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Biotic Indicators for Ecological State Change in Amazonian Floodplains

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Riverine floodplains are biologically diverse and productive ecosystems. Although tropical floodplains remain relatively conserved and ecologically functional compared to those at higher latitudes, they face accelerated hydropower development, climate change, and deforestation. Alterations to the flood pulse could act synergistically with other drivers of change to promote profound ecological state change at a large spatial scale. State change occurs when an ecosystem reaches a critical threshold or tipping point, which leads to an alternative qualitative state for the ecosystem. Visualizing an alternative state for Amazonian floodplains is not straightforward. Yet, it is critical to recognize that changes to the flood pulse could push tropical floodplain ecosystems over a tipping point with cascading adverse effects on biodiversity and ecosystem services. We characterize the Amazonian flood pulse regime, summarize evidence of flood pulse change, assess potential ecological repercussions, and provide a monitoring framework for tracking flood pulse change and detecting biotic responses.

Keywords: Global change, climate change, river, flooded forest, aquatic ecosystems

Riverine floodplains, particularly those in tropical and subtropical regions, are some of the most biologically diverse and productive ecosystems on Earth, as they provide a tremendous variety of economic and cultural services (Goulding et al. 1996, Ward et al. 1999, Tockner and Stanford 2002). Floodplain biodiversity and productivity stem from natural flooding when the water rises above the river channel into the alluvial plain, carrying sediments and replenishing nutrients therein (Meade 2007). In the northern hemisphere, the function and services of 90% of the floodplain ecosystems have been radically diminished through deforestation and anthropogenic hydrological modifications (Tockner and Stanford 2002, Opperman et al. 2017). In contrast, numerous riverine floodplains in tropical regions remain relatively conserved and ecologically functional but face the threat of rapid land-use alteration and environmental change. The extent to which these changes are already pushing floodplain ecosystems to profound ecological state change remains poorly known. State change can occur when an ecosystem reaches a critical threshold or a tipping point that leads to an alternate qualitative state for the ecosystem (Scheffer et al. 2001). State change can be quantified relative to a baseline, but the temporal scale at which a state change can occur is variable (Lenton 2011). Significant ecosystem state changes are becoming apparent in disparate terrestrial and aquatic ecosystems across the globe. They are driven

by various causes, including climate variability and change, deforestation, nutrient addition, and overharvest, among others (Scheffer et al. 2001).

The outcomes of state change in ecosystems are context-dependent and include shifts in dominant species to shifts in entire biomes. For tropical terrestrial ecosystems in general, such as the Amazonian rainforest biome, large-scale deforestation is predicted to induce a shift from a forest-dominated to a savanna-dominated state by altering the biotic pump that regulates the hydrologic cycle (Nobre and Borma 2009, Lovejoy and Nobre 2018). In temperate river floodplains, documented state changes include: (i) a shift from a clear-water state dominated by submerged aquatic vegetation to a turbid-water state with sparse vegetation induced by reduced natural hydrologic-disturbance after river impoundment (Bouska et al. 2020); (ii) a shift from a diverse native fish community to a non-native-dominated fish community induced by floodplain habitat degradation, overfishing, and the introduction of non-native invasive carp species (Bouska et al. 2020); and (iii) a shift from a mosaic of native meadows and forests to a persistent monospecific meadow induced by deforestation and non-native grass invasion (Bouska et al. 2020 and reference therein). In nearshore temperate marine ecosystems, the shift from a kelp forest-dominated state to an algal-dominated barren state is driven by local-scale drivers such as sea urchin overgrazing (Filbee-Dexter and

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Scheibling 2014, 2017) or global-scale drivers such as ocean warming and eutrophication (Filbee-Dexter and Wernberg 2018). The alternative states are often maintained through positive feedback mechanisms involving abiotic or biotic factors. In temperate river floodplains, for instance, alternative states are maintained by bioturbation (e.g., increased turbidity by grazing carp) and species interactions (e.g., predation and competition) (Bouska et al. 2020). The barren state of kelp forests is maintained by sea urchin demographics (Filbee-Dexter and Scheibling 2017), while the savanna state of rainforests is maintained by complex relationships between precipitation, evapotranspiration, runoff, and surface air temperature (Nobre and Borma 2009).

In alluvial floodplains, like in many other aquatic ecosystems, flooding constitutes the primary mechanism that both modulates natural succession and contributes to maintaining biodiversity (Odum and Barrett 1971, Junk et al. 1989). This occurs because flood-generated disturbance keeps floodplain ecosystems at an intermediate point between early and late successional stages. In addition to creating a disturbance, periodic and predictable flooding promotes speciation because it constitutes a selective pressure that generates adaptive responses by plants and animals to cycles of flood and drought (Odum and Barrett 1971, Lytle and Poff 2004). Many lowland river ecosystems are subject to natural periodic and predictable flood pulses that connect river channels to adjacent floodplains (Junk et al. 1989). However, a change in flooding attributes could cause significant and unpredictable effects on essential ecosystem functions and the biodiversity these ecosystems sustain. Human-driven modifications to floodplain ecosystems can affect natural flood pulse regimes and possibly lead to state change by, for example, creating unpredictable, strong, and/or arrhythmic floods that result in oscillatory rather than stable ecosystems and lead to biodiversity losses (Odum and Barrett 1971). In rivers where arrhythmic and unpredictable flash floods occur, frequent disturbance resets and maintains ecosystems at an early successional stage (Winemiller 2004, Jardine et al. 2015). Floodplains in arrhythmic rivers generally have much lower aquatic species richness and productivity than those with a predictable flood pulse (Jardine et al. 2015).

The Amazon River drainage basin has some of the most extensive floodplains of any river in the world (Keddy et al. 2009). Amazonian floodplains are under the pressure of multiple stressors that could synergistically promote large-scale ecological state change in the mid-to-long term. Climate change, deforestation, and the development of hydropower dams have already affected the natural flow regime of some Amazonian rivers (Almeida et al. 2020, Melack and Coe 2013, Marengo and Espinoza 2016, Timpe and Kaplan 2017), possibly leading to flood-pulse disruption across a variety of river basins. Substantial deviations from the baseline flood pulse could disturb Amazonian floodplains sufficiently to transition from biodiverse and functional ecosystems that provide essential ecosystem services (State A) to depauperate ecosystems with loss, or

considerable reduction, of ecosystem services provided (State B).

Although it is difficult to foresee a single alternative state for Amazonian floodplains, it is critical to recognize the role of the flood pulse regime as a potential driver of state change. This realization would allow evaluating how fauna and flora may respond to flood pulse alterations and identifying biological changes that may indicate the onset of profound longer-term changes at the ecosystem level. Here we briefly describe Amazonian floodplains, characterize the Amazonian flood pulse regime, summarize evidence of flood pulse change, and assess the potential ecological repercussions of flood pulse alterations. We then provide a monitoring framework for tracking changes in the flood pulse and propose four proxies to monitor how key flora and fauna, and ecological processes modulated by the flood pulse, would respond to alterations to the flood pulse regime.

The flood pulse and its change

Floodplains form along lowland tributaries under 500 meters above sea level (m.a.s.l.), occupying 16.8% of the lowland Amazon basin (i.e. total wetland area minus river channels and permanent to semi-permanent lakes; Hess et al. 2015). Beginning with the Andean uplift during the Miocene (23-10 Mya), a predictable annual flood pulse created stable lateral connectivity in lowland Amazonia, linking habitats and ecological processes in river channels and floodplains (Figure 1) (Junk et al. 1989, Wittmann et al. 2010, Wittmann and Householder 2017). Longitudinally, Amazonian floodplains extend over thousands of kilometers and have distinct geomorphology, water quality, and seasonally flooded plant communities (Junk et al. 2012, Hess et al. 2015). The flooded forests are the most extensive wetland types on the Amazonian floodplains covering ≈ 70 -80% of all wetland area (Amaral et al. 2020, Melack and Hess 2010).

