Goulding (1980). Other studies have investigated this relationship, providing insights into how intraspecific size variations affect seed dispersal; however, most studies have focused on a single target species and a single facet of seed dispersal. Thus, the generality of this pattern remains unclear. As larger individuals are expected to be the most effective seed dispersers and the preferred targets of fisheries, size-selective overharvesting threatens seed dispersal mutualism in flooded forests (Correa *et al.* 2015a).

Most studies on ichthyochory in natural habitats have focused on conspicuous, large-bodied frugivorous fish species, such as tambaqui (*Colossoma macropomum*) and pacu (*Piaractus* spp.). However, small-bodied species also consume many fruits and play an important role as dispersers of small-seeded plants, particularly in shallow-flooded habitats (Costa-Pereira *et al.* 2011,

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Silveira & Weiss 2014). Small freshwater fish can be threatened by extinction as much as large ones (Olden *et al.* 2007) and because of their shorter lifespan, intense harvesting can quickly bias population size (Nusslé *et al.* 2016). In particular, some small-bodied frugivorous species (*e.g.*, *Triportheus*, *Myloplus*, *Mylossoma*) are widely used as food (for humans or domestic animals) and live bait across South America (Junk 1984, Fabr e & Alonso 1998).

It is increasingly evident that fishing-down within-populations has detrimental effects on fish–plant interactions. However, we lack a general understanding of how individual fish size affects seed dispersal efficiency. Here, we combined a literature review and empirical data to elucidate how within-population differences in fish size influence seed dispersal effectiveness: (1) we reviewed the literature, testing the hypothesis that fish size affects quantitative and/or qualitative facets of seed dispersal; and (2) we investigated whether the pattern of larger individuals swallowing more and higher proportion of intact seeds, which is commonly observed among large-bodied species, extends to small-bodied species. We hypothesize that even narrow size ranges of variation among small-sized fish species can impose gape limitation and affect quantitative components of seed dispersal effectiveness for small-seeded plants. Finally, we discuss conservation implications of size-selective harvest on fish–plant mutualistic interactions.

METHODS

LITERATURE REVIEW.—We conducted a search in Google Scholar with the key words fruit-eating fish, ichthyochory, fish frugivory, fruit fish diet, seed fish diet, and body size. We selected articles that statistically investigated the relationship between intraspecific body size and some aspect of seed dispersal. We classified seed dispersal effectiveness into six categories: (1) proportion of fruit in the diet relative to other food types; (2) presence, number, and/or volume of intact seeds in gut contents; (3) proportion of intact seeds in gut contents relative to seeds destroyed by mastication; (4) seed richness; (5) seed dispersal distance; and (6) germination success. We coded the reported effects of increased body size on these components as positive (+), negative (-), or null (0).

SEED DISPERSAL BY SMALL FISH SPECIES.—To investigate if the relationship between body size and quantitative components of seed dispersal (*i.e.*, number and proportion of swallowed intact seeds) holds true for small-bodied species, we studied two characids inhabiting seasonally flooded savannahs in the Pantanal wetland: the tetra *Astyanax lacustris* (up to 120 mm standard length [SL]) and the freshwater sardine *Triportheus nematurus* (up to 180 mm SL). These species patrol trees dropping ripe fruits, which constitute a substantial proportion of their diet during the flood season (Costa-Pereira *et al.* 2011, 2017b). Both species are consumed locally and commonly used as bait for recreational and commercial fisheries.

We captured individuals of *A. lacustris* using cast nets and *T. nematurus* using barbless hooks on the Miranda River

floodplain, Mato Grosso do Sul, Brazil (19°34'36" S, 57°01'06" W) for 4 days during the flood season (May 2011). We killed fish by overdosing them with clove oil and measured body size (SL) and gape width using a digital caliper (0.1 mm precision). We analyzed gut contents under a stereomicroscope and counted the number of intact and masticated seeds. These are key quantitative aspects of seed dispersal effectiveness (Schupp *et al.* 2010).

