Biological Conservation 315 (2026) 111692

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Water and fire: Wildfires threaten fish habitats across Brazilian biomes, and protected areas offer insufficient safeguards

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ARTICLE INFO

Keywords:
Annual killifishes
Fire ecology
Freshwater fish
Intermittent ponds
Protected areas
Rivulidae
Temporary wetlands

ABSTRACT

Temporary wetlands are aquatic ecosystems shaped by alternating wet and dry periods, but the influence of wildfires on their water regimes and biodiversity dynamics remains insufficiently investigated. This study compares fire frequency in temporary wetlands inhabited by annual fishes (Rivulidae) across biomes differing in fire propensity and protection, using a comprehensive spatiotemporal framework across 1161 sites over four decades (1985–2024), and drawing on occurrence records of 187 species, 102 of which are threatened with extinction in Brazil. Results show that wildfires were subject to 57 % of annual fish species and burned 28 % of the temporary wetlands in which they occur. Fire-dependent biomes (Cerrado, Pantanal; with the exception of the Pampa) experienced significantly higher fire frequency than fire-independent (Caatinga) and fire-sensitive (Amazon, Atlantic Forest) biomes. Fire frequency peaked between 2020 and 2024, with regions such as the Amazon exhibiting increasing vulnerability. The majority of burned wetlands in the Caatinga, Atlantic Forest, and Pampa were associated with small fire scars (<50 ha), while large-scale fire events were predominantly concentrated in the Cerrado and Pantanal. Protected areas did not consistently mitigate fire frequency; in some biomes, reserves recorded higher fire frequencies than unprotected areas. Fire can affect annual fish both directly, through egg mortality caused by burning, and indirectly, by altering or destroying the temporary wetland habitats on which they depend. Our findings reveal significant gaps in existing conservation frameworks and underscore the urgent need to integrate proactive fire-management strategies into protected-area governance and broader aquatic-biodiversity planning under intensifying global fire regimes.

1. Introduction

Wildfires are intrinsic components of terrestrial natural systems, shaping ecosystem patterns and processes, carbon cycling, and climate regulation (Bowman et al., 2009). However, natural fire regimes have been profoundly disrupted by human activities—deforestation, agricultural expansion, and poor fire management have driven unprecedented patterns of fire intensity, frequency, and extent over recent decades (e.g., Pivello et al., 2021; Feron et al., 2024). Globally, approximately 774 × 10^6 ha are burned annually (or 5.9 % of ice-free land; Chen et al., 2023), releasing an estimated 2.4 Pg C (≈ 8.8 $GtCO_2$) into the atmosphere between 2023 and 2024 alone (Jones et al., 2024). These emissions fuel a self-reinforcing feedback loop between fire and climate: fires reduce biological carbon sinks by burning vegetation, emit greenhouse gases that accelerate global warming, and in turn intensify droughts and heatwaves, ultimately increasing lightning activity and the likelihood and severity of future fires (Burton et al., 2024; Verjans et al., 2025). Recurrent fires drive biodiversity loss and habitat degradation (e.g., Pivello et al., 2021; Malecha et al., 2025), while the release of fine particulate matter ($PM_{2.5}$) exacerbates respiratory and cardiovascular diseases, with associated health costs estimated at US$160 billion in the United States alone between 2006 and 2020 (Law et al., 2025). Understanding the drivers and consequences of fire is therefore critical, as it has become one of the most pervasive and impactful threats to global socio-environmental systems.

Fire occurs across nearly all biomes, from Arctic boreal forests to tropical savannas and Mediterranean regions (e.g., Hardesty et al., 2005; Bowman et al., 2009; Martín et al., 2023; Feron et al., 2024; Jones et al., 2024b). In Brazil, fire plays contrasting ecological roles depending on the biome, which are classified by their fire propensity based on dominant vegetation types (Hardesty et al., 2005; Pivello et al., 2021; Viegas et al., 2022). Fire-dependent biomes—such as the Cerrado (savannas), Pantanal (wetlands), and Pampa (grasslands)—exhibit various fire-adaptive traits and may benefit from post-fire conditions (Pivello

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https://doi.org/10.1016/j.biocon.2025.111692
Received 27 August 2025; Received in revised form 22 November 2025; Accepted 29 December 2025

et al., 2021). In these biomes, fire sustains key ecological processes, promotes species coexistence, and supports nutrient cycling and vegetation renewal (Miranda et al., 2002; Durigan, 2020). Its exclusion can lead to woody encroachment, the loss of open-habitat species, and structural changes in ecosystems (Durigan and Ratter, 2016; Costa et al., 2020). In contrast, fire-sensitive biomes like the Amazon and Atlantic Forest, dominated by moist tropical forests, experience severe biodiversity losses when burned (Pivello et al., 2021; Feron et al., 2024). The Caatinga, a seasonally dry tropical forest in northeastern Brazil, is considered fire-independent; under natural conditions, its sparse vegetation fails to form a continuous fuel bed, limiting the spread of surface fires (Hardesty et al., 2005; Pivello et al., 2021; Viegas et al., 2022). Even within biomes, landscape heterogeneity creates a mosaic of fire-dependent, fire-sensitive, and fire-independent zones (Pivello et al., 2021). However, widespread land-use change and the replacement of natural ignition sources with anthropogenic ones have decoupled fire occurrence from its natural regimes, leading to severe ecological impacts across all Brazilian biomes (Libonati et al., 2021; Marques et al., 2021; Oliveira et al., 2022a; Rocha et al., 2024; Braga and Laurini, 2024; Malecha et al., 2025). The scale of wildfires in Brazil is extraordinary: approximately 24 % of the country ($\approx$ 2.06 million km^2) burned at least once between 1985 and 2024 (RAF, 2025), which exceeds the combined land area of France (0.54), Germany (0.36), the United Kingdom (0.24), Italy (0.30), and Spain (0.51) (total $\approx$ 1.95 million km^2; United Nations Statistics Division, 2025). As a consequence, Brazilian recurrent fires are causing severe biodiversity declines, public health problems, and economic impacts, and we still know very little about how to properly measure these effects (Sobreira et al., 2025).

