Neotropical Ichthyology

Original article

https://doi.org/10.1590/1982-0224-2025-0043

Diving into temporary pools: a global perspective on freshwater fish research

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Freshwater temporary pools are ephemeral habitats with high structural and physicochemical variability. Many dry out during the dry season and host seasonal killifishes, among the most threatened freshwater fishes. These ecosystems support diverse fish communities and are highly vulnerable to climate change. This systematic review aimed to uncover global research trends and gaps concerning fish inhabiting freshwater temporary pools and to test the hypothesis that public policies influence scientific production. Covering the period from 1981 to 2024, it analyses 115 peer-reviewed articles. Geographically, research was concentrated in South America and Africa, particularly in Brazil. Reproduction and taxonomy were the most common study areas, with the focus primarily on Rivulidae and Nothobranchiidae. Notably, 62 species of Rivulidae and 12 of Nothobranchiidae were studied, while other 100 species from other families received limited attention. Knowledge gaps persist in areas such as ecotoxicology, physiology, trophic ecology, behavior and parasitology. Our findings suggest that public policies did not directly influence publication trends about fish in freshwater temporary pools and emphasize the need to integrate scientific knowledge with conservation planning. A broader focus on other fish clades and ecological aspects will be critical for protecting the biodiversity of these vulnerable ecosystems.

Keywords: Biodiversity, Conservation, Research trends, Systematic review, Temporary habitats.

Submitted March 12, 2025
Accepted July 14, 2025
Epub December 19, 2025

Associate Editor Franco Teixeira de Mello
Section Editor Fernando Pelicice
Editor-in-chief José Birindelli

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Online version ISSN 1982-0224
Print version ISSN 1679-6225

Neotrop. Ichthyol.
vol. 23, no. 3, Maringá 2025

Poças temporárias de água doce são habitats efêmeros com alta variabilidade estrutural e físico-química. Muitas delas secam durante a estação seca e abrigam *killifishes* sazonais, que estão entre os peixes de água doce mais ameaçados. Esses ecossistemas abrigam comunidades de peixes diversas e são altamente vulneráveis às mudanças climáticas. Esta revisão sistemática teve como objetivo revelar tendências e lacunas na pesquisa global sobre peixes que habitam poças temporárias de água doce e testar a hipótese de que as políticas públicas influenciam a produção científica. Abrangendo o período de 1981 a 2024, a revisão analisou 115 artigos revisados por pares. Geograficamente, as pesquisas se concentraram na América do Sul e na África, particularmente no Brasil. Reprodução e taxonomia foram as áreas de estudo mais comuns, com foco principalmente em Rivulidae e Nothobranchiidae. Notavelmente, 62 espécies de Rivulidae e 12 de Nothobranchiidae foram estudadas, enquanto outras 100 espécies de outras famílias receberam atenção limitada. Lacunas de conhecimento persistem em áreas como ecotoxicologia, fisiologia, ecologia trófica, comportamento e parasitologia. Nossos resultados sugerem que as políticas públicas não influenciaram diretamente as tendências de publicação sobre peixes em poças temporárias de água doce e enfatizam a necessidade de integrar o conhecimento científico ao planejamento da conservação. Um foco mais amplo em outros clados de peixes e aspectos ecológicos será crítico para proteger a biodiversidade desses ecossistemas vulneráveis.

Palavras-chave: Biodiversidade, Conservação, Habitats temporários, Revisão sistemática, Tendências de pesquisa.

INTRODUCTION

Freshwater temporary pools are unique ecosystems characterized by high levels of endemism, as they can act as aquatic islands (Coronel *et al*., 2007), functioning also as both important refuge and habitats of allopatric speciation for some animal taxa (King *et al*., 1996; Williams, 2007), resulting in an exclusive and specialized fauna (Williams, 1997; Williams *et al*., 2010; Boix *et al*., 2020). However, these temporary environments are extremely vulnerable to anthropogenic activities such as urban expansion, pollution and deforestation (Volcan, Lanés, 2018). Temporary pools are found worldwide associated to rivers and streams or isolated in the landscape and, despite their regional differences, they typically undergo a marked dry phase. They can be formed by rainfall, flooding of streams and rivers and by the seasonal heightening of phreatic waters (Williams, 2007). Their connectivity and species composition vary over time and space, with changes occurring both laterally and longitudinally (Couto *et al*., 2018), with fish frequently utilizing these temporary environments as part of their reproductive strategies (Espírito-Santo *et al*., 2013; Espírito-Santo, Zuanon, 2017). These pools not only support distinct fish assemblages but also influence the composition of nearby streams (Espírito-Santo *et al*., 2009), and, in some cases, the abundance of fish in temporary pools may exceed that of adjacent channels due to seasonal dynamics, as seen in upland streams of the Central Brazilian Amazon (Espírito-Santo, Zuanon, 2017).

Survival in such environments can be challenging especially due to the rapid changes in environmental physicochemical parameters (such as water temperature, dissolved oxygen concentration, and accumulation of decaying organic matter), and especially in function of their ephemeral nature. For fish, life in such extreme environments has led to the evolution of remarkable functional traits, such as exceptional physiological tolerance, effective dispersal ability (including overland displacements, *e.g.*, Gibb *et al.*, 2011) and life history modifications (Williams, 2007; Riesch *et al.*, 2015), concentrated in a few lineages that have specialized in inhabiting these habitats permanently (Polačik, Podrabsky, 2015). Only a small percentage of fish, less than 1%, have evolved an amphibious lifestyle, allowing them to survive on land during parts of their life (Gordon *et al.*, 1969; Turko *et al.*, 2021). To cope with the challenges of terrestrial environments, some species have developed mechanisms to manage factors such as dehydration across all life stages, including behaviors like seeking moist microhabitats or forming a mucus cocoon (Barton, 1985; Fishman *et al.*, 1986; Turko *et al.*, 2021), or even the aptness to perceive environmental cues to move into more favourable habitats (Espírito-Santo *et al.*, 2017). Additionally, many fish species found in temporary pools exhibit air-breathing strategies utilizing specialized organs, such as gas bladders, lungs, or parts of the gastrointestinal tract, to breathe air (Turko, Wright, 2015; Lederoun *et al.*, 2020; Turko *et al.*, 2021). In addition, amphibious species can use the skin as a respiratory surface (Graham, 1997) and some even have the ability to remodel gill structures to avoid branchial water loss (Turko *et al.*, 2011).

Several evolutionary drivers have shaped these air-breathing adaptations and amphibious lifestyle in such habitats, including severe aquatic hypoxia and other challenging abiotic conditions (Sayer, Davenport, 1991; Bayley *et al.*, 2019; Damsgaard *et al.*, 2020; Turko *et al.*, 2021). The intermittent nature of some aquatic habitats, where water may be absent for minutes, hours, days, or even months, has also played a crucial role (Turko *et al.*, 2021). These adaptations offer other significant evolutionary advantages, such as enhanced locomotion, the colonization of new environments (Courtenay, Miley, 1975; Taylor *et al.*, 2008), and even the ability to escape predators (Turko, Wright, 2015; Ord *et al.*, 2017; Espírito-Santo *et al.*, 2019), with these characteristics present in fish from distinct families (Ord, Cookie, 2016). This is particularly relevant from a metacommunity perspective, as dispersal ability in patchy and dynamic environments plays a key role in shaping biodiversity and structuring ecological communities (Vanormelingen *et al.*, 2008; Logue *et al.*, 2011; Padial *et al.*, 2014; Cunillera-Montcusí *et al.*, 2021).

