Fish Frugivory in Neotropical Wetlands: Past, Present and Future of a Unique Interaction

Sandra Bibiana Correa[1]

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RESUMO – Frugivoria de Peixes em Áreas Úmidas Neotropicais: Passado, Presente e Futuro de uma Interação Única. A frugivoria é um hábito de alimentação generalizado entre os peixes, particularmente nas zonas úmidas tropicais da América do Sul. Essa antiga interação evoluiu há cerca de 70 milhões de anos e, provavelmente, contribuiu para moldar comunidades de plantas em zonas úmidas neotropicais. Após quase quatro décadas de pesquisa, estamos apenas começando a entender os mecanismos que influenciam a dispersão de sementes por peixes frugívoros. Hoje, a persistência da interação única entre peixes e florestas é ameaçada por mudanças no uso da terra e no clima global. Aqui, destaco algumas das principais lacunas de conhecimento em nossa compreensão da frugivoria dos peixes, sintetizo as ameaças atuais para as interações entre peixe e floresta, e discuto estratégias de manejo para floresta e pesca em áreas alagáveis, incluindo a adoção da Abordagem de Ecossistemas para Pescas (EAF), proposta pela Organização das Nações Unidas para a Alimentação e a Agricultura (FAO). Neste artigo, sintetizo cada componente da EAF e ofereço ideias sobre sua implementação no contexto das pescarias das planícies de inundação da América do Sul.

Palavras-chave: Abordagem ecossistêmica das pescarias; mudanças climáticas; dispersão de sementes; floresta de planície de inundação; reflorestamento.

ABSTRACT – Frugivory is a widespread feeding habit among fishes particularly in tropical wetlands of South America. This ancient interaction evolved nearly 70 Mya and has likely contributed to shaping plant communities in Neotropical wetlands. After nearly four decades of research, we are just starting to understand the mechanisms that influence fish frugivory and seed dispersal. Today, the persistence of the unique interaction between fishes and forests is threatened by changes in land use and global climate. Here, I highlight some of the major knowledge gaps in our understanding of fish frugivory, summarize current threats to fish-forest interactions, and discuss management strategies for floodplain forests and fisheries, including the adoption of The Ecosystem Approach to Fisheries (EAF) proposed by the Food and Agriculture Organization of the United Nations (FAO). Here, I summarize each EAF component and offer insights on its implementation in the context of South American floodplain fisheries.

Keywords: Climate change; ecosystem approach to fisheries; floodplain forest; reforestation; seed dispersal.

Afiliação

[1] Department of Wildlife, Fisheries and Aquaculture, Mississippi State University, Box 9680, Mississippi State, MS 39762, USA.

E-mail

sbc257@msstate.edu

RESUMEN – Frugívoro de Peces en Humedales Neotropicales: Pasado, Presente y Futuro de una Interacción Única. La frugivoría es un hábito de alimentación común entre los peces, especialmente en los humedales tropicales de América del Sur. Esta interacción antigua evolucionó hace casi 70 Ma y probablemente contribuyó a definir la configuración de las comunidades de plantas en los humedales Neotropicales. Después de casi cuatro décadas de investigación, apenas estamos empezando a comprender los mecanismos que influencian la frugivoría y la dispersión de semillas por peces. Hoy en día, la persistencia de la interacción única entre los peces y los bosques se ve amenazada por los cambios en el uso de la tierra y el cambio climático global. En este artículo, resalto algunas de las principales brechas de conocimiento en nuestra comprensión acerca de la frugivoría en peces, resumo las amenazas actuales a las interacciones entre peces y bosques, y discuto estrategias de manejo para los bosques de llanuras inundables y la pesca, incluida la adopción del Enfoque de Ecosistemas en la Pesca (EEP), propuesta por La Organización de las Naciones Unidas para la Agricultura y la Alimentación (FAO). Específicamente, resumo cada componente de la EEP y ofrezco perpectivas sobre su implementación en el contexto de las pesquerías en planos de inundación de América del Sur.

Palabras clave: Enfoque de ecosistemas en la pesca; cámbio climático; dispersión de semillas; bosques de planes de inundación; repoblación forestal.

