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AQUATIC ECOSYSTEM SERVICES

Review Paper

Ecosystem services provided by river-floodplain ecosystems

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Abstract River-floodplain ecosystems (RFEs) provide multiple ecosystem services. However, their importance may be underestimated because they are not summarized yet. In this paper, we review and update the benefits that RFEs provide to society, including supporting, regulating, provisioning, and cultural ecosystem services. Although considered a unique ecosystem service category, we advocate that supporting services, like soil formation, nutrient cycling, primary production, and habitat provisioning can be comprehended as ecosystem processes that generate other services. RFEs provide valuable regulating services, including water regulation, storm protection, erosion control, water purification, waste treatment, and disease control. The society also benefits from provisioning services from RFEs, such as water for drinking and irrigation, food (e.g., fishes and crops), fiber, ornamental and biochemical resources, and energy production. RFEs also provide cultural services including recreation, ecotourism, religiosity, and spirituality. Most ecosystem services from pristine and human-altered RFEs are primarily regulated by the flood pulse because it maintains temporal and spatial habitat variability, high biodiversity, and biotic and abiotic interactions. Despite providing many benefits to society, RFEs are seriously threatened, mainly due to river regulation, land-use changes, pollution and invasive species. Consequently, the multiple demands and uses of RFEs worldwide raise challenges of conservation and restoration.

Keywords Flood pulse · Environmental services · Wetland · Human wellbeing

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Introduction

River-floodplain ecosystems (RFEs) are highly biodiverse areas subject to seasonal inundation by lateral overflows of rivers, where the biota responds with adaptations to alterations of habitats caused by water level fluctuations, producing singular community structures (Junk et al., 1989). RFEs are wetlands that differ from other aquatic ecosystems because flood pulses (or simply "pulses", according to Neiff, 1990) promote the existence of a mosaic of habitats from aquatic to terrestrial, with different degrees of connectivity among themselves and with the main river (Junk et al., 1989; Ward et al., 1999). Another characteristic that differentiates RFEs from other wetlands, like mangroves, bogs and peats, is that the water level oscillations in the former are associated with lateral rivers and the flood pulse is seasonal.

The importance of the water level oscillations to ecology of RFEs, and the recognition that these ecosystems provide benefits to society are much older (Forbes, 1887, reprinted 1925; Table 1). It is worth quoting the words of Forbes: "…fluviatile lakes are most important breeding grounds and reservoirs of life, especially as they are protected from the filth and poison of towns and manufactories by which the running waters of the state are yearly more deeply defiled." In the first half of this sentence, Forbes recognizes the importance of lakes in the Illinois River floodplain for fish production (a provisioning service) and provisioning of habitat (a supporting service essential for biodiversity), while in the second half, it is explicit that the lakes alleviate pollution (a regulating service).

The recognition of RFEs importance for biodiversity conservation and to provide several ecosystem services and benefits for societies have increased in recent decades (Wantzen et al., 2016; Estrada-Carmona et al., 2020; Jakubínský et al., 2021; Table 1; Fig. 1). For example, the large floodplain areas (known as 'aquatic-terrestrial transition zone' – ATTZ – sensu Junk et al., 1989) are subject to periodical water accumulation, making RFEs to reduce catastrophic flooding downstream (Akanbi et al., 1999; Talbot et al., 2018; Jakubínský et al., 2021). RFEs also help improve water quality by retention of nutrients and sediments (Zehetner et al., 2009; Vaikasas & Dumbrauskas, 2010; Walalite et al., 2016; Hopkins et al., 2018) and they provide cultural services such as recreation and ecotourism (Wantzen et al., 2016; Funk et al., 2019; Jakubínský et al., 2021). The benefits provided by these ecosystems (along with swamps) worldwide are highly valuable, representing ca. 25,021 to 27,021 $/ha/yr (values in 2007 International dollars, Costanza et al., 1997, 2014; de Groot et al., 2012).

Despite providing many benefits, RFEs are seriously threatened, especially in temperate regions, owing to river regulation, pollution and invasive species, among other impacts (Schindler et al., 2014). The contrast between benefits provided by RFEs and the immediate threats they suffer makes urgent the identification of ecosystem services they provide, which may help to highlight the importance of these ecosystems and to tackle and monitor nature-based solutions to resolve and mitigate the effects of anthropogenic impacts (Díaz et al., 2015). Others have demonstrated the importance of wetlands in general as providers of ecosystem services (Maltby & Acreman, 2011; Mitsch et al., 2015). Thus, our goal was to advance and provide a discussion about how specific functions are essential to ecosystem processes that underlie the provisioning of ecosystem services in RFEs (a particular type of wetland) and how it is regulated by the flood pulse. We also raise the discussion about the benefits and services provided by RFEs because we still lack a structured orientation in this regard, to better understand the intermediate and final services classification. We used a non-systematic survey to identify and update information about ecosystem services provided by RFEs. In addition, (i) we discussed the implication of some definitions of ecosystem services in the evaluation of these services in RFEs, (ii) we identified how ecosystem services are mediated and modified seasonally by flood pulses (a unique feature of RFEs), and (iii) we discussed the main threats to ecosystem services provided by RFEs. We highlight that our objective was not to give monetary values on ecosystem services but to identify and exemplify how services and benefits (and sometimes, disservices) are provided by RFEs. We included examples from different continents and different latitudes to get our survey as broad as possible.

Defining ecosystem services and their application to floodplains

Defining ecosystem services is not an easy task, and there are different approaches and typologies to classify them. The Millennium Ecosystem Assessment (MEA, 2003, 2005) typified ecosystem services in

Table 1 Ecosystem services categories and ecosystem services provided by river-floodplain ecosystems (according to the Millennium Ecosystem Assessment Report, 2003, 2005), along with examples of benefits for humans

