The Influence of Forests on Freshwater Fish in the Tropics: A Systematic Review

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Tropical forests influence freshwater fish through multiple pathways, only some of which are well documented. We systematically reviewed the literature to assess the current state of knowledge on forests and freshwater fish in the tropics. The existing evidence is mostly concentrated in the neotropics. The majority of studies provided evidence that fish diversity was higher where there was more forest cover; this was related to the greater heterogeneity of resources in forested environments that could support a wider range of species. Studies quantifying fish abundance (or biomass) showed mixed relationships with forest cover, depending on species-specific habitat preferences. We identify the key challenges limiting our current understanding of the forest–fish nexus and provide recommendations for future research to address these knowledge gaps. A clear understanding of the functional pathways in forest–freshwater ecosystems can improve evidence-based policy development concerned with deforestation, biodiversity conservation, and food insecurity in the tropics.

Keywords: ecosystem function, land use, inland, functional diversity, conservation management

Forest and freshwater ecosystems are inextricably linked, exchanging flows of water, energy, and organic and inorganic materials (Studinski et al. 2012, Tanentzap et al. 2014, Chase et al. 2016). These flows form the physical habitats and ecological pathways that structure aquatic communities (Shaw and Bible 1996). There is a weak understanding of the extent and nature of the relationships among forests, freshwater ecosystems, and fish in the tropics, posing a challenge to effective policy-making (Ramírez et al. 2008). Forest–water ecosystems feature on several international agendas, including the Convention on Biological Diversity's Aichi targets, the United Nations Framework Convention on Climate Change, and the Ramsar Convention on Wetlands (Springgay et al. 2019), attesting to its increasing recognition in the sociopolitical sphere. Active management of the forest–water nexus is also highlighted as a crucial component in supporting the fulfillment of the Sustainable Development Goals (SDGs) related to poverty reduction (SDG 1), food and nutrition security (SDG 2), good health and well-being (SDG 3), clean water (SDG 6), sustainable fisheries management (SDG 14), and forest and biodiversity conservation (SDG 15).

Despite their significance to global environmental policy agendas, tropical forests and freshwater biodiversity are rapidly declining. Tropical forests include some of the most biodiverse ecosystems in the world (Barlow et al. 2018); however, they face tremendous pressures from anthropogenic disturbances with persistently high rates of deforestation and degradation (Barlow et al. 2016, Austin et al. 2017, Curtis et al. 2018). Meanwhile, freshwater species populations have declined by 83% since 1970, and, among all vertebrates, freshwater fish had the highest extinction rate worldwide in the twentieth century (WWF 2018).

Freshwater fish populations provide food security for many tropical forest-dwelling rural communities and are often one of the most important sources of protein and micronutrients (Dounias et al. 2016). Fish contribute more than half of the protein intake for over 400 million people in the poorest countries of Africa and Asia (Béné et al. 2012). Wild capture of freshwater fish is also a vital source of income for rural livelihoods (Béné et al. 2009, Dounias et al. 2016). The potential impact of an ongoing decline in forests and freshwater fish populations on human health and well-being is vast. A clear understanding of the pathways linking tropical forests and freshwater fish is therefore urgently required for designing policies that can effectively address the management of forests, the conservation of freshwater biodiversity, and the contribution of these fish to local livelihoods and food security.

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Temperate models and tropical systems

Strong coherent models inform our understanding and management of temperate systems. Beginning with the river continuum concept in 1980 (Vannote et al. 1980), river ecologists have built their understanding of the relationship between forests and fish on the hypothesis that predictable gradients in physical conditions correspond to expected response patterns in aquatic communities. The model has been modified to include variability in flow (Junk et al. 1989) and the implications of hydrological variability for stream fish assemblages (Poff and Allan 1995), as well as variability in temperature and implications for individual species distributions (Steel et al. 2017). The multiple linkages among forested riparian systems, flow and temperature, habitat structure, and fish growth or biodiversity were identified in a wide range of studies and reviews (e.g., Pusey and Arthington 2003, Smokorowski and Pratt 2007).

Our collective understanding of temperate streams has also been scaled up by a large body of research investigating relationships between landform and land use, including forested areas, across entire catchments with in-stream physical and biological conditions. The collective relevance of this body of work was introduced by Allan (2004), who concluded that a high proportion of forest cover is normally associated with positive stream conditions. Two syntheses of developments were later published (Johnson and Host 2010, Steel et al. 2010), both of which emphasized the growing understanding that forested riparian zones and catchments benefit fishes through a range of functional pathways. However, the reviews also emphasized the context-dependent nature of these relationships and identified challenges in providing quantitative evidence of the influence of forests on freshwater systems at catchment scales.

