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ORIGINAL PAPER

Trophic niche partitioning among non-native fish species coexisting in a Colombian high Andean reservoir

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Abstract The introduction of non-native species to a new environment poses a threat to local biological diversity, causing instability in the functioning of the ecosystem. The ecological effects caused by these species have been scarcely documented in the Magdalena basin. By studying predator–prey interactions, we characterized the trophic niche of three non-native species (*Cyprinus carpio, Micropterus salmoides,* and *Oncorhynchus mykiss*) that dominate a high Andean reservoir in the Magdalena basin. This study allows us to understand their specific feeding behaviors and how these behaviors facilitate their establishment in the reservoir. We evaluated the diversity of the prey they consume, their feeding strategy, and possible differences in the feeding scheme. Forty individuals were analyzed, with the highest representation of *M. salmoides* with 17 individuals, followed by *C. carpio* (13 individuals), and finally *O. mykiss* with 10 individuals. We identified twenty categories of food as prey for these species, with aquatic invertebrates and vegetation material being the predominant prey. The analysis of stomach contents in these samples suggested that they are representative for determining specialized or generalist feeding strategies. There were no differences in the number of prey items consumed by these three species. The analysis revealed that the feeding strategies are specific for each species. There was no overlap in the diet of *C. carpio* with the other two species, however, the composition of the diet is similar between *M. salmoides* and *O. mykiss.* Analyzing the diet of these non-native fish provides a useful tool for describing trophic interactions in this aquatic environment. Our results contribute information on the existing interactions amongst non-native species in the Magdalena basin, which is important for the development of strategies to manage and mitigate their impact.

Keywords Habitat fragmentation · Species introduction · Ecological impacts · Species interactions · Magdalena river basin

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Introduction

The introduction of fish species is often a result of human activities that facilitate the entry of non-native species into ecosystems, such as aquaculture, sport fishing, fishkeeping, and dam construction (Ortega et al. 2015; Vitule et al. 2019). The new interactions that occur in aquatic environments due to species introductions can have detrimental effects on native species and can alter ecosystem functioning (Toussaint et al. 2018; Milardi et al 2019). Additionally, species introduction is increasingly recognized as an important contributor to the risk of local species extinction (Jeschke et al. 2014; Villéger et al. 2015), as well as the global loss of species (Clavero and Garcia Berthou 2005; Vitule et al. 2009).

There are several ecological aspects that characterize non-native fish species and make them particularly successful as invasive species, such as the ability to establish rapidly, exploit favorable conditions, outcompete native species and expand their populations (Liu et al. 2017). A means of characterizing biological invasions is understanding the trophic interactions of the species in its new environment (McKnight et al. 2017). Successful invaders tend to have relatively broad trophic niches or ones that are different from other species in the recepient community (Herbold and Moyle 1986), thus enabling them to use trophic resources unexploited by the other species (Araújo et al. 2011). It has been reported that predation and increased competition for resources caused by invader fish lead to a decrease in native fish diversity in aquatic environments (Pelicice and Agostinho 2009; Pereira and Vitule 2019). Therefore, identifying the competition and distribution of food resources (i.e. the trophic niche) of the invasive species in an aquatic environment is a fundamental component in understanding both the community structure and the ecological functions that these organisms can perform in the environment (Bezerra et al. 2018; Restrepo-Santamaria et al. 2022a).

The Magdalena River basin in Colombia is recognized for harboring a remarkable diversity of fish (DoNascimiento et al. 2023), which is characteristic of the Neotropics (Albert et al. 2020). This region stands out as the home of numerous endemic species (Garcia-Alzate et al. 2020), displaying a wide variety of morphologies and sizes. However, this valuable biological wealth faces a latent threat due to the introduction of invasive species (Lasso et al. 2020). These non-native species pose a significant challenge to the conservation of diversity in the Magdalena basin. On the other hand, it has been identified that the loss of river connectivity due to dam construction in the basin may play an important role in the establishment of invasive species in the lentic environment of the reservoir (Valencia-Rodríguez et al. 2022). The altered habitat conditions bring about modifications in fish distribution, restructuring of assemblages, and homogenization of habitat characteristics (Martínez-Toro et al. 2022; Valencia-Rodríguez et al. 2022; Restrepo-Santamaria et al. 2022b) that favor ecological aspects of non-native species (Vitule et al. 2012). Once established in these environments, non-native species can affect resident assemblages through numerous interactions, such as predatory competition for resources, habitat alteration, transmission of new diseases, or hybridization, among other impacts (Gozlan et al. 2010; Cucherousset and Olden 2011). Therefore, understanding the trophic niche the invaders occupy, which is one of the key factors that favor the successful establishment of non-natives species in this basin, is crucial for implementing appropriate management measures that reduce negative effects and safeguard the unique biodiversity of this region.

