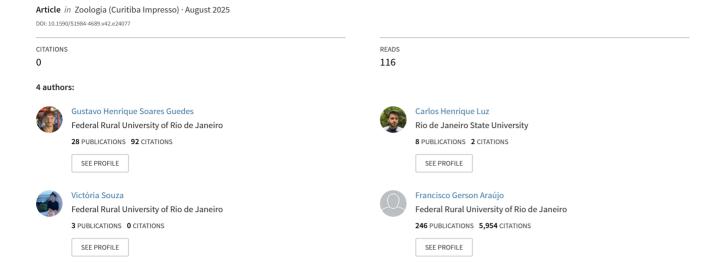
A fish frontier? Itatiaia expedition and biodiversity repositories reveal gaps in fish occurrences in Brazil's high-altitude aquatic ecosystems





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RESEARCH ARTICLE

A fish frontier? Itatiaia expedition and biodiversity repositories reveal gaps in fish occurrences in Brazil's high-altitude aquatic ecosystems

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ABSTRACT. Brazil harbors one of the highest number of fish species in the world; however, the occurrence of fish in high-altitude aquatic ecosystems remains largely underexplored. This study aimed (1) to investigate the occurrence of fish species in the Itatiaia Plateau (Itatiaia National Park), at altitudes ranging from 2,140 to 2,543 m; and (2) to analyze gaps in the altitudinal distribution of fish above 2,000 meters in Brazil. This was accomplished by compiling approximately one million occurrence records from digital biodiversity repositories and digital elevation models. The results indicate that there are no records of fish in high-altitude aquatic ecosystems (> 2,000 m) in Brazil. The highest altitudinal record (~ 1,944 m) is for *Psalidodon* cf. *scabripinnis*. There are many possible reasons for this: challenging climatic conditions, physical barriers to dispersal, isolation, historical absence, sampling gaps, and repository biases. This study highlights the gaps in knowledge regarding fish distribution and emphasizes the potential for future research to discover previously unknown species or species adapted to high altitudes in Brazil.

KEYWORDS. Altitudinal gradients, biodiversity, freshwater fishes, Linnean shortfall, Parque Nacional de Itatiaia.

INTRODUCTION

Alexander von Humboldt (1799–1804) paved the way for understanding the unique patterns and processes that shape biodiversity in mountainous environments (Wulf 2015). Each altitudinal level harbors complex and diverse ecosystems where life adapts to challenging climatic, spatial, and geomorphological conditions (Fischer et al. 2011). Biodiversity patterns in mountains do not follow a uniform trend. Species richness, for example, can decrease with altitude, either monotonically or after a plateau of high richness at lower altitudes, or exhibit a unimodal pattern, with peaks at mid-altitudes, which aligns with the mid-domain effect (McCain and Grytnes 2010, Costa et al. 2023, Valente-Neto et al. 2025). These altitudinal gradients in species richness are attributed to four main characteristics of mountainous

systems: changes in area along the elevation, climatic gradients, geographic isolation of mountain communities, and feedback between zonal communities (Lomolino 2001).

Mountains function as natural barriers for fish by delimiting distinct watersheds and, consequently, promoting specialization (Ribeiro 2006, Buckup 2011, Schluter and Pennell 2017, Cassemiro et al. 2023). In Brazil's megadiverse basins, such as the Tocantins-Araguaia River Basin, new species' descriptions have focused on streams in high-altitude regions, often involving endemic species with restricted distributions and smaller body sizes (Reis et al. 2024). Overall, Brazil harbors one of the highest freshwater fish bio diversities in the world, dominated by Characiformes, Siluriformes, and Cichliformes dominating freshwater ecosystems (Buckup et al. 2007, Albert and Reis 2011). The richness, abundance, biomass, and trophic groups of these



native fish orders are highly sensitive to gradients of altitude and temperature (e.g., Ferreira and Petrere 2009, Viana et al. 2013, Terra et al. 2016, Borges et al. 2020, Gonçalves et al. 2020, Valente-Neto et al. 2025, Fernando et al. 2024).

