


RESEARCH ARTICLE

Fish on Fire: Shifts in Amazonian fish communities after floodplain forest fires

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Abstract

1. Severe droughts can lead to fires that cause massive tree mortality in even the wettest and most isolated Amazonian forests. After repeated fires, blackwater floodplain forests can remain in an open vegetation state of arrested succession that facilitates a transition towards a white-sand 'savanna-like' vegetation. These vegetation shifts, from closed-canopy floodplain forests to open fire scars and eventually white-sand savannas, may have profound implications for fish communities that depend on floodplain forests for food and recruitment. In turn, changes in fish communities may contribute to the arrested forest recovery after fires as fish are important seed dispersal agents for many floodplain tree species.
2. To explore the impacts of floodplain forest fires on fish communities, we sampled fish in unburnt forests, fire scars, and white-sand savannas in the middle Rio Negro basin (Brazil) during two consecutive flooding seasons. We compared the abundance, species richness, and the taxonomic and trophic composition of fish assemblages across the three habitat types.
3. We found significant shifts in fish assemblages in fire scars compared to unburnt floodplain forests. Also, as fire scars increased in size, total fish biomass decreased strongly. Fish communities in unburnt floodplain forests seem to be characterized by a higher proportion of smaller and omnivorous fish species than fish communities in burned floodplain forests and white sand savannas. Fish assemblages in fire scars and white-sand savanna were not significantly different.
4. *Synthesis and Applications.* Amazonian fish communities change after floodplain forest fires. Unburnt forests have diverse fish communities, with a large proportion of unique and small omnivorous species. In contrast, carnivores and detritivores become more common in fire scars and white-sand savannas formed after forest fires. Less omnivore fish after forest fires can reduce tree seed dispersal and forest regeneration, affecting ecosystem functioning and the services provided by Amazonian forests. Fish are also a primary source of food and income for people living in Amazonian floodplains. Preventing forest fires is therefore of

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fundamental importance for the conservation of Amazonian aquatic and terrestrial ecological communities as well as for the livelihood of people.

KEYWORDS

aquatic-terrestrial interaction, ecological network, plant–animal interaction, resilience, seed dispersal, tropical forest, white-sand savannas

1 | INTRODUCTION

Aquatic and terrestrial biodiversity are highly intertwined in tropical and temperate floodplains (Horn et al., 2011; Junk, 2005; Opperman et al., 2017). In Amazonian floodplain forests, many fish species expand their distribution, from main river channels onto inundated floodplain forests, during the annual high-water season (e.g. Carvalho et al., 2009; Goulding, 1980; Goulding et al., 1988). These inundated forests provide crucial feeding and nursery grounds, where fish feed extensively on terrestrial arthropods, fruits, and seeds, building up fat reserves that increase fish survival during the low-water season when food availability is limited (Carvalho et al., 2009; Correa & Winemiller, 2018; Gottsberger, 1978; Goulding, 1980; Kubitzki & Ziburski, 1994; Saint-Paul et al., 2000). Floodplain forests are also key environments for fish reproduction and rearing (e.g. Menezes & Vazzoler, 1992; van der Sleen et al., 2020). Fish, in turn, play an important role as seed dispersers for many floodplain trees. Fish provide essential upstream dispersal, in contrast to the exclusive downstream dispersal provided by water, and they can also scarify seeds, increasing germination rates (Carvalho et al., 2009; Weiss et al., 2016).

These tight ecological interactions, between aquatic and terrestrial organisms, can be disrupted by disturbances affecting either the forest or the river compartments of floodplain ecosystems. Severe droughts have impacted the Amazon Basin during the last two decades (Jiménez-Muñoz et al., 2016; Marengo et al., 2011; Phillips et al., 2009), a trend that is predicted to increase as climate change progresses (Cai et al., 2014). These droughts not only reduce the extent of the flooding, but they also dry out forests sufficiently to facilitate the ignition and spread of fires (Phillips et al., 2009). Floodplain forests show a lower resilience to drought-induced forest fires than non-floodplain (or upland) forests (Flores et al., 2017). Especially floodplain forests along blackwater rivers (known locally as *igapós*), recover very slowly or may fail to recover at all after forest fires, remaining in an open vegetation state of arrested succession for decades (Flores et al., 2016). This open state of arrested forest succession, which is more susceptible to reburning, may facilitate a transition towards a white-sand savanna-like vegetation with a distinct tree species composition, higher herbaceous cover and more sandy soils compared to unburnt closed-canopy floodplain forests (Flores & Holmgren, 2021a). These vegetation shifts, from closed floodplain forests to white-sand savannas, appear to be driven by both nutrient erosion (Flores & Holmgren, 2021a) and seed dispersal limitation (Flores & Holmgren, 2021b).