Characterizing the natural flow regime of rivers as deviations from baseline streamflow provides a conceptual framework to understand the hydrological dynamics of unregulated rivers (Poff et al. 1997). The predictability (date of peak flooding), the magnitude of change (m^3/s difference between the maximum and minimum flow), and the duration of flooding (number of days above mean flow) are essential for characterizing the hydrological regime of floodplains, given that these factors regulate most ecological processes therein (Ward 1989, Poff et al. 1997).

Characterization of the Amazonian flood pulse. A generally predictable monomodal flood pulse characterizes the flow regime in most of the Amazonian lowlands, with a mean amplitude over the year of approximately 10 m (Junk et al. 1989, Goulding et al. 2003), corresponding to mean streamflow of $\sim 170,000 \text{ m}^3/\text{s}$ at the Óbidos gauge (Brazil) (Siddiqui et al. 2021). This annual flood pulse is primarily driven by precipitation in the upper catchment area which explains the time lag in flood peaks that exists between upstream and downstream reaches (Figure 2A). In turn, precipitation

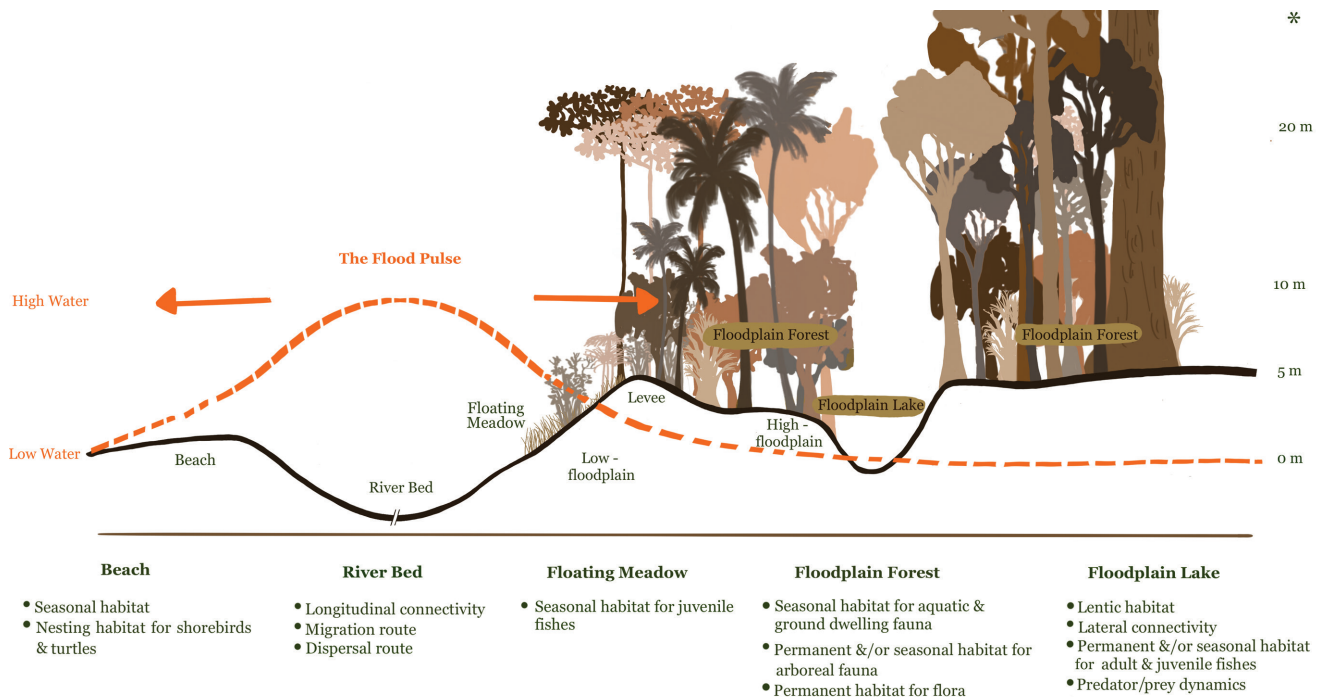


Figure 1. Conceptual model representing the Amazonian floodplain ecosystem and the ecological processes occurring in each habitat which in turn are modulated by the flood pulse. The double dash on the river bed indicates variable river-bed width. The asterisk indicates emergent trees up to 30-40 m in height. Diagram produced by Yira Tatiana Onzaga Barreto, Social Communicator, the Wildlife Conservation Society.

regimes across the Amazon, and their interannual variability, are influenced by topography, distance from the sea, and global air circulation (i.e., the Intertropical Convergence Zone (ITCZ) and El Niño Southern Oscillation (ENSO; Hamilton et al. 2002, Schöngart and Junk 2007, Furley 2007). As the ITCZ moves north, the surface trade winds carry moisture-laden air from the Atlantic Ocean westward, generating heavy rainfall in Western Amazonia from April to July; the ITCZ then moves to the south and causes heavy rain in Central Amazonia from August to March (Furley 2007). The effect of the ITCZ, paired with the extensive latitudinal range of the Amazon Basin, results in a bimodal distribution in the timing of peak flooding, with the northern Amazon peaking in June, while the southern Amazon peaking earlier in mid-March. Moreover, the east to west movement of the ITCZ seems to slightly amplify upstream to downstream timing differences in Southern Amazonia and do the opposite in the Northern part of the basin. As a result, in southern tributaries peak flood generally occurs later closer to the mainstem Amazon River (i.e., peak flooding occurs earlier in upper portions of tributaries). But an opposite pattern is observed in northern tributaries. The date of peak flooding is generally later away from the mainstem Amazon (Figure 2A) (Siddiqui et al. 2021). The flooding magnitude, measured as deviations from baseflow, is more variable in the northern Amazon than the generally low dry-season baseflows in the southern Amazon (Figure 2B). In turn, the north and south bimodality in the timing of flooding leads to a longer than

expected flooding season, or backwater effect, for the main stem Amazon River and the 400-800 km lower reach of its tributaries which have monomodal flooding (Figure 2C) (Meade et al. 1991). Thus, climate and rainfall patterns, coupled with variable baseflows, result in the formation of diverse floodplain habitats across the basin.

Evidence of flood pulse change in Amazonia. Across the Amazon basin, the construction and operation of hydroelectric dams have been shown to alter nearly all components of the flow regime, but especially those related to the frequency of high and low pulses, the predictability and magnitude of flooding, and rate of change (or flashiness) from low to high water-level conditions (e.g., Assahira et al. 2017, Forsberg et al. 2017, Timpe and Kaplan 2017, Almeida et al. 2020). For example, computer simulations of the downstream effects of large dams planned in Western Amazonia showed a reduction in the maximum floodplain inundated area in Peru's Loreto region (Forsberg et al. 2017). On the Uatumã River (Brazil), a small tributary of the Amazon River, the Balbina dam delayed the flood pulse timing, altered its magnitude (i.e., lower maximum and higher minimum flows), and increased the frequency of high pulses downriver of the impoundment (Assahira et al. 2017). In the Madeira River (Brazil), the construction of two large dams, Santo Antonio and Jirau, affected downstream hydrology with significant increases in short-term (i.e., daily and hourly) flow variability (flashiness) and moderate changes in the annual flood