Although tropical and temperate freshwater systems share many similarities, there are key differences limiting our ability to apply the temperate conceptual model of freshwater systems described above or to apply specific findings from the relatively vast body of literature describing the influence of forests on fish abundance, distribution, and community structure. One of the most important differences is temperature, implicit in the very definitions of temperate and tropical ecosystems. As a result of higher temperatures, tropical systems are also characterized by higher metabolic rates and higher species diversity, both terrestrial and aquatic. Sensitivity of species to habitat disturbance has also been shown to be higher in the tropics than in higher latitudes as a result of lower rates of historical disturbance (Betts et al. 2019). We also note that much of temperate research has been focused on commercially valuable fish species (e.g., salmonids) that demand cool water, high oxygen levels, and coarse substrates. Even in temperate systems, less is known about species with lower or no commercial value; these are often less widely distributed, locally adapted, and smaller.

Systematically reviewing forest and freshwater fish research in the tropics

The need for a better understanding of the mechanisms through which forests affect freshwater fish in the tropics is garnering attention, particularly in light of growing pressures on these ecosystems and the overlapping threats they face. We provide a comprehensive synthesis of available research describing the role of tropical forests in supporting freshwater fish. In the present article, we investigate the overall effects of forests on freshwater fish and the multiple ecological pathways that structure forest and freshwater ecosystems in the tropics. From the pool of relevant studies, we identify the geographical distribution; assess the effects between forests and fish diversity, abundance, and biomass; synthesize key patterns; and summarize the strength of evidence for the potential pathways by which forests structure freshwater ecosystems. We assess the methodological challenges that limit our understanding of the forest–freshwater nexus and recommend a future research agenda to advance our knowledge of tropical forest–freshwater interactions. We intend our findings to support the development of future research agendas and evidence-based policies to reduce tropical deforestation, conserve biodiversity, and address both poverty and food insecurity.

We follow a systematic approach as outlined in Petticrew and Roberts (2008) to identify relevant studies within the existing literature. Literature searches carried out on 29 June 2019 in Scopus and in the Web of Science yielded 12,150 results (16,992 studies including duplicates). In the next step, selection criteria were applied to the title and abstract of each potential study. In the third step, a full-text screening was conducted on all 305 studies selected at the title and abstract stage. Via the above steps, we identified 61 relevant studies. For each of these 61 studies, we record the geographical location, type of inland water body (floodplains or reservoirs, streams or rivers), the types of outcome measures used, the direction of effect, and the functional pathways linking forests and freshwater bodies. Last, we assess and compare the types of spatial and temporal approach implemented across all studies, and identify knowledge gaps (see the supplemental material for a more detailed description of the systematic literature searches).

Spatial and temporal biases in tropical research

We found that the geographical location of studies was unevenly distributed, with 44 (72%) studies concentrated in Brazil alone. A further 4 (7%) studies were from other countries in South and Central America, 10 (16%) from South and Southeast Asia, and 3 (5%) from Sub Saharan Africa. The oldest study was published in 1984, whereas the number of publications sharply increased in 2015, most notably with studies in the neotropics (figure 1). Studies from the Indomalaya or Afrotropical region have been sporadic overtime. Africa and Southeast Asia face severe rates of forest loss (Sodhi et al. 2010, Aleman et al. 2018); however, little is known about the conditions of freshwater habitats

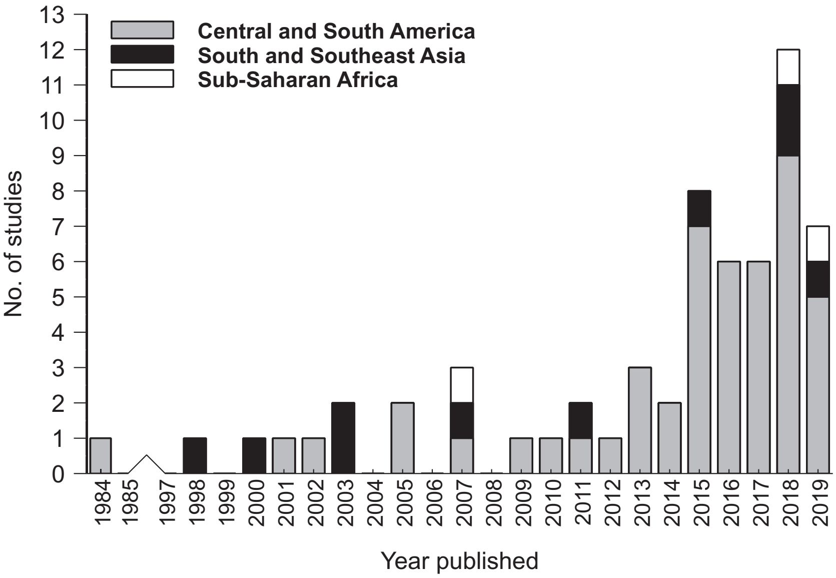

Figure 1. The number of published studies as a function of publication date and geographical region. We found no studies that met our selection criteria between 1985 and 1997; for the purpose of visuals, we include an axis break during this period.

prior to these land use changes, and more importantly, what influence recent deforestation or degradation has had on freshwater environments. The geographical imbalance of scientific evidence of forest–freshwater interactions also reflects the asymmetrical distribution of existing policies and recommendations on the appropriate management of riparian forest ecosystems across the tropics; Central Africa and South Asia, in particular, lack riparian-specific policies that target the conservation of freshwater biodiversity (Luke et al. 2019).