Ecosystem service category	Ecosystem service provided by RFEs	Benefits for humans
Supporting services	1. Soil formation	Improve habitat quality for plants, increase macrophyte primary productivity, provide a sink and source of nutrients (e.g., Baveye et al., 2016; Barbosa et al., 2019)
	2. Nutrient cycling	Flux and exchange of organic and inorganic matter, biomass production, ecosystem functioning, water purification (e.g., Talbot et al., 2018; Thomaz, 2022a)
	3. Primary production	Biomass for higher trophic levels and provisioning services (e.g., Junk et al., 1989; Grabowska et al., 2014)
	4. Habitat provisioning	Habitat area suitable for biodiversity (e.g., Thomaz et al., 2007; Deosti et al., 2021)
Regulating services	5. Water regulation	Reduce catastrophic floods, regulate runoff and recharge aquifers (e.g., Pithart et al., 2010)
	6. Erosion control	Shore protection, soil protection (e.g., Christine et al., 2005; Mori et al, 2021)
	7. Water purification and waste treatment	Improvement of water quality, nutrient cycling (Walalite et al., 2016)
	8. Disease regulation	Improvement of water quality by reducing coliforms and other pathogens (e.g., Henriot et al., 2019)
	9. Climate regulation	Short term control of local climate and long-term control of global changes (Lu et al., 2005; Cole et al., 2007)
Provisioning services	10. Water supply	Provision of water of quality for human consumption and ecological balance and maintenance of biodiversity (e.g., Grygoruk et al., 2013)
	11. Food provisioning	Provision of living biomass including fish for food consumption and as a social and economic asset for society (e.g., Welcome, 2008; Opperman et al., 2009; Thomaz, 2022a)
	12. Ornamental market	Provision of fish and macrophytes for the ornamental market (e.g., Pelicice & Agostinho, 2005; Thomaz, 2022a)
	13. Genetic resource	Provision of genetic diversity can buffer anthropogenic pressures and maintain biodiversity production (Enriquez-Quiroz et al., 2006)
	14. Hydropower generation	Energy source and water retention for consumption and leisure (e.g., Schindler et al., 2014)
Cultural services	15. Spiritual and religious	Space for the local community to practice their religious rituals, sense of belonging (e.g., Matthews, 2012; Wantzen et al. 2016; Shah et al., 2018; Rinku & Singh, 2019)
	16. Recreation and ecotourism	Water sports, freshwater beach recreation, bird watching (e.g., Sanon et al., 2012; Funk et al., 2020)
	17. Aesthetic	Contemplation of nature (e.g., Gilvear et al., 2013; Wantzen et al., 2016)
	18. Cultural	Practice of regional and historical gatherings and popular festivities (e.g., Begossi, 2014; Begossi et al., 2019)

four categories: supporting, provisioning, regulating, and cultural services. One limitation of using the MEA typology is distinguishing between the functions (or processes) that generate services and ecosystem services themselves (Boyd & Banzhaf, 2007; Wallace, 2007; Haines-Young & Potschin, 2010). Within this context, some authors do not consider supporting services (e.g., nutrient cycling and productivity) as ecosystem services, since they provide the basis for ecosystem functioning and, indirectly,

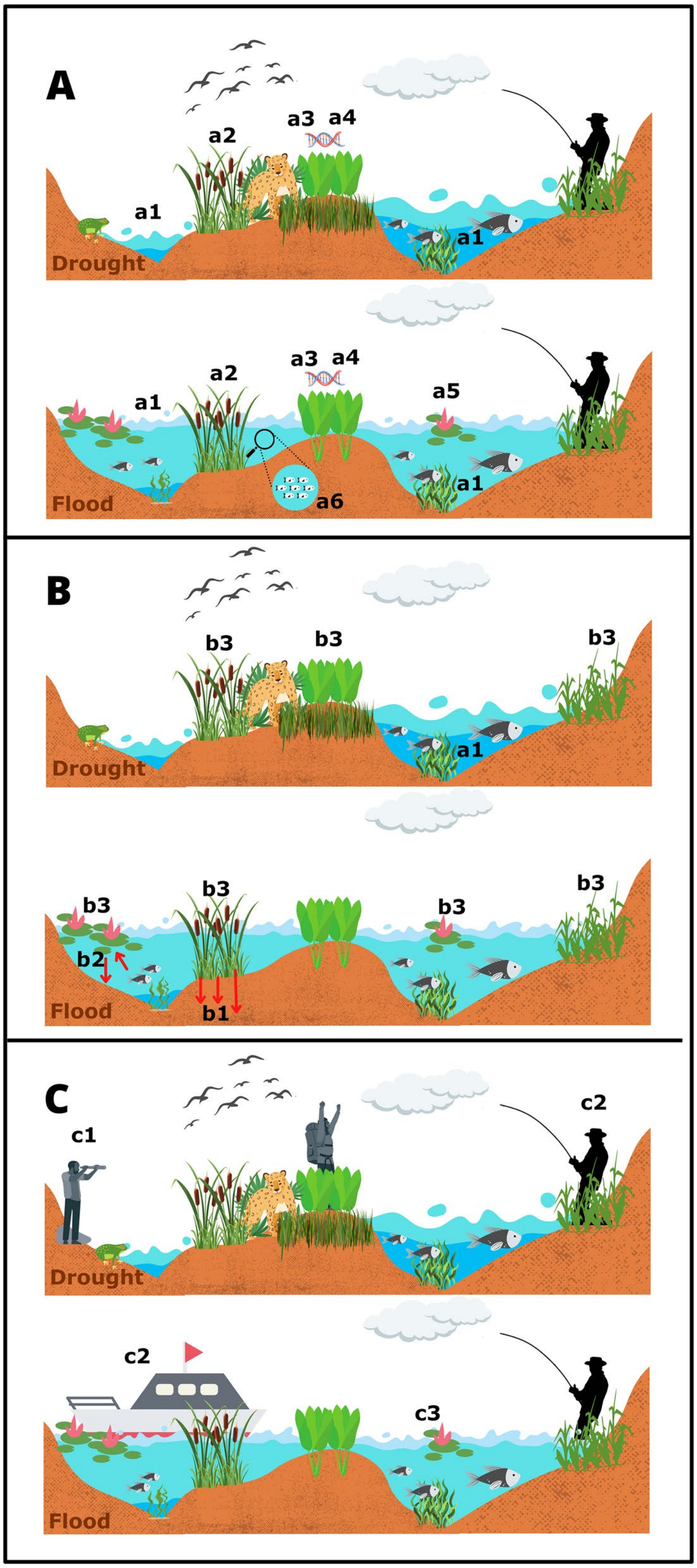

Fig. 1 Selected examples of ESs provided by RFEs and the influence of the flood pulse on some of them. **A** *Provisioning Services*: biomass of plants, fish and other animals (*a1*), fiber (*a2*), genetic resources (*a3*), biochemicals (*a4*) and ornamental resources (*a5*), all obtained from aquatic and terrestrial plants; **B** *Regulating Services*: water regulation, related with timing and magnitude of runoff, flooding and aquifer recharge (associated with plants physical structure and water infiltration, indicated by arrows, mainly during high waters) (*b1*), water regulation and waste treatment (absorption by macrophytes, microorganisms, sedimentations indicated by a arrow) (*b2*), climate regulation (*b3*); **C** *Cultural Services*: bird and other animal observation, which changes with the flood pulse (*c1*), fishing and boating (*c2*), use of products like macrophytes (e.g., lotus) with religious purposes (*c3*)

provide the basis for ecosystem services which will benefit humans (Boyd & Banzhaf, 2005; Haines-Young & Potschin, 2010).