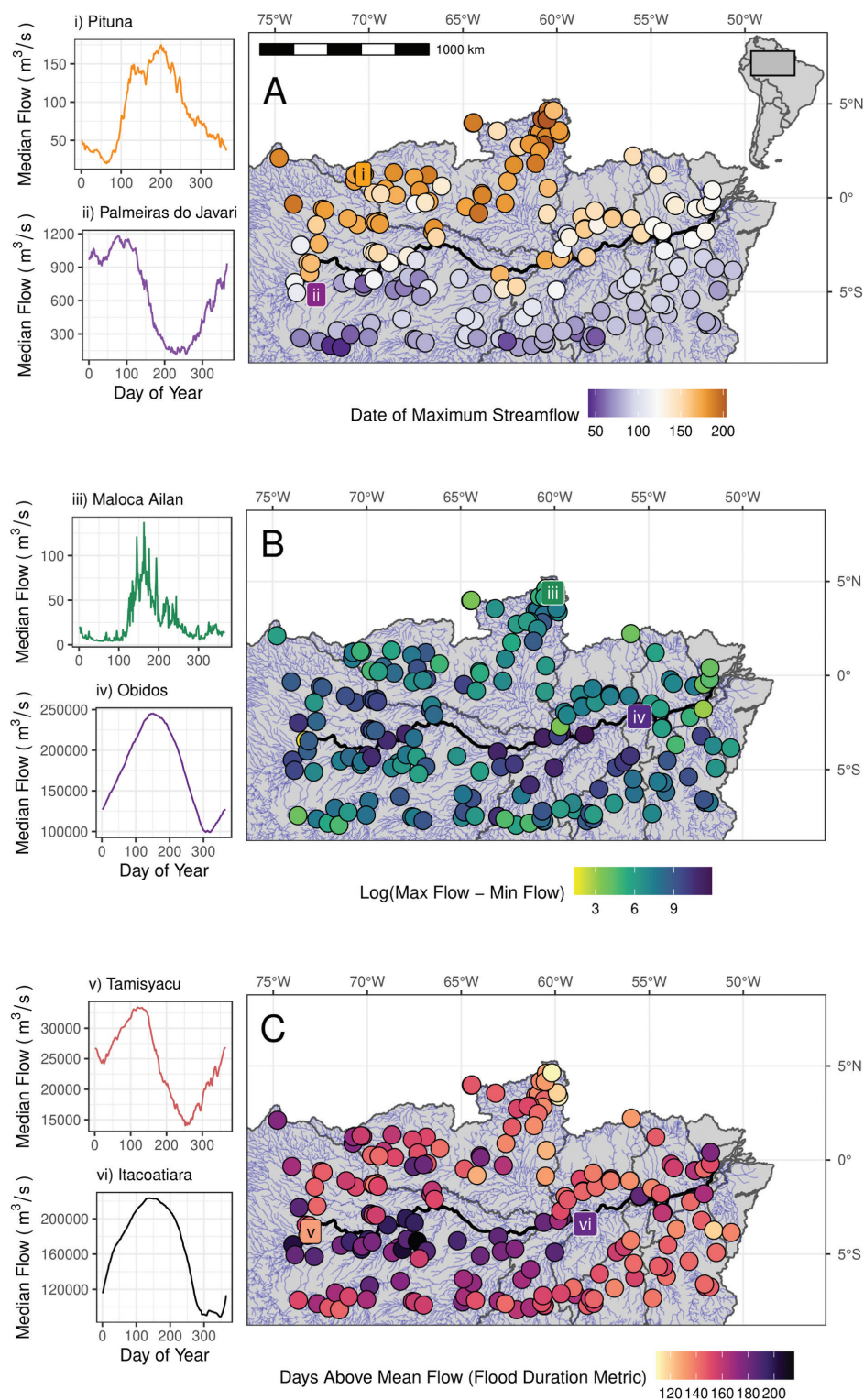


Figure 2. Hydrographs represent contrasting conditions in flood pulse attributes across Amazonia, including (A) timing (date of peak flooding), (B) the magnitude of change (m^3/s difference between maximum and minimum flow), and (C) flood duration (number of days above mean flow (m^3/s)). Notice differences in median streamflow magnitude. Gauge stations for hydrographs include (i) Pituna (Colombia), (ii) Palmeiras do Javari (Brazil), (iii) Maloca Ailan (Brazil), (iv) Óbidos (Brazil), (v) Tamisyacu (Peru), and (vi) Itacoatiara (Brazil). Streamflow stations mapped were selected as those within floodplain areas (designated by Venticinque et al., 2016) under 500 masl. Location of study area is shown in a rectangle in (A) with reference to the South American continent. Major tributaries are outlined as thick lines (Lehner & Grill, 2013) and the river network (Mayorga et al., 2012) is shown as thinner lines.

pulse (Almeida et al. 2020). Hydrological analysis of 33 dams in the Brazilian Amazon showed downstream alterations to the frequency and rate of change attributes of the flood pulse; the magnitude of such alterations increased at lower elevations with reservoir size (Timpe and Kaplan 2017). Despite efforts to quantify the downstream effect of dams on the flood pulse, we ignore how many floodplains basin-wide show evidence of flood pulse change, the size of affected areas, and the magnitude of such change.

In addition to dams, climate change may influence the flood pulse through increased variability of the strength of the El Niño and La Niña Southern Oscillations, effectively decreasing or increasing precipitation and streamflow, respectively (Costa et al. 2009). During the twentieth century, the extent of inundated floodplains was reduced by up to 12% in El Niño years (e.g., in 1952 and 1982; Foley et al. 2002). When El Niño coincides with the dry phase of the flood pulse (e.g., 1992–1993), exceptional low streamflow can result in a 45% reduction of the inundated floodplain area (Melack and Coe 2013). Moreover, such extreme drought events reduce the amount of water stored in floodplain lakes which play a crucial role in the basin's hydrological cycle by replenishing in-channel river flow (reviewed by Melack and Coe 2013). Climate change-induced variation in precipitation and concomitant effects on discharge and flooding can be exacerbated by deforestation, given the forest's contribution to the hydrological cycle (Nobre and Borma 2009).

Computer simulations of basin-wide deforestation scenarios show contrasting effects on climate and flooding. Modest deforestation (i.e., 35%) can decrease potential evapotranspiration rates relative to precipitation, thereby increasing runoff rates (Costa et al. 2009) and the extent of the inundated area by 6% average on the main stem Amazon River floodplain. However, drastic deforestation (i.e., 55% of the basin) can decrease precipitation relative to evapotranspiration, leading to a 5–10% decrease in the inundated floodplain area, particularly in El Niño years (Melack and Coe 2013). Drastic deforestation also can reduce flood duration. For instance, the number of years in which the inundated floodplain area was 50% smaller during four consecutive months nearly doubled in a 51-year time series simulation (Melack and Coe 2013).

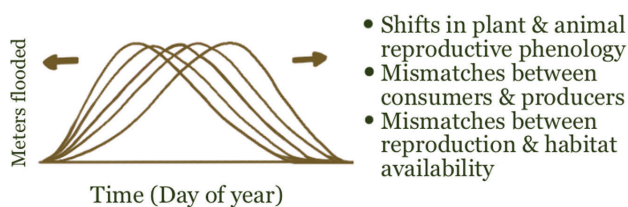
Long-term consequences of flood pulse alteration for floodplain ecosystems. On the basis of their exceptionally high biodiversity and numerous species interactions, Amazonian floodplains are home to complex ecosystems. Therefore, the ecological consequences of flood pulse change might be neither immediately apparent nor easily measurable. However, through progressive cascading effects, even subtle hydrological change could, in the longer term, lead to a substantial loss of biodiversity and ecosystem services in Amazonian floodplains. We focus here on the potential ecological consequences of change in three different aspects of the flood pulse: the timing, duration, and magnitude of

flooding (Figure 3). While we acknowledge that changes in other components of the flood pulse (e.g., water velocity) may also impact floodplain ecosystems, these three components exert a dominant effect on the composition and functioning of floodplain ecosystems (Ward 1989; Poff et al. 1997). In addition, we acknowledge that the components of flood pulse change listed below have partially overlapping ecological effects. Thus, some of the potential ecological consequences discussed are not restricted to only one hydrological change factor.

