Insights

Seed consumption by small fish follows peak seed availability in a tropical dry forest river

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Abstract
We evaluated seed consumption by fish in an altered tropical dry forest river in Mexico. Non-natives fishes more than natives ingested significantly more seeds in the rainy season. Fishes follow the peak of seed availability after a flood pulse released them from the soil seed banks.

Abstract in spanish is available with online material

KEYWORDS
Amacuzac River, Balsas River Basin, dry deciduous forest, non-native species, freshwater ecosystem, ichthyochory, riparian Corridors, Seasonal Variation, seed ecology

1 INTRODUCTION

Consumption of fruits by fishes is a widespread interaction (Anderson et al., 2009; Mendes Araujo et al., 2020) that influences reproductive dynamics of plant communities in riparian and floodplain habitats of tropical regions (Correa et al., 2015). Many trees in Amazonian floodplains have adapted to concentrate their fruiting period during the flooding season, making fruits and seeds available to fish (Parolin et al., 2004). In turn, physiological, morphological, and behavioral adaptations in fish correlate with the consumption of fruits and seeds (Correa et al., 2007; Costa-Pereira et al., 2011; Drew et al., 2004). Although large-bodied frugivorous fish species are commonly the effective seed dispersers (Anderson et al., 2009; Correa, Costa-Pereira, et al., 2015; Galetti et al., 2008), small- or medium-sized fishes play an important role as dispersers of small-seeded plants (Costa-Pereira et al., 2011, 2017; Silveira et al., 2019; Silveira & Weiss, 2014).

Seed consumption and dispersal by fish have been more extensively described in natural Neotropical large river systems of Amazonia, where ichthyochory follows a seasonal gradient associated with a flood pulse that creates long-lasting seasonally flood zones (Wantzen et al., 2002). This is important in maintaining the plant community structure of wetlands (Correa et al., 2007), and seasonal inundated floodplains (Anderson et al., 2009, 2011), but its effects on plant communities in seasonal dry forests are largely unknown. The Amacuzac hydrological system, which runs through one of the most extensive seasonal tropical dry forests of Central Mexico, shows the concurrence of two interesting environmental and ecological characteristics. One is a marked climatic seasonality, which in turn determines a transient increase in river flow and its potential to overflow, resulting in a drag effect on banks, and in the river carrying three times more seeds in the rainy than in the dry season (Esper-Reyes et al., 2018). Therefore, we hypothesize that rates of seed consumption by fish would correspondingly increase during rainy seasons.
The other peculiar characteristic of the system is the coexistence of native and non-native fish species. The presence of non-native fish is due to the fact that the middle part of the Amacuzac river receives discharges from four tributaries that cross important urban, industrial, and agricultural districts as well as an extensive network of ornamental fish farms (Ortega et al., 2009; Ramírez et al., 2010). The improper handling and the escape of fish into adjacent rivers have drastically changed the fish fauna over the last 100 years (Jordan & Snyder, 1899; Miller, 1986), altering the local aquatic trophic chain (Mejía-Mojica et al., 2012, 2015). Invasions represent one of the most pervasive aquatic habitat transformations, and a central issue in biodiversity conservation around the world (Rajeev et al., 2008; Simberloff, 2010), as invasive species can lead to a loss of native biodiversity and the homogenization of aquatic systems (Olden et al., 2016). However, ichthyochory by non-native fish species may benefit dispersal of native plants as well as invasive aquatic plant seeds (VonBank et al., 2018). The antecedents suggest that successful non-native fish species would be opportunistic and have a broad trophic niche, switching between food sources depending on their abundance (Córdova Tapia et al., 2015). We expect that in the Amacuzac river both native and non-native fish would consume seeds in similar proportions due to the high availability of seeds in water during rainy seasons. In order to assess the role of native and non-native fish in the ecological dynamics of the Amacuzac system, here our aims were (a) to identify and estimate the frequency and number of fish species whose stomachs contained seeds, and to determine the percentage of each fishes’ diet corresponding to seeds with respect to total food items, and (b) to evaluate whether there were seasonal differences in the consumption of intact seeds by fish and between native versus. non-native species.

The study was carried out in the Amacuzac River (Figure 1), one of the main tributaries of the Balsas River basin. The basin covers an area of 8,946 km² (Cotler, 2004), and the volume due to precipitation is around 4,200 million m³. The climatic regime is seasonal hot sub-humid with summer rains (Jun–Oct) and a dry season (Nov–May); mean annual temperature is 21.5°C and annual precipitation ranges between 900 and 1,500 mm (Bolongaro, 2006). These features correspond to a tropical deciduous forest, evergreen and deciduous riparian forest (Bonnilla-Barbosa & Villaseñor, 2003), and aquatic vegetation in small transient flooded areas along the edges of the river (Bonnilla-Barbosa & Villaseñor, 2006; Bonilla-Barbosa 2007).

