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Limnological perspectives on conservation of floodplain lakes in the Amazon basin

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Abstract

1. Limnological aspects of Amazon floodplain lakes are examined in the context of aquatic conservation.
2. A prerequisite to detecting and evaluating changes that could threaten the ecological health and organisms in floodplain lakes is understanding variation under present conditions. Based on one of the few studies with regular measurements over 2 years, chlorophyll, total phosphorus, dissolved oxygen, transparency, and total suspended solids in Lake Janauacá indicate that the lake is naturally quite variable with a mesotrophic to eutrophic status.
3. Direct threats to ecological health of floodplain lakes include mining operations that can increase turbidity and trace metals and reduce nutritional quality of sediments. Mercury contamination and methylation leads to bioaccumulation in aquatic organisms.
4. Deforestation in uplands increases nitrogen and phosphorus inputs to floodplain lakes and can alter trophic status. Deforestation in floodable forests alters the habitat and food of the fish that inhabit these forests.
5. Cumulative limnological responses as catchments are altered by urban, agricultural, and industrial developments, and as inundation is altered by changes in climate and construction of dams, have major implications for the ecology of floodplain lakes.
6. To improve understanding and management of threats to the conservation of aquatic Amazon biota and ecosystems requires considerably expanded and coordinated research and community-based management that includes the spectrum of floodplain lakes throughout the basin.

KEYWORDS
climate change, ecosystem approach, floodplain, impoundment, lake, mining, water quality

1 | INTRODUCTION

Floodplains with their lakes and associated vegetated habitats are an integral part of the complex hydrological and biogeochemical systems of the Amazon basin. As a consequence of recent, integrated research programmes, such as the Large-scale Biosphere–Atmosphere experiment, an understanding of atmospheric, terrestrial, and aquatic processes, their variability and changes in the Amazon basin has advanced substantially (Gash, Keller, & Silva-Dias, 2009; Nagy, Forsberg, & Artaxo, 2016). Field measurements, remote sensing, and modelling have contributed to an appreciation of the important role of aquatic habitats within the basin (Costa, Coe, & Guyot, 2009;

Melack, 2016; Melack, Novo, Forsberg, Piedade, & Maurice, 2009; Richey, Krusche, Johnson, da Cunha, & Ballester, 2009). Major threats to the ecological integrity of the aquatic habitats are becoming apparent (Castello & Macedo, 2016).

Floodplain lakes, a major aquatic habitat throughout the Amazon basin, are critical for the conservation of aquatic ecosystems and organisms. This article synthesizes threats to Amazon floodplain lakes caused by human activities in light of their limnological characteristics, and discusses implications for promoting their conservation. To do so, key limnological concepts, general aspects of Amazon floodplain lakes, and aquatic conservation issues related to Amazon lakes are presented. Since a prerequisite to detecting and evaluating changes is understanding current natural variability, temporal variability in one well-studied floodplain lake (Janauacá) and comparative data from other lakes are presented. Examples of specific threats to Amazon lakes are examined, and likely limnological changes in the future and their implications for aquatic conservation are discussed.

1.1 | Limnological concepts

Limnology, a synthetic science, includes aspects of geology, geomorphology, hydrology, ecology, hydrodynamics, environmental chemistry, biogeochemistry, public health, and most areas of biology, as they pertain to inland waters (Kalff, 2002; Wetzel, 2001). Hence, the inherently multidisciplinary nature of limnology can synergistically combine understanding of the physical, chemical and biological characteristics of aquatic systems and their interactions. With appropriate data, experiments, and modelling, cumulative impacts of environmental changes and threats can be identified and possibly managed.

Physical aspects, such as optical properties, temperature and frequency and depth of mixing, influence chemical and biological conditions. Underwater optical conditions are determined by amounts of phytoplankton, dissolved organic carbon (DOC) and suspended sediments. Hydrological inputs via precipitation, groundwater, streams and mainstem rivers, and losses via surface and sub-surface outflows convey dissolved and particulate material into and out of lakes. Many substances with a wide range of concentrations including major solutes, nutrients (nitrogen, phosphorus, silicon, and some metals) and pollutants (e.g. pesticides, mercury) occur in lakes. Interactions of physical and chemical conditions with the rich biological diversity of lakes, spanning archaea, bacteria, phytoplankton, attached algae, aquatic plants, invertebrates, amphibians, fish, aquatic birds, and mammals, combine to influence the functioning of these aquatic ecosystems.

1.2 | Amazon floodplain lakes

Amazon floodplains contain thousands of lakes and associated wetlands (Hess et al., 2015; Sippel, Hamilton, & Melack, 1991), characterized by large seasonal and inter-annual variations in depth and extent of inundation (Paiva et al., 2013). At low water, floodplain lakes are shallow, and parts are dry, allowing growth of rooted herbaceous plants (Junk, 1997). During rising and high water, lakes expand and encompass flooded forests (Junk, Piedade, Wittmann, Schöngart, & Parolin, 2010) and seasonal growths of floating aquatic plants (Engle, Melack, Doyle, & Fisher, 2008; Silva, Melack, & Novo, 2013). Junk, Bayley, and Sparks (1989) defined this seasonally flooded region as the aquatic–terrestrial transition zone. Melack and Forsberg (2001) discussed the hydrology and limnology of floodplain lakes and biogeochemical aspects of carbon, nitrogen and phosphorus with a focus on lakes near Manaus (e.g. Calado and Camaleão). Analyses of energy balances, winds, and thermal structure indicate that latent energy losses, convective mixing and wind-induced motions are all important physical processes (Augusto-Silva, MacIntyre, Rudorff, Cortes, & Melack, 2019; MacIntyre & Melack, 2009). Complete vertical mixing can occur daily at low water but is less frequent at high water levels (MacIntyre & Melack, 1988). Underwater light attenuation varies seasonally in Amazon floodplain lakes, with the highest attenuation usually occurring at low water when lakes are shallow (Forsberg, Melack, Richey, & Pimentel, 2017).