Protected areas (PAs) are cornerstones of biodiversity conservation, however, there remains considerable uncertainty and debate regarding their effectiveness in safeguarding biodiversity from fire (Nelson and Chomitz, 2011; Lucas et al., 2023). More broadly, Brazilian PAs are embedded in a heterogeneous legal framework that regulates deforestation, fire use and environmental enforcement (e.g., Law No. 9.985/2000; Law No. 12.651/2012). Since the 1970s, the country has been gradually shifting from a policy of complete fire exclusion toward an adaptive fire management approach (Pivello et al., 2021), a process that culminated in the recent National Integrated Fire Management Policy (Law No. 14.944/2024), which formally recognizes both the ecological role of fire and the legitimacy of traditional fire-management practices (Pereira et al., 2025). Yet, integrated fire management is still implemented in a relatively small subset of protected areas, especially in fire-dependent biomes such as the Cerrado, while large portions of the landscape — particularly on private lands outside PAs — remain subject to weak enforcement and poorly coordinated fire management (Oliveira et al., 2022a). In practice, the intensity of monitoring, the application of sanctions and compliance with regulations vary widely among agencies, protection categories (sustainable use vs. strict protection), states and biomes, leading to contrasting outcomes in terms of fire occurrence and severity (Nepstad et al., 2006; Nelson and Chomitz, 2011; Oliveira et al., 2021; Neto and Evangelista, 2022; Pessôa et al., 2023). Despite advances in fire policy, management, and understanding the drivers of fire across Brazilian biomes, critical gaps remain, particularly for aquatic ecosystems, where the relationship between water and fire is still commonly (and mistakenly) perceived as strictly antagonistic — that is, where there is water, there is no fire.

Ephemeral aquatic ecosystems—also referred to as temporary wetlands or temporary ponds—are generally small, shallow aquatic features that dry out either seasonally or unpredictably, and support specialized flora and fauna adapted to alternating wet and dry phases (Junk et al., 2014; Calhoun et al., 2017; Biggs et al., 2017). In Brazil, such habitats occur across all biomes and host a remarkable group of fishes adapted to life without water: the annual fishes (Cyprinodontiformes: Rivulidae). During the dry season, temporary pools desiccate and become essentially terrestrial environments, leading to the death of all adult fish (Martin and Podrabsky, 2017; Guedes et al., 2020). However, prior to dying, these fish reproduce and deposit desiccation-resistant eggs in the substrate, which can remain viable through a complex process of embryonic diapause (Costa, 2013; Berois et al., 2015; Loureiro et al., 2018). Under these metabolic constraints, the eggs can survive for months—or even years—buried in the dry sediment (Furness, 2016; Lajus and Alekseev, 2019; Weber et al., 2025). With the onset of the next rainy season, the temporary wetlands refill, the eggs hatch, and a new generation of annual fish emerges—without generational overlap (Guedes et al., 2023a, 2023b). The evolution of an annual life cycle in vertebrates is highly unusual and aligns these fishes with survival strategies seen in desert-adapted plants (e.g., seeds) or invertebrates (e.g., eggs and cysts) inhabiting temperate zones with freezing winters (Furness, 2016).

Annual fishes belong to the family Rivulidae, but not all rivulids are annual life cycle (Guedes et al., 2025a). Rivulidae comprises at least 488 valid species in the Neotropical region (Fricke et al., 2025), of which 266 exhibit an annual life cycle (Guedes et al., 2025a). In Brazil, 200 annual species are known to occur, of which 115 are officially listed as Possibly Extinct (PEX), Critically Endangered (CR), Endangered (EN), or Vulnerable (VU); 66 are classified as Least Concern (LC) or Near Threatened (NT); 19 remain unassessed or Data Deficient (DD) (ICMBio, 2025). The threat to annual fishes is unparalleled: they comprise 115 threatened species—surpassing the combined total of at-risk Brazilian mammals (105 spp.), or reptiles (79 spp.), or amphibians (74 spp.) (ICMBio, 2025). Thus, annual fishes represent the most numerically vulnerable group of vertebrates to extinction in the world's most biodiverse country. Habitat loss is the primary threat to rivulids (Volcan and Lanés, 2018). Temporary wetlands are being systematically converted into croplands, drained and filled to make way for pastures, urban sprawl, and industrial developments (Calhoun et al., 2017; Castro and Polaz, 2020). In addition, microplastic (Guedes et al., 2025b) and chemical pollution linked to the widespread use of agrochemicals in Brazilian agriculture exerts negative effects even at concentrations below the legal safety thresholds (Gonçalves et al., 2024; Godoy et al., 2025).

Despite this critical scenario, several additional threats—such as invasive species, climate change, and wildfires—remain virtually unexplored and are still poorly understood by science. Overall, most of the literature on fire effects in aquatic systems and associated fauna is focused on streams, with limited data available on the impacts of fire on wetlands (Bixby et al., 2015; Erdozain et al., 2024; Moreira et al., 2025). Temporary wetlands and annual fishes may be particularly vulnerable to fire regimes due to the seasonal desiccation of their habitats, which removes the hydrological barrier to fire and leaves diapause eggs in the substrate highly exposed to incineration. In the absence of robust data on the susceptibility of these populations to multiple stressors, there is a real risk of underestimating key drivers of decline and failing to implement effective conservation measures. Filling these knowledge gaps is just as urgent as the physical protection of their habitats: only with comprehensive information on potential impacts will it be possible to reverse the alarming trajectory of extinction vulnerability.

