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Influence of Habitat on the Impact of Non-Native Fishes on Native Ichthyofauna in a Group of Lakes of the Lower Doce River, Espírito Santo, Southeastern Brazil

Eduardo Hoffmam de Barros [1,2,*], Nuno Caiola [3], Renan Luxinger Betzel [2], Ronaldo Fernando Martins-Pinheiro [4] and Luisa Maria Sarmento-Soares [1,4]

[1] Centro de Ciências Humanas e Naturais, Campus Goiabeiras, Universidade Federal do Espírito Santo, Vitória 29075-910, ES, Brazil; luisa@nossosriachos.net
[2] Ello Ambiental Consultoria Ltda., Colatina 29700-480, ES, Brazil; renan@elloambiental.com.br
[3] Eurecat, Technology Center of Catalonia, Climate Resilience Center, C/Lligallo de Lorente 3, 43870 Amposta, Spain; caiola.nuno@gmail.com
[4] Instituto Nossos Riachos, Niterói 24348-095, RJ, Brazil; pinheiro.martins@gmail.com
* Correspondence: eduardohbarros@elloambiental.com.br or ello@elloambiental.com.br; Tel.: +55-27999095559

Abstract

The Doce River basin is the largest river system in southeastern Brazil. Over the last century, the Doce River has been undergoing a serious process of degradation, culminating in a huge environmental disaster due to Fundão tailing dam bursting in Mariana (Minas Gerais) and causing severe damage to biodiversity and local human communities. Near its mouth, the Doce River harbors an extensive lake area, with over ninety lakes on coastal lowlands. These lakes are of fluvial origin and connected to each other and to the main Doce River by small tributary streams. In this area, one of the main sources of impact on the fish fauna is the presence of non-native fish species. We compared richness, taxonomic diversity, beta diversity, species composition and proportion of non-native species in lakes and streams, and related these variables to each other and to environmental variables. We used the indicator species index (IndVal) to identify species associated with each type of environment. We used multivariate analyses to test the influence of stream habitat on the fish fauna in streams and Generalized Linear Models (GLMs) to test the influence of distance to lakes on the proportion of non-native species in streams, and the influence of this proportion on total and native fish richness and diversity. The results showed that some non-native species originating from lentic environments have adapted to the lakes and are spread throughout the internal lake system. In streams, there are proportionally fewer non-native fish and their distribution is more fragmented, as some stretches do not provide the conditions for the establishment of some of these species, making them potential refuges for native ichthyofauna. As the streams move away from the lakes, the proportion of non-native species tends to decrease. In streams, the richness and diversity of native species are affected by the proportion of non-native species, but not in lakes. The native vegetation in the landscape showed no potential for reducing the invasion of non-native species. The depth and width of the streams are directly related to the proportion of non-native species within the streams and are structural characteristics that should be considered in strategies for the conservation of the fish fauna.

Keywords: fishes; streams; lagoon; invasion; non-native species

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1. Introduction

An understanding of the factors which govern biodiversity is key for development of integrative concepts in aquatic ecology and conservation [1]. Understanding how various processes shape fish assemblages is challenging, and researchers often disagree about the relative importance of biotic and abiotic factors [2].

The introduction of non-native species is recognized as one of the main factors linked to the extinction of species [3,4]. Although habitat destruction is usually considered the main risk factor for fish species, the introduction of non-native species can be an even more problematic factor, because once established, these species can become permanent fixtures on the landscape and their eradication can become impossible [5]. For this reason, prevention has been mentioned as a more appropriate measure than eradication to deal with this problem [5,6].

In freshwater lentic environments, predation is considered the main factor in population regulation and consequently in the structuring of communities [7] and the impact of the introduction of predatory alien species on native species is quite significant [8], but this is not the only mechanism that acts in this sense [9]. Effects of non-native species on native ichthyofauna are well documented in lake regions [10,11], including the lakes of the middle Doce River [8,9]. These effects include changes in ecological conditions related to the reproduction, growth and development of native species, hybridization, introduction of diseases and parasites, competition and predation, which can lead to the decline or disappearance of native fish populations.

If a native fish population is not competitive or does not possess an efficient anti-predatory mechanism, its chances of persisting in invaded communities, before the presence of the alien species, can be linked to its ability to use refugia inside the lakes [8]. Thus, it is expected that areas of high heterogeneity within aquatic systems will reduce the effectiveness of superior predators and competitors [12] and increase the chances of persistence of less efficient prey and competitors [13]. However, a study conducted in the middle Doce River showed that greater habitat heterogeneity within lakes containing non-native species apparently did not function as a refuge for native fish populations [8].

Key characteristics of biological communities include the spatial patterns of species distribution, composition, and diversity [14], which are largely determined by habitat-related factors. Physical space is regarded as one of the fundamental dimensions of the niche [15]; the habitat, however, provides not only space but also a variety of additional resources for organisms [16]. A central theme in community ecology is understanding the factors that determine species richness across different habitats [17]. Habitat information has multiple applications in biodiversity conservation, such as understanding the requirements for species survival and persistence [18–20] and guiding actions aimed at restoring and maintaining suitable conditions for their conservation [21].

Species-specific adaptations integrate with biotic and abiotic factors to shape organismal parameters such as growth, survival, and reproductive success [22]. Therefore, habitats that exhibit greater similarity to the environments of origin of native species, rather than those of non-native species, are expected to reduce the ecological impacts of the latter and provide refuges for the native ichthyofauna in the region.

We present a comparative study of the fish fauna from nine internal lakes of the Lower Doce River and their associated streams. The main question addressed is whether there are habitats within streams that can provide refuges that mitigate the negative impacts of non-native species on native species.

The specific objectives of this study were to answer the following questions: 1. Do lakes and streams differ in richness, taxonomic diversity, composition, and diversity partitioning (beta diversity)? 2. Are there characteristic species associated with each environment type (lakes and streams)? 3. Does the ratio of non-native to native species differ between lakes and streams? 4. Does proximity to lakes influence the proportion of non-native species in streams? 5. Does the proportion of non-native species affect the richness and diversity of native species in lakes and streams? 6. Which habitat characteristics influence fish community composition and the proportion of non-native species in streams within the lacustrine system?

2. Materials and Methods

2.1. Study Area

The Doce River basin is the largest in southeastern Brazil, encompassing approximately 85,000 km^2 of watercourses across the states of Minas Gerais and Espírito Santo. The river flows into the Atlantic Ocean at the district of Regência, Espírito Santo state [23]. From its headwaters to its mouth, Doce River extends 929 km, traversing a gradient from the Cerrado in the Espinhaço Range to the floodplains of the Atlantic Forest in the coastal lowlands. Its highest headwaters are located in the Córrego da Cachoeira Alta, at an elevation of 1230 m in the municipality of Desterro do Melo, Minas Gerais. The river is named as “Doce” after the confluence of the Piranga and Carmo rivers.

Historically, the Doce River valley was inhabited by Indigenous peoples collectively known as the Krenak, Aymorés or Botocudos. These communities inhabit areas from the middle valley to near the river’s mouth [24]. Since colonial times, the development of Espírito Santo was constrained by its proximity to Minas Gerais, which hindered the expansion and integration of the state’s interior [25]. Between 1725 and 1758, seven royal decrees were issued prohibiting the construction of routes from Minas Gerais to Espírito Santo, in an effort to preserve the royal monopoly over gold trade [25]. By 1888, only 15% of Espírito Santo’s territory was occupied, mainly limited to coastal regions. The expansion into the interior began with the rise in coffee cultivation [26]. The northern part of the state remained largely unoccupied until the mid-20th century, when logging activities began to exploit this region [27].

The Suruaca Valley was one of the last regions in southeastern Brazil to be colonized due to its swampy terrain, inaccessibility, high incidence of yellow fever, and the high investment required for drainage [28]. Originally, the lower Doce River course formed a vast wetland. However, beginning in 1968, this area suffered severe degradation due to channel drainage initiatives promoted by the Federal Government through the National Department of Works and Sanitation (DNOS) for agricultural purposes [28–31]. These actions caused irreversible damage to the biodiversity of the entire Suruaca Valley, effectively transforming it into a “chemical desert” [32]. As a consequence of the Fundão tailings dam collapse, the lakes of the lower Doce River were specifically targeted by an emergency intervention aimed at mitigating fish mortality. This initiative, known as the “Noah’s Ark” operation, received widespread media coverage at the time [33–37] and involved the translocation of fish from the Doce River into nearby lakes. Although intended as a conservation measure, the action likely resulted in additional introductions of non-native species into the lacustrine system.

The lower Doce River region (Figure 1) includes approximately 90 lakes of highly variable sizes, ranging from 0.8 ha to 6200 ha [38], within a complex that spans an area of 165 km^2 [39]. The lacustrine genesis allows for classification into two main types: barrier lakes, located on the tertiary plateau of the Barreiras Formation, and coastal lakes, or the Monsarás system [40,41]. Barrier lakes are directly influenced by the Doce River and can be grouped into two subtypes based on their morphology and landscape setting. The first subtype, known as external lakes, is found at the boundary between the Barreiras Formation plateaus and the Quaternary coastal plain. These lakes typically range from 1 to 10 km in length, aligned in directions from NW-SE to WNW-ESE, with Lagoa Aguiar—south of the Doce River—being the most prominent example. The second subtype, internal lakes, is primarily located on the river’s left bank atop the tertiary plateaus of the Barreiras Formation, though their outlets extend into the fluvial deposits of the Doce River [40]. This extensive lacustrine area contains the largest coastal lake in Brazil, Lagoa Juparanã [42]. Internal lakes generally exhibit greater size and depth, whose depths can reach 27 m below sea level [43].

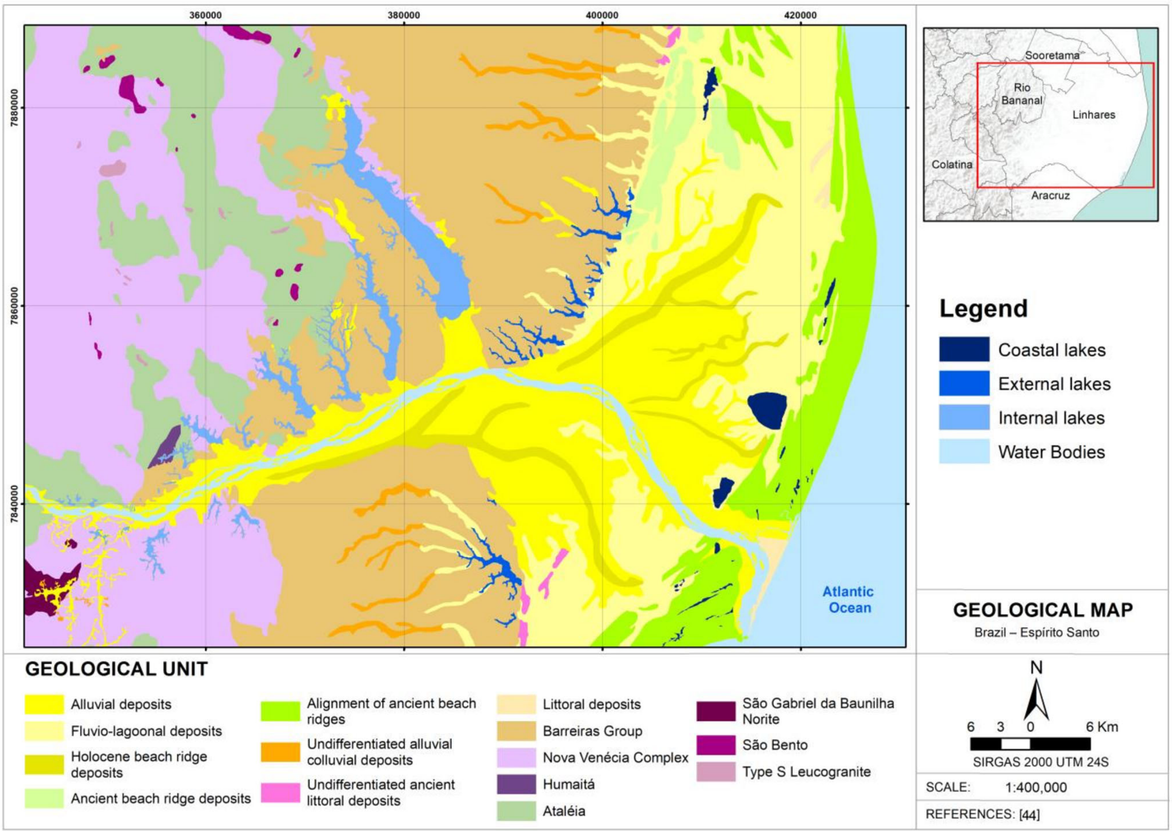

Figure 1. Lacustrine system of the lower Doce River, state of Espírito Santo, southeastern Brazil, and its spatial relationship with underlying geological formations [44].

The four largest internal lakes were described based on their physical characteristics [45]. Lake Juparanã, the largest in the region, extends 25 km, covers an area of 47 km^2, has a drainage basin of 1942 km^2, and reaches a maximum depth of 16 m. Lake Lagoa Nova is 18 km long, with an area of 16 km^2, a basin of 368 km^2, and a maximum depth of 32 m. Lake Lagoa das Palminhas extends 12 km, covers 8 km^2, has a basin of 70 km^2, and a maximum depth of 29 m. Lake Lagoa das Palmas measures 8.5 km in length, has an area of 12 km^2, a drainage basin of 86 km^2, and a maximum depth of 45 m. However, a more recent study reports that this lake reaches a depth of 50.7 m, identifying it as the deepest natural lake in Brazil [46].

2.2. Sample Design

Nine internal lakes were sampled, locally known as: Lagoa Nova, Lagoa das Palmas, Lagoa Palminhas, Lagoa Piabanha, Lagoa Terra Alta, Lagoa Terra Altinha, Lagoa do Óleo, Lagoa do Limão and Lagoa Juparanã. Lagoa Piabanha and Lagoa do Óleo were each sampled once, whereas the other lakes were sampled twice, on different days and at distinct locations. Sampling locations in the lakes were selected visually during surveys conducted by motorboat. Priority was given to choosing two shoreline segments with visibly distinct physical characteristics, located near opposite extremities of each lake. Areas with visible anthropogenic interference—such as recreational zones, access points used by fishers or swimmers, residential areas, exposed soil, and livestock access—were deliberately avoided. In total, 16 lake sampling events were conducted, each over two consecutive days using the gillnet method.

In the streams connected to these lakes, 37 sampling events were carried out at sites distributed upstream and downstream at varying distances from the lakes Juparanã, Nova, Palmas, Palminhas, Limão, Terra Alta, Terra Altinha, and Óleo. No streams connected to Lagoa Piabanha were sampled. To ensure sample independence, the sites within each lake were placed on opposite shores or in different arms of the lake, maintaining a minimum straight-line distance of 2 km between them.

Within the streams, sampling sites were preferentially assigned to three distance categories relative to the lakes: (1) proximal—up to 900 m; (2) intermediate—from 900 m to 5 km; and (3) distal—more than 5 km. In some cases, only two sites per stream were sampled, each from a different distance category. In the streams, sampling points were selected a priori based on aerial imagery. Priority was given to: including more than one stream per lake; selecting stretches both upstream and downstream of the lakes; covering three different distance categories relative to the lakes; and choosing segments with the greatest possible distance within the same stream. Areas with visible anthropogenic interference were avoided. In two stream segments, no fish were recorded; thus, only 35 stream sites were considered in the analyses (Figure 2).