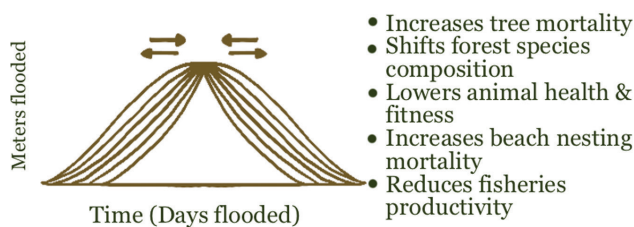
When?—The effects of changes in the timing (predictability) of flooding. Numerous plant families that dominate Amazonian flooded forests originated ≈ 100 million years ago (Correa et al. 2015). Flooded forests have persisted and dominated wetlands and river floodplains since the Andes uplift during the Miocene, which facilitated the evolution of adaptations to the flood pulse and strong species interactions (Wittmann and Householder 2017). Changes in the timing and predictability of flooding can affect plants and animals' life-history adaptations (i.e., synchronized life-cycle events) (Lytle and Poff 2004). For example, one remarkable adaptation of trees in Amazonian floodplains involves the community-wide synchronicity of fruit ripening with the annual flood season (Haugaasen and Peres 2005a, Hawes and Peres 2016). This adaptive strategy facilitates seed dispersal by water (Parolin et al. 2013, Correa et al. 2018) and by the numerous vertebrate frugivores that migrate to the flooded forest during the annual flood, including fish (Correa et al. 2015, Correa and Winemiller 2018), birds, and mammals (Haugaasen and Peres 2007, Bodmer et al. 2018). These interdependencies also suggest that alterations to the flood pulse and its predictability could lead to mismatches between tree fruiting and the presence of dispersal agents, such as fish, disrupting coevolutionary seed dispersal networks (Valiente-Banuet et al. 2015). The importance of effective seed dispersal for plant community resistance (ability to withstand disturbance) and resilience (recovering ability) is well established. Therefore, the disturbance of seed dispersal networks could profoundly affect forest regeneration (Araujo et al. 2021) and the abundance of animals dependent on tree seeds and fruits.

Alterations to the flood pulse and concomitant trophic mismatches between frugivores and fruit can also lead to behavioral and physiological changes in vertebrate frugivores. Under a normal flood pulse regime, the seasonal hyper-abundance of fruit drives seasonal shifts in the diet of frugivores from a fruit-dominated diet during the flood season to alternative, less preferred food types during the dry season (Correa and Winemiller 2014). If fruits are no longer available or become scarce, permanent diet shifts are likely. Permanent diet shifts among frugivorous fishes have been reported in response to translocation (e.g., *Piaractus brachypomus*, Serrasalminidae; Correa et al. 2014) or hydrological alteration after damming (e.g., *Mylossoma duriventre*, Serrasalminidae, *Brycon gouldingi* and *B. falcatus*, Bryconidae;

A. Timing / Predictability



B. Duration



C. Magnitude

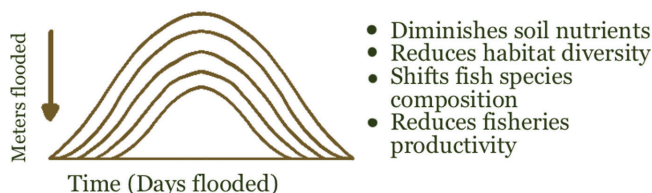


Figure 3. Conceptual model representing the ecological consequences of alterations to three attributes of the flood pulse: (A) timing, (B) duration, and (C) magnitude of flooding. Diagram produced by Yira Tatiana Onzaga Barreto, Social communicator, the Wildlife Conservation Society.

Albrecht et al. 2009, Melo et al. 2019). A fruit-dominated diet, rich in carbohydrates, provides the energy that supports the metabolism of frugivores (Correa and Winemiller 2018). Trophic mismatches between frugivores and fruit availability would no longer sustain fat deposits in frugivores (Junk 1985). Such mismatch can affect the health of frugivores through a reduction in body condition (i.e., lower weight for a given length), and alterations to their reproductive phenology. Community-wide alterations in body condition, with increasing or decreasing trends, driven by changes in food availability and quality have been reported in a broad array of consumers (e.g., Neotropical freshwater fish, Pereira and Agostinho 2019; frugivorous birds, Campo-Celada et al. 2022; marine fish, birds, and mammals, Harwood et al. 2015). Long-term consequences of low body condition include decreased growth rate, shorter individuals, smaller stocks, and reduced fitness (Harwood et al. 2015).

The flood pulse also triggers fish migrations at different times relevant to spawning, dispersal and feeding. For

migrating species, most of which spawn at the onset of the flooding season, a fast-rising river constitutes a strong signal to start the spawning migration and accelerate gonad development (e.g., Brito and Petrere 1990, Barthem et al. 2017). Other behavioral aspects of fish reproductive cycles—not just for regional or continental migratory species but also for sedentary or locally migratory species—rely on cues related to the flood pulse. For example, falling waters prompt *Arapaima* spp. (Arapaimidae) populations to migrate from flooded floodplains to permanent lakes and their connecting channels, where they build nests and spawn (Castello 2008). Loss of reliable hydrological cues relevant for successful spawning may reduce and delay reproductive output, with negative effects on the age class of that year (Ribeiro and Petrere-Jr 1990).

How long? – The effects of changes in the duration of flooding. The effects of changes in flooding duration are complex and highly species-specific. For floodplain trees, long-term flooding is ultimately a stress factor. Tree root systems are susceptible to oxygen deprivation during prolonged flooding. Floodplain trees exhibit strategies to alleviate hypoxic and anoxic conditions (e.g., Parolin et al. 2004, Haase and Rättsch 2010, Piedade et al. 2010). Therefore, the ability to withstand prolonged flooding is a strong driver of tree species composition in Amazonian floodplain forests (e.g., Ferreira 1997; Wittmann et al. 2004; Householder et al. 2021). An increase in flooding duration can lead to tree mortality, as it was recently shown for tree species at the lowest floodplain topographies on the Uatumã River in the Central Amazon basin (Assahira et al. 2017, Resende et al. 2019). Tree mortality occurred during periods of consecutive years of inundation caused by implementing a hydro-power dam. Although many floodplain tree species also occur outside floodplains (Wittmann et al. 2013), shortening of the flooding duration, on the other hand, may cause an increased dominance of tree species primarily associated with higher topographies on the floodplain and upland forest. Thus, changes in flooding duration could lead to floodplain truncation (see below) and to a substantial turnover of species in floodplain forests (Wittmann et al. 2019).

For most Amazonian fish in main river channels, the dry season is a period of limited food availability due to low in-situ productivity (Goulding et al. 1988). In contrast, the flooding season furnishes a period of plenty due to the elevated availability of allochthonous foods in a greatly expanded aquatic environment. Many fish species, and most migratory characiforms, rely primarily on fat reserves, built up by heavy feeding during the floods, to survive the dry season (Goulding 1980, Junk 1985). The dry season is also a period of high predation risk for fish, given that in most areas, their aquatic habitat retracts to a volume that is only a fraction of that during the flooding season (Crampton 2011). Therefore, changes in the duration of flooding affect the productivity of fish populations and survival rates, ultimately affecting fishery yields. Long floods have been found

to boost fishery yields in subsequent years (Castello et al. 2015, Lima et al. 2017), whereas long dry seasons promote smaller-than-normal catches. Alternatively, in some areas, the accumulation of dry organic matter can be an important driver for aquatic productivity during the following flood season. This means that the duration of the dry period could also be significant for some aquatic species (Sabo et al. 2017).