Non-native species have been observed in a high Andean reservoir within the Magdalena basin, including largemouth bass *Micropterus salmoides* (Lacepède 1802), rainbow trout *Oncorhynchus mykiss* (Walbaum 1792), and common carp *Cyprinus carpio* (Linnaeus 1758), which dominate this lentic environment. Notably, no catches of native species have been recorded in the reservoir (Martínez-Toro et al. 2022). In contrast, lotic environments, such as rivers, streams, and creeks that flow into the reservoir are primarily inhabited by small native fish species of the genera *Hemibrycon, Astroblepus*, and *Trichomycterus* (Martínez-Toro et al. 2022). The prevalence of non-native species in the lentic environment and the absence of natives raise questions about their specific feeding habits and how these behaviors facilitate their establishment in the reservoir. Furthermore, by identifying predation and competition for native aquatic resources, we gain knowledge to predict the impacts of invasive species on native communities and ecosystem functioning. This information is crucial for developing targeted management strategies, allowing for proactive measures to mitigate the negative effects of invasive species. Understanding these interactions helps protect and restore native biodiversity, promoting the overall health of freshwater ecosystems. Ultimately, this study aims to enhance our ability to preserve and restore the ecological integrity of freshwater systems and protect the unique biodiversity they harbor.

Materials and methods

Study area

The Riogrande II reservoir is situated in the mountainous region of the Magdalena and Cauca Rivers basin in Colombia, at an elevation of 2267 m above sea level (masl) (Fig. 1). This reservoir is formed by damming the waters of the Grande and Chico rivers, through a dam on the Grande river located two kilometers downstream from the confluence of these two rivers. The use of the reservoir is for the supply of drinking water to the inhabitants of populated