Thus, this study aims to map fire frequency in ephemeral aquatic ecosystems that host annual fishes, comparing patterns across different Brazilian biomes and across areas with contrasting territorial protection policies. Two hypotheses were tested. H1 — Occurrence sites located within fire-dependent biomes (Cerrado, Pantanal, and Pampa) exhibit higher fire frequency than those located in fire-sensitive (Amazon and Atlantic Forest) or fire-independent biomes (Caatinga). This hypothesis is grounded in the premise that fire-dependent biomes are more prone to wildfires due to the combination of seasonally dry climates, grass–shrub vegetation, and natural ignition sources, whereas fire-sensitive and fire-independent biomes are less conducive to fire propagation (Pivello et al., 2021; Viegas et al., 2022). H2 — Occurrence sites located within protected areas experience significantly lower fire frequency compared to those in unprotected areas, although the degree of protection varies by biome. This hypothesis is based on studies showing that protected areas—particularly in fire-sensitive biomes such as the Amazon—can effectively inhibit fire occurrence (Nepstad et al., 2006; Nelson and Chomitz, 2011; Pessôa et al., 2023), whereas protected areas in fire-dependent biomes often perform poorly in fire mitigation (Oliveira et al., 2022a). These outcomes may reflect differences in legal restrictions on deforestation, fire use, and enforcement (Oliveira et al., 2021). By integrating novel data on long-term fire regimes, threatened species distributions, and protected area effectiveness, this study aims to inform decision-making and strengthen fire management and conservation strategies to safeguard ephemeral aquatic ecosystems and their uniquely adapted fauna in Brazil.

2. Materials and methods

2.1. Fish occurrences

Occurrence records of annual fishes from the family Rivulidae were compiled from the comprehensive distribution dataset provided by Guedes et al. (2025a,b), which includes all known species in the Neotropical region up to the year 2023. This occurrence records were obtained from multiple sources, including articles, books and public digital repositories that aggregate data from biological collections and museums, such as the Global Biodiversity Information Facility (GBIF, gbif.org), the Brazilian Biodiversity Information System (SIBBR, sibbr.gov.br), SpeciesLink (splink.org.br) and Biodiversity Extinction Risk Assessment System (SALVE, salve.icmbio.gov.br) (Guedes et al., 2025a, b). From this dataset, the data were processed following the steps outlined below: (1) selection of records and species occurring in Brazil; (2) exclusion of localities with low geographic precision (e.g., coordinates reported only in degrees and minutes); and (3) inclusion of newly published occurrence localities and species descriptions (e.g., Volcan et al., 2025; Nielsen et al., 2025) up to June 2025. The final dataset comprises 1161 occurrence records (Fig. 1), representing 187 annual species across 32 genera, of which 102 are classified as threatened with extinction in Brazil (ICMBio, 2025; Table A.1 – Appendix A). For each occurrence site, a circular buffer with a 180 m radius (approximate area = 101,787 m^2) was generated following Guedes et al. (2023b). This spatial unit, referred to as the "biotope", encompasses both the temporary wetland and its immediate buffer zone, thereby capturing the broader landscape-matrix context in which annual fishes occur.

2.2. Fire mapping

Burned area mapping in Brazil was obtained from the MapBiomas Fire Collection 4.0 project (https://brasil.mapbiomas.org). MapBiomas is a global, multi-institutional network—comprising universities, NGOs, and technology companies—that monitors transformations in land cover and land use across territories and their impacts. Fire uses annual and monthly mosaics of Landsat imagery (30 × 30 m resolution), covering the period from 1985 to 2024. The input data correspond to surface reflectance (SR) mosaics from the USGS Landsat Collection 2 – Tier 1, processed for each year in the time series. Fire scars are classified using a Deep Neural Network (DNN), trained with Red, Near-Infrared (NIR), and Shortwave Infrared (SWIR1 and SWIR2) (Alencar et al., 2025). For further technical details regarding training sample collection, model classification, post-classification procedures, and validation, see Alencar et al. (2022; 2025) and RAF (2025).

Species occurrence records were overlaid with data from MapBiomas Fire Collection 4.0 to extract four variables: (1) year of last fire