Many Amazonian fish species also depend on floodplain forests as breeding and rearing grounds (e.g. van der Sleen and Albert 2017, van der Sleen et al. 2020). A shortening of the flooding period may reduce the recruitment season for several species. In addition, lengthening of the low-water season may reduce fish body condition and thus reproductive output at the start of the flooding season. Indeed, the recruitment of long-distance migratory fish is known to be positively related to flooding duration and timing (Agostinho et al. 2004, Suzuki et al. 2009). On the other hand, a shorter dry season may affect species that depend on sandbanks for nesting sites, such as bird and reptile species (e.g., birds—*Phaetusa*, *Rhynchops*, *Sternula*: Zarza et al. 2013; turtles—*Podocnemis*: Escalona et al. 2009). For turtles, shortening the time when unflooded areas are available could increase mortality by drowning of unhatched turtles and by increased nest disturbance by predators and other laying females (Eisemberg et al. 2016). Interspecific differences in breeding behavior make some species more vulnerable than others to changes in flood regimes. *Podocnemis expansa*, for instance, nests on the upper part of sandbanks, while *P. unifilis* nests closer to the water (Ferreira Júnior and Castro 2010). For sandbank-using birds, reductions in physical areas available for nesting are expected to be severe (Austad 2016). As nesting requirements are quite precise, populations are likely to decline not only from the loss of available breeding space but also because of increased aggression between nest-holders which is already a significant cause of mortality (Ramos 2003; Villanueva-Gomila et al. 2009). In addition, nesting sites for several species of river turtles (e.g., *Peltocephalus dumerilianus*, Vogt et al. 1994) and crocodilians (e.g., *Melanosuchus niger*, Villamarín-Jurado and Suárez 2007) often is limited due to their prolonged incubation times and need of large volumes of vegetation for nest construction (e.g., *M. niger*, Banon et al. 2019). This may lead to an increased frequency of communal nesting sites (e.g., *Caiman crocodilus*, Cunha et al. 2016) under climate change conditions (Villamarín et al. 2011). Changes in water levels following dam construction have been recorded as severely disrupting caiman reproductive patterns (Campos 2019). In addition, all Neotropical crocodilians have temperature-related sex-determination (Piña et al. 2003), thus alterations to nesting sites driven by flood pulse changes may also have long-term effects on sex-ratios (Valenzuela 2001).

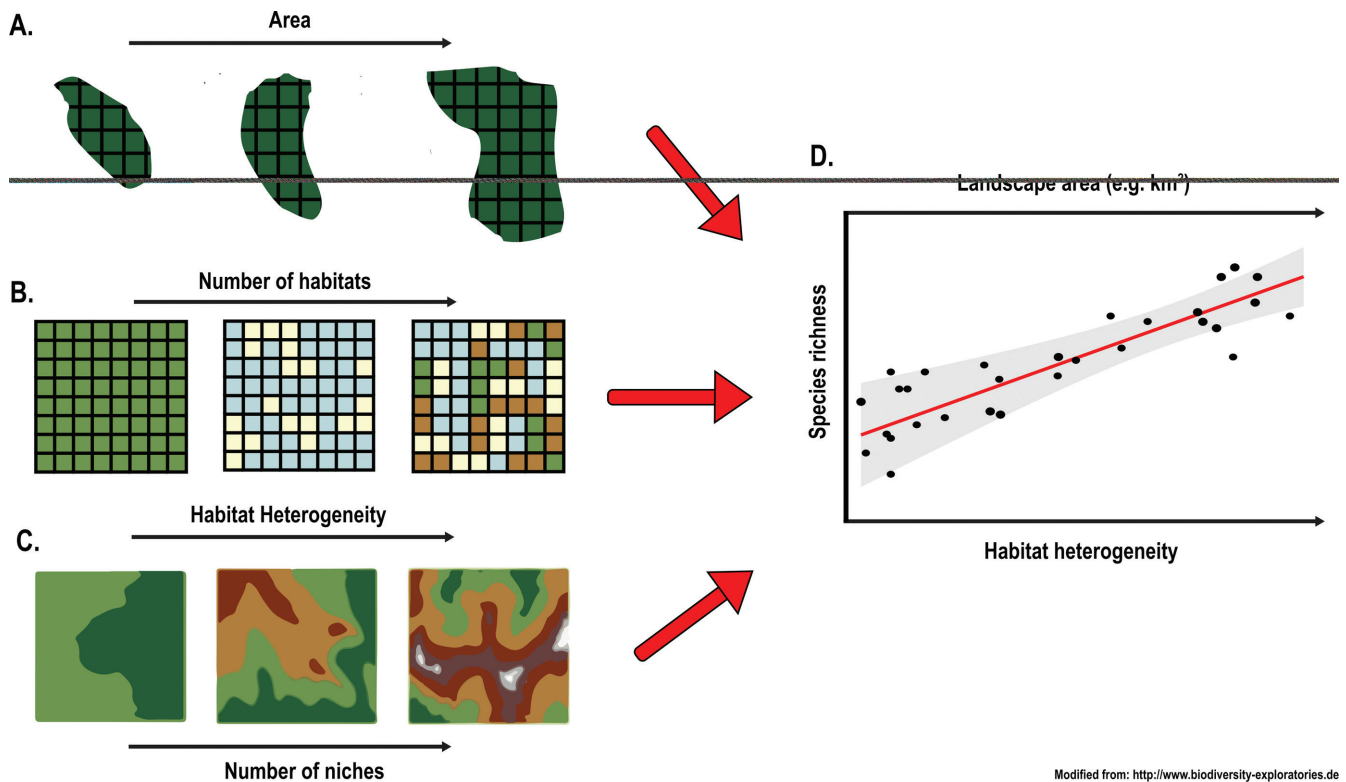
Changes in flooding duration causing tree mortality and turnover of tree species in floodplains can have cascade effects on dependent mammal communities. While some primate species visit flooded forests occasionally (Haugaasen and Peres, 2005b, 2007, 2009), several primate

species spend most of the year within flooded forests. Yet others are entirely dependent on flooded forests (e.g., *Cacajao calvus calvus*, *Saimiri vanzolinii*: Paim et al. 2019) and may respond strongly. Leaf and fruit production timing in flooded and non-flooded adjacent habitats is non-synchronous (Haugaasen and Peres 2005a; Hawes and Peres 2016). Such divergence in the temporal distribution of food resources influences the movement of flooded-forest specialist primates (e.g., *Cacajao ouakary*, Barnett et al. 2005; *Chiropotes albinasus*, de Oliveira et al. 2016) to the adjacent non-flooded forest when suitable resources are no longer present in viable quantities. The presence of the two adjacent habitats appears key to population survival; uakari monkeys (*Cacajao* spp.) are absent from areas of the lower Rio Negro that lack flooded forest, while populations are sparse in flooded forests that lack an adjacent non-flooded hinterland (Rocha 2016).

How high? – The effects of changes in the magnitude of flooding. The annual advance and retreat of river waters over their adjacent floodplains induce lateral exchanges of organic and inorganic materials between river channels and floodplains that increase primary production (Melack and Forsberg 2001). Andean-origin tributaries deposit nearly 500 Tg of sediment and nutrients onto their floodplain annually (Dunne et al. 1998, McClain and Naiman 2008), and in the process create and maintain thousands of square kilometers of floodplain habitat in the lowland Amazon (Lessmann et al. 2016). Lower or higher flooding magnitude may affect deposition rates and floodplain soil fertility in the long term.

Reduction of flooding magnitude will also effectively reduce the size of the floodplains as it will inhibit flooding at higher topography. As mentioned above, numerous herbivorous, insectivorous, and omnivorous fishes store fat by exploiting foods seasonally available in floodplain forests during the annual flood pulse's high- and falling-water periods (Junk 1985). As a result, they time gonad maturation and spawning to the subsequent dry- and rising-water seasons, respectively, to capitalize on accumulated fat (Röpke et al. 2019). Fish fecundity, for instance, increases in females reproducing a year after a strong flood season (i.e., long duration and magnitude; Röpke et al. 2019). A decline in floodplain forest extent will lower fish biomass and decrease fisheries yields for all if not most trophic groups, including surface and benthic dwellers (Castello et al. 2018, Arantes et al. 2019b, de França Barros et al. 2020). Consequently, shrinkage of floodplain forest extent will ultimately affect the livelihoods of millions of people who are dependent on fishery resources in the Amazon basin.

