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RESEARCH REVIEW

Large-scale degradation of Amazonian freshwater ecosystems

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Abstract

Hydrological connectivity regulates the structure and function of Amazonian freshwater ecosystems and the provisioning of services that sustain local populations. This connectivity is increasingly being disrupted by the construction of dams, mining, land-cover changes, and global climate change. This review analyzes these drivers of degradation, evaluates their impacts on hydrological connectivity, and identifies policy deficiencies that hinder freshwater ecosystem protection. There are 154 large hydroelectric dams in operation today, and 21 dams under construction. The current trajectory of dam construction will leave only three free-flowing tributaries in the next few decades if all 277 planned dams are completed. Land-cover changes driven by mining, dam and road construction, agriculture and cattle ranching have already affected ~20% of the Basin and up to ~50% of riparian forests in some regions. Global climate change will likely exacerbate these impacts by creating warmer and dryer conditions, with less predictable rainfall and more extreme events (e.g., droughts and floods). The resulting hydrological alterations are rapidly degrading freshwater ecosystems, both independently and via complex feedbacks and synergistic interactions. The ecosystem impacts include biodiversity loss, warmer stream temperatures, stronger and more frequent floodplain fires, and changes to biogeochemical cycles, transport of organic and inorganic materials, and freshwater community structure and function. The impacts also include reductions in water quality, fish yields, and availability of water for navigation, power generation, and human use. This degradation of Amazonian freshwater ecosystems cannot be curbed presently because existing policies are inconsistent across the Basin, ignore cumulative effects, and overlook the hydrological connectivity of freshwater ecosystems. Maintaining the integrity of these freshwater ecosystems requires a basinwide research and policy framework to understand and manage hydrological connectivity across multiple spatial scales and jurisdictional boundaries.

Keywords: climate change, conservation, dams, fragmentation, hydrological connectivity, land-cover change, mining, policy, watershed

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Introduction

Freshwater ecosystems provide a range of key ecosystem services. They regulate climate, support nutrient cycling, transport water and materials, and maintain water quality and natural communities (Millennium Ecosystem Assessment, 2005). They also provide food, energy, fiber, and water for human consumption, being necessary for the survival and well-being of people (Brauman *et al*., 2007).

The volume, timing, quality, and variability of water flows play key roles in maintaining the integrity of freshwater ecosystems because they control their hydrological connectivity – defined as the 'water-mediated transport of matter, energy, and organisms within and between elements of the hydrological cycle' (Rosenberg *et al*., 2000; Pringle, 2001; Freeman *et al*., 2007b). Disruptions of hydrological connectivity, referred to here as hydrological alterations, can degrade freshwater ecosystems. Dam construction, for example, disrupts river flows by changing their seasonality and establishing lentic (still water) conditions (e.g., Pelicice *et al*., 2014).

Hydrological alterations are escalating worldwide as human populations grow and global climate change shifts the planetary energy and water balance (Vörösmarty *et al*., 2000). These environmental changes are widespread in tropical regions, particularly in large river basins such as the Congo, Mekong, and Amazon (Wohl *et al*., 2012). In the Amazon (the largest of these basins), construction of dams, mining, land-cover

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change, and global climate change are driving rapid degradation of freshwater ecosystems through changes to the hydrological cycle (Castello *et al*., 2013b; Macedo & Castello, 2015). Freshwater ecosystems cover over 1 million km^2 of the Amazon Basin, draining ~6.9 million km^2 of moist tropical forests and savannas and discharging 20% of global surface river flows into the Atlantic Ocean (Coe *et al*., 2008).

Maintaining the integrity of freshwater ecosystems requires understanding the full range of ecosystem effects caused by hydrological alterations occurring in adjoining freshwater, terrestrial, atmospheric, and oceanic systems. However, predicting the impact of hydrological alterations on large tropical basins is difficult due to a lack of integration of available knowledge. Most studies of drivers on hydrological alteration of freshwater ecosystems have focused on single dams in tributary watersheds, but they have largely disregarded the cumulative effects of multiple dams on the hydrological connectivity of freshwater ecosystems systems. Similarly, most studies assessing the consequences of hydrological alteration have focused on specific ecosystem components (i.e., species composition, biogeochemical cycling), but have paid little attention to whole ecosystem structure and function.

This review provides a comprehensive framework for understanding the linkages among Amazon freshwater ecosystems, drivers of hydrological alteration, ecosystem responses and feedbacks to these changes, and the role of management policies. The framework hinges on four research questions: (i) What is the role of hydrological connectivity in maintaining the structure and function of freshwater ecosystems? (ii) How and to what extent are dams, land-cover change, mining, and global climate change altering the hydrological connectivity of Amazon freshwater ecosystems? (iii) What are the consequences of these hydrological alterations for freshwater ecosystems at the Amazon Basin scale? and (iv) What deficiencies in existing policies may hinder protection of freshwater ecosystems from hydrological alteration?

Hydrological connectivity

Macroscale patterns

The hydrological connectivity of Amazon freshwater ecosystems operates in four dimensions, one temporal and three spatial (Fig. 1; adapted from Ward, 1989). In the temporal domain, connectivity refers to seasonal and interannual changes in water flows (e.g., rainfall). In the spatial domain, it consists of longitudinal (headwater–estuary), lateral (river–land or stream–land), and vertical (river–atmosphere or land–atmosphere) connections.

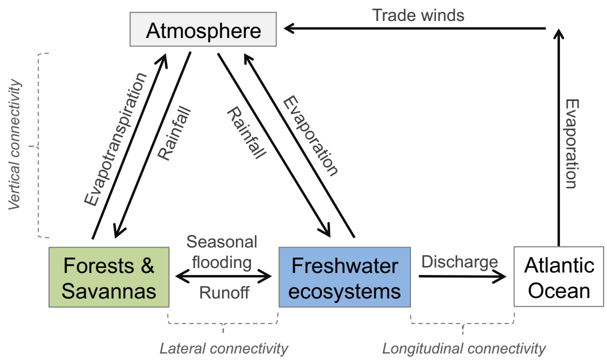

Fig. 1 Schematic diagram of the main pathways involved in the hydrological connectivity of Amazon freshwater ecosystems.

Rainfall in the Amazon depends on the trade winds and the South American Monsoon System (Fig. 1), which transfer moisture from the Atlantic Ocean to the Basin (Marengo *et al*., 2012; Jones & Carvalho, 2013). Average annual rainfall over the Basin is ~2200 mm yr^{-1} and highly seasonal (Huffman *et al*., 2007). Between 50 and 75% of this annual rainfall (~9600 km^3 yr^{-1}) is intercepted by forests and savannas and recycled back to the atmosphere via evapotranspiration (Shuttleworth, 1988; Malhi *et al*., 2002; D'Almeida *et al*., 2007). The remainder falls over freshwater ecosystems, or drains through forests and savannas (i.e., surface runoff) and enters a vast network of streams, lakes, and rivers, transporting terrestrial organic and inorganic materials into freshwater ecosystems. Downstream flows transport these materials and discharge an estimated ~6700 km^3 yr^{-1} of freshwater into the Atlantic Ocean (Coe *et al*., 2008).

Influence on freshwater ecosystems

Rainfall and geomorphology control the physical and chemical properties of rivers (Sioli, 1984; Junk *et al*., 2011; Hess *et al*., 2015). Whitewater rivers originate in the Andes Mountains and carry heavy sediment loads. Clearwater rivers originate in the southeastern region of the basin and drain the weathered soils of the Brazilian and Guianan Shields, carrying some dissolved minerals but few suspended sediments. Blackwater rivers (e.g., the Negro River) drain the sandy, nutrient-poor soils of the central Amazon, carrying few suspended sediments but high levels of acidity and tannins. These rivers form a diverse array of freshwater ecosystems throughout the Basin (Fig. 2).