Although Brazil stands out for its vast continental territory, its range of mountains and altitudinal gradient are relatively narrow, especially compared to neighboring countries in the Andes Mountain range. The Pico da Neblina, at 2,993 m a.s.l., located in the Amazon biome, is Brazil's highest peak (IBGE 2023). Although advances have expanded our understanding of biodiversity in Brazil (e.g., Boeger et al. 2024), the distribution of fish species in high-altitude mountains (> 2,000 m) represents an uncharted frontier. This knowledge gap is not exclusive to Brazil: fish remain among the least studied taxonomic groups along high-altitudinal gradients (Fischer et al. 2011). This is not only the case for fish. For example, expeditions to the Pico da Neblina National Park led to the discovery of new frog species (e.g., Fouquet et al. 2024) and insights into insect community distribution patterns along elevation gradients (Shimabukuro et al. 2023).

Another significant high-altitude site is Pico das Agulhas Negras. It is the fifth-highest peak in Brazil at 2,789 m a.s.l. in the Atlantic Forest biome (Itatiaia National Park, (IBGE 2023). Its relative height, however, is approximately 489 m a.s.l., as it rises from the Itatiaia plateau, which is situated around 2,300 m a.s.l. (Faria 2005). This plateau hosts high-altitude fields that develop on the upper terraces of the alkaline massif (Safford 1999), interwoven with an extensive drainage network of streams, temporary marshes, small lakes, and waterfalls. In addition to its impressive elevations and abundant water resources, the plateau sustains a rich biodiversity, including plants, invertebrates, amphibians, reptiles, birds, and mammals adapted to high altitudes (e.g., Ribeiro et al. 2007, Carvajalino-Fernández et al. 2013, Abreu et al. 2017, Aximoff et al. 2020). This is a complex ecosystem and essential biodiversity refuge in the Serra da Mantiqueira (southeastern Brazil). To date, ca. 21 species have been reported in Itatiaia National Park and its surroundings (Miranda Ribeiro 1906, Costa 1992, Migliari 2022, Martins 2023, Luz et al. 2024, Uzeda et al. 2024). A pattern of decreasing species richness along the altitudinal gradient is obvious, with 16 species recorded on the edges of this conservation unit (between 400-530 m a.s.l. - Martins 2023, Migliari 2022), 12 species at intermediate elevations (700-1,200 m a.s.l. - Luz et al. 2024), ca. 7 species from 1,250-1,500 m a.s.l. (Luz et al. 2024, Uzeda et al. 2024), and only four species reaching higher elevations (1,570–1,600 m a.s.l. - Luz et al. 2024). In this highest altitudinal range, only Siluriformes were recorded, including Pareiorhina rudolphi (Miranda Ribeiro, 1911) and *Trichomycterus* cf. *auroguttatus* Costa, 1992, suggesting a possible environmental filter limiting the occurrence of other lineages at higher elevations (Luz et al. 2024). The only known expedition referencing fish on the Itatiaia plateau (> 2,000 m) was conducted over 120 years ago (1901–1903) when naturalists Carlos Moreira and Alípio de Miranda Ribeiro explored the area. Miranda Ribeiro (1906) described a new species of toad and noted that no fish was found. The survey did not focus on fish, and no specific sampling locations, sampling effort, or capture methods were described. Thus, whether fish are present or not in these high-altitude aquatic ecosystems remains an open question.