The loss of floodplain forest extent induced by a lower flood pulse may also influence ecosystem processes and functions via a decline in structural complexity (Mensah et al. 2020) and by reducing or eliminating permanent water bodies such as oxbow lakes (Reis et al. 2019). Habitat heterogeneity at a landscape scale, in combination with habitat size, likely explains the high concentration of species in



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Figure 4. The habitat heterogeneity—largely determined by the mosaic structure of meadow and forest habitats associated with the floodplains (A)—most likely promotes the number of niches (B) (Carvalho et al. 2016) and species diversity per unit area (C, D) (Henderson and Robertson 1999).

many animal and plant groups associated with floodplain landscapes (Figure 4). Studies of a variety of Amazonian taxa provide support for this hypothesis. For example, the structural complexity of floodplain habitats in the Central Amazon drives fish species richness (Henderson and Robertson 1999) and beta diversity (Siqueira-Souza et al. 2016). Floodplain forest loss has been directly linked to spatial homogenization of fish assemblages and reduced functional diversity (Arantes et al. 2018, 2019b). A lower flood pulse can also affect the availability of floating meadow habitat for juvenile fishes (Petry et al. 2003), with negative consequences for biodiversity as adjacent floodplain meadow and forest habitat support different fish assemblages (Correa et al. 2008; Siqueira-Souza et al. 2016). Thus, habitat heterogeneity is fundamental at a local scale because it facilitates spatial segregation, species coexistence, and the maintenance of biodiversity (Rosenzweig 1995, Morris 2003, Leibold and McPeck 2006).

A lower flood pulse may also increase the area covered by relatively shallow water. Shallower habitats support lower fish species diversity and abundance (Petry et al. 2003, Arantes et al. 2013). A change in depth shifts community composition (Miranda 2005). In particular, shallower waters associated with low dissolved oxygen (DO) favor air-breeding and hypoxia-tolerant species (Miranda 2005) and negatively affect pelagic piscivore species that are intolerant

of hypoxic conditions (Junk et al. 1997). Even species that tolerate hypoxia (e.g., *Arapaima* spp. and *Hoplias malabaricus*) can be affected by hydrogen sulfide (H_2S), which is often associated with low DO (Petry et al. 2003). Therefore, a smaller flood pulse and the associated reduction, or loss, of floodplain habitat can have profound cascading effects on biodiversity.

A lower flood pulse may also affect dry-season food availability within the floodplain forest, with potential community-level consequences. Numerous terrestrial vertebrates consume seeds as receding water deposits floating seed mats on the forest floor (Antunes et al. 2019). A lower flood pulse will reduce the size of the inundated area and hence restrict the extent of such seed mats to the river's shore. These seed mats are present at a period when seed availability is low in the adjacent non-flooded forest, leading to high visitation rates and voluminous seed removal (Haugaaen and Peres 2005a). Consumers include floodplain-forest-dependent primates that descend from the canopy (Barnett et al. 2012), as well as granivores (e.g., rodents) and herbivores (e.g., deer and tapir that feed on the germinating shoots) that migrate from the adjacent non-flooded forest (Antunes et al. 2019). Carnivores (e.g., jaguar and ocelots) track both groups (Barnett et al. 2012; Antunes et al. 2019). Lower seed availability could increase the frequency of caiman-egg removal by primates (Torralvo et al. 2017) and nest-guarding caiman

predation by jaguars (da Silveira et al. 2017). The importance of resource pulses such as these seed mats in supporting terrestrial vertebrate diversity has yet to be quantified (e.g., see Correa and Winemiller 2014 for fish).

In contrast, a higher flood pulse may affect the survival of sandbank-nesting turtles and birds in the Amazon. Some river turtles excavate nests up to 60 cm deep, creating the potential to place them below the water table as waters rise (Norris et al. 2018a). Low elevation coupled with lateral infiltration of water in sandy soils, means that effective areas suitable for nesting may be much smaller than what appears above the water level (Norris et al. 2020). For sandbank-nesting turtles and birds, inundation and erosion of existing sites are likely to lead to crowding, resulting in reduced reproductive success because of interference (Santos Arraes et al. 2016). In addition, some nesting sites may be lost completely, and the capacity for adjustment at the individual- and population-level is currently little studied, although transplantation is a management option (Ribeiro and Navarro 2020; Norris et al. 2018b).

Tracking flood pulse alterations in Amazonian

Within a floodplain, slight differences in elevation of a few centimeters per kilometer make a difference in flood duration (i.e., water retention time) and the direction of water flow (Melack and Coe 2021). Hydrological (vertical flow) and hydraulic (lateral flow) modeling of Amazonian floodplains advanced tremendously over the last three decades thanks to improved remote sensing technology and multi-satellite analytical approaches (reviewed by Fassoni-Andrade et al. 2021). Yet modeling the flood pulse within dense floodplain forests and floating macrophytes is still hindered by the lack of high-resolution digital elevation models that capture fine-scale changes in topography (Fassoni-Andrade et al. 2021, Melack and Coe 2021). Although the daily discharge of many large rivers is currently monitored by water-level gauges, mainly in the Brazilian Amazon, these gauges are located in river channels and do not capture fine-scale hydrological variability within floodplains (e.g., overbank flooding versus flooding through channels; Melack and Coe 2021). Exacerbating these challenges is the reality that different institutions independently manage river gauges within the eight countries and one overseas territory that comprises the Amazon basin. Limited coordination between institutions and governments makes it extremely difficult to access data for basin-level analyses.

Monitoring flood pulse change in Amazonia. As climate change and dam construction progress, the flood pulse needs to be monitored at a high temporal and spatial resolution that reflects hydrological influences on ecological processes (e.g., plant zonation and lateral fish migrations). Adequately monitoring alterations to the flood pulse requires establishing a network of regional observatories that are equipped with sensors within floodplains at different reaches (upper, middle, lower) in the large northern and southern tributaries

(e.g., Japura, Negro, Madeira, Trombetas, and Tapajos rivers). Other priority areas are wetlands in large depressions (e.g., Pacaya-Samiria National Reserve, Peru). A network can be established by building upon existing infrastructure in national parks, sustainable use and nature reserves, and biological stations across the basin and creating infrastructure within indigenous territories. Training local staff and indigenous peoples and investing in internet connectivity can facilitate the maintenance of equipment and data collection in remote areas. Protocols from ongoing efforts to monitor flood pulses in other regions (e.g., United States Environmental Protection Agency, <https://www.epa.gov/wetlands/how-do-i-develop-wetlands-monitoring-program>) can be adapted to the context of the Amazon region. Data loggers that record flooding on an hourly basis can be deployed in transects within floodplains to access spatiotemporal variability. Other variables of importance that influence the flood pulse include precipitation, temperature, and groundwater storage. A network approach will allow data sharing, standardization of methodologies (sensor types, variables recorded, and frequency of data collection), data access to the scientific community, calibration of remote sensing data, and data integration.