Also, some fish species can opportunistically inhabit temporary pools (Florencio, Lamelas-López, 2016), but few studies investigate their community composition and the mechanisms that enable their survival in such extreme environments. On the other hand, killifishes, found in both the Neotropical region and Africa, have garnered significant scientific interest due to their unique reproductive and developmental traits, such as ontogenetic diapause stages, which have been a research focus since the 1970s (*e.g.*, Polačik, Podrabsky, 2015). More recently, Nothobranchiidae species have attracted researchers aiming to better understand aging mechanisms due to their limited lifespan (Polačik *et al.*, 2011; Bartáková *et al.*, 2013). These seasonal (usually annual) killifishes, in particular, are also fascinating models for studying ecology and evolution (Polačik, Reichard, 2011; Dorn *et al.*, 2011; Polačik *et al.*, 2014).

Species that inhabit freshwater temporary pools are extremely threatened (Castro, Polaz, 2020; Becker *et al*., 2024) and have been receiving increasing attention (Furlan *et al*., 2023). These environments are under growing pressure from habitat loss, particularly due to urban expansion, which heightens extinction risks for many associated species (Volcan, Lanés, 2018). In a world facing intensifying climate change, extreme weather events, such as prolonged droughts and heatwaves, are becoming more frequent and severe (Behera, 2024), with direct consequences including mass fish mortality in aquatic habitats (Braz-Mota, Val, 2024). Temporary pools, due to their small size, isolation, and reliance on seasonal rainfall, are especially vulnerable to these changes. Understanding the current state of knowledge on these systems is therefore critical, not only to anticipate how they may respond to ongoing environmental change, but also to guide effective conservation planning. In this context, synthesizing available scientific data can inform and support the development of public policies aimed at protecting these fragile ecosystems and the highly specialized species they host.

However, most studies are dispersed in the literature, and it is essential to identify and quantify the existing knowledge, research trends and information gaps regarding these environments and their ichthyofauna. Therefore, through a systematic review, we sought to evaluate the global research effort on the freshwater fish fauna of temporary pools. We specifically examined the number of articles published annually, the countries where those studies were conducted, the most covered research areas and the main fish clades studied. This comprehensive review aimed to identify patterns in research efforts, highlight the primary areas of focus, and pinpoint significant gaps in the current knowledge of temporary pools fish assemblages. Since research efforts in certain taxa can be dictated by factors such as resource allocation and public awareness (Clark, May, 2002; Ducatez, Lefebvre, 2014; Guedes *et al*., 2023), we also decided to test the hypothesis that public policies can positively influence scientific production on fish that inhabit these habitats. We hope this work will guide new research efforts to fill the evidenced gaps and, consequently, help protect fish in temporary pools worldwide. Additionally, our findings may assist policymakers and conservationists in developing more targeted and effective strategies for the preservation of these unique ecosystems and the diverse species that inhabit them.

MATERIAL AND METHODS

In August 2024, a literature review was carried out using the Scopus database, searching for articles published up to 2023, and in May 2025 a search for articles from 2024 was conducted and these were also obtained. The Scopus database was chosen because it has a higher journal coverage than others, such as Web of Science (Mongeon, Paul-Hus, 2016). For this, article titles, abstracts and keywords were searched applying the following Boolean combinations: fish* AND temporary habitat* OR temporary pool* OR transient pool* OR seasonal pool* OR ephemeral pool* OR intermittent pool* OR temporary pond* OR transient pond* OR seasonal pond* OR ephemeral pond* OR intermittent pond*. A total of 383 articles were obtained, ranging from 1981 to 2024. For filtering, seeking to identify which articles were suitable for inclusion, PRISMA guidelines were followed (Moher *et al*., 2009). Firstly, only peer-reviewed articles

written in English or with at least a title and abstract in English were considered. English was chosen as it returned the highest number of papers using the applied Boolean combinations. The same articles search was also carried out in Spanish, Portuguese, French and Italian, and not a single article was found with these combinations (see Tab. **S1** for the terms searched in each idiom).

Articles that addressed larger floodplains, major wetlands, intermittent streams, lakes or tide pools were discarded, and only those articles that actually addressed freshwater temporary pools were analysed. For this, we used the concept of freshwater temporary pools following the description of Costa (2002) and Castro, Polaz (2020), defined as shallow water bodies formed by the accumulation of rainwater or flooding caused by water courses, with the pools at least temporarily cut apart from these water courses. Many articles do not present data regarding pool size; however, the information gathered from articles included in this review show that pools depth ranged 0.05–2 m (average = 0.59 m, standard deviation = 0.47 m, number of observations = 38), from 0.2 to 336 m in length (average = 7.17 m, standard deviation = 9.93 m, number of observations = 10), 0.3–150 m in width (average = 38.28 m, standard deviation = 5.05 m, number of observations = 10), and 8–32,000 m^2 in surface area (average = 3,331 m^2, standard deviation = 8,163.04 m^2, number of observations = 25).

Based on these criteria, 268 articles were excluded from the analysis. Of these, 148 did not focus on fish, with the majority addressing amphibians (38) or crustaceans (25). Additionally, 98 papers were excluded because they did not fit the concept of temporary pools, most of them focusing on major wetlands (14), floodplains (7), or streams (9). A smaller number of articles were excluded for being reviews, opinion notes, technical notes, or editorials. To ensure transparency, an Excel file detailing each excluded article and the reason for its exclusion has been made available as supplementary material on Zenodo (https://zenodo.org/records/15460113). Thus, after the exclusion procedures, a total of 115 articles were reviewed.

Information obtained from each article included the publication year, country where the research was carried out, main study area, environment type, and fish clade (Tab. 1). We also obtained all species cited by paper, which had their updated nomenclatures consulted in the Eschmeyer's Catalog of Fishes (Fricke *et al*., 2025). An exponential regression was employed to investigate the temporal trend in the number of articles published per year. The number of studies per environment type and country were compared, as well as the number of articles published by study area and fish clade. For both categories, temporal trends were also explored. Spearman correlations were used to assess the relationship between the number of unique authors per year (*e.g.*, the same author with more than one paper per year was considered only once), the average number of authors per paper per year, and the total number of papers published annually.

To provide a more balanced interpretation of geographic patterns in scientific output, we normalized the number of publications per country using national indicators of research capacity and demographic scale. Data on population size, land area (km^2), and researchers per million people were obtained from the online database OurWorldInData.org (Ritchie, Roser, 2018), as these factors have been shown to influence country-level scientific production in studies on temporary lentic waterbodies (Olmo *et al*., 2024). To ensure comparability, scaling factors were applied by dividing population and land area by one million. This approach helps identify countries with disproportionately high scientific output relative to their size or research infrastructure.

TABLE 1 | Extracted information from each article regarding fish in temporary pools and their respective classification.