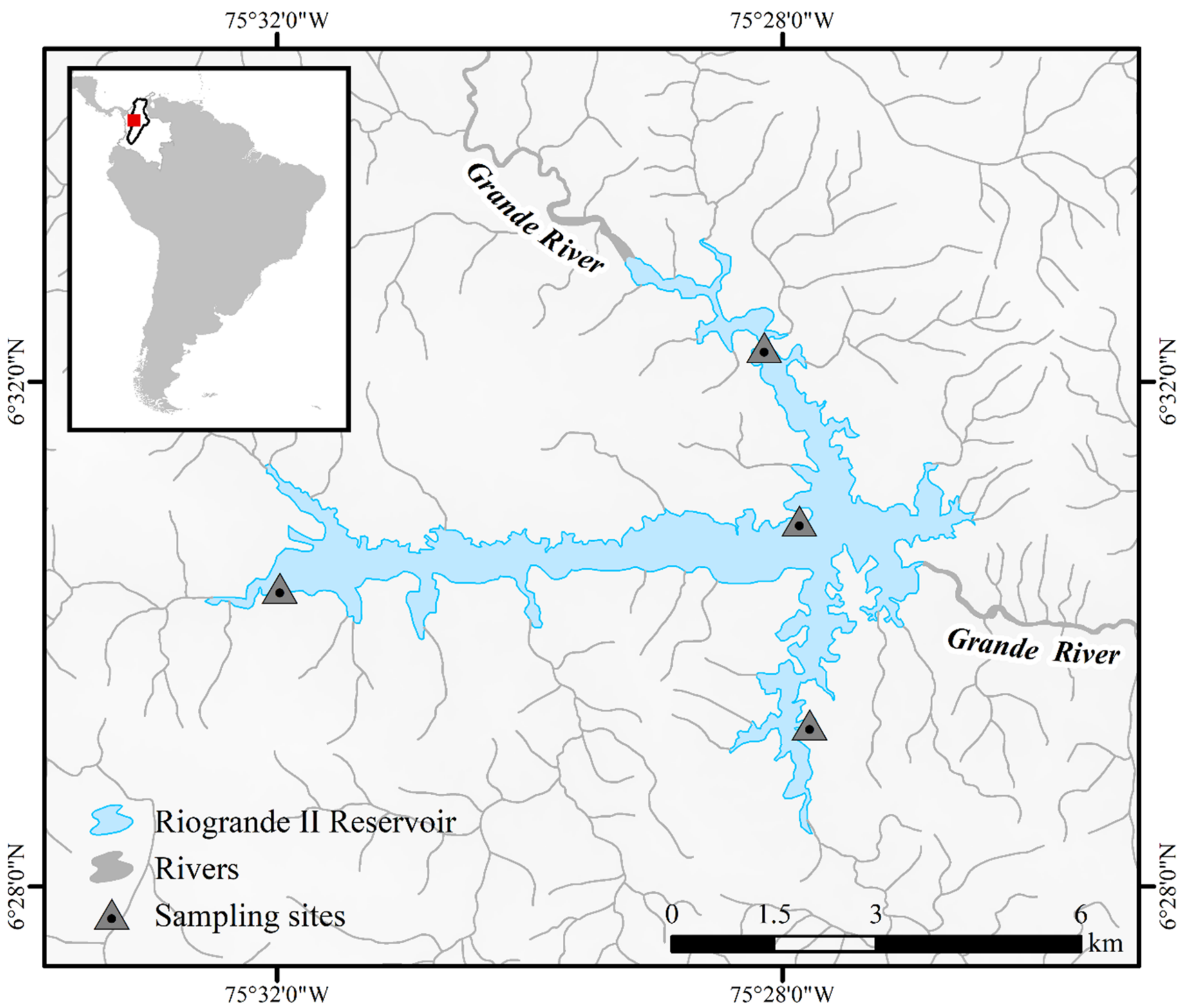

Fig. 1 Sampling sites in the Riogrande II reservoir: all locations were monitored in both surveys. The upper inset highlights the Magdalena Basin in Colombia. The shapefiles representing the water bodies, Riogrande II reservoir, and Magdalena basin were obtained from the IGAC (https://geoportal.igac.gov.co/)

centers and hydroelectric generation. It has a depth ranging from 35 to 45 m and a total storage capacity of 253 million m^3. The reservoir inundated an area of 11 km^2, and its average retention time is 73 days (Mazo et al. 2015). These favorable conditions contribute to the high chemical quality of the water released from the reservoir after passing through the turbines. The temperatures in this area range from 12 to 18 degrees Celsius (°C), and the average annual rainfall is approximately 1,324 mm. During the months of October and November, the humidity reaches an average of 83% (Mazo et al. 2015).

Sampling design

Samples were collected in August and October of 2020 at four sites within the reservoir. This time frame was selected because it corresponds to the months with the lowest estimated rainfall periods for that year, thereby increasing the chances of detecting organisms. The sampling effort involved the use of three gill nets, each measuring 100 m in length and 3 m in height; one net was placed in each site's littoral zone. The gill nets were left in place for a duration of six hours, which was the maximum time allowed by the reservoir administration, specifically from 7:00 to 13:00. These nets were equipped with ten different mesh sizes, ranging from 1 to 10 cm. Only the three non-native fish species were caught. Subsequently, these species were anesthetized with eugenol (Javahery et al. 2012), sacrificed, and their stomachs were removed and preserved in Transeau solution (1:1 proportion) for further analysis in the laboratory. Only stomachs containing food were considered for analysis. The stomach contents were observed using a stereoscope and an inverted microscope. Food items recognized in the stomachs were classified as: animal remains (i.e. parts of some unidentified vertebrate animal), fish remains (remains of scales, spines, etc.), aquatic invertebrates (larval stages, nymphs, or parts of invertebrates), terrestrial invertebrates (terrestrial insects or spiders in adult stages), vegetation material (leaves, stems, fruits, seeds, filamentous algae), and unidentified food (mud, soil, debris). The lowest possible taxonomic resolution was identified for each item.

Data analysis

The frequency of occurrence and volumetric index were estimated for each item found in the sample of the diet of each species (Hyslop 1980). The frequency of occurrence was defined as the number of stomachs containing a prey item, divided by the total number of stomachs of the specific predatory species, and expressed as a percentage (%) (Hyslop 1980). Volumetric analysis was conducted both directly and indirectly. In the direct estimation, the displacement of each type of food or group of food selected from the stomach contents was measured in a graduated cylinder, where the volume of liquid displaced equaled that of the food (Hyslop 1980). Indirect volumetric analysis was carried out by comparing food with blocks of a known volume, matching the shape of the organism to be measured (Hyslop 1980). Both volumetric methods were employed for the descriptive analysis of trophic strategy.