Ecosystem services and benefits are considered the same within the MEA context; however, some authors use ecosystem services as the aspects of ecosystems used by humans to produce well-being, while benefits are considered as something that impacts human welfare (Boyd & Banzhaf, 2005; Fisher & Turner, 2008). For example, recreation is a benefit rather than a service provided by ecosystems (Boyd & Banzhaf, 2005; Fisher & Turner, 2008). In addition, benefits can be derived from intermediate or final services (Boyd & Banzhaf, 2005; Fisher & Turner, 2008). Taking one example for RFEs (Fisher & Turner, 2008), primary productivity (by riparian vegetation and macrophytes) helps water regulation (an ecosystem service provided by RFEs) which in turn enhances drinking water (a benefit provided by RFEs). Primary productivity can also directly enhance timber production (another benefit in a variety of RFEs). In the former example, primary productivity is an intermediate service, while it is a final service in the latter.

Another consideration is related to the fact that ecosystem services are considered by some authors as being ecological in nature (Fisher & Turner, 2008). In this sense, cultural contentment and recreation, for example, would not be considered ecosystem services (Fisher & Turner, 2008). Also, in accordance with this point of view, flood regulation is an ecosystem service (similarly to MEA, 2005), although others disagree with this view and consider flood regulation a process, not a service (Boyd & Banzhaf, 2005; Wallace, 2007).

The benefits provided by RFEs to humans are also circumstantial. For example, these ecosystems reduce flow velocity and retain water, which can be translated into flood control, one of the most critical ecosystem services provided by RFEs (see below). However, whether this is an ecosystem service or not depends on the benefits it provides for a given population (Haines-Young & Potschin, 2010). Societies leaving far from areas subject to flood will not recognize or will not be willing to pay for this type of service. Using a different perspective, floods that occur in pristine, unpopulated areas do not represent harm for humans, which makes flood control not be perceived as a benefit for society in these areas. In the same sense, enhanced evaporation in a RFE is necessary to maintain ecosystem functioning and is positive from this perspective. Still, it is a loss of water for those who leave downstream, being considered negative in certain circumstances (Bullock & Acreman, 2003). Because ecosystem services are context-dependent, the examples we show in this survey should be considered as ’potential ecosystem services’, because they can benefit humans in some RFEs but not in others.

Another consideration is that the same ecosystem service may belong to different categories. For example, food is a typical provisioning service, but it is also a cultural service in numerous cultures. It is also important that nature may contribute negatively to humans (in the form of "disservices") and for this reason, the International Platform for Biodiversity and Ecosystem Services prefers to use the term "Nature Contribution to People", instead of ecosystem services (Pascual et al., 2017).

Despite the above considerations, the original MEA framework is still largely used to evaluate ecosystem services and its flexibility helps to capture different types of services (Talbot et al., 2018). However, taking the above considerations into account, we were also flexible regarding ecosystem services definitions. Thus, sometimes we recognize that an ecosystem service can belong to different categories. We will also discuss the supporting services categorization (proposed by MEA, 2005) in the light of recent research that brings up the classification of environmental processes important to the functioning of RFEs as intermediate ecosystem services.

Supporting services

Supporting services classification is highly dependent on the context of the ecosystem evaluation because the ecosystem properties can be described as intermediate services that underpin the output of final services (Haines-Young & Potschin, 2018). Haines-Young & Postchin (2018) argue that supporting services such as soil formation and nutrient cycling would be better documented in other ecosystems properties accounting the structure, processes, and functions that give rise to services. Ecosystem properties ultimately determine the capacity of the ecosystem to deliver particular services and can be measured as the ecosystem condition.

Floodplains supporting services are strongly related to the hydrological and biogeochemical cycles, and to the differential provision of habitats through seasons (Baigún et al., 2008), which are processes primarily driven by the flood pulse dynamics (Talbot et al., 2018). **Soil formation**, for instance, is an essential ecosystem process because many provisioning services depend on soil availability, fertility, and the rate of soil formation. Floodplain soil is formed through the sedimentation of alluvial sediments over a long time (> decades and centuries) (Ivanov et al., 2019). The accumulation and erosion rates, granulometry, and nutrient contents vary with floodplain distance from the active river channel, flood pulse magnitude and frequency, and the uses given to the area (Aalto et al., 2003; Oliveira Junior et al., 2019; Schomburg et al., 2019), that drive differential ecosystem services in each context (Baveye et al., 2016). In pristine systems, soil moisture and fertility support primary production and nutrient cycling and are directly influenced by the preserved natural vegetation (Barbosa et al., 2019). In these systems, soil formation supports plant growth and animal survival, enhancing the energy transfer between the aquatic-terrestrial interface and buffering flooding (Talbot et al., 2018). Through infiltration, nutrients and matter are filtered and aquifers are recharged (Baveye et al., 2016). Soil also serves as a physical buffer in the global water cycle and medium that fosters biological/biochemical transformations of toxic compounds (Baveye et al., 2016).

In human-altered RFEs, drainage of the river terraces and reduction in the soil moisture (i.e., river regulation and land-use changes) disrupts soil formation and nutrient cycling, changing forest species composition, reducing energy and matter exchange between the river and its floodplain and lowering the groundwater levels (Kawalko et al., 2021). In these systems, ecosystem processes are altered, with a consequential shift in the provisioning ecosystem services. For example, eliminating floods and lowering the groundwater table allow deeper penetration of the soil by plant roots, soil fauna, and microorganisms, and creates more favorable conditions for the agricultural use of soils (Kawalko et al., 2021). The soil itself is a source of raw materials, such as clay and sand, for buildings, industry, and manufacturing (Baveye et al., 2016).

Photosynthesis and **primary production** are also two crucial supporting services provided by RFEs. In freshwater ecosystems, these ecosystem services are associated mostly with microalgae (Naselli-Flores & Padisák, 2022) and macrophytes (Piedade et al., 1991; Junk et al., 2011; Thomaz, 2022a). In RFEs, most biomass produced by microalgae occurs in lakes and other lentic habitats (Carvalho et al., 2001; Devercelli et al., 2014; Grabowska et al., 2014) and in the ATTZ for macrophytes (Junk et al., 1989). Photosynthesis and primary production are also provided by flooded forests in these ecosystems (Ward et al., 2002; Junk et al., 2021). In RFEs, microalgae contribute conspicuously to higher trophic levels, being very important for fish production (e.g., Araújo-Lima et al., 1986), despite the small area covered by lakes in the floodplain. In contrast, macrophytes are more important in fueling microbial food-webs in RFEs, directly contributing to nutrient cycling (Thorp & Delong, 2002). Indirectly, floating macrophyte roots provide shelter to zooplankton assemblages that can control microalgae through trophic interactions and contribute to nutrient cycling and primary production regulation (Keckeis et al., 2003; Burdis & Hoxmeier, 2011; Higuti & Martens, 2016).