As intermittent rainfall flows from land into stream channels, it creates aquatic–terrestrial interfaces (referred to as riparian zones of small streams) that are the

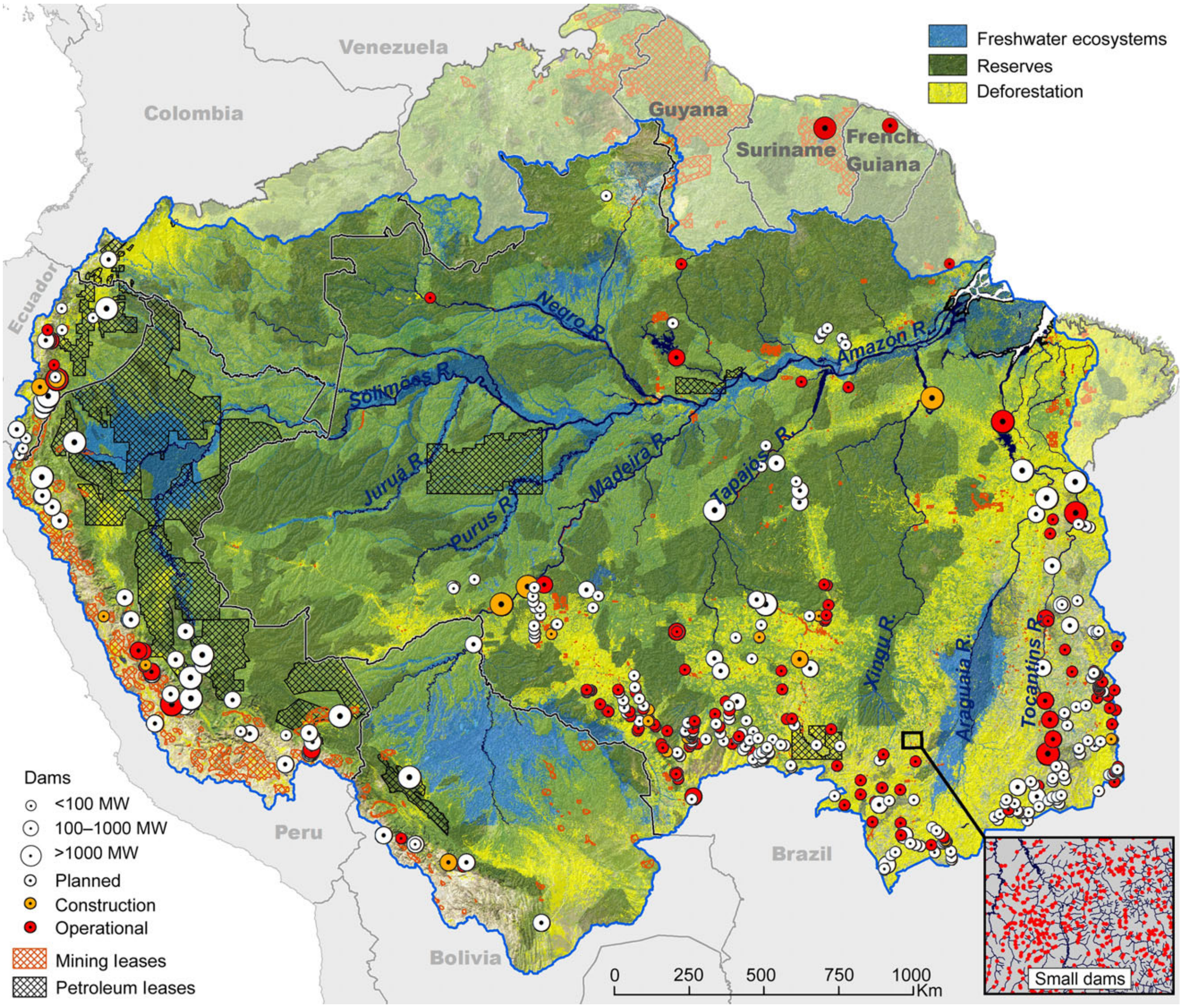

Fig. 2 Drivers of hydrological alteration in Amazon freshwater ecosystems. Figure by Paul Lefebvre (adapted from Castello *et al.* 2013b).

principal zone of exchange of water, nutrients, sediments, and organic matter between terrestrial and freshwater ecosystems (Junk, 1993; Godoy *et al.*, 1999; McClain & Elsenbeer, 2001; Naiman *et al.*, 2005). Despite their size, small streams and their riparian zones are numerous and likely the most extensive freshwater ecosystem of the Basin (Junk, 1993; Beighley & Gummadi, 2011). Although their extent is unknown, headwater streams are thought to represent two-thirds of total stream length in typical watersheds and thus underpin basinwide freshwater connectivity (Freeman *et al.*, 2007a).

In the lower reaches of large rivers, seasonal inundation cycles (i.e., flood pulses) with mean amplitude of 10 m (to as high as 15 m in the Purus River) control floodplain ecosystems supporting diverse forest stands and aquatic macrophyte communities (Junk *et al.*, 1989). These floodplains, which can span tens of kilometers (Hess *et al.*, 2003), are fertile and productive in whitewater rivers due to their heavy sediment loads. The annual rise and fall of river waters induce lateral exchanges of organic and inorganic materials between river channels and floodplain habitats that influence most biogeochemical processes in these ecosystems (Junk *et al.*, 1989; Melack *et al.*, 2009).

Local precipitation and inputs from streams and rivers form several extensive wetlands in depressed or flat areas of the basin. As river networks traverse large inland depressions in the Basin, they form extensive wetlands in the Marañon-Ucayali region (Peru), Llanos de Moxos (Bolivia), and Bananal Island (Brazil), among others (Kalliola *et al.*, 1991; Hamilton *et al.*, 2002). Seasonal rainfall and high water tables form swamps and flooded savannas in interfluvial regions (e.g., in the

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Negro Basin; Junk, 1993). Precipitation and seasonal inundation driven by flood pulses and tides create a diverse wetland mosaic on Marajó Island in the estuary (Smith, 2002).

Ecosystem services

The hydrological connectivity of Amazon freshwater ecosystems enables the provision of several services that are vital for local, regional, and global communities. Key ecosystem services include biodiversity maintenance; water quality, climate and flow regulation; nutrient and carbon (C) cycling; and food and fiber production. The diversity of freshwater ecosystems found in the Basin sustains a wealth of life forms. According to available estimates, the Basin contains between 6000 and 8000 fish species (Schaefer, 1998; Reis *et al*., 2003), of which only about 2320 have been described to date (Abell *et al*., 2008). About half of those fish species are thought to inhabit river floodplains, while the rest occupy headwater streams, where geographic isolation promotes endemism (Junk & Piedade, 2004). The diversity of bird and tree species is similarly high, with an estimated 1000 flood-tolerant tree species and over 1000 bird species inhabiting the lowland forests of the Central Amazon (Junk, 1989; Stotz *et al*., 1996). Much of this diversity occurs along river networks, as ecological corridors with specific environmental conditions determine species occurrence and mediate movement through the landscape (e.g., Van Der Windt & Swart, 2008).

As rainwaters drain through terrestrial ecosystems, riparian zones regulate water quality by filtering the organic and inorganic materials they carry (Alexander *et al*., 2000). Terrestrial inputs are transported downstream, deposited, and remobilized in river floodplains until they are discharged into the ocean (Wipfli *et al*., 2007; McClain & Naiman, 2008). During this transport, freshwater ecosystems regulate water flows, buffering flows during high discharge periods and maintaining them during low discharge periods. This regulation of flows promotes soil infiltration, recharges groundwater stores, and facilitates regular river navigation and hydropower generation.