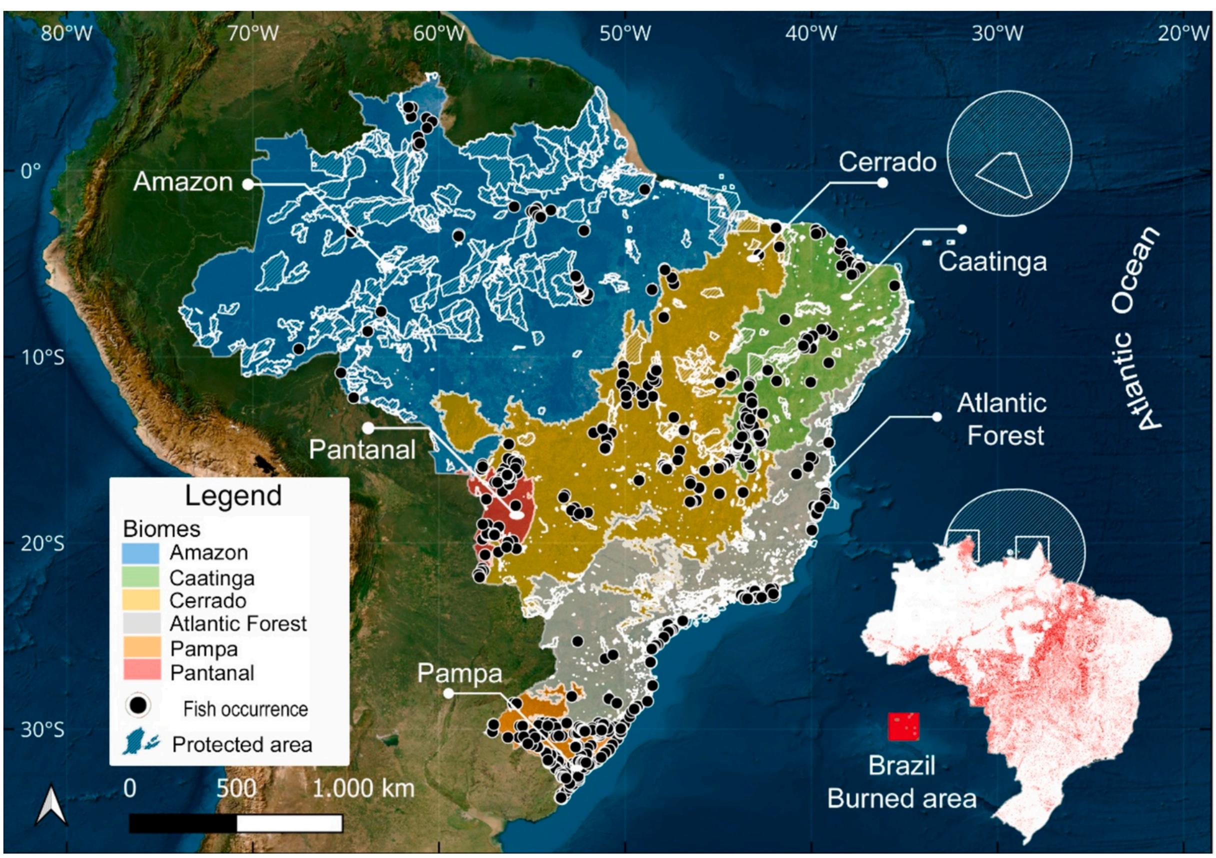

Fig. 1. Occurrences of annual fish species (black circles) across Brazilian biomes. The small map in the lower right corner shows burned areas (red), representing cumulative fire scars from 1985 to 2024 (MapBiomas Fire, Collection 4). Protected areas (white outlines) include conservation units under the National System of Conservation Units (SNUC) and indigenous lands. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

occurrence, (2) fire frequency and (3) annual burned area by scar size. Year of last fire occurrence indicates the last year each pixel was mapped as burned, between 1985 and 2024, and is useful for identifying areas recently affected by fire. The Fire frequency represents the number of times a given pixel was affected by fire during the period, ranging from 1 to 39 events, allowing for the assessment of fire recurrence across the landscape. The annual burned area by scar size classifies annual fire scars into ten size classes (1: <10 ha; 2: 10–50 ha; 3: 50–100 ha; 4: 100–500 ha; 5: 500–1000 ha; 6: 1000–5000 ha; 7: 5000–10,000 ha; 8: 10,000–50,000 ha; 9: 50,000–100,000 ha; 10: ≥100,000 ha), with each scar defined as a contiguous group of burned pixels within a given year; this metric helps characterize the magnitude of fire events (Alencar et al., 2022, 2025).

2.3. Protected areas and Brazilian biomes

Spatial data for biome boundaries were obtained from Instituto Brasileiro de Geografia e Estatística - IBGE (www.ibge.gov.br), and protected-area boundaries from the Sistema Nacional de Unidades de Conservação da Natureza (CNUC) of the Ministry of the Environment, including municipal, state, and federal units and encompassing both sustainable-use and strictly protected categories (https://cnuc.mma.gov.br/map).

2.4. Statistical analyses

To determine (H1) that biotopes located within fire-dependent biomes exhibit higher fire frequency than those located in fire-sensitive or fire-independent biomes; and (H2) that protected areas experience significantly lower fire frequency compared to unprotected areas—a Generalized Linear Mixed Models (GLMM) approach was employed. The response variable, fire frequency (the sum of all fire events from 1985 to 2024 across all pixels within the buffer), exhibited strong heterogeneity of variances, high positive skewness (skewness ≈ 9.5), and elevated kurtosis (kurtosis ≈ 128), consistent with long-tailed, sharply peaked distributions. Moreover, ≈ 66 % of the records were zeros, indicating pronounced zero-inflation—a common pattern in fire frequency datasets (Sá et al., 2018; Raveendran et al., 2024).

Given the data structure, we fitted zero-inflated negative binomial (GLMM - ZINB) models with a log link using the *glmmTMB* package (Brooks et al., 2017). Fixed effects comprised Biome, classified by fire propensity following Pivello et al. (2021) and Viegas et al. (2022) into fire-dependent (Cerrado, Pantanal, Pampa), fire-independent (Caatinga), and fire-sensitive (Amazon, Atlantic Forest); protection status (protected vs. unprotected); and their interaction (Biome × Protection status), each specified in both the conditional and zero-inflation components. Model significance for main effects and interactions was assessed using Type III Wald χ^2 ANOVA via the *car* package, with $\alpha = 0.05$. Post hoc estimated marginal means (EMMs) for main effects were obtained using the *emmeans* package, with pairwise comparisons conducted using Tukey's adjustment. Pairwise comparisons were performed for main effects only, as the interaction was not statistically significant. Model assumptions and adequacy were checked using the simulateResiduals function from the *DHARMa* package (Hartig, 2024). Diagnostic plots (QQ plots and residuals versus predicted values; Fig. A.1) were used to verify distributional assumptions, check for overdispersion, and identify potential outliers. No significant violations were detected (Fig. A.1 - Appendix). All spatial analyses and overlays were conducted using QGIS version 3.34.11 (QGIS Development Team, 2025), and all statistical analyses were performed in R version 4.3.1 (R Core Team, 2024). Data and scripts used in the analyses are available in Appendix B.

3. Results

3.1. Burned area and year of last fire occurrence

Of the 187 annual fish species analyzed, 108 (57 %; Table A.1 – Appendix B) had at least one biotope reached by fire in Brazil between 1985 and 2024. Overall, 321 (28 %) of the 1.161 biotopes examined were burned during this period, comprising 111 (34.2 %) within protected areas and 1.050 (27.0 %) within unprotected areas (Table 1). Pantanal exhibited the most severe scenario: all 11 species analyzed (e.g., *Plesiolebias glaucopterus*, *Pterolebias phasianus*, *Trigonectes balzanii*, *Moema heterostigma, Austrolebias ephemerus*) had at least one occurrence locality affected by fire between 1985 and 2024, both inside and outside protected areas (Table 1). By contrast, the Pampa showed the lowest proportion of species and biotopes impacted by fire among the biomes examined (e.g., *Cynopoecilus fulgens*, *Matilebias periodicus*, *Garcialebias nachtigalli*) (Table 1; Table A.1 – Appendix A).