To evaluate the representativeness of the diet for each species, rarefaction curves were used based on the number of stomachs analyzed and the interpolation/extrapolation of the Hill numbers, where the confidence interval was constructed using the bootstrap resampling method (Chao et al. 2014), implemented in the iNEXT package (Hsieh et al. 2016). Asymptotic behavior in the extrapolation curve indicates that the diversity of prey observed is representative of the species' feeding habits, which is supported by the estimation of the sampling coverage, which varies between zero and one, where values near one suggest a good representativeness in the number of stomachs analyzed for the estimation of prey diversity (Hsieh et al. 2016). The diversity of the prey consumed by the species evaluated was calculated using the effective number of species or Hill numbers (q0, q1, and q2) (Hill 1973), following the method proposed by Jost (2006) and Chao et al. (2014). Where q0 represents the effective richness, taking into account the amount of prey identified for each species, regardless of its frequency of occurrence. q1 is equivalent to the Shannon diversity exponent and is sensitive to prey with low to medium frequency of occurrence (i.e., common prey), while q2 is equivalent to the inverse of the Simpson index and is more sensitive to prey with higher frequency (i.e., dominant prey) (Jost 2006).

The trophic strategy was described using the Amundsen graphic method, which is based on a representation of two dimensions – the specific abundance of a prey (Pi), and its frequency of occurrence in the diet of species x (Amundsen 1996). The specific abundance of each prey was expressed as its percentage with respect to the total volume ($\sum$ volume i…n) of the sample and is expressed as follows: $\text{Pi} = \sum \text{Si}/\sum \text{Sti} * 100$; where Pi is the specific abundance of prey i. Si is the volume represented by prey i; and Sti is the total volume of the stomach contents ($\sum$ volume i…n) in the sample (Amundsen 1996). In the graphical representation, the vertical axis illustrates the feeding strategy of the predator in terms of specialization or generalization. Predators that specialize in particular prey types are positioned at the top of the graph, while those at the bottom indicate occasional consumption or generalization. Prey points located in the upper left of the diagram suggest specialization among individual predators, whereas those in the upper right represent specialization of the predator population (Amundsen 1996). These relationships are visualized in three scatterplots created using the ggplot package (Wickham 2016).

To evaluate the differences in the feeding scheme of the species in the reservoir, we used non-parametric, multivariate methods. Similarity matrices were generated by using the Jaccard similarity index (presence/absence), which were compiled in a distance matrix of food items (prey) for each species. The differences in diet amongst species were evaluated with a permutational multivariate ANOVA (PERMANOVA), using the adonis function of the vegan package (Oksanen et al. 2022). To evaluate the differences amongst each pair of species we calculated the p-values corrected by Bonferroni with the pairwise adonis function from the pairwise Adonis package (Martínez Arbizu 2020). The results are shown on a non-metric multidimensional scaling (nMDS) plot to demonstrate the structure of the diet composition of each species, considering a tension of 0.2 as an acceptable goodness adjustment (Clarke et al. 2014). SIMPER analysis was used to identify the prey that most contributed to the dissimilarity of diets between fish species (Clarke 1993). All statistical analyses and graphs were done using R software (R version 4.2.2; R Development Core Team 2022).

Results

A total of 40 individuals were analyzed, representing three non-native fish species. The highest number of individuals belonged to *M. salmoides*, with a total of 17 individuals ranging in size from 170 to 430 mm standard length (SL). This was followed by *C. carpio* with 13 individuals (320–520 mm SL), and finally *O. mykiss* with 10 individuals (234–410 mm SL) (Table S1). The analysis of stomach contents revealed a coverage estimate of over 90% for all three species, with a statistical confidence interval of 95% (Fig. 2). This suggests that the dietary analysis conducted on these species is representative. Twenty categories of food were identified as prey for these species. The most frequent prey items in their diet were aquatic invertebrates and vegetation material (Table S1).

Diversity of consumed prey

There were no differences observed in the number of prey items consumed by these three species (Fig. S1). No significant differences were observed in the number of common or dominant prey consumed (Table S2). When examining the amount of prey consumed by *C. carpio* using the effective number of species, it was found that 89.6% of the expected prey items were present in their diet (13.3 expected prey, standard error, s.e. = 2.1) (Fig. 2). *M. salmoides* had a broader diet, with 56.1% of the identified items being classified as their prey (21.4 expected prey, s.e. = 10). However, *O. mykiss* exhibited a lower consumed prey compared to the other evaluated fish species (Fig. 2). It was determined that 95.3% of the prey items were successfully identified, with an expected prey count of 9.4 (s.e. = 0.9).