Extracted information	Classification
Year	All years ranging from 1981 to 2024.
Country	Each country where the study was carried out.
Environment	Classified into two categories: natural or artificial temporary pools (formed in artificial environments such as roadside ditches).
Study area	Classified into 11 categories: reproduction, taxonomy, community ecology, genetics, trophic ecology, behavior, physiology, new occurrences, species interactions, ecotoxicology and parasitology.
Fish clade	Fish clade of the study, with the taxonomic level of family being standardized. When the study addressed the entire community, and not specific species, the category "Community" was adopted.

To test the hypothesis that public policies can influence scientific production about fish in temporary pools, we focused on the Rivulidae, once it is the group with the largest number of published articles. Given that the conservation policies considered are specific to Brazil, we restricted this analysis to articles authored in Brazil. For this, we employed segmented regression models with the *segmented* R package (Muggeo, 2008). Initially, two hypothesized breakpoints were tested: 2012 (after the beginning of the Extinction Risk Assessment of Brazilian Fauna Species) and 2013 (which marks the first National Action Plan for the Conservation of Endangered Rivulid Fish in Brazil). For each hypothesis, a linear model was fitted to the data, with the year as the independent variable and the number of publications as the dependent variable. After the hypothesis-driven analyses, we performed an exploratory segmented regression without specifying a breakpoint, allowing the model to estimate the most appropriate year for a possible shift in publication trends. In this case, the *segmented* function was used without predefined breakpoints, and the model was free to identify the optimal point of change in the trend. The models were bootstrapped with six samples to ensure convergence, and the resulting breakpoints and coefficients were analysed to assess the presence of significant shifts in the data.

Given the high number of taxonomic studies on Rivulidae, the year of first description for each species identified in the review was recorded and analysed to assess the frequency of species discoveries over time. All analyses and data visualizations were conducted using R software (v. 4.2.1). The raw data and a detailed code walkthrough are available in a GitHub repository (see data availability statement) to enhance the reproducibility of our work.

RESULTS

From the total of 115 articles reviewed here (Tab. **S2**), the analysis demonstrated a significant – but moderate – increase in publications over the years ($R^2 = 0.56$, $p < 0.001$, Fig. 1). For example, the cumulative number of articles jumped from 30 in 2013 to 115 in 2024, that is, with a rate of 8.5 articles per year during this decade, in contrast to the previous decade, with a rate of 2.4 articles per year between 2003 and 2013. The

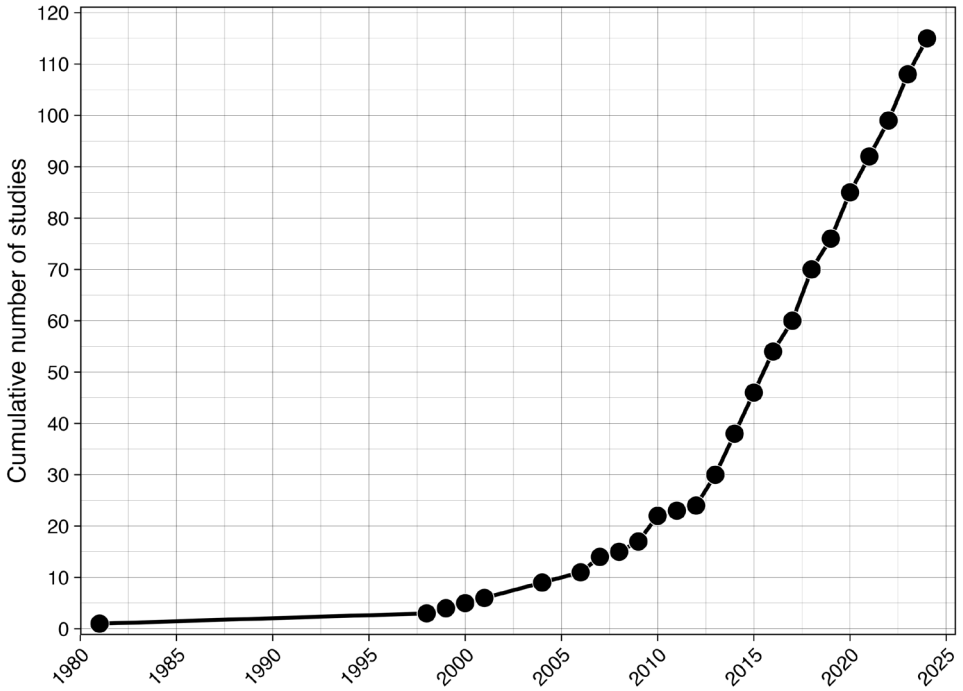

FIGURE 1 | Cumulative number of studies published annually on fish in temporary pools, between 1981 and 2024.

number of unique authors per year showed a strong and significant positive correlation with the total number of papers published annually (S = 162.1, rho = 0.94, p < 0.001) (Fig. **S3**). Similarly, the average number of authors per paper for each year was also positively correlated with the number of papers published per year (S = 680.34, rho = 0.74, p < 0.001) (Fig. **S3**). These results suggest a relationship between the growing research capacity, reflected in both individual and collaborative contributions, and the overall increase in scientific output.

Most studies addressed natural temporary pools (n = 114), with just one study addressing artificial temporary pools, in this case roadside ditches. Most of the work focused on South America and Africa, with Brazil (n = 45) in first place among the countries, followed by Mozambique (n = 16), Uruguay (n = 12), United States (n = 9) and Mexico (n = 6) (Fig. 2A). However, when considering normalized values, Uruguay emerges as the top country in papers per million inhabitants (n = 3.54), followed by Mozambique (n = 0.47), Bolivia (n = 0.32) and Brazil (n = 0.21). A similar trend is seen for papers per million km², with Uruguay again leading (n = 68.65), followed by Mozambique (n = 20.34), with Brazil ranking fifth. For papers per thousand researchers, Mozambique (n = 0.36) and Tanzania (n = 0.16) rank highest, with Bolivia (n = 0.06) and Brazil (n = 0.05) following. Between 1981 and 1990, studies were concentrated in the United States, with contributions from Brazil arising only between 1991 and 2000, but after 2011 most of studies on temporary pools are mainly from Brazil and Mozambique (Fig. 2B). In just the last four years (2021–2024), the number of studies has been high (Fig. 2B), close to the number of articles published in the last decade.

