Chapter 13 The Fishes and the *Igapó* Forest 30 Years After Goulding



Mauricio Camargo Zorro

13.1 Introduction

The natural flow regime of the rivers is crucial for maintenance of processes as water dynamics, flood pulse, nutrient cycling, passive transport of carbon sources, and top-down control (Poff and Zimmerman 2010; Winemiller et al. 2014). About 14% of the Amazon Basin is covered by floodplains, which are key to biological production, biogeochemical cycling, and trophic flows (Luize et al. 2015).

In the three kinds of Amazon waters, the regular and prolonged lateral flooding is the main determinant factor of phenological patterns in *várzea* (flooded forests by white waters) (Junk et al. 2010) and *igapó* (flooded forest by black or clear waters) (Haugaasen and Peres 2005; Camargo et al. 2015a). In the first months of flooding season, the riparian forest has peaks of fructification (Parolin et al. 2004; Haugaasen and Peres 2005; Camargo et al. 2015a), providing food resources and temporally habitats for fish. These hydrological dynamics maintain resident aquatic biodiversity.

Floods stimulate nutrient remineralization as well as primary and secondary production in floodplain habitats (Welcomme 1985; Junk et al. 1989). The new habitats created by floods and the movement of fishes into flooded forests cause a dynamic seasonal rearrangement of fish communities, and many fish species are adapted to take advantage by reproducing at the beginning of the wet season, which allows early life stages to feed and grow within inundated floodplain habitats (Lowe-McConnell 1987).

In contradiction, oligotrophic waters of the Negro River support a higher fish diversity (750 described species; Petry and Hales 2013) and sustain important fisheries (Inomata and Freitas 2015); yet what energy sources maintain the blackwater

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M. C. Zorro (🖂)

Instituto Federal de Educação, Ciência e Tecnologia da Paraíba, Belem, Brazil e-mail: camargo.zorro@gmail.com

fish production? During the lateral inundation, the *igapó* of clear and black waters provides important links for food chains, transferring energy from the riparian forest and other terrestrial low trophic levels like arthropods for the fishes (Camargo et al. 2014; Correa and Winemiller 2018). As a response to periodical allochthonous terrestrial sources, omnivorous and opportunistic feeding habits may have evolved.

13.2 Food Web Structure in Black Waters

Food webs are diagrammatic descriptions of trophic connections among species in communities (Fig. 13.1). Understanding the main sources of primary production that support the trophic levels in the Amazon waters is crucial to know the structure of food webs, perceive ecosystem flows, and promote sustainability of the natural processes. For the Negro River basin, detritus and other allochthonous sources are the main pathways for energy and nutrients that are provided by the forest to transfer into higher consumer levels (Goulding et al. 1988).

Isotopic studies performed in the middle Negro River concluded that the main autotrophic sources are the flooded forest, aquatic herbaceous vegetation, and algae (periphytic and phytoplanktonic), which utilize a C3 photosynthetic pathway (Marshall et al. 2008). Thus, the importance of phytoplankton in blackwater environments in trophic food webs could be underestimated. Isotope studies have demonstrated that phytoplankton and periphytic algae are more important than their abundance suggests (Hamilton et al. 1992; Forsberg et al. 1993).

Both algae and aquatic macrophytes enter in aquatic food webs mostly in form of detritus (fine and coarse particulate organic matter) or being transported by water flow and settling onto substrates (Winemiller 2004). Particulate organic matter in the stream of rapids and waterfalls is mostly associated with biofilm and epilithic diatoms that grow on rocks, submerged wood, and herbaceous plants and compose the main energy sources for macroinvertebrates and other trophic links (Camargo 2009a).