The relationship between tropical forests and fish diversity

From the pool of relevant studies, we identified 47 directional responses of fish diversity to forest presence and cover (figure 2); of these, 35 and 12 responses were observed at the species and functional level, respectively. We report and summarize the influence that forests have on fish diversity by type of inland water body.

Streams and rivers. From the 42 (67%) studies that measured the diversity and compositional structure of fish communities in lotic systems, we were able to record the direction of effect (positive, negative, or no detected effect) from 40 taxa or functional measures of fish diversity; from these, the majority (50%) of responses reported a positive association with forest cover and presence (figure 2). Studies reported terrestrial inputs from forested streams providing multiple benefits that supported a wider range of preferences than can be found in nonforested streams. In addition, inputs from forests such as woody debris and leaf litter were found to support a diversity of habitat niches that can provide nursing grounds and refuges against predators (Juen et al. 2016). Substrate size was also larger in forest stream habitats, adding to the complexity and variety of microhabitats that can accommodate a greater and more diverse range of fish species (Zeni et al. 2019). Nonforested and deforested streams lack large substrate materials from terrestrial sources, and experience higher levels of sedimentation and siltation. These factors contribute to homogenizing the condition of in-stream habitats and, consequently, encourage the homogenization of freshwater communities (Wilkinson et al. 2018a). In particular, the influx of unconsolidated substrates negatively affects benthic communities; stable and coarse substrates are required for benthic fish species to attach themselves, particularly in lotic freshwater systems (Iwata et al. 2003b). Instability in substrate composition could lead to biological instability in benthic communities (Gurtz and Wallace 1984).

Forests can further diversify and stabilize the types of food available for fish by supplying both allochthonous inputs from leaf litter and increased availability of terrestrial insects that fall directly into the water (Zeni and Casatti 2014). Forest habitats can support a diverse range of trophic guilds including terrestrial insectivores and herbivores (Zeni and Casatti 2014). Riparian forests deliver leaf litter in streams attracting insects, algae, and biofilm, each of which may be vital for particular fish species (Giam et al. 2015, Juen et al. 2016). In contrast, nonforested streams may lack the allochthonous food inputs that support terrestrial feeding fish species (da Costa and da Rocha 2017). Pasture streams, for example, are associated with trophic homogenization, only benefitting species that consume aquatic diets (Zeni and Casatti 2014).

Four (10%) negative responses of forests on fish diversity were reported; for example, pasture streams experienced high primary productivity of aquatic plants from greater light exposure, and therefore increased the availability of aquatic food for fish (Lorion and Kennedy 2009, Fernandes et al. 2013). It should be noted that studies showing negative effects were considered as the number of species rather than the functional diversity of fish communities.

We found six (15%) indicators that did not detect an effect of forests on fish. Again, it is worth noting that most studies applied diversity measures at the taxa level rather than using trait-based indicators. The timing of studies can have an important effect on findings because biological responses in freshwater fish communities may not yet be detectable in recent conversions from forest to agriculture along streams and exhibit time lag effects (Zeni et al. 2017). In other cases, species richness were similar between comparators, but dissimilarities in species composition were observed;

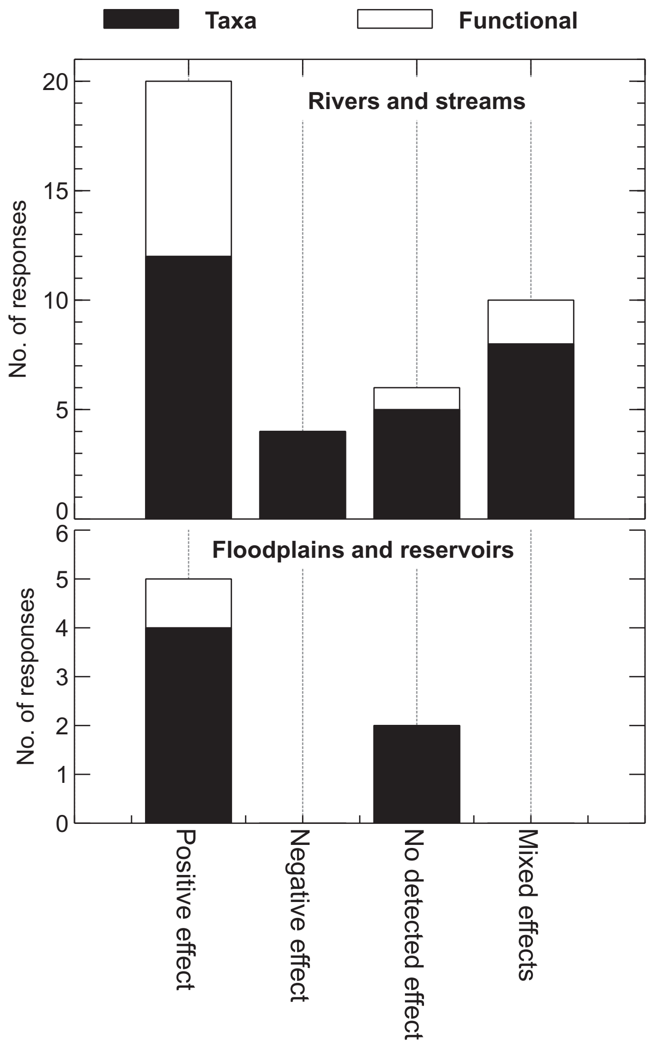

Figure 2. The number of responses that reported on the effect of forests and trees on fish diversity in stream or river systems (top) and floodplain or reservoir systems (bottom). The outcomes are divided by type of indicator, functional or taxonomic.