Introduction

Fruit consumption is widespread among tropical fishes. In the Neotropics alone, fruit consumption involves >150 fish species and >500 plant species (Horn *et al*. 2011, Correa *et al*. 2015b). Ancestral diet reconstructions demonstrated that frugivory evolved independently in multiple families of Neotropical and African characiform fishes and likely originated from omnivory (Correa *et al*. 2007). In South American wetlands, highly specialized frugivorous fishes evolved ~70 Mya, during the radiation of flowering plants (Thompson *et al*. 2014), which pre-dates the origin of all other major vertebrate frugivores including birds, bats and monkeys (Correa *et al*. 2015b). Such a long shared evolutionary history between fishes and fruits has likely promoted co-evolutionary processes resulting in the diversification of fish- and fruit-traits associated with fruit consumption and seed dispersal by fishes (Correa *et al*. 2018).

There is great variation in body shape and size of frugivorous fishes, as well as in dentition, morphology and length of their digestive tract, all of which influence interactions with fruits (Correa *et al*. 2007). Frugivorous fishes can serve as seed dispersers when they swallow seeds intact or as seed predators when they damage seeds through mastication. Seed dispersal by fish (i.e., ichthyochory) has been widely studied in South American wetlands since the publication of “The fishes and the forest” (Goulding 1980), a seminal monograph that brought international attention to fish frugivory in Amazonian floodplain forests. Although numerous field studies have documented fruit consumption (reviewed by Correa *et al.* 2015b), we are just starting to gain a better understanding of the mechanisms that influence fish frugivory and ichthyochory.

Fish size is positively related to multiple qualitative and quantitative metrics of seed dispersal effectiveness (Schupp *et al.* 2010). Large fish within and among species tend to swallow more seeds intact, therefore the rates of seed dispersal, relative to seed predation, increase with body size (Galetti *et al*. 2008, Anderson *et al*. 2009, Correa *et al*. 2015a). Furthermore, large fish have big stomachs with a greater capacity to consume fruits, possess a greater mouth-gape which allow them to consume small-and large-seeded fruits, and are more mobile, which increases the probability of encountering the fruits of more plant species and dispersing seeds farther distances (Anderson *et al*. 2009, Anderson *et al*. 2011, Correa *et al.* 2015a, Costa-Pereira *et al.* 2017). The passage of seeds through the digestive tract of fishes can have positive, neutral or negative effects on germination success (reviewed in Correa *et al*. 2007, and Horn *et al*. 2011). Boedeltje and colleagues (2015), recently demonstrated that the seed traits (i.e., shape, hardness and size) that increased germination rate after consumption by one fish species, decreased germination success when those seeds were consumed by another fish species with different morphological and physiological digestive-tract traits. Correa and collaborators (2015a) showed that consumption by large fishes increased germination rates for seeds of some species but have no effect for others. Such variable outcomes are likely driven by the interaction between intestinal length, retention time and seed hardness.

The aim of this article is to highlight some of the major knowledge gaps in our understanding of fish frugivory and ichthyochory, summarize current threats to the interactions between fishes and forests, and discuss management strategies for floodplain forests and fisheries with a particular emphasis on South American wetlands.

Research gaps on fish frugivory and seed dispersal

Although we know that diverse fish species consume fruits and transport huge numbers of viable seeds of numerous plant species in tropical floodplain forests and savannas, we still have limited direct evidence of how fish contribute to shape plant community structure. Assessing deposition patterns and recruitment of fish-dispersed seeds in natural settings are two research areas that can contribute toward filling this knowledge gap.

Evidence from a telemetry-based movement study of Tambaqui (*Colossoma macropomum*), the largest frugivorous fish in the Amazon, demonstrated that Tambaqui mostly forage within floodplain forests and have limited movement across river channels (Anderson *et al*. 2011). Such strong habitat affinity increases the probability that seeds defecated by Tambaqui would be deposited in habitats suitable for germination and recruitment (Anderson *et al*. 2011). It is also likely that different fish species may have distinct seed dispersal patterns due to differences in morphology and movement. Dorso-ventrally compressed or streamlined fish species, for instance, may disperse seeds to shallow areas that are not accessible to large deepbodied species. Likewise, small fishes may be able to forage in habitats with greater structural complexity, while large fishes may be restricted to more open habitats. Differences in deposition patterns among fishes may directly influence plant recruitment dynamics given that microhabitat conditions in the understory (e.g., gap vs. closed canopy) determine the identity of recruiting species (Terborgh *et al*. 2017). In order to develop a stronger understanding of these dynamics, further studies are needed to assess foraging and fine-scale movement patterns of frugivorous fishes with diverse morphological and behavioral traits.