This study aims to expand our knowledge on fish distribution in high-altitude ecosystems and highlight these underexplored areas as potential sites for significant discoveries. More specifically, it aimed (1) to investigate the occurrence of fish on the Itatiaia Plateau (Itatiaia National Park) at altitudes from 2,140 to 2,543 m through field sampling; and (2) to analyze the occurrence of fish species in Brazil's high-altitude aquatic ecosystems (> 2,000 m) using data from digital biodiversity repositories (SpeciesLink, Salve, SIBBr/GBIF) and digital elevation models. Three possibilities were expected with regards to objective 1: (i) discovery of species that occur at lower altitudes, expanding their distribution to the Itatiaia Plateau; (ii) discovery of species unknown to science; and (iii) absence of fish.

MATERIAL AND METHODS

Study area

The Itatiaia National Park (Fig. 1) is in the Mantiqueira Mountain Range (southeast Brazil; 22°23'02.6"S; 44°40' 06.1"W), covering an area of approximately 300 km². The park is dominated by mountainous and rocky elevations, with altitudes ranging from 540 to 2,791 m, at its highest point, Pico das Agulhas Negras (IBGE 2023). The area is considered a high-priority site for biodiversity conservation, being the first national park established in Brazil in 1937 and part of the Atlantic Forest Biosphere Reserve (ICMBio 2013). In the region known as the Itatiaia Plateau, also referred to as the Upper Part, high-altitude grasslands and hanging valleys are present (Safford 1999), characterized by an extensive network of springs that feed small streams, temporary marshes, lakes, and waterfalls. The waters from this region drain into two main river basins: Alto Paraná and Paraíba do Sul River Basins (ICMBio 2013). Sampling was carried out under permit ICMBio/SISBio 94739 issued by the Chico Mendes Institute for Biodiversity Conservation



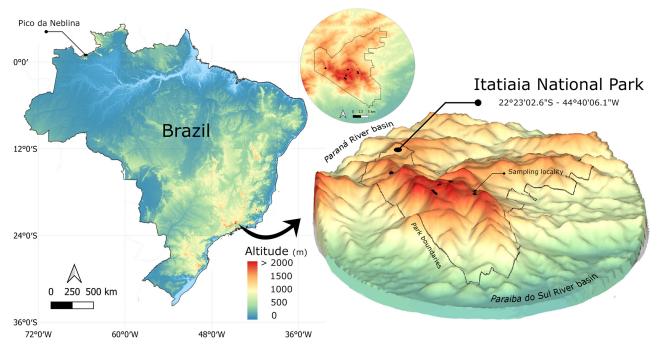


Figure 1. Digital Surface Model of Brazil and Itatiaia National Park. Color scale according to altitude. Black polygon representing the park boundaries. Black points represent sampling localities. Layer: ALOS AW3D30 – Japan Aerospace Exploration Agency.

and approved by the Animal Use Ethics Committee (CEUA/ ICBS/UFRRJ; protocol 12.28.01.00.00.00.45).

Abiotic and biotic sampling

Fish samplings were carried out on the plateau of the Itatiaia National Park (altitude between 2,140 and 2,543 m) in October 18–20,2024 using an oval hand net (50 × 40 cm, 1 mm mesh), covering different environments (small lakes and dams, streams, waterfalls, and swamps; Table 1 and Fig. 2). Each site was sampled by three researchers, with sampling time ranging from 30 to 60 minutes, depending on the characteristics of the area. Small lakes and swamps were fully sampled, while stream sections were surveyed over a length of 150 to 200 m. Abiotic parameters of the water were measured using a multi-sensor device (Hanna HI98194 model). The following variables were recorded: water temperature (°C), dissolved oxygen saturation (%), pH, electrical conductivity (mS/cm), turbidity (FTU), and total dissolved solids (g/L).

Biodiversity repositories

To identify potential knowledge gaps regarding fish occurrences above 2,000 m of altitude in Brazil, data were compiled from public digital repositories that aggregate open-access information from museums and biological col-

lections, such as SpeciesLink (https://specieslink.net), Salve (https://salve.icmbio.gov.br), and the Brazilian Biodiversity Information System (SiBBr; https://sibbr.gov.br), which serves as the Brazilian node of the Global Biodiversity Information Facility (GBIF). These repositories were selected for their relevance and scope in aggregating biological data. SpeciesLink and SiBBr compile data from major biological collections in Brazil, while Salve includes records associated with collection permits issued, threatened species, and sampling within Brazilian conservation units (ICMBio 2024). This latter aspect is particularly important because the highest-altitude locations in Brazil are situated within protected areas.