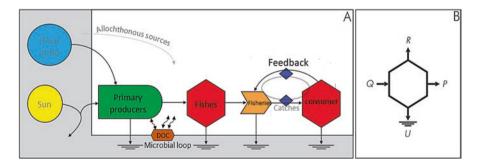


Fig. 13.1 (a) Simplified model flow of energy in Amazon River during the flood period. (b) Flows to each box: Q=Consumption; P=Production; R=Respiration; U=Unassimilated

In tropical blackwater rivers, the aquatic insect abundance is low with most species and biomass concentrated in leaf litter and wood debris providing important habitats (Benke et al. 1984) but supporting large populations of atyid and palaemonid shrimp (Winemiller 2004). Isotope mixing models in a blackwater system concluded that the first link of secondary production during the annual flood is composed by terrestrial arthropods that bond with forests and fishes and made a greater proportional contribution to fish biomass (Correa and Winemiller 2018).

The blackwater systems have patterns with high richness of fish species, low primary production, and a large piscivore abundance (Winemiller and Jepsen 2004). For the Negro basin, even an amount in fish exceeding 750 described species (Petry and Hales 2013), partitions of abundance in the communities are usually skewed having very few highly abundant species and outnumbered rare (uncommon) species (Magurran and Henderson 2003). Those abundant species have an important role transferring most material in food webs and short food chains (Winemiller 2004).

The average of isotopic ¹³C for in situ blackwater fish assemblage revealed that benthivorous fishes feed primarily on burrowing midge larvae that are fed mostly with organic matter derived from terrestrial plants and midwater characids that consume fruits and seeds of terrestrial plants plus smaller fractions of terrestrial insects (Winemiller and Jepsen 2004). Through values of ¹³C for *Semaprochilodus insignis*, the view of Fernandez (1993) who concluded that the route of carbon assimilation is consistent with the fish migration from white water to black water for Negro and Amazonas rivers was confirmed. With fish migration, ecosystems can be linked by transfer production from rich nutrient whitewater to poor nutrient blackwater systems (Winemiller and Jepsen 2004).

Large piscivorous like *Cichla temensis* (Aguiar-Santos et al. 2018), *Hidrolycus* and *Serrasalmus* in a wider range of habitats allowing consumption of a great range of prey sizes. It should have greater potential to exert top-down effects on the food web. Moreover, reduction of body size (miniaturization) (Weitzman and Vari 1988) seems to constitute a very common trait among fishes that inhabit environments with food limitation like the black waters of the Negro River. That evolutionary strategy is a response to minimize the energetic demand among fishes.

13.3 The *Igapó* of the Middle Xingu River

The stretch of the Xingu River between Xingu-Irirí confluence and Belo Monte waterfalls is a homogenous geomorphologic region named middle Xingu (Camargo et al. 2004), comprising a unique geographic feature of lower Amazon Basin, with its relative steep terrain and sinuous configuration (Fig. 13.2). This physiography is resulted by ancient orogenic processes, dating two billion years ago. The numerous rapids carved by the river into the faults of giant granite and gneisses blocks created interfacial environments that suffer considerable seasonal modifications resulting in annual variations in volume of water (Camargo et al. 2013).

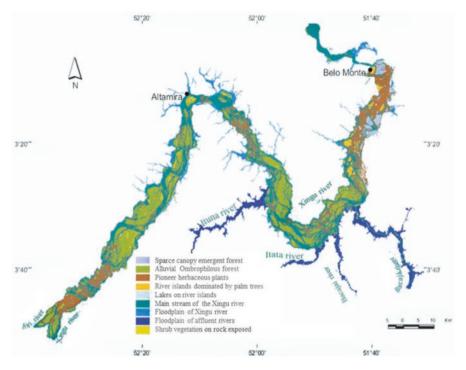
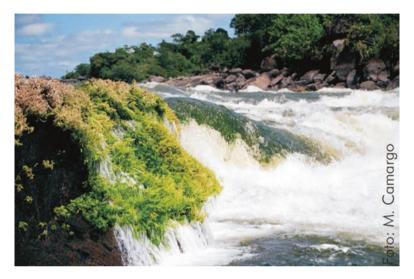


Fig. 13.2 The stretch of the Xingu River between Xingu-Irirí confluence and Belo Monte waterfalls



The middle Xingu River differs in a geomorphological way from the lowland Amazon floodplain. By its wavy geomorphology and rocky bottom that expands or contracts in function of the river flow regime, there is a definition of a flooding limited area. By the way, the inundate areas correspond to their own waterway that, by a high dynamics of alluvial transport and sedimentation, generates flooded terraces with many succession of vegetable stages in pioneer ways till the alluvial dense ombrophilous forest (Estupiñan and Camargo 2009).