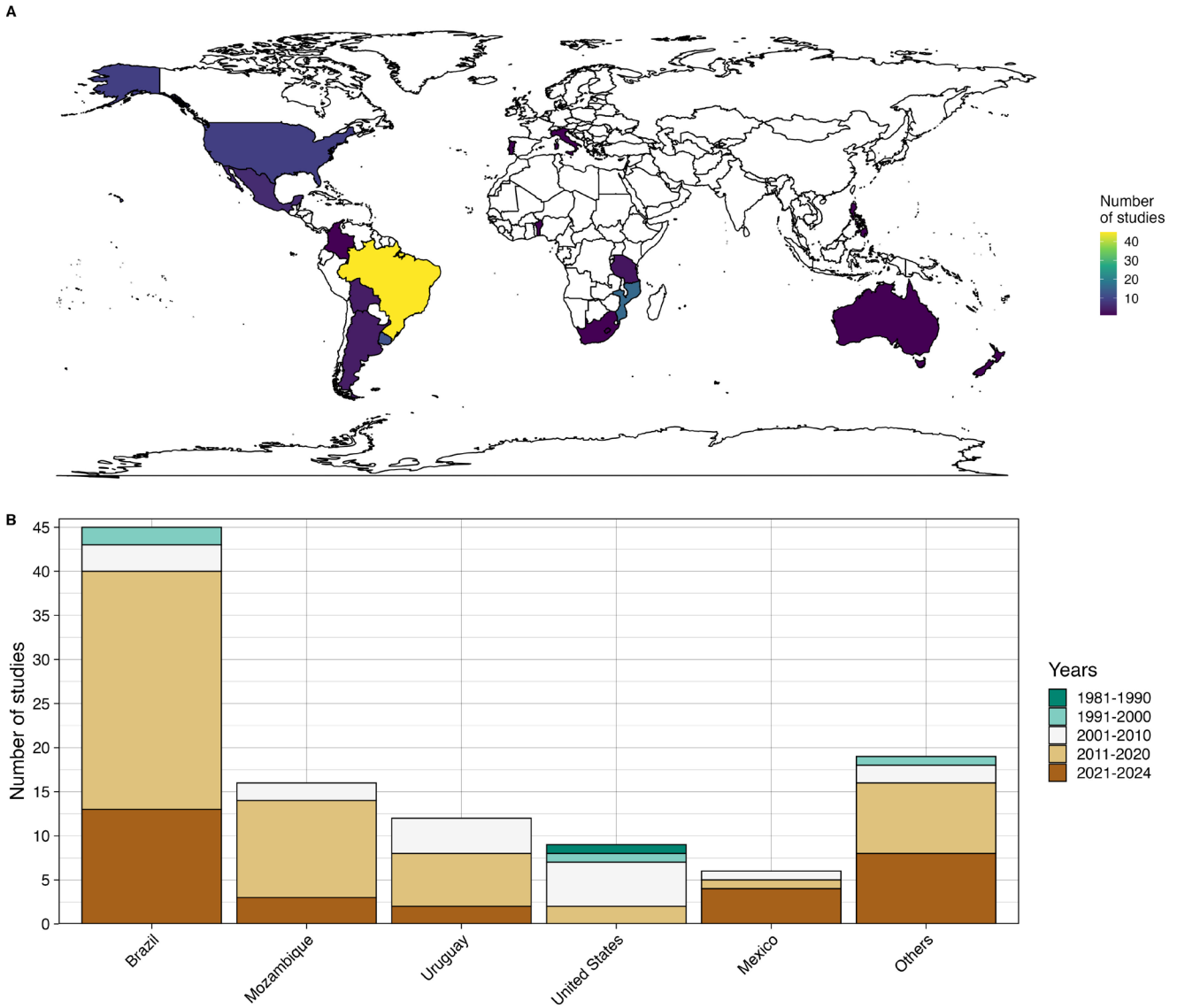

FIGURE 2 | World map with the number of studies on fish in temporary pools by country (**A**). Barplots representing the number of studies by the five countries with the highest number of studies; "Others" include the remaining countries. Studies were separated by decades since 1981 (**B**). Number of analysed articles = 115.

In total, 174 fish species were identified across the reviewed articles (details on each species and the number of papers in which they appear are available in Tab. **S4**, and paper-specific species citations and study areas covered are provided in the raw data). Of these 174 species, 62 belong to Rivulidae (approximately 35.63%) and 12 to Nothobranchiidae, both families commonly associated with temporary pools. The remaining 100 species, representing various families, were predominantly studied at the community level. Within the Rivulidae, the species appearing in the highest number of papers were *Garcialebias minuano* (Costa & Cheffe, 2001) and *Austrofundulus limnaeus* Schultz, 1949 (both cited in six papers). For Nothobranchiidae, *Nothobranchius furzeri* Jubb, 1971 appeared in 20 papers, and *Nothobranchius orthonotus* (Peters, 1844) in nine.

Among the 100 species from other families, *Pyrrhulina brevis* Steindachner, 1876 and *Hoplias malabaricus* (Bloch, 1794) were the most frequently cited, each appearing in four papers.

Regarding the fish clades studied, more than half of the articles focused on Rivulidae (n = 72), followed by Nothobranchiidae (n = 28) and community level studies (n = 10) (Fig. 3A); only five articles focused on other specific families (Protopteridae, Poeciliidae, Lepidogalaxiidae, Lebiasinidae and Galaxiidae), with one article per family. As for the research areas covered in the articles, the most studied was reproduction (n = 34), followed by taxonomy (n = 28) (Fig. 3B), with a considerable occurrence of works on genetics (n = 11) and community ecology (n = 10). The least discussed topic was parasitology (n = 2), with few other studies focusing on physiology (n = 7), behavior (n = 6), trophic ecology (n = 6), species interactions (n = 5), ecotoxicology (n = 3) and new occurrences of species (n = 3) (Fig. 3B).