To download data from these repositories, specific primary filters were applied to suit the distinct characteristics of each search system. In the SpeciesLink repository, the primary filter used was "Actinopterygii", yielding 426,125 records. In the Salve/ICMBio repository, the main filter was "continental fishes", resulting in 246,313 records. In SIBBr, the primary filters applied were "Actinopterygii", "present", and "Brazil", with the attribute set to "collection", yielding 325,445 records. A total of ~1 million (997,893) occurrences records were extracted from the three repositories. The searches in digital repositories were conducted in October





Figure 2. Photographic records of different sampled locations on the plateau of Itatiaia National Park, southeastern Brazil: (A) small lake; (B) Lapa Swamp; (C) Aiuruoca Waterfall downstream; (D) upstream views.

Table 1. Geographic coordinates, altitude (meters a.s.l.), and drainage of the sampled locations on the plateau of Itatiaia National Park, southeastern Brazil. Altitude according ALOS AW3D30 – Japan Aerospace Exploration Agency. Geographic coordinate system: WGS84.

Sample	Locality	Latitude	Longitude	Drainage	Altitude
1	Small lake	22°22'40.84"S	44°40'27.15"W	Paraíba do Sul	2,543
2	Aiuruoca Waterfall	22°21'41.82"S	44°40'05.27"W	Alto Paraná	2,373
3	Aiuruoca Waterfall	22°21'41.73"S	44°40'05.69"W	Alto Paraná	2,373
4	Rancho Caído Waterfall	22°22'04.17"S	44°38'19.21"W	Paraíba do Sul	2,258
5	Stream	22°22'18.77"S	44°38'11.91"W	Paraíba do Sul	2,279
6	Small dam	22°23'06.47"S	44°40'43.34"W	Paraíba do Sul	2,385
7	Flores Waterfall	22°23'14.73"S	44°40'31.24"W	Paraíba do Sul	2,333
8	Flores Waterfall	22°23'16.48"S	44°40'27.52"W	Paraíba do Sul	2,312
9	Lapa Swamp	22°21'28.78"S	44°44'09.52"W	Alto Paraná	2,143
10	Lapa Swamp	22°21'28.80"S	44°44'12.60"W	Alto Paraná	2,138
11	Lapa Swamp	22°21'25.94"S	44°44'11.35"W	Alto Paraná	2,140

2024. All records consulted in the repositories are available and accessible through the Zenodo repository (Guedes 2025).

To determine the altitude of each occurrence record, geographic coordinates were overlaid onto a global Digital Surface Model (DSM) layer set with an approximate horizontal resolution of 30 m (~ 1 arc second), provided by the Japan Aerospace Exploration Agency (https://www.eorc.jaxa.

jp). The overlay and layer sampling were conducted in QGIS software, version 3.32 Lima (QGIS Core Team 2024), using the "Point Sampling Tool" plugin and based on the WGS 84 geographic coordinate reference system. All occurrence records with altitudes above 2,000 m a.s.l. were individually verified to assess whether the coordinates matched the sampling locations described in the metadata.



RESULTS

Itatiaia expedition

The physico and chemical variables of the streams on the plateau of Itatiaia National Park are characterized by neutral pH (mean \pm s.d., 7.1 \pm 0.2), cold (11.4 \pm 0.2 °C) and clear water characterized by low turbidity (2.0 \pm 0.2 FNU) and minimal dissolved solids (5.5 \pm 0.5 mg/L). Additionally, the water exhibited low conductivity (11 \pm 1.1 μ S/cm) and oxygen saturation levels nearing 80% (\pm 8.4). Notably, no fish species were recorded at any of the 11 sampled locations on the plateau, situated at altitudes ranging from 2,140 to 2,543 m.