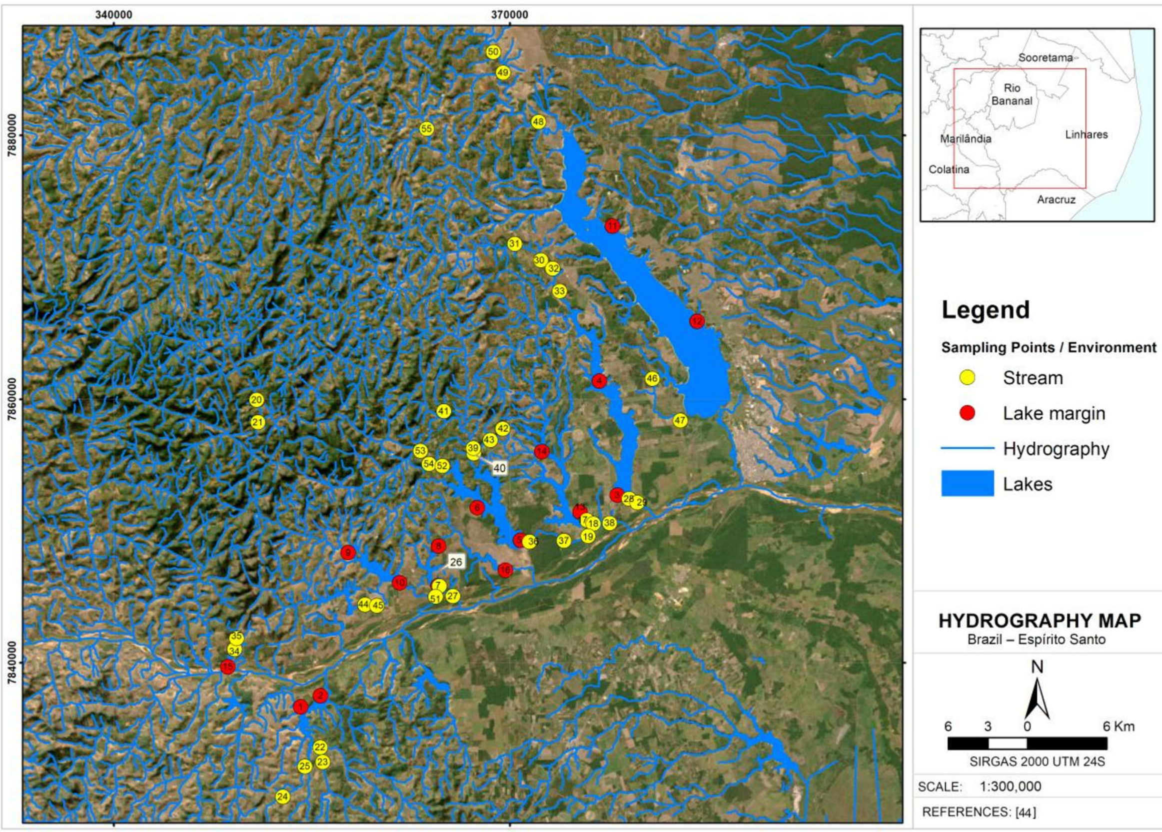

Figure 2. Sampling sites for fish and habitats in internal lakes of the lower Doce River basin (red dots) and their tributary streams (yellow dots). Blue lines represent the hydrographic network, and blue polygons indicate the lakes. The inset map shows the study area location within the state of Espírito Santo, southeastern Brazil [44].

2.3. Data Collection

2.3.1. Fishes

In the lakes, sampling sites were selected near the margins. To ensure sample independence, approximately 200 m shoreline segments were delineated at each location, where the same fish capture methods used in streams were applied. Capture efforts included the exhaustive use of cast nets, seines with different mesh sizes, and ichthyological sieves across the greatest possible variety of microhabitats (e.g., varying depths, slopes, vegetation types, and substrates). Additionally, each lake was sampled with a set of nine gillnets (10 m × 1.5 m) with mesh sizes of 30 mm, 40 mm, 50 mm, 60 mm, 70 mm, 80 mm, 100 mm, 120 mm, and 140 mm (measured between opposite knots). These nets were equipped with sinkers and floats at the ends and deployed randomly from the shoreline toward the lake center. Nets were set in the late afternoon and retrieved the following morning, remaining in the water for approximately 17 h per sampling.

Stream fish sampling followed the RAPELD protocol for aquatic environments [47]. Sampling units were 50 m stretches, where fish were collected using cast nets, seines of different mesh sizes, and ichthyological sieves, with repeated efforts until both margins and the full length of the stretch were thoroughly sampled.

Voucher specimens of all recorded species were collected and deposited in the zoological collections of the Instituto Nacional da Mata Atlântica (INMA) and the Centro Universitário Norte do Espírito Santo (CZNC) (see list in Appendix B). Native species identified in the field were released back into their respective capture sites after sampling. Surplus individuals of non-native species not destined for collections were either discarded or donated. The classification of fish as native or non-native and taxonomic identification was based on specific literature [48,49].

2.3.2. Structural Data

Structural data in streams were collected from three cross-sections located at 5 m, 25 m, and 45 m along each 50 m stretch. Parameters recorded included depth (cm), width (m), water velocity (m/s), substrate composition (percentage), riparian vegetation cover (percentage), canopy cover density (percentage), presence or absence of sewage or dams, and the percentage of exposed soil in the surrounding area, following RAPELD methodology [47]. In streams narrower than 2 m, a single measurement was taken at each cross-section. In wider streams, average values were calculated from measurements taken at both margins (1 m from the edge toward the center of the stream) and in the middle of each cross-section.

2.3.3. Physicochemical Parameters

Water physicochemical parameters included pH, temperature (°C), dissolved oxygen (mg/L), salinity (ppt), electrical conductivity (MsC), and total solids (ppt), measured using a multiparameter probe. Dissolved oxygen values were converted to percent saturation to account for the influence of temperature on solubility. This conversion followed the solubility formula and temperature-specific reference table [50], assuming a constant atmospheric pressure of 1 mmHg at all sampling locations.

2.3.4. Native Vegetation in the Landscape

The percentage of native vegetation in the landscape was assessed at two spatial scales: local and riparian. The local scale was defined as a 250 m radius buffer around the central point of each sampling site. The riparian scale encompassed a 30 m buffer along the entire upstream drainage network feeding into each site (Figure 3), based on the Brazilian Institute of Geography and Statistics (IBGE) [44] shapefile of watercourses. To estimate native forest cover, land use and land cover data from State Institute for the Environment and Water Resources of Espírito Santo (IEMA) [51] were clipped at both scales. Areas classified as "native forest" and "native forest in early regeneration stage" were selected and summed to obtain the total native vegetation area. Metrics generated at the local and riparian scales were referred to as "Forest250" and "Forest30", respectively.

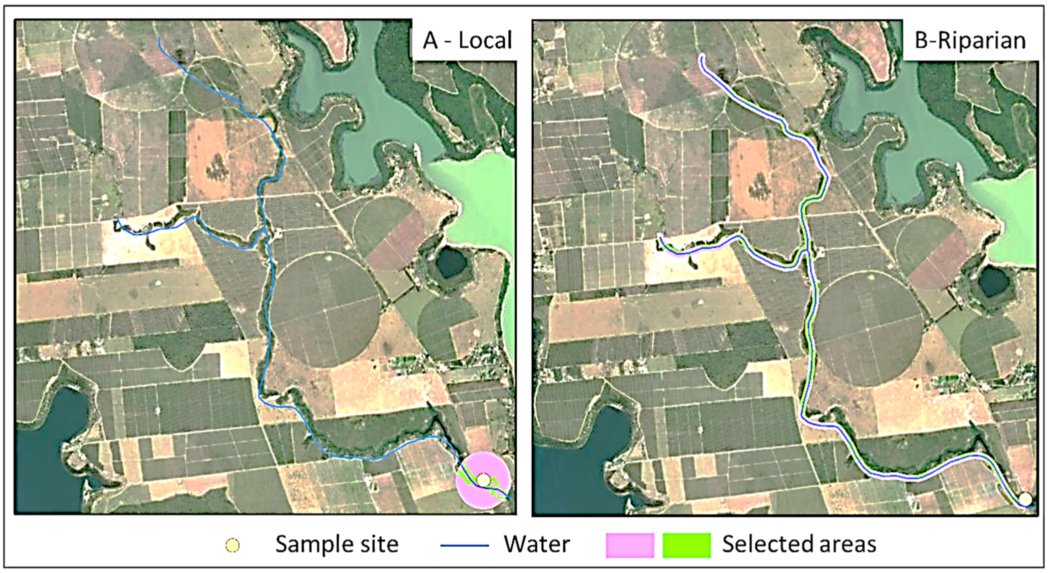

Figure 3. Representation of the local (**A**) and riparian (**B**) scales used to assess the percentage of native vegetation—a metric applied in the study of environmental variables influencing the ichthyofauna of the lacustrine complex of the lower Doce River.

2.4. Data Analysis

2.4.1. Comparisons Between the Ichthyofauna of Lakes and Streams

To compare the richness between lakes and streams, rarefaction curves based on individuals were constructed [52], in which comparisons are made considering the abundance of the community standardized by the smallest number of individuals. In order to compare the diversity between lakes and streams, we used a diversity profile based on "*Rényi series*" [53], in which values of the different indices are placed on a continuum, called an α, whose lower values indicate the attribution of greater weight to the number of species, and higher values indicate greater weight attributed to dominance. In addition, the differences between the types of environments (lakes and streams) were tested in relation to the parameter's richness, diversity and dominance in the analysis of paths, explained further on. Diversity was represented by the Shannon index [54] and dominance by the Simpson index [55].

To compare species composition in lake and stream communities, a matrix was organized with the presence and absence of all species recorded by type of environment (lake or stream) and the Principal Coordinate Analysis (PCoA) was performed using the Jaccard index [56]. Then, to test whether the species composition is significantly different between lakes and streams, permutational multivariate analysis of variance—PERMANOVA was performed [57]. These analyses were performed with the aid of the Past software, version 4.03 [58].

To determine whether there are species strongly associated with any of the types of environments, an analysis of indicator species (IndVal) was carried out [59]. This analysis uses the combined abundance and frequency to identify indicator species, that is, more characteristics of a given habitat type, when these are predominantly associated with that type. The analyses were carried out in an R environment version 4.3.2 [60] with the "indicspecies" package version 1.7.6 [61].

Beta diversity and its subcomponents (diversity partition) were evaluated to determine if the processes of differentiation of native and non-native fish communities are different between lakes and streams. Beta diversity was calculated by the Sorensen index and the turnover (Simpson) and nestedness (Nested) components [62] considering: 1—lakes and streams as local communities (alpha) and total sample of both environments as regional community (gamma); 2—each sampling area as local community (alpha) by type of environment (lake or stream) and the total set within each environment as regional community (gamma). In the two scales, the analyses were made separately for native species, non-native species and for the total set of species. The analyses were developed using the R (version 4.3.2) programming language, and beta functions: SOR, beta; YES and beta; and NES from the betapart package version 1 [63].

2.4.2. Distribution of Non-Native Ichthyofauna Across the Internal Lake Complex

A chi-square (x^2) test was used to test for differences in the frequency of non-native fishes between lakes and streams, and between upstream and downstream sections of streams relative to the connected lake. These analyses were performed using the Past software, version 4.03 [58]. A generalized linear model (GLM) was used to test the influence of the distance of each stretch of stream sampled from the nearest lake and the proportion of non-native species in each sampling. The proportion of non-native species (response variable) was logarithmized and normal distribution was used. One of the sampling sections (JES1B) was excluded from this analysis because it is located between two small artificial lakes (i.e., small reservoirs on private properties) and less than 150 m from each one. The analyses of the models and residuals (Figures S1–S9) were carried out in the R environment (version 4.3.2) [60,64] and the graphs were generated with the Past software version 4.03 [58].

2.4.3. Influence of Non-Native Ichthyofauna on Native Fish Communities

To assess the effect of non-native ichthyofauna on the native fish community, two complementary approaches were employed: generalized linear models (GLM) and path analysis. The GLMs were applied separately for lakes and streams and individually for pairs of variables, always using as an explanatory variable the proportion of non-native species per sample and response variable richness, diversity and dominance, considering separately the total fish community and the native fish community. To represent diversity, the Shannon index was used, and the Simpson index was used for dominance. Diversity and dominance were logarithmized and the normal distribution for the models was used. The models that considered richness as a dependent variable used the untransformed values and the Poisson distribution.

To examine multiple influences and multiple responses simultaneously, path analysis or "piecewise Structural Equation Modelling" [65] was used. This is an analysis that allows the testing of multiple hypotheses, in which the same variables can be used simultaneously as explanatory variables and response variables, and allows for the separate analysis of the direct and indirect effects of these variables [66]. Environment type—lakes (0) and streams (1) and the distance from each stream stretch to the nearest lake (with a value of 0 for lakes) were defined as explanatory variables. As response variables, richness, diversity represented by the Shannon index and dominance represented by the Simpson index were defined, considering separately the total fish community and the native fish community. The proportion of non-native fishes in relation to the total number of fish in each sampled area was used as a response variable in relation to the type of environment and the distance to the nearest lake and as an explanatory variable in relation to diversity, richness and dominance. The values of the variables proportion of non-native species, diversity and dominance were logaritimized. The models that employed diversity and dominance as response variables used normal distribution and, for wealth analyses, Poisson distribution. In all stages, the model residues were checked. These analyses were developed in the R environment (version 4.3.2) [60,64].

2.4.4. Influence of Habitat on the Fish Community in Streams

To investigate the influence of stream structural characteristics on fish community composition, we performed a Redundancy Analysis (RDA) [67], relating the Bray–Curtis dissimilarity matrix of community structure to a matrix of independent environmental variables. Species abundance was transformed into relative abundance using the Hellinger method [68]. As the R^2 can be inflated by collinearity between variables [65], the "vif.caa" function of the "Vegan" package version 2.7 [64] was used to remove the correlated variables that can inflate the variance. Variables with an inflation factor of variance greater than 10 were removed from the analysis. First, an RDA was performed using all uncorrelated variables; variables with a p-value < 0.1 were selected, and a partial RDA was subsequently conducted using only these variables. The significance of the RDA was evaluated by permutation testing using the "permutest" function, with 999 randomizations and the r^2 value adjusted for the RDA was calculated using the "RsquareAdj" function of the "Vegan" package [62].

Generalized linear models were used to test the direct influence of each of the environmental variables—physicochemical, structural and landscape—on the proportion of individuals belonging to non-native species. The proportion of individuals belonging to non-native species (response variable) was logarithmized and normal distribution was used. The analyses of the models and residuals (Figures S1–S9) were carried out in the R environment (version 4.3.2) [60] and the graphs were generated with the Past software version 4.03 [58].

3. Results

3.1. Overall Results

A total of 1577 individuals were sampled, including 677 from lakes and 900 from streams. Thirty-eight distinct species were identified (Appendix A), with comparable species richness observed in lakes (S = 25) and streams (S = 28). Among these, 27 species were classified as native and 11 as non-native.

Native species represented approximately 75% of all individuals (n = 1187), while non-native species accounted for 25% (n = 390). The proportion of non-native individuals was notably higher in lakes (41%) compared to streams (12%). This elevated presence of non-native species in lakes is largely due to the high abundance of *Metynnis lippincottianus* (n = 109) and *Pygocentrus nattereri* (n = 107), which were recorded in nearly all lakes sampled.

3.2. Comparisons Between the Ichthyofauna of Lakes and Streams

The stabilization trend observed in the rarefaction curves suggests adequate sampling coverage across both environments (Figure 4). The overlap of the 95% confidence intervals indicates that species richness does not differ significantly between streams and lakes. However, there is a tendency for higher richness in streams when considering only native species (right panel), as the overlap of confidence intervals is reduced.