The rewetting of dry sediment during flooding mobilizes nutrients and organic matter from locally mineralized and decomposed organic matter in the soil (Padial & Thomaz, 2006; Schönbrunner et al., 2012), and drives a high potential for nutrient cycling in the aquatic and terrestrial environmental interface. **Nutrient cycling** is a major ecosystem process because it drives biomass production, supports food webs, and maintains water quality (Clawson et al., 2001; Talbot et al., 2018). Seasonal floods contribute with nutrients to aquatic and terrestrial systems and stimulate primary production (Junk et al., 1989), that might initially be inhibited while water is high and nutrients are still held in the sediment or in the living biomass, but will then be available to support the fluxes of energy and matter (Lindholm et al., 2007; Talbot et al., 2018). In human-altered REFs, increased nutrient inputs from anthropogenic sources may induce eutrophication whenever flooding and flushing rates are low, and can prejudice food and water provisioning and reduce aesthetic and cultural benefits from RFEs (Talbot et al., 2018), because it surpasses the natural nutrient cycling from the ecosystem.

Because **soil formation** rates and typologies are so variable and discontinuous over space and time in RFEs, and because **nutrient cycling** fluxes (sources and sinks) and **primary production** can be better understood by means of the final services they provide, they can be better assessed as ecosystem processes, rather than ecosystem services themselves. The rates of erosion and soil formation, nutrients, and sources that sustain food webs, water quality, and recreational potential are all benefits from the processes of **soil formation, nutrient cycling,** and **primary production** (Table 1, Fig. 1).

Habitat provisioning is another important supporting service provided by RFEs. The hydrological variation associated with the flood pulse, and the different degrees of connectivity between the river and the floodplain habitats, enhance the spatio-temporal heterogeneity of habitats, both in terms of physical and chemical characteristics (Tockner & Ward, 1999; Ward et al., 1999; Marchese & Ezcurra-Drago, 2002; Thomaz et al., 2007). High habitat heterogeneity in RFEs is also provided by the presence of terrestrial, amphibian, and aquatic plants belonging to different life forms (Junk & Wantzen, 2004). The composition of plants changes spatially and temporally, in response to the flood pulse (Bini, 1996; Neiff & Poi de Neiff, 2003; Murray-Hudson et al., 2014) and to connectivity (Pozzobom et al., 2021), creating different habitats for invertebrates, fish, and aquatic birds. These sources of habitat variability make RFEs to be very important systems in terms of habitat provisioning, which in turn helps explaining the high biodiversity of RFEs (Junk et al., 1989; Tockner & Ward, 1999; Marchese & Ezcurra-Drago, 2002; Agostinho et al., 2004; Conceição et al., 2018; Deosti et al., 2021).

Regulating services

Regulating services are related to benefits obtained from the regulation of ecological processes (MEA, 2003, 2005). **Water regulation** is a typical benefit and in RFEs it is related to timing and magnitude of runoff, flooding, and aquifer recharge. Flood mitigation (associated with water regulation) is among the most typical and important benefits of RFEs (Ming et al., 2007; Pithart et al., 2010), and it can be considered similar to **storm protection,** another benefit also provided by coral reefs and mangroves (MEA, 2005). A systematic review showed that floods reduced or delayed, or that recession increased, in 23 out of 28 studies, suggesting that flood mitigation is more important in RFEs than in other types of wetlands (Bullock & Acreman, 2003). The storage of water is provided by morphometric features (e.g., floodplain lakes, channels, and by floodplain surface), by water infiltration and by macrophytes that colonize the ATTZ, which reduce flow velocity (Keddy, 2000; Liao, 2012).

Flood mitigation is more valuable in populated regions located downstream from RFEs, which are the ones that receive most of the benefits from flood control (Akanbi et al., 1999; Jakubínský et al., 2021). This benefit has long been recognized and the recovery of floodable areas and other storage structures is a strategy that has been used to reduce catastrophic flood impact in urban areas where humans impacted or subtracted RFEs (Lee et al., 2008; Liao, 2012). These interventions will be even more important in future scenarios of global changes subject to extreme climatic events (da Silva et al., 2018), although sometimes they are not enough to impede flood damages (e.g., Amaral & Ross, 2020).

In addition to flood mitigation, water regulation is also provided in **aquifer recharge**. This ecosystem service depends on the size of the inundation area (i.e., the ATTZ), and this service enhances during flooding in RFEs, when the contact between water and soils increases (Talbot et al., 2018). For example, groundwater recharge occurred in all 13 studies surveyed by Talbot et al. (2018) and in nine of 10 RFEs surveyed by Bullock & Acreman (2003), evidencing the importance of this ecosystem service in RFEs.

Erosion control is another benefit provided by RFEs related to flood mitigation (e.g., Mori et al., 2021) because erosion intensity is positively associated with river flow and water velocity. Thus, features of RFEs that reduce flooding downstream also contribute to erosion control. For example, promoting overflowing, increasing roughness, and implementing 'dry reservoirs' are strategies suggested to increase flood mitigation and erosion control (Christine et al., 2005).

Water purification and waste treatment are essential benefits provided by RFEs and they are mostly related to nutrient cycling. Studies show that these ecosystems function as sinks of nutrients, including nitrogen and phosphorus (Vaikasas & Dumbrauskas, 2010; Filoso & Palmer, 2011; Walalite et al., 2016; Hopkins et al., 2018). Several mechanisms cause the retention of nutrients laterally to rivers, including absorption by macrophytes (Hes et al., 2021), trapping and filtering activity of the ATTZ vegetation (Walalite et al., 2016) and denitrification (Carignan & Neiff, 1992).

Water purification and waste treatment go beyond nitrogen and phosphorus retention since RFEs retain organic and inorganic pollutants other than these two macronutrients (Lair et al., 2009). Deposition of contaminants associated with sediment involves a variety of processes, like sorption of contaminants into sediment (Sposito, 1989) and diffusion into solid structures (Pignatello, 1990; see Lair et al., 2009 for a synthesis about these processes). The dynamics of pollutants change according to physical and chemical properties in the floodplain and deposition usually occurs at long term during periods of slow flow, when discharge is below bank, while episodic release of pollutants from the floodplain may occur during flooding (Lair et al., 2009). This temporal trend of pollutant retention is evidence that ecosystem services related to pollutant retention are also regulated by the flood pulse.