Morphological and physiological mechanisms in the digestive tract of frugivorous birds interact with seed traits and other foods in their guts to increase seed germination speed (Traveset *et al*. 2008). Early seedling emergence has positive effects on recruitment in terrestrial systems (Verdú and Traveset 2005). In floodplain forests, however, faster seed germination induced by passage through the digestive track of frugivores would only be advantageous to plant species dispersed to shallow or higher elevation floodplain areas that remain flooded for short periods of time, or that produce fruit toward the end of the flooding season. In fact, recruitment dynamics in floodplain forests are driven by the hydrological cycle, where germination and establishment are restricted to the dry season (Parolin 2001). Feeding experiments revealed no effects on germination speed in seeds consumed by fish without gastric mills, but positive or negative effects on seeds consumed by fish with gastric mills (Boedeltje *et al*. 2016). Given that the dominant fishes involved in seed dispersal in Neotropical wetlands (i.e., characiforms and siluriforms; Horn *et al*. 2011) lack gastric mills, it is likely that seeds passing throughout the digestive tract of most fishes will not increase seed germination speed. Further laboratory studies need to assess the interacting effects of digestive enzymes, fish digestive tract length and retention time on seed germination speed. Such laboratory studies should be coupled with planting experiments of fish-egested seeds in field settings that can account for spatial differences in soil and light conditions across microhabitats.

Another major knowledge gap in our understanding of fish-forest interactions is assessing reciprocal dynamics between forests and fishes in floodplain ecosystems. So far we know that fishes provide important seed dispersal services which likely have contributed to shape and maintain forest diversity in South American floodplains (Correa *et al*. 2015b, Correa *et al*. 2017). Very few studies, however, have examined how floodplains forests contribute to maintain fish productivity and diversity.

Fish biomass and diversity, in general, is greater in floodplains with higher forest canopy cover (Lobón-Cerviá *et al*. 2015, Arantes *et al*. 2017). Fish species that eat terrestrial foods (i.e., herbivores, invertivores, omnivores and detritivores), prefer habitats with high structural complexity and are positively associated with forest cover (Correa 2008, Arantes *et al*. 2017). The protein provided by canopy arthropods that fall into the water during the flood season support diverse fish assemblages in floodplain forests of oligotrophic rivers (Correa and Winemiller 2018). Fruits also are a dependable and valuable food resource to fishes due to the community-wide synchrony in fruit production with the flood season (Correa *et al*. 2017) and their high nutrient content (Waldhoff *et al*. 1996, Waldhoff and Maia 2000). As such, fruits constitute a resource pulse that facilitates the coexistence of ecologically similar fish species (Correa and Winemiller 2014). To better understand the role of floodplain fruits on fish diversification, future studies should use a phylogenetic approach to assess whether fruits have influenced speciation rates of fruit-eating fishes.

Threats to fish-forest interactions

Reluctance to protect freshwater biodiversity is a global conservation issue (Saunders 2002, Abell *et al.* 2011). Although riverine floodplains are some of the most biodiverse and productive ecosystems on Earth, they also are among the most threaten (Costanza *et al*. 1997, Tockner and Stanford 2002). A projected 80% increase in hydroelectric dam construction across the Amazon Basin will disrupt the natural hydrologic cycle of many large lowland rivers, leading to reduced floodplain connectivity (Finer and Jenkins 2012, Winemiller *et al*. 2016). By altering floodplain connectivity, the proliferation of dams would have unforeseen impacts on ecosystem functions via biodiversity loss (Tilman *et al*. 2014). In South American wetlands, fish-fruit interactions have contributed to maintain biodiversity over tens of millions of years (Correa *et al*. 2015b, Correa *et al.* 2018), yet reduced floodplain connectivity will constrain fish's access to habitat and food within floodplain forests and their ability to contribute seed dispersal and seed predation services. For fishes, impacts of such disturbance could lead to lower fecundity, increased juvenile mortality, reductions in the population size of multiple species, shifts in local species assemblages, and overall declines in diversity and fisheries productivity. Moreover, the observed high genetic flow within populations of migratory frugivorous fishes in the Amazon and Pantanal (i.e., *C. macropomum*, *Piaractus brachypomus*, *P. mesopotamicus* and *Brycon hilarii*; Santos *et al*. 2007, Calcagnotto and DeSalle 2009, Escobar *et al.* 2015, Okazaki *et al*. 2017), makes evident that the long-term persistence of these species depends on having access to continuous floodplains at a river basin scale. For plants, reduced floodplain connectivity leads to less seeds of fewer species being dispersed by fishes, increased seed dispersal limitation for nonbuoyant large-seeded species (Correa *et al*. 2015b), lower gene flow in plant populations, changes in local species assemblage structure, and diminished plant diversity.