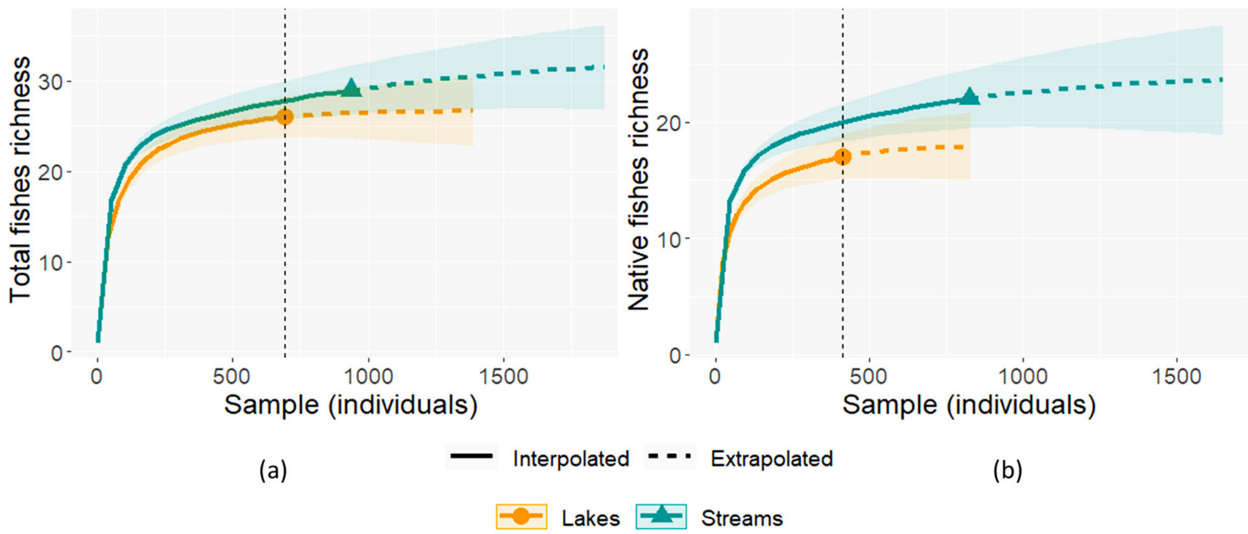

Figure 4. Rarefaction curves for fish samples collected in lakes of the Lower Doce River and its tributary streams, considering all species (**a**) and only native species (**b**).

The diversity profiles (Figure 5) indicate that streams are more diverse than lakes, regardless of the diversity index used, because the profiles do not intersect and their confidence intervals (95%) do not overlap. The difference in diversity between the two environments is more pronounced considering only the native ichthyofauna (graph on the right).

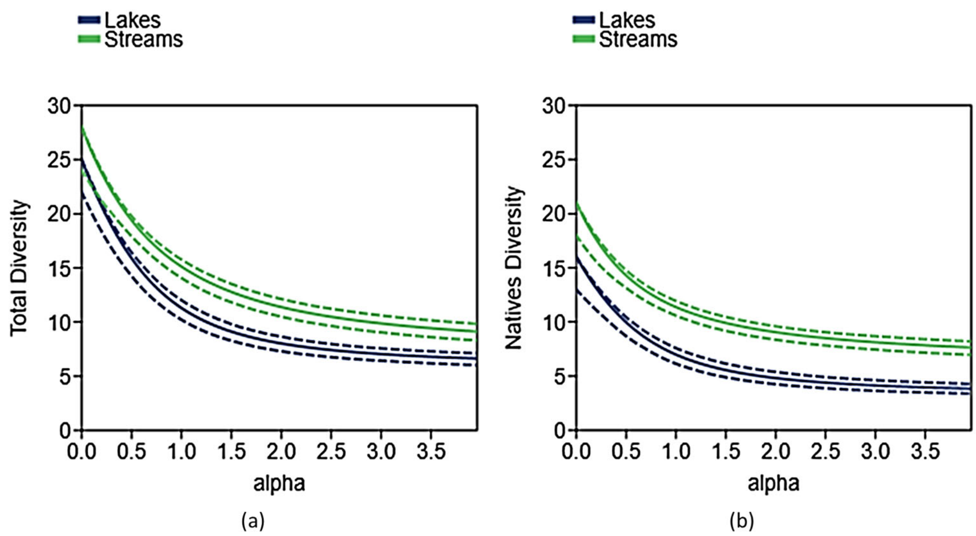

Figure 5. Diversity profiles following Hill's series for fish samples from lakes of the lower Doce River and their tributaries (streams). On the left considering all the ichthyofauna (**a**) and on the right only the native species (**b**). Solid lines represent calculated values, and dashed lines represent the 95% confidence interval.

Lakes and streams showed communities with significantly different compositions (Permanova, F = 5.15; $p < 0.01$). The PCoA ordering, using the Jaccard index, showed an explanation percentage of 26.48% for the first two axes (Axis 1 = 14.26%; axis 2 = 12.22%) and there was little overlap between the set of points sampled in lakes (light blue) and streams (black) (Figure 6).

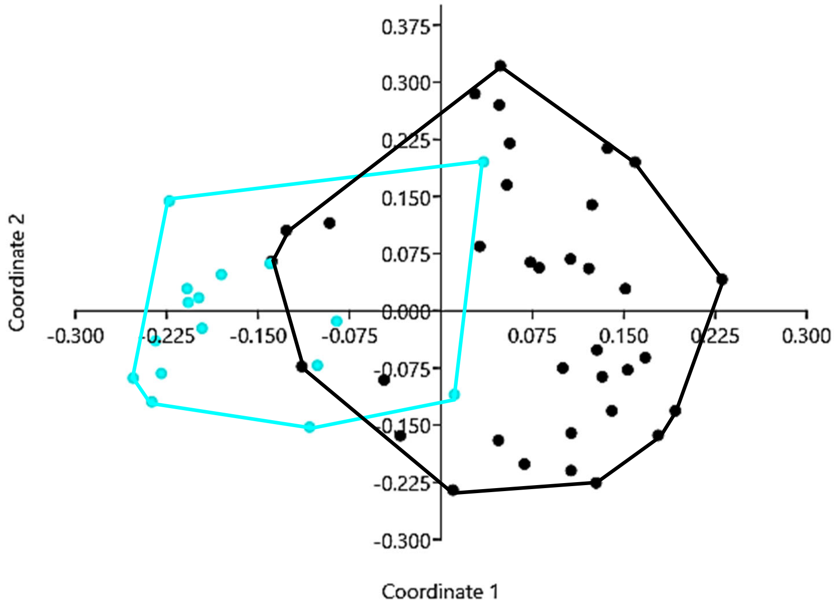

Figure 6. Ordering of fish communities in internal lakes of the lower Doce River and their tributaries by PCoA using Jaccard's index. The light blue dots represent the lakes and the black dots represent the sampled stream stretches. Percentage of explanation of the axes: Axis 1—14.26%; axis 2—12.22%. Permanova: F = 5.15; $p < 0.01$.

The indicator species that showed a strong association with the type of lake environment, according to the index of indicator species (IndVal), were *Trachelyopterus striatus*, *Pygocentrus piraya*, *Pigocentrus nattereri*, *Prochilodus lineatus*, *Pachyurus adspersus*, *Hoplosternum littorale* and *Astyanax lacustris*. The species *Crenicichla lacustris* was associated both with lakes and with stretches of streams close to and intermediate in relation to lakes, and the species *Metynis lippincottianus* was associated with lakes and nearby streams (Figure 7). Among the nine species associated with the type of lake environment, four—*P. piraya*, *P. nattereri*, *P. lineatus* and *M. lippincottianus*—are considered of non-native origin for the region, and *P. nattereri* was the one that presented the highest indicator value (IndVal) among all, indicating a more evident association.

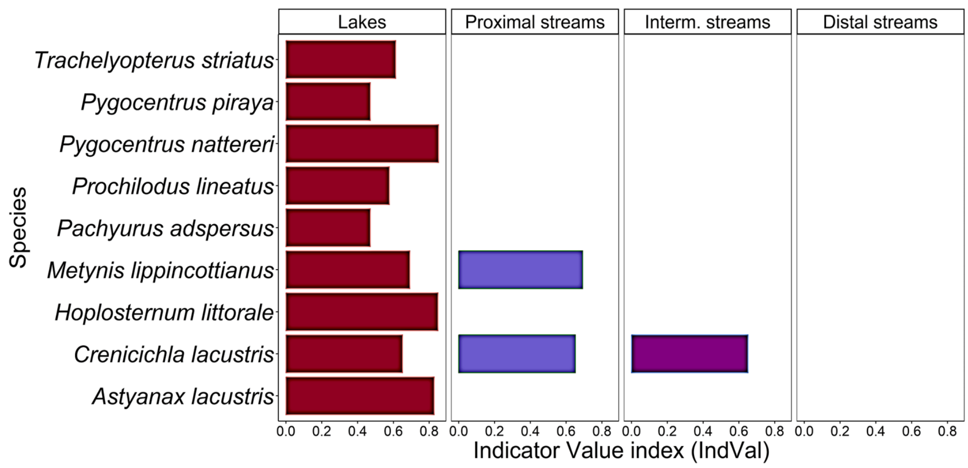

Figure 7. Index of indicator species (IndVal) for significant values ($p < 0.05$) indicating association with the types of environments sampled in the lakes of the lower Doce River and their tributaries by distance category: Distal_streams—stretches of streams far from the lakes (>5 km); Interm._streams—stretches of intermediate streams (between 1 and 5 km in relation to the lakes; Proximal_streams—stretches of streams near lakes (>1 km) and lakes.

The total beta diversity (Sorensen index), considering two communities—lakes and streams—was 0.43, with a turnover component of 0.40 and nestedness of 0.03 (Table 1), indicating that 40% of the species recorded occur only in one or another type of environment and that very little of the diversity found represents a subset of the total diversity (nestedness). Beta diversity is greater in streams than in lakes, varying little between non-native, native and total within each of these environments. The nestedness component is greater considering only the non-native species in both types of environments, but mainly in the lakes (Figure 8), indicating that the diversity of non-native species in each sampled area, more than in the native ones, are represented by the same subgroup of the total diversity (gamma) that occurs in various environments, especially in the lakes.

Table 1. Values of beta diversity (Sorensen index) and of the turnover and nestedness components for the total, native and non-native fish community in internal lakes of the lower Doce River and their tributaries, considering: 1—lakes and streams as distinct assemblages of the same community; 2—considering each sampling site as an assemblage within lakes and streams separately.

Type of Environment Considered	Community Considered (According to the Origin of the Species)	Number of Assemblages Considered	Beta Diversity (Sorensen)	Replacement (Simpson)	Nested
Lakes and streams	Total	2	0.43	0.4	0.03
	Natives	2	0.56	0.48	0.08
	Non-native	2	0.38	0.29	0.09
Lakes	Total	16	0.84	0.77	0.07
	Natives	16	0.84	0.75	0.09
	Non-native	16	0.85	0.65	0.20
Streams	Total	35	0.94	0.91	0.03
	Natives	35	0.93	0.89	0.04
	Non-native	35	0.95	0.86	0.09

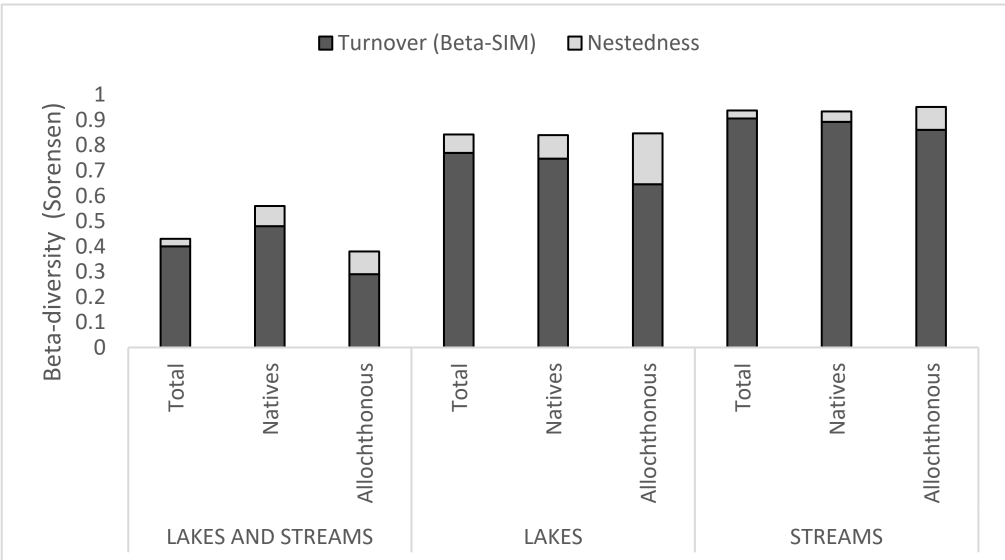

Figure 8. Beta diversity (Sorensen index) and turnover and nestedness components for the total, native and non-native fish community in internal lakes of the lower Doce River and their tributaries, considering: 1—lakes and streams as distinct assemblages of the same community; 2—considering each sampling site as an assemblage within lakes and streams separately.

3.3. Distribution of Non-Native Ichthyofauna Across the Internal Lake Complex

The frequency of non-native species differed significantly between lakes and streams ($\chi^2 = 170.6$; df = 1; $p < 0.01$). In lakes, 399 individuals (59%) were native species and 278

(41%) were non-native. In streams, 790 individuals (88%) were native and 110 (12%) were non-native (Table 2). Among streams, the frequency of non-native species also varied significantly between upstream and downstream sites ($\chi^2 = 119.4$; df = 1; $p < 0.01$), with a higher proportion of non-native species in downstream sites (31.5%) compared to upstream sites (5%) (Table 3).

Table 2. Frequency of native and non-native fishes in internal lakes of the lower Doce River and their tributaries. ($x^2 = 170.6$; gl = 1; $p < 0.01$).

	Environment	
Origin	**Lakes**	**Streams**
Native	399 (59%)	790 (88%)
Non-native	278 (41%)	112 (12%)

Table 3. Frequency of native and non-native fish in streams, by position relative to the adjacent lake (upstream/downstream) ($x^2 = 119.4$; gl = 1; $p < 0.01$).

	Position	
Origin	**Upstream**	**Downstream**
Native	612 (95%)	174 (68.5%)
Non-native	31 (5%)	80 (31.5%)

Within the streams, there is a slight trend ($p = 0.10$) of decreasing proportions of non-native species with increasing distance, despite high variability in the dataset, although it is not statistically significant ($p > 0.05$) (Figure 9).

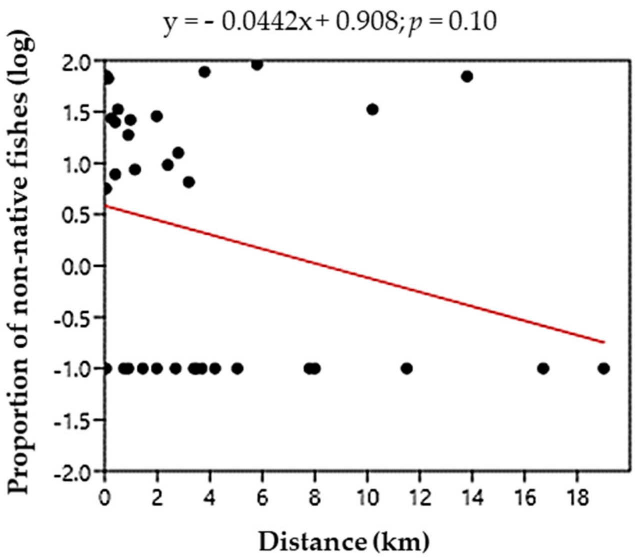

Figure 9. Influence of distance to the nearest lake on the proportion of non-native fish by sampling in streams of the lower Doce River lake complex (Normal distribution, $p = 0.10$). Relationship between Y and X, illustrated by the red line, with black points denoting individual samples.