Seasonal inundation induces the constant recycling of nutrients in river floodplains, leading to primary production rates (~17 Mg C ha^{-1} yr^{-1}) that are five times higher than those of upland forests (Melack & Forsberg, 2001; McClain & Naiman, 2008). About 93% of this production occurs in levee forests and C4 macrophyte communities (i.e., *Echinochloa polystachya*; Piedade *et al*., 1991), which in whitewater rivers reach one of the highest primary productivity rates on the planet (Melack & Forsberg, 2001). Net primary production along river floodplains in a 1.77 million km^2 region of the Central Amazon has been estimated at ~298 Tg C yr^{-1}, of which ~210 Tg C yr^{-1} are outgassed as carbon dioxide (CO_2) and subsequently recycled as net primary production (Melack *et al*., 2009). These natural carbon fluxes are comparable in scale to net carbon emissions attributed to land-cover change in the Brazilian Amazon during the 1990s (Houghton *et al*., 2000), making them an important part of the global carbon cycle.

Seasonal inundation promotes secondary productivity by allowing fish populations to exploit plant-based resources in the floodplains (Lagler *et al*., 1971; Goulding, 1980; Castello, 2008a). Fish migrate laterally onto the floodplains during rising river waters to avoid predators and feed on nutritious plant materials (Welcomme, 1985; Gomes & Agostinho, 1997; Castello, 2008a,b). Conversely, declining waters force fish to migrate back to river channels and lakes, where water quality is generally poor and fish are more vulnerable to predation (Welcomme, 1985; De Mérona & Gascuel, 1993; Arantes *et al*., 2013). These lateral migrations are performed by resident floodplain species (e.g., *Cichla* spp.), as well as migratory species that travel longitudinally along river channels (e.g., *Prochilodus nigricans*; Ribeiro *et al*., 1995; Barthem & Goulding, 2007). Some large-bodied catfish species migrate exclusively along river channels from the estuary to the headwaters (e.g., *Brachyplatystoma rousseauxii*), but they prey on floodplain-dependent species (Barthem & Goulding, 1997). The productivity of Amazon river floodplain fish populations sustains high mean per capita fish consumption rates of 40–94 kg yr^{-1}, well above the global average of 16 kg yr^{-1} (Isaac & Almeida, 2011).

Spatial and seasonal patterns of water flows influence many other animals at different points in their life histories. Turtles (*Podocnemis* spp.), caimans (e.g., *Melanosuchus niger*), otters (*Pteronura brasiliensis*), and dolphins (*Inia geoffrensis*, *I. boliviensis*, and *Sotalia fluviatilis*) have life cycles dependent on seasonal colonization of the floodplains during high waters (Martin & Da Silva, 2004; Martin *et al*., 2004; Fachín-Terán *et al*., 2006; Da Silveira *et al*., 2010, 2011). Many terrestrial animals inhabit riparian zones year-round or during the dry season to access water and feed on fruits, leaves, and other animals (Naiman & Decamps, 1997; Bodmer *et al*., 1999). Riparian zones also serve as important migratory corridors for wide-ranging terrestrial species such as jaguars (*Panthera onca*), tapirs (e.g., *Tapirus terrestris*), and peccaries (e.g., *Tayassu pecari*; Lees & Peres, 2008; Keuroghlian & Eaton, 2008). Some terrestrial and migratory bird species use wetlands as seasonal feeding grounds (Petermann, 1997).

Productive whitewater river floodplains allow Amazonians to generate important economic activities while diversifying their diets. Hunting along riparian zones is widespread (Bodmer *et al.*, 1999; Parry *et al.*, 2014), as is exploration of palm fruits (e.g., *Euterpe oleracea*), timber (e.g., *Calycophyllum spruceanum*), and fish (e.g., *Arapaima* spp.; Pinedo-Vasquez *et al.*, 2001; Brondízio, 2008; Castello & Stewart, 2010). Together, these activities often contribute as much as two-thirds of rural household income (McGrath *et al.*, 2008, 2015; Ewel, 2009).

Drivers of hydrological alterations

Amazon freshwater ecosystems are becoming increasingly degraded due to human development activities, including the construction of dams, mining, land-cover change, and global climate change (Fig. 2). Many of these activities were historically driven by domestic markets and national development interests, which prompted construction of roads and conversion of native forests and savannas to croplands and rangelands (Laurance *et al.*, 2001; Nepstad *et al.*, 2014). Although these domestic forces remain strong, the growing engagement of Amazonian countries in export-oriented markets for agricultural and mineral commodities has made the region increasingly susceptible to international forces. For example, multilateral development initiatives, including the Initiative for the Integration of the Regional Infrastructure of South America (IIRSA) and the South American Council on Infrastructure and Planning (COSIPLAN), have invested heavily in the construction of waterways, hydroelectric dams, and other infrastructure in the Amazon. The result has been large-scale disruptions to the hydrological connectivity of Amazon freshwater ecosystems via a variety of mechanisms, including: (i) storage of water in hydroelectric reservoirs; (ii) changes in seasonal flood dynamics; (iii) reduced rainfall, water quality, and evapotranspiration at regional scales; and (iv) increases in the frequency and intensity of extreme weather events (i.e., droughts, floods; Fig. 3).

Dams

Some of the most direct impacts on streams and rivers stem from dams (Fig. 4a). Storage of water in reservoirs regulates water flows, blocks animal movements, and disrupts downstream transport of materials. Water storage in reservoirs can drastically alter stream or river thermal regimes, depending on the depth from which water is released and the reservoir's physical characteristics (e.g., depth, surface area; Olden & Naiman, 2010;

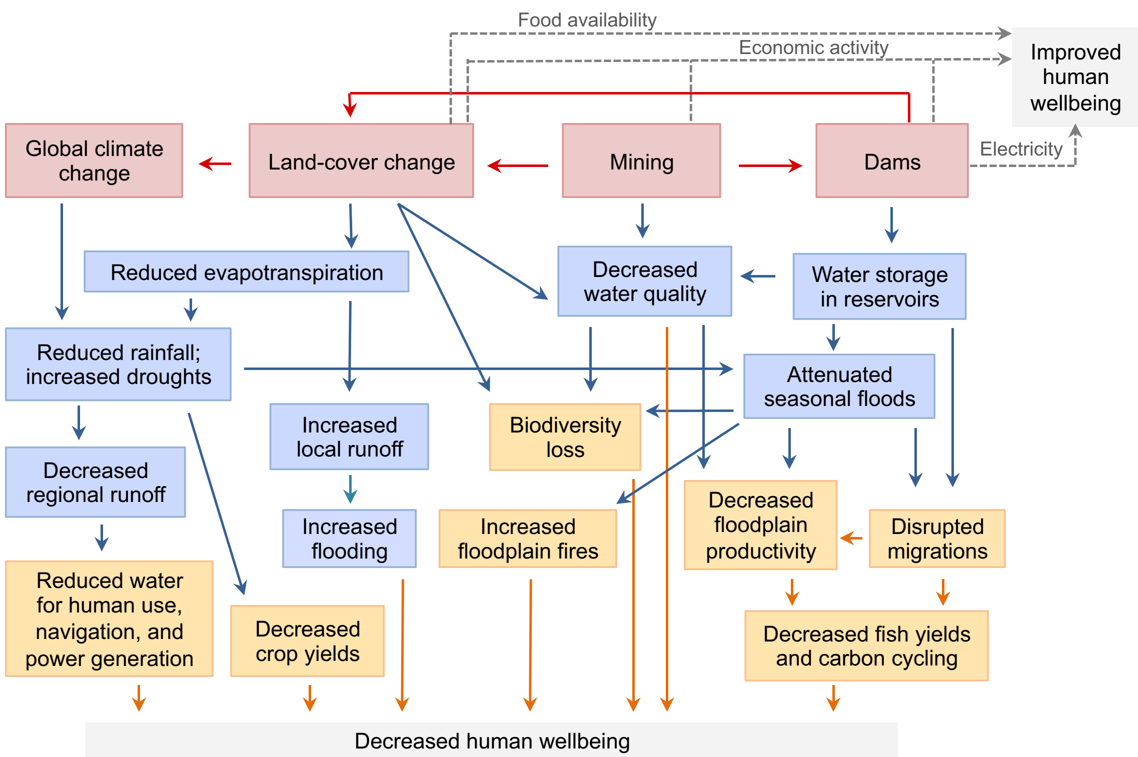

Fig. 3 Interactions among freshwater ecosystems, drivers (*Red rectangles*), hydrological alterations (*Blue rectangles*), and ecosystem impacts (*Yellow rectangles*). Dashed lines denote effects not addressed by this review.