Feeding strategies

Specifically, the studied population of *C. carpio* exhibited a specialized feeding strategy, primarily consuming animal remains (Fig. 3). It was also observed that some individuals of this species focus on consuming insect remains and vegetation material (Fig. 3). On the other hand, *M. salmoides* feeds on a variety of resources simultaneously, predominantly preying on aquatic invertebrates, with a particular focus on Diptera, Trichoptera, and Odonata insect larvae. However, some individuals of this species

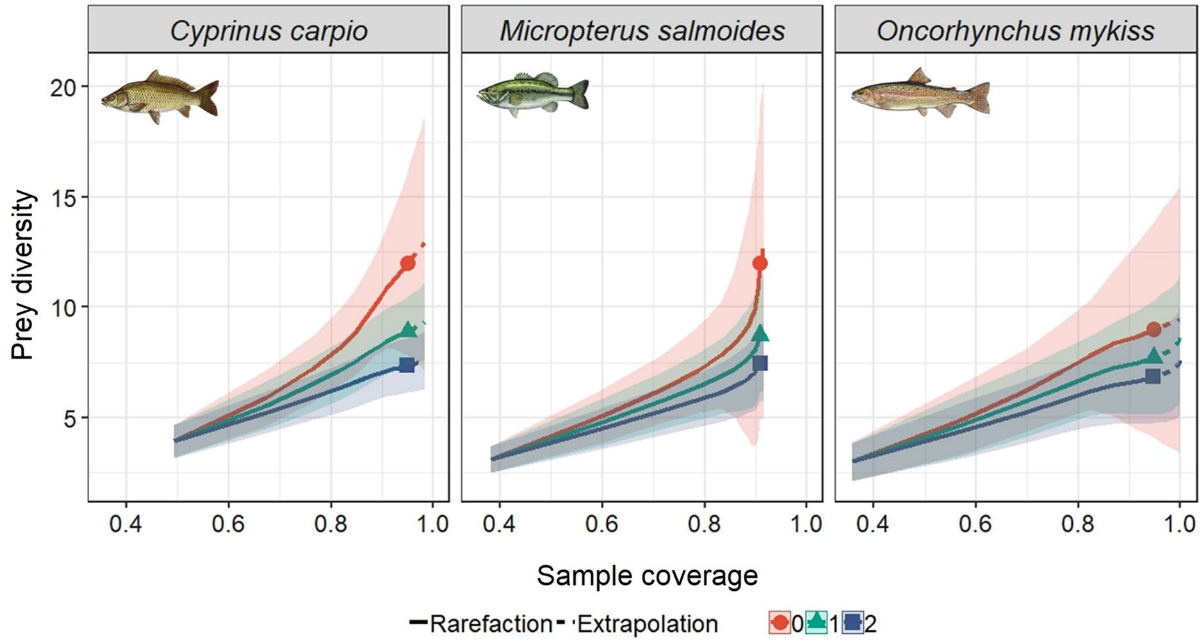

Fig. 2 Coverage-based rarefaction (solid lines) and extrapolation (dashed lines) sampling curves with 95% confidence intervals (shaded areas, based on a bootstrap method with 50 replications) for comparing number of prey items consumed by three non-native fish species in the Riogrande II reservoir. These curves are based on Hill numbers (q0, q1, and q2)