Biodiversity repositories

There are five records of fish found at altitudes above 2,000 m at Serra dos Órgãos, Caparaó, and Mantiqueira (southeast of Brazil) (Table 2). The geographic coordinates of these records, however, are not very consistent and precise. All coordinates corresponding to the highest-altitude records in the Salve repository are arbitrary (coordinate precision = approximate). They were estimated using the centroid method, representing the geographic center of a set of locations (e.g., midpoint of a protected area), as described in the metadata (see Appendix 1). Records of Trichomycterus brunoi Barbosa & Costa, 2010 (catalog number: MBML-4482) were duplicates, appearing in Salve and SpeciesLink. The precision of these records is also low, with coordinates indicating a steep rocky escarpment without any water, contradicting the described collection locality (Table 2). Therefore, out of all records analyzed, none corresponding to altitudes above 2,000 m are accurate. The highest recorded altitude (~ 1,944 m) for a fish collected in Brazil goes to Psalidodon cf. scabripinnis (Jenyns, 1842) (Table 2).

DISCUSSION

Itatiaia expedition

The fish sampling conducted during the Itatiaia expedition represents one of the highest-altitude studies (2,140–2,543 meters) in Brazil's aquatic ecosystems. However, it was not the first to record the absence of fish in the Itatiaia plateau (Miranda Ribeiro 1906). Several hypotheses explain the absence of fish at high altitudes in Itatiaia National Park. One possibility is that fish were either never present in these ecosystems due to ancient geological and climatic conditions, or they were there at some point but were later extirpated due to landscape evolution processes (e.g., Val et al. 2022). During the Pleistocene, it is speculated that the Itatiaia plateau has been covered by ice due to extremely cold climatic conditions, and today, Itatiaia represents one of the coldest areas in eastern South America because of its geographic exposure to southern polar fronts (Safford 1999). The average annual temperature is about 14°C, with colder temperatures sometimes dropping below -10°C during the approximately 56 nights of freezing temperatures per year (Ribeiro et al. 2007). Local flora and fauna species show adaptations to these extreme climatic conditions. For example, the toad Melanophryniscus moreirae (Miranda-Ribeiro, 1920) goes through dormancy (Carvajalino-Fernández et al. 2013), and C3 plants dominate the landscape (Ribeiro et al. 2007).

Additionally, physical barriers to dispersal, such as waterfalls, rapids, and steep, rugged terrain, may prevent fish from migrating to higher altitudes (e.g., May et al. 2017), hindering the arrival and colonization of fish species (e.g., *Trichomycterus* cf. auroguttatus, *Pareiorhina rudolphi*, *Neoplecostomus altimontanus* Uzeda et al., 2024) that reach the known altitudinal distribution peaks (~1500 m) in Itatiaia National Park (Luz et al. 2024, Uzeda et al. 2024). In general, a decrease

Table 2. Fish occurrence records at high altitudes (meters a.s.l.) according to biodiversity repositories (Salve, SpeciesLink, and SiBBr), with comments on coordinate.

Source	Species	Latitude	Longitude	Altitude	Remarks
Salve	Trichomycterus brunoi Barbosa & Costa, 2010	-20.4584	-41.7851	2,122	Imprecise coordinate based on centroid method
Salve	Trichomycterus itatiayae Miranda Ribeiro, 1906	-22.3566	-44.6837	2,111	Imprecise coordinate based on centroid method
Salve	Characidium vidali Travassos, 1967	-22.4888	-43.0597	2,098	Imprecise coordinate based on centroid method
Salve	Parotocinclus maculicauda (Steindachner, 1877)	-22.4888	-43.0597	2,098	Imprecise coordinate based on centroid method
Salve/Specieslink	Trichomycterus brunoi Barbosa & Costa, 2010	-20.4201	-41.828	2,073	Imprecise coordinate, with coordinates indicating a steep rocky escarpment, devoid of apparent water bodies, contradicting the described collection locality.
Specieslink	Psalidodon scabripinnis (Jenyns, 1842)	-22.7167	-45.45	1,944	Literature supports species' occurrence at altitudes around 1,920 m (e.g., Néo et al. 2000)