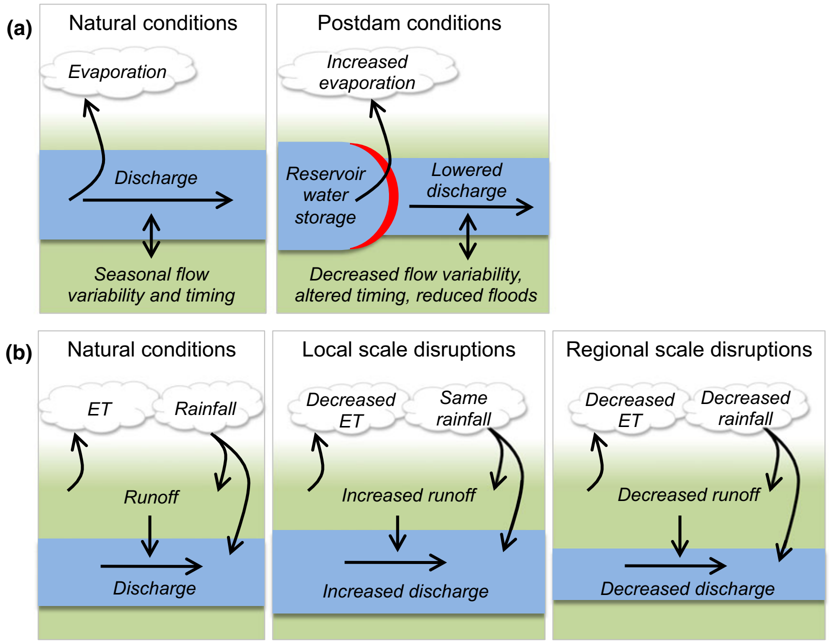

Fig. 4 Schematic diagram depicting the main hydrological alterations caused by dams and land-cover change on Amazon freshwater ecosystems. (a) Relative to undisturbed conditions (*Left*), dams store water in reservoirs, lower discharge and flow variability, alter flood seasonality, and decrease high-flood maxima (*Right*). (b) Relative to undisturbed conditions (*Left*), local land-cover change (*Middle*) generally decreases evapotranspiration (ET), increasing runoff and discharge but not rainfall. Land-cover change at regional scales (*Right*) may decrease ET sufficiently to also decrease rainfall. Runoff and discharge may experience a net increase or decrease (+/−), depending on the balance between rainfall and ET (rainfall − ET = runoff).

Macedo *et al.*, 2013). Reservoirs can also reduce river discharge as stored water evaporates or is diverted for other uses (e.g., irrigation). Flow regulation by dams also disrupts lateral connectivity by decreasing seasonal flow variability, most notably by attenuating flood maxima (Poff *et al.*, 1997; Poff & Hart, 2002).

Dam-induced hydrological alterations are increasingly common in the region as dams of all types and sizes proliferate. Although there is uncertainty in available data, the total installed power generation capacity in the basin is expected to double from ~18 000 megawatts (MW), provided by 154 large hydroelectric dams currently in operation, to ~37 000 MW with the completion of ~21 additional dams now under construction (Fig. 2; Table 1; ANEEL, 2012; Proteger, 2012; Castello *et al.*, 2013b). Construction of an estimated 277 planned hydroelectric dams (now in the initial planning stages) could add as much as ~58 000 MW of installed capacity in the region, although many dams operate below capacity. Most hydroelectric dams are relatively small (<100 MW) and are or will be located in the Araguaia-Tocantins, Tapajós, and Madeira tributary basins (Table 1). Although global attention has focused on the construction of large hydroelectric dams, the most abundant dams in the Amazon are actually small farm impoundments, which are constructed in headwater stream reaches to provide drinking water for cattle, facilitate road construction in flat areas, or enable small-scale energy or irrigation. In 2007, an estimated 10 000 such impoundments existed in the headwaters of the Xingu Basin alone (Macedo *et al.*, 2013), averaging one impoundment per seven kilometers of stream length. The cumulative impacts of many small dams may be significant, particularly in the sensitive headwaters regions where they are most common.

Land-cover change

Land-cover change, particularly the conversion of native forests and savannas to other land uses (e.g., agriculture, pastures), alters the surface water balance and partitioning of rainfall into evapotranspiration, discharge, and soil moisture (Abell *et al.*, 2007; Brauman *et al.*, 2007; Sterling *et al.*, 2012; Wohl *et al.*, 2012). In general, crops and pasture grasses use less water than native vegetation due to their lower height, less complex canopy, shallower rooting depth, and lower leaf area index (Calder, 1998; Giambelluca, 2002). As a result, at local scales, deforestation tends to decrease evapotranspiration and increase runoff and stream discharge (Sahin & Hall, 1996; Andreassian, 2004; Coe *et al.*, 2011; Hayhoe *et al.*, 2011). Over large spatial scales, deforestation is likely to reduce regional rainfall and alter rainfall seasonality (Butt *et al.*, 2011; Spracklen

Table 1 Amazon hydroelectric dams by installed potential, country, and subwatershed

	Operational	Construction	Planned
Dam capacity			
<100 MW	135	14	206
100–1000 MW	14	4	56
>1000 MW	5	3	15
Country			
Brazil	138	16	221
Peru	7	2	30
Ecuador	5	2	17
Bolivia	4	1	8
Colombia	0	0	1
Subwatershed			
Araguaia-Tocantins	56	2	101
Madeira	43	8	44
Tapajós	33	6	73
Ucayali	6	1	15
Xingu	6	1	2
Marañon	5	3	22
Amazon drainage	4	0	8
Negro	1	0	1
Purus	0	0	6
Napo	0	0	4
Caqueta-Japurá	0	0	1

et al., 2012; Yin *et al.*, 2014), which in turn would decrease stream and river discharge (Fig. 4b; Bruijnzeel, 2004; Stickler *et al.*, 2013).

Land-cover change has affected about 1.4 million km^2 (~20%) of the Amazon Basin (Hansen *et al.*, 2013; Fig. 2), primarily driven by expansion of cattle ranching and crop production into native forest and savanna regions (Nepstad *et al.*, 2014). Most land-cover change to date has occurred in the headwaters of the Araguaia-Tocantins, Xingu, and Tapajós Rivers (i.e., the 'arc of deforestation'); more recently, it has extended to the south and southwestern regions of the basin. High rates of deforestation observed in the early 2000s decreased significantly after 2005, particularly in Brazil (Macedo *et al.*, 2012; Nepstad *et al.*, 2014). They remain low relative to historic rates, but have shown an increasing trend since 2012 (INPE 2014). Growing demands for agricultural products and weakening of environmental legislation in some countries have increased pressures on the region's native vegetation, especially in the Andes (Gutiérrez-Vélez *et al.*, 2011) and *Cerrado* savannas (Soares-Filho *et al.*, 2014).

Mining

Mining involves rapidly expanding operations to extract gold, oil, gas, bauxite, and iron ore. Although gold mining activities have existed in the Amazon for decades, they have recently surged following a 360% increase in gold prices after 2000 (Fig. 2; Nevado *et al.*, 2010; Swenson *et al.*, 2011; Asner *et al.*, 2013; De Miguel *et al.*, 2014; Marinho *et al.*, 2014). Artisanal miners extract gold by dredging sediments from the river bottom and using mercury (Hg) to amalgamate fine gold particles, thereby altering stream and river morphology, increasing suspended sediment loads, and polluting waters via the release of Hg. Mercury can be transformed by microorganisms into Methylmercury (MeHg), which is a powerful endocrine disruptor that can damage the nervous system, be assimilated into living tissue, and become magnified in food webs via bioaccumulation (Zhang & Wong, 2007).