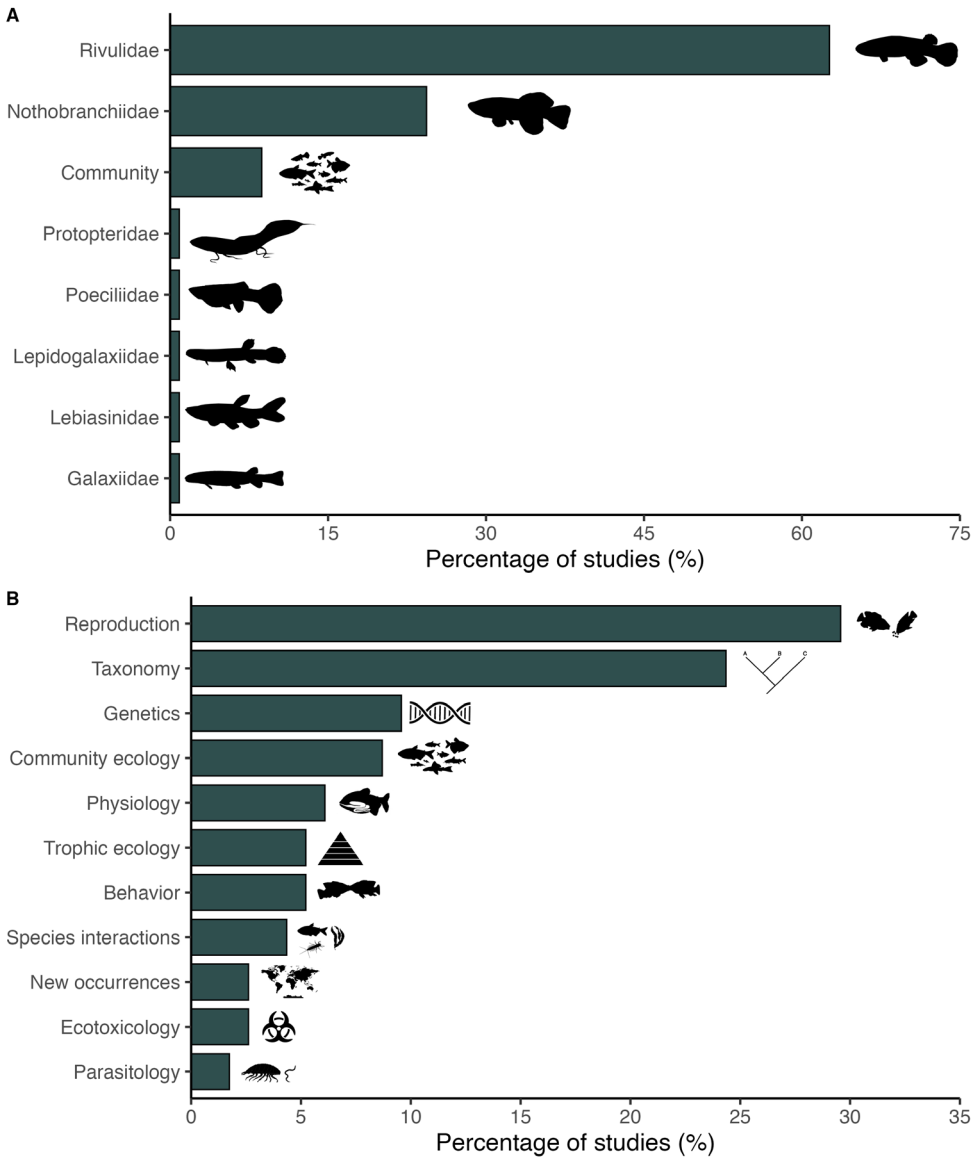

FIGURE 3 | Percentage of studies of fish in temporary pools by fish clade studied (**A**) and by research area (**B**). Number of analysed articles = 115.

Regarding temporal trends in publications, Rivulidae shows an increasing trend, maintaining a high number of articles published per year. Nothobranchiidae also shows an increase, but with a lower intensity. Community level studies have been less numerous (Fig. 4). As for study area over the years, reproduction was the most frequent approach especially after 2014, followed by taxonomic studies. Parasitology and ecotoxicology had the lowest number of studies, appearing just recently. Other topics appeared mostly in the last two decades (Fig. 5).

Combining the fish families studied and research areas, the articles with Rivulidae are mainly about taxonomy (n = 23) and reproduction (n = 18). For Nothobranchiidae, reproduction (n = 14) was the main biological aspect studied, whereas for community ecology most studies focus on describing the community and its environmental predictors (n = 9), with only one study relating the fish community with a bird assemblage. For Poeciliidae, only one study was found and its focus on the interaction with aquatic beetles, while the only study with Protopteridae focuses on reproduction. For Lepidogalaxiidae, the only study was on reproduction, meanwhile for Lebiasinidae was on behavior and for Galaxiidae was a physiology study (Tab. 2).

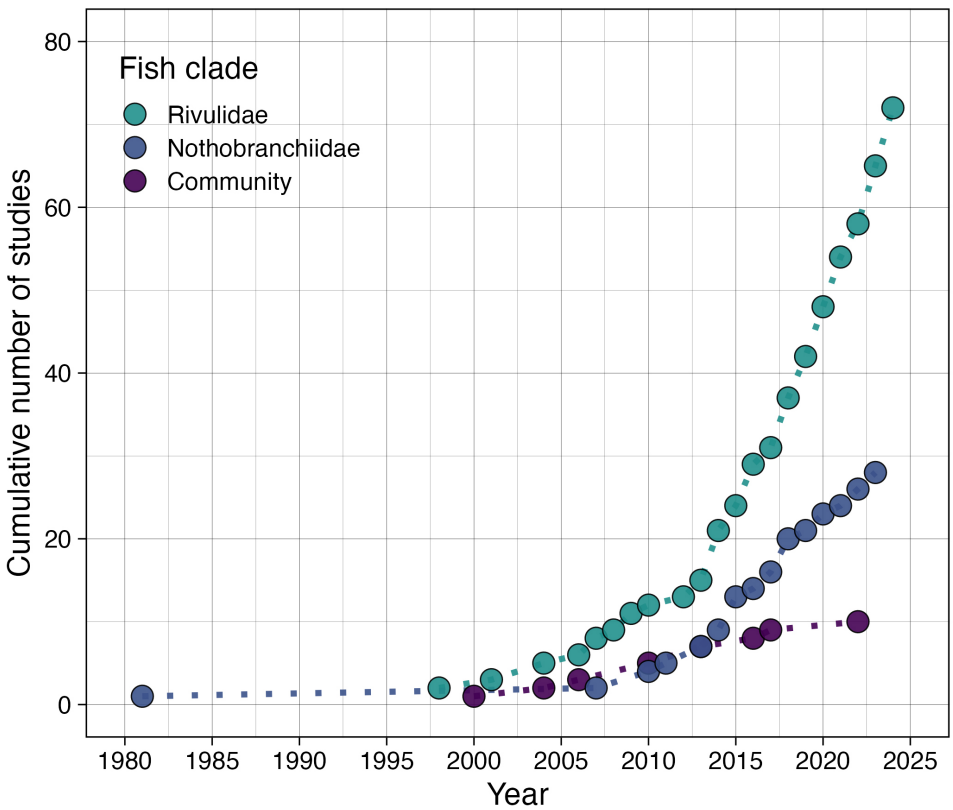

FIGURE 4 | Cumulative number of fish studies in temporary pools per year, considering the three fish clades with more than one study (Rivulidae and Nothobranchiidae) and community-level studies. Number of analysed articles = 115.