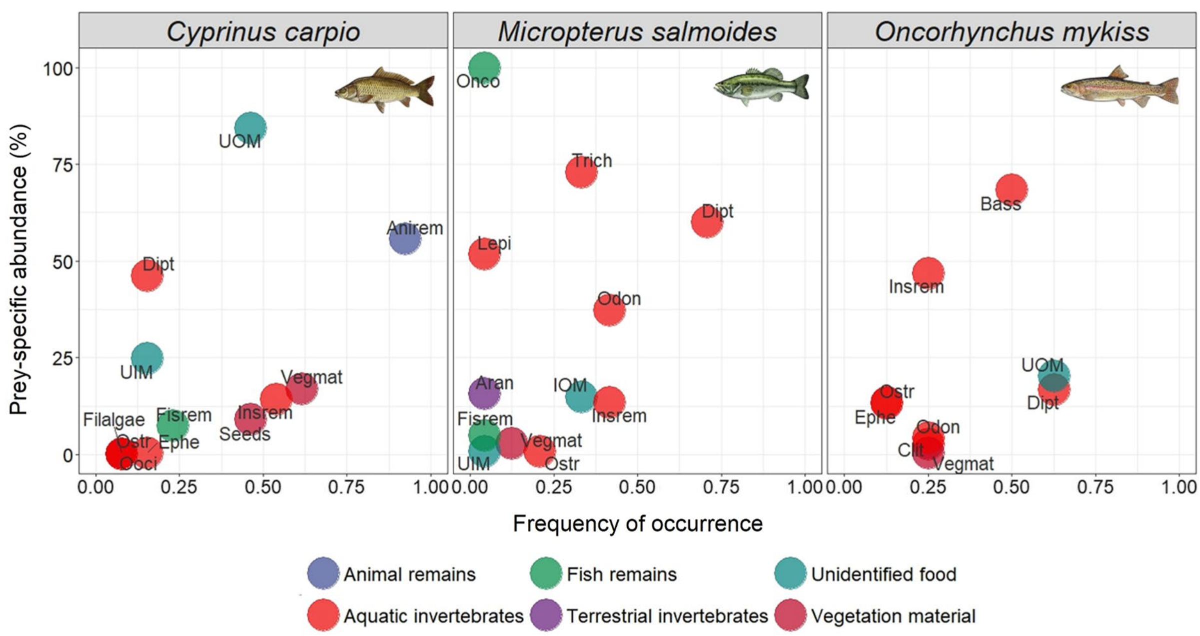

Fig. 4 Amundsen Diagram. Indicates the feeding strategy of three non-native fish species in the Riogrande II reservoir. Abbreviations on Online Resource 1.

are also predators of juvenile individuals of the non-native species *O. mykiss* (Fig. 3). In the case of *O. mykiss*, most individuals present a generalist strategy, given that they feed on prey with low specific abundance and high occasional occurrence, dominated by mollusks (Basommatophora) and insect remains (Fig. 3). No evidence was found that non-native species in this reservoir prey on native fish.

Variation in diet composition amongst species

The PERMANOVA showed that the diet analysis composition is different amongst the species (Table 1); however, no differences were observed between *M. salmoides* and *O. mykiss* (Table 1). The nMDS analysis revealed the spatial structure of diet composition among the species studied (Fig. 4). The diet compositions of *C. carpio* and *M. salmoides* displayed distinct and discrete units. In contrast, the diet of *O. mykiss* exhibited a broader composition, overlapping with the diets of the other analyzed species (Fig. 4). This finding suggests that *O. mykiss* is a generalist species (Fig. 4). SIMPER analysis showed that the most frequent prey type contributing to differences in diet composition between *C. carpio* and *M. salmoides* were animal remains, fish remains, diptera, vegetation material, seeds, oocytes, and filamentous algae (Table S3). While prey such as animal remains, seeds, and aquatic invertebrates such as Basommatophora contributed to the differences in diet between *C. carpio* and *O. mykiss* (Table S3).

Table 1 Differences in diet composition amongst species

PERMANOVA

df = degrees of freedom; SS = sum of squares

Significant values in bold print

	Df	SS	R^2	Pseudo-*F*	*P*-values
Between species	2	3.449	0.234	6.282	**< 0.001**
C. carpio vs. *M. salmoides*	1	2.771	0.234	10.39	**< 0.001**
C. carpio vs. *O. mykiss*	1	1.463	0.227	5.588	**< 0.001**
M. salmoides vs. *O. mykiss*	1	0.687	0.075	2.351	0.092
Residual	41	11.255	0.55		
Total	43	14.705	1.00		