Large-scale mining for iron ore, bauxite, oil, and gas impacts freshwater ecosystems (both directly and indirectly) by promoting deforestation, dam construction, and roads in remote regions. Because smelting of iron ore and bauxite is energy intensive, the steel and aluminum industries have motivated the construction of many dams in the Amazon (Switkes, 2005; Fearnside, 2006), including the Tucuruí Dam, which flooded an area spanning 2860 km^2 and displaced more than 24 000 people (WCD, 2000). Where hydroelectric power is insufficient to meet mining demands, smelters consume charcoal that is produced by burning native vegetation (Fearnside, 1989; Sonter *et al.*, 2014a,b). The Carajás Mining Complex (Pará, Brazil), for example, is the world's largest iron ore mine with large stores of bauxite, copper, manganese, and gold. Since construction in the 1970s, the Greater Carajás Project has led to the construction of a railroad, many roads, and a large hydroelectric dam, all of which have led to significant land-cover changes. Leases for oil and gas extraction drive similar land-cover changes and infrastructure development. Today, more than two-thirds of the Peruvian and Ecuadorian Amazon are covered by oil and gas leases (Fig. 2), many of which overlap protected areas and indigenous reserves in remote regions (Finer *et al.*, 2008). As energy demand grows, controversial projects like the Camisea gas pipeline in Peru are likely to become more common, particularly in the Andean Amazon (Finer *et al.*, 2008).

Climate change

Increases in atmospheric greenhouse gas (GHG) concentrations are driving global climate changes that will likely exacerbate the impacts of ongoing hydrological alterations on freshwater ecosystems (Fig. 3; Melack & Coe, 2013). Climate predictions for the future of the Amazon generally indicate that temperatures will increase, promoting melting of snow and ice in the Andes Mountains (IPCC, 2014) and reducing the water storage and discharge buffer capacity of freshwater ecosystems (Junk, 2013). Projections also indicate that total rainfall will likely decrease, while seasonal variability will increase and extreme weather events (i.e., droughts, floods) will become more frequent and severe (Mahli *et al.*, 2007; Malhi *et al.*, 2009; IPCC, 2014). Such dry–warm conditions would likely dampen annual flood pulses and increase the frequency and severity of low-water events in large rivers (Costa *et al.*, 2003). Low-order rivers could experience dramatic changes in discharge and flood pulses, while many perennial headwater streams may become intermittent (Junk, 2013).

Regional land-cover changes have been linked to decreases in water recycling and increased land surface temperatures, driving local climate changes beyond those attributed to atmospheric GHG concentrations (Silvério *et al.*, 2015). By causing near-term shifts in the energy and water balance, land-cover changes may provoke shifts in regional rainfall regimes, increased land surface temperatures, and changes in river flows (Panday *et al.*, 2015). Land-cover change in the western Amazon, for example, has been linked to decreased precipitation, longer dry seasons, and higher amplitude of seasonal water flow (Lima *et al.*, 2013). Cumulative land-cover changes in the western Brazilian Amazon (Rondônia state) have been linked to delays in the onset of the wet season, decreasing its length by an estimated six days per decade (Butt *et al.*, 2011; Yin *et al.*, 2014).

Climate and land-use change often act synergistically (Fig. 3). Regional deforestation appears to amplify the magnitude of droughts, making them dryer and more severe than they would be with full forest cover (Bagley *et al.*, 2014). Severe droughts, in turn, can fuel further land-cover changes by killing trees directly (Lewis *et al.*, 2011) or triggering more widespread and intense wildfires (Brando *et al.*, 2014), both of which release carbon stored in vegetation back to the atmosphere. These changes are expected to disproportionately impact dryer transitional forests (~40% of the Amazon basin) and their associated freshwater ecosystems (Brando *et al.*, 2014).

Ecosystem impacts

Hydrological alterations trigger a wide range of impacts on Amazon freshwater ecosystems, many of which have complex feedbacks and synergistic interactions. The available information indicates that the cumulative impacts of dams, land-cover changes, mining, and global climate changes can substantially alter biogeochemical cycling, transport of organic and inorganic materials, freshwater community composition, and productivity (Fig. 3). These changes may hinder the provision of key ecosystem services by causing biodiversity loss and increasing disturbances such as floodplain fires and extreme droughts and floods. Decreases in hydrological connectivity can also drive changes in water quality, carbon cycling, and fish yields, and may limit the availability of water for human use, navigation, and power generation (Fig. 3).

Disrupted biogeochemical cycles

The biogeochemistry of freshwater ecosystems is governed primarily by hydrology, soil type, nutrient availability, and terrestrial inputs of organic and inorganic matter. Biogeochemical cycling, in turn, is largely controlled by biota, temperature, light availability, and water chemistry. All of these factors vary geographically throughout the Amazon, and changes to any of them can indirectly affect others. In temperate watersheds, conversion of forests to croplands has been associated with increased stream flow and nutrient loading, causing large-scale eutrophication (Carpenter *et al.*, 1998; Schindler, 2006). However, little is known about how similar changes affect tropical systems, where soils require different fertilization regimes and differ in their capacity to retain and cycle nutrients. In the southeastern Amazon (Xingu Basin) fertilizer use in soy croplands has not affected stream nutrient concentrations due to the high binding capacity of regional soils (Neill *et al.*, 2013). On the other hand, land-use practices in the same region have degraded riparian vegetation and led to the establishment of thousands of small farm impoundments, which together have warmed headwater streams by 2–3 °C and increased discharge fourfold relative to streams in forested watersheds (Hayhoe *et al.*, 2011; Macedo *et al.*, 2013).

In addition to these physical changes to stream water, mining exploration, agricultural development, and dam construction can introduce new pollutants into freshwater ecosystems. Mercury, for example, is one of several pollutants that are produced or accumulated in reservoirs, dispersed downstream, and magnified in food webs (Schwarzenbach *et al.*, 2006; Ashe, 2012; Marinho *et al.*, 2014). The anoxic conditions commonly found in dam reservoirs increase natural levels of MeHg. For example, MeHg levels in water, plankton, and fish downstream of the Balbina Dam on the Uatumã River have been shown to be higher when reservoir water is stratified, because stratification fosters the anoxic conditions required for methylation (Kasper *et al.*, 2014).

Reservoirs often flood large forested areas, killing trees that produce large quantities of methane (CH_4) as they decay. As a result, tropical reservoirs can have high concentrations of CH_4 and CO_2 in their deeper anoxic layers (Kemenes *et al*., 2007), although there are few reliable estimates of the rate at which these GHGs are emitted to the atmosphere. Estimates from the Balbina hydroelectric dam (Amazonas state, Brazil) suggest that emissions from within and downstream of the reservoir totaled 3 Tg C yr^{-1} (Kemenes *et al*., 2007, 2011). Other studies of tropical dams likely underestimate GHG emissions because they exclude downstream fluxes (St Louis *et al*., 2000; Demarty & Bastien, 2011). Sediment deposition in reservoirs (particularly in whitewater rivers) has the potential to trap C, lowering CO_2 and methane (CH_4) emissions that would normally occur from biological processing downstream (Smith *et al*., 2001). It is unclear whether C storage in sediments could be sufficient to compensate emissions, but Amazon reservoirs are likely net producers of GHGs (St Louis *et al*., 2000; Fearnside, 2004; Kemenes *et al*., 2011).