Disease regulation is also an important benefit provided by some RFEs. Considering the critical role of macrophytes in reducing pathogens by physical (e.g., filtration by plant roots attached to the substrate), biological (e.g., plant-microbes interaction within biofilms) and chemical (e.g., exposure to biocides excreted by some plants; Alufasi et al., 2017; Biedunkiewicz et al., 2020), and that these plants occur in high abundances in the ATTZ and in floodplain lake shores, RFEs likely have an essential role in reducing the abundance of a myriad of microorganisms related to human diseases. For example, wetlands connected to a floodplain exhibited resilience to *Escherichia coli* (Migula, 1895) contamination and a lower abundance of particular antibiotic-resistant pathogens than the main river channel, indicating that floodplains may contribute to reducing contamination (Henriot et al., 2019). In contrast, the flood pulse may stimulate and spread mosquito larvae which are disease vectors (Sánchez-Ribas et al., 2017), which can in these cases be considered a ’disservice’.

Climate regulation is provided by ecosystems at local and global scales by emitting and sequestering greenhouse gases (MEA, 2003, 2005). At local scales, for example, there is evidence that RFEs change the wind circulation (dos Santos et al., 2014), moisture transport (dos Santos et al., 2014) and contributes to atmospheric CO_2 variations (Lu et al., 2005). At the global scale, carbon dynamics become important. Most freshwater ecosystems release carbon incorporated by terrestrial vegetation to the atmosphere (Cole et al., 2007), which is probably an important carbon source in RFEs. Carbon emissions in RFEs also occur through litterfall and submerged root respiration of flooded forests and floating macrophytes (Abril et al., 2014), to cite a few examples. In contrast, carbon is accumulated from a variety of sources in RFEs, like through riparian regeneration that enhances soil C stock (Matzek et al., 2020), through detritus accumulation of highly productive C4 grasses in floodplain lake sediments (Piedade et al., 1991) and through particulate organic carbon overbank sedimentation (Walling et al., 2006). In addition, carbon is buried in floodplain lakes at rates that can be several folds greater than those reported for other aquatic ecosystems (Sanders et al., 2017).

It is challenging to conclude about the role of RFEs at the global scale (and thus, about their role in climate regulation) because of tremendous differences in their metabolism and biomass stocks (Homeier et al., 2017), percentage covered by vegetation (Abril et al., 2014) and wetland surface in relation to the catchment surface (Borges et al., 2015). To our knowledge, there is no global analysis of the carbon budget for RFEs. However, other freshwater ecosystems that suffer from seasonal desiccation (like RFEs) indicate they represent important net C sources for the atmosphere (Keller et al., 2021). In contrast, a survey conducted in RFEs in British rivers suggested that they function as carbon sinks (Walling et al., 2006), while the CO_2 net ecosystem exchange of particular RFEs is nearly neutral in the central Amazon (Abril et al., 2014) and the carbon budget is nearly neutral in an Australian floodplain (Webb et al., 2018). Considering the sources of variation in RFEs characteristics mentioned above, it is expected that some RFEs function as carbon sinks, while others would function as carbon sources. For the latter ones, a "disservice", in terms of climate regulation would occur.

Provisioning services

River-floodplain ecosystems provide many valuable benefits to society that are included in the provisioning service category, such as water for drinking and irrigation, food (e.g., fishes and crops), fiber, biochemical resources, ornamental species, and energy production. The **water supply** is vital for ecological balance and human needs, and consequently, it is one of the most relevant ecosystem services provided by RFEs. For example, a study from Poland identified that the water storage volume of a floodplain was greater in magnitude than all artificial reservoirs summed in a determined area (Grygoruk et al., 2013). However, the water quality provided by RFEs mainly depends on surrounding native vegetation (Koschke et al., 2014). Human land use may decrease water quality through native vegetation reduction, pollutants, and silting. Consequently, the conservation and restoration of riparian vegetation in RFEs are essential for providing drinking water. The use of water from floodplains for irrigation is also relevant for many crops worldwide (Barbier & Thompson, 1998; Shankar et al., 2005; Chitu et al., 2020). However, the loss of other ecosystem services caused by reduced floodplain inundation due to irrigation areas (e.g., fishing, fuelwood, and agriculture) may be higher than the irrigation benefits (see Barbier & Thompson, 1998).

River-floodplain ecosystems are among the most productive ecosystems on earth due to the continual enrichment from the upstream and lateral sources caused by the flood pulse (Tockner & Stanford, 2002; Opperman et al., 2010). Because of the high nutrient and water concentration, RFEs are essential to **food provisioning** since various crops are developed in their fertile lands, such as rice, corn, and soybeans (Chitu et al., 2020; Bhatt et al., 2021; Tariq et al., 2021). Also, other agricultural practices such as pasture and timber are developed in floodplain areas (Opperman et al., 2009) and some macrophytes associated with floodplains provide fiber and potential biomass fuel (Ciria et al., 2005; Thomaz, 2022a). Particularly macrophytes may provide valuable **biochemical** metabolites for commercial products (e.g., natural products such as pharmaceuticals), including species with potential antineoplastic, anti-inflammatory, antifungal, antibacterial, and antioxidant activities (Kurashov et al., 2016; Adelodun et al., 2020; Musara & Aladejana, 2020).

Fishery is one of the most socially and economically valuable ecosystem services provided by RFEs (Opperman et al., 2010). Floodplain habitats are the nursery of many economically valuable species. Also, the fishes' reproduction highly depends on the flood regime (Gomes & Agostinho, 1997; Bailly et al., 2008; Oliveira et al., 2020), especially for long-distance migratory species because the flood is a trigger for migration and reproduction (Oliveira et al., 2020). Examples of long-distance migratory species include *Salminus brasiliensis* Valenciennes, 1850, *Pseudoplatystoma corruscans* (Spix & Agassiz, 1829) and *Brachyplatystoma rousseauxii* (Castelnau, 1855) in South America, *Pangasianodon gigas* (Chevey, 1931) in the Mekong River (Barlow et al., 2008) and *Coreius guichenoti* (Sauvage & Dabry de Thiersant, 1874), *Acipenser dabryanus* (Duméril, 1869), and *Psephurus gladius* (Martens, 1862) in the Yangtze River (Cheng et al., 2015). Although most of these species are threatened, some are highly appreciated in culinary and, consequently, monetarily valued, providing an essential income for fishers. River floodplain ecosystems also may generate billions of dollars worldwide through **ornamental** fisheries. In South America, most of the ornamental fish trade is restricted to the Amazon region because of its high fish diversity that includes many species regarded as ornamentals (Pelicice & Agostinho, 2005; Sampaio et al., 2019). However, other RFEs also have a huge potential for ornamental activity. For example, in the Upper Paraná River floodplain (Brazil), from a total of 101 species of fishes captured, 40.6% were cited as ornamental in the literature and an additional 42.6% are considered as potentially ornamental (Pelicice & Agostinho, 2005).