the relative abundance of species that were nektonic had reduced in nonforest streams and the abundance of species that possessed the traits of being tolerant to hypoxia and siltation was higher (Zeni et al. 2017). One case in Brazil showed that functional beta diversity was similar between forested and agriculture streams (Roa-Fuentes et al. 2019). However, the land use composition was measured at the catchment level and sample sites were located in landscapes that were already dominated by agriculture; where there is little variability in land use between catchments, it can be difficult or impossible to observe effects on fish diversity.

Ten (25%) measures presented mixed effects of forests on fish diversity, which were partly attributed to different results of outcome indicators. The studies reported negative or nonsignificant effects of forests on species richness, but beta diversity measures were higher among forested areas (Bojsen and Barriga 2002, Teresa and Casatti 2011). This suggests that the heterogeneity in fish species composition is higher among forested streams than among deforested streams. Similarly, other studies observed insignificant differences in the number of species measured, but the taxonomic and functional composition of fish communities were dissimilar between forest and nonforest streams, particularly when observed at the trophic guild level (Lorion and Kennedy 2009, dos Santos et al. 2015).

The variety of land use comparisons applied also contributed to the mixture of results. For example, fish communities in natural forested areas were found to have intermediate levels of diversity when compared to sugarcane (de Carvalho et al. 2017), but fish trophic diversity in natural forested areas was lower than in pasture streams.

Floodplains and reservoirs. Only seven diversity responses were measured in floodplain systems (figure 2). Five (70%) responses reported flooded forests having positive effects on species and functional groups; the heterogeneity in habitat structure provided by floodplain forests accommodate species that require unique and specific habitats for survival (Arantes et al. 2018, Loebens et al. 2019). Flooded forests contain significantly more species than open waters, even when factoring in seasonal changes in the rising and falling of waters (Loebens et al. 2019).

Carvalho Freitas and colleagues (2018) observed no detected effect of fish diversity along the floodplain forest cover gradient; fish communities, instead, significantly responded to the amount of shrub vegetation bordering floodplain lakes as well as the area of open waters.

In the Amazon Basin, floodplain forests contained significantly higher diversity of species than open waters, but macrophyte and flooded forest habitats were similar across all measures of fish diversity (Siqueira-Souza et al. 2016). This suggests that macrophytes may contain similar refuge properties to flooded forest habitats that protect prey species from predators compared to open waters where prey species are more vulnerable to predators.

The relationship between tropical forests and the biomass or abundance of fish

Compared to diversity measures, we recorded fewer responses of fish biomass and abundance to forests with 32 responses in total (figure 3). The majority of responses were from stream and river ecosystems (84%, 27 out of 32 responses). Again, we report results and findings of fish abundance and biomass outcomes by type of inland freshwater systems.

Streams and rivers. From a total of 27 studies, we found 9 (33%) and 18 (67%) biomass or abundance responses at the species and community level, respectively (figure 3). Five (19%) responses reported positive associations between forests and the density of fish at the species and community level. In Indonesia, species with complementary