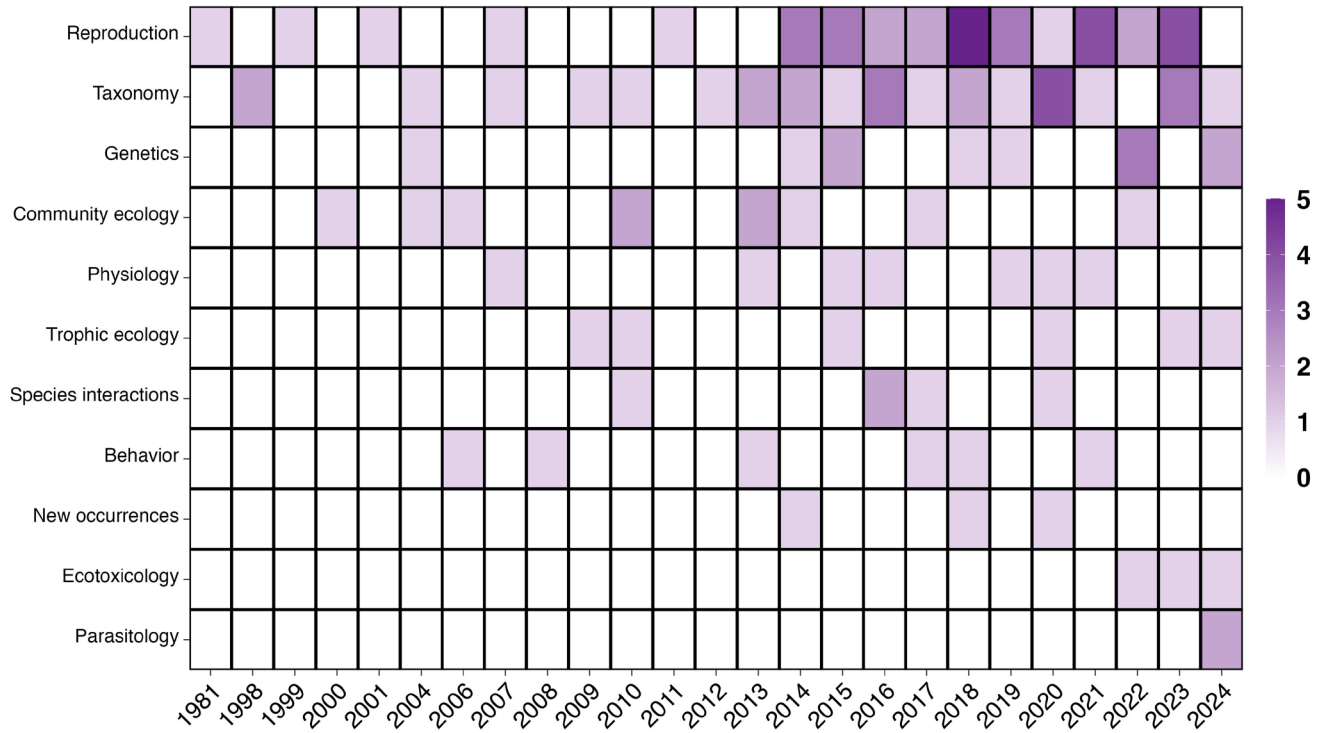

FIGURE 5 | Heatmap of research areas of studies with fish in temporary pools globally, according to the year of publication (1981–2024). Color intensity is proportional to the number of studies. Number of analysed articles = 115.

TABLE 2 | Study area developed with fish from temporary pools by fish clades, with the respective number of articles. Riv. = Rivulidae, Not. = Nothobranchiidae, Poe. = Poeciliidae, Pro. = Protopteridae, Lep. = Lepidogalaxiidae, Leb. = Lebiasinidae, Gal. = Galaxiidae, Com. = Community. Number of analysed articles = 115.

	Fish clades							
Study topics	Riv.	Not.	Poe.	Pro.	Lep.	Leb.	Gal.	Com.
Reproduction	18	14	0	1	1	0	0	0
Taxonomy	23	5	0	0	0	0	0	0
Community ecology	1	0	0	0	0	0	0	9
Genetics	9	2	0	0	0	0	0	0
Physiology	5	1	0	0	0	0	1	0
Trophic ecology	4	2	0	0	0	0	0	0
Species interactions	1	2	1	0	0	0	0	1
Behavior	5	0	0	0	0	1	0	0
New occurrences	3	0	0	0	0	0	0	0
Ecotoxicology	1	2	0	0	0	0	0	0
Parasitology	2	0	0	0	0	0	0	0
Total	72	28	1	1	1	1	1	10

The high number of taxonomic studies on Rivulidae, based on the 62 species identified in this review and their respective years of first description, reveals that the rate of species descriptions has remained relatively steady from 1863 to 2024 (Fig. **S5**). However, in the last two decades, there has been a marked increase in the frequency of species descriptions, with fewer gaps between discoveries (Fig. **S5**). We also tested the hypothesis that public policies can influence scientific production about fish in temporary pools, focusing on two breakpoints for Rivulidae using segmented regression models: 2012 and 2013. However, neither hypothesis was supported by the data. Without specifying a priori breakpoints, the model estimated 2006.76 (Standard Error = 6.80, R^2 = 0.29) as the most likely breakpoint, with the following coefficient estimates: -0.1250 for the years prior to 2006.76 (p = 0.641) and 0.2943 after 2006.76 (t = 1.05). Despite the model's ability to detect a change in trend around 2007, the lack of a provided p-value for the post-2006.76 coefficient, coupled with a weak overall significance for the model, suggests that the breakpoint is not highly reliable. Model details are available as supplementary material (Tab. **S6**; Fig. **S7**).

DISCUSSION

The results of our literature search revealed a relatively low number of published studies on the fish fauna of temporary pools, although research has remained consistent with a slight increase in recent decades. Most studies were concentrated in South America and Africa, primarily targeting Cyprinodontiformes, especially Rivulidae and Nothobranchiidae, and focusing on reproduction and taxonomy. While species from other families were also reported, mainly through community-level studies, these remain limited in comparison. Key research areas such as physiology, ecotoxicology, parasitology, behavior, trophic ecology, species interactions, and species occurrences were less frequently explored. Contrary to our initial hypothesis, we found no evidence that public policies directly influenced scientific production in this field. Although studies on Rivulidae have increased over time, this trend may be driven by other factors, such as socioeconomic and cultural dynamics. In summary, despite the global distribution of temporary pools, the literature on their fish fauna remains scarce, geographically and taxonomically biased, and narrowly focused on terms of research scope.

Our review covers studies from 1981 to 2024, addressing various aspects of fish inhabiting temporary pools worldwide. The earliest study (Inglima *et al*., 1981) examined diapause in *Nothobranchius guentheri* (Pfeffer, 1893), marking the onset of research in this field. Since then, especially after 2010, publications have increased, reflecting growing interest in the ecology of these ephemeral environments. Although the number of studies correlates with time, the modest strength of this relationship, based on exponential regression, suggests that other unaccounted factors may be influencing publication trends, such as availability of funding, presence of active research groups, academic interest in model organisms, or regional access to temporary waterbodies.

We tested whether public policies influenced scientific production using segmented regressions with two hypothesized breakpoints for Rivulidae: 2012 (after the start of Brazil's Extinction Risk Assessment) and 2013 (launch of the National Action Plan for Rivulidae conservation). Although the latter has been linked to increased sampling requests (Furlan *et al*., 2023), our analysis did not support this hypothesis. While such

policies may help to identify knowledge gaps and promote data publication, other factors likely contribute. The positive correlation between the number of unique authors and published papers suggests that research capacity may be a limiting factor. Cultural aspects, such as established research lines led by prolific mentors, could also influence productivity, though these are harder to quantify. Studies on reptiles have shown that socioeconomic conditions and proximity to biodiversity institutions affect research effort (Guedes *et al*., 2023). Moreover, ecological and conservation research tends to be less frequent for amphibians, reptiles, and fish than for mammals and birds, a pattern known as "taxonomic chauvinism" (Bonnet *et al*., 2002). Temporary pools may also receive less attention due to their low public appeal and lack of economically valuable species. We suggest that future studies explore how traits like body size, threat level, and public awareness shape research trends across clades and regions.

Of the 115 articles reviewed, 114 focused on fish from natural temporary pools. Only one addressed artificial habitats, examining anthropogenic structures such as roadside ditches in Florida, USA, thereby underscoring the scarcity, but also the ecological importance, of such environments (Hohausová *et al*., 2010). Despite limited research, artificial temporary habitats offer valuable opportunities for conservation studies. For example, tire tracks were shown to host unique macroinvertebrate assemblages, including rare species (Armitage *et al*., 2012). Similarly, some Rivulidae have been found exclusively in ditches near highways, rather than in natural habitats (Costa, 2002).

Another study involving artificial environments, though not retrieved in our literature search, used field mesocosms (bowls) to investigate social influences on overland movement in *Anablepsoides micropus* (Steindachner, 1863) (Espírito-Santo *et al*., 2019). The absence of such *in situ* experiments in our dataset may reflect limitations in indexing of titles, abstracts, and keywords. In the context of rapid environmental change, understanding how adapted species use artificial habitats, coexist with other species, and respond to stressors like contamination and heat in structures such as road ditches is a promising direction for future research.