Vegetation shifts caused by forest fires, from closed-canopy unburnt *igapó* forests to open fire scars and eventually white-sand savannas, may have profound implications for fish communities. Previous studies have found that floodplain forest loss can have large impacts on fish abundance and diversity in the Amazon (Arantes et al., 2018; Bojsen & Barriga, 2002; Castello et al., 2018). However, the impacts of forest fires on fish communities have not been studied. Here, we assess the changes in the composition and structure of fish communities after forest fires in blackwater floodplains. We expect fire-driven vegetation shifts to strongly change food sources and the availability of refuges to fish. Massive tree mortality after fires (Flores et al., 2016) could reduce the availability of fruits and a large diversity of terrestrial invertebrates associated with the forest that are often part of the fish diet in floodplain forests. At the same time, the higher availability of exposed sandy soils in burned areas (Flores & Holmgren, 2021a) could favour fish species that forage by sifting finely particulate detritus associated to the substrate. The loss of woody biomass in fire scars may also reduce the availability of refuges that could facilitate hiding from predators and safe reproduction (Ferreira et al., 2015; Gois et al., 2012; Wright & Flecker, 2004), making burned areas good hunting grounds for (large) predatory fish, but poor and dangerous places for (smaller) herbivorous and omnivorous fish species. We therefore expected these ecological changes to be reflected in the relative abundance of different fish trophic categories as well as in the size structure of the fish communities after forest fires. In particular, we expected that: (1) fish communities in fire scars have a lower relative abundance of frugivorous fish species and a higher abundance of predatory fish species than those found in unburned floodplain forests; (2) fish communities in fire scars have a higher proportion of larger fish sizes than unburned forests; and (3) fish communities in white sand savannas have a larger abundance of benthic fish species associated with sandy substrates compared to fish communities in unburnt forests and fire scars.

2 | MATERIALS AND METHODS

2.1 | Study area

We studied fish communities in blackwater floodplains of the middle Rio Negro region in Central Amazonia, including the Mariuá Archipelago and the Quiuni River, close to the city of Barcelos, Brazil (Figure 1). This study area is flooded annually from May to September, with a 5.5m water level mean amplitude between the