Altered sediment dynamics

Dams and land-cover changes affect river discharge and sediment transport and mobilization, which are key determinants of river geomorphology, but their net effects are scale dependent and context specific. In the Upper Xingu Basin, for example, a fourfold increase in stream flow in agricultural watersheds had little effect on sediment loads or the morphology of small headwater streams (Hayhoe *et al*., 2011). On the other hand, in the Araguaia River Basin a 25% increase in annual discharge (due to large-scale land-cover change) increased bed load transport by 31% and completely restructured the river's morphology (Latrubesse *et al*., 2009; Coe *et al*., 2011). In contrast, hydroelectric projects on whitewater rivers such as the Madeira are expected to trap large amounts of sediments, reducing sediment transport and potentially altering river floodplain morphology (Fearnside, 2013). Such changes in sediment dynamics and water temperature may affect incubation and development time, sex determination, growth rates, and metabolism of some species, particularly ectotherms (e.g., fish, reptiles). The nesting outcomes of turtle species such as the giant Amazon river turtle (*Podocnemis expansa*) and yellow-spotted sideneck turtle (*Podocnemis unifilis*) have been linked to river dynamics, temperature, and the grain size of sediments in the nesting area (Lubiana & Ferreira Júnior, 2009; Ferreira Júnior & Castro, 2010).

Deforestation of riparian areas

Human settlements and development activities have disproportionately impacted stream riparian zones and river floodplain ecosystems. Over 50% of floodplain forests in the Lower Amazon region were deforested by 2008 (Renó *et al*., 2011), compared to ~20% of upland forests in 2012 (Hansen *et al*., 2013). In addition to reducing biodiversity, deforestation of riparian areas reduces filtration of terrestrial inputs flowing into streams and rivers, causing erosion, lowering water quality, and altering aquatic primary production (Williams *et al*., 1997; Neill *et al*., 2001). In whitewater rivers, floodplain deforestation reduces the abundance of C3 plant communities that sustain herbivorous and detritivorous animal populations, as well as C4 macrophyte communities that are key biological producers (Araujo-Lima *et al*., 1986; Forsberg *et al*., 1993). Riparian deforestation also removes structures that provide habitat for aquatic biota (e.g., macrophytes, woody debris) and reduces shading of small streams, often increasing incident sunlight and water temperature, which may directly affect species composition and metabolism (Bojsen & Barriga, 2002; Sweeney *et al*., 2004; Macedo *et al*., 2013).

Changing inundation regimes

Disruption of seasonal inundation regimes impacts species composition and biogeochemical cycling in river floodplains. Floodplain forest trees have a number of adaptations to cope with the physiological stress caused by regular seasonal flooding (Haugaasen & Peres, 2005). Global climate change (coupled with large-scale land-cover change) is expected to shift these hydrological regimes by decreasing mean annual rainfall and increasing the frequency of extreme weather events (e.g., droughts and floods). Such changes in the inundation regime, particularly reduced flood maxima, could reduce selection for flood-tolerant species and alter the species composition of floodplain forests (Nilsson & Berggren, 2000). Reduced flood maxima could reduce lateral exchanges between river channels and floodplains, decreasing nutrient recycling and associated biological productivity (Nilsson & Berggren, 2000) and hence altering regional C budgets, including GHG emissions. Reduced flood maxima can also increase the frequency, severity, and ecological impact of fires, given that floodplain trees lack many traits associated with fire and drought resistance (Brando *et al*., 2012; Flores *et al*., 2012). In the Middle Rio Negro, for example, severe droughts have caused fires that killed over 90% of floodplain forest trees, which showed little sign of regeneration even a decade later (Flores *et al*., 2012).

Disruption of seasonal inundation regimes by dams also disrupts the migrations of fish and other fauna (Jackson & Marmulla, 2001). Most dams in the Amazon are constructed in the middle and upper reaches of riv-

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ers (Fig. 2), affecting resident and long-distance migrants whose home ranges encompass the area. Depending on river and reservoir characteristics, attenuation of seasonal inundation regimes and reductions in high-flood maxima can restrict access to floodplain food and habitat resources for fish populations far downstream. Many other animal groups (e.g., turtles, caimans, otters, dolphins) are similarly affected by attenuated inundation. Lateral and longitudinal restrictions of fish migrations by dams have led to dramatic fishery impacts in the Araguaia-Tocantins Basin and elsewhere in the world (Ribeiro *et al*., 1995; Limburg & Waldman, 2009; Fei *et al*., 2015). Continued hydroelectric development in the Amazon is thus likely to disrupt the ecosystem roles of many animals and reduce fisheries yields, with the potential to threaten regional income and food security (Castello *et al*., 2015). Such hydrological alterations also limit animal dispersal and recolonization after extreme events, increasing the likelihood of biological extinctions over the long run (Hess, 1996; Fagan, 2002), particularly in headwater streams with high species diversity.

Establishment of reservoir conditions

By replacing lotic habitats with lentic ones, the storage of water in reservoirs threatens specialist endemic species and favors generalist species, leading to biotic homogenization and reduced biodiversity (Poff *et al*., 1997; Liermann *et al*., 2012). As a result, Amazonian reservoirs are often heavily vegetated with macrophytes and dominated by species adapted to lentic conditions (Junk & Mello, 1990; Gunkel *et al*., 2003). In the Araguaia-Tocantins River Basin, for example, construction of the Tucuruí Dam led to a dominance of predator species, and increased the abundance and biomass of detritivorous Prochilodontids and planktivorous *Hypophthalmus spp*. (Ribeiro *et al*., 1995). It is often argued that reservoirs create additional habitat, but habitat quality may be poorer than the natural habitats they replace. For example, today the 4500 km^2 Balbina Reservoir supports giant otter (*Pteronura brasiliensis*) populations twice as large as those before construction, but four times smaller than those predicted by available habitat (Palmeirim *et al*., 2014).

Policy limitations

Some policies pertinent to freshwater ecosystem conservation exist, including laws governing protected areas, conservation of forests on private properties, water resource management, and environmental licensing of hydroelectric dams (Fig. 5). However, each of these policies has limited capacity to protect freshwater ecosystems, and combined they fail to address the full range of drivers of hydrological alteration (Fig. 5). The main limitation of these policies is their disregard for the role of hydrological connectivity in freshwater ecosystem structure and function.

Protected areas

The Brazilian Amazon enjoys a relatively high level of protection, with a network of nature reserves, indigenous lands, and sustainable use areas covering ~54% of its area (Soares-Filho *et al*., 2010; Castello *et al*., 2013b). Although it is touted as the model of Amazonian conservation, this protected area network has limited capacity to protect freshwater ecosystems because its design was largely based on the biogeography of terrestrial taxa, with little regard for hydrological connectivity (Peres & Terborgh, 1995; Abell *et al*., 2007). A large proportion of headwater streams, rivers, and other wetland types are unprotected, and many freshwater ecosystems within protected areas are vulnerable to upstream threats (e.g., dams) outside their boundaries (Pringle, 2001; Hansen & Defries, 2007). Furthermore, many protected areas overlap competing land designations or are governed by laws that allow mining, forest exploration, or hydroelectric development within their boundaries (Veríssimo *et al*., 2011; Ferreira *et al*., 2014). For example, the original design of Brazil's Belo Monte Hydroelectric Complex contemplated five separate reservoirs within federal indigenous reserves upstream of the Belo Monte Dam in the Xingu River. Although the five reservoirs are not yet being constructed, they may eventually be built to allow Belo Monte to function at capacity (Stickler *et al*., 2013). Brazil's Congress is also debating several new laws (i.e., the 'Mining Code', PEC215, PL 3.682) that could open protected areas and indigenous reserves to mining exploration. In addition, Amazonian protected areas have been increasingly downgraded, downsized, degazetted, and reclassified since 2008, mainly to enable the generation and transmission of hydroelectric power (Bernard *et al*., 2014; Ferreira *et al*., 2014).