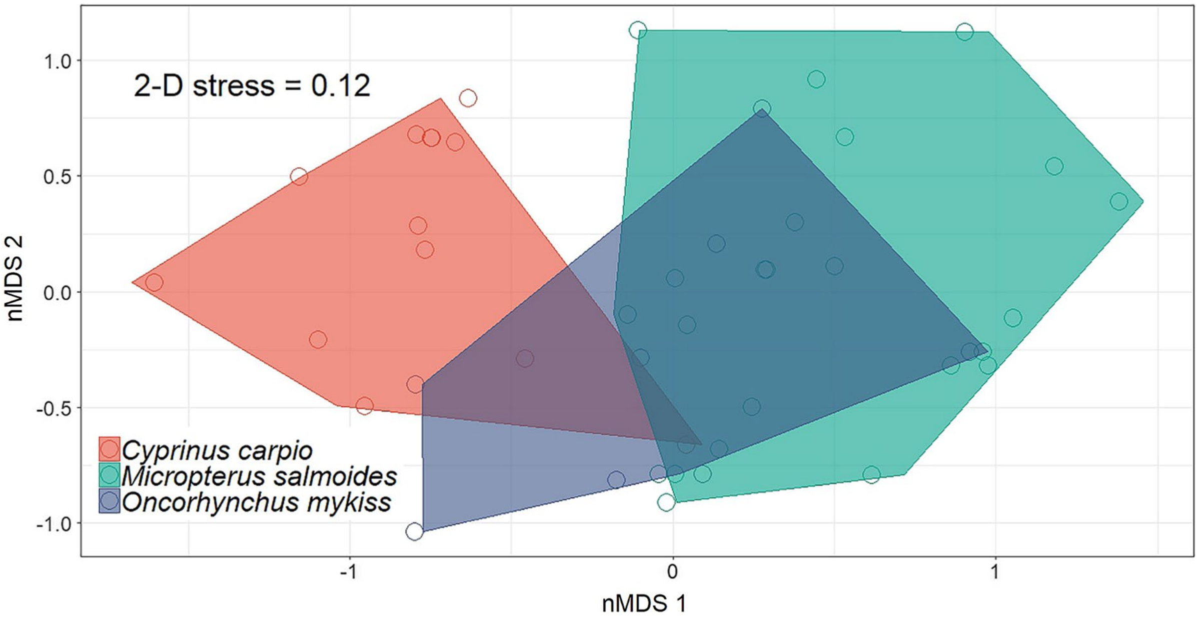

Fig. 4 nMDS analysis of the diet composition of non-native species in the Riogrande II reservoir, Magdalena basin, Colombia

Discussion

In this study, we investigated the trophic niche partitioning among three dominant non-native fish species (*C. carpio, M. salmoides,* and *O. mykiss*) in a high Andean reservoir in the Magdalena basin, Colombia. Our findings provide information on the feeding behaviors and potential interactions of these species, contributing to the understanding of the factors that promote the establishment and persistence of these species. Obtaining a deeper understanding of the trophic interactions of non-native fish species is crucial to contribute to their local management in the Colombian Andes. This research may have broader implications for conservation efforts in similar aquatic environments around the world.

The number of prey items consumed by the three fish species was similar, suggesting their ability to exploit the distribution of food resources and thus facilitate their coexistence (de Carvalho et al. 2019; Pennock et al. 2021). The most frequently consumed prey items by these three non-native species included various aquatic invertebrates, aquatic and terrestrial vegetation material, and animal remains. This observation aligns with findings in other aquatic environments. For instance, Di Prinzio et al. (2013) identified the impact of *O. mykiss* on native fauna in two rivers located in the mountains of Patagonia, Argentina. Huser and Bartels (2015) conducted a comprehensive literature review to elucidate the feeding ecology of *C. carpio*, while Pereira and Vitule (2019) undertook a global examination of the influence of *M. salmoides* on other freshwater fish species. Collectively, these studies provide valuable insights into the adaptability and resource utilization of these non-native fish species, underlining their capacity to effectively establish themselves in various environments. Additionally, the absence of evidence of predation on native fish species may suggest that these native species are absent from the lentic environment, possibly due to the diverse abilities and morphological characteristics of the native fish, which lead them to prefer the tributaries of this reservoir.

The feeding strategies differ among the three fish species, indicating specific feeding patterns for each of them. Specifically, the *C. carpio* population showed a specific feeding strategy, while the *M. salmoides* and *O. mykiss* populations exhibited generalist feeding behavior. We found that *C. carpio* has a diet that is primarily composed of animal remains and unidentified organic and inorganic material (i.e., detritus and soil), suggesting that this species feeds in the benthic area of this aquatic environment. It should be noted that some individuals in this population also consume various types of resources simultaneously, such as aquatic invertebrates and vegetation material. This feeding pattern has been reported in its native habitat, where its diet consists mainly of aquatic plants and benthic invertebrates (Magalhães 1993; Rahman et al. 2010). In environments such as lakes and reservoirs, it has been documented as an opportunistic species that primarily feeds on detritus, vegetation material, amphipods, and dipteran insect larvae (Colautti and Freyre 2001; García-Berthou 2001). Thus, the feeding behavior of this species may help reduce competition for food with the other two coexisting species (Rahman et al. 2010).