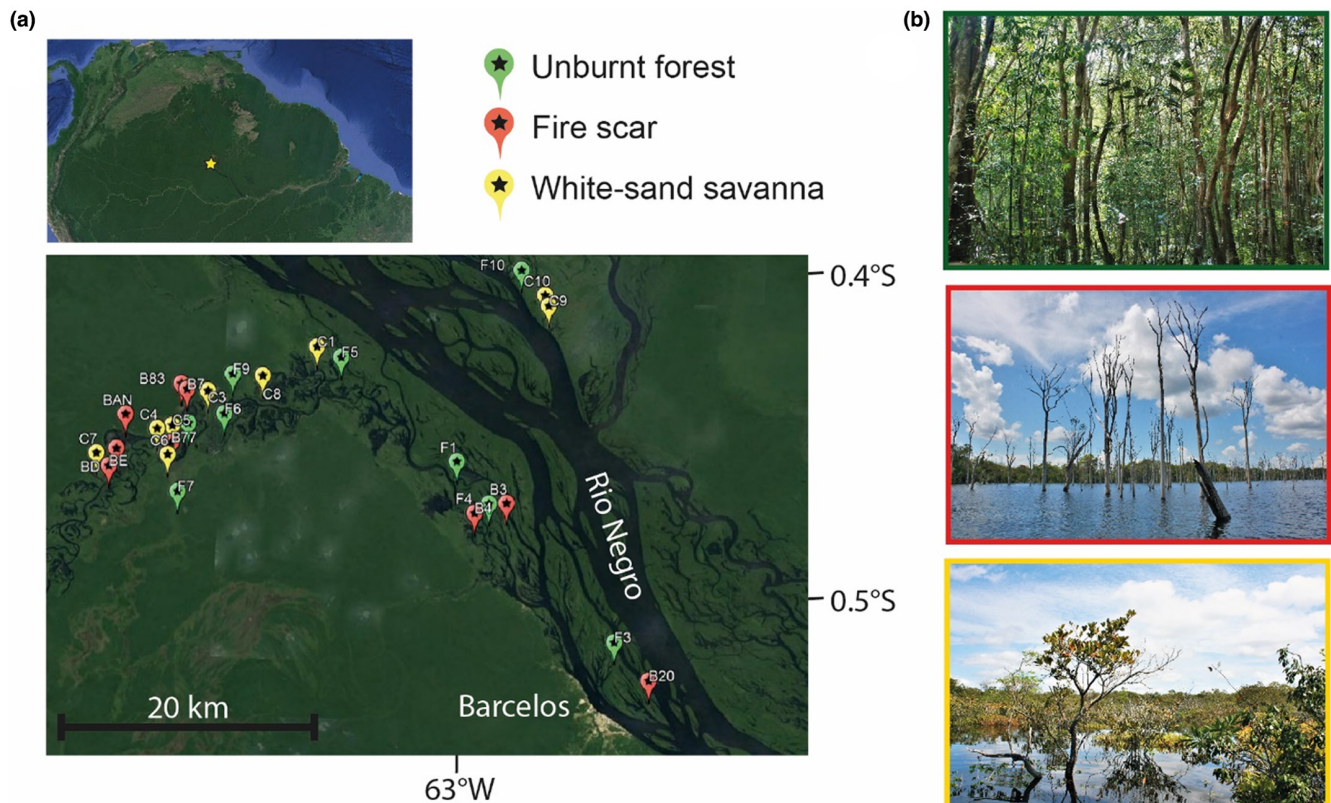


FIGURE 1 Map of the studied area in the middle Rio Negro, Brazil, with locations of the 27 sampling sites (a). Images of the three types of sampled habitats (b): unburnt floodplain forest (green), containing high habitat heterogeneity and structural complexity; burnt floodplain forest (i.e. fire scars; red) that lost most woody vegetation and persist in an open-vegetation state; and white-sand savanna (i.e. *campina*; yellow), characterized mainly by 'stunted' shrubs.

highest and the lowest water level (Goulding et al., 2003). We sampled 27 sites in three different flooded habitats (Figure 1): (1) Unburnt floodplain forests ($n=9$), that based on remote sensing images did not burn in the past three decades (this was also confirmed by interviewing local residents); (2) fire scars ($n=9$) of floodplain forests that burnt twice in the past decades and currently persist in an open-canopy vegetation state that lacks signs of forest recovery; and (3) floodplain white-sand savannas ($n=9$), which are locally known as *campinas* and described by Goulding et al. (1988) and Adeney et al. (2016) as white-sand grass or shrublands, with stunted stature and sclerophyllous leaves in comparison to adjacent rainforests. The vegetation and soil conditions in the same study sites were previously described by Flores et al. (2016) and Flores and Holmgren (2021a, 2021b).

2.2 | Fish sampling

We sampled fish communities during the high-water seasons (from May to July) of 2018 and 2019. Fish were captured in all sites using a set of nine 20-m long gillnets of different mesh sizes (40–200 mm) during 24 consecutive hours at each sampling year. Distance of the nets to the nearest river edge varied across sites, but was less than 1 km for all sites (range 24–710 m). Fish were retrieved from the

gillnets every 6–8 h. Each collected individual was photographed and identified to species level, and its standard length and total weight recorded. Unidentified fish were preserved in a 10% formaldehyde solution and stored for further identification at the Fish Systematics and Ecology Laboratory of the National Institute for Amazonian Research (INPA) in Manaus, Brazil. This research was conducted under permit by the ethics committee for the use of animals in scientific research (CEUA) of the National Institute for Amazonian Research (INPA, Portuguese acronym), Manaus, Amazonas state, Brazil (Protocol nr. 033/2012) and by SISBIO/IBAMA permanent sampling permit to Jansen Zuanon (#10199-3).

2.3 | Data analysis

Data from the two sampling years were pooled prior to statistical analyzes. Differences among the three habitats in number of individuals and species were tested with an ANOVA. Shannon diversity (H) and Dominance (D; calculated as 1-Simpson index) indexes were calculated for every sampled site and differences across habitat types assessed using a Kruskal-Wallis test as the data did not follow a normal distribution.

We also used an a Kruskal-Wallis test to assess differences in mean fish size across the three habitat types using all collected

individuals and the most abundant species only: *Serrasalmus gouldingi* ($n = 171$). Because fire scars differed greatly in size (5–150 ha), we used linear regressions to assess the effect of fire scar size on the number of species, individuals, total biomass, and mean fish size.

To study potential shifts in community composition across the three habitats, we first visualized fish community composition across habitats. To this end, we plotted the relative abundance of collected fish species in each of three main habitat types, considering only species with more than five individuals. We 'assigned' species to a habitat if they had $\geq 50\%$ of their relative abundance in that specific habitat. Next, a non-metric multidimensional scaling (NMDS) was performed on fish abundance in the sampling sites and across habitat types by using the Bray–Curtis similarity index (all collected fish individuals were included in this analysis). A PERMANOVA test was used to assess differences in species composition between the three habitats. Lastly, fish were classified in four trophic categories: (1) carnivore, (2) herbivore, (3) detritivore and (4) omnivore, based on their main diet according to previous studies (Goulding et al., 1988; Röpke et al., 2016) and the online database FishBase (Froese & Pauly, 2021). A Chi-square test was used to assess differences in the relative abundance of these trophic categories across the three habitat types.

Because geographical distance across sites could potentially influence species similarity, we used a Mantel test in which we compared matrices of Bray–Curtis similarity index and geographical distances between sites. In addition, we assessed the potential confounding effect of distance of the samples sites to the nearest open-water body, such as river or lake edges, on species abundance and richness using correlation tests. All the statistical tests were performed in R (R Core Team, 2020), IBM SPSS Statistics for Windows (Version 26.0) and PAST statistical software (Hammer et al., 2001).