Inflows of nutrient-rich water from the Amazon River, other tributaries and local catchments help sustain lake productivity (Melack & Forsberg, 2001). Complex flow patterns (Alsdorf, Bates, Melack, Wilson, & Dunne, 2007) and differences in the sources of water (Bonnet et al., 2017; Ji et al., 2019; Lesack & Melack, 1995; Rudorff, Melack, & Bates, 2014) account, in part, for variations in the levels of nutrients and productivity both within and among lakes (Forsberg, Devol, Richey, Martinelli, & Santos, 1988; Forsberg, Melack, et al., 2017). Log–log relationships between mean annual chlorophyll and total phosphorus (TP) and total nitrogen (TN; linear regressions, r^2 = 0.85 and 0.88, respectively), indicate that both of these nutrients can limit phytoplankton biomass in these lakes (Trevisan & Forsberg, 2007). Evidence from algal bioassays (Setaro & Melack, 1984) and regional variations in algal photosynthesis and nutrients (Forsberg, Melack, et al., 2017) has also indicated a variable pattern of nutrient limitation. The nutrient dependence of phytoplankton and other aquatic plants is a fundamental factor affecting the levels of biomass and production of the flora and fauna. Human activities that alter the concentrations of phosphorus and nitrogen in Amazon floodplain lakes can, therefore, have significant effects on their productivity. While progress has been made in understanding Amazon floodplain lakes, the vast size and aquatic variety of the Amazon basin means much is unknown. To date, there is no regular, Amazon-wide or lake-specific monitoring of the limnological conditions in these lakes.

2 | TROPHIC STATUS AND TEMPORAL VARIABILITY IN FLOODPLAIN LAKES

Trophic status is relevant to ecological health and support of biodiversity in lakes. It is typically assessed based on measurements of algal productivity or biomass (usually as chlorophyll), transparency (often as Secchi depth) and total phosphorus and/or total nitrogen (Wetzel, 2001: Table 13–18). Dissolved oxygen concentrations below

2 mg L^{-1} are often considered hypoxic and potentially stressful for fishes. However, chlorophyll–nutrients relationships developed elsewhere may not apply to floodplain lakes with their large seasonal inflows and outflows. Bomfim et al. (2019) provide a demonstration that phytoplankton functional groups are related to trophic status of Amazon floodplain lakes.

Temporal variations in limnological conditions are relevant to ecosystem functioning and biodiversity and to lacustrine responses to natural and human impacts. The coefficient of variation (CV, standard deviation divided by the mean, expressed as a percentage) is a simple metric of temporal variability previously applied to tropical lakes (Melack, 1979). Multi-year measurements in Lake Janauacá are used as an illustrative case study of ecological conditions in an Amazon floodplain lake and for an assessment of trophic status and temporal variability.

Lake Janauacá (3°23′S, 60°18′ W; altitude 32 m; Figure 1) is representative of floodplain lakes common in the central Amazon basin that receive major inputs from the sediment and nutrient-rich waters of the Solimões River, a so-called 'white-water' river. As is typical of these lakes, aquatic habitats include open water, flooded forests. and floating herbaceous plants, all of which vary considerably in extent as water levels rise and fall each year (Figure 2). The uplands around the lake have a long history of human occupation with increased agricultural and fishing activity over the last few decades (Forsberg, 2018). Measurements were made at two sites about monthly between August 2014 and September 2016, representing low, rising, high and falling water. One site was in an embayment, a common feature around the lake, and the other site represented large areas of open water. Sampling and analytical methods are described in Amaral et al. (2020) and Barbosa et al. (2020). Publications with information about limnology, biogeochemistry and hydrology of Lake Janauacá include Amaral et al. (2018, 2020), Barbosa et al. (2020), Bonnet et al. (2017), Brito et al. (2017), Forsberg, Melack, et al. (2017), Junk (1970), and Schmidt (1973a, 1973b). Tables 1 and 2 summarize ranges, means, and coefficients of variation for DOC, TN, TP, total suspended solids (TSS), chlorophyll-*a* (Chl-*a*), and near-surface dissolved oxygen (DO) and temperature.

Based on the seasonal range of mean Chl-*a* (2.8–50.5 μg L^{-1}), TP (1.9–3.8 μM), and TN (21–108 μM) in open water, Lake Janauacá would be considered mesotrophic during high water and eutrophic during low and rising water. DO in near-surface waters ranged from hypoxic to supersaturated (1.2–10.3 mg L^{-1}), and water temperatures were usually around 30°C. Transparency was often low (Secchi depth, 0.2–1.9 m), DOC moderately high (2.5–6.6 mg L^{-1}), and TSS varied seasonally from up to 115 mg L^{-1} during low and rising water to 2.4 mg L^{-1} during high water. The seasonal CV for chlorophyll ranged