The largest flooding area is composed by outnumbered fluvial islands representing 21.89 Km² of the studied area. Only 8.3% of the total area is covered by a strait riparian ombrophilous forest and 1.0% by pioneering regularly flooded shrub vegetation (Estupiñan and Camargo 2009). The increase of the river's flow rate and the rise of waters in rainy season favor the progressive flooding margin areas that are topographically lower turning into waterways, locally denominated *sangradouros*. Those, while flooding, turn into important access channels and connect alluvial forest areas with the river's main stream (Giarrizzo and Camargo 2009).

13.3.1 The Igapó and the Piracemas in the Middle Xingu River

The use of the word *piracema* is still misunderstood. For some, the term is related with the rise of fishes through the rivers till its spring for spawning. The other way associates the *piracema* with the season when fishes go into reproduction. Etymologically, the word comes from Tupi language, with the assembling of the prefix *pirá* (fish) and *sema* (grouping), which means "meeting of fishes for spawning."

In the vision of local Xingu fishermen, a *piracema* is understood as an aquatic habitat located on the margins of fluvial islands and even in the river, where shoals of many species like the piaus (Anostomidae), curimatã and ariduia (Prochilodontidae), branquinas (Curimatidae), sardinhas (*Triportheus*) and even trairas (Erithrynidae) and other fish species meet for spawning. Then, the term applies for fishes, in general, that migrate small distances for reproduction.

In the Amazon River system, the hydrological regime strongly influences all the ecological processes (Poff and Allan 1995); by the way, the periodical flood pulse constitutes an inductive process for reproduction of many fishes (Junk et al. 1989). So, a big group of fishes migrate in search of appropriate sites for spawning in synchrony with the start of regional floods in a more or less restrictive season (Welcomme 1979; Araujo-Lima et al. 1995). During this migration, fishes use temporally the flooded forest, which warranties a habitat rich in food and refuge from predators (Goulding et al. 1988; Waldhoff et al. 1996).



Piracema waterways or sangradouros

13.3.2 The Source of Piracema Fishes

The association of the phenomenon denominated by fishermen as *repiquete*, which consists in a sudden increase on water level in the main waterway still in the end of dry season (November), and the flooding of the *sangradouros* in the pluvial islands of Xingu stimulate a process of short migration and spawning in small periods of time (hours), in superficial depths (30 cm). This process can be explained by the possible changes on some parameters of the aquatic environment, which works as a start signal for fishes to get ready physiologically and behaviorally for spawning.

In that way, the association of factors like: I. The currency of migrant adult fishes concentrated in the waterfall areas of Xingu in dry season; II. Environmental signals indicating changes on the physicochemical attributes of aquatic environment, and III. the flooding of *sangradouros* by the sudden increase of the water level with the *repiquete*, causing short displacements in countercurrent to reach those *sangradouros*, for spawning.

Even with the existence of seasonal insular lakes, forming a surface of approximately 5.0 km², representing 0.31% of the studied area in Xingu, these and the *sangradouros* possibly don't support in an exclusive way the fishery production of the middle Xingu. A hypothesis proposal in relation to the source of migrant fishes is associated with the displacement of metapopulations in Xingu's tributary rivers, like Bacajá, Bacajaí, Itatá, and Ituna that drain into its margin. All those rivers have big traces of marginal floodable forests covering an area of approximately 152 km² (an estimated extension of 20 km) representing 10% of the researched area.