in the number of species toward mountain headwater streams is a broad pattern of the river continuum concept (Vannote et al. 1980). This decline can be attributed to low temperatures and the steep slopes of mountain streams, which act as natural filters for species dispersal, as observed for fish communities in the Iberian Peninsula (Oliveira et al. 2012) and in the Andes-Amazon transition zone (Bogota-Gregory et al. 2024). In Itatiaia National Park, the mean water temperature in the lower section (20.6 ± 1.1 °C; Martins 2023) is approximately 10 °C higher than that recorded in the upper Itatiaia Plateau $(11.4 \pm 0.2 \, ^{\circ}\text{C})$. Additionally, the occurrence of surface freezing in aquatic habitats during winter on the Itatiaia Plateau may act as an ecological barrier to fish colonization and persistence at these elevations. Other possibilities, such as food scarcity, low habitat complexity, or unfavorable physical and chemical water conditions, are unlikely to be limiting factors. The water bodies in this region present diverse microhabitats (e.g., rapids, pools, rocks, branches), a high diversity of invertebrates (e.g., Macedo et al. 2016, Ribeiro et al. 2019), which provide ample food resources for fish, as well as water with typical characteristics (excluding temperature), such as neutral pH and good oxygenation, conducive to fish development (Tundisi and Tundisi 2016).

The absence of fish records in the Itatiaia plateau is supported by (1) the current data collected in this study, (2) historical records (Miranda Ribeiro 1906), and (3) extreme environmental fluctuations, such as the freezing of aquatic habitat surfaces and steep geomorphology, which are known ecological barriers to fish colonization and persistence. However, this absence may also be attributed to methodological limitations that were not fully addressed in this study, highlighting the need for future investigations. Alternative collecting methods, beyond the hand nets employed here, such as electrofishing and environmental DNA (eDNA) analysis, could provide promising tools for detecting fish in high-altitude aquatic environments (Xing et al. 2022). Nonetheless, these methods also face inherent limitations: the low water conductivity in the region may impair the efficiency of electrofishing, and the high diversity of bird species could introduce confounding factors for eDNA analysis (e.g., fish remnants in bird feces, potentially leading to false positives). These challenges underscore the necessity of methodological refinements and complementary approaches in future research.

Gaps in fish occurrences in high-altitude aquatic ecosystems

The maximum recognized altitude record for a fish in the biodiversity repositories analyzed (SpeciesLink, SALVE/

ICMBio and SiBBr) corresponds to Psalidodon cf. scabripinnis (1,944 m a.s.l.). This record is located approximately 87 km from the Itatiaia Plateau, in streams of the Serra da Mantiqueira that drain into the Paraíba do Sul River basin (Néo et al. 2000, Castro et al. 2014). The species was originally described from specimens collected by Charles Darwin in the city of Rio de Janeiro and was recently repositioned into Psalidodon (Terán et al. 2020). These fish are regarded as a "species complex," with some populations isolated for millions of years in different hydrographic basins, separated by hundreds of kilometers (Moreira-Filho et al. 2004, Bertaco and Lucena 2006). Allopatric populations at varying altitudes exhibit differences in morphometric, reproductive, and chromosomal characteristics, including B chromosomes, which may reflect distinct selective pressures in each altitudinal zone (Néo et al. 2000, Moreira-Filho et al. 2004, Castro et al. 2014, 2015, Silva et al. 2022). Although the population of P. scabripinnis represents a remarkable example of occurrence at high altitude, the question persists: could this mark the altitudinal distribution limit for Brazilian freshwater fish?