3.4. Influence of Non-Native Ichthyofauna on Native Fish Communities

Path analysis indicated that the type of environment had a marginally significant influence ($p = 0.051$) on the proportion of non-native species and significant ($p < 0.05$) influence on richness, diversity (Shannon index) and dominance (Simpson index), both on the total ichthyofauna (Figure 10) and on the native ichthyofauna (Figure 11). The richness and diversity were positively affected by the environment, indicating that it was greater in the streams than in the lakes. The distance from the lakes had a marginally significant negative influence (p = 0.078) on the proportion of non-native fishes in streams, but did not significantly affect the parameters of richness and diversity (neither total nor native). The proportion of non-native fishes affected richness and diversity of the native ichthyofauna negatively ($p < 0.05$) and showed a marginally positive effect on dominance ($p < 0.1$). Significant relationships ($p < 0.05$) are represented by solid lines; Relationships with a p-value between 0.05 and 0.1 were represented by dotted lines; The relationships with $p > 0.1$ were represented by light gray lines. The blue color indicates positive relationships and the red color indicates negative relationships between the continuous variables. For the variable "Environment" the relationship was considered positive when the response variable was higher in the streams in relation to the lakes. The variables total richness, total dominance, native richness and Shannon native richness did not present variances with completely homogeneous distributions, although they presented normal distribution. The distribution and analysis of the residues of the models are presented in the Appendix C.1.

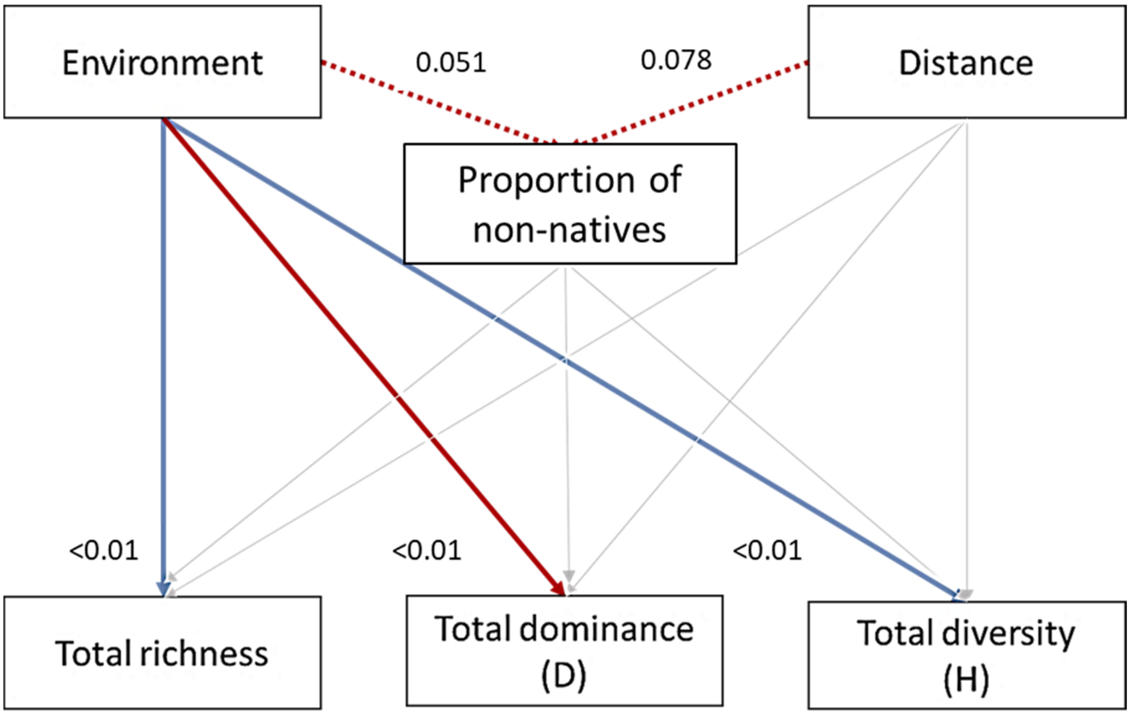

Figure 10. Results of path analysis for total ichthyofauna sampled in internal lakes of the lower Doce River and their tributaries. Variables analyzed: environment (lake or stream); proportion of non-native species by sampling; distance from the sampling site in relation to the lakes (zero value for sampling within the lakes); Shannon's richness, diversity, and Simpson's dominance. Non-significant relationships ($p > 0.1$) are represented by light gray lines; Significant relations ($p < 0.05$) are represented by solid lines and marginally significant relationships ($p < 0.1$) are represented by dotted lines. The blue color indicates positive relationships and the red color indicates negative relationships between the continuous variables. For the variable "Environment" the relationship was considered positive when the variable was higher in the streams in relation to the lakes. The numbers in the figure indicate the p value of each ratio.

Considering each environment separately, generalized models (GLM) that tested the influence of the proportion of non-native species on the richness, diversity and dominance of ichthyofauna in lakes showed non-significant results ($p > 0.05$). In the streams, the proportion of non-native species significantly reduced the richness and diversity of native species, increased native species' dominance, and reduced total diversity ($p < 0.05$). The decrease in total richness was marginally significant (p = 0.059) (Figure 12).

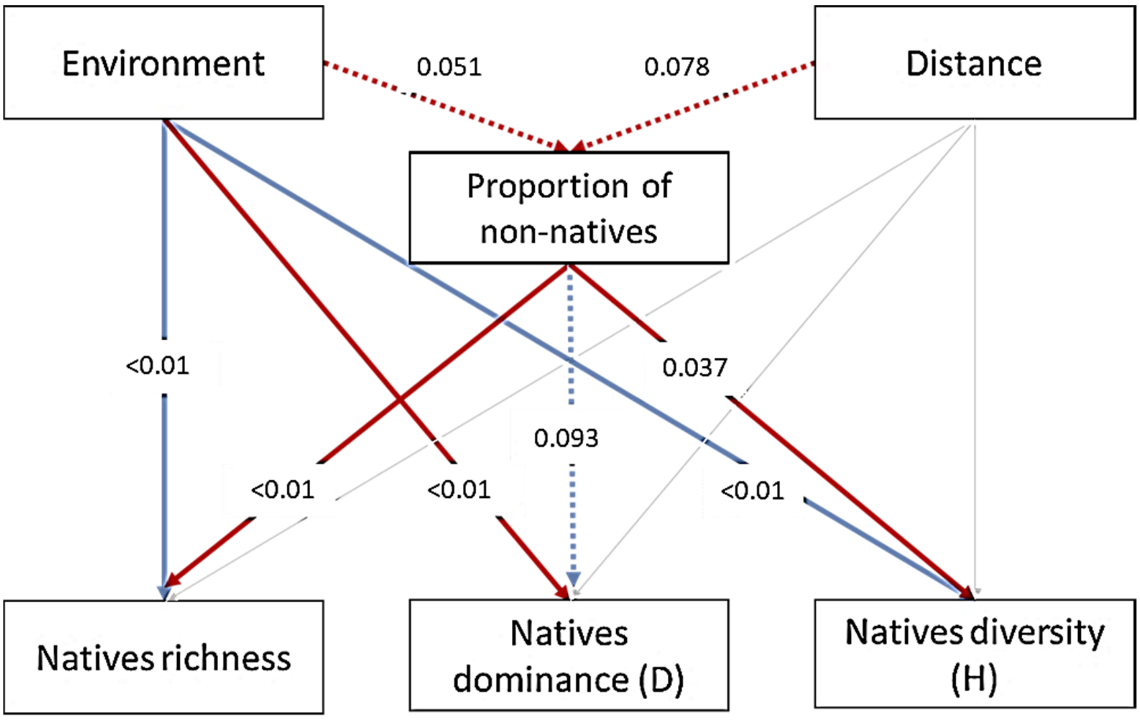

Figure 11. Results of path analysis for native ichthyofauna sampled in internal lakes of the lower Doce River and their tributaries. Variables analyzed: environment (lake or stream); proportion of non-native species by sampling; distance from the sampling site in relation to the lakes (zero value for sampling within the lakes); Shannon's richness, diversity, and Simpson's dominance. Non-significant relationships ($p > 0.1$) are represented by light gray lines; Significant relations ($p < 0.05$) are represented by solid lines and marginally significant relationships ($p < 0.1$) are represented by dotted lines. The blue color indicates positive relationships and the red color indicates negative relationships between the continuous variables. For the variable "Environment" the relationship was considered positive when the variable was higher in the streams in relation to the lakes. The numbers in the figure indicate the p value of each ratio.

3.5. Influence of Habitat on the Fish Community in Streams

For the complete RDA, the variable "block", referring to the type of substrate, presented a high variance inflation factor (>10) and was removed. The complete RDA showed an explanation percentage of 69% and an adjusted r^2 of 0.05, but the model was not significant (permutation test, $p > 0.05$). The variables with significance <0.10 were: percentage of native forest in 30 m of the upstream surroundings (mat30); percentage of silt in the substrate; average depth in the sampling section; percentage of vegetation on the banks; covering leaves in the substrate; canopy cover in the sampled section and presence of a sandbar in the substrate (Table 4). These variables were selected to perform the final RDA.

The final RDA, performed only with the selected variables ($p < 0.1$), was significant (permutation test, $p = 0.002$), presented an explanation percentage of 28% and an adjusted r^2 of 0.09 (Figure 13; Appendix C.2). The most representative species in the analysis were *Astyanax lacustris*, *Astyanax* sp., *Poecilia reticulata*, *Deuterodon intermedius*, *Knodus moenkhausi*, *Crenicichla lacustris* and *Coptodon rendalli*. In the second level, the species *Australoheros capixaba*, *Hyphessobrycon eques*, *Mugil curema*, *Hoplosternum littorale*, *Hoplias malabaricus* were representative.

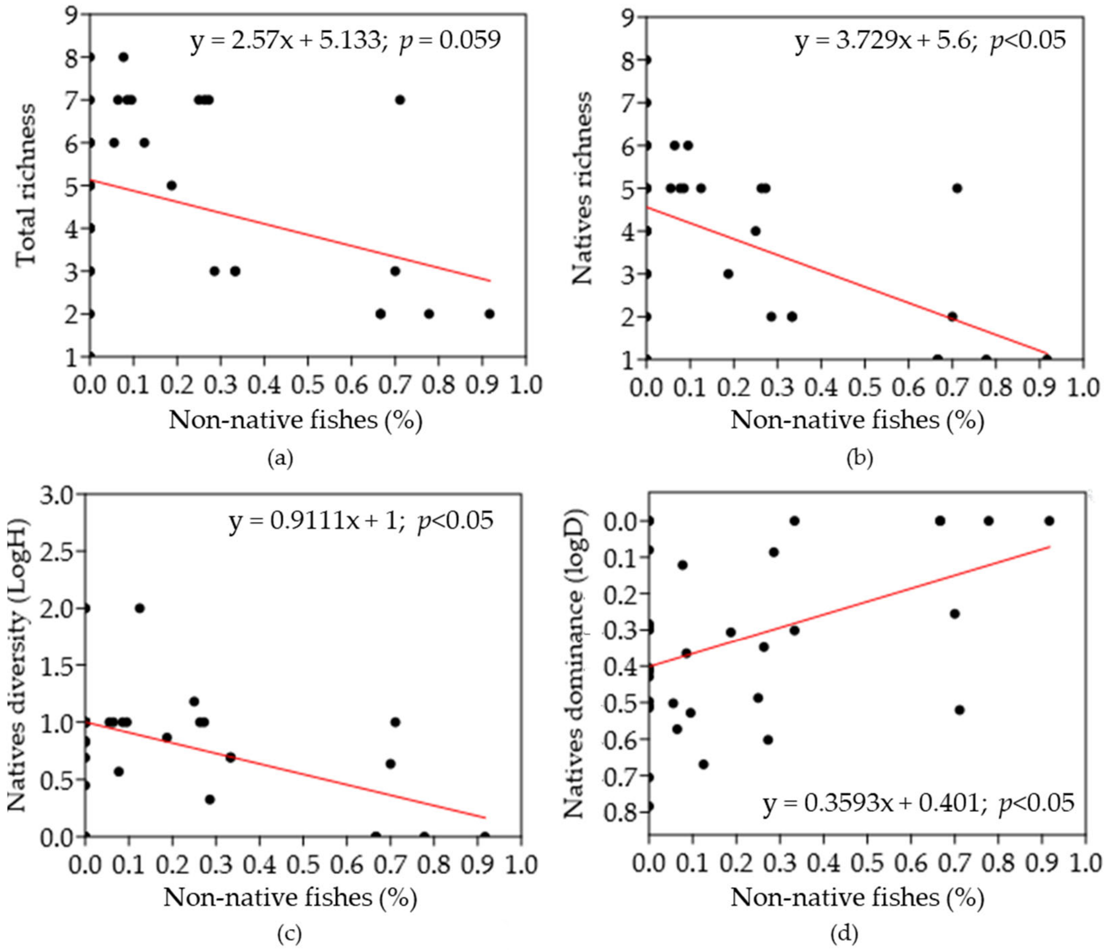

Figure 12. Generalized Linear Models (GLM) for the influence of the proportion of non-native species in fish samples from streams of the lower Doce River internal lake complex on the variables: (**a**) total richness; (**b**) natives' richness; (**c**) natives' diversity represented by Shannon index (log) and (**d**) natives' dominance represented by Simpson index (log). Relationship between Y and X, illustrated by the red line, with black points denoting individual samples.

Table 4. Significance of main variables for the RDA (redundancy analysis) between the environmental variables and the fish community sampled in the streams of the lower Doce River lacustrine complex. Adjusted $r^2 = 0.05$.

Variable	Abbreviation	AIC	F	*p*
Proportion of native vegetation within a 30 m riparian buffer upstream of the streams	Forest30	−4.23	2.16	0.010
Proportion of silt in the substrate	Silt	−4.42	2.00	0.010
Average depth of the reach	Depth	−4.8	1.69	0.040
Riparian vegetation	MargVeg	−4.68	1.79	0.045
Leaf litter cover on the substrate	Leaves	−4.98	1.54	0.075
Canopy cover	CanCov	−4.91	1.60	0.085
Presence of sandbars	Sand	−4.98	1.54	0.090

The most notable associations between fish species and stream environmental variables were as follows: *Knodus moenkhausi* and *Coptodon rendalli* showed a positive association with the "mat30" variable; *Poecilia reticulata*, *Hyphessobrycon eques*, *Mugil curema*, *Australoheros capixaba*, *Crenicichla lacustris* and *Mugil curema* showed a positive association with the variables depth and vegetation on the margins; *Deuterodon intermedius* and *Poecilia* with the vegetation variables on the margins and canopy cover and *Astyanax* sp. and *Astyanax lacustris* with the silt variable. Other milder positive associations were of *Hoplosternum littorale* and *Hoplias malabaricus* with mat30, leaves in the substrate and sand; in addition to *Otothyris travassosi*, *Oligosarcus acutirostris* and *Gymnotus carapo* with canopy cover.