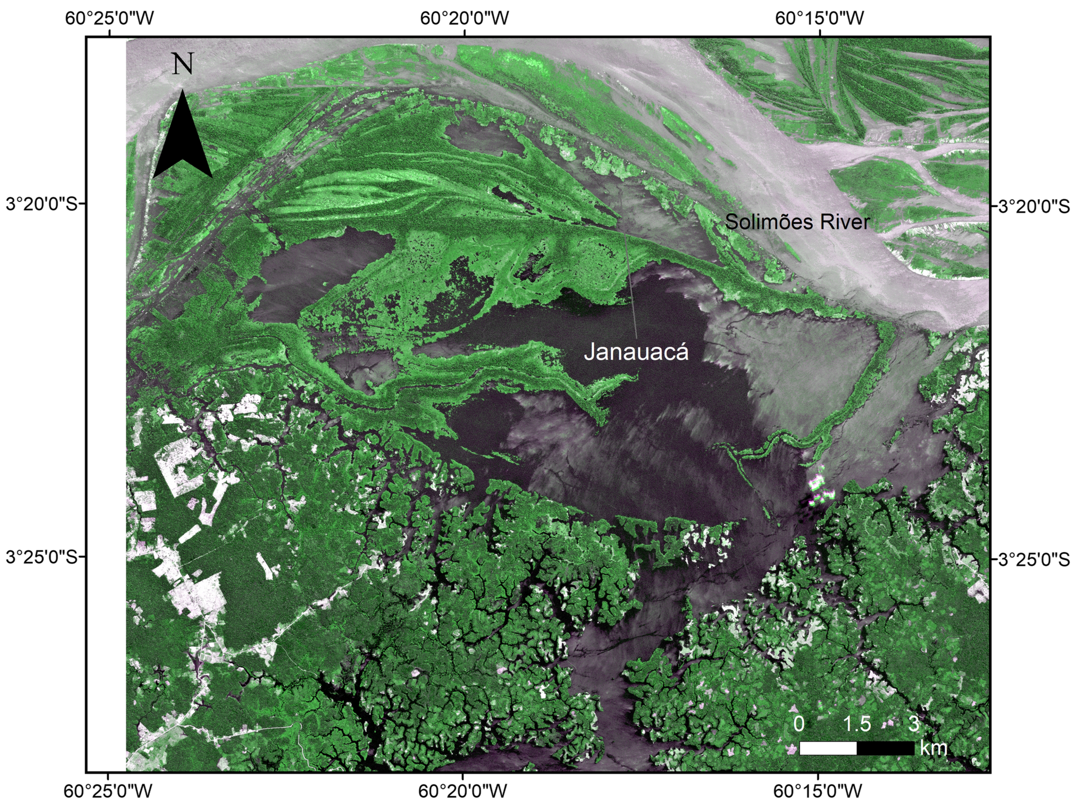

FIGURE 1 Janauacá floodplain in the central Amazon basin. Composite early falling water image (Planet® RapidEye-L3A, 5-m resolution – 15 August 2015) showing the environmental heterogeneity of Amazon floodplains. In the northern portion of the Janauacá, close to the Solimões River, herbaceous plants are abundant (light green) and associated with flooded forests, that remain flooded for longer periods (6–9 months) compared with the forests located in the southern portion. Dendritic bays are evident around the open lake margins. Floodplain channels are draining to the river at this time

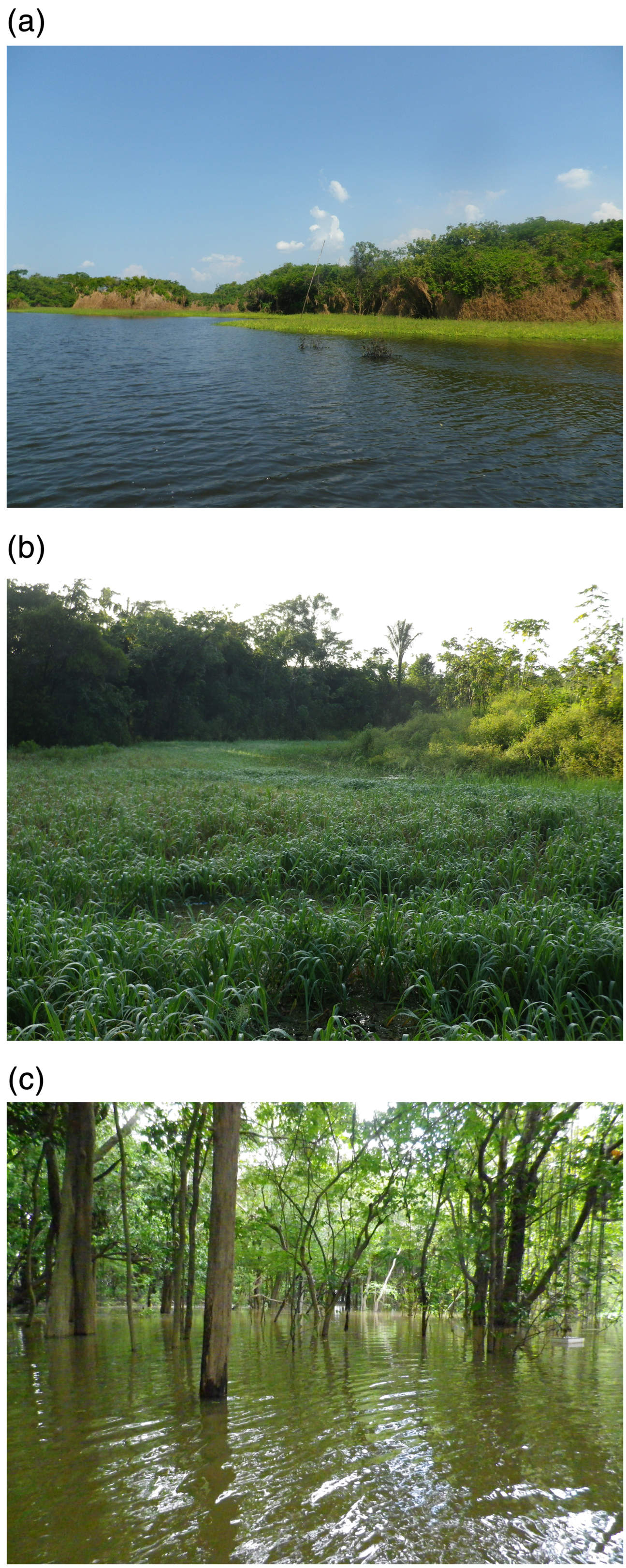

FIGURE 2 Photographs of Amazon floodplain lake habitats, Lake Janauacá. (a) Flooded forest and floating plants fringing the lake during falling water with decaying plants draping the forest. (b) Floating plants and fringing forest in bay. (c) Flooded forest

from 21 to 156%, spanning the range reported by Melack (1979) for many tropical lakes. Compared with criteria applied to other types of lakes, the large seasonal variation in trophic status, low transparency, high temperatures, and variable TSS and DO result in conditions that, although typical of Amazon floodplains, would appear to suggest degraded water quality. Instead, floodplain flora and fauna are adapted to these conditions (Goulding, 1980; Junk, 1997; Junk et al., 2010), and muting this variability has been shown to be detrimental (Assahira et al., 2017).

2.1 | Comparative studies in other floodplain lakes

Regular sampling over at least 1 year with measurements similar to those done in Lake Janauacá are available for very few of the thousands of Amazon floodplain lakes. Data from lakes associated with white-water rivers in the western, central, and eastern Amazon support conclusions regarding the range in trophic status and temporal variability observed in Lake Janauacá. Lakes associated with so-called black and clear water rivers tend toward mesotrophic or oligotrophic states.

Affonso, Queiroz, and Novo (2011) examined limnological characteristics of floodplain lakes at the confluence of the Solimões and Japurá rivers within Mamirauá Sustainable Development Reserve, a region where human activities have had little impact. Mean chlorophyll concentrations were 0.3 μg L^{-1} during high water and 113 μg L^{-1} during low water, a range that extends from oligotrophic to eutrophic based on standard trophic classification. Both Secchi depths (means of 1.6 m and 0.3 m, high and low water) and total phosphorus (means of 0.5 and 7 μM, high and low water) would classify the lakes as eutrophic. In the sparsely inhabited basin of the Juruá, a meandering tributary of the Solimões River, Campos-Silva et al. (2020) examined floodplain lakes distributed within and outside two protected areas of sustainable use. Average Chl-*a* concentration during low water (40 μg L^{-1}) was greater than average values recorded during high water (0.1 μg L^{-1}). Average TP values of 2.6 μM (low water) to 1.7 μM (high water)) and average Secchi depth (0.42 to 0.49 m) varied only slightly. These values indicate that the lakes would be considered oligotrophic during high water and eutrophic during low water according to indices of trophic state.