Genetic resources can be considered a provisioning or supporting service (MEA, 2005; Zhang et al., 2007). Genetic diversity, through genotypic complementarity, can buffer against extreme climatic events (Reusch et al., 2005). Regarding provisioning, for example, a high fish genetic diversity found in floodplains may allow the fisherman to be more readily responsive to changing market demands or environmental variations that might affect fisheries (e.g., changes in flood intensity and frequency).

Finally, **hydropower generation** in RFEs can be considered another relevant ecosystem service provided by large rivers (Schindler et al., 2014), mainly where hydro is the primary energy source (e.g., Brazil, Canada and Norway; IEA, 2020; Alfredsen et al., 2022). However, dam construction and operation can negatively affect the provision of other ecosystem services, such as water supply (Grygoruk et al., 2013) and fishery (Agostinho et al., 2004; Oliveira et al., 2020). Consequently, benefits provided by hydropower generation may not compensate for the loss of valuable ecosystem functions and benefits provided by RFEs free of dams (see below).

Cultural services

Throughout human history, civilizations have influenced ecosystems and their constituent elements (Pretty et al., 2009; Espinoza-Toledo et al., 2021), developing cultures capable of predicting and responding to seasonal environmental variations imposed by adjacent ecosystems (Turner & Clifton, 2009). For example, the great empires of Mesopotamia and Egypt were consolidated in the adjacencies of RFEs (Wantzen et al., 2016) and developed cultural traditions associated with the pulse of the waters. The Egyptians used irrigation methods based on the natural rise and fall of the Nile's seasonal fluctuations and hydrology. Flood pulses provided nutrients and sediment to the floodplain areas maintaining high productivity (Klaver, 2012). The flood pulses of the Nile River also played an essential role in scientific development. The first numerical system was created to distribute land for planting after the floods, which spurred the development of mathematics (Klaver, 2012). RFEs are natural systems that provide a range of non-material benefits to humanity (Funk et al., 2019), capable of promoting the social and cultural development of a region. The long history of human-nature interaction in the RFEs (Tockner & Stanford, 2002) reveals that the flood pulse is the driving force for the establishment and development of cultural practices in many rivers (Junk & Wantzen, 2004; Wantzen et al., 2016).

Cultural ecosystem services (CESs hereafter) are classified as 'the non-material benefits people obtain from ecosystems through spiritual enrichment, recreation, cognitive development and aesthetic experiences' (MEA, 2005). The recognition of non-monetary benefits provided by river ecosystems to humanity dates back to the 1960s (Leopold, 1969). Recently, the significant contributions to the satisfaction of essential individual and social necessity provided by rivers were summarized by Wantzen et al. (2016) by the concept "River Culture". These authors emphasize the influence of flood regimes and biological characteristics of adjacent areas in the expression of elements of human culture, as well as the need to ''learning from the river" with pulsating flow regimes for more sustainable management. However, the minimum river flows necessary to maintain ecological balance and human needs differ from those for cultural purposes. This can be visualized with the social and cultural practices of indigenous peoples, which date back thousands of years, but the pulses needed to sustain cultural ways of life are sometimes overlooked (Morgan, 2012). This fact requires water planning for the sustainability of cultural practices (Johnston et al., 2012). Human/water engagement in floodplains is manifested in many ways and CESs can be classified as spiritua, religious and sense of belonging, recreation and ecotourism, aesthetic and educational.

Spiritual, religious and sense of belonging services are also manifested in association with aquatic environments. For example, in India, the river Ganges (also referred to as Ganga) has been a symbol of India's age-long culture and civilization, whose waters are responsible for the material and spiritual sustenance of more than 500 million people (Rinku & Singh, 2019). Holy to Hindus, the Ganges has provided livelihoods, food, and water for Nepal, India, and Bangladesh. The 'Mother Ganga' is the scene of numerous religious manifestations, bringing together thousands of people in daily bathing rituals and funeral ceremonies (Shah et al., 2018). People have immense faith in the powers of Ganga water in healing and regeneration. But this close relationship of beliefs and traditions with the river has caused degradation and pollution. In Southeast Asia, religious beliefs and practices are related to protecting rivers and fish by the Naga spirit, especially among ethnic minorities in the Mekong River (Matthews, 2012). Small offerings such as bowls of fruit or bouquets used in religious rituals are often found on the African floodplains (Klaver, 2012) in addition to spiritual cleansing and cultural rituals to drive evil spirits into the wetland (Ondiek et al., 2016).

Recreation and ecotourism are two important cultural services. Floodplains offer different types of related recreational activities like hiking, wildlife observation, swimming, boating, fishing, and ice skating (Sanon et al., 2012; Funk et al., 2020). For example, in temperate zones, in winter, flood pulses can promote frozen floodplain areas, which are often used for recreational activities such as ice skating (Wantzen et al., 2016). The Amazon floodplain includes recreation and tourism associated with knowledge of indigenous cultures for modern cultures (Marcinek & Hunt, 2018). The tourist numbers in the Amazon region are constantly increasing, even though the tourist potential in the region is underused. In this sense, the community-based tourism (CBT) has provided several economic benefits, increasing the financial income of traditional communities located on Ilha do Marajó, at the mouth of the Amazon River, as well as social benefits, including skills development and the creation of local identity (Rodrigues & Prideaux, 2018). On the banks and tributaries of the river Ganges, there are several holy temples that receive millions of people to pray and bathe in the waters on important holidays of the Hindu calendar. In this plain, there are several forms of tourism that include religious, heritage, adventure, sports, and ecosystem tourism (Kumar, 2017).

Aesthetic values are reported for floodplains and their pulses (Wantzen et al., 2016). For example, numerous species of macrophytes that grow in RFEs [e.g., *Nymphaeae* spp., *Victoria amazonica* (Poepp.) J.C. Sowerby and *Nelumbo nucifera* (Gaertn.)] are used in water gardens (Thomaz, 2022a). RFEs are attractive, awakening a sense of place and can improve physical and mental wellbeing (Haines-Young & Potschin, 2010). This fact is pointed out by Ondiek et al. (2016) who showed that most of the people in the Kano floodplain recognize the natural wetland as an important aesthetic service mainly because of its beauty. Biodiversity was the main factor that triggered the sensation of aesthetic value, with the birds, macrophytes and the microclimate provided by the floodplains being the main characteristics considered. These benefits, associated with other ecosystem services, have led to actions aimed at the rehabilitation of floodplains (Gilvear et al., 2013). In many cities such as Frankfurt and Berlin, there has been a huge appreciation and development of architecture in areas adjacent to the Main and Spree rivers following restoration efforts (Wantzen et al., 2016).