During 2015, an intensive monthly sampling of fish was performed in six locations along the Amacuzac River (Figure 1). Sampling was carried out in 200 m of river stretches, covering different types of habitats (raptids, parallel pools, backwaters, and canals). The sampling effort was one hour. Fish were collected using cast nets of 2 m diameter and 20 mm mesh, and were kept cold for later analysis in the laboratory. We randomly selected 10–15 fish specimens per site from each species collected. Fish were dissected ventrally, leaving the visceral cavity exposed for extraction and for contents analysis by means of a stereoscopic microscope (Nikon SMZ-2T). Specimens were deposited in the fish collection (CICIB) at the Autonomous University of the State of Morelos (UAEM). The taxonomic identification of species was based on the criteria shown in Table S1, and with the help of the specialized staff at CICIB-UAEM. We determined the proportion of seeds with respect to total food items observed in stomachs using the numerical grid method (Lagler, 1956; Windell & Bowen, 1978).

Once we knew which fish species had seeds in their stomachs, we did a second field survey during the dry and rainy season of 2016, collecting only the four species identified in 2015 (Table S2). The sampling protocol and objectives were similar to that of the previous year, and were based on the methodology used by Mejía-Mojica et al. (2012). We sampled five locations in the same area of previous years’ sampling (Figure 1). Between 15 and 30 specimens were taken per species and location. Seeds were identified to the genus level and classified according to known original dispersal syndromes (Table S3 and S4).

Data from the two years were combined to evaluate differences in the number of fish individuals containing at least one seed in their stomachs between two seasons (rainy and dry), and between native and non-native fishes represented by four species (two species of each type) collected from nine study locations. Statistical analyses were performed using a generalized linear mixed-effects model (GLMMs) with binomial option family using the “glmer” function of the “lme4” package (Bates et al., 2015), of the R statistical computing program (R Core Team, 2020). The response variables were the number of fish with seeds in their stomach content and the number of fish without seeds, in each sampling location/year/season/species (N = 68). The model included season, fish origin (native, non-native), and their interaction as fixed effects, with year, locations nested within year and species as random effects. To find the best (simplest) model, we applied a backwards comparison starting with the most complex model (including all terms and interactions), and arrived at the final model by retaining only those terms that were statistically significant (p < 0.05). From stomach content analysis, the proportion of seeds with respect to the rest of food consumed by fishes were grouped into three categories (0, 1%–25%, and > 25% seeds). We used a G test of independence to assess possible differences among the four fish species and the categories of seed proportions. To establish differences between species, we ran pairwise comparisons, controlling family-wise error rate (Hommel, 1988).

We identified and analyzed 1,621 individuals from 13 fish species: 723 native and 898 non-native individuals (Table S1). Of these, 144 had at least one seed in their stomach (64 native/80 non-native; 9%) (Table S1). This corresponded to four fish species: two native species—Astyanax aeneus and Notropis moralesi, and two non-native species—Aequidens rivulatus and Amatitlania nigrofasciata. The native A. aeneus and the non-native species A. nigrofasciata had the greatest number of individuals containing seeds—21% and 26%, respectively, of the total number of individuals of each species collected in both periods. Of 1,621 individuals analyzed, 848 (52%) belonged to the four seed-consumer species; of these, 152 (18%) had at least one intact seed in their stomach (Table S2). The number of individuals with seeds was significantly higher in the rainy season than in the dry season (χ² = 82.06; df = 1; p < 0.001), with a higher proportion...
of non-native fishes carrying seeds, but only in the rainy season, indicated by a significant interaction \( (\chi^2 = 4.98; \ df = 1; \ p = 0.025) \), Figure 2a). The model that included only fish origin was not significant \( (\chi^2 = 1.12; \ df = 1; \ p = 0.28) \). The variance contributions of random factors were as follows: 17.5% for year, 34.1% for locations within year, and 14.1% for species. We found significant differences between the fish species in the proportion of seeds consumed, \( (G = 54.723, \ df = 6, \ p < 0.001) \). N. moralesi showed the lowest proportion of seeds ingested (N. moralesi versus A. aeneus: \( p < 0.001 \); versus A. nigrofasciata: \( p < 0.001 \); and versus A. rivulatus: \( p = 0.042 \); Figure 2b). The number of seeds found in fish stomach was too low in the dry season to test the season effect. Seeds constituted a fraction in the composition of the fish diet, and an estimation of a subsample showed that 46% of seeds were found intact in fish stomachs (n = 73 stomachs).

Seeds from 11 families, 12 genera, and 16 species could be identified to the genus and species level (Tables S3 and S4). Including five morpho-species of seeds, and three taxa identified at the family level, we found a total of 21 different seeds in fish stomachs, representing eight aquatic and eight terrestrial plants. Seeds from the aquatic genus Echinodorus (Solanaceae) appeared in all fish species at least once; but of all species, aquatic seeds of Polygonum were the most frequently found (Table S3). As many fish species in the Neotropics (see Correa, Costa-Pereira, et al., 2015), here we found seeds of one tree species, Inga vera. However, most of the seeds ingested were from herbaceous species and were water- or animal-dispersed, including agricultural weeds such as Sorghum halepense and Chenopodium album (Table S3 and Table S4).