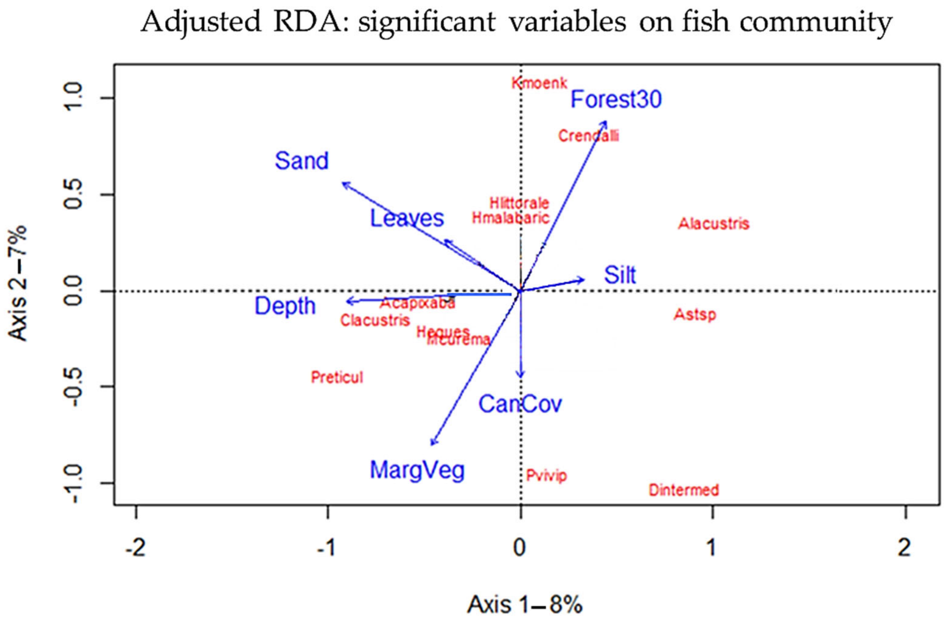

Figure 13. Adjusted redundancy analysis between the most significant environmental variables ($p < 0.1$) and the fish community sampled in the streams of the lower Doce River lake complex. $r^2 = 0.36$; $p < 0.001$. Legend of the species: Kmoenk = *Knodus moenkhausii*; Crendalli—*Coptodon rendalli*; Alacustris = *Astyanax lacustris*; Astsp = *Astyanax* sp.; Dintermed = *Deuterodon intermedius*; Pvivip = *Poecilia vivipara*; Preticul = *Poecilia reticulata*; Heques = *Hyphessobrycon eques*; Otravassosi = *Otothyris travassosi*; Oacuti = *Oligosarcus acutirostris*; Haffinis = *Hypostomus affinis*; Mcurema = *Mugil curema*; Clacustris = *Crenicichla lacustris*; Acapixaba = *Australoheros capixaba*; Hlittorale = *Hoplosternum littorale*; Hmalabaric = *Hoplias malabaricus*.

Among all environmental variables measured in the streams, only depth and width showed a significant positive relationship with the proportion of non-native species (width—$r^2 = 0.11$; $p = 0.045$; depth—$r^2 = 0.11$; $p = 0.042$) (Figure 14).

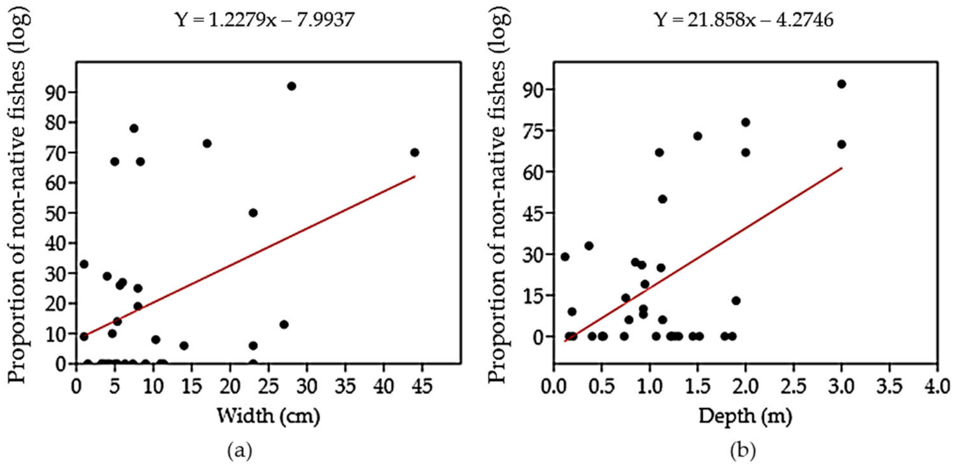

Figure 14. Influence of the variables width (**a**) and depth (**b**) on the proportion of non-native fishes sampled in streams of the lower Doce River lacustrine complex. $p < 0.01$. Relationship between Y and X, illustrated by the red line, with black points denoting individual samples.

4. Discussion

4.1. Comparisons Between the Ichthyofauna of Lakes and Streams

Although Atlantic Forest streams generally exhibit lower richness when compared to other aquatic environments, such as lagoons and rivers [6], the present study recorded higher richness and diversity in the streams than in the internal lakes of the lower Doce River, particularly for native species. It should be noted, however, that lake sampling was conducted along the margins, while central and deeper regions were not surveyed. Deeper lake areas may harbor species not recorded in this study, as depth creates microhabitat segregation and provides refuge from unstable conditions and intense predation common at shallower depths [69]. Marceniuk et al. [70] mention that the persistence of the critically endangered species *Paragenidens granducolis* in Lagoa Nova (one of the internal lakes sampled in the present study) is possibly associated with the high depth found in this lake, which allows the species to survive in deep areas rarely occupied by potential predators, such as piranhas.

The ichthyofauna of the internal lakes differs markedly from that of the tributary streams, confirming that these two environments possess distinct ecological characteristics that shape different fish communities. The species strongly associated with the lakes were precisely some of the largest found within the complex (*Trachelyopterus striatulus*, *Pygocentrus piraya*, *Pigocentrus nattereri*, *Prochilodus lineatus*, *Pachyurus adspersus*, *Metynis lippincottianus*, *Hoplosternum littorale*) which were adapted to the lentic environment and/or to large water bodies [71–75]. An exception was *Astyanax lacustris*, a small species associated with the lake environment. It has already been observed that in Atlantic Forest small streams, *Astyanax* species can be partially replaced by species of the genus *Deuterodon*, possibly because these are specialized in feeding on leaves that fall from marginal trees [76].

Of the nine species associated with this environment, four are considered non-native to the region (*P. piraya*, *P. nattereri*, *P. lineatus* and *M. lippincottianus*). Among them, *M. lippincottianus* was also associated with the stretches of streams near the lakes, indicating that the habitat of this species is not restricted to the lakes, but presents some limitation in relation to the proximity to them. Similarly, *Crenicichla lacustris* seems to have a preferential occurrence in and near lakes, a little less restricted than that of *M. lippincottianus*, since *C. lacustris* was associated with nearby and intermediate streams.

Among the species we recorded in the region, 13 occurred exclusively in the streams, but four of them had only one or two captures, and this exclusivity is possibly due to their rarity in the sampling. The species recorded exclusively in streams with more than ten individuals were *Mugil curema*, *Otothyris travassosi*, *Hypostomus affinis*, *Hyphessobrycon* sp., *Poecilia reticulata*, *Deuterodon intermedius* and *Knodus moenkhausi*, with emphasis on the last two, which had 75 and 132 individuals, respectively. However, no indicator species were identified for the streams, because the index of indicator species takes into account not only the abundance, but also the frequency of occurrence of the species among the sampling areas. Due to the high heterogeneity among local stream communities, even typical stream species were absent from many sampling locations within this environment. On the other hand, in the lakes, the indicator species were found with high abundance and frequency, as they are widely distributed among the internal lakes.

This result cannot be attributed to easier dispersion within lakes, as they are distinct water bodies connected only through streams. Therefore, this effect could be attributed to the greater environmental heterogeneity in the streams or to the possibility of species being released differently in the two types of environments. However, if this result were related only to releases, it would be valid only for the species preferred by fishermen and breeders, and would not be valid for most native and smaller species. This indicates that environmental characteristics and the sharing of these characteristics among lakes determine the association of certain species with this type of environment.

Beta diversity is higher in streams than in lakes, indicating greater differentiation among local fish communities in streams. This result is an indication that in lakes there should be greater biotic homogenization, a process in which the introduction of non-native species and consequent loss of native species (often endemic) reduces the distinction of biota [77,78], resulting in ecological and evolutionary losses [78–80]. One of the characteristics of biotic homogenization is that it leads to a reduction in beta diversity [81].

Analysis of turnover and nestedness components of beta diversity illustrated that fish communities are structured by different processes in lakes and streams. In addition, the differentiation of native and non-native fish assemblages is different in both environments. The nestedness component is higher for non-native fish than for native fish, particularly in lakes. The turnover, in turn, is more expressive in streams than in lakes, both for native and non-native species. The turnover component reflects an exchange of species or relative abundances between communities and can be caused by species gain or loss as a result of competition, environmental filtering, or historical dispersal factors [82–84]. Nestedness indicates a process of non-random loss of species, which generates a pattern in which sites with a lower number of species are subsets of sites with a higher number of species [62]. Therefore, nestedness can be the result of different processes, such as habitat reduction [85], reduction in environmental heterogeneity [86], disturbances in the environment [87], selective extinction of species [88], or even selective colonization, in which the isolation of habitats generates nestedness due to limited dispersion [89,90].

The observed pattern indicates that in local lakes, communities with lower numbers of species represent subsets of communities with higher numbers of species, mainly for non-native species. This is because the same subset of non-native species is common in most lakes. In the tributary streams of these lakes, different stretches have subsets of non-native species that differ more from each other, so the turnover component is larger. The non-native species *Metynnis lippincottianus* and *Pygocentrus nattereri* were collected in nine and eight of the nine lakes sampled, respectively; in the streams, the non-native species present in the largest number of stretches presented a proportionally much lower frequency. The species *Poecilia reticulata*, *Hyphessobrycon eques* and *Cichla kelberi*, were present, respectively, in seven, six and five of the 35 stretches.

In this study we did not quantify the introductions of non-native species, but it is likely that over decades the same set of non-native species has been introduced throughout the region and that subsets of species more adapted to lentic environments and with a large volume of water have been established and disseminated through the internal lakes. The introduction of fish into the middle Doce River began to occur in the 1970s, with the introduction of species originating mainly from the Amazon, Paraguay and Paraná basins [91,92]. In the lower Doce River, the introductions must have occurred at the same time, since it was the period in which they occurred in other places in southeastern Brazil [93,94] and when the region of Linhares began to be strongly impacted by human occupation and economic activities [26,27,95]. *Metynnis lippincottianus* is a species native to South America, found in the Amazon Basin and distributed in the Amazon Basin and the Guiana Shield [96,97]. It is a pelagic which is essentially herbivorous [98–100]. *Pygocentrus nattereri* is a predatory species typical of lentic environments [101] whose biological and demographic characteristics indicate adaptations to floodplain lakes [102].

In tributary streams, although the same species are potential colonizers, non-native species compose more distinct assemblages from each other and with a greater turnover component. This seems to be a consequence of an isolation, at least partial, within stretches of streams that have favorable characteristics for the species that were introduced. Of the nine non-native species present in the lakes, five also occur in the streams, but their occurrence is much more punctual, generating greater beta diversity and turnover.

Considering that the depth and width of streams positively affect the proportion of alien species, then narrow and shallow stretches are less favorable to alien species and it is plausible to assume that they hinder their dissemination, thus generating some degree of isolation from their local assemblages. Another implication of this isolation is that the composition of non-native communities in streams should be more affected by the recurrence of punctual introductions than by colonization, generating high beta diversity and high turnover component. In lakes, on the other hand, a few events of introductions of non-native species adapted to their conditions can result in a colonization of the entire environment.

Another factor influencing fish dispersal in this system is its directional flow. Waterfalls hinder or prevent transit upstream but not downstream [103]. Thus, in a lake that receives several tributaries, presumably the colonization of the tributaries upstream to the lake is more intense than the opposite direction. In this way, a lake receives species present in several tributaries, while each tributary tends to receive fewer species coming from the lake, especially in higher stretches, although this depends a lot on the morphology of the channels and the ability of the introduced species to overcome them.

4.2. Distribution of Non-Native Ichthyofauna Across the Internal Lake Complex

The results indicate that non-native fish are proportionally more abundant in the internal lakes of the Lower Doce River than in the connected streams, and that stream assemblages exhibit greater differentiation among themselves. The results show that there are proportionally more non-native fish in the internal lakes of the lower Doce River than in the streams connected to these lakes and that in the streams there is greater distinction between their local assemblages.

There is also a trend toward a reduction in the proportion of non-native species in streams with increasing distance from the lakes. This trend suggests two possible explanations: (1) with increasing distance from the lakes, streams accumulate stretches of unfavorable habitat for non-native species, limiting their dispersal and reducing their proportion; and/or (2) with increasing distance from the lakes, streams progressively decrease in width and depth, characteristics that influence the proportion of non-native species. However, distance did not influence stream depth or width—probably because both upstream and downstream stretches were considered relative to the lakes, and due to the presence of numerous small dams throughout the region—thereby ruling out the second explanation.

The proportion of non-native species was significantly higher in streams downstream than upstream of the lakes. This suggests that the dispersal of non-native fish from the lakes to the streams is an important factor, as the dispersal downstream is easier than upstream, since waterfalls hinder or prevent transit upstream but not downstream [103]. Thus, the first explanation is more plausible, as the distance from the lakes itself seems to be the primary factor influencing the proportion of non-native species, rather than correlated physical attributes such as width and depth.

Therefore, the results of this study indicate that regional streams contain habitats less favorable to introduced fish species than lakes, where the pressure they exert on native species is greater. It is unlikely that these environments completely prevent the passage of non-native species, but the accumulation of stretches with these characteristics along the watercourse likely acts as an ecological filter, gradually limiting their spread and establishment.

4.3. Influence of Non-Native Ichthyofauna on Native Fish Communities

Streams contain habitat stretches less impacted by non-native fish than lakes, and therefore represent potential refuges for native ichthyofauna. However, native ichthyofauna appeared more sensitive to the presence of non-native species in streams than in lakes. In streams, the proportion of non-native species is related to the reduction in richness and diversity and increased dominance among native fish, whereas in lakes no significant influence on these parameters was detected. This suggests that coexistence between native and non-native species is more stable in lakes than in streams.

However, this does not imply that the impact of non-native fish on lakes is lower than on streams. Considering the time that has elapsed since the first introductions and the way in which non-native species are disseminated in the internal lakes of the lower Doce River, the current ichthyofauna is certainly different from the original. Currently, the native ichthyofauna in both environments consists of species that persisted through historical and contemporary impacts in the region, including those caused by non-native species. Precisely because they present refuges for native fauna, there are places in the streams with a low proportion of non-native and high richness of natives and on the contrary, places with a high proportion of non-native and low richness of natives, which explains the relationship between these two variables. Moreover, the smaller size of stream habitats makes them more vulnerable to local species extinctions. The probability of local extinction is higher in smaller areas with clustered individuals than where species occupy multiple sites forming meta-populations [104]. The influence of migrations on community structure tends to be greater in smaller and more simplified habitats than in larger and more complex habitats [105]. Considering the entire network of streams within the system, this environment is more heterogeneous, less impacted by non-native species, and harbors greater native species diversity. On the other hand, in portions of habitat that allow the expressive presence of non-native, the native ichthyofauna is more sensitive to their impacts.