Another peculiarity of the middle Xingu River is its altitude variation. Its dip is 85 m in an extension of 160 km, and the pluvial islands topographical heterogeneity demonstrate that the migration process doesn't occur in a synchronized way in this stretch of the river. While in the main channel, some kilometers upstream, the *sangradouros* is being flooded, in the downstream way, some waterways even have achieved its minimal level to induce fishes that are spawning. In shallow flooded areas, the fertilized eggs form big floating clouds in the surface. There is a belief that with this mechanism, species can minimize mortality by predators and maximize juveniles' chance of survival with water level decrease, occupying marginal areas.

Afterward, some species stay in flooded areas throughout the flood period or just turn back to the main waterway. This cross-border migration cycle (river > *sangradouros* > flooded areas > *sangradouros* > river) is known by the local population. Some riverside communities take advantage of those concentration of fishes and build "fences" or wood barriers allowing the entrance of fish that are ready to spawn but limit its exit, making an easy target to be captured, and impairing the reproduction process of migrant fishes.



"Fences" or wood barrier allowing the entrance of fish that are ready to spawn

13.3.3 Is Expected a Reproduction Pattern to Piracema Fishes?

The available info about the behavior of reproductive migration of the Amazon fishes have been described for white, clear, and darkwater environments (e.g., Fernandes 1997; Brito Ribeiro 1983; Carvalho and Merona 1986). Although some study relate reproductive behavior and kinds of migrant fishes in different Amazonian environments (Welcomme 1979; Junk et al. 1983; Tejerina-Garro et al. 1998), those were made in environments where the flood surface is significantly big and the flood of the river lasts for months.

With the help of local fishermen, a cartographical survey about *piracemas* was made, along the middle Xingu (Giarrizzo and Camargo 2009). Totalling 198 places were recorded where *piracema* occurs. Nearly 58% of identified places (114) are registered in fluvial islands, and the others at the river margins. Most part of *piracemas* (73%) happen in places with ombrophilous forest, those acting as an incident solar radiation filter over water surface, providing food and used as refuge and protection from predators.

These findings show that the same fish species with migratory habits for reproduction have a broad plasticity in its response to perform long and short displacements according to the regional hydrological dynamics. In this way, for some Amazon environments, migratory fishes like curimatã (*Prochilodus nigricans*) need a long displacement through the main stream for reproduction. In the middle Xingu River, the curimatã develops its gonads in rapids and after doing small displacements entering in the available narrow waterways with the water level increasement at the *repiquete* time, in the flooded forest (Fig. 13.3).

It's possible that in the middle Xingu River the stocks of migratory species have a homing ability to return in spawning season, for its area of nursery and growth in the same *piracema* channel. This assumption is supported by fishermen that know different morphotypes inside the same species and associate with a particular habitat of *piracema*. Other fishes, like the pacus (Serrasalmidae), even spawning in synchrony with the flooding season, can show an asynchrony spawn peak, during dry season in the Xingu main stream. The occurrence of juveniles during the regional drought indicates this asynchrony in some fishes that are spawning (Camargo and Lima Jr. 2007).



Mature fishes come into the piracema habitat



Metynnis hypsauchen (Müller & Troschel, 1844)

Myleus torquatus (Kner, 1858)



Poptella orbicularis (Valenciennes, 1850) - Mature females

Migrations made by fishes during annual flooding warrant, even reproduction success, the access to primary allochthonous sources. High rates of primary annual production of plant fractions that make up the alluvial forest and the tight sync in fruit production with the flood indicate a mutualism where plants provide food to fishes and release seeds in other areas by ichthyochory (Gottsberger 1978).

From 26 abundant plant species recorded in the alluvial forest of the middle Xingu River, 22 feature fruiting in synchronic with the flood, when fishes inhabit flooded areas (Fig. 13.4). Araça (*Myrcia* sp.), caferana (*Quiina florida*), piranheira (*Piranha trifoliata*), and seringueira (*Hevea brasiliensis*) are included as a preference of frugivorous fish (Giarrizzo and Camargo 2009), while other pioneer plant fruits like embauba (*Cecropia* sp.), even if digested, do not constitute the main food base of many fishes, probably because of its low nutrition value, when compared with primary forest plants (Waldoff et al. 1996).