The global distribution of studies on fish in temporary pools is notably uneven, with most research concentrated in South America and Africa, particularly Brazil and Mozambique, where interest has grown markedly since 2010. This pattern reflects the distribution and diversity of the two most studied families: Rivulidae in the Americas and Nothobranchiidae in Africa. Brazil stands out as a major hotspot, hosting high Rivulidae diversity (Costa, 2002). This family represents 40% of Brazil's threatened small freshwater species (Castro, Polaz, 2020), many of which face extinction risks before formal description (Böhlke *et al*., 1978; Volcan, Lanés, 2018). Notably, research activity in Brazil from 2021 to 2024 nearly equaled that of the entire previous decade, signaling growing recent interest. However, when accounting for differences in country size, population, and research capacity, Brazil ranks behind several smaller nations. Uruguay, for instance, leads in normalized publication per million inhabitants and per million km². This highlights Uruguay's disproportionately high contribution relative to its geographic and demographic size, consistent with several Rivulidae species or populations restricted to seasonal environments of Uruguay (Loureiro, García, 2008; Loureiro *et al*., 2011; Loureiro *et al*., 2018; Teixeira-de-Mello *et al*., 2021), and probably very productive research groups. Notably, Uruguay has also been identified as the most productive country in general research on temporary lentic waterbodies when adjusted by population size (Olmo *et al*., 2024).

Mozambique is the second-largest contributor, with 16 studies, and also stands out in normalized analyses, ranking second in papers per million inhabitants and per million km², and first in papers per thousand researchers. This reflects Africa's rich killifish diversity (Murphy, Collier, 1997). Nothobranchiidae inhabit seasonal and marginal habitats, as the Rivulidae species (Wildekamp, 2004; Bartáková *et al*., 2013; Furness *et al*., 2015). In Mozambique, *Nothobranchius* species have become important models in biology, evolution, and toxicology (Polačik *et al*., 2011), especially *N. furzeri* and *N. orthonotus*, which appeared most frequently in our review and are widely used in aging research (Polačik *et al*., 2011; Bartáková *et al*., 2013). However, many species face threats from agriculture, mining, and urbanization, highlighting the urgency of conservation efforts (Bragança *et al*., 2022).

The predominance of reproductive studies on Rivulidae and Nothobranchiidae likely reflects the importance of reproductive strategies for survival in temporary habitats. Species in these extreme environments rely on physiological, morphological, and life cycle adaptations, making reproduction a key focus (Wiggins *et al*., 1980; Polačik, Podrabsky, 2015). Nothobranchiidae show a higher proportion of studies on reproduction and have become important models in this field due to their short life cycles (Podrabsky, 1999; Arezo *et al*., 2005; Cellerino *et al*., 2016; Thompson *et al*., 2022), especially *N. furzeri* (Api *et al*., 2018; Polačik, Vrtílek, 2023). In contrast, Aplocheilidae, despite being widely distributed, were absent from our review, likely because their species are associated with streams, paddy fields, swamps, and estuaries rather than temporary pools (Yeo, Lin, 2010; Fernando *et al*., 2018).

The larger number of studies on Rivulidae, addressing both reproduction and taxonomy, likely reflects the group's diversity in Neotropical ichthyofauna and its distinct evolutionary and ecological traits (Loureiro *et al*., 2018). *Garcialebias minuano*, cited in six studies, has been examined for sex ratio (Lanés *et al*., 2016), physiology (Godoy *et al*., 2020), diet (Keppeler *et al*., 2015), and interactions with invertebrates (Vendramin *et al*., 2020). Likewise, *A. limnaeus* has been studied for reproduction (Podrabsky, Somero, 2007), genetics (Wagner *et al*., 2018), and physiology (Wagner *et al*., 2016). Although some species are well-studied, most of the 62 Rivulidae species identified in this review remain poorly known and warrant further research.

The growing number of studies reflects increasing interest in the complex reproductive strategies of annual fish, particularly egg diapause, a key trait from both biological and evolutionary perspectives (Berois *et al*., 2012; Domínguez-Castanedo *et al*., 2022). Concerns over habitat loss, driven by urbanization and other anthropogenic pressures, have also spurred conservation efforts (Godoy *et al*., 2023; Weber *et al*., 2023). Understanding reproductive cycles is essential for effective conservation planning (Williams, 2007; Volcan, Lanés, 2018). However, there remains a notable gap regarding reproduction in non-killifish groups, emphasizing the need for future research on other fish families in ephemeral habitats to better understand adaptive strategies and support ecosystem conservation.

Taxonomy accounted for over 25% of the studies reviewed, with a noticeable rise after 2010. This trend was most evident in the Neotropical region, where most of Rivulidae studies focused on taxonomy, compared to a few on Nothobranchiidae, despite its scientific prominence (Reichard, 2010). Rivulidae dominate research on temporary pools in countries like Brazil and Uruguay, likely due to their high

endemism and ecological relevance (Volcan, Lanés, 2018). Although not the only family present (Pazin *et al*., 2006), their restricted distributions and the geographic isolation of temporary pools hinder sampling and gene flow (Costa, 2002; Menezes *et al*., 2007), contributing to their vulnerability: nearly 40% of threatened Neotropical fish species belong to this group (Tagliacollo *et al*., 2021; Alonso *et al*., 2023). New Rivulidae species continue to be described in several biomes (Costa, 2017a,b, 2019; Alonso *et al*., 2018; Ramos *et al*., 2023).

The high number of taxonomic papers and ongoing species descriptions (Fig. **S5**) underscore major knowledge gaps in Rivulidae diversity. However, our review may underestimate this, as not all relevant studies use searchable terms like "temporary pool" in titles or abstracts. For instance, important early works (Costa, 1988, 1992) were excluded for this reason. This suggests that the species listed here represent only a fraction of the actual diversity of Rivulidae in temporary pools.

We also acknowledge that some foundational and important studies, particularly those focused on annualism (Wourms, 1972a,b,c; Furness *et al*., 2015) and on many aspects of Rivulidae (Costa, 2001, 2006, 2008, 2010, 2011; García, 2006; Ferrer *et al*., 2008, 2014; Loureiro, García, 2008; García *et al*., 2009, 2012, 2014, 2015; Arim *et al*., 2010; Loureiro *et al*., 2011, 2024; Passos *et al*., 2013; Ortiz, Arim, 2016; Furness *et al*., 2018; Zebral *et al*., 2018; Teixeira-de-Mello *et al*., 2021; Gonçalves *et al*., 2024), were not captured through our search strategy. Although our search was designed to detect broader trends across taxa and research areas, we emphasize that a more targeted search using clade-specific terms (*e.g*., "annualism", Rivulidae, or specific genera) would be more appropriate for taxon-focused syntheses. We suggest that future reviews investigate specific clades in more detail, incorporating not only biological patterns (*e.g*., research trends by genus, microhabitat preference, biomes) but also socioeconomic factors (*e.g*., proximity to research institutions, author profiles) that may influence publication trends.