3 | RESULTS

3.1 | Fish species composition and relative abundance

We collected 938 individuals of 80 fish species during the two flood seasons: 144 specimens of 41 species in 2018 and 794 specimens of 76 species in 2019. About 37% of all species (30 out of 80) were collected in all three habitat types. Unburnt floodplain forests had the largest proportion of unique species (21.3%; 17 out of 80) followed by fire scars (16.3%; 13 out of 80) and white-sand savannas (8.8%; 7 out of 80).

We found that total fish abundance, number of species, Shannon diversity and dominance indices did not significantly differ across the three habitat types, but variability among replicates was larger in unburnt forests than in the two other habitats (Figure 2). Yet, we found shifts in fish species composition and species relative abundance across the three habitats (Figure 3). There were significant

differences in the assemblage composition across trophic categories among the three habitat types (Chi-squared = 42.989, $df = 6$, p -value < 0.001). Unburnt floodplain forests showed the largest proportion of omnivores, a functional group that became less abundant in fire scars and white-sand savannas. In contrast, detritivores showed a slight increasing trend from unburnt forests, to fire scars and white-sand savannas (Figure 3). These changes were also detected in fish species composition, which differed among the three habitat types (PERMANOVA, $F = 1611$; $p < 0.005$); unburnt sites differed from fire scars ($p = 0.021$) and white-sand savannas ($p = 0.018$), while the latter two habitats did not differ from each other (Figure 4).

3.2 | Fish size and biomass

Mean fish length was larger in fire scars ($19.23 \text{ cm} \pm 0.27 \text{ SE}$) than in unburnt forests ($17.94 \pm 0.42 \text{ SE}$; Kruskal–Wallis Test, $p = 0.02$). Mean fish length in white-sand savannas ($18.74 \text{ cm} \pm 0.41 \text{ SE}$) was not significantly different from the other two habitat types. Differences in mean individual fish length between the three habitats seem to be mostly driven by the most abundant fish species, the piranha *Serrasalmus gouldingi* (Figure 5). Excluding *S. gouldingi* individuals from the dataset resulted in no significant differences in mean fish size across the three habitats.

The total fresh fish biomass captured was 160 kg, of which 39% were captured in unburnt forests, 32% in fire scars, and 28% in white-sand savannas. We found no overall significant difference in total fish biomass or in mean fish weight among the three habitats. Interestingly, we found strong and negative relationships between fire scar size and total fish biomass ($p = 0.013$, adjusted $r^2 = 0.56$), and between fire scar size and mean fish size ($p = 0.024$, adjusted $r^2 = 0.47$) (Figure 6).

We verified if our results were affected by spatial distance between sites (i.e. if nearby sites were more similar regardless of habitat type) or by differences in the distance to the nearest open-water body (as fish species diversity could be higher closer to open-water bodies), but found no significant effect of geographic distance on species similarity across sites (Mantel test using Bray–Curtis index, p -value = 0.57), nor a significant correlation between the distance to the nearest open-water body and Shannon diversity index, total fish biomass, number of species and individuals.

4 | DISCUSSION

Fire perturbations are a relatively recent, but increasingly pressing, threat to the integrity of Amazonian forests, including those covering the vast floodplains of the Amazon basin (Jiménez-Muñoz et al., 2016; Marengo et al., 2011; Phillips et al., 2009). We found significant shifts in Amazonian fish assemblages of blackwater floodplains after forest fires. Fish species composition and the relative abundance of trophic groups change after blackwater forests burn and remain as open fire