Several lakes fringing the Solimões, Amazonas, and Negro rivers near Manaus in the central Amazon have been sampled for parameters appropriate to evaluate trophic status. Catalão Lake, located on a peninsula between the Solimões and Negro rivers, reflects the contrasting influence of the black-water Negro River during rising water and the Solimões River during high water: Secchi depth, 0.45–1.15 m; near surface TSS, 3–45 mg L^{-1}; Chl-*a*, 3.4–24.7 μg L^{-1} (Brito, Alves, & Espírito-Santo, 2014). In Lake Rei, located within Careiro Island at the confluence of the Solimões and Negro rivers, during falling and rising water, TP varied considerably from 0.2 to 3 μM as did Chl-*a* (7 to 57.5 μg L^{-1}) (Ribeiro & Darwich, 1993). Both lakes Catalão and Rei would be considered mesotrophic to eutrophic.

TABLE 1 Environmental variables measured in open water of embayment in Lake Janauacá during the low (LW), rising (RW), high (HW), and falling (FW) water periods about monthly between August 2014 and September 2016

Embayment	Hydroperiod							
	LW		RW		HW		FW	
Variable	Mean Min	CV Max	Mean Min	CV Max	Mean Min	CV Max	Mean Min	CV Max
Chl-*a*, μg L^{-1}	34.3	13.8	10.2	76	10.1	44	15.4	84
	30.9	37.6	4.4	26.2	6.0	15.0	4.3	29.7
DO, mg L^{-1}	6.9	49.2	3.0	57	3.9	62	4.9	47
	4.5	9.3	1.5	6.6	1.2	6.8	2.3	7.7
DOC, mg L^{-1}	4.3	3.3	5.1	17	5.1	30	5.0	19
	4.2	4.4	4.0	6.3	2.5	6.6	4.1	6.0
TN, μM	50	13	93	182	24	74	31	62
	45	55	10	474	7	52	7	55
TP, μM	4.7	105.3	1.6	95	2.2	84	1.2	86
	1.2	8.2	0.2	3.9	0.5	4.3	0.4	2.7
Secchi, m	0.3	28.3	0.7	53	1.4	27	1.5	21
	0.2	0.3	0.2	1.2	0.7	1.8	1.2	1.9
Temp, °C	31.0	2.1	29.8	2	30.1	2	30.8	2
	30.5	31.4	28.6	30.8	29.1	30.9	30.2	31.8
TSS, mg L^{-1}	50.1	55.3	22.9	88	4.0	39	4.4	25
	30.5	69.7	5	62.3	2.4	6.1	3.2	5.3

Note: Samples for Chl-*a*, DOC, TSS, TN and TP analyses were collected from ~0.3 m; DO and temperature at 0.1 m.
Abbreviations: Chl-*a*, chlorophyll-*a*; CV, coefficient of variation (%); DO, dissolved oxygen; DOC, dissolved organic carbon; Max, maximum; Min, minimum; Secchi, Secchi depth; Temp, temperature; TN, total nitrogen; TP, total phosphorus; TSS, total suspended solids.

In contrast to the lakes in the western Amazon, the large Curuai floodplain in the eastern Amazon has 20,000 rural inhabitants who graze cattle on the exposed floodplain during low water and about half of the floodable forest has been cut in the last 40 years (Renó, Novo, Suemitsu, Renno, & Silva, 2011). Barbosa, Novo, Melack, Gastil-Buhl, and Waterloo (2010) reported chlorophyll values of 8, 29, 69, and 33 μg L^{-1} during rising, high, falling, and low water, respectively. This criterion would classify the Curuai floodplain as eutrophic year-round. The combination of the use of the exposed floodplain for cattle, reduced riparian forest, and shallow depths in this floodplain is likely to contribute to its eutrophic state.

Further evidence for the range of trophic conditions and their relationship with nutrient levels are provided by regional surveys along the Negro, Solimões, and Amazonas rivers and their tributaries. Forsberg, Melack, et al. (2017) found that average Chl-*a* and TP in lakes associated with white-water rivers were significantly higher than those in lakes fed by black- and clear-water rivers. The white-water floodplain lakes were classified between mesotrophic and eutrophic whereas the black- and clear-water floodplain lakes surveyed were mesotrophic. The levels of Chl-*a* and TP were significantly higher in all lakes at low water than at high water. During four hydrological stages, lakes along the Solimões and Amazonas rivers had near-surface DO concentrations from 2 mg L^{-1} to 8.3 mg L^{-1}, Chl-*a* concentrations as low as 0.1 μg L^{-1} and up to 79.9 μg L^{-1}, total dissolved phosphorus values from 0.1 to 1.8 μM, and TSS from 1 to 150 mg L^{-1} (Amaral et al., 2019; Barbosa et al., 2016; Table 3). Monthly samples from lakes along the floodplains of the Solimões and Negro rivers indicated trophic states between mesotrophic and eutrophic (Trevisan & Forsberg, 2007).

3 | ENVIRONMENTAL ISSUES IN FLOODPLAIN LAKES AND THEIR IMPLICATIONS FOR AQUATIC CONSERVATION

Floodplain lakes can be affected by a variety of human activities that can threaten their ecological health and conservation (Castello & Macedo, 2016; Castello et al., 2013; Melack, 2005; Melack & Forsberg, 2001; Table 4). Perturbations can be local or regional with impacts on airsheds and catchments as well as lakes directly. Ecological impacts and responses associated with deforestation and land use changes, mining, urbanization, hydroelectric dams, and climate variability and change are discussed here. Other articles in this special issue focus on issues related to fish, other organisms, and hydrological conditions.