Assessing flood pulse change in Amazonia. Leveraging tools from the early warning signals and tipping point literature (e.g., Scheffer et al., 2012; Dakos et al., 2012) may further contextualize the scale and pace of ongoing and future hydrologic alterations in the Amazon Basin. Yet, the concept of tipping points has been scarcely applied in hydrological studies for several reasons. A major issue is that hydrology tends to be used both as a driver and a control variable in tipping point studies, which hinders inference on cause-effect (Jaramillo et al., 2020). The spatial-temporal scale at which hydrologic tipping points are identified requires long-term data series which often are not available (e.g., time series when the hydrologic record has greater length and sampling frequency relative to its potential drivers – climate and deforestation; Krueger et al., 2019). In addition, hydrologic tipping points are often thought to be driven by shifts in climate and landscape which precludes searching for other drivers (Jaramillo et al., 2020). Acknowledging these shortcomings, we propose that the inclusion of hydrological tipping point analyses (e.g., early warning signal analysis; Scheffer et al. 2012, Dakos et al. 2012) could be used to quantify the effects of large-scale drivers of change on hydrological systems. In general, the determination of early warning signals may use metrics-based and/or model-based approaches. Metrics such as variance, critical slowing down, and conditional heteroskedasticity have been shown to be useful at monitoring signals of early warning tipping points in climate and forest cover change (Scheffer et al. 2012, Dakos et al. 2012). A model-based approach quantifies changes in time-series data (i.e. time-varying or threshold-based autoregressive models) to simulate environmental conditions and occasional shifts in alternative stable states. The advantage of a

Table 1. Proposed monitoring proxies to detect large-scale ecological change induced by alterations to the flood pulse regime in Amazonian floodplains

Biotic Proxies	Drivers	Responses	Indicators
1) Floodplain forests	<ul style="list-style-type: none"> • Flooding stress • Drought stress • Fire 	<ul style="list-style-type: none"> • Tree mortality 	<ul style="list-style-type: none"> • % forest cover • Floodplain extent • Habitat heterogeneity
2) Fish assemblages	<ul style="list-style-type: none"> • Flow regime • Environmental cues 	<ul style="list-style-type: none"> • Predictable shifts in assemblage composition (functional groups) • Loss of early life stages • Reduced fisheries 	<ul style="list-style-type: none"> • Species composition • Distribution • Abundance • Life stage • Catch per effort • Body size
3) Floodplain-forest-specialist fauna	<ul style="list-style-type: none"> • Trophic mismatches 	<ul style="list-style-type: none"> • Permanent diet shifts • Lower survival • Decreased fitness 	<ul style="list-style-type: none"> • Diet • Health (weight/length) • Reproductive timing • Reproductive effort
4) Beach-specialist fauna	<ul style="list-style-type: none"> • Flow regime 	<ul style="list-style-type: none"> • Loss of beach nesting habitat • Loss of riparian nursery habitat 	<ul style="list-style-type: none"> • Sex ratio • Age structure • Birth rates • Mortality rates

model-based approach is that sensitivity analysis and testing model parameters can isolate the role of a driver on short to long-term hydrologic variability (Ives & Dakos, 2012). Prior to calculation, it should be noted that the data is appropriately related to a hydrologic response variable, be of sufficiently long-time span, and have a measurement frequency suitable for determining proximity to a tipping point (Thompson and Seiber, 2011).

Biotic indicators of ecosystem state change in Amazonian floodplains

Given the potential ecological consequences of changes in the flood pulse to biodiversity, as described above (figure 3), here we identify biotic indicators that could flag the onset of significant ecosystem change, and that should have a high priority in long-term monitoring efforts. We identify four biotic proxies likely to show strong responses to alterations of the flood pulse and that may serve as indicators of floodplain ecosystem state change (Table 1, Figure 5).

Floodplain forests. Tree mortality can follow almost immediately after inundation periods that extend beyond a tree’s maximum flooding tolerance (Assahira et al. 2017, Resende et al. 2019). Thus, tree mortality, particularly at the lowest part of the flooding gradient, could be one of the first apparent consequences of flood pulse change. However, changes in the flood pulse can also lead to tree mortality at higher topographies since shorter flooding seasons may induce drought stress for trees during the dry season and/or increase the risk of forest fire (Flores et al. 2016, 2017). Tree mortality could ultimately lead to a loss of tree cover in floodplains, and a shift to a more open vegetation state, as observed in the Rio Negro basin (Figure 5A-B; Flores and Holmgren 2021). Thus, the percentage of tree cover per unit area can be used as one of the primary indicators of floodplain ecosystem state change. In addition, monitoring landscape attributes can help identify landscape complexity losses and if mitigation is implemented, avoid species losses

given the positive relations between habitat area and heterogeneity with species richness (Figure 4). We recommend monitoring changes in floodplain extent and the percent of habitat types (e.g., lakes, channels, forests) per unit area.

Changes in tree cover, habitat area, and landscape heterogeneity in floodplains could be identified using remote sensing data (but see Kalacska et al. 2020 for methodological considerations), as well as by extending the network of permanent forest sampling plots in Amazonian floodplains (e.g., Amazon Tree Diversity Network, Amazon Forest Inventory Network-Rainfor and Center for Tropical Forest Science-CTFS). Still, vast areas in the Amazon currently lack any inventory- and/or long-term monitoring plots, particularly in the western and southeastern Amazon. For both inventory plot- and remote sensing data, it is essential to recognize that floodplains consist of gradients in flooding duration that drive patterns in tree species composition (Ferreira 1997; Wittmann et al. 2004; Householder et al. 2021). Such gradients, and thus site selection, are important to acknowledge and account for when using monitoring networks or remote sensing approaches to assess the impact of flood pulse change, as its impact may depend on site topography.

Fish assemblages. Alteration of the flood pulse, and associated changes in floodplains, can result in relatively predictable shifts in fish assemblage composition (Arantes et al. 2019a). Thus, monitoring fish assemblage structure can serve as an indicator of state change. For example, generalist species with pelagic behavior and low dispersal capacity (including piscivores adapted to lentic environments) and species with high diet plasticity may be relatively tolerant to change in the duration and magnitude of flooding. Indeed, some species in the genera *Cichla* (Cichlidae), *Serrasalmus* (Serrasalminidae), and *Hypophthalmus* (Pimelodidae) have been reported to increase in abundance in areas affected by hydrologic alterations from hydropower dams (Figure 5C-D; Arantes et al. 2019a). On the other hand, periodic strategists (i.e., those