The overall trend indicates a marked increase in fire events in the biotopes, particularly after 2010, with a peak observed during the 2020–2024 period (Fig. 2a). The Pantanal stands out due to a pronounced rise in fire occurrences in recent years (2020–2024), whereas the Caatinga and Pampa show a temporal decline, with peaks in 2000–2004 and 1995–1999, respectively. Biotopes located in fire sensitive biomes, such as the Atlantic Forest (e.g., *Leptopanchax opalescens*, *Ophthalmolebias constanciae*, *Nematolebias whitnei)* and the Amazon (e.g., *Pituna xinguensis*, *Spectrolebias reticulatus*, *Plesiolebias altamira),* exhibit a gradual increase in fire occurrence over time (Fig. 2).

Most fish of the burned biotopes in the Caatinga (e.g., *Hypsolebias adornatus*, *Cynolebias rectiventer*, *Hypsolebias guanambi*), Atlantic Forest, and Pampa biomes were associated with small fire scars, predominantly within the <10 ha ($n = 258$) and 10–50 ha ($n = 164$) size classes, which together account for over 60 % of all recorded events. The Amazon exhibited an intermediate pattern, with most records concentrated in the smaller classes, but also with occurrences in larger size categories, including fire scars exceeding 10,000 ha. In contrast, species from biotopes affected by large-scale fire events were primarily concentrated in the Cerrado (e.g., *Maratecoara Formosa*, *Simpsonichthys boitonei*, *Cynolebias griseus*) and Pantanal biomes (Fig. 2b), the only ones with consistent records in the highest size classes, including scars ≥50,000 ha.

3.2. Fire frequency

Fire frequency in annual-fish biotopes differed significantly among

Table 1
Number of annual fish species and temporary wetland localities analyzed by biome and protection status in Brazil. FI % = percentage of species or localities reached by fire at least once between 1985 and 2024. Fire freq ± SD = mean total Fire Frequency ± standard deviation. Fire categories: FS = fire-sensitive; FI = fire-independent; FD = fire-dependent.

Biome	Protection status	Species (FI %)	Localities (FI %)	Fire freq ± SD
Amazon (FS)	Protected	4 (100)	14 (42.8)	256 ± 546
	Unprotected	14 (71)	59 (57.6)	33 ± 71
Atlantic Forest (FS)	Protected	14 (50)	44 (36.3)	16 ± 83
	Unprotected	40 (35)	129 (18.6)	11 ± 43.6
Caatinga (FI)	Protected	3 (33)	7 (14)	1.7 ± 4.5
	Unprotected	50 (66)	207 (32.3)	17 ± 43.3
Cerrado (FD)	Protected	7 (43)	12 (50)	192 ± 319
	Unprotected	50 (66)	125 (70)	157 ± 345
Pampa (FD)	Protected	10 (20)	28 (10.7)	1.1 ± 5.2
	Unprotected	35 (17.1)	440 (2)	0.3 ± 4
Pantanal (FD)	Protected	5 (100)	6 (100)	716 ± 287
	Unprotected	11 (100)	90 (68)	78 ± 111
Total	Protected	41 (51 %)	111 (34.2 %)	98.9 ± 287
	Unprotected	182 (56 %)	1050 (27 %)	32.3 ± 136.3