Cecropia pachystachya (Cecropiaceae) and *Banara arguta* (Salicaceae) were, respectively, the most abundant fruits consumed by *A. lacustris* (70% of the individuals) and *T. nematurus* (84%); thus, our analysis focused on these species. We modeled the number of intact seeds and the proportion of intact seeds (intact seeds/intact + masticated seeds) in gut contents as a function of fish size (SL), species, and their interaction via separated negative binomial regressions in the R package *MASS* (R Development Core Team 2017). Prior to analyses, we beta-transformed the proportional data (beta transformation = $p \times (N - 1) + 0.5$)/ N , where n = sample size) to reduce it to a range between 0 and 1. *P*-values were obtained using Type III Wald Chi-square tests in the R package “car” (Fox & Weisberg 2011).

RESULTS

We found 13 studies in the literature that presented results for 39 statistical tests on the relationship between intraspecific body size variation and aspects of seed dispersal effectiveness for 15 fish species. Most (87.18%, $N = 34$) tests found a positive effect of

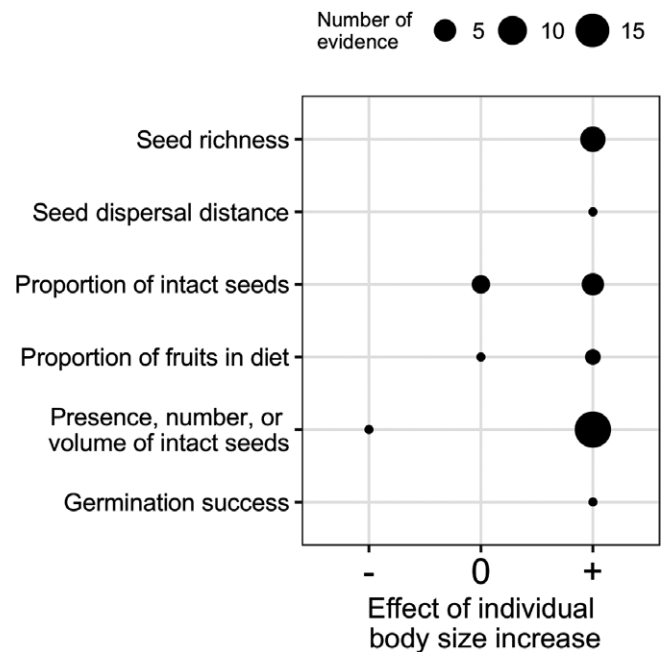


FIGURE 1. Predominantly positive effects (+) of individual body size within-species on different aspects of seed dispersal by fish. The size of each point is proportional to the number of statistical tests presented in Table 1.

TABLE 1. Increases in intraspecific body size positively affect different aspects of seed dispersal effectiveness. We obtained data on max length from FishBase (Froese & Pauly 2017). The effect of increased individual fish body size on these aspects is represented as positive (+), negative (−), or null (0).

Fish	Fruit/seed	Max length (cm)	Proportion of fruits in diet	Presence, number, or volume of intact seeds	Proportion of intact seeds	Seed richness	Seed dispersal distance	Germination success	Reference*
<i>Ictalurus punctatus</i>	Many	132		+					1
<i>Cyprinus carpio</i>	Many	120		−					2
<i>Colossoma macropomum</i>	Many	108			+				3
<i>Colossoma macropomum</i>	Many	108		+	0				4
<i>Colossoma macropomum</i>	Many	108		+				+	5
<i>Colossoma macropomum</i>	Many	108					+		6
<i>Litbodoras dorsalis</i>	Many	100		+					7
<i>Piaractus brachypomus</i>	Many	88		+	0				4
<i>Piaractus brachypomus</i>	Many	88		+					5
<i>Piaractus mesopotamicus</i>	<i>Bactris glaucescens</i>	75		+					8
<i>Piaractus mesopotamicus</i>	Many	75		+	+	+			9
<i>Brycon bilarii</i>	Many	56		+		+			10
<i>Hephaestus fuliginosus</i>	Many	54	+						11
<i>Brycon amazonicus</i>	Many	46.2			+	+			9
<i>Brycon amazonicus</i>	Many	46.2		+					12
<i>Leporinus friderici</i>	<i>Banara arguta</i>	40		+	+				13
<i>Brycon melanopterus</i>	Many	38				+			9
<i>Brycon melanopterus</i>	Many	38		+					12
<i>Brycon falcatus</i>	Many	37		+					12
<i>Myloplus torquatus</i>	Many	28		+		+			9
<i>Mylossoma duriventre</i>	Many	25		+		+			9
† <i>Triportheus nematurus</i>	<i>Banara arguta</i>	18.3		+	0				14
<i>Myloplus tiete</i>	Many	16	0	+		+			9
† <i>Astyanax lacustris</i>	<i>Cecropia pachystachya</i>	15	+	+	+				14