TABLE 2 Environmental variables measured in open water of Lake Janauacá during the low (LW), rising (RW), high (HW) and falling (FW) water periods about monthly between August 2014 and September 2016

Open Lake	Hydroperiod							
	LW		RW		HW		FW	
Variable	Mean Min	CV Max	Mean Min	CV Max	Mean Min	CV Max	Mean Min	CV Max
Chl-*a*, μg L^{-1}	50.5	21	26.1	156	2.8	50	6.0	37
	43.0	57.9	3.9	116.1	0.9	5.0	4.0	9.0
DO, mg L^{-1}	8.9	23	5.6	38	3.1	34	4.7	30
	7.4	10.3	2.7	9.0	1.7	4.4	2.6	5.7
DOC, mg L^{-1}	4.6	12	4.7	18	4.3	19	4.2	42
	4.2	5.0	3.5	5.4	3.3	5.3	3.1	6.2
TN, μM	108	6	34	46	21	75	25	62
	103	113	12	53	5	45	5	41
TP, μM	2.3	35	3.8	96	1.9	85	2.1	73
	1.7	2.8	0.5	5	0.3	4	0.6	3.9
Secchi, m	1.0	97	0.6	40	1.1	36	1.3	20
	0.3	1.6	0.2	0.9	0.7	1.5	1.0	1.6
Temp, °C	31.8	3	29.6	3	29.5	1	31.1	4
	31.1	32.4	28.7	30.7	29.1	29.9	30.0	32.8
TSS, mg L^{-1}	36.5	15	35.0	106	11.0	52	27.4	116
	32.7	40.2	8.6	115.0	4.5	17.2	6.5	64.0

Note: Samples for Chl-*a*, DOC, TSS, TN, and TP analyses were collected from ~0.3 m; DO and temperature at 0.1 m.
Abbreviations: Chl-*a*, chlorophyll-*a*; CV%, coefficient of variation; DO, dissolved oxygen; DOC, dissolved organic carbon; Max, maximum; Min, minimum; Secchi, Secchi depth; Temp, temperature; TN, total nitrogen; TP, total phosphorus; TSS, total suspended solids.

3.1 | Deforestation

Deforestation and associated agricultural development can alter aquatic habitats critical for fish (Castello et al., 2018; Goulding, 1980; Lobón-Cervia, Hess, Melack, Varella, & Araújo-Lima, 2015), increase nutrient inputs (Nóbrega et al., 2018; Williams & Melack, 1997) and cause pesticide contamination (Schiesari, Waichman, Brock, Adam, & Grillitsch, 2013; Waichman, Römbke, Ribeiro, & Nina, 2002). Fires associated with deforestation and agriculture mobilize nutrients and particles transported by surface waters and the atmosphere, and influence rain chemistry (Guyon et al., 2005; Lesack & Melack, 1991).

Deforestation in uplands influences the amount and chemical composition of water entering floodplain lakes. Catchment studies in the Amazon basin in intact forests provide a baseline to compare with deforested catchments. Lesack (1993a, 1993b) determined the water balance and measured fluxes of solutes exported by streamflow and sub-surface outflow for an undisturbed upland rain forest adjacent to the Amazon floodplain, and Williams and Melack (1997) and Williams, Fisher, and Melack (1997) measured water and solute fluxes from the same catchment after partial deforestation had occurred. Nitrate increased by a factor of five in groundwater after cutting and burning, although mean volume-weighted concentrations in the stream water were similar before and after partial deforestation. Runoff was higher in the catchment after deforestation, TN yield doubled, and the TP yield increased by a factor of seven. The conversion of forest to pasture in low-order streams in the Jamanxim River basin (Pará) increased carbon and nutrient fluxes (Nóbrega et al., 2018). Deforestation increases vulnerability of soil to erosion and leads to higher concentrations of suspended sediments in floodplain lakes (Forsberg, Godoy, Victoria, & Martinelli, 1989; Roulet et al., 2000).

Renó and Novo (2019) assessed deforestation along the floodplain of the Solimões and Amazonas rivers and observed a west to east gradient of increased forest depletion resulting from the history of human occupation and public policies. Deforestation in floodable forests can directly alter the habitat and food of the fish that inhabit these forests (Arantes et al., 2017). For example, *Colossoma macropomum* feeds on fruits and seeds from trees and shrubs of the floodplain (Goulding & Carvalho, 1982), and *Osteoglossum bicirrhosum* supplements its diet by leaping from the water to obtain terrestrial and arboreal prey (Goulding, 1980). In the 1980s, Goulding and Carvalho (1982) noted long-lasting effects of floodplain deforestation on fish populations caused by adverse impacts on their diet. The floodplain and its floodable forests are also important for fish reproduction as nursery grounds (Fernandes, 1997); for example, the giant pirarucu, *Arapaima gigas*, builds nests in lakes and channels of the Amazon floodplain (Castello, 2008). Correlations between the density of floodplain forests and fish diversity and yield (Arantes et al., 2017;

TABLE 3 Environmental variables measured in nine lakes along the Solimões and Amazonas rivers: Paupixuna, Curupira, Tefé, Coari, Mamiá, Ananás II, Cabaliana, Calado, and Tia Dora (listed upstream to downstream; locations shown in Amaral et al., 2019) during the low (LW), high (HW), early falling (EFW), and late falling (LFW) water periods

Lakes	Hydroperiod							
	LW		HW		EFW		LFW	
	Mean		Mean		Mean		Mean	
Variable	Min	Max	Min	Max	Min	Max	Min	Max
Chl-*a*, μg L^{-1}	19.2		5.7		7.1		1.22	
	2.2	79.9	1.6	12.6	0.9	13	0.6	2.1
DO, mg L^{-1}	6.2		4.1		5.3		5.5	
	3.6	8.3	2.0	6.8	2.5	7.3	3.7	8.3
DOC, mg L^{-1}	4.7		5.8		4.4		6.3	
	3.5	7.1	3.4	9.5	3.1	6.6	4.9	8.3
TDN, μM	20.7		22.8		24.9		21.4	
	10.3	48.9	16.4	31.6	17.5	40.1	13.6	25.6
TDP, μM	0.1		0.9		0.5		0.5	
	0.1	0.5	0.4	1.8	0.1	1.2	0.2	0.9
Secchi, m	NA		1.2		1.5		1.2	
	NA	NA	0.6	1.8	0.6	2.3	0.6	2.1
Temp, °C	30.2		29.7		30.5		31.8	
	28.7	31.8	27.6	32.7	28.4	32.7	31.2	32.9
TSS, mg L^{-1}	85		7		7		9	
	19	150	1	19	2	18	4	21

Note: EFW and LFW periods shown in Figure 2, Amaral et al. (2019). Samples for Chl-*a*, DOC, TDN, TDP and TSS analyses were collected from ~0.3 m; DO and temperature at 0.1 m.
Abbreviations: Chl-*a*, chlorophyll-*a*; DO, dissolved oxygen; DOC, dissolved organic carbon; Max, maximum; mean; Min, minimum; NA, not measured; Secchi, Secchi depth; TDN, total dissolved nitrogen; TDP, total dissolved phosphorus; Temp, temperature; TSS, total suspended solids.