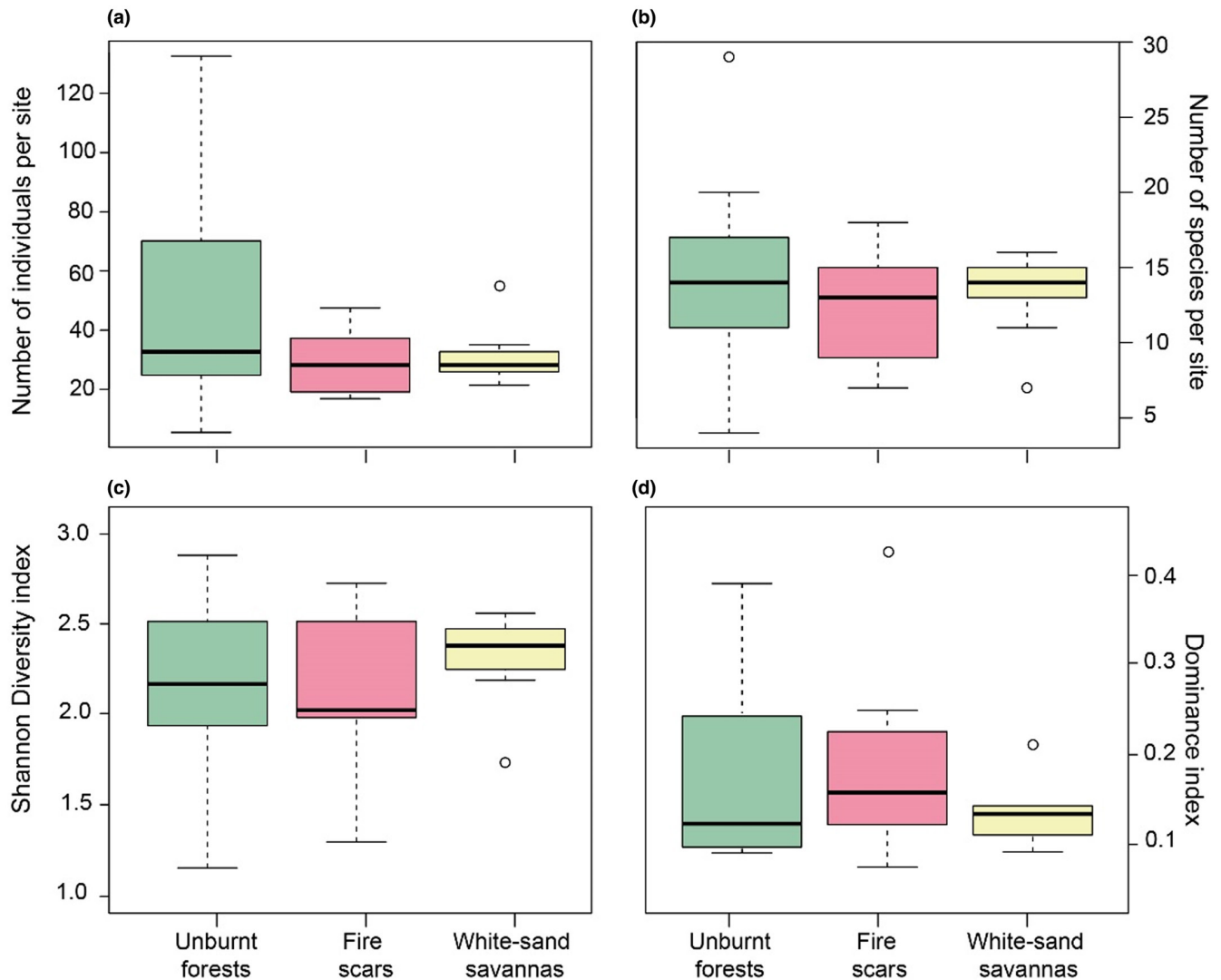


FIGURE 2 Box plots of collected fish individuals (a), number of species (b), mean Shannon diversity (c) and dominance values (d) in sites across the three habitat types. Thick black line in boxes represents mean values.

scars or as they transition to white-sand savannas. Unburnt forests were characterized by diverse fish communities, with a large proportion of unique and (smaller) omnivorous species. In contrast, carnivores and detritivores appear to become more common in fire scars and white-sand savannas. Our study is the first assessment of changes in fish communities after fires in Amazonia. Remarkably, the patterns we found are comparable to those reported on changes in fish community structure and composition after other types of disturbances that cause forest loss (Arantes et al., 2018; Bojsen & Barriga, 2002; Castello et al., 2018). Interestingly, the turnover in fish species composition after floodplain forests are burnt resembles the community shifts reported earlier for tree species (Flores & Holmgren, 2021a) and birds (Ritter et al., 2012) in the Rio Negro.

Fish communities are potentially interconnected during the flood season, as fish can move freely among the three habitat types in search for food or more adequate environmental conditions. So, the observed differences in fish assemblage composition and trophic groups among interconnected habitat types suggest

that there are strong ecological processes driving shifts in species composition across unburnt forests, fire scars and white-sand savannas. The differences in the relative abundance of trophic groups across habitats were consistent with our main expectations and could be partially explained by changes in food availability. Smaller fish, in particular, are mostly insectivorous and omnivorous (e.g. Goulding et al., 1988), depending strongly on the terrestrial, allochthonous material, that falls from the forest canopy into the water. Since fires can kill up to 90% of the trees in blackwater floodplain forests (Flores et al., 2016), fish that depend on organisms associated to the forest canopy may find less food resources in burnt floodplains. Increased predation risk may also contribute to changes in fish communities after forests burn. The fish size distribution of the most abundant fish species, *S. gouldingi* (18% of all individuals caught), shows a shift from smaller-sized individuals in unburned floodplain forests to larger-sized individuals in fire scars and white-sand savannas (Figure 5b,c). Fire scars have an open vegetation with less trees (Flores et al., 2016) and therefore