Climate change will also likely imperil ichthyochory owing to increased drought stress with cascading consequences for the plant communities that are structured by this mutualism. Even in humid areas such as the Amazon Basin, global climate change is already altering the timing and magnitude of precipitation and increasing the severity of drought episodes (Malhi *et al*. 2008, Marengo *et al*. 2011). These changes can disturb natural hydrologic cycles by diminishing high and low water-level peaks, shortening the length of the flood season, and shifting environmental cues that trigger plant phenology. A disruption in the synchrony of fruiting and flooding will reduce fruit availability for fishes and potentially lead to depleted frugivorous fish populations and increased seed dispersal limitation. Because, water flow influences patterns of seed deposition and the availably of suitable habitats for seedling establishment along rivers (Merritt and Wohl 2002), lower water-levels induced by climate change could alter plant community structure in floodplains.

To evaluate how floodplain forest communities are responding to global climate change, it is critical to establish year-round and multi-year monitoring of long-term trends in precipitation, water levels and fruiting phenology.

Floodplain forests in Central and Southern Amazonia have suffered large-scale deforestation since the late 19th century due to logging, agriculture, and cattle and water buffalo ranching (Sheikh *et al*. 2006, Junk and Piedade 2010). These activities have led to a dominance of species-poor secondary forests in floodplains along the lower Amazon River (Junk *et al*. 2010). The largest watersheds in Western Amazonia still have ≈85% forest cover (Melack and Hess 2010). The lack of road access to non-flooding forests, however, concentrates logging in floodplain forest areas (Schongart and Queiroz 2010). In the Pantanal wetland, low-intensity cattle ranching introduced by European colonizers in the middle 18th century has maintained ecosystem function and biodiversity in natural grasslands (Junk and Nunes da Cunha 2005). Increased pressure for greater cattle productivity has unfortunately led to clear cutting of seasonally flooded riparian and monodominant cambará (*Vochysia divergens*) forests (Mittermeier *et al*. 1990) in this region. Moreover, expansion of sport-fishing operations since the 1960's has led to widespread clear cutting of riparian forests to build lodging (Artioli and Resende 2005). Floodplain deforestation reduces fish abundance (Lobón-Cerviá *et al*. 2015, Arantes *et al*. 2017), and the contribution of frugivorous fishes to seed dispersal and natural forest regeneration. To mitigate this problem, conservation efforts should focus on protecting remnant old growth floodplain forests and accelerating succession in degraded areas through reforestation and afforestation. A recently developed anthropization index for floodplain forests can help identifying priority areas for recovery (Magalhães *et al*. 2015).

Reforestation of degraded flooded forests

Reforestation of degraded Amazonian and Pantanal floodplains represents an opportunity to restore ecosystem function and services in these megadiverse wetlands (Chazdon 2008, Lindell *et al*. 2013, Lindell and Thurston 2013, Mukul *et al*. 2016). Floodplain forest fruits are commonly used as fishing bait by local fishers (Wittmann and Wittmann 2010). By replanting fruit producing trees, "fish orchards" (M. Goulding, personal communication) would increase food for fish, enhance floodplain fisheries (Correa and Winemiller 2018) and create economic opportunities for local people via harvesting of fruits and fibers (Wittmann and Wittmann 2010, Adams *et al*. 2016, Londres *et al*. 2017). A basin-wide replanting approach is, however, necessary given that many frugivorous fishes are migratory (Goulding 1980). The implementation of large-scale restoration efforts would be an enormous challenge and require multinational cooperation and the involvement of local communities in the decision (e.g., natural history knowledge to decide what species to plant where and when) and execution stages (e.g., assistance in propagation, planting and monitoring). In addition, because floodplain ecologic and socioeconomic dynamics are highly influenced by precipitation and flooding, reforestation strategies would need to adapt to climate change, as well as to shifts in the goals and needs of stakeholders (Locatelli *et al*. 2015, Lazos-Chavero *et al*. 2016). First steps include identifying priority areas and target species that would maximize ecosystem services (Thomson *et al*. 2009, Comín *et al*. 2018); developing best management practices for plant propagation that use native species and locally available materials; and educating the public on the environmental and social benefits of "replanting forests for fishes".