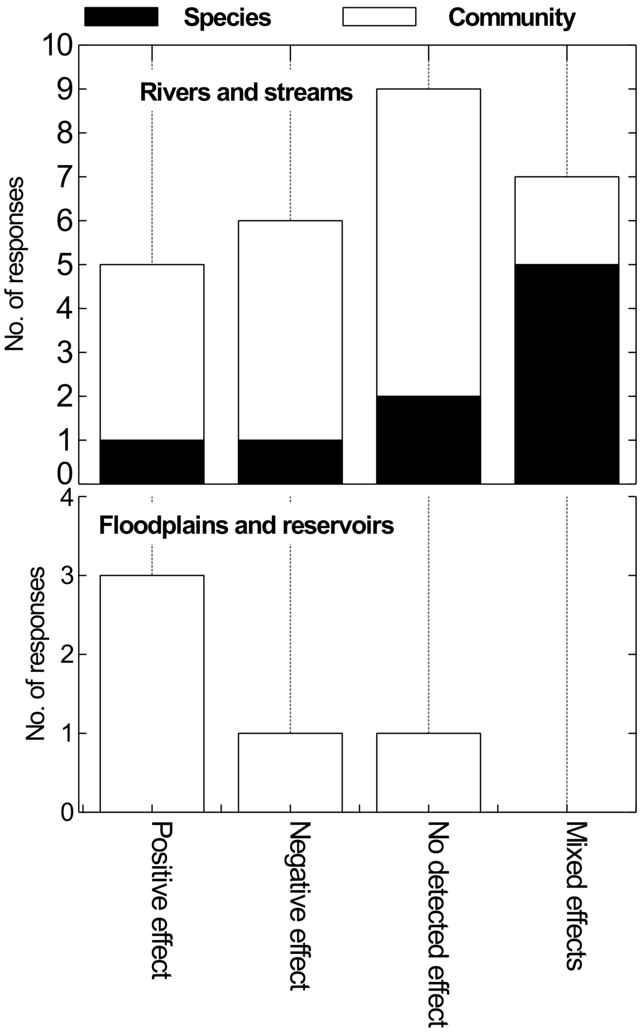

Figure 3. The number of studies that reported on the effect of forests and trees on the abundance and biomass of fish at the species and community level in stream or river systems (top) and floodplain or reservoir systems (bottom).

feeding niches combined with greater energy transfer from forest inputs led to higher fish production within streams (Giam et al. 2015). In Malaysia, sedimentation occurring in degraded (secondary) forest streams lowered the density of freshwater shrimp species (Iwata et al. 2003b). Despite deforestation having occurred 9–20 years prior to this study, it was evident that aquatic populations had still not fully recovered, emphasizing the long-term effects of land use change on stream biodiversity. Shrimp species appear to be especially sensitive to changes in water velocity and sedimentation preferring fast currents with coarse substrates that act as refuges to reserve energy (Iwata et al. 2003a). Higher fish biomass in forested streams compared to nonforested streams was also found. This was attributed to greater food availability and niche complementary from the diversity of fish species, both providing conducive conditions for greater energy transfer and increased production (Giam et al. 2015). Ilha and colleagues (2018) also suggests that warmer temperatures from greater sun exposure in deforested streams decrease growth rates, which lead to reduced fish body mass.

Six (22%) responses reported inverse patterns between fish abundance or biomass and forest presence. At the species level, Algae-grazing catfish found in Panama prefer to reside in sunny open stream habitats that have a greater availability of periphyton to feed on (Power 1984). The reduced abundance at the community level found in several studies was primarily driven by only a few species that mainly fed on aquatic food materials (Esteves et al. 2008, da Costa and da Rocha 2017, Virgilio et al. 2018, Ilha et al. 2019) or displayed generalist feeding behaviors (Ferreira et al. 2018).

In total, nine (33%) responses reported no effect between forests and biomass or abundance. One (4%) study reported no effects between forest and biomass or abundance at the individual species level. For *Enteromius neumayeri*, a highly abundant predatory cyprinid fish species in Uganda, warmer waters from greater sun exposure in deforested sites increased metabolic rates and energy intake and consequently reduced growth and reproduction (Fugere et al. 2018). Nonetheless, greater availability and increased consumption of invertebrates compensated for metabolic costs, therefore explaining why changes in biomass were not observed.

Other studies pointed to other factors that had a greater influence on species and community abundance, including water velocity (Teresa and Casatti 2013), stream order (Dias and Tejerina-Garro 2010), in-stream habitat space (dos Santos et al. 2015), and urbanization within close proximity to streams (Junqueira et al. 2016). Riparian zones that were subjected to reduced impact logging activities did not significantly differ from undisturbed forested streams regarding fish abundance, which suggests that managing ecological alterations in riparian forests can minimize the negative effects of deforestation on freshwater communities (Prudente et al. 2017). Wilkinson and colleagues (2018b) found that fish communities were resilient to land use changes in Sabah, Malaysia; however, the authors caution that the interpretation of findings should consider methodological choice of using cast nets to capture fish and may not fully represent the response of freshwater fish communities.

Seven (26%) responses showed that forests have contrasting effects on abundance and biomass. Mixed effects of forests on fish abundance and biomass were usually related to the feeding preferences of fish species and their association with specific physical habitat conditions (Abes and Agostinho 2001, Bojsen 2005, Barbosa et al. 2019). In Kenya, crab abundance was higher in riverine forested sites than in nonforested sites; however, biomass remained the same because of the high presence of crab juveniles; consequently, altering riverine forests could negatively affect the reproduction of crab species and lead to the extirpation of local crab populations (Dobson et al. 2007). In contrast,