In the Amacuzac river, there was a higher seed consumption by fish during rainy than during dry seasons, consistent with the occurrence of a flood pulse that increased the potential of the river to overflow and release seeds accumulated in soil seed banks toward the water. This sweep effect has also been shown in other systems with a seasonal within-channel flow variability and stream bank removal of seeds, and is a critical factor determining the number of seeds available in water (Middleton, 2000). Thus, we suggest that fishes consume fruits/seeds on a seasonal basis, as has also been suggested by Horn et al. (2011); however, in this case it is explained by a different mechanism other than the timing of seed production by trees. In the rainy season seeds transported in water can arrive in diverse habitat types and transient flooded areas and are available for consumption by fishes.

Seed consumption was higher by non-natives than by native fishes. Most of the study was carried out in the middle portion of the Amacuzac river, which coincides with deforested- agriculture areas and human impacts including the presence of ornamental fish farms (Ramirez et al., 2010), and in turn, with low water quality conditions and warmer temperatures (Meija-Mojica et al., 2015; Trujillo-Jiménez et al., 2010). We consider that these conditions could be more favorable for non-native fish species, since they are generally characterized by high environmental tolerance and a broad diet (Marvier et al., 2004; Shea & Chesson, 2002).

The two species with the highest seed consumption—the native characid A. aeneus and the non-native cichlid A. nigrofasciata, are omnivorous. A. aeneus usually obtains its food from materials that float or are carried by the current, swimming vigorously in all
environments and temperatures (Maya & Mejia-Mojica, 1991). Characids are recorded as common seed dispersers in tropical regions of South America (Correa, Costa-Pereira, et al., 2015; Horn et al., 2011; Reys et al., 2009; Vilella et al., 2002). It is interesting that several studies have reported seed consumption/dispersion by Astyanax in the Neotropics (e.g., Costa-Pereira et al., 2017; Gomiero & Braga, 2003; Silveira & Weiss, 2014), and Silveira et al. (2019) found that A. lacustris is an efficient seed disperser in the wetlands of Central South America. This evidence suggests that A. aeneus could be a good seed disperser in our system as well. A. nigrofasciata with a maximum standard length of 10 cm (Trujillo-Jiménez, 1998) is highly territorial and aggressive fish. This non-native species had the highest seed consumption, but its more restricted home range resulting from its territorial behavior may limit its effectiveness as a seed disperser. In contrast, the cyprinid, N. Moralesi, and the cichlid, A. rivulatus, consumed very few seeds in our study; Trujillo-Jiménez and Castro-Lara (2008) considered them opportunistic–omnivorous species in the Amacuzac river and recorded their intake of plant components as incidental. The native N. Moralesi has been described as the most important seed disperser in temperate regions (Correa et al., 2007; Horn et al., 2011); however, in our study its abundance is limited and it is considered threatened according to the protection criteria set by Mexican legislation NOM-059-ECOL (2001) and IUCN Red List 2019. The non-native A. rivulatus is a large cichlid (males can reach 30 cm and females 20 cm; Rodríguez, 2004; Sifuentes, 1992), highly territorial, aggressive that inhabits the lower riverbed and muddy bottoms where seed inputs may be more scarce.

In conclusion, our results showed that in the Amacuzac river, two native and two non-native fish species consumed seeds more frequently in the rainy than in the dry season. Because of rainy season overflows transient flood areas, remove seeds from banks, and triples the amount of seeds in water compared to dry seasons (Esper-Reyes et al., 2018), we suggest that fish have greater opportunities to consume seeds. In the rainy season, non-native fish consumed more seeds than native fish, perhaps resulting from greater plasticity in the use of habitats and wider trophic habits. Because half of the

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**FIGURE 2** (a) Proportion of fish individuals consuming seeds for native and non-native species in rainy and dry seasons; columns represent back-transformed means with standard error bars estimated by GLMM model; (b) Proportion of fish with different contributions of seeds to their diet (0, <25%, > 25% of food items consist of seeds). Different letters indicate significant differences (N. Moralesi versus. A. nigrofasciata and A. aeneus: p < 0.001; and versus. A. rivulatus: p = 0.042)
seeds ingested were found intact in fish stomachs, we suggest these small fish species may have a role as seed dispersers of herbaceous species along the riparian corridor of the Amacuzac River. Further experimental approaches are needed to assess the disperser role of non-specialized opportunistic small fish in diverse environments. As with hydrochory in tropical dry forests, seed consumption and dispersal by fish inhabiting rivers within this ecosystem have been overlooked in the ecology and conservation literature. This evidence is relevant for tropical dry forest ecosystem dynamics and management strategies in riparian corridors.

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CONFLICT OF INTEREST

There have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.sqv9s4n2m (Oca et al., 2020).

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