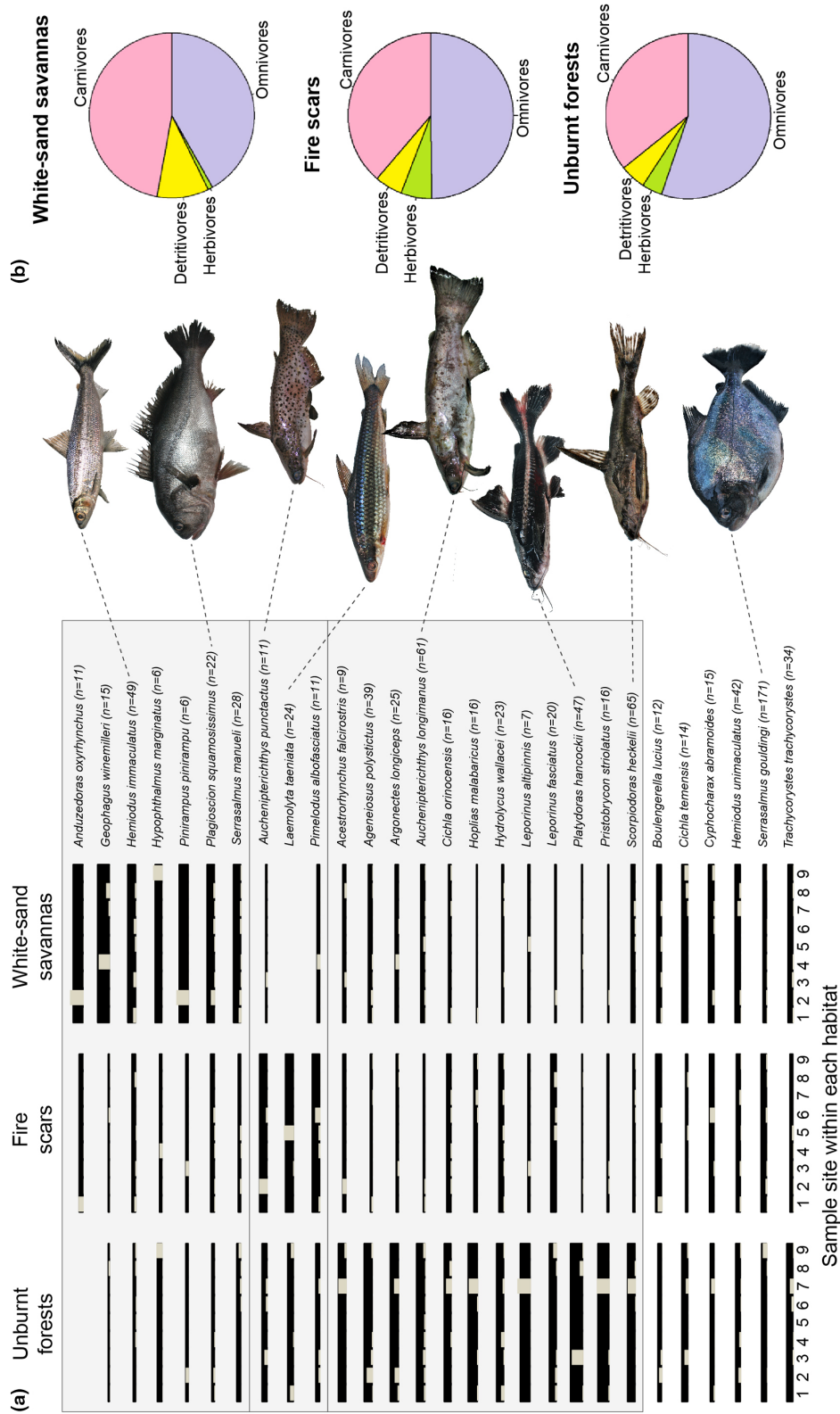


FIGURE 3 Fish relative abundance for species with more than five total collections across the three habitats where line thickness represents relative abundance (a); species were assigned to a habitat when they had ≥50% of their relative abundance in it (species are ordered alphabetically within the habitats). Total number of individuals collected in brackets after species name. Relative abundance of different trophic groups in white-sand savannas, fire scars and unburnt forests (b).

FIGURE 4 NMDS ordination based on species abundance in the three habitats. The ordination used the Bray-Curtis similarity index; stress value: 0.289. Collecting sites names are as follow: unburn forest sites (F, in green), burned forests sites (B, in red); dot size representing variance in fire scar size and white-sand savannas (C, in yellow).