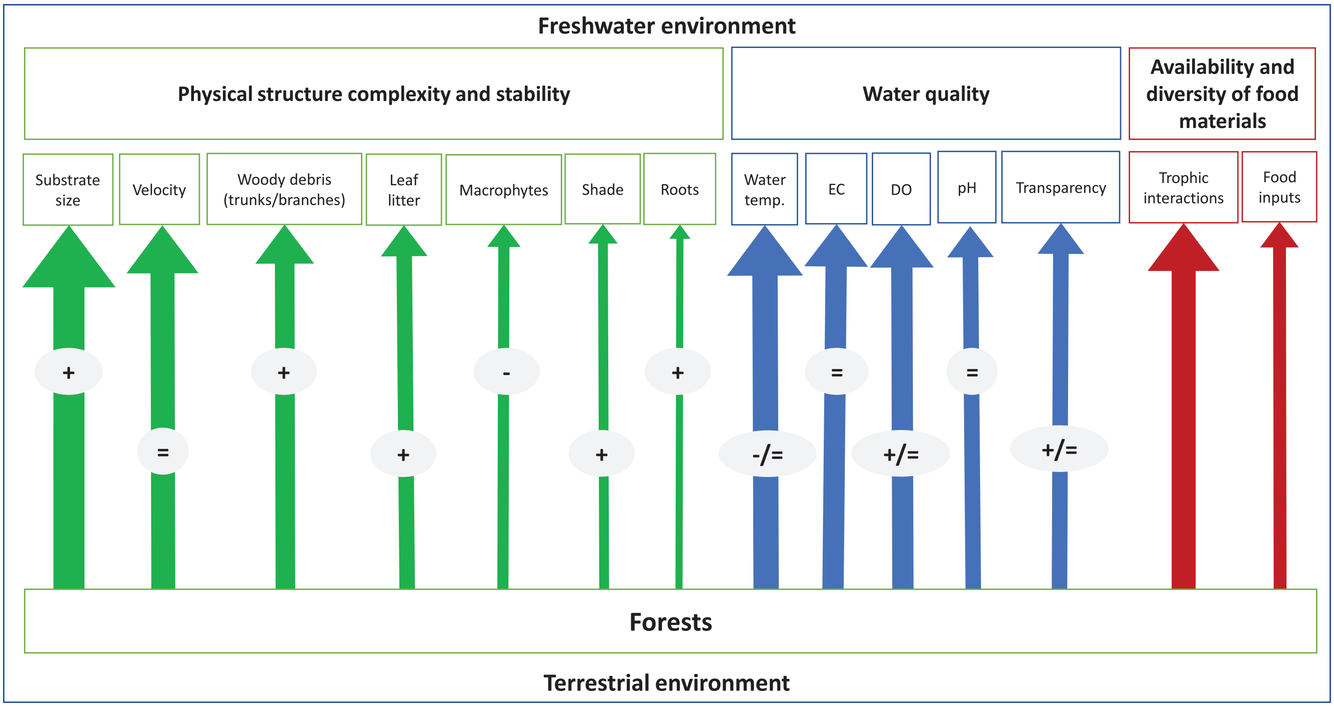

Figure 4. The strength and direction of correlations between forests or trees and freshwater environments that are broadly categorized into physical structure, water quality, and food. The thickness of the arrows represents the number of studies in which the linkages between forests and the characteristics of freshwater habitats were measured. The grey circles show the direction of the correlation, which may be positive (+), negative (–), or similar (=).

higher abundance of fish at the community level was found in nonforested streams, but again, biomass remained the same, suggesting that smaller fish prefer open stream habitats (Bojsen and Barriga 2002). Other mixed effects were due to varying responses to different types of land use: In Sabah, Malaysia, *Nematabramis everetti* were lower in logged forests but abundant in both oil palm and primary forested streams (Wilkinson et al. 2019). This could be because of sedimentation from recent logging activities.

Floodplains and reservoirs. Only five (8%) responses in our review showed measured abundance or biomass in relation to forest floodplains or reservoirs. The large majority (60%) of responses showed a positive effect (figure 3). In floodplains, fish species migrate between different land uses following the rise and fall of water levels at which certain species show a greater preference for flooded forests during high water levels (Castello 2008). Forests also appear to help maintain connectivity between habitats, which support the life cycle of fish species and movement between habitat patches across the landscape (Fernandes et al. 2015, Hurd et al. 2016). Floodplain deforestation effects on fish communities have been suggested to influence fish habitat selection patterns, with the removal of forests leading to lower than normal fish densities (Castello 2008, Castello et al. 2018).

One (20%) study in a Brazilian reservoir showed that the presence of submerged trees—riparian trees growing along river banks—was associated with lower fish abundance overall; however, the density of juvenile fish was significantly higher in reservoirs with rather than without submerged trees (Gogola et al. 2016). This reinforces existing notions that the structural complexity provided by forests is crucial to support the development of aquatic organisms at the early stages of the life cycle (Agostinho and Zalewski 1995).

One (20%) study showed that overall fish abundance did not significantly differ along forest cover gradients within local catchments in floodplains; however, as the compositional structure varied with percentage of forest cover, community density appeared to have been compensated with species replacement (Arantes et al. 2018).

Functional mechanisms by which forests shape freshwater habitats in the tropics

In the present article, we examine the strength of scientific evidence for functional mechanisms by which forests shape freshwater fish habitats (figure 4). We categorized these mechanisms into three groups: physical habitat structure, water quality, and food supply.

Physical structure. Forests were widely cited for contributing to habitat complexity by providing direct terrestrial inputs from trees as well as controlling for sedimentation and siltation. A total of 32 (52%) studies linked forests with changes in physical structure with a high proportion of studies showing strong evidence pointing toward forested habitats having a higher abundance of leaf litter, woody debris, and submerged roots (figure 4). From the all the studies that recorded substrate size (36%, 22 of 61 studies), 18 (82%) studies reported that forested water bodies contained larger substrate composition from large terrestrial in-stream materials deposited in freshwater habitats. Furthermore, lower proportions of fine sediments were found in areas with a higher forest presence; this was attributed to the role forests have in reducing siltation and sedimentation and consequently maintains the complexity and availability of microhabitats (Kamdem Toham and Teugels 1999). From all the studies that measured velocity between land use comparators (31%, 19 of 61 studies), nine (50%) studies showed that the velocity of river and stream habitats remained similar.