Some cultural services are strongly related and often linked to provision and regulation services. For example, artisanal fishing is not just about food and salary income, but a way of life while water purification allows for the safe use of aquatic sports during low waters. **Culture** is represented in the way of life of traditional populations (Roosevelt, 1999), which may have alterations related to changes in flood pulses. This fact is reflected in fish traps and nets, places of traditional fishing practices and traditional knowledge of fish ecology. The construction of houses on stilts to adapt to the annual floods, always built-in front of the river, is also a clear example of a culture associated with flood pulses (Lira & Chaves, 2016). The Amazon floodplain has provided fish that help maintain cultural and economic activities (Smith, 1985; Begossi, 2014). Historically, most fishing in this floodplain is done by small-scale fishers, predominantly from the "ribeirinhos" culture, that rely mainly on fish protein for their diet and economic livelihood (Silva & Begossi, 2009; Begossi et al., 2019). Thus, these traditional populations affect and have their ways of life affected by flood pulses and availability of freshwater resources (Begossi et al., 2019). The way of life of riverine Amazonian communities has particular social aspects, such as the collective management of local resources, guided by their traditional knowledge (Lira & Chaves, 2016). A powerful example of a management system for these communities is the sustainable extractive reserve of Mamirauá, in the State of Amazonas (http://www.mamiraua.org.br/), which promotes the management of natural resources and other social aspects for local populations. Another important cultural service are the festivals related to resources provided by the floodplain, such as the "Ecofestival de Novo Airão" in the Brazilian Amazon. This festival invokes elements of nature, myths, legends and songs in defense of the preservation of the Amazon (Verde et al., 2021), and promotes the strengthening of the bond between humans and river systems.

The flood pulse and its relation with ecosystem services

Numerous ecosystem services are maintained or regulated by the flood pulse in a variety of ways and this is what makes RFEs different from other ecosystems in terms of ecosystem services dynamics (Fig. 1). For example, many benefits associated with regulating services in RFEs (e.g., water regulation, water purification, and waste treatment) depend on the capacity to retain water in the floodplain (Jakubínský et al., 2021), meaning that flooding is crucial for the maintenance of these benefits (Fig. 1B). Preservation of organic matter in sediments is influenced by hydrological variations (Bertassoli et al., 2017) and emission of greenhouse gases in large rivers is also affected by river connectivity with the floodplains (Teodoru et al., 2015), indicating that the flood pulse highly influences the carbon budget (and climate regulation). Even local climate changes in response to flooding, which is shown by intensification of river breezes during high waters (Santos et al., 2019). As a corollary, rivers without lateral floodplains or areas where the floodplains were extirpated, levees were constructed or where the flood pulse was regulated, will lose these benefits compared with areas where the natural flood pulse still regulates the floodplains.

Another example about the importance of the flood pulse relates to provisioning services (Fig. 1A). The flood pulse maintains high productivity in the ATTZ because it contributes with nutrients to the floodplain in a variety of RFEs habitats (Pedrozo & Bonetto, 1987; Camargo & Esteves, 1995; Houser & Richardson, 2010) and maintains vegetation in the early successional stages (Junk et al., 1989). Consequently, numerous floodplains have high biomass production of different trophic levels, including fish (Fernandes et al., 2009; Alford & Walker, 2013), one of the most important provisioning services provided by RFEs. Similarly, the ATTZ provides highly fertile soils during the low water (Wantzen et al., 2016). In addition to provisioning services, the high primary productivity typical of pristine RFEs is also related to various other ESs. For example, biomass production (e.g., timber) enhances flood control and climate regulation (Haines-Young & Potschin, 2010), two regulating services also provided by RFEs.

Cultural services also change with the flood pulse (Fig. 1C). One example is tourism and nature observation, which depends on the seasonal response of plants and animals to water level oscillations. In the Pantanal Wetland in South America (the largest RFEs in the world), for example, densities of numerous animal species that attract tourism, like caiman *Caiman crocodillus* Linnaeus, 1758, capybara *Hydrochaeris hydrochaeris* Linnaeus, 1766, marsh deers *Blastocerus dichotomus* Illiger, 1815, and waterfowl respond to the seasonal flood pulse (Alho, 2008). Migratory species of fish also respond to the flood pulse and thus, recreational fishing associated with these species also change during the year (Massaroli et al., 2021). As a consequence, the tourism activity associated with animal observation and recreational fishing changes seasonally, and the same occurs with the use of beaches, which appear during low water periods. In a broad sense, one can say that the flood pulse dictates the "rhythm of life", including cultural aspects of local people living in these areas or near them (Junk & Wantzen, 2004; Wantzen et al., 2016), who lives in the "rhythm of the waters" (Silva & Silva, 1995).

The seasonal variation associated with the flood pulse also allows replacement of species with different traits over the year, as shown for primary producers in general, and macrophytes in particular (Junk et al., 1989; Bini, 1996; Pan et al., 2011). Because ecosystem functions and their services are positively related to species traits (complementarity theory; Engelhardt & Ritchie, 2001; Loreau & Hector, 2001), we also expect that the complementarity of species traits resulting from flood pulse is important to maintain regulating and provisioning services related with biomass production. For example, nutrient retention, which translates into water purification (an ecosystem service provided by RFEs), enhances with macrophyte (and trait) diversity in wetlands (Engelhardt & Ritchie, 2001; Moi et al., 2021), and thus, the flood pulse potentially enhances this particular ecosystem service.

In addition to these examples above, the flood pulse generates benefits outside the aquatic ecosystem (Schindler et al., 2014). The flooding of terrestrial areas that remain exposed during periods of the year enhances soil nutrient and oxygen exchanges and provides fertile substrate for natural plant growth in pristine systems, and cultivated crops or pasture in altered systems (Pithart et al., 2010; Schomburg et al., 2019). Because flood zones are considered ecotones, they possess unique abiotic and biotic characteristics, and boost the provision of biodiversity of terrestrial and water-dependent species (e.g., otters, birds, capybara, jaguar) (Tockner & Stanford, 2002)..

Impacts and management

Impacts in RFEs are usually associated with ecosystem services losses. The most pervasive impacts that affect floodplain ecology and provisioning of ecosystem services are those related to transformations of the flood pulse and lack of connectivity. A variety of human impacts, such as dam construction and operation, levee construction, floodplain drainage, and other engineering and hydraulic works (e.g., Bowen et al., 2003; dos Santos et al., 2021; Jakubínský et al., 2021; Meyer et al., 2021; Kuehne et al., 2022; Vieira et al., 2022) can cause river regulation and decrease connectivity. Because community structure and ecosystem functioning of RFEs depend on flood pulses, the transformation of the natural water level fluctuations impacts the biota and ecosystem functioning, with consequences for ecosystem services provided by these ecosystems.