An additional possible explanation for these results—requiring more specific investigation—relates to niche occupation. The internal lakes of the Doce River are of fluvial origin and the native species that colonized these lakes evolved in fluvial environments of the Atlantic Forest, which are typically small streams [76]. For this reason, the occupation of niches by native species in streams must be more complete than in lakes, since the longer evolutionary time of the species in this environment provides greater ecological specialization. Therefore, native species in streams are expected to occupy a greater number of ecological niches, albeit with narrower specialization, whereas in lakes, niche occupation is likely broader but less specialized. From this scenario, two additional possible explanations emerge for the observed patterns:

1—richer communities are more resistant to invasion than poorer communities, because in them the use of resources is more complete and the establishment of invaders becomes more difficult [79]. This is another factor that may contribute to the low proportion of non-native and high richness of native streams in stretches that preserve typical characteristics of Atlantic Forest streams, and the opposite in stretches that had their fluvial regime more severely altered.

2—It is known that species tend to occupy smaller niches in the presence of competitors and predators than in their absence [106]. Thus, considering a lower specialization of native species in the use of lake conditions and resources, the exclusion of a species would be less likely in these environments, due to the greater possibility of realized niche variation in the presence of non-native species, reducing the pressure exerted by them. In addition, predation is one of the factors that can prevent competitive exclusion and, in some cases, the presence of the predator can even increase the richness of prey [16]. One of the main non-native species in the lakes is *Pygocentrus nattereri*, a predator that feeds on various types of prey [107,108], typical of lentic environments [101]. Despite its impact on native fish, this generalist predator may primarily feed on the most abundant species, alternating prey according to availability and thereby preventing population declines from reaching exclusion levels. This could even favor the coexistence of more competing species, whether native or non-native, counterbalancing the impact of piranhas on the richness and diversity of native species in the lakes. To further investigate this issue, it would be interesting for future studies to evaluate whether in the presence of piranhas there is a greater coexistence of functionally more similar species.

4.4. Influence of Habitat on the Fish Community in Streams

Given that stream fish communities are often species rich, and that each species is necessarily influenced by a shared suite of habitat factors, a complex web of direct and indirect effects arises whenever we attempt to include multiple habitat variables and populations in the same empirical analysis [2]. In a classic study in the Central Valley stream of California on the influence of environmental characteristics on the fish community, Marchetti and Moyle [109] identified a separation between native and non-native species, indicating a clear relationship of native species with a combination of variables that reflect the natural conditions of the water body. However, ordination of fish species along environmental gradients in the lower Doce River streams did not reveal a clear separation between native and non-native species.

Local environmental conditions have a stronger relationship with ichthyofauna in more preserved locations, while regional conditions affect this fauna more significantly in environments degraded by human actions, where the association of ichthyofauna with local habitat conditions has already been lost [103]. This appears to be the case in the Lower Doce River lake region, where the impacts on the ichthyofauna—especially the introduction of non-native species—are so severe that the associations between fish assemblages and local environmental conditions are weak. A positive association of the species *Coptodon rendalli* with the percentage of native forest around the streams (30 m) upstream of the sampled stretches and a slightly weaker association of *Hyphessobrycon eques* with the vegetation variables at the margin, depth and canopy cover were detected. This indicates that riparian vegetation recovery, including legally mandated APPs, although necessary and recommended, is not by itself sufficient to reduce the impact of non-native fish on native species in streams. In fact, the establishment of preservation areas based on attributes of the terrestrial environment has not been shown to be effective for the conservation of aquatic environments [110]. However, the depth and width of the streams are variables that influenced the percentage of non-native species in this region and, therefore, should be considered in conservation initiatives, especially aiming to reduce the impact of non-native fish species.

The Lower Doce River lake region is impacted by multiple human activities, original vegetation has been replaced, and the remaining forest fragments are scarce and no longer represent the original habitats in which species evolved. Thus, the influence of the current native vegetation on the native ichthyofauna may be less due to the direct supply of resources and more to the influence of this vegetation on the structural conditions of the environment, such as shading, type of substrate, organic matter (leaves), etc. Species with more specialized relationships with the original vegetation, such as frugivorous species, no longer occur in most of the region. However, even the mostly secondary vegetation that makes up the region can maintain less specialized native species.

Therefore, combining APP recovery with the preservation of long stretches of undammed small streams is a strategy that can both favor native species and hinder non-native species, thereby mitigating their impacts on native communities.

One factor that is usually considered in relation to the structure of lakes communities is their insular characteristics [105,111]. In these environments, the introduction of species can be seen as a factor in the change in the balance between colonization and extinction [112]. The connection between lotic and lentic habitats in the lacustrine complex of the middle Doce River in Minas Gerais is pointed out as a factor responsible for the invasion of the lakes of this region by non-native species [8,9]. The same occurs in the lower Doce River, where the connection between different lakes and the Doce River itself is made by a network of streams. In these streams, the distribution of non-native species is fragmented and their predominance is associated with stretches of greater depth and width. The connection between environments within the complex can allow gene flow, the replacement of individuals and even recolonization by native species, due to the possibility of movements, migratory or not. However, this connectivity also influences the probability of colonization by invasive species, as they are also subject to the constraints imposed by the spatial structure that limits their dispersal [9]. Since connectivity through the river network can favor both native and non-native species, the ideal scenario is one in which this network exhibits characteristics more favorable to native species and less favorable to non-native species. In this way, these streams can represent a reservoir for native fish and act as a filter for the dispersion of non-native fish, mitigating their impacts in the region.

5. Conclusions

One of the main factors affecting native fish assemblages in the Lower Doce River lake complex is the presence of non-native species. These species are widespread throughout the region, but are more prevalent in lakes than in tributaries, as most introduced species are better adapted to lentic environments with larger water volumes. In contrast, non-native species are less prevalent and more unevenly distributed in tributaries, due to greater environmental heterogeneity and the presence of shallower and narrower stretches that limit their dispersal. As a result, local streams provide refuges for native fish species and may function as filters against the spread of dominant non-native species, particularly upstream. However, native fish assemblages in streams are more sensitive to the presence of non-native species than those in lakes. Therefore, conservation or restoration efforts targeting aquatic environments in the region should take into account physical habitat characteristics—especially depth and width—alongside the more commonly considered variable of riparian vegetation. These efforts should focus primarily on local streams, particularly those upstream, closer to the headwaters. Raising awareness about the impacts of non-native species on native fauna and ecosystems is essential, as many well-intentioned conservation actions may inadvertently cause additional harm to native fish populations.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d17090650/s1. Figure S1: Residual analysis of the variable proportion of non-native species in tributary streams of the internal lakes of the lower Doce River. Figure S2: Residual analysis of the variable total fish richness in tributary streams of the internal lakes of the lower Doce River. Figure S3: Residual analysis of the variable total fish Shannon diversity in tributary streams of the internal lakes of the lower Doce River. Figure S4: Residual analysis of the variable total fish Simpson dominance in tributary streams of the internal lakes of the lower Doce River. Figure S5: Residual analysis of the variable native fish richness in tributary streams of the internal lakes of the lower Doce River. Figure S6: Residual analysis of the variable native fish Shannon diversity in tributary streams of the internal lakes of the lower Doce River. Figure S7: Residual analysis of the variable native fish Simpson dominance in tributary streams of the internal lakes of the lower Doce River. Figure S8: Residual analysis of the variable stream width in tributary streams of the internal lakes of the lower Doce River. Figure S9: Residual analysis of the variable stream depth in tributary streams of the internal lakes of the lower Doce River.

Author Contributions: All authors designed the study; E.H.d.B., R.L.B., L.M.S.-S. and R.F.M.-P. participated in fieldwork. R.F.M.-P. built the species vochers list and checked species distribution ranges. L.M.S.-S. performed data curation and taxonomic validation. Statistical analysis was performed by E.H.d.B. and N.C. All authors wrote the manuscript. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest: Authors Eduardo Barros and Renan Betzel were employed by the company Ello Ambiental Consultoria Ltda. The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Appendix A

Table A1. Fish species recorded in internal lakes of the lower doce river and their tributaries, including the total number of individuals per species and their distribution across habitat types.

Taxa	Origin	Total Individuals	Individuals on Lakes	Individuals on Streams
Atheriniformes				
Atherinopsidae				
Atherinella brasiliensis	Native	13	13	0
Characiformes				
Anostomidae				
Hypomasticus copelandii	Native	19	19	0
Characidae				
Astyanax lacustris	Native	183	107	76
Astyanax sp.	Native	129	0	129
Psalidodon rivularis	Native	75	0	75
Hyphessobrycon eques	Non-native	19	0	19
Hyphessobrycon luetkenii	Native	22	0	22
Knodus moenkhausi	Native	132	0	132
Moenkhausia vittata	Native	1	0	1
Oligosarcos acutirostris	Native	7	2	5
Curimatidae				
Cyphocharax gilbert	Native	1	0	1
Erythrinidae				
Hoplias malabaricus	Native	42	25	17
Prochilidontidae				
Prochilodus lineatus	Non-native	10	10	0

Table A1. *Cont.*

Taxa	Origin	Total Individuals	Individuals on Lakes	Individuals on Streams
Serrasalmidae				
Metynnis lippincottianus	Non-native	145	109	36
Pygocentrus nattereri	Non-native	120	107	13
Pygocentrus piraya	Non-native	12	12	0
Cichliformes				
Cichlidade				
Astronotus ocellatus	Non-native	4	4	0
Australoheros capixaba	Native	42	6	36
Cichla kelberi	Non-native	24	17	7
Coptodon rendalli	Non-native	17	5	12
Crenicichla lacustris	Native	57	7	50
Geophagus brasiliensis	Native	107	47	60
Oreochromis niloticus	Non-native	2	2	0
Clupeiformes				
Engraulidae				
Lycengraulis grossidens	Native	3	3	0
Cyprinodontiformes				
Poeciliidae				
Poecilia reticulata	Non-native	24	0	24
Poecilia vivipara	Native	137	18	119
Gymnotiformes				
Gymnotidae				
Gymnotus carapo	Native	12	1	11
Mugiliformes				
Mugilidae				
Mugil curema	Native	11	0	11
Perciformes				
Sciaenidae				
Pachyurus adspersus	Native	7	7	0
Siluriformes				
Auchenipteridae				
Trachelyopterus striatulus	Native	10	8	2
Callichthyidae				
Hoplosternum littorale	Native	146	133	13
Heptapteridae				
Pimelodella aff. vittata	Native	1	0	1
Rhamdia quelen	Native	2	0	2
Loricariidae				
Hypostomus affinis	Native	13	0	13
Loricariichthys castaneus	Native	1	1	0
Otothyris travassosi	Native	12	0	12
Pimelodidae				
Pimelodus maculatus	Non-native	13	12	1
Synbranchiformes				
Synbranchidae				
Synbranchus marmoratus	Native	2	2	0
RICHNESS		38	25	28

Appendix B

Table A2. Voucher specimens collected in internal lake system of the lower Doce River deposited in public scientific collections.

Sample Date	Local Id	Locality	Environment	Lat	Long	Specie	Collection Code	Voucher Number
30 March 2022	L. JUPARANÃ	Lagoa Juparanã	Lago	−1,923,160	−4,016,285	*Anchoviella lepidentostole*	CZNC	4899
31 March 2022	L. PALMAS	Lagoa Palmas	Lago	−1,944,636	−4,023,067	*Astronotus ocellatus*	CZNC	4930
13 April 2021	ANG 1A	Córrego Timirim, proximo a cachoeira de Angeli	Córrego	−1,934,915	−4,042,013	*Astyanax* cf. *intermedius*	CZNC	4845
13 April 2021	ANG 1B	Afluente da Lagoa Terra Alta	Córrego	−1,936,425	−4,041,918	*Astyanax* cf. *intermedius*	CZNC	4815
17 April 2021	LIM 3A	Afluente da Lagoa do Limão	Córrego	−1,962,088	−4,040,378	*Astyanax* cf. *intermedius*	CZNC	4842
7 April 2021	NOV 1A	Lagoa Nova	Córrego	−1,941,836	−4,015,389	*Astyanax* cf. *intermedius*	CZNC	4814
10 April 2021	OLE 1A	Afluente da Lagoa do Batista	Córrego	−1,951,966	−4,043,761	*Astyanax* cf. *intermedius*	CZNC	4890
11 April 2021	SÃO 1A	Rio São José	Córrego	−1,915,960	−4,021,523	*Astyanax* cf. *intermedius*	CZNC	4874
19 January 2020	Palmas	Lagoa das Palmas, Linhares	Lago	−19,447,222	−4,022,9444	*Astyanax lacutris*	MBML-PEIXES	14,006
13 April 2021	ANG 1A	Córrego Timirim, proximo a cachoeira de Angeli	Córrego	−1,934,915	−4,042,013	*Astyanax lacutris*	CZNC	4848
20 December 2020	INTERMED AB	Afluente da Lagoa Palmas	Córrego	−1,938,783	−4,029,887	*Astyanax lacutris*	CZNC	4881
12 April 2021	JES 1B	Afluente sem nome da Lagoa Juparanã	Córrego	−1,916,424	−4,029,590	*Astyanax lacutris*	CZNC	4904
30 March 2022	L. JUPARANÃ	Lagoa Juparanã	Lago	−1,923,160	−4,016,285	*Astyanax lacutris*	CZNC	4897
19 April 2020	L. LIMÃO	Lagoa do Limão	Lago	−1,955,946	−4,039,027	*Astyanax lacutris*	CZNC	4956
31 March 2022	L. PALMAS	Lagoa Palmas	Lago	−1,944,636	−4,023,067	*Astyanax lacutris*	CZNC	4929
1 April 2022	L. PIABANHA	Lagoa Piabanha	Lago	−1,946,710	−4,024,168	*Astyanax lacutris*	CZNC	4961
15 April 2021	LIM 1C	Afluente da Lagoa do Limão	Córrego	−1,958,801	−4,037,719	*Astyanax lacutris*	CZNC	4822

Table A2. *Cont.*

Sample Date	Local Id	Locality	Environment	Lat	Long	Specie	Collection Code	Voucher Number
17 April 2021	LIM 3A	Afluente da Lagoa do Limão	Córrego	−1,962,088	−4,040,378	*Astyanax lacutris*	CZNC	4907
6 May 2021	LSD 1A	Lagoa Terra Altinha	Córrego	−1,947,708	−4,028,962	*Astyanax lacutris*	CZNC	4863
7 April 2021	NOV 1A	Lagoa Nova	Córrego	−1,941,836	−4,015,389	*Astyanax lacutris*	CZNC	4810
April 2021	NOV 2B	Lagoa Nova	Córrego	−1,926,074	−4,020,624	*Astyanax lacutris*	CZNC	4860
10 April 2021	OLE 1A	Afluente da Lagoa do Batista	Córrego	−1,951,966	−4,043,761	*Astyanax lacutris*	CZNC	4889
2 May 2021	PAL 1C	Afluente da Lagoa Palminhas	Córrego	−1,943,500	−4,016,622	*Astyanax lacutris*	CZNC	4832
20 December 2020	PALMAS 4	Lagoa Palmas	Lago	−1,942,385	−4,026,169	*Astyanax lacutris*	CZNC	4936
10 April 2022	PAU 1B	Afluente da Lagoa Pau Grosso	Córrego	−1,949,099	−4,033,457	*Astyanax lacutris*	CZNC	4851
2 May 2021	RES 1B	Afluente da Lagoa Juparanã	Córrego	−1,936,511	−4,011,470	*Astyanax lacutris*	CZNC	4886
11 April 2021	SÃO 1A	Rio São José	Córrego	−1,915,960	−4,021,523	*Astyanax lacutris*	CZNC	4872
11 April 2021	SÃO 1B	Rio São José	Córrego	−1,914,903	−4,022,318	*Astyanax lacutris*	CZNC	4877
20 December 2020	INTERMED AB	Afluente da Lagoa Palmas	Córrego	###########	-4.02989×10^{12}	*Astyanax* sp.	CZNC	4883
17 April 2021	LIM 3A	Afluente da Lagoa do Limão	Córrego	−1,962,088	−4,040,378	*Astyanax* sp.	CZNC	4906
April 2021	NOV 2B	Lagoa Nova	Córrego	−1,926,074	−4,020,624	*Astyanax* sp.	CZNC	4859
20 December 2020	PALMAS 4	Lagoa Palmas	Lago	−1,942,385	−4,026,169	*Astyanax* sp.	CZNC	4937
19 January 2020	Palmas	Lagoa das Palmas, Linhares	Lago	−19,447,222	−40,229,444	*Atherinella brasiliensis*	MBML-PEIXES	14,000
30 March 2022	L. PALMINHAS	Lagoa Palminhas	Lago	−1,938,574	−4,021,471	*Australoheros capixaba*	CZNC	4941
April 2021	NOV 2B	Lagoa Nova	Córrego	−1,926,074	−4,020,624	*Australoheros capixaba*	CZNC	4861
10 April 2022	PAU 1B	Afluente da Lagoa Pau Grosso	Córrego	−1,949,099	−4,033,457	*Australoheros capixaba*	CZNC	4852