*References: 1) Adams *et al.* (2007), 2) Boedeltje *et al.* (2015), 3) Kubitzki & Ziburski (1994), 4) Lucas (2008), 5) Anderson *et al.* (2009), 6) Anderson *et al.* (2011a), 7) Barbosa & Montag (2017), 8) Galetti *et al.* (2008), 9) Correa *et al.* (2015a), 10) Reys *et al.* (2009), 11) Davis *et al.* (2010), 12) Correa *et al.* (2015b), 13) Costa-Pereira *et al.* (2011), 14) this study.

†Empirical data presented in this study.

fish size on quantitative aspects of seed dispersal effectiveness (Fig. 1, Table 1). Specifically, our literature review indicated that increases in size positively affected the (a) proportion of consumed fruits relative to other food types (2 positive effects/3 tests), (b) the amount (presence, number, or volume) of intact seeds in guts (18/19), (c) the proportion of intact relative to masticated seeds (5/8), (d) seed richness (7/7), (e) seed dispersal distance (1/1), and (f) germination success (1/1) (Table 1). Increases in fish size had a null effect on seed dispersal in only four tests (10.25%) and decreased seed dispersal effectiveness in only one (Fig. 1; Table 1).

We retrieved 1096 *B. arguta* seeds from freshwater sardines ($N = 51$, 72.6–155.3 mm SL), 63 percent of which were masticated, and 321 *C. pachystachya* seeds from tetras ($N = 63$, 46.92–82.71 mm SL), 22 percent of which were masticated. The mean number of intact seeds dispersed by individual fish was higher for *B. arguta* (mean = 11.22, SD = 9.70, max = 41) relative to *C. pachystachya* (mean = 8.72, SD = 7.84, max = 33) (Costa-Pereira *et al.* 2017a). In addition to *C. pachystachya*, tetras also dispersed few intact seeds

of *Trichilia* sp., *B. arguta*, and Malvaceae gen. sp., whereas *B. arguta* was the only species consumed and dispersed by sardines.

The number of intact seeds increased with fish size for both species (Fig. 2, Table 2). There was no significant effect of species on the number of intact seeds ($P = 0.25$), suggesting that this pattern is consistent for both species. However, the pattern for proportion of intact seeds relative to all seeds consumed is more complex. We found a significant effect of the interaction between species and body size on the proportion of intact seeds ($P = 0.02$), but not an individual effect of body size ($P = 0.25$) or species ($P = 0.13$) (Table 2). The proportion of intact *C. pachystachya* seeds clearly increased with body size for *A. lacustris*, but the opposite pattern (with much larger variability) was observed for the consumption of *B. arguta* by *T. nematurus* (Figs 2 and S1).

DISCUSSION

Size-selective harvest can result in quick demographic changes, shifting population size structure and influencing species

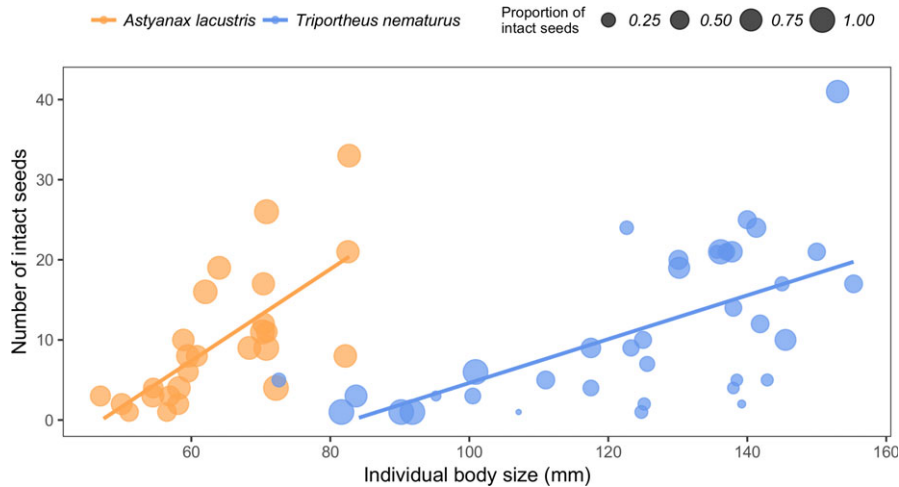


FIGURE 2. The number of intact seeds increases with individual body size ($R^2 = 0.39$) for two small fish species in the Pantanal wetland, but the proportion of intact seeds (represented by point size) shows different responses to interspecific body size.