Castello et al., 2018; Freitas et al., 2018; Goulding et al., 2018; Lobón-Cervia et al., 2015) have demonstrated the critical importance of conserving alluvial forests.

3.2 | Mining

Mining activities can cause severe local pollution and siltation. Forsberg et al. (1989) attributed a tenfold increase in sedimentation rates in a floodplain lake on the Jamari River over a period of 20 years to erosion associated with cassiterite mining and agricultural development in the Jamari basin upstream of the lake. Mine tailings have been released directly into natural lakes. In Lake Batata, a floodplain lake on the Trombetas River, tailings from bauxite mining released directly into the lake covered about 30% of the lake bottom (Esteves, Bozelli, & Roland, 1990). This material was shown to have a lower calorific content (Callisto & Esteves, 1996) and lower levels of phosphorus, carbon, and nitrogen (Roland & Esteves, 1993) than uncontaminated sediments. During low water, resuspension of the clays associated with the tailings reduced transparency and primary production (Roland & Esteves, 1998; Roland, Esteves, & Barbosa, 2002). Increased turbidity can alter fish composition by decreasing the abundance of the igapó-associated and visually oriented fish (Lin & Caramaschi, 2005).

Some of the severest impacts of erosion linked to mining have been reported in the Madre de Dios River basin, where extensive gold mining on alluvial floodplains and uplands has resulted in massive siltation in streams and floodplain lakes. Dethier, Sartain, and Lutz (2019) used a series of Landsat images and an algorithm to detect total suspended sediment concentrations to evaluate temporal changes in TSS in 32 river reaches in the Madre de Dios region between 1984 and 2019, when a major increase in mining activities occurred. TSS concentrations in rivers below some mining sites increased by orders of magnitude relative to pre-impact levels, resulting in extensive siltation of aquatic habitats in these regions (Figure 3).

Gold mining releases mercury and sometimes cyanide, both of which represent risks for aquatic organisms. The fate of the anthropogenic mercury inputs in the Amazon's diverse aquatic habitats and their consequences for aquatic biota depend on the hydrological and limnological conditions encountered in these environments. When cyanide is used in sites contaminated by mercury, it can lead to the formation of mercury cyanide, and all are highly toxic to the biota (Da Silva, 2020). Cyanide can inhibit mercury methylation close to mining discharge (Guimarães et al., 2011), and thus mercury bioaccumulation occurs mainly due to inorganic forms.

Some of the highest levels of mercury contamination in surface waters and predatory fish occur in floodplain lakes associated with black-water rivers such as the Negro River (Belger & Forsberg, 2006;

TABLE 4 Main drivers and impacts of perturbations to Amazon floodplain lakes

Drivers	Primary impacts	Secondary impacts
Deforestation	Loss of flooded forests	Loss of critical aquatic habitat
	Fires	Increased nutrients and sediments
	Enhanced soil erosion	
Agriculture and ranching	Nutrient increases	Excessive algae and plants
	Enhanced soil erosion	Increased nutrients and sediments
	Pesticide releases	Biota contamination
		Biodiversity loss
River regulation	Altered discharge	Loss or gain of flooded forests
	Reduced connectivity	Fish migrations and movements
	Flooding of forests	Deoxygenation and methane increase
	Stratification and deoxygenation	Changes in mercury speciation
	Altered sediment fluxes	Changes in optical conditions
Mining	Increased sediments	Degraded water quality
	Mercury contamination	Biota loss and contamination
Urbanization	Organic pollution	Deoxygenation
	Plastic and toxic pollution	Biota loss and contamination
Climate change	Altered precipitation	More or less runoff and inundation
	Increased temperature	Altered metabolism and trophic status

Note: Modified from Castello et al. (2013).

FIGURE 3 Massive siltation impacts along the main channel and floodplain of the Colorado River, Madre de Dios basin, Peru, associated with gold mining operations. Image Google Earth

Fadini & Jardim, 2001). Relatively little gold mining has occurred in the Negro basin and mercury inputs are derived predominantly from atmospheric deposition (Lacerda, Ribeiro, Cordeiro, Sifeddine, & Turq, 1999) and chemical weathering (Souza, 2015). A gradual increase in the mercury levels in the sediments of Lake Cristalino, a floodplain lake along the Negro River, beginning in the 1940s, was attributed to increased atmospheric deposition derived from regional and global human sources (Melack & Forsberg, 2001). Lacerda et al. (1999) found a similar trend in isolated Amazon lakes that they attributed to atmospheric inputs from modern artisanal small-scale gold mining activities, and an increase in mercury deposition during the colonial period from silver and gold mining operations (Guerrero, 2016). Regions with artisanal small-scale gold mining often have elevated mercury in fishes (Roach, Jacobsen, Fiorello, Stronza, & Winemiller, 2013). Roulet et al. (2000) showed that discharge of particulate mercury in the Tapajos River and its accumulation in floodplain lakes had increased significantly since 1940 with the expansion of mining and agricultural activities in the basin.

The high levels of mercury encountered in fish in the Negro basin also reflect factors that promote the methylation and bioaccumulation of mercury. Methylation occurs preferentially in anoxic waters with low pH and high concentrations of DOC. These conditions are prevalent at high water in lakes and wetlands along the Negro floodplain and year-round in the groundwater of hydromorphic podzols, as evidenced by the high levels of dissolved methylmercury encountered in these environments (Kasper et al., 2017) and the elevated levels of mercury encountered downstream (Belger & Forsberg, 2006).

3.3 | Urbanization

Expansion of cities and attendant urban runoff and sewage releases cause local pollution (Couceiro, Hamada, Forsberg, Ferreira, &

Silva, 2007; Melo et al., 2019; Thomas et al., 2014). Leaching from landfill and fish farms can cause trace elements contamination (Capparelli et al., 2020; Silva-Filho et al., 2014), and plastic waste has been found in aquatic organisms (Andrade et al., 2019). Overharvesting of water for human consumption may be a concern in the future in urban environments as basic sanitation is precarious in the region according to ABES (2019). Road crossings block streams and alter instream habitat, connectivity, and biological assemblages (Leal et al., 2016; Leitão et al., 2018). Control of insect vectors of diseases has employed widespread use of DDT (now prohibited, although persistent) and other pesticides that contaminate aquatic ecosystems and their biota (Mendez et al., 2016).