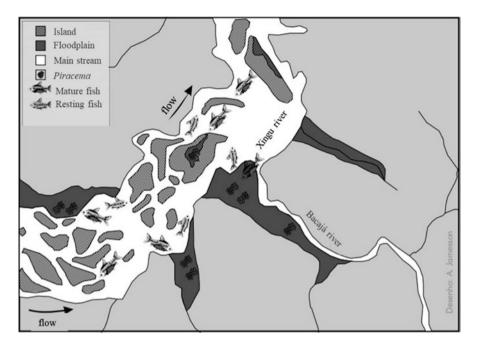


Fig. 13.3 Model of lateral migration - fish reproduction in the middle Xingu River

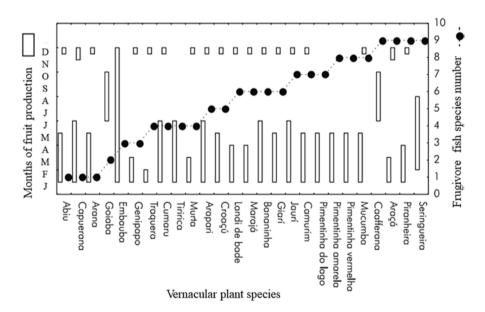


Fig. 13.4 Synchrony of fruit production, seasonal flooding, and use by frugivore fishes in the middle Xingu River

13.3.4 Trophic Ecology of Fishes in the Igapó of the Middle Xingu River

Facing seasonal changes in the quality and availability of food resources, consumers should adjust their foraging behavior in a way to maximize energy and nutrient intake (Correa et al. 2015a). Floodplains of the Amazon Basin are characterized by a strong, predictable, hydrological seasonality providing fruits, seeds, and other terrestrial-originated food resources. Therefore, rivers with rhythmical annual floods have a higher richness of fish species and elevated rates of riparian forest production comparing those with arrhythmic flood pulses (Jardine et al. 2015).

Frugivory is a key plant–animal interaction that contributes to maintain biological and functional diversity. Ichthyocory is a seed long-distance dispersal mechanism that maintains the reproductive dynamics of plant communities and possibly the radiation of early angiosperms in flooded forests (Correa et al. 2015a), while fishes gain access to rich sources of carbohydrates, lipids, and proteins (Horn et al. 2011). In clear waters of the middle Xingu, Serrasalmidae were the most diverse and also the more abundant species as frugivore fish with 0.63 g.m⁻² d.w (Camargo 2009b).

In clear waters of the middle Xingu River, the flooding forest consumption includes other plant parts such as leaves and flowers, as well as terrestrial and aquatic invertebrates. Juveniles of pacus (*Myleus*, Serrasalmidae) were observed jumping some centimeters over the water to consume seeds and flowers of marginal grasses (Camargo 2004). Litterfall production per month, during the seasonal flooding, achieved 33 g.m⁻² of dry weight (d.w) for fruits ($r = 0.48 \pm 0.32$ s.d), 137 g.m⁻² d.w for leaves ($r = 0.42 \pm 0.09$ s.d), and 10 g.m⁻² d.w for flowers ($r = -0.61 \pm 0.02$ s.d) (Camargo et al. 2015b).

Feeding studies for 126 fish species of main stream backwater, riffles, fluvial lakes, and riparian forest environments in the middle Xingu stretch revealed 8 trophic guilds (Table 13.1). A PCA based on the relative abundances (CPUEg) of guilds exposes four spatial patterns: I the insular lakes, similar composition of iliophages (preference of epilithon-benthic algae), carnivores, piscivores, and insectivores; II. Main stream of Xingu and Iriri river environments are very similar by the abundance of piscivores, frugivores, and omnivores; III backwaters near waterfalls, the higher affinity was defined, mainly, by piscivore fishes; IV riffles with iliophage habits (preference on biofilm and epilithic organism associated with rocks, for macroinvertebrates and another trophic link as important energy sources) (Camargo 2009a).