TABLE 2. Individual body size, species identity, and their interaction affect the number and proportion of intact seeds swallowed by two fish species in the Pantanal wetland. Bold values indicate significant effects ($P < 0.05$)

Fixed effect	df	Number of intact seeds		Proportion of intact seeds	
		χ^2	<i>P</i>	χ^2	<i>P</i>
Species	1	1.32	0.25	2.34	0.13
Body size	1	34.48	<0.0001	1.37	0.25
Species * Body size	1	6.39	0.01	5.70	0.02

interactions (Pérez-Méndez *et al.* 2015, McConkey & O’Farrill 2016). Although we have begun to understand how selective harvest affects seed dispersal by freshwater fish (Correa *et al.* 2015a, b), the detrimental effects of fishing-down within populations remain unclear. We addressed this issue by reviewing the literature to understand how individual body size relates to seed dispersal efficiency. We found that larger individuals within populations are more effective seed dispersers than smaller ones, both qualitatively and quantitatively. Furthermore, as most studies have focused on large-bodied frugivorous fish, we used empirical data from a Neotropical wetland to investigate if a similar pattern holds true for small fish species. We observed that even within small-bodied species, large individuals swallow a higher number of intact seeds, but not necessarily a higher proportion. Our findings provide new insights into the negative effects of size-selective overharvest on seed dispersal by fish. This key role of large-bodied individuals on seed dispersal dynamics has important ecological and conservation implications.

WITHIN-SPECIES SIZE VARIATION AND SEED DISPERSAL EFFICIENCY.—Our results reinforce the long-standing hypothesis that body size

influences seed dispersal by fish (Gottsberger 1978, Goulding 1980). However, our literature review indicated that large-bodied individuals might play an even more important role than previously thought, because size not only affects the number of consumed seeds (Galetti *et al.* 2008), but also quantitative and qualitative aspects of seed dispersal. Overall, bigger individuals within populations consume more fruits, masticate a lower proportion of seeds, and swallow more seeds intact, enhancing germination success and dispersing seeds over longer distances.

Life-history aspects of frugivorous fish explain the positive effect of size on quantitative and qualitative aspects of seed dispersal. Large individuals have higher demands for energy, particularly during the reproductive season when their diet can be composed of more than 90 percent fruits in flooded forests (Goulding 1980). Large fish also have longer retention times, which may influence germination success and dispersal distance (Anderson *et al.* 2011a). Moreover, larger individuals have wider mouths, increasing the likelihood of swallowing intact seeds across a broad range of sizes (Anderson *et al.* 2009, Correa *et al.* 2015b).

Beyond biomechanical mechanisms, ontogenetic changes in foraging behavior can also lead to differences in seed dispersal effectiveness (Adams *et al.* 2007). For instance, underwater observations revealed that adult *Leporinus friderici* ingest whole *B. arguta* fruits, whereas young individuals consume small fragments, even if their gape size is sufficient to swallow whole fruits (Costa-Pereira *et al.* 2011). Dietary ontogenetic changes in fruit-eating fish are well documented, where individuals shift from an insectivorous to a frugivorous diet (Goulding 1980, Cotta-Ribeiro & Molina-Ureña 2009). Curiously, these dietary changes are coupled with shifts in the production of digestive enzymes to break down carbohydrates (Drewe *et al.* 2004), which could also affect qualitative aspects of seed dispersal (*e.g.*, germination success).

In only one case, increases in individual size led to a decrease in seed dispersal effectiveness. In a feeding experiment,

Boedeltje *et al.* (2015) found that, as carps (*Cyprinus carpio*) grew, increased bite force reduced seed survival. Therefore, seed dispersal efficiency may not only depend on gape size, but also on other morphological and physiological traits that covary with body size (*e.g.*, dentition and jaw morphology, bite force, digestive capability); this is an important aspect that should be investigated in future studies.