Ecosystem approach to floodplain fisheries management

The Ecosystem Approach to Fisheries (EAF) accounts for biotic, abiotic and human components of ecosystems (FAO 2003). According to Rice (2011), there are four components of the EAF. The first is accounting for environmental effects on stock dynamics. In marine ecosystems, environmental effects on growth, maturation and natural mortality often have strong effects on stock abundance (Rice 2011). In tropical fluvial systems with annual flood pulsing, strong seasonal fluctuations in food and habitat availability affect fish feeding dynamics, reproductive phenology, fecundity, juvenile mortality and recruitment. In Amazonian floodplains, omnivorous fishes generally accumulate fat during the flood season when food resources are most available, and then catabolize these energy reserves during the dry season when food quality and quantity is reduced (Junk 1985). These energy stores also are used to support reproduction; some species reproduce throughout the year while others reproduce during a narrow window at the end of the dry season or beginning of the annual flood pulse. Thus, an effective EAF for South American floodplains needs to consider the contribution of forest cover to foraging success, reproduction and recruitment.

The second EAF component is accounting for effects of fisheries on ecosystems. In marine ecosystems, decades of research have demonstrated cascading effects of overfishing on food-web structure and coral reef stability (e.g., Pauly *et al*. 1998, Jackson *et al*. 2001, Myers *et al.* 2007, Adam *et al*. 2015). Evidence of ecosystem-level impacts on riverine fisheries is, however, scarce. In tropical rivers, frugivorous fishes provide important process subsidies via seed dispersal and seed predation (Flecker *et al*. 2010). Overexploitation of large frugivorous fishes in the Amazon Basin has depleted the largest size classes of these stocks (Tregidgo *et al*. 2017), and these large individuals are the most efficient seed dispersers (Galetti *et al*. 2008, Correa *et al*. 2015a). The loss of large frugivorous fishes could impact tree dispersal and recruitment, especially for trees with seeds too large to be ingested by smaller fishes (Anderson *et al*. 2011, Correa *et al*. 2015a, Costa-Pereira and Galetti 2015). EAF in South American floodplains needs to consider the ecological role of fish species. The implementation of a maximum capture size limit for large-bodied frugivorous fish species, for example, would not only protect individuals with the greatest reproductive potential, but also safeguard their role in the ecological processes of floodplain forests (Correa *et al*. 2015a, Costa-Pereira *et al.* 2018).

The third and fourth EAF components include achieving inclusive governance and integrated management. Tropical rivers and their floodplains support diverse fishery practices, including subsistence and commercial fisheries that provide the principal source of animal protein for many millions of people in developing countries (Gragson 1992, McIntyre *et al.* 2016), as well as sport-fisheries that contribute to ecotourism economies (i.e., Moraes 2002). In addition, floodplain fisheries target medium- and large-bodied species with diverse life history traits and trophic levels. Most of these species complete part of their lifecycles within floodplain habitats. Thus, EAF in tropical floodplains needs to take into account the goals of different stakeholders as well as the ecological requirements of fishes with diverse life history traits. For longlived marine species (~80 years), recruits should make <5% of the annual catch (Rice 2011). Large-bodied frugivorous fishes such as Tambaqui in the Amazon live up to 65 years (Loubens and Panfili 1997), yet the mean length of individuals captured by this fishery corresponds to that of non-reproductive fish (Campos *et al*. 2015).

Concluding remarks

In nearly four decades since the publication of Goulding's "The fishes and the forest" (1980), we have made tremendous progress in understanding the evolutionary origin and ecological dynamics of fruit-eating fishes. In the next decades, our challenge is to expand this knowledge toward a mechanistic understanding of reciprocal dynamics between fishes and floodplain forests. Key areas of research include investigating how fish movement influences plant population and community dynamics, how fish morphology and physiology affect fruit trait evolution and plant recruitment, and how forests influence fish population dynamics and productivity. Climate change and dam construction are major threats to fish-forest interactions. The long-term persistence of biodiversity in South American riverine floodplains depends on developing a collective consciousness about the interdependence between fishes and forests which would foster interdisciplinary research, inclusive governance and ecosystem-based management.

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