A wide spectrum of trophic guilds recorded in the middle Xingu River indicated a development system with various base sources of energy and with rapid transference along the different links, involving physical and ecological processes. The physical processes are related with the water flow, rains, and transport–deposition of particulate material along the stream. Ecological processes include decomposition and recycling of biogenic material via microbial-loop and their availability to primary and secondary production. The abundance of piscivores in the spatial-temporal

Guild/habitat	Main stream	Fluvial lakes	Tributary stream	Waterfalls
Detritivores	0.015-0.020	0.013-0.027	0.012-0.035	0.013-0.014
Iliophagous fishes	0.014-0.017	0.041-0.021	0.020-0.017	0.013-0.011
Plankton feeders	0.006-0.013	-	-	0.082-0.00
Frugivores	0.034-0.043	0.007-0.002	0.048-0.00	0.014-0.03
Insectivores	0.005-0.009	0.011-0.005	0.002-0.027	0.002-0.013
Omnivores	0.039-0.022	0.012-0.012	0.064-0.027	0.005-0.003
Carnivores	0.027-0.014	0.035-0.021	0.013-0.010	0.015-0.004
Piscivores	0.034-0.036	0.027-0.038	0.027-0.052	0.032-0.032
Total	0.173-0.176	0.126-0.145	0.187-0.162	0.176-0.107

Table 13.1CPUEg $(g.m^{-2}.h^{-1})$ – trophic guild and habitat in seasonal variation – middle XinguRiver

variation of the Xingu River confirms the important role of the top-down control in the system production.

Comparison of the middle Xingu riffles and the blackwater rapids of the Negro River in relation with rheophilic fish assemblages evidenced that the former is more complex. The Xingu River revealed a higher diversity of feeding tactics, different foraging areas, and periods of activity (Zuanon 1999; Camargo 2004). The main light incidence on submerged rocks in clear waters, associated with deposition of fine particulate material, promotes a major microbial-loop via detritus and the development of the biofilm on rocks. Most of this production is derived from algae and, during the wet season, from vascular plants. Limited light penetration caused by high levels of humic acids that stain in the black waters reduces its transparency and restricts growth of epilithon.

13.3.5 Food Webs in the Middle Xingu

Studies in the fluvial compartments of the ecosystem in the middle Xingu River identified its main functional groups tracing and quantifying the flow of biomass through the system (Camargo et al. 2004; Brito et al. 2009; Camargo et al. 2009; Costa et al. 2009; Estupiñan and Camargo 2009; Jesus et al. 2009; Giarrizzo and Camargo 2009; Camargo 2009a, b; Bastos et al. 2011; Camargo et al. 2015a, b) of 24 components which were analyzed using Ecopath with Ecosim software (Camargo et al. 2014).

The model was developed for wet seasons (December–February), when the riparian forest is flooded. The results indicate that the main flow of biomass into the food web is made by alluvial forest. Also in the backwater, the floating submerged leaves of marginal vegetation are colonized by dense aggregations of epiphytes. In contrast with the riparian forest, on long stretches of rapids and waterfalls, rocks of the riffles support other sources of primary production, such as the mats of epiliths, which in turn provide substrate for the complex of organisms composing the "auf-

Piscivoro		Weasel aronura brasiliensis)	Large i	liophagous fish	Small piscivorous fish	Medium pisch fish	vorous I	arge predator sh
3	Crocodilians (Caiman cocrodilus)	Invertebra para:			Insectivorous	1		
	rtles mis unifilis)	Invertebrate t	penthic		Invertebrate benthic	phagous fish		Omnivorous
2	Zooplankton (Keratella, Lecane)	Invertebrate benthic collecters		Invertebrate benthic predators		tivorous fish	Frugivorous fish	

Fig. 13.5 Trophic model of the aquatic ecosystem of the middle Xingu River including the area affected by the Belo Monte hydroelectric project. The size of each circle corresponds to its contribution to biomass of each compartment. The numbers correspond to the trophic level of each compartment

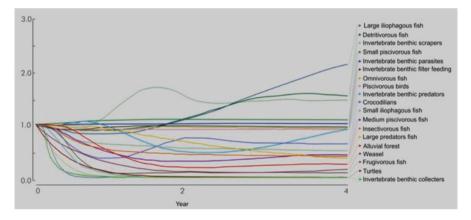


Fig. 13.6 Simulation of reduction on biomass of the alluvial forest and its effects on selected compartments of the ecosystem

wuchs" that generates important carbon sources supporting a large rheophilic fish biomass. The model had four distinct trophic levels (Fig. 13.5).