Table A2. *Cont.*

Sample Date	Local Id	Locality	Environment	Lat	Long	Specie	Collection Code	Voucher Number
12 April 2021	JES 1B	Afluente sem nome da Lagoa Juparanã	Córrego	−1,916,424	−4,029,590	*Cichla kelberi*	CZNC	4903
30 March 2022	L. JUPARANÃ	Lagoa Juparanã	Lago	−1,923,160	−4,016,285	*Cichla kelberi*	CZNC	4898
30 March 2022	L. PALMINHAS	Lagoa Palminhas	Lago	−1,938,574	−4,021,471	*Cichla kelberi*	CZNC	4947
7 April 2021	NOV 1A	Lagoa Nova	Córrego	−1,941,836	−4,015,389	*Cichla kelberi*	CZNC	4812
11 April 2021	SÃO 1A	Rio São José	Córrego	−1,915,960	−4,021,523	*Cichla kelberi*	CZNC	4870
19 January 2020	Palmas	Lagoa das Palmas, Linhares	Lago	−19,447,222	−40,229,444	*Cichla* sp.	MBML-PEIXES	14,004
12 April 2021	SAO 1C	Rio São José	Córrego	−1,911,154	−4,024,773	*Coptodon rendalli*	CZNC	4835
8 April 2021	3 MA 1B	Ribeirão das Palmas	Córrego	−1,943,544	−4,017,800	*Crenicichla lacustris*	CZNC	4910
19 April 2020	L. LIMÃO	Lagoa do Limão	Lago	−1,955,946	−4,039,027	*Crenicichla lacustris*	CZNC	4950
31 March 2022	L. PALMAS	Lagoa Palmas	Lago	−1,944,636	−4,023,067	*Crenicichla lacustris*	CZNC	4923
30 March 2022	L. PALMINHAS	Lagoa Palminhas	Lago	−1,938,574	−4,021,471	*Crenicichla lacustris*	CZNC	4946
27 October 2022	L.TERRA ALTINHA	Lagoa Terra Altinha	Córrego	−1,944,994	−4,028,975	*Crenicichla lacustris*	CZNC	4912
15 April 2021	LIM 1C	Afluente da Lagoa do Limão	Córrego	−1,958,801	−4,037,719	*Crenicichla lacustris*	CZNC	4823
15 April 2021	LIM 1C	Lagoa do Limão	Córrego	−1,958,801	−4,037,719	*Crenicichla lacustris*	CZNC	4830
6 May 2021	LSD 1A	Lagoa Terra Altinha	Córrego	−1,947,708	−4,028,962	*Crenicichla lacustris*	CZNC	4864
7 April 2021	NOV 1A	Lagoa Nova	Córrego	−1,941,836	−4,015,389	*Crenicichla lacustris*	CZNC	4811
12 June 2021	PAL 1A	Ribeirão das Palmas	Córrego	−1,944,742	−4,022,411	*Crenicichla lacustris*	CZNC	4817
10 April 2022	PAU 1B	Afluente da Lagoa Pau Grosso	Córrego	−1,949,099	−4,033,457	*Crenicichla lacustris*	CZNC	4849
6 May 2021	TAL 1B	Lagoa Terra Alta	Lago	−1,948,494	−4,029,217	*Crenicichla lacustris*	CZNC	4902
20 December 2020	INTERMED AB	Afluente da Lagoa Palmas	Córrego	###########	-4.02989×10^{12}	*Cyphocharax gilbert*	CZNC	4885
April 2021	NOV 2B	Lagoa Nova	Córrego	−1,926,074	−4,020,624	*Cyphocharax gilbert*	CZNC	4858

Table A2. *Cont.*

Sample Date	Local Id	Locality	Environment	Lat	Long	Specie	Collection Code	Voucher Number
13 April 2021	ANG 1A	Córrego Timirim, proximo a cachoeira de Angeli	Córrego	−1,934,915	−4,042,013	*Geophagus brasiliensis*	CZNC	4846
4 May 2021	DES 1C	Lagoa Juparanã	Córrego	−1,936,319	−4,011,679	*Geophagus brasiliensis*	CZNC	4828
20 December 2020	INTERMED AB	Afluente da Lagoa Palmas	Córrego	###########	-4.02989×10^{12}	*Geophagus brasiliensis*	CZNC	4880
30 March 2022	L. NOVA	Lagoa Nova	Lago	−1,933,768	−4,017,302	*Geophagus brasiliensis*	CZNC	4918
30 March 2022	L. PALMINHAS	Lagoa Palminhas	Lago	−1,938,574	−4,021,471	*Geophagus brasiliensis*	CZNC	4945
1 April 2022	L. PIABANHA	Lagoa Piabanha	Lago	−1,946,710	−4,024,168	*Geophagus brasiliensis*	CZNC	4962
6 May 2021	LSD 1A	Lagoa Terra Altinha	Córrego	−1,947,708	−4,028,962	*Geophagus brasiliensis*	CZNC	4866
10 April 2021	OLEO 1B	Afluente da Lagoa do Batista	Córrego	−1,951,219	−4,043,625	*Geophagus brasiliensis*	CZNC	4840
20 December 2020	PALMAS 4	Lagoa Palmas	Lago	−1,942,385	−4,026,169	*Geophagus brasiliensis*	CZNC	4934
16 April 2021	PAU 1A	Afluente da Lagoa Pau Grosso	Córrego	−1,948,928	−4,034,423	*Geophagus brasiliensis*	CZNC	4820
19 January 2020	Palmas	Lagoa das Palmas, Linhares	Lago	−19,447,222	−40,229,444	*Geophagus brasiliensis*	MBML-PEIXES	14,003
28 October 2022	L. TERRA ALTA	Lagoa Terra Alta	Lago	−1,945,396	−4,035,517	*Gymnotus carapo*	CZNC	4914
6 May 2021	LSD 1A	Lagoa Terra Altinha	Córrego	−1,947,708	−4,028,962	*Gymnotus carapo*	CZNC	4865
10 April 2021	OLE 1A	Afluente da Lagoa do Batista	Córrego	−1,951,966	−4,043,761	*Gymnotus carapo*	CZNC	4891
20 December 2020	PALMAS 4	Lagoa Palmas	Lago	−1,942,385	−4,026,169	*Gymnotus carapo*	CZNC	4938
11 April 2021	SÃO 1B	Rio São José	Córrego	−1,914,903	−4,022,318	*Gymnotus carapo*	CZNC	4875
4 May 2021	DES 1C	Lagoa Juparanã	Córrego	−1,936,319	−4,011,679	*Hoplias malabaricus*	CZNC	4827
20 December 2020	INTERMED AB	Afluente da Lagoa Palmas	Córrego	###########	-4.02989×10^{12}	*Hoplias malabaricus*	CZNC	4878
19 April 2020	L. LIMÃO	Lagoa do Limão	Lago	−1,955,946	−4,039,027	*Hoplias malabaricus*	CZNC	4952
30 March 2022	L. NOVA	Lagoa Nova	Lago	−1,933,768	−4,017,302	*Hoplias malabaricus*	CZNC	4921
1 April 2022	L. PIABANHA	Lagoa Piabanha	Lago	−1,946,710	−4,024,168	*Hoplias malabaricus*	CZNC	4966

Table A2. *Cont.*

Sample Date	Local Id	Locality	Environment	Lat	Long	Specie	Collection Code	Voucher Number
17 April 2021	LIM 3A	Afluente da Lagoa do Limão	Córrego	−1,962,088	−4,040,378	*Hoplias malabaricus*	CZNC	4844
10 April 2021	OLEO 1B	Afluente da Lagoa do Batista	Córrego	−1,951,219	−4,043,625	*Hoplias malabaricus*	CZNC	4837
20 December 2020	PALMAS 4	Lagoa Palmas	Lago	−1,942,385	−4,026,169	*Hoplias malabaricus*	CZNC	4931
11 April 2021	SÃO 1A	Rio São José	Córrego	−1,915,960	−4,021,523	*Hoplias malabaricus*	CZNC	4869
30 March 2022	L. JUPARANÃ	Lagoa Juparanã	Lago	−1,923,160	−4,016,285	*Hoplosternum littorale*	CZNC	4896
30 March 2022	L. NOVA	Lagoa Nova	Lago	−1,933,768	−4,017,302	*Hoplosternum littorale*	CZNC	4920
31 March 2022	L. PALMAS	Lagoa Palmas	Lago	−1,944,636	−4,023,067	*Hoplosternum littorale*	CZNC	4926
30 March 2022	L. PALMINHAS	Lagoa Palminhas	Lago	−1,938,574	−4,021,471	*Hoplosternum littorale*	CZNC	4948
1 April 2022	L. PIABANHA	Lagoa Piabanha	Lago	−1,946,710	−4,024,168	*Hoplosternum littorale*	CZNC	4967
20 December 2020	PALMAS 4	Lagoa Palmas	Lago	−1,942,385	−4,026,169	*Hoplosternum littorale*	CZNC	4940
2 May 2021	RES 1B	Afluente da Lagoa Juparanã	Córrego	−1,936,511	−4,011,470	*Hoplosternum littorale*	CZNC	4888
11 April 2021	SÃO 1A	Rio São José	Córrego	−1,915,960	−4,021,523	*Hoplosternum littorale*	CZNC	4871
20 December 2020	PALMAS 4	Lagoa Palmas	Lago	−1,942,385	−4,026,169	*Hyphessobrycon bifasciatus*	CZNC	4932
8 April 2021	3 MA 1B	Ribeirão das Palmas	Córrego	−1,943,544	−4,017,800	*Hyphessobrycon eques*	CZNC	4909
27 October 2022	L.TERRA ALTINHA	Lagoa Terra Altinha	Córrego	−1,944,994	−4,028,975	*Hyphessobrycon eques*	CZNC	4911
15 April 2021	LIM 1C	Afluente da Lagoa do Limão	Córrego	−1,958,801	−4,037,719	*Hyphessobrycon eques*	CZNC	4825
6 May 2021	LSD 1A	Lagoa Terra Altinha	Córrego	−1,947,708	−4,028,962	*Hyphessobrycon eques*	CZNC	4868
10 April 2022	PAU 1B	Afluente da Lagoa Pau Grosso	Córrego	−1,949,099	−4,033,457	*Hyphessobrycon eques*	CZNC	4854
13 April 2021	ANG 1B	Afluente da Lagoa Terra Alta	Córrego	−1,936,425	−4,041,918	*Hypostomus affinis*	CZNC	4816
20 December 2020	INTERMED AB	Afluente da Lagoa Palmas	Córrego	###########	-4.02989×10^{12}	*Hypostomus affinis*	CZNC	4879

Table A2. *Cont.*

Sample Date	Local Id	Locality	Environment	Lat	Long	Specie	Collection Code	Voucher Number
April 2021	NOV 2B	Lagoa Nova	Córrego	−1,926,074	−4,020,624	*Hypostomus affinis*	CZNC	4856
20 December 2020	INTERMED AB	Afluente da Lagoa Palmas	Córrego	###########	-4.02989×10^{12}	*Knodus aff. Moenkhausii*	CZNC	4884
10 April 2021	OLE 1A	Afluente da Lagoa do Batista	Córrego	−1,951,966	−4,043,761	*Knodus aff. Moenkhausii*	CZNC	4893
10 April 2021	OLEO 1B	Afluente da Lagoa do Batista	Córrego	−1,951,219	−4,043,625	*Knodus aff. Moenkhausii*	CZNC	4841
20 December 2020	PALMAS 4	Lagoa Palmas	Lago	−1,942,385	−4,026,169	*Knodus aff. Moenkhausii*	CZNC	4935
19 December 2020	PALMAS INTER 2/4	Afluente da Lagoa Palmas	Córrego	−1,942,385	−4,026,169	*Knodus aff. Moenkhausii*	CZNC	4829
12 April 2021	SAO 1C	Rio São José	Córrego	−1,911,154	−4,024,773	*Knodus aff. Moenkhausii*	CZNC	4834
28 October 2022	L. TERRA ALTA	Lagoa Terra Alta	Lago	−1,945,396	−4,035,517	*Loricariichthys castaneus*	CZNC	4915
19 April 2020	L. LIMÃO	Lagoa do Limão	Lago	−1,955,946	−4,039,027	*Lycengraulis grossidens*	CZNC	4958
19 April 2020	L. LIMÃO	Lagoa do Limão	Lago	−1,955,946	−4,039,027	*Metynnis lippincottianus*	CZNC	4955
30 March 2022	L. NOVA	Lagoa Nova	Lago	−1,933,768	−4,017,302	*Metynnis lippincottianus*	CZNC	4917
31 March 2022	L. PALMAS	Lagoa Palmas	Lago	−1,944,636	−4,023,067	*Metynnis lippincottianus*	CZNC	4927
30 March 2022	L. PALMINHAS	Lagoa Palminhas	Lago	−1,938,574	−4,021,471	*Metynnis lippincottianus*	CZNC	4943
1 April 2022	L. PIABANHA	Lagoa Piabanha	Lago	−1,946,710	−4,024,168	*Metynnis lippincottianus*	CZNC	4963
16 April 2021	PAU 1A	Afluente da Lagoa Pau Grosso	Córrego	−1,948,928	−4,034,423	*Metynnis lippincottianus*	CZNC	4821
10 April 2022	PAU 1B	Afluente da Lagoa Pau Grosso	Córrego	−1,949,099	−4,033,457	*Metynnis lippincottianus*	CZNC	4850
19 January 2020	Palmas	Lagoa das Palmas, Linhares	Lago	−19,447,222	−40,229,444	*Metynnis maculatus*	MBML-PEIXES	14,002
15 April 2021	LIM 1C	Afluente da Lagoa do Limão	Córrego	−1,958,801	−4,037,719	*Moenkhausia doceana*	CZNC	4826
11 April 2021	SÃO 1B	Rio São José	Córrego	−1,914,903	−4,022,318	*Oligosarcus acutirostris*	CZNC	4876