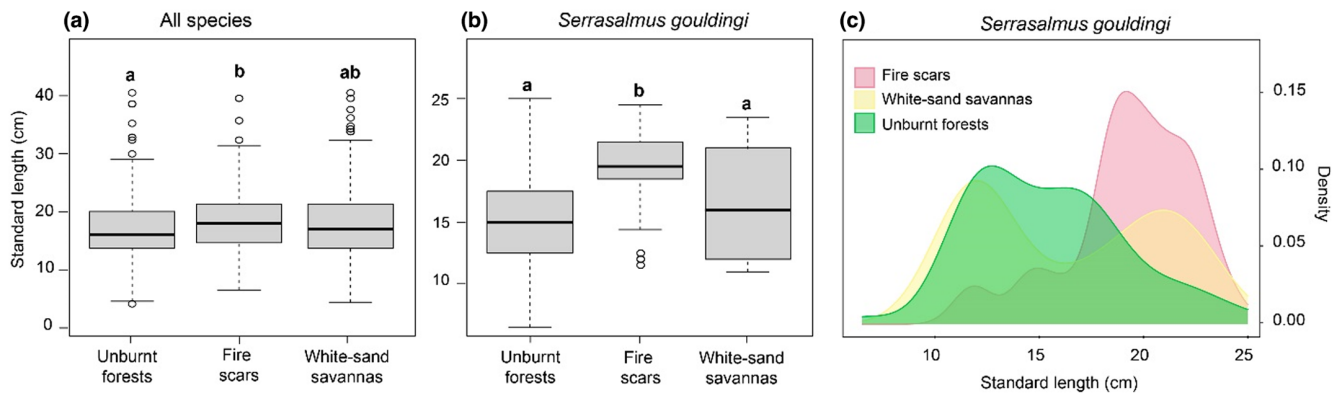
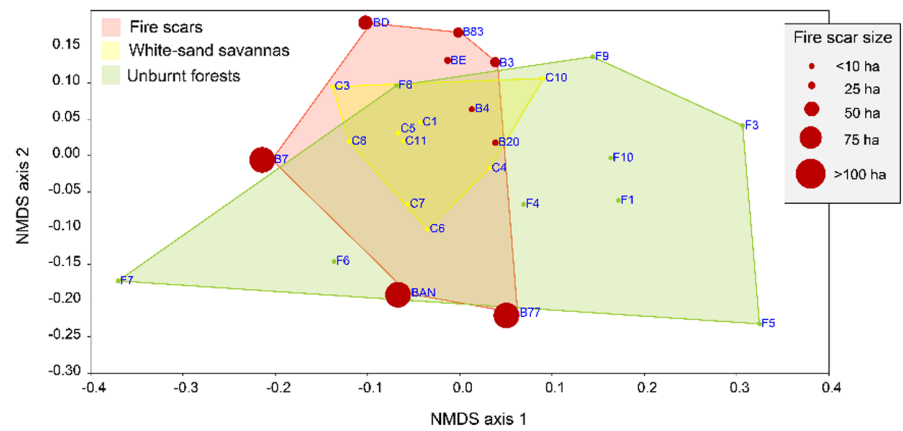


FIGURE 5 Mean fish length across the three habitats: all species together (a), and for *Serrasalmus gouldingi* (b). Small letters (a, b) indicate significant differences. Size distribution of *S. gouldingi* ($n=171$) across the three habitats (c).

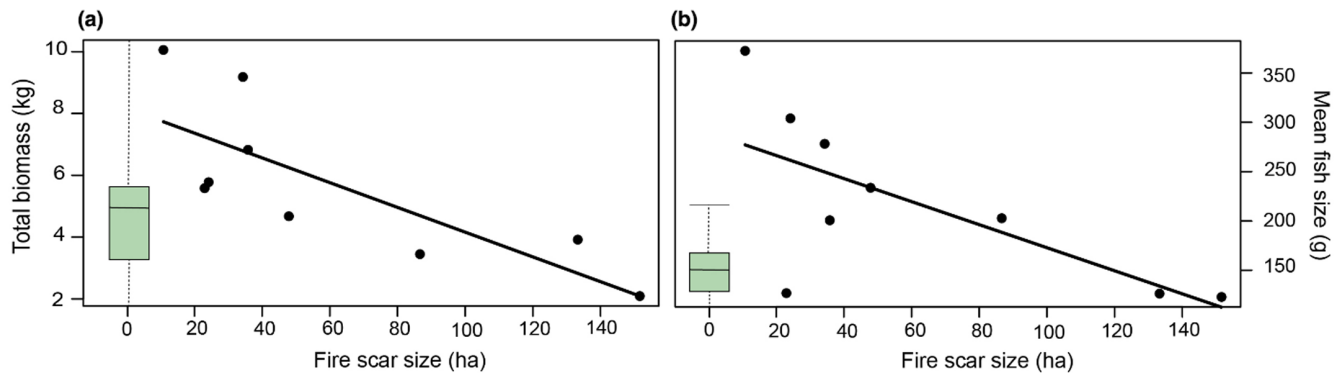


FIGURE 6 Changes in total biomass (a; $p=0.013$, adjusted $r^2=0.56$) and mean fish size (b; $p=0.024$, adjusted $r^2=0.47$) with fire scar size ($n=9$). Green boxplot shows data from unburnt forests, for comparison (in panel a, maximum value for total biomass was 25 kg in unburnt forests).