For example, regulating services like retention of nutrients, water regulation, and flood regulation are related to the capacity to retain water and nutrients during extreme discharges (Jakubínský et al., 2021). Because of these important roles of the flood pulse and the connectivity it provides, river regulation tends to decrease groundwater recharge and reduce nutrient retention, pollutant retention, and water purification (Zehetner et al., 2009; Talbot et al., 2018). The transformation of the flood pulse and break of connectivity between the river and the floodplain habitats consistently reduce ecosystem services in biomass production, water regulation, flood control, and nutrient retention, for example.

One typical example of provisioning service that decreases with flood regulation and lack of connectivity is the fish catch. In numerous RFEs throughout the world, there are many highly appreciated species of fish that migrate long distances and whose young depend on lateral areas for growing and survival (see the previous "Provisioning services" section). If the flood pulse does not follow the natural seasonality and/or its intensity is not large enough to promote connectivity, fish stocks are seriously damaged (Agostinho et al., 2016). The barriers created by the dams disrupt upstream spawning migration and compromise the downstream drift of fish eggs and larvae that sustain fisheries in large RFEs (Dugan et al., 2010), compromising this important provisioning service.

The links between the flood pulse, connectivity, and ecosystem services in RFEs bring important lessons for the management of these ecosystems. For example, it has been shown that interventions related to production and river regulation decrease, while restoration of connectivity and rehabilitation of RFEs promotes recovery of ecosystem floodplain multifunctionality and enhanced supply of ecosystem services (Schindler et al., 2014).

Reservoirs are a particular case in terms of impact on RFEs. Besides flow regulation, reservoirs retain nutrients and seston (Barbosa et al., 1999; Zanon, 2021), with consequences for RFEs located downstream. For example, reservoirs substantially reduce the phosphorus concentration and enhance the Secchi depth of RFEs located downstream (Roberto et al., 2009; Cheng et al., 2017). As a consequence, RFEs located downstream from reservoirs may experience a potential long-term oligotrophication (Thomaz et al., 2004; Junk et al., 2021). In the Nile River, for example, the construction of the Aswan Dam caused oligotrophication and significant reduction of fish production (Nixon, 2003). Owing to oligotrophication, one can predict losses of various ecosystem services in the long term (e.g., biomass production, fish stocks, and carbon storage) in RFEs situated downstream of reservoirs.

In addition to the above impacts, more related to flood pulse transformations, a variety of others compromise ecosystem services in RFEs, like urbanization and agriculture, only to cite a few examples. For instance, urbanization is related to changes in sediment deposition and erosion (Chin, 2006). In the Czech Republic, transformations of a floodplain that straightened the river made the floodplain to become flattened, which was followed by a decrease of 64% of its value in terms of flood mitigation, carbon sequestration, biodiversity and biomass production (Pithart et al., 2010). The transformation of grasslands and forests growing in a floodplain in Zambia into monocultures also compromised several ecosystem services associated with native biodiversity, decreasing natural benefits to local populations, like for example the provision of nutritious food year-round (Estrada-Carmona et al., 2020).

Biological invasions are also considered important impacts in RFEs and in the ecosystem services they provide. Invasions tend to reduce biodiversity and for this reason, invasive species may be important sources that disrupt ecosystem services outputs (Haines-Young & Potschin, 2010). Numerous RFEs are hot spots of invasions (Müller & Okuda, 1998; Tonella et al., 2018), facilitated by disturbances regimes mediated by humans and propagule pulses associated with flood pulses (Amo et al., 2021; Thomaz, 2022b). For these reasons, invasions may be of paramount importance in terms of impacts on ecosystem services in RFEs, especially in those affected by multiple stressors, where biodiversity may experience even higher decreases. At the same time, however, the facilitated invasion provided by RFEs in its areas and downstream (Thomaz, 2022b) may sometimes be considered a disservice provided by these ecosystems.

The above impacts are important individually, but they must be boosted by extreme climatic events, expected to occur in a scenario of global changes (Diez et al., 2012), which has already been experienced on the planet. A systematic literature review conducted by Talbot et al. (2018) found that extreme floods have the potential to cause losses in almost every ecosystem services they identified, while small floods had neutral or positive effects on half of these ecosystem services. Considering that some regions of the globe will experience higher levels of rainfall caused by climate changes (IPCC, 2021), one can predict that RFEs will be seriously affected in terms of ecosystem services they provide. Still in regard to extreme climatic events, and considering the critical role of RFEs in catastrophic flood regulation (Pithart et al., 2010), maintaining these ecosystems functional may be fundamental to provide flood mitigation in several parts of the planet. Catastrophic droughts are also expected to have huge impacts in regions where rainfall will decrease with climate change, which is already occurring in many areas (e.g., IPCC, 2021; de Necker et al., 2022). The Pantanal wetland in Brazil and Bolivia, for example, experienced one of its strongest droughts in 2019–2020, with severe consequences for biota and ecosystem services (Marengo et al., 2021). According to these authors, this extreme event can be associated with land-management and current climate changes, reducing rainfall transported from the Amazon towards the southern latitudes. Extreme drought events can impact many ecosystem services provided by RFEs, such as fish stock (because flood is crucial for reproduction of many fish species; Castello et al., 2015; Alves et al., 2021), water security (UNU-INWEH, 2013), navigability (Marengo et al., 2021) and recreational activities, because droughts decrease fisheries (Fernandes et al., 2009) and enhance eutrophication (Carvalho et al., 2001).

In summary, there are a myriad of impacts that cause losses of benefits provided by ecosystem services to local populations. However, the disruption of the flood pulse is a cause of concern because this driving force mediates a variety of ecosystem services in RFEs, and this association between seasonal flood pulses and ecosystem services is a unique feature of these ecosystems. Within this context, holistic approaches have to be taken into account for the maintenance of RFEs functionality and restoration purposes. Several studies have emphasized the importance of management options that respect the river dynamics and that the same threat menaces apparently different things like human well-being, cultural, and biological diversity (Junk & Wantzen, 2004; Wantzen et al., 2016). The use of "multifunctional floodplain management", which aims at a balanced provision of multiple ecosystem services (Jakubínský et al., 2021), is a tool to maintain and restore RFEs biodiversity, functioning, and their ecosystem services.

Concluding remarks

Here, we show that RFEs are providers of several benefits to society that are mainly driven by the flood pulse dynamics. The provision of ecosystem services in RFEs is influenced by the pronounced temporal and spatial environmental variability that allows the maintenance of high biodiversity and ecosystem multifunctionality. The complexity of functions and processes in RFEs makes them biodiversity hotspots and raises the challenges of conservation and restoration. The multiple demands and uses from RFEs worldwide generate conflicts that are not always easy to solve. Because of that, the synthesis of their major benefits to society is essential.

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