Water quality. Out of the 35 (57%) studies that included water quality indicators, 22 (63%) were linked to forest presence (figure 4). This suggests that hydrological factors of freshwater habitats are assumed to be independent from the presence of forests in more than one-third of these studies. Indeed, we found several cases where water quality parameters were controlled for between land use types. Both pH and electrical conductivity were similar between forested and nonforested areas. Lower solar radiation levels from riparian canopy cover is expected to reduce water temperatures and maintain dissolved oxygen levels (de Paula Ferreira et al. 2015); these findings were present in seven (39%) and eight (53%) studies measuring these indicators, respectively. Specific studies have focused on forest, water temperature, and biomass changes in depth, such as Ilha and colleagues (2018), in which they found a 3.5 degree Celsius increase in temperature from deforestation in southeastern Amazonia streams was linked to a reduction in both fish body size and growth. However, there remains ambiguity because of the relatively high number of results that detected no differences in water temperature (61%, 11 of 18 studies) and dissolved oxygen (47%, 7 of 15 studies) between comparators. Water transparency is also mediated by forests via greater sedimentation and siltation control (Lobon-Cervia et al. 2016); and similarly, seven (64%) studies showed that transparency levels were similar between forest and nonforest or degraded freshwater bodies, and four (30%) studies reported clearer waters in forested sites. Some evidence suggests that forest root systems improve the quality of water via natural infiltration processes (Neary et al. 2009), but it is unclear how this affects specific water quality parameters, particularly in freshwater ecosystems. In part, this is influenced by the type of land use that is being compared to forested sites.

Food materials. We found 22 (36%) studies that examined the relationship between forests and fish through the availability and distribution of food materials (figure 4), which were broadly categorized into aquatic and terrestrial sources. We would expect a greater abundance of aquatic plants and insects in open freshwater habitats with greater exposure of sunlight (Power 1984, Lin and Caramaschi 2005, Esteves et al. 2008) and a greater abundance of terrestrial food inputs in forested areas (Bojsen 2005, Zeni and Casatti 2014). Feeding traits of individual fish species are, therefore, likely to influence fish community response to land use (Bojsen 2005, Zeni and Casatti 2014, de Paula Ferreira et al. 2015, Giam et al. 2015). However, what creates a more complex picture is the indirect mediating factors that forests exhibit through the availability and distribution of aquatic food materials. For example, benthic species depend on coarse substrate materials, which are proportionally higher in forested sites, because they create favorable conditions for the growth of algae and periphyton (Casatti et al. 2015). Siltation, a characteristic of degraded environments, has also been reported to reduce zoobenthic food resources (Giam et al. 2015). Like fish communities, resources derived from forests support aquatic insects by providing terrestrial food materials (Boyero et al. 2012) and shelter (Abdul Hamid and Md Rawi 2011).

Multiscale mechanisms. Several studies reported the influence of scale on the observed responses of freshwater fish. Differences in spatial scales have a profound effect on how we observe forest and fish interactions and which attributes influence fish species and the community structure (Smokorowski and Pratt 2007). Riparian forests have a direct role in the habitat structure and the distribution of food materials, as well as mitigating negative impacts from agriculture in landscapes (Giam et al. 2015, Juen et al. 2016). However, other characteristics of freshwater habitats are shaped by processes occurring at the wider landscape and watershed level. The functional complementarity of freshwater fish communities, for example, is strongly associated with regional changes in forest cover (Bordignon et al. 2015, Arantes et al. 2018, Leitao et al. 2018). Some studies suggest that environmental variables have hierarchical scaling effects on fish assemblage structure: catchment and landscape compositional factors are ultimately mediated by the ecological condition of local riparian buffers that determine the overall composition (Tanaka et al. 2016, Terra et al. 2016, Leal et al. 2018).

Key findings and knowledge gaps

Forests positively influence the diversity of freshwater fish communities in the tropics via increased heterogeneity in physical structure and food materials in freshwater habitats. This tropical pattern conforms to the conceptual model of forest influences on aquatic systems in temperate ecosystems (e.g., Allan 2004, Smokorowski and Pratt 2007). The collective body of tropical research can ascribe change in the compositional structure of freshwater fish assemblages to the influence of terrestrial environments. Such relationships are similar to what was originally described in temperate streams as the river continuum concept (Vannote et al. 1980), but the downstream patterns and particular relationships differ.

Forest versus nonforest environments provide alternative ecological conditions in freshwater habitats, and these environmental filters determine the distribution of fish species (Córdova-Tapia et al. 2018) that can be reasonably well predicted by functional traits and tolerance to changes in resources. For example, fish species that have narrow habitat preferences may require specific resources derived from forested environments. This is evident in several cases where specialized and rare species were found in forested areas, whereas generalists flourished in disturbed environments (Zeni et al. 2019).