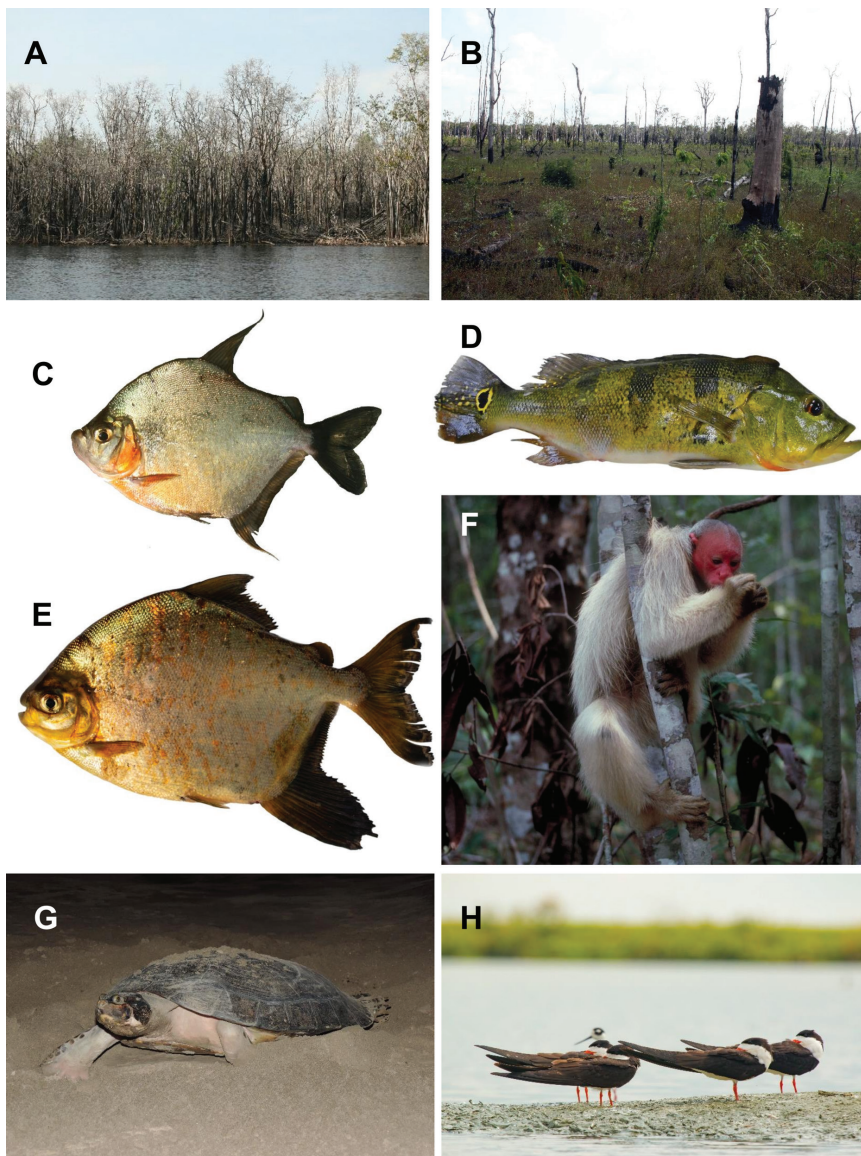


Figure 5. Proposed biotic indicators of state change in Amazonian floodplains. Floodplain forest tree mortality in the middle Rio Negro (Brazil), photographed in 2017, at a recently burned site (A), and at a site that remains in an open vegetation state after burning in 2010 (B). Species adapted to lentic environments include *Catoprion mento* (C) and *Cichla* spp. (D). Flooded forest specialist fauna includes frugivorous species such as *Myloplus asterias* (E) and White Uakari (*Cacajao calvus calvus*) (F). Beach specialist fauna includes beach-nesting *Podocnemis expansa* (G) and *Rynchops niger* (H). Photo credits: (A-C) Peter van der Sleen, (D) Caroline Arantes, (E, H) Jorge Garcia-Melo, (F) Michael Goulding, (G) Barthira Rezende de Oliveira.

with late maturity, high fecundity and low juvenile survival), rapid (rheophilic) and/or bottom dwellers, and feeding specialists may be particularly vulnerable to changes in flow characteristics, and so are likely to experience rapid declines (Miranda 2005, Arantes et al. 2019a). Likewise, reduction of floodplain extent can be followed by declines in the abundance/biomass of species that have strong associations with flooded forests. These include frugivores, detritivores, and

equilibrium strategists (i.e., those with late maturity, low fecundity, and high juvenile survival) (Arantes et al. 2019b). The resulting would be a fish assemblage likely dominated by species that benefit from increased primary production in open waters (e.g., planktivores). Fish monitoring-data can be used as input for threshold indicator analysis (e.g., TITAN, Gradient Forest; Baker and King 2010, Chen and Olden 2020) to detect effects of flood pulse change and landscape disturbance on fish assemblages.

Additionally, the monitoring of earlier life stages of fish assemblages has been relatively overlooked (Zacardi et al. 2020) but can provide insights into flood-pulse-change influences on reproduction dynamics, spawning grounds, and fish species recruitment. Like incubation of eggs and larval development, the initiation of fish spawning is strongly related to flood pulse timing, magnitude, and duration and responds to these attributes in various degrees depending on species identity (Zacardi et al. 2020, Mariac et al. 2021). Monitoring data on egg and larval composition, distribution, and abundance can thus provide valuable early indicators of the effects of flood pulse change and ecosystem state change.

Ultimately, alterations in fish assemblage composition can cause profound effects on fisheries, with potential declines in the yields of those species that are less resilient to changes in flooding attributes. Thus, although responses are likely to be slower than observed for the fish assemblages (e.g., potential delays in responses may be observed), or can be initially hidden by shifts in fishing gear and fishing effort, monitoring fishery aspects, including catch per unit effort, as well as species composition, body size and weight in yields can inform the status of fishery production in relation to flood pulse changes.

Floodplain forest specialists. Floodplain forest specialists can act as sentinels for floodplain ecosystems, based on their dependence on floodplain habitat and food resources. Specialists include frugivorous fishes such as *Colossoma macropomum*, *Piaractus brachypomus*, *Myloplus* spp. and *Myleus* spp., birds such as the Varzea Piculet (*Picumnus varzeae*) and Scaled Spinetail (*Cranioleuca muelleri*), and primates such

as Golden-backed uacari (*Cacajao ouakary*), White Uakari (*Cacajao calvus calvus*), and Black Squirrel Monkey (*Saimiri vanzolinii*) (Figure 5E-F). Monitoring floodplain frugivores' feeding habits and health could help detect permanent diet shifts or lower body condition, respectively, which can serve as indicators of ecosystem state change. Lastly, the detection of delays in reproduction or lower fecundity by monitoring the reproductive phenology and reproductive effort of floodplain-forest specialists can also serve as indicators of ecosystem state change. Multi-year monitoring should focus on small-sized/short-living vertebrates that are likely to respond faster than long-living species to changes in the flood pulse. Ideally, monitoring of consumers should be coupled with monitoring of food production.

Beach specialists. Animals specialized in foraging and nesting in fluvial beaches have their natural histories deeply connected to the hydrological cycle and, as such, are susceptible to flood pulse alterations. Detection of demographic changes in populations of beach-dependent species (e.g., turtles and shorebirds) can be a highly effective indicator of ecosystem state change (Figure 5G-H). This strategy can capitalize on an existing network of nest-site conservation programs (Fagundes et al. 2021; Mogollones et al. 2010) and combine academic and citizen science approaches (Norris et al. 2018b) to facilitate implementation.

Conclusions and recommendations

River floodplains constitute a critical ecosystem that supports unique biodiversity and ecosystem services in the Amazon. Just as rainfall modulates ecosystem processes in rainforests (Malhi et al. 2008) and can drive ecosystem state change (Lovejoy and Nobre 2018), we emphasize how flood pulses drive the functioning of Amazonian floodplain ecosystems. Along with controlling headwater, upland, and wetland deforestation and pollution effects on water quality, the long-term conservation of aquatic biodiversity in the basin also depends on maintaining the key attributes of the flood pulse: timing, duration, and magnitude (Figure 3). Aside from a few studies assessing changes to the flood pulse downstream from hydropower dams and computer simulations of the effects of climate change and deforestation, there is very limited documentation of how the flood pulse of Amazonia is changing. To advance this knowledge gap, it is critical to track flood pulse change and monitor biotic indicators of ecosystem state change which will provide crucial information for policy decisions aimed at mitigation.

Long-term environmental and biological monitoring in the Amazon is challenging due to the region's enormous size, remoteness, and lack of institutional monitoring infrastructure in many areas, the scarcity of research institutions, and limited funding for long-term monitoring. Given these challenges, proxies are needed to identify ecological state changes. Such biotic proxies could include tree mortality, fish assemblage structure, the abundance and health of floodplain-forest plant and animal specialists, and beach

specialist species. In addition, we recommend creating a basin-wide network of automated data loggers to monitor hydrological change in floodplains specifically, to complement the current monitoring of river channel flow dynamics. A network approach will ensure adapting standardized protocols and create opportunities for remote sensing and in-situ data integration.

Scientists working in collaboration with subsistence fishers and hunters will benefit from their long-term local ecological knowledge of past and current conditions (García-Quijano 2007). Local communities can play an essential role in monitoring change, while their involvement can empower youth to pursue advanced education and training. Such an approach would be fruitful for ensuring the continuity and quality of data collection and enhancing stakeholders' understanding of the long-term consequences of environmental change for Amazonian aquatic ecosystems and the people that depend on them.

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