they likely offer less refuges for smaller fish than unburnt forests (Ferreira et al., 2015; Gois et al., 2012). In addition, higher light penetration in the aquatic environment of fire scars could increase visibility and hunting success of diurnal, visually oriented predatory fishes, such as *S. gouldingi*, which in turn could influence local fish assemblages (Rodríguez & Lewis Jr, 1997). Higher visibility has also been suggested as an explanation for the increased abundance of predatory fish in natural habitats and in newly created

reservoirs after hydropower dam constructions (Melo et al., 2009; Rodrigues et al., 2020). Lower food availability and higher predation risk may thus reduce the abundance of smaller-size fishes in fire scars compared to unburnt forests. It is possible that other factors, such as differences in water temperature and oxygen availability, could also contribute to changes in species composition across the habitats (Arrington & Winemiller, 2006; Ceneviva-Bastos et al., 2017; Willis et al., 2005).

We found that total fish biomass and mean individual fish size decreases steadily as fire scars became larger (Figure 6). This suggests that large fire scars become different aquatic environments than smaller fire scars, and may be used differently by fish. Indeed, we found that *S. gouldingi*, which was the most abundant species throughout our sampling sites, had a very low abundance in the two largest fire scars, with only one individual caught in each one. A low abundance of fish in general could make the largest fire scars unfavourable feeding habitats for large fish in particular given their high energy demands (Weitzman & Vari, 1988). Alternatively, higher temperatures and low oxygen availability in these unshaded large fire scars could limit the abundance of large-sized fish species as they have lower tolerance to these conditions (Anjos et al., 2008). The loss of fish abundance and diversity in the largest fire scars of the Rio Negro basin are worrisome, because the presence of large fire scars may increase strongly in these blackwater forests due to the combination of very slow forest recovery rate and expected increases in fire occurrence as climate changes.

The lack of more pronounced differences in overall abundance and diversity among habitat types in general may have been caused by heterogeneity among sites within the main habitat types, which is clearly reflected in the variance observed in each of the habitats (Figure 2). Unburnt forest sites have a very high heterogeneity in terms of tree species composition, vegetation density, canopy openness and height (Flores et al., 2016; Flores & Holmgren, 2021a). This likely creates patchiness in food availability for aquatic organisms which is in turn reflected in a clustered presence of fish. In contrast, white-sand savanna sites are more similar in canopy height and tree species composition (Flores & Holmgren, 2021a). Lastly, fire scar sites are structurally very homogeneous, with few isolated trees scattered in largely open areas, covered by herbaceous plants and with abundant dead wood from trees that died in the fire. High heterogeneity across forest sites may explain the lack of statistical differences in overall mean values. Such an effect could be accentuated by the fact that gillnets are likely less effective in forested habitats, because the high density of submerged woody vegetation can lead to incomplete unfolding of the nets (Knight & Bain, 1996). Our sampling method could thus underestimate the actual diversity and abundance of fish in unburnt flooded forests. In addition, some of the burnt sites were relatively small and located within a large well-preserved forest matrix. Consequently, differences in fish species composition and abundance across habitats may be relatively small in these cases.

4.1 | Conservation and management implications

Because productivity is exceptionally low in the Rio Negro basin, floodplain forests may need several centuries to recover a close canopy and the late-successional species after fire disturbances (Flores & Holmgren, 2021a; Junk et al., 2015). Our study shows that forest lost by fire could have pervasive negative effects on local fish communities. These negative effects include changes in fish species composition, abundance of trophic groups and lower fish population densities in fire scars. Changes in fish functional groups may have

large implications for the conservation of the forest itself as omnivorous and frugivorous fish are key seed dispersers for many tree species. These persistent changes in biological communities after floodplain forests burn may compromise the capacity of these forests to recover after perturbations. Indeed seed dispersal limitation has proved to be a major barrier for the regrowth of blackwater forests after fire (Flores & Holmgren, 2021b). Future studies should assess the relative contribution of different fish functional groups and species in seed dispersal and their sensitivity to different types of perturbations to better understand the tight interactions between species across terrestrial-aquatic environments and plant-animal groups.

Persistent loss of floodplain forests can ultimately impact human welfare in the region. Fish are a fundamental source of food (Barthem & Goulding, 2007), income through ornamental fish (Ladislau et al., 2019; Zehev et al., 2015) and sport fishing (Holley et al., 2008; Sobreiro, 2015). Conservation efforts should focus on prevention of forest fires. One effective tool could be the development of educational campaigns for local communities that explain the risk and consequences of using fires during drought events as well as providing alternatives to burning for agriculture purposes. Preventing forest fires will become increasingly important as climate change progresses and the conditions for forests to easily burn become more frequent.

AUTHOR CONTRIBUTIONS

Milena Holmgren, Jansen Zuanon and Peter van der Sleen conceived the ideas and designed methodology; Arnold Lugo collected the data; Arnold Lugo and Peter van der Sleen analysed the data; Arnold Lugo and Milena Holmgren led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.vdncjsz0h> (Lugo-Carvajal et al., 2023).

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