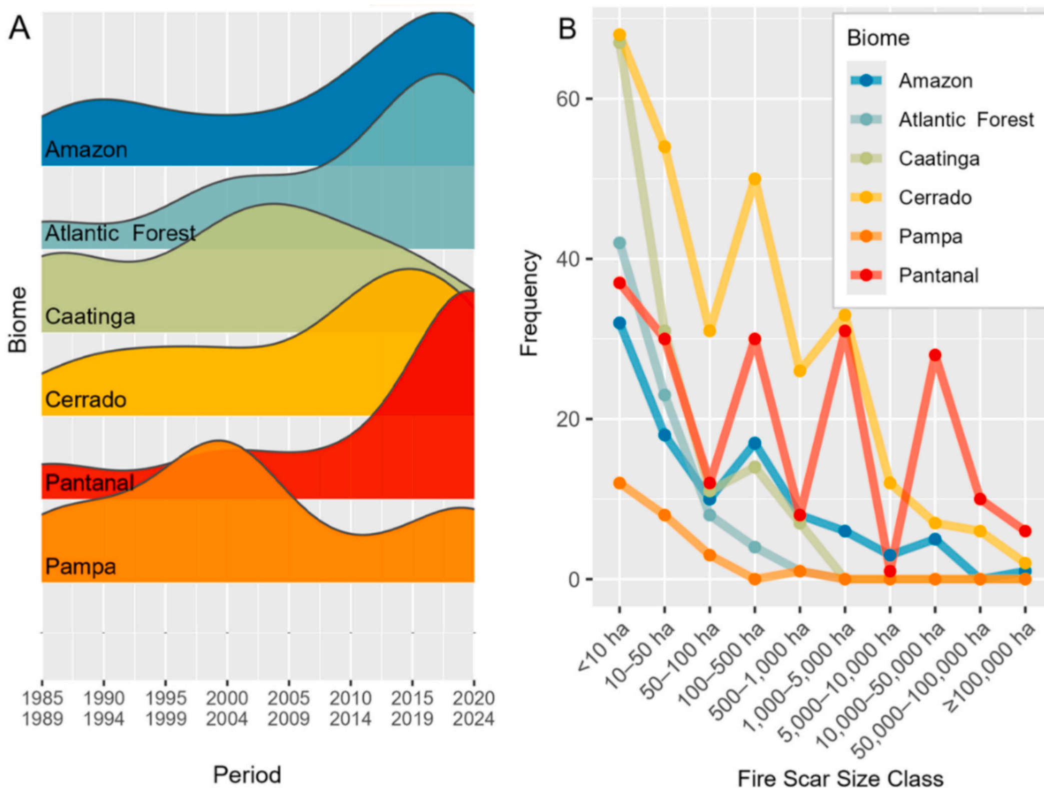

Fig. 2. Temporal and spatial patterns of fire occurrence in the biotopes of annual fish species across Brazilian biomes from 1985 to 2024. On the left (A), the curves represent the Year of Last Fire Occurrence records, grouped into five-year intervals, with peaks indicating periods with more records and valleys indicating periods with fewer fire records. The curves are based on a smoothed kernel density (KDE) along the x-axis (time periods), calculated separately for each biome. On the right (B), the line chart shows the distribution of fire scar counts across ten size classes (Annual burned area by scar size).

biomes ($\chi^2 = 8.17$, $p = 0.016$) and between protection status ($\chi^2 = 6.04$, $p = 0.013$); whereas the Biome × Protection status interaction was not significant ($\chi^2 = 3.78$, $p = 0.150$). In line with H1, fire-dependent biomes (Cerrado, Pantanal, Pampa) exhibited substantially higher fire frequency than fire-independent biomes (Caatinga; estimate = 2.53, $p = 0.002$) and fire-sensitive biomes (Amazon, Atlantic Forest; estimate = 0.95, $p = 0.001$). Within the fire-dependent category, Cerrado and Pantanal showed the highest fire frequency, whereas Pampa registered the lowest (Fig. 3). Although protection status exerted a significant overall effect—indicating a tendency toward higher fire frequency in protected areas (Table 1; Fig. 3)—Tukey-adjusted pairwise comparisons revealed no significant difference between protected and unprotected sites (estimate = 0.18, $p = 0.71$; Table 2), thereby failing to support H2.

4. Discussion

This study reveals three main findings. First, fire poses a pervasive threat to the habitats and populations of annual fish species across Brazil, reaching 57 % of the 187 species evaluated, including 55 of the 102 threatened species, and consuming over one-third (28 %) of the temporary wetlands they inhabit. Second, temporary wetlands situated within fire-dependent biomes (with the exception of the Pampa) experienced significantly higher fire frequencies than those located in fire-independent or fire-sensitive biomes, partially supporting H1. Third,

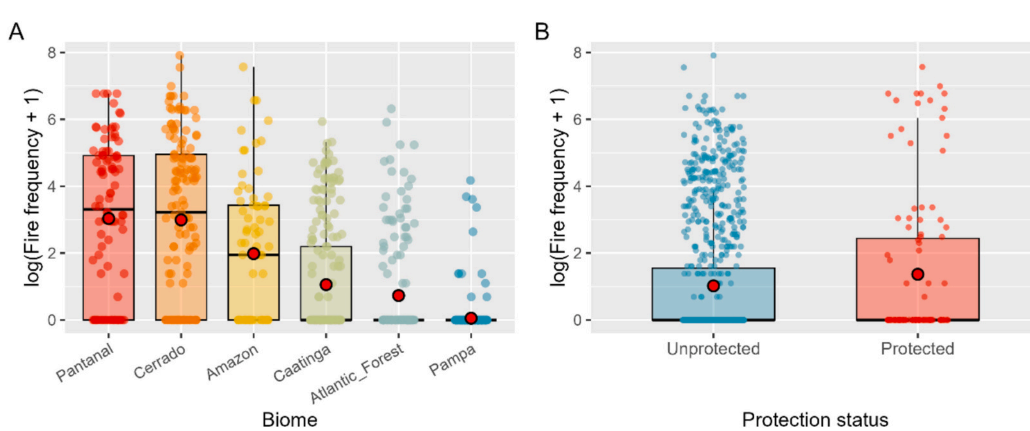

Fig. 3. Boxplots of fire frequency (log +1) in annual fish biotopes, shown for (A) biomes (Pantanal, Cerrado, Amazon, Caatinga, Atlantic Forest, Pampa) and (B) protection status (Unprotected, Protected). Individual sites are plotted as semi-transparent points, and red circles mark group means. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Pairwise contrasts of marginal means (estimated marginal means, emmeans) from the zero-inflated negative binomial generalized linear mixed model (GLMM) fitted to fire frequency in annual fish biotopes. "Contrast" indicates the pairwise comparison between factor levels.
Estimate: difference in log-transformed fire frequency between groups; SE: standard error; CI: lower and upper bounds of the 95 % confidence interval; z-ratio: test statistic for the contrast; *p*-value: significance of the difference (Tukey-adjusted for multiple comparisons).

Contrast	Estimate	SE	CI	z-ratio	p
Biome category					
Fire dependent vs. Fire independent	2.538	0.749	0.78–4.29	3.387	0.002
Fire dependent vs. Fire sensitive	0.959	0.272	0.32–1.59	3.532	0.001
Fire independent vs. Fire sensitive	−1.579	0.745	−3.32–0.16	−2.118	0.086
Protection status					
Protected vs. Unprotected	0.188	0.514	−0.82–1.20	0.366	0.714

territorial protection policies, particularly the establishment of protected areas, have proven insufficient to curb the spread of wildfires, exhibiting, in some biomes, lower efficacy than unprotected regions, which contradicts H2, originally posited in the opposite direction. These novel results, derived from detailed spatial mapping combined with nearly four decades of fire-frequency data (1985–2024), constitute the first comprehensive assessment of wildfire risk for endangered annual fishes in Brazil's temporary wetlands.

4.1. Spatiotemporal patterns of fire across biomes

Biotopes of annual fishes situated within fire-dependent biomes (Cerrado and Pantanal) experienced significantly higher fire frequencies than those in fire-independent (Caatinga) or fire-sensitive (Amazon and Atlantic Forest) biomes. This result partially supports our first hypothesis (H1), although the Pampa—also classified as fire-dependent—exhibited comparatively lower burn frequencies, deviating from the expected pattern.