Significant gaps remain in the study of fish in temporary pools, with underrepresentation of topics such as parasitology, ecotoxicology, physiology, trophic ecology, and behavior. Only three ecotoxicological studies were identified, most of them focusing on insecticide effects in Nothobranchiidae (Kafula *et al*., 2022, 2023). The impacts of other pollutants on Rivulidae, Nothobranchiidae, and their fragile habitats remain largely unknown. For instance, a global review on microplastics found just one relevant study, also on a Nothobranchiidae species (Sacco *et al*., 2024), pointing to a critical and promising area for future research.

Behavioral studies were also scarce, with only five focusing on Rivulidae. Few addressed reproductive behaviors like courtship (García *et al*., 2008), and territoriality was rarely explored (Shibatta, 2006). Physiology was similarly underrepresented, with five studies on Rivulidae and one on Nothobranchiidae. Among these, two examined oxidative stress (Godoy *et al*., 2020; Castro *et al*., 2021) and two focused on anoxia tolerance, an essential adaptation in temporary habitats (Podrabsky *et al*., 2007; Wagner *et al*., 2016). A recent review highlighted the general lack of physiological traits in functional ecology (Gomes *et al*., 2023), emphasizing the need for more species-level studies.

Trophic ecology studies were scarce, with only four on Rivulidae and two on Nothobranchiidae. This gap is critical, as understanding diet and feeding behavior is essential for conserving these species and the resources they rely on in ephemeral environments (Pacheco *et al*., 2023). Flexibility in diet can support survival under

fluctuating conditions (Lu *et al*., 2016), making this knowledge especially relevant for temporary pools. Yet, studies on food webs in both Afrotropical (Necker *et al*., 2020) and Neotropical regions (Laufer *et al*., 2009) remain scarce. Resource partitioning, both inter- and intraspecific, has been addressed in a few cases (Laufer *et al*., 2009; Keppeler *et al*., 2015).

Few studies have explored the diet of other fish families in temporary pools, such as Poeciliidae that are also common in these environments (Florencio, López, 2016). Additionally, species like *Callichthys callichthys* (Linnaeus, 1758), *Hoplosternum littorale* (Hancock, 1828) and *H. malabaricus* are often found in temporary pools as juveniles (Espírito-Santo *et al*., 2017). However, their feeding habits in these environments remain understudied. Although the diet of these species has been examined in other habitats, such as swamps (Winemiller, 1987; Mol, 1995) and lakes (Hahn *et al*., 1997), further research is required to understand their roles in temporary pools.

Similarly, species interactions in temporary pools have received little attention, despite the growing calls for multi-taxa approaches (Luza *et al*., 2023). Only a few studies have addressed these interactions: one explored the relationship between birds and fish in temporary ponds (Keppeler *et al*., 2016), another examined the role of Nothobranchiidae in mosquito larvae control (Matias, Adrias, 2010), and a third investigated the effect of Rivulidae on aquatic invertebrate communities (Vendramin *et al*., 2020). Additionally, just one study focused on non-killifish species interactions, specifically the impact of *Gambusia holbrooki* Girard, 1859 on endemic water beetles (Florencio, Lamelas-López, 2016).

Furthermore, few studies have examined other fish families at the species level in temporary pools. One study on Protopteridae evaluated reproductive aspects of *Protopterus annectens* (Owen, 1839) (Lederoun *et al*., 2020), a species coexisting with Nothobranchiidae (Bartáková *et al*., 2013). For Lebiasinidae, *Pyrrhulina brevis*, also one of the two non-killifish species most frequently studied, showed the highest number of records in temporary pools of Central Brazilian Amazon, as reported by Espírito-Santo, Zuanon (2017). Moreover, this Amazonian pencil fish presents seasonal use of both stream channel and temporary pools, with its spatial dynamics being well explored (Espírito-Santo *et al*., 2017), where the species seems to enter the pools mainly for spawning (Espírito-Santo *et al*., 2013, 2017). Additionally, for Lepidogalaxiidae, *Lepidogalaxias salamandroides* Mees, 1961, a species restricted to highly acidic and ephemeral pools in southern Western Australia, has been studied for its larval development (Gill, Morgan, 1999). On the other hand, for Galaxiidae, *Neochanna apoda* Günther, 1867 and *Galaxias fasciatus* Gray, 1842 have also been studied, with research measuring niche breadth through ecophysiological aspects and predicting their occurrence probability in forest pools (White *et al*., 2015). We recommend that future research should focus specifically on species from other numerous families that inhabit temporary pools, as highlighted in Tab. **S4**, particularly since many of those are cited from community-level assessments describing fish assemblages in these habitats.

Only nine articles addressed temporary pools at the community level, with few studies in the Neotropical region that evaluated seasonal variation and environmental gradients in the Amazon and Pantanal in Brazil (Pazin *et al*., 2006; Espírito-Santo *et al*., 2013; Tondato *et al*., 2013; Espírito-Santo, Zuanon, 2017; Couto *et al*., 2018), and none have been conducted in temporary pools in Africa. Furthermore, while much

attention has globally been paid to functional ecology in different environments (Gomes *et al*., 2023), no article was found investigating the functional space within fish communities in temporary pools, an essential aspect for understanding such vulnerable and misunderstood communities.

In conclusion, our study highlights a growing global interest in freshwater temporary pool fishes, while also revealing major knowledge gaps in research areas. These gaps are critical, as understanding species biology and ecological roles is essential for effective conservation, particularly in the face of increasing habitat degradation and the accelerating effects of climate change on temporary aquatic systems. The limited attention to species interactions and community-level dynamics, especially for non-killifish species, further contributes to an incomplete understanding of these ecosystems. Addressing these gaps is vital for conserving both local biodiversity and the functional integrity of temporary pools. Future research should adopt a broader and more integrative perspective, exploring ecological interactions, population dynamics, and functional diversity across underexplored regions and biomes. Studies on artificial habitats and the role of temporary pools within broader ecological networks should also be prioritized.

As extreme weather events become more frequent and intense globally, these temporary pools are likely to experience rapid and profound ecological shifts. Such environmental changes may not only alter the persistence of individual species but also disrupt existing communities, potentially giving rise to novel assemblages governed by new ecological dynamics (Pecl *et al*., 2017; Outhwaite *et al*., 2022). Anticipating these transformations requires a deeper understanding of current community composition and structure of temporary pools, which can inform conservation strategies that are resilient and adaptive in the face of global change.

ACKNOWLEDGMENTS

We thank the editor and anonymous reviewers for their constructive feedback, which helped improve the quality of this manuscript.

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AUTHORS' CONTRIBUTION

João Henrique Alliprandini da Costa: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing-original draft.

Jansen Zuanon: Conceptualization, Investigation, Methodology, Writing-original draft, Writing-review and editing.

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ETHICAL STATEMENT

Not applicable.

DATA AVAILABILITY STATEMENT

The datasets generated during the current study are available in the https://github.com/JH-All/freshwater_temporary_pools_fish_review repository.

COMPETING INTERESTS

The authors declare no competing interests.

FUNDING

This study was financed, in part, by the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP), process number #2023/14344–5, and by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Finance Code 001.

HOW TO CITE THIS ARTICLE

- **Costa JHA, Zuanon J, Selinger A, Castilho AG, Souza UP, Duarte RF.** Diving into temporary pools: a global perspective on freshwater fish research. Neotrop Ichthyol. 2025; 23(3):e250043. https://doi.org/10.1590/1982-0224-2025-0043

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