This study highlights the lack of valid records of fish occurrences above 2,000 m in Brazil. Despite extreme climatic conditions, high altitudes do not seem to limit fish distribution in other mountainous regions worldwide. An example is the Altiplano of the Andes Mountain Range, which hosts fish species at altitudes between 3,600 and 4,500 m (Vila et al. 2007). Another example is the cyprinid Herzensteinia microcephalus (Herzenstein, 1891), recorded on the northern slope of Mount Tanggula on the Qinghai-Tibet Plateau in the Himalayas, considered the highest-altitude fish occurrence known, reaching 5,350 m a.s.l. (Zhu et al. 2021). In addition to the historical, biogeographical, and ecological factors previously discussed for the Itatiaia Plateau, the absence of records at high altitudes in Brazil (> 2,000 m) may be attributed to several other factors. First, this particularly suggests a sampling gap in fish data from high-altitude areas in Brazil, characterizing a Linnean shortfall (the lack of formal description of species that have not yet been discovered or documented by science) or a Wallacean shortfall (lack of knowledge about species distributions) (Hortal et al. 2015). This gap may reflect a sampling bias, as fish research in Brazil tends to focus on more accessible, low-altitude regions where ecosystems are easier to sample (e.g., Junqueira et al. 2020, Lima et al. 2021). When occurring at higher altitudes, studies have revealed a sharp decline in the richness, abundance, and biomass of fish with increasing altitude (e.g., Ferreira and Petrere 2009, Viana et al. 2013, Terra et al. 2016, Borges et al. 2020, Gonçalves et al. 2020, Valente-Neto et al. 2025), and



no species were found near 2,000 m a.s.l. (Sarmento-Soares and Pinheiro 2011). Second, although Brazil has a vast territory, altitudes above 2,000 m are restricted to mountainous areas (e.g., Serra dos Órgãos, Mantiqueira, Imeri, Caparaó, Pacaraima), which are proportionally rarer. Consequently, the likelihood of discoveries at high altitudes in Brazil is reduced to specific and limited mountainous regions, which remain largely under-sampled.

Third, biases related to records, communication, data availability, and inadequate, incomplete, or absent data reporting represent major barriers to understanding species distributions (Oliveira et al. 2016). For instance, research conducted in high-altitude regions may not have fully reported findings, leading to an underestimation of species presence in these areas. Another contributing factor is the use of secondary databases, where species may have been collected but not formally recorded in biological collections or may be housed in collections without public access via open data platforms. Furthermore, imprecise geographical information, such as the lack of exact coordinates, can underestimate the actual altitude of sampling sites, leading to the exclusion of records that, in reality, occurred above 2,000 m a.s.l.. This set of factors highlights the need for a rigorous review involving collaboration between field researchers, collection curators, museums, and digital repository administrators. The shared goal should be to ensure the availability of accurate and open data, allowing for a more reliable biodiversity analysis.

Final remarks

This study advances knowledge of Brazilian biodiversity by: (1) exploring extreme-altitude aquatic ecosystems in the Itatiaia National Park, representing one of the highest-altitude fish surveys ever conducted in the country; (2) identifying Psalidodon cf. scabripinnis as the species with the highest recorded altitude (1,944 m); (3) presenting evidence from primary and secondary data that converge on the absence of cataloged fish distribution records above 2,000 m in Brazil; and (4) identifying, for the first time, high-altitude aquatic ecosystems as a frontier for ichthyological research in Brazil. Reporting absences is crucial for understanding species distributions but is often overlooked in biodiversity studies, posing challenges for species modeling and conservation strategies (e.g., Lobo et al. 2010). Consequently, the findings of this study are expected to encourage further research and future expeditions to determine whether Brazil's high-altitude mountains represent a frontier for fish.

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Data availability

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