Table A2. *Cont.*

Sample Date	Local Id	Locality	Environment	Lat	Long	Specie	Collection Code	Voucher Number
10 April 2021	OLE 1A	Afluente da Lagoa do Batista	Córrego	−1,951,966	−4,043,761	*Otothyris travassosi*	CZNC	4894
10 April 2021	OLEO 1B	Afluente da Lagoa do Batista	Córrego	−1,951,219	−4,043,625	*Otothyris travassosi*	CZNC	4838
19 April 2020	L. LIMÃO	Lagoa do Limão	Lago	−1,955,946	−4,039,027	*Pachyurus adspersus*	CZNC	4957
1 November 2022	L. OLEO	Lagoa do Óleo	Lago	−1,945,711	−4,025,622	*Pachyurus adspersus*	CZNC	4913
April 2021	NOV 2B	Lagoa Nova	Córrego	−1,926,074	−4,020,624	*Pimelodella* cf. *lateristriga*	CZNC	4862
30 March 2022	L. NOVA	Lagoa Nova	Lago	−1,933,768	−4,017,302	*Pimelodus maculatus*	CZNC	4922
13 April 2021	ANG 1A	Córrego Timirim, proximo a cachoeira de Angeli	Córrego	−1,934,915	−4,042,013	*Poecilia vivipara*	CZNC	4847
20 December 2020	INTERMED AB	Afluente da Lagoa Palmas	Córrego	###########	-4.02989×10^{12}	*Poecilia vivipara*	CZNC	4882
12 April 2021	JES 1B	Afluente sem nome da Lagoa Juparanã	Córrego	−1,916,424	−4,029,590	*Poecilia vivipara*	CZNC	4905
30 March 2022	L. JUPARANÃ	Lagoa Juparanã	Lago	−1,923,160	−4,016,285	*Poecilia vivipara*	CZNC	4900
30 March 2022	L. PALMINHAS	Lagoa Palminhas	Lago	−1,938,574	−4,021,471	*Poecilia vivipara*	CZNC	4942
1 April 2022	L. PIABANHA	Lagoa Piabanha	Lago	−1,946,710	−4,024,168	*Poecilia vivipara*	CZNC	4959
15 April 2021	LIM 1C	Afluente da Lagoa do Limão	Córrego	−1,958,801	−4,037,719	*Poecilia vivipara*	CZNC	4824
15 April 2021	LIM 1C	Lagoa do Limão	Córrego	−1,958,801	−4,037,719	*Poecilia vivipara*	CZNC	4831
17 April 2021	LIM 3A	Afluente da Lagoa do Limão	Córrego	−1,962,088	−4,040,378	*Poecilia vivipara*	CZNC	4843
17 April 2021	LIM 3A	Afluente da Lagoa do Limão	Córrego	−1,962,088	−4,040,378	*Poecilia vivipara*	CZNC	4908
6 May 2021	LSD 1A	Lagoa Terra Altinha	Córrego	−1,947,708	−4,028,962	*Poecilia vivipara*	CZNC	4867
7 April 2021	NOV 1A	Lagoa Nova	Córrego	−1,941,836	−4,015,389	*Poecilia vivipara*	CZNC	4813
April 2021	NOV 2B	Lagoa Nova	Córrego	−1,926,074	−4,020,624	*Poecilia vivipara*	CZNC	4857

Table A2. *Cont.*

Sample Date	Local Id	Locality	Environment	Lat	Long	Specie	Collection Code	Voucher Number
10 April 2021	OLE 1A	Afluente da Lagoa do Batista	Córrego	−1,951,966	−4,043,761	*Poecilia vivipara*	CZNC	4895
10 April 2021	OLEO 1B	Afluente da Lagoa do Batista	Córrego	−1,951,219	−4,043,625	*Poecilia vivipara*	CZNC	4839
12 June 2021	PAL 1A	Ribeirão das Palmas	Córrego	−1,944,742	−4,022,411	*Poecilia vivipara*	CZNC	4818
2 May 2021	PAL 1C	Afluente da Lagoa Palminhas	Córrego	−1,943,500	−4,016,622	*Poecilia vivipara*	CZNC	4833
20 December 2020	PALMAS 4	Lagoa Palmas	Lago	−1,942,385	−4,026,169	*Poecilia vivipara*	CZNC	4933
16 April 2021	PAU 1A	Afluente da Lagoa Pau Grosso	Córrego	−1,948,928	−4,034,423	*Poecilia vivipara*	CZNC	4819
10 April 2022	PAU 1B	Afluente da Lagoa Pau Grosso	Córrego	−1,949,099	−4,033,457	*Poecilia vivipara*	CZNC	4853
2 May 2021	RES 1B	Afluente da Lagoa Juparanã	Córrego	−1,936,511	−4,011,470	*Poecilia vivipara*	CZNC	4887
11 April 2021	SÃO 1A	Rio São José	Córrego	−1,915,960	−4,021,523	*Poecilia vivipara*	CZNC	4873
12 April 2021	SAO 1C	Rio São José	Córrego	−1,911,154	−4,024,773	*Poecilia vivipara*	CZNC	4836
6 May 2021	TAL 1B	Lagoa Terra Alta	Lago	−1,948,494	−4,029,217	*Poecilia vivipara*	CZNC	4901
19 January 2020	Palmas	Lagoa das Palmas, Linhares	Lago	−19,447,222	−40,229,444	*Poecilia vivipara*	MBML-PEIXES	14,005
30 March 2022	L. NOVA	Lagoa Nova	Lago	−1,933,768	−4,017,302	*Prochilodus lineatus*	CZNC	4916
31 March 2022	L. PALMAS	Lagoa Palmas	Lago	−1,944,636	−4,023,067	*Prochilodus lineatus*	CZNC	4924
30 March 2022	L. PALMINHAS	Lagoa Palminhas	Lago	−1,938,574	−4,021,471	*Prochilodus lineatus*	CZNC	4949
19 April 2020	L. LIMÃO	Lagoa do Limão	Lago	−1,955,946	−4,039,027	*Pygocentrus nattereri*	CZNC	4954
30 March 2022	L. NOVA	Lagoa Nova	Lago	−1,933,768	−4,017,302	*Pygocentrus nattereri*	CZNC	4919
31 March 2022	L. PALMAS	Lagoa Palmas	Lago	−1,944,636	−4,023,067	*Pygocentrus nattereri*	CZNC	4928
30 March 2022	L. PALMINHAS	Lagoa Palminhas	Lago	−1,938,574	−4,021,471	*Pygocentrus nattereri*	CZNC	4944
1 April 2022	L. PIABANHA	Lagoa Piabanha	Lago	−1,946,710	−4,024,168	*Pygocentrus nattereri*	CZNC	4964
20 December 2020	PALMAS 4	Lagoa Palmas	Lago	−1,942,385	−4,026,169	*Pygocentrus nattereri*	CZNC	4939

Table A2. *Cont.*

Sample Date	Local Id	Locality	Environment	Lat	Long	Specie	Collection Code	Voucher Number
19 January 2020	Palmas	Lagoa das Palmas, Linhares	Lago	−19,447,222	−40,229,444	*Pygocentrus nattereri*	MBML-PEIXES	14,001
10 April 2021	OLE 1A	Afluente da Lagoa do Batista	Córrego	−1,951,966	−4,043,761	*Rhamdia quelen*	CZNC	4892
19 April 2020	L. LIMÃO	Lagoa do Limão	Lago	−1,955,946	−4,039,027	*Synbranchus marmoratus*	CZNC	4951
1 April 2022	L. PIABANHA	Lagoa Piabanha	Lago	−1,946,710	−4,024,168	*Synbranchus marmoratus*	CZNC	4960
19 April 2020	L. LIMÃO	Lagoa do Limão	Lago	−1,955,946	−4,039,027	*Trachelyopterus striatulus*	CZNC	4953
31 March 2022	L. PALMAS	Lagoa Palmas	Lago	−1,944,636	−4,023,067	*Trachelyopterus striatulus*	CZNC	4925
1 April 2022	L. PIABANHA	Lagoa Piabanha	Lago	−1,946,710	−4,024,168	*Trachelyopterus striatulus*	CZNC	4965
10 April 2022	PAU 1B	Afluente da Lagoa Pau Grosso	Córrego	−1,949,099	−4,033,457	*Trachelyopterus striatulus*	CZNC	4855

Appendix C

Appendix C.1 Redundancy Analisis Plot

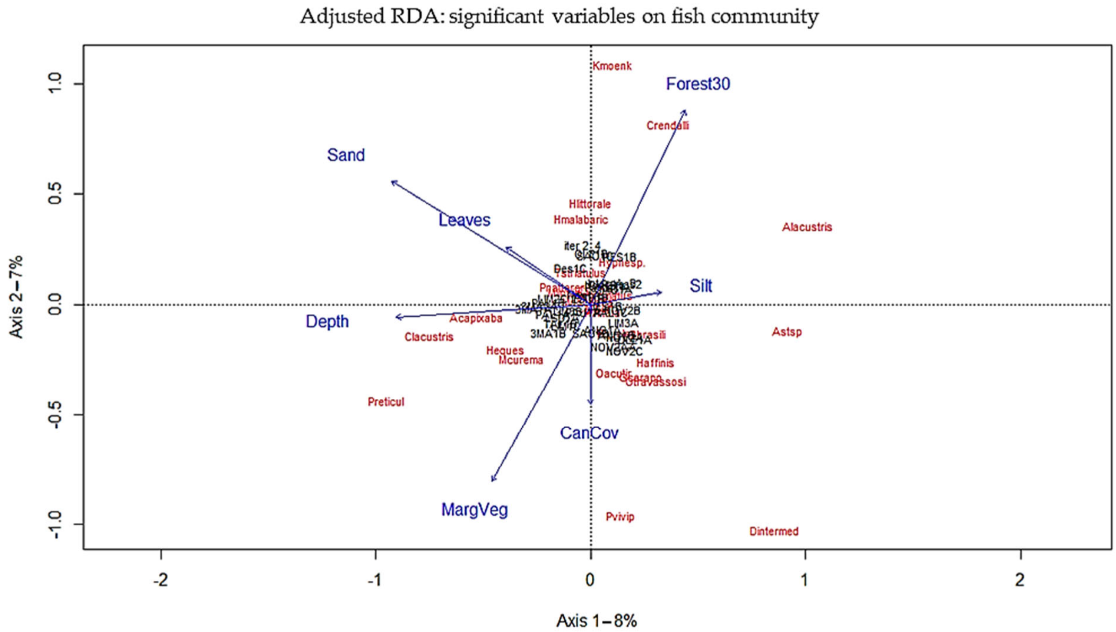

Figure A1. Redundancy analysis (RDA) original plot.

Appendix C.2 Redundancy Analysis (RDA) Abbreviation

Table A3. Redundancy analysis (RDA) abbreviations for significant environmental variables and fish species.

Abbreviation	Variable/Fish Species
Forest30	Proportion of native vegetation within a 30 m riparian buffer upstream of the streams
Silt	Proportion of silt in the substrate
Depth	Average depth of the reach
MargVeg	Riparian vegetation
Leaves	Leaf litter cover on the substrate
CanCov	Canopy cover
Sand	Presence of sandbars
Alacustris	*Astyanax lacustris*
Astsp	*Astyanax* sp.
Acapixaba	*Australoheros capixaba*
Ckelberi	*Cichla kelberi*
Crendalli	*Coptodon rendalli*
Clacustris	*Crenicichla lacustris*
Cgilbert	*Cyphocharax gilbert*
Dintermed	*Deuterodon intermedius*
Gbrasili	*Geophagus brasiliensis*
Gcarapo	*Gymnotus carapo*
Hmalabaric	*Hoplias malabaricus*
Hlittorale	*Hoplosternum littorale*
Heques	*Hyphessobrycon eques*
Haffinis	*Hypostomus affinis*
Kmoenk	*Knodus moenkhausi*
Mlippin	*Metynnis lippincottianus*
Mdoceana	*Moenkhausia doceana*
Mcurema	*Mugil curema*
Oacutir	*Oligosarcos acutirostris*
Otravassosi	*Otothyris travassosi*
Pvittata	*Pimelodella aff. vittata*
Pmaculatus	*Pimelodus maculatus*
Preticul	*Poecilia reticulata*
Pvivip	*Poecilia vivipra*
Pnattereri	*Pygocentrus nattereri*
Rquelen	*Rhamdia quelen*
Tstriatus	*Trachelyopterus striatulus*

Appendix C.3 Redundancy Analisis Scores

Table A4. Scores of redundancy analysis (RDA) obtained for fish species sampled in the lower Doce River lakes system.

	RDA1	RDA2	RDA3	RDA4	RDA5	RDA6
Alacustris	0.2871774	0.095098	−0.2346368	0.117138	−0.0127829	6.675×10^{-2}
Astsp	0.2599233	−0.033125	0.2497147	0.102720	−0.0616100	2.079×10^{-2}
Acapixaba	−0.1502863	−0.016744	−0.0946923	0.001056	0.0206506	-1.272×10^{-1}
Ckelberi	0.0095291	0.018361	−0.0247578	0.095438	−0.0211341	3.295×10^{-2}
Crendalli	0.1020989	0.218210	−0.0589342	−0.249312	0.0239482	7.438×10^{-2}
Clacustris	−0.2121435	−0.037414	−0.1022061	0.128475	0.0368650	5.359×10^{-2}
Cgilbert	0.0067282	−0.004576	0.0032906	−0.003626	−0.0136688	-1.737×10^{-2}
Dintermed	0.2424275	−0.273372	−0.0201323	−0.059099	−0.0207313	2.390×10^{-2}
Gbrasili	0.0742925	−0.034724	0.0691402	0.003919	0.0405709	-1.393×10^{-2}
Gcarapo	0.0666279	−0.087901	−0.0084166	−0.012176	−0.0204309	-3.183×10^{-2}
Hmalabaric	−0.0120460	0.103393	0.0517551	0.036565	0.0009784	5.490×10^{-2}
Hlittorale	0.0005268	0.123535	−0.0270564	0.007960	0.0843419	-4.524×10^{-4}
Heques	−0.1112137	−0.056053	−0.0315570	0.021358	0.0397048	$2.462e \times 10^{-2}$
Hyphesp.	0.0423203	0.050411	0.2355081	0.034440	0.1861800	3.289×10^{-2}
Haffinis	0.0860899	−0.069194	−0.0075782	−0.052764	−0.0432219	4.489×10^{-3}
Kmoenk	0.0286509	0.290509	−0.0002278	0.038631	−0.1936251	-6.439×10^{-2}
Mlippin	−0.0347366	0.014004	−0.0905114	0.046688	0.0543380	6.154×10^{-2}
Mdoceana	−0.0038226	0.003703	−0.0099426	0.020586	0.0030692	7.139×10^{-3}
Mcurema	−0.0903952	−0.065431	−0.0295016	−0.082196	0.0109884	-2.252×10^{-4}
Oacutir	0.0310391	−0.082284	−0.0165534	−0.033329	0.0109820	2.075×10^{-2}
Otravassosi	0.0870227	−0.092579	−0.0143259	−0.010101	−0.0065022	-5.057×10^{-3}
Pvittata	0.0168954	−0.008149	−0.0049234	−0.007834	0.0008022	3.438×10^{-3}
Pmaculatus	0.0193803	0.012132	−0.0180206	−0.010730	−0.0073229	8.691×10^{-5}
Preticul	−0.2684137	−0.116375	0.1445372	−0.033484	−0.1578284	1.019×10^{-1}
Pvivip	0.0392636	−0.256204	−0.1306801	0.010152	−0.0237046	-4.814×10^{-3}
Pnattereri	−0.0354041	0.021581	−0.0270983	0.032740	−0.0106518	1.061×10^{-2}
Rquelen	0.0350051	−0.035740	0.0008839	−0.007965	−0.0183521	-6.632×10^{-3}
Tstriatulus	−0.0124126	0.038993	−0.0160142	0.011482	0.0256772	-4.121×10^{-3}

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