3.4 | Hydroelectric dams

Demand for electric energy has led to the construction of hydroelectric dams in the Amazon basin and plans to build many more in the coming decades (Almeida et al., 2019; Finer & Jenkins, 2012). These dams can have multiple impacts on floodplains related to impoundment, altered discharge and aquatic connectivity (Anderson et al., 2018; Forsberg, Dunne et al., 2017; Latrubesse et al., 2017). Dams built in lowlands generally inundate forested areas, and the decomposition of the inundated organic matter consumes dissolved oxygen, resulting in anoxic conditions and high concentrations of DOC. These conditions lead to generation of high concentrations of greenhouse gases (CO_2 and CH_4) that are released both above and below the dams (Kemenes, Forsberg, & Melack, 2007, 2011, 2016). The anoxic conditions in reservoirs also promote the methylation and bioaccumulation of mercury, contaminating aquatic biota above and below the dam (Forsberg, Dunne et al., 2017; Kasper et al., 2014). By transforming a lotic to a lentic environment, impoundment also affects fish communities, selecting for species adapted to lentic conditions (Winemiller et al., 2016).

Dam construction reduces river and floodplain lake connectivity that is important to meta-population dynamics, evolution, and speciation and essential to migratory fish species (Anderson et al., 2018; Pelicice, Pompeu, & Agostinho, 2015; Pompeu, Agostinho, & Pelicie, 2012). An exceptional example of fish migration is the Amazonian catfish, *Brachyplatystoma rousseauxii*, a species that begins to grow in the Amazon estuary and gradually migrates to the Andes mountains to spawn, the longest strictly freshwater fish migration in the world (Barthem & Goulding, 1997; Barthem et al., 2017). Fish ladders have been constructed at some Amazonian dams to mitigate impacts on fish migration, but little is known about their efficacy (Lira et al., 2017) and they may actually have detrimental effects on fishes (Pelicice & Agostinho, 2008).

Alterations of flows downstream of dams have major implications for floodplain ecosystems adapted to and dependent on a natural flood regime. Increases in the flood period of the Uatumã River floodplain downstream from Balbina Reservoir resulted in the mortality of alluvial tree species (Assahira et al., 2017). Hydroelectric dams trap suspended sediments which alters sediment and nutrient supplies downstream. Forsberg, Dunne et al. (2017) predicted an 80% reduction in the supplies of phosphorus and nitrogen to the lowland Amazon basin if six dams planned in the western Amazon are constructed. Regulated flows decrease the supply of riverine sediments and nutrients to floodplains limiting agricultural and aquatic production (Barrow, 1988). Forsberg, Dunne et al. (2017) predicted that a reduction of peak flooding below three dams planned for the western Amazon could lower regional fish yields.

3.5 | Climate variability and changes

Natural variability and human-induced climate change leading to global warming and altered precipitation can have impacts on hydrological and biogeochemical processes that directly and indirectly affect floodplain lakes (Costa et al., 2009; Melack & Coe, 2013; Roland et al., 2012; Sorribas et al., 2016). Melack and Coe (2013) considered how climate changes might influence limnological conditions in Amazon floodplain lakes. As temperatures increase owing to climatic warming, increased vapour pressure gradients are likely to increase latent energy changes and cause deeper and more frequent mixing. If convective storms with intense rains and winds increase, vertical mixing would be further enhanced. These changes would increase the frequency of water-column anoxia and fish kills (Caraballo, Forsberg, Almeida, & Leite, 2014). Major changes in river discharge and flooding patterns are expected as a result of climate change (Sorribas et al., 2016). Altered flooding could alter the patterns of anoxia in floodplain environments affecting the levels and dynamics of CO_2, CH_4, and methylmercury (Amaral et al., 2018; Barbosa et al., 2020; Kasper et al., 2017). Changes in discharge alters the balance between mainstem river and local basin inputs of nutrients and water, affecting the levels and dynamics of limiting nutrients (Forsberg et al., 1988; Setaro & Melack, 1984). Changes in the spatial distribution of flood duration would also alter the phenology, distribution and productivity of floodplain plants and associated fauna (Junk, 1997; Junk et al., 2010). All these changes, especially when acting together, are likely to have impacts on aquatic diversity and ecosystem functioning.

The frequency of exceptional droughts and floods has increased in the last two decades in the Amazon region, and is related to a combination of climatic changes and deforestation (Duffy, Brando, Asner, & Field, 2015; Gloor et al., 2013). For example, exceptionally high water was reported in the central Amazon in 2012 and 2015, and severe droughts occurred during 2005 and 2010 (Marengo & Espinoza, 2016). Barbosa et al. (2020) reported high concentrations and fluxes of methane following an extended period with low water in Lake Janauacá in 2016, probably linked to the colonization by herbaceous plants in the exposed sediments, followed by their decomposition as water levels rose. Furthermore, Röpke et al. (2017) reported that low water associated with a regional drought led to changes of the fish assemblage in a central Amazon lake and that subsequent hydrological conditions hampered recovery.

4 | APPLICATION OF LIMNOLOGICAL PERSPECTIVES TO CONSERVATION OF FLOODPLAIN SYSTEMS

The high species diversity and productivity of aquatic biota in the Amazon basin is linked to the spatial and temporal variety of floodplains and the biological adaptations associated with these habitats. Fishing and exploitation of other aquatic organisms can directly alter food webs and biodiversity, if not done sustainably (Goulding et al., 2018; Tregidego, Barlow, Pompeu, Rocha, & Parry, 2017). Improved understanding of the limnology of floodplain lakes would contribute to efforts for ecosystem management. At present, community-based ecosystem management identifies spatial zones for fishing access and lakes protected from fisheries based mainly on local knowledge about the occurrence of a target species and its ecological behaviour (Campos-Silva, Hawes, & Peres, 2019; McGrath, De Castro, Futemma, Amaral, & Calabria, 1993). Seldom are limnological characteristics considered in the establishment or evaluation of management strategies. In one example, Campos-Silva and Peres (2016) and Campos-Silva et al. (2020) examined the occurrence and abundance of *A. gigas* and limnological characteristics of floodplain lakes along a 600-km reach of the Juruá River, within and outside two protected areas. Lakes outside protected areas had no or low abundance of *A. gigas* and higher chlorophyll biomass, compared with lakes in protected areas, suggesting a trophic cascade influencing phytoplankton.