A simulation developed to predict the impacts of the Belo Monte dam on the middle Xingu River revealed alterations to the natural hydrological regime of the river and indicates major impacts on the vegetation associated with the rocky outcrops and the areas of fluvial forest. The effects of gradual processes of suppression of the alluvial forest, following the filling of the Belo Monte reservoir (Fig. 13.6), indicated a rise of epilithon, in the case of primary producers, with an increase of benthic scrapers and iliophagous fish, while frugivores fish, which constitutes an important source of protein for local communities, declined.

In addition to a general loss of biodiversity, the model indicates clearly the potential loss of fishery productivity on the stretch of the river that will be affected by the inundation of the Belo Monte reservoir. The reduction in these habitats, which are dependent on the annual flood pulse, would likely result in a drastic reduction in abundance of commercially important frugivores, such as pacus (Serrasalmidae), and large-body detritivores like the curimatã and ariduia (Prochilodontidae), leading to major changes in the composition of local catches (Camargo 2009b).

13.4 Amazon Wetlands: Implications for Conservation and Management



Overfishing could eliminate the most effective seed dispersers from floodplain ecosystems, with negative consequences for plant regeneration dynamics, species diversity, and genetic flow among plants in wetland habitats (Correa et al. 2007; Harrison et al. 2013; Kurten 2013; Correa et al. 2015b).

A review about the consequences of suppressing riparian forest in drainage areas of freshwater ecosystems, made by Pinheiro et al. (2015), exposed their important role on maintaining the local biodiversity acting as a corridor for animal migration (Metzger 2010), promoting deposition of particulate and dissolved organic matter (POM and DOM) and nutrients via mineralized accumulated litterfall (Moss 2010), removing pesticides and fertilizers inserted at adjacent agricultural areas (Wantzen et al. 2008; Gücker et al. 2009), and decreasing their harmful effects on biotic components (Ramírez et al. 2008; Winemiller et al. 2008).

In addition, Pinheiro et al. (2015) alert that watershed deforestation may diminish the DOM and nutrient inflow into aquatic systems and change water chemical composition, unbalancing the food chains and decreasing primary productivity (Lampert and Sommer 2007). Likewise, the authors highlight that large-scale removal of riparian forest may cause negative impacts on the resident biota and also on the communities of aquatic bodies. For example, intense deforestation of marginal areas along the Negro River may interfere with DOM input (Moss 2010), reducing the concentration of humic compounds and, therefore, decreasing the water darkness and allochthonous biomass.

Brazil's original Forest Code of 1965 established a proportion of rural land that should be maintained permanently as forest (legal reserves) and also prohibited the clearing of vegetation in fragile areas – such as along the margins of rivers and streams (APP, areas of permanent protection). In turn, the new 2012 forest law, promoted by rural and agribusiness interests, allows opening wide new forest areas for agriculture. Areas formerly held for being too steep or vital on protecting watersheds and watercourses are now open to destruction. A study made by IPEA, an organization linked with the federal government, concluded that the area that could be deforested due to the changes in the Brazilian Forest Law could be sized as much as 79 million hectares with a release amount of 28 billion tons of carbon release into the atmosphere (WWF 2018).

For the restoration and conservation of riparian forest, Pinheiro et al. (2015) proposed to implement ecological corridors in the deforested regions, allowing natural restoration and thus ensuring that the seed bank or allochthonous propagules can help in the recovery of suppressed vegetation, adding them to the APP strips and renouncing some of the taxes paid by landowners.

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