INDIVIDUAL SIZE AND SEED DISPERSAL IN SMALL-BODIED FISHES.—The positive relationship between individual fish size and the number of seeds swallowed intact is widely supported in the literature for large- and medium-bodied species (Table 1). Interestingly, our empirical data indicate that this same pattern can be observed in small frugivorous fish species. Thus, even within populations of small-bodied species (<16 cm) with a substantially narrower intraspecific body size range, fish size affects the total number of seeds swallowed intact. This pattern suggests that size-selective harvest affects seed dispersal by small-bodied frugivorous species.

Our empirical results reveal that the rates of seed mastication appear to be context dependent. While we found the expected positive relationship between body size and the proportion of intact seeds for the tetra *A. lacustris*, this relationship was not apparent for the freshwater sardine *T. nematurus*. Instead, the proportion of intact seeds consumed by *T. nematurus* greatly fluctuated across body sizes (Fig. S1), as reflected in the small amount of variation explained by the regression ($R^2 = 0.06$). Other factors besides body size, including intra and interspecific variation in fruit and seed size or seed coat hardness and intraspecific differences in foraging behavior (Costa-Pereira *et al.* 2011), might influence seed predation rates. How mastication rates change across fish species and fruit and seed traits is unknown. Most studies evaluating seed dispersal by fish focused on one or two fish species (Table 1). Thus, future studies should follow a community approach, tracing changes in fruit availability across years, intra and interspecific variation in fruit and seed traits, and individual variation in foraging behavior. Such an approach would better illuminate the complexity and context-dependency of fish–fruit interactions.

IMPLICATIONS FOR FISH–PLANT MUTUALISMS IN FLOODED FORESTS.—The harvest of fish populations is a nonrandom process, since humans usually target larger individuals. Size-selective harvest of historically overfished large-bodied Neotropical frugivorous species, such as *Colossoma macropomum* and *Piaractus* spp., has likely reduced population sizes and potentially shifted size structure toward smaller individuals (Costa-Pereira & Galetti 2015). Our review suggests that downsized populations might have a lower seed dispersal potential, both in qualitative and quantitative terms. Thus, the maintenance of large individuals within populations is important to promote natural forest regeneration dynamics in floodplains. An interesting way to achieve this goal would be to legally establish a maximum size limit for capture of frugivorous fishes, in addition to the current minimum size limits (Correa *et al.* 2015b). This management strategy has been implemented for few species and locations in Brazil and Argentina (Costa-

Pereira & Galetti 2015); however, it needs to be broadly expanded to improve size structure and the seed dispersal potential of wild populations.

Our results indicate that size-selective harvest of small-bodied fish species used as bait or food can negatively affect natural forest regeneration. Worryingly, small-bodied fish species are poorly represented in inland fisheries statistics and are not protected by fishing regulations in Neotropical countries. These species likely play a significant role as seed dispersers of small-seeded plants (Correa *et al.* 2015b), many of them pioneer species triggering ecological succession (*e.g.*, *Cecropia*). This can be particularly relevant in highly impacted and/or grassy areas, where natural roosts for birds and bats are scarce, decreasing the likelihood of seed dispersal by these animals. For example, shallow streams and lowland areas have historically suffered clearance in South America, and small generalist-frugivorous fish can exhibit high abundances in these impacted habitats (*e.g.*, *Astyanax*) (Lorion & Kennedy 2009, dos Santos *et al.* 2015).

CONCLUSION

At the interspecific scale, the disproportional importance of larger fish species in seed dispersal networks compared to small ones was recently demonstrated (Correa *et al.* 2016). Here, we added a new level of complexity to this pattern, showing that intraspecific size variations also affect quantitative and qualitative aspects of seed dispersal by fish. These findings support the recently debated idea of cryptic function loss: seed dispersal effectiveness can be disrupted due to changes in population structure, even though the species is still present in the system (Pérez-Méndez *et al.* 2015, Valiente-Banuet *et al.* 2015, McConkey & O’Farrill 2016). Overall, our results call attention to the negative impacts of fishing-down and size-selective harvest on seed dispersal in wetlands.

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DATA AVAILABILITY

Data available from the Dryad Repository: <https://doi.org/10.5061/dryad.f6p6r> (Costa-Pereira *et al.* 2017a,b).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

FIGURE S1. Proportion of intact seeds increases with individual body size for *Astyanax lacustris*, but not for *Triportheus nematurus*, in the Pantanal wetland.

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