In savanna biomes such as the Cerrado, fires are frequent due to the combination of grass- and shrub-dominated vegetation, a highly seasonal climate, and an extended dry season (Oliveira et al., 2022a). This seasonality, together with the abundant herbaceous biomass accumulated during the rainy season, creates a highly flammable fuel load that is primarily ignited by anthropogenic activities in the dry season (Arruda et al., 2024). Similarly, the Pantanal—the world's largest freshwater wetland—also experiences high fire frequency: during the dry season, vast expanses of grasslands and reeds desiccate, conferring the biome with elevated intrinsic flammability (Pivello, 2011; Marques et al., 2021; Garcia et al., 2021; Pivello et al., 2021; Neto and Evangelista, 2022). Grasslands and savannas exhibit fire spread rates and intensities higher than those observed in forests (Gomes et al., 2020), which corroborates our findings that temporary wetlands embedded within large fire events (i.e., the largest fire-scar size classes) were particularly prevalent in the Pantanal and Cerrado. Moreover, both biomes have shown an increasing trend in fire frequency over the past decades (Pivello et al., 2021), a pattern that is also reflected in our results.

In contrast, the Pampa—despite its grassland character and classification as "fire-dependent"—exhibited lower burn rates and a temporal decline in the number of burned biotopes. This is likely due to milder, more humid seasonal conditions compared to other Brazilian grassland biomes: rainfall is more evenly distributed year-round, and lower winter temperatures reduce extreme vegetation desiccation (Araújo et al., 2012). Moreover, unlike in the Amazon, Cerrado, and Pantanal, agricultural and livestock practices in the Pampa rarely employ fire for pasture renewal or deforestation (Pivello, 2011), thereby limiting the spread of anthropogenic fires into the temporary wetlands inhabited by rivulid fishes.

The intermediate fire patterns observed in tropical rainforests (Amazon and Atlantic Forest) are driven primarily by anthropogenic ignitions, since high humidity and a dense canopy inhibit natural fires (Gomes et al., 2020) and, when they do occur, inflict severe damage due to these forests' lack of fire adaptations (Pivello et al., 2021). Forests have increasingly become affected by fire. In 2024, for the first time, the Forest Formation class was the most impacted land-cover type by fire in Brazil, with a record nearly 7.7 million hectares burned—287 % above the historical average (RAF, 2025). Although this study focused on temporary wetlands inhabited by annual fishes—representing only 0.003 % of Brazil's land area—its findings align with broad geographical analyses that report high burn rates in the Pantanal and Cerrado; intermediate levels in the Amazon, Atlantic Forest, and Caatinga; and low rates in the Pampa (Oliveira et al., 2022a). Thus, fires in temporary wetlands mirror Brazil's broad-scale spatial fire gradient and underscore each biome's distinct vulnerabilities, confirming that fire propensity directly reflects regional vegetation types and climatic regimes, now exacerbated by human activities.

4.2. Protected areas offer insufficient safeguards

Contrary to the second hypothesis (H2), which proposed that occurrence sites within protected areas would experience significantly lower fire frequency than those in unprotected areas, our results showed no reduction in fire frequency inside protected areas compared to unprotected sites. This finding challenges the conventional assumption that legal designation alone would suffice to safeguard annual fish biotopes from fire in Brazil and aligns with a growing body of literature indicating that legal protection in isolation often proves insufficient to mitigate wildfires (e.g., Oliveira et al., 2022a; Carvalho et al., 2023; Moreira et al., 2024). Indeed, it has been documented that only through concrete measures—such as the deployment of indigenous fire-management brigades—was a reduction of up to ~80 % in fire frequency achieved in historically heavily burned areas (Oliveira et al., 2022b). Similarly, it was found that certain categories of protected areas permitting sustainable use failed to prevent fires without strengthened enforcement and appropriate management (Carvalho et al., 2023). In other words, the effectiveness of protected areas in containing fire is heavily dependent on the implementation of management policies and control of ignition sources, rather than on legal status alone.

Several factors have been identified to explain the high incidence of fires in protected areas. A majority of fire events in Brazilian PAs has been concentrated in sustainable-use reserves, where human presence and agricultural burning occur in surrounding lands (RAF, 2025). Anthropogenic fires originating in adjacent areas, which then escape unchecked into the reserves, have been recognized as one of the principal drivers of interior fires (Almeida-Rocha and Peres, 2021; Moreira et al., 2024). In response to this alarming scenario, the National Policy on Integrated Fire Management (Law No. 14944/2024) was enacted in 2024. This new policy proposes a paradigm shift in fire governance: instead of relying solely on fire prohibition and repression, an integrated strategy is adopted that incorporates fire ecology, traditional knowledge, and the controlled use of prescribed burns to prevent large wildfires. By reinforcing interagency coordination, holding parties accountable for improper fire use, and supporting community brigades, it is anticipated that integrated management will reduce uncontrolled fires both inside and adjacent to protected areas—thereby contributing to the protection of biodiversity in the face of wildfires.

4.3. Potential direct and indirect impacts of fire on annual fishes

While the flora of many Brazilian biomes displays fire-adaptive traits, the associated aquatic fauna appears to lack comparable resilience. Annual fishes, for example, may be particularly vulnerable to fire regimes for three main reasons. First, during the dry season—the period when fires are most prevalent in Brazil (Pivello et al., 2021)—the complete loss of surface water removes any hydrological barrier to fire (Mason et al., 2023), leaving diapausing eggs buried in the substrate highly susceptible to incineration. Second, the margins and beds of temporary wetlands are typically dominated by dense herbaceous vegetation and accumulated organic matter which, once desiccated, supply abundant fine fuel (Marques et al., 2021). Third, the small size, spatial isolation, and high degree of fragmentation of temporary wetlands across the landscape (Guedes et al., 2025a) restrict potential escape routes for annual fishes. As a result, temporary wetlands and their annual fishes may be structurally more exposed to fire-related impacts than perennial fish species inhabiting rivers, lakes, or permanent marshes. Therefore, during the dry season, fire can directly cause mortality by incinerating eggs and reducing recruitment, thereby threatening the next generation of fish populations.