Climate and land-use policies

Brazil and Peru regulate forest cover on private properties. The Brazilian Forest Code requires landowners in the Amazon biome to conserve native vegetation on 80% of their property in forested regions and 20–35% in Cerrado regions. It also designates riparian forest buffer zones as Areas of Permanent Preservation (Soares-Filho *et al*., 2014). Peru's Forest and Fauna Law also mandates the conservation of a 50 m riparian buffer zone along rivers and lakes. By requiring conservation of

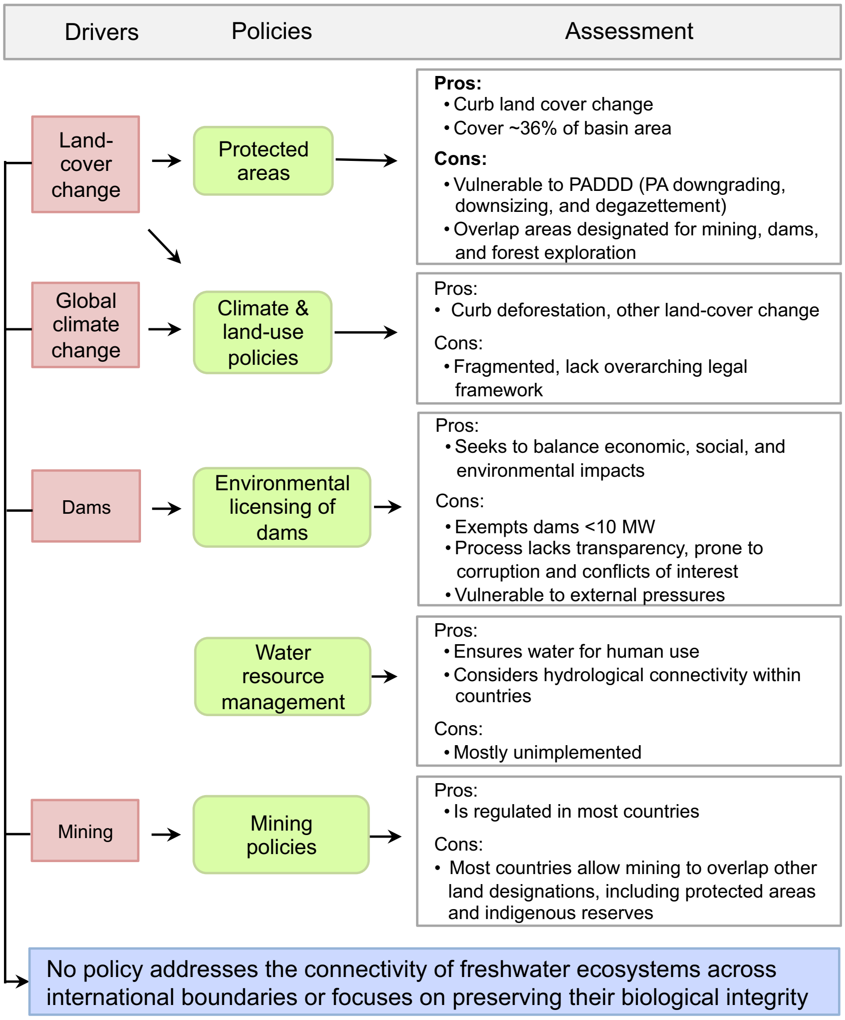

Fig. 5 Schematic diagram depicting the main drivers of hydrological alteration (*Red rectangles*), existing policies (*Green rectangles*) that address them, and respective pros and cons (*White boxes*).

native vegetation in riparian zones, both laws have the potential to mitigate the negative impacts of land-cover change on freshwater ecosystems. However, compliance with these regulations has been notoriously low due to poor monitoring and enforcement. In Peru, for example, the average protected riparian buffer is only about half the legally required width (McClain & Cossio, 2003).

A substantial reduction in Brazil's deforestation rates from 2005 to 2012 has been attributed to domestic policies, including Brazil's National Climate Change Plan and Low Carbon Agriculture program, which created financial incentives (e.g., low-interest loans) and disincentives (e.g., restrictions on credit) to reduce deforestation (Nepstad *et al.*, 2014). Expansion of protected areas and improvements in monitoring and enforcement of environmental laws were also key factors in reducing illegal deforestation, particularly in the southeastern Amazon (Nepstad *et al.*, 2009; Arima *et al.*, 2014). These national efforts were aided by non-profit campaigns to boycott products produced in illegally deforested areas; voluntary moratoria aimed at restricting market access for commodities produced on newly deforested lands; and restrictions on access to credit for illegal deforesters. Continued efforts to establish deforestation-free supply chains in Brazil have shown some promise in curbing the impact of crop and cattle production on native ecosystems (Gibbs *et al.*, 2015a,b). However, recent increases in deforestation rates in the Brazilian Amazon suggest that these initiatives are still vulnerable to external market pressures, political administrations, and changes in consumer demand. That vulnerability is due in part to a fragmented policy environment and lack of an overarching legal framework to protect Amazon terrestrial and aquatic ecosystems.

Water resource management

All Amazonian countries are implementing water resource management laws to protect the availability and quality of water. Although these laws vary across countries, they rely on the common principle that water is a finite resource that is vulnerable to human activities and should be managed at the watershed scale (Setti, 2004). Because these laws focus almost exclusively on water as a resource to satisfy human needs, they cannot ensure preservation of freshwater ecosystems. Furthermore, they are generally national in their jurisdiction, contradicting the very principle of watershed-scale management and ignoring the international connectivity of Amazon freshwater ecosystems. Even though water resource laws encompass many large tributary basins (e.g., the Caqueta-Japurá, Napo, and Juruá), the lack of international coordination undermines their potential effectiveness.

Colombia possesses a more comprehensive water resource management framework than its neighboring Amazonian nations. It complements standard water resource management principles by establishing goals for conserving the integrity of freshwater ecosystems, while recognizing their diversity and the need to use all available information and work across administrative boundaries. However, there are no data on the effectiveness of the Colombian framework for water resource management. This scarcity of data, along with limited human and financial resources for management activities, presents a major challenge to effective freshwater ecosystem management (Oliveira, 2002; Castello *et al*., 2013a,b; Brum *et al*., 2015; Cavole *et al*., 2015).

Environmental licensing of dams

Some countries (e.g., Peru and Brazil) have decision-making processes to ensure that new hydroelectric dams are economically viable and minimize environmental and social impacts, while other countries do not (e.g., Bolivia; World Bank, 2008; Balbín & La Rosa, 2012). Here, we focus on Brazil's process because it has been studied and is similar to that of other nations. The first step in Brazil's 'environmental licensing' process is an inventory of the river basin and viability assessment of the proposed project, followed by an Environmental Impact Assessment (EIA) and a Report on Impacts to the Environment (RIMA). The next step is public hearings in the affected area, which may lead to revisions of the EIA-RIMA documents. Once approved, governmental agencies (e.g., IBAMA in Brazil) issue preliminary licenses enabling firms to bid for construction contracts.

Although the EIA-RIMA process appears adequate on the surface, this licensing process has several deficiencies that negatively impact freshwater ecosystems (La Rovere & Mendes, 2000; Switkes, 2002, 2007; Fearnside, 2013). First, hydroelectric dams smaller than 10 MW of installed energy production capacity are exempt from the process. Over half (~90) of the operational dams in the Amazon have an installed capacity of 10 MW or less, compared to ~64 dams with a capacity greater than 10 MW (Table 1). Although the individual impacts of large dams may be great, the cumulative effects of many small dams can surpass those of the larger dams.