As summarized by Melack and Forsberg (2001), Melack et al. (2009), and Melack and Engle (2009), organic carbon supply to Amazon floodplain lakes is derived from phytoplankton and periphyton, aquatic herbaceous plants, and litterfall from flooded forests together with inputs of dissolved and particulate carbon from local catchments and rivers. This organic carbon is metabolized by a rich diversity of organisms from microbes to fish (Forsberg, Araújo-Lima, Martinelli, Victoria, & Bonassi, 1993; Waichman, 1996). Hence, a relationship between organic carbon supply and fish production or perhaps fishery yield could be a guide to fishery management (Bayley, 1989). An integrated measure of productivity that combines photosynthetic activity by phytoplankton with planktonic respiration is gross primary productivity. Melack (1976) demonstrated a semilog relationship between fish yields and gross primary productivity for tropical lakes, that could be explored for Amazon floodplain lakes. However, as noted by Campos-Silva and Peres (2016) and Campos-Silva et al. (2020), proximity to fisher communities, and lake size and connectivity to rivers, are also relevant to evaluating potential fish yield.

Conservation of aquatic systems usually requires strategies different from those applied to terrestrial systems (Castello & Macedo, 2016). Owing to the structure of river and floodplain networks, effects are connected and linked at multiple landscape scales. For example, Leal et al. (2020) demonstrated that terrestrially focused conservation planning provides limited incidental conservation of freshwater species, but when conservation planning integrates terrestrial and freshwater environments, the percentage of aquatic species conservation increases up to 600%, compared with the potential conservation of aquatic species when only terrestrial planning is considered. Frederico, Zuanon, and De Marco (2018) showed that protected areas, delineated with a focus on terrestrial systems, did not satisfactorily protect fish in Amazon streams.

As the countries within the Amazon basin continue economic developments, including building roads and navigation channels and expanding agriculture and urban areas, individual and collective impacts on floodplains are likely. As floodplain forests and upland catchments are cut, the transport of sediments, and nutrients and other solutes to floodplain environments is likely to accelerate and algal growth, siltation, and mercury contamination are expected to increase. Furthermore, the loss of floodplain forests is expected to reduce the diversity and production of Amazon fish communities. Although strategic basin-wide planning could optimize energy production and other resource uses and minimize environmental impacts, as illustrated by Almeida et al. (2019), this approach is not being practised.

In the Amazon basin, there are a few conservation initiatives that include floodplain lakes and seasonally flooded areas. Floodplain lakes are protected or sustainably managed in several International Union for Conservation of Nature protected area categories: Anavilhanas National Park, Mamirauá Sustainable Development Reserve, Amanã Sustainable Development Reserve, Rio Trombetas Biological Reserve, Medio Jurua Extractive Reserve, Uacari Sustainable Development Reserve, Reserva de Desenvolvimento Sustentável do Tupé, and Piagaçu-Purus Sustainable Development Reserve. Indigenous areas also include floodplain lakes (e.g. Terra Indígena Espírito Santo, Terra Indígena Itixi Mitari, Terra Indígena Paumari do Lago Marahã, and Terra Indígena Jurubaxi-Téa). The Jaú National Park is the only reserve that protects almost all catchments of a large river (Jaú River; www.icmbio.gov.br). Maintenance of these protected areas, however, can be difficult owing to scarce financial and human resources, and inherent surveillance difficulties.

One type of protected area, called RDS and RESEX, allows local communities inhabiting the protected areas to exploit the natural resources in a sustainable way. This approach builds formal alliances with reserve residents, decentralizes resource management, strengthens full-time surveillance and reduces overall conservation costs. Moreover, these types of protected areas favour the generation of income opportunities that bring social and economic benefits to the inhabitants. One especially successful example is the Mamirauá Sustainable Development Reserve (Castello, Viana, Watkins, Pinedo-Vasquez, & Luzadis, 2009). Another example is in the Juruá river basin where there is an unusual level of socio-political organization of the local communities in two reserves (Medio Jurua Extractive Reserve and Uacari Sustainable Development Reserve). Campos-Silva and Peres (2016) provide a quantitative assessment of how community-based management promoted the recovery and conservation of *Arapaima* spp., while generating significant income and food. Lessons from the Juruá sustainable-use reserves show that protecting floodplain lakes is important in maintaining harvest-sensitive stocks and providing favourable conditions for successful community-based management.

5 | RESEARCH DIRECTIONS

Improving understanding of threats to the conservation of Amazon floodplain lakes requires considerably more studies that represent the spectrum of floodplain lakes throughout the basin. Measurement programmes of sufficient length to evaluate the current status and variability of the lakes need to be implemented. For example, whereas increased inputs of nutrients are known to lead to reduced water quality as eutrophication occurs, the extent to which Amazon floodplain lakes are susceptible to increased nutrients is uncertain. The annual filling and draining of their water may reduce impacts. Nutrient input–output budgets are lacking, and whole-system experimental treatments have not been done. Furthermore, evaluation of trophic status requires more than nutrient levels, and integrated biological approaches, such as identification of phytoplankton functional groups, are worth exploring.

Although mechanistic models of limnological conditions are improving, the complex seasonal variations of floodplain lakes require considerable development of these models and their rigorous testing. Remote sensing systems can provide multi-year and synoptic spatial data on inundation, sediment and chlorophyll levels and land cover. However, applications to Amazon floodplains are challenging given that clouds are common, flooded forests cover large areas and seasonal changes are large. Although in situ sensors can monitor thermal structure, DO, turbidity, chlorophyll, and water velocities, their deployment on Amazon floodplains is a logistical challenge. Hence, field measurements by trained personnel remain essential complements.

Incorporating limnological perspectives into conservation is likely to strengthen management efforts and improve their evaluation. To do so requires active, effective communication and interaction among scientists, resource managers, stakeholders, and local communities. To establish long-term measurement programmes that underpin sound management would benefit from expanded coordination between Amazonian institutes and international scientists and programmes. Establishment of publicly available datasets that combine results from different regions and programmes would lead to synergistic analysis.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest with regard to the content of this publication.

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