We identified three key research and knowledge gaps for understanding and managing integrated forest and freshwater habitats in the tropics. There is an underrepresentation of interlinkages between forests and functional diversity of fish communities in lentic ecosystems (1 of 61 studies). In addition, there is a scarcity of studies assessing environmental filtering as a key driver of functional structure in fish assemblages in tropical wetland ecosystems (Córdova-Tapia et al. 2018). Finally, it is important to consider the spatial biases of existing tropical studies; most of the research describes river or stream systems in Brazil. The forest–freshwater literature will benefit from more studies focused on floodplain systems, as well as research carried out in the Indomalaya and African tropics.

Methodological caveats

Although most studies point to forests enhancing fish diversity as compared with nonforested environments, we found several studies presenting divergent findings. Divergent findings could represent complex relationships but could also be because of differences in the methodological design and the type of outcome indicators. To prevent misinterpretation of findings and to identify knowledge gaps that help to improve our understanding of the forest–fish nexus, we highlight the issues and constraints limiting our ability to compare results across studies.

First, some studies addressed taxonomic diversity alone, which may limit our ability to identify the drivers of structural changes in fish communities (Mouillot et al. 2013). Functional diversity based on species traits provides a more rigorous lens for quantifying and predicting the effects of land use changes and identifying the type of disturbances that occur and which species will be affected (Frimpong and Angermeier 2010, Mouillot et al. 2013). Second, differences in spatial scale can have a profound effect on how we observe forest and fish interactions and on which attributes appear to influence fish species and the community structure (Smokorowski and Pratt 2007, Feist et al. 2010). Third, long-term consequences of recent forest degradation and deforestation may not be observable in research conducted soon after the disturbance event (Zeni et al. 2017). This may be particularly true for land use changes that occur at broader spatial scales (Leal et al. 2018, Roa-Fuentes et al. 2019). Fourth, temporal dynamics including seasonality (which are particularly important in floodplain systems), fish migrations between habitat types, and seasonal shifts in habitat preferences across life stages of any particular species (Gogola et al. 2016) may obscure relationships between tropical forests and fish. Last, approaches to measuring and controlling environmental variables in freshwater habitats varied across studies, creating difficulties in harmonizing results, particularly in understanding the range of pathways that occur between forests, freshwater habitats, and the biological responses of fish species. For example, we found studies in which the local characteristics of freshwater systems were measured independently of forest and forest cover; other studies alternatively took an analytical pathway approach by modeling freshwater variables as a result of forest cover first and then measuring the fish response to these variables. This method provides a stronger analytical approach in understanding the interactions between forests and the ecological processes that occur within freshwater environments. Other statistical analyses test for interacting factors between land types and, in some cases, removed forest cover from the models (e.g., Carvalho Freitas et al. 2018), which could therefore misrepresent the importance of forests within the aquatic–terrestrial interface. Freshwater habitat area and stream order are key factors that also influence species richness and abundance (Angermeier and Schlosser 1989, Dias and Tejerina-Garro 2010, Fernandes et al. 2013); our inability to account for these determinants could result in the misinterpretation of findings from observed results.

Directions for science and policy

Quantifying the relationships between forests and freshwater fish communities is challenging, in part, because of the need to match the spatial and temporal scales of the processes involved in such linkages. Forests are stationary whereas freshwater ecosystems can flow over hundreds of kilometers and fish in them can move; they are affected not just by habitat changes but also by associated food web effects. In the present article, we reveal the integral contribution of forests to fish in freshwater ecosystems; they can provide regulatory and provisioning functions that support the aquatic habitat, water quality, and availability of food for freshwater fish. The response of freshwater fish communities is tightly linked to these deterministic environmental conditions that filter both the occurrence and abundance of species. We also highlight the potential impacts of deforestation and land degradation on freshwater fish and how different fish species may respond to changes in the landscape. Land use change is one of the greatest and most immediate threats to biodiversity (Titeux et al. 2016); further research on its impact on freshwater biodiversity is necessary to develop land use policies that support freshwater habitats and prevent further depletion of freshwater fish communities. We identify three key priorities for future research to enhance our understanding of forests and freshwater ecosystems in the tropics: (1) greater investment is needed in research from Asia and Africa, especially considering the high rates of deforestation and habitat degradation occurring in these regions. (2) wider use of metrics that assess species by functional traits to better understand the consequences of land use change on freshwater fish assemblages. This approach also helps to identify which species are sensitive to changes along environment gradients and therefore, highly important for informing effective conservation management. (3) accounting and reporting of covariates in methodological design to help harmonize findings and prevent the misinterpretation of results.

Although the existing literature reviewed in the present article offers a solid base for understanding how tropical forests and freshwater fish interact, many interesting questions remain about the underlying mechanisms determining these interactions and how they differ by species and context. Answering these questions is not only of academic interest but is key for guiding informed choices about land use with important consequences for biodiversity, livelihoods, and food security.

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Supplemental material

Supplemental data are available at *BIOSCI* online.

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