Second, EIA-RIMAs consistently underestimate the socio-environmental impacts observed after dam construction because the process lacks transparency, is prone to corruption, and is riddled with conflicts of interest. EIA-RIMA studies are developed by consulting firms, which have monetary incentives to minimize negative findings because they are hired directly by the construction firms. Construction firms control study results because their contracts specify that they own the data and contents of the reports, whose publication is subject to their approval. EIA-RIMA studies are thus generally narrow in scope, often based on erroneous information, address only the immediate effects of dams, and are usually focused on collection of data instead of integrated evaluation of socio-ecological impacts (Kacowicz, 1985; Magalhaes, 1990; Fearnside, 2001, 2005, 2014; Switkes, 2002). Furthermore, EIA-RIMA studies only consider the direct impacts of the dam in question, ignoring cumulative impacts on watersheds.

Finally, the licensing process is vulnerable to external pressures. In some cases, the process has been hijacked by federal agencies or via legal mechanisms that allow judges to intervene and overrule the process (e.g., Law no. 8437 of 30 June 1992, in Brazil). Individuals or corporations can thus influence the process for political or economic gains. For example, in 1998, despite severe impacts associated with the Santo Antonio and Jiraú Dams on Brazil's Madeira River, 'the decision to build them was made before impacts were evaluated and the licensing proceeded under political pressure despite concerns raised by technical staff in the licensing agency' (Fearnside, 2014).

Lack of data and policy integration

The fragmented and incomplete nature of policies pertinent to freshwater ecosystem conservation has led management agencies throughout the Amazon to respond to freshwater impacts on a case-by-case basis, with little if any consideration of cumulative impacts over the whole Basin. Construction of Brazil's Belo Monte dam is a clear case where cumulative impacts have been ignored. Discussions regarding the dam's effect on freshwater ecosystems paid little attention to the five additional reservoirs required for it to operate at full capacity. They also ignored the environmental impacts of new deforestation occurring around the construction site at Altamira in the lower Xingu Basin.

The lack of a basinwide perspective on the capacity of multiple stressors to affect freshwater ecosystems is exacerbated by a widespread lack of data on freshwater ecosystems, making it virtually impossible to detect ongoing degradation trends (Junk & Piedade, 2004). Except for land-cover change, which has been monitored since the 1980s, there is a lack of baseline information on the location and extent of pollution, small dams, or deforestation of floodplains and riparian zones (Castello *et al*., 2013b). Consequently, even though hydrological alterations are widespread over the basin, most studies and environmental impact assessments likely underestimate the overall impacts while the public remains uninformed about the ongoing impoverishment of Amazon freshwater ecosystems.

Conclusions

The drivers of hydrological alteration of freshwater ecosystems are dynamic and multifaceted. As Amazonian countries pursue prevailing economic development strategies, there has been a surge in dam construction, mining activities, and land-cover changes, suggesting that hydrological alterations will mark the next phase in Amazonian development. The current trajectory of dam construction will leave only three free-flowing tributaries in the next few decades (i.e., Juruá, Trombetas, and Iça-Putumayo) if all planned dams are completed.

The available evidence indicates that dams, land-cover change, and mining are affecting all four dimensions of hydrological connectivity. Vertical connectivity, in particular, links freshwater ecosystems over large areas, as rainfall over any river basin depends on evapotranspiration by vegetation elsewhere. Maintaining freshwater ecosystems in large tropical river basins thus requires moving beyond the traditional catchment-based approach and managing forest cover over large areas to avoid negative land-climate feedbacks.

As drivers of hydrological alterations advance from southeastern tributaries into southern and western tributaries, geographic differences in hydrology, geomorphology, and water chemistry will likely determine different ecological impacts. The cumulative ecological impacts will also depend on the mix of drivers found in each basin, as they interact in complex ways. For example, climate and land-cover changes can degrade forests and associated streams and rivers through synergistic effects (Brando *et al*., 2014). On the other hand, increases in discharge associated with local forest loss could be partially offset by reductions in discharge due to dam reservoirs (Petts, 1984; Bruijnzeel *et al*., 1990). Ecological impacts will thus be heterogeneously distributed throughout the Basin, requiring intensive study across many tributary basins.

The ecological impacts of hydrological alterations encompass ecosystem processes ranging from hydrology and geomorphology to biotic composition, energy, and carbon flows. Impacts on any one of these have the potential to trigger cascading effects that can significantly degrade these freshwater ecosystems. If current trends continue, more tributary basins will be degraded, compromising ecosystem services such as biodiversity maintenance, water quality, flow regulation, C cycling, and food production (Fig. 3). In the face of these threats, the fate of Amazon freshwater ecosystems depends on a weak and fragmented set of policies that is wholly insufficient to address the growing array of impacts.

Managing hydrological connectivity

Maintaining the integrity of Amazon freshwater ecosystems requires a research and policy framework to understand and manage the drivers of hydrological alteration in aquatic, terrestrial, and atmospheric systems. A basinwide management framework for the Amazon could be developed through multiple-use zoning strategies that integrate various uses of aquatic and terrestrial resources across multiple watershed scales (Castello *et al*., 2013b). Existing management efforts focused on collaborative partnerships and stakeholder involvement are promising first steps toward such a framework (McGrath *et al*., 2008; Nepstad *et al*., 2014). The knowledge gaps identified here offer direction for future research efforts. Many of the existing policies, if revised to address their deficiencies, could form the basis for a unified framework for conserving the hydrological connectivity of freshwater ecosystems.

Development and implementation of a unified framework could build on the principles established by the European Union Water Framework Directive, which was developed around ecosystem-based objectives after decades of failed experiences through disjointed policies (Kallis & Butler, 2001). The process of constructing such a framework could begin with tributary basins within countries and scale up to encompass the whole Amazon Basin. The framework could ultimately be implemented by a new institution, or integrated into the objectives of existing pan-Amazonian institutions such as the Amazon Cooperation Treaty Organization (ACTO) or the Union of South American Nations

(UNASUR). Its effectiveness would be strengthened if Amazonian countries ratify the UN Watercourses Convention, which aims to 'ensure the utilization, development, conservation, management and protection of international watercourses' (Rieu-Clarke *et al.*, 2012).

The history of Amazonian conservation suggests that collecting and disseminating sound environmental monitoring data is a crucial first step toward management. Regular satellite-based monitoring of forest cover has fstered public awareness and policy developments, enabling the improved enforcement of regulations and significant reductions in deforestation rates that have been observed in recent years. We suggest that satellite-based measurements provide the most practical approach to monitoring Amazon freshwater ecosystems, as they are the only data source that permits basinwide inferences about hydrological connectivity and freshwater ecosystem integrity over time. Although satellite records cannot directly measure water quality or composition of biotic communities, they can provide useful proxies for ecosystem integrity when combined with other data sources. Radar data have been used to map inundation extent and habitat structure of wetlands in the Amazon (Hess *et al.*, 2003). Newer sensors (e.g., ALOS-2) could be used to monitor the volume, variability, and timing of water flows, allowing detection of hydrological alterations over time. Given that seasonal and interannual variability in hydrological connectivity is the norm in freshwater ecosystems, such indicators would have to focus on metrics of interannual and seasonal variability (i.e., the variability of the variability).

Recent advances in curbing deforestation are laudable, but they have been largely due to interventions at the local scale, informed by satellite-based monitoring. Managing hydrological alterations in the Amazon will be more difficult. It will require basinwide management arrangements and monitoring of hydrological connectivity over vast areas. Metrics of hydrological connectivity will need to be linked to human development activities to determine their full ecological impacts, which often interact in complex ways and accumulate as water flows downstream. Such metrics will need to be developed in a way that is understandable and responsive to large constituencies and can evaluate cumulative changes over huge geographic areas. This scale of environmental management complexity is unprecedented globally.

Fortunately, public awareness about the impacts of ongoing hydrological alterations (e.g., dams, droughts, and deforestation) is increasing, building the social momentum necessary to begin managing hydrological connectivity. Although the challenge is enormous, a basinwide management framework with a focus on hydrological connectivity would maintain ecological functions that are critical to both aquatic and terrestrial ecosystems in the Amazon and beyond. It can thus provide more benefits than management frameworks focused on terrestrial ecosystems.

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