In the rainy season, substantial potential indirect effects of fire may manifest through multiple synergistic pathways, including (but no limited): increased water toxicity due to the adsorption of ammonium ions from ash inputs (Gomez et al., 2022; Edwards et al., 2024); environmental alkalosis—a chemical imbalance that stresses fish by raising water pH and disrupting blood pH and physiological processes (Kwan et al., 2024)—which may particularly affect annual species adapted to acidic waters (Guedes et al., 2023b); loss of vegetation cover and leaf litter that normally retain moisture, causing ephemeral pools to dry more rapidly and shortening the inundation period vital for fish (Shakesby and Doerr, 2006); direct alterations of trophic dynamics, linking fire-induced changes to biomass trajectories of periphyton, invertebrates and fish (Erdozain et al., 2024; Roon et al., 2025); and sublethal behavioral and physiological changes that render species more lethargic and less inclined to forage or form cohesive shoal (Gonino et al., 2019). Therefore, although some perennial fish species exhibit resilience to sporadic burns through active dispersal (e.g., Severo-Neto and Volcan, 2018; Erdozain et al., 2024), high-frequency or high-severity fires can exceed the tolerance thresholds of annual species—which inhabit isolated, shallow, small-scale environments with pronounced edge effects, where the synergistic impacts of fire may become unpredictable.

4.4. Implications, limitations and future directions

Until now, fire has been listed as a threat for only one annual fish species (*Simpsonichthys boitonei*) in Brazil's Red List of Threatened Fauna (ICMBio 2018). The results presented here demonstrate, for the first time, that this risk is far more widespread and general across one of the world's most imperiled vertebrate groups. In a highly agricultural country like Brazil—where the "trinity" of agricultural impacts includes land-use change and intensification (Volcan and Lanés, 2018), agrotoxical application (Gonçalves et al., 2024; Godoy et al., 2025), and now fire—it is essential to recognize fire not merely as an episodic event, but as an omnipresent, interacting disturbance.

Although this study provides valuable insights, there are inherent limitations warrant consideration. First, there is a pronounced Wallacean shortfall for annual fish species distributions, as for most taxa in the Neotropical region, with occurrence data remaining incomplete and spatially biased (Diniz Filho et al., 2023; Tonella et al., 2023; Guedes et al., 2025a,b). Most sampling efforts concentrate along roads (Costa et al., 2025), near research stations, and around urban centers that are more accessible and frequently surveyed, whereas remote wetlands, protected areas, and relatively pristine regions (notably in central Amazonia) receive much less attention (Guedes et al., 2025c). Consequently, this uneven geographic coverage may lead to under- or overestimation of fire exposure. Second, we did not distinguish between natural fires (e.g., lightning-ignited), anthropogenic fires (e.g., agricultural burns, deforestation), or controlled burns (preventive management), as these data are unavailable. Yet such differentiation is essential to guide targeted interventions: reinforcing firefighting brigades in areas prone to natural ignitions; enhancing enforcement and reviewing agricultural practices in zones dominated by anthropogenic burning; and delineating areas suitable for preventive burns while explicitly excluding temporary wetlands. Third, our database includes only 111 localities within protected areas, without differentiating between strict-protection and sustainable-use categories—classes that entail different degrees of fire-use restriction and land-management practices (Nelson and Chomitz, 2011; RAF, 2025). This limited sample size in protected areas not only highlights the territorial underprotection of annual fish habitats but also precludes incorporating this subdivision because of the assumptions inherent in statistical models.

This study represents a first step toward understanding how annual fishes and their habitats are exposed to fire regimes, and it opens several fundamental avenues for future research. Among these, experimental and field studies are needed to test the direct and indirect effects of fire on egg mortality in rivulid fishes (e.g., for other taxa Branson and Vermeire, 2007 and Shine et al., 2016). An important next step is to incorporate, in the analysis, the interval between the most recent fire event and fish occurrence records. This would help clarify how fire affects our ability to detect species in the field (Southwell et al., 2022). In addition, areas with high fire frequency often experience low-intensity burns, whereas areas with low fire frequency may be affected by high-intensity fires—a trade-off (Keeley, 2009). Because fire intensity and frequency largely determine ecological impacts, fire frequency alone may mask important differences in how wetlands and fishes respond to burning. This reinforces the need for a comprehensive fire-management program that brings together traditional, local, and scientific knowledge (Garcia et al., 2021) and explicitly incorporates temporary wetlands, even when dry, into its principles and practices, recognizing them as frequently overlooked habitats that harbor highly endemic and threatened species. Furthermore, future approaches that consider fire not only as an agent of impact but also as a historical force shaping the current biogeographical patterns of temporary wetlands and the distribution of annual fishes will be valuable. Finally, this work did not aim to exhaustively address every dimension of wildfires in temporary wetlands occupied by annual fishes, and future investigations can further elucidate and refine the patterns identified here.

CRediT authorship contribution statement

Gustavo Henrique Soares Guedes: Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Francisco Gerson Araújo:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision.

Funding

This study was funded by Fundo Brasileiro para a Biodiversidade – FUNBIO Conservando o Futuro, and Instituto HUMANIZE (Proc. # 028/2023), Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (E-26/200.897/2021, E-26/210.103/2023), and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq 140.512/2022–5).

Declaration of competing interest

The author declares no competing interests.

Acknowledgements

Special thanks to the developers and collaborators of MapBiomas,

whose continuous updates and improvements have made this work possible.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111692.

Data availability

Data and scripts used in the analyses are available in Appendix B.

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