M. salmoides individuals have a generalist feeding strategy in this reservoir. The results suggest there is a variation in the consumption of resources amongst individuals of the population evaluated. For instance, while some individuals fed on various terrestrial and aquatic invertebrates, others fed on juvenile fish of *O. mykiss*. This behavior was expected, since it is reported as a voracious predator in the environment. Such feeding habits could potentially reduce the diversity of non-native fish species and lead to the local extinction of aquatic biota (Jackson 2002; Pereira and Vitule 2019; Cárdenas-Mahecha et al. 2022). In its native environment it is also an important predator, juveniles feed on terrestrial and aquatic invertebrates, while adults feed on vertebrates such as fish, amphibians, mammals, and even opt for cannibalism (Howick and O'Brien 1983; Hodgson and Hansen 2005; Braun and Walser 2011). Besides, it's important to highlight that *M. salmoides* acts simultaneously as predator and competitor of *O. mykiss*, this could be attributed to the fact that the search for similar resources amongst these predators in the same environment could increase the rate of encounter with an opportunist predator, thus turning juvenile fish into potential prey (Costantini et al. 2018; Luo et al. 2022). This behavior of *M. salmoides* could be a response to competition, broadening its diet to reduce any other niche amongst coexisting species (Araújo et al. 2011).

The generalist feeding strategy of *O. mykiss* in the reservoir involves feeding on mollusks and various types of aquatic invertebrates. Its prey includes aquatic insects found both within the water column and on the water's surface, and it may acquire a substantial portion of its diet from terrestrial invertebrates that fall from riverine or lacustrine areas (Nakano et al. 1999; Luque and González-Trujillo 2019). In addition to its presence in the reservoir, *O. mykiss* has been observed in rivers and tributary streams within this lentic environment (Martínez-Toro et al. 2022). In these streams, it likely obtains additional food resources, potentially leading to competition for food resources with native fish species (Musseau et al. 2018; Shelton et al 2017). However, more studies are needed to estimate predation by this species on native fauna and gather data to understand its impact on aquatic environments in the Colombian Andes.

We found that the three non-native fish species analyzed exhibited specific feeding behaviors and occupied different trophic niches in the reservoir. Although overlap was observed between *M. salmoides* and *O. mykiss*, these species generally find available niche opportunities and underutilized resources for feeding in their new environment. In addition to their generalist feeding strategy, they have particular adaptations that give them a competitive advantage, which facilitates their dispersal and population growth in this aquatic environment (Angulo-Valencia et al. 2023). However, their trophic interactions must be closely monitored to assess their potential ecological impacts on this aquatic environment, such as alterations in nutrient cycling, changes in the abundance of primary producers, and modifications in the trophic structure of native fish assemblages (Gozlan et al. 2010). Moreover, it is essential to consider the potential impacts these invasive species may have on the entire ichthyofauna of the Magdalena basin. While this study focuses on a high-mountain reservoir where species richness is lower compared to lower elevation areas (Valencia-Rodríguez et al. 2023), the distribution of these three species in the Magdalena basin extends beyond the Grande and Chico rivers, and their impact on native fauna could go beyond mere competition for food resources.

The reservoirs of the Magdalena basin have been subject to the repopulation of non-native species over the years from time to time as a means of food security for inhabitants living near these environments (Jiménez-Segura et al. 2014; Lasso et al. 2020); however, it was unknown that invaders could carry negative effects to an already modified environment (Jiménez-Segura et al. 2016; Valencia-Rodríguez et al. 2022). For example, through its ecological interactions, it has been reported that *C. carpio* could modify the concentrations of nutrients and turbidity of the water by means of its benthic foraging, as well as decrease the diversity of benthic fauna and macrophytes associated to the environment (Weber and Brown 2009). The introduction of *M. salmoides* could lead to a decrease in the diversity of non-native fish species and to the local extinction of aquatic biota where it settles (Pereira and Vitule 2019). Changes in the food web are attributed to *O. mykiss* in addition to altering the structure of the communities (Nakano et al. 1999; Shelton et al. 2017). In some countries, addressing environmental damage caused by non-native species incurs substantial costs (Haubrock et al. 2022; Turbelin et al. 2022). Therefore, it is important to develop more efficient and proactive strategies for handling these species, aiming to prevent their introduction and mitigate their impact (Green and Grosholz 2021). Achieving a deeper understanding of their ecological and behavioral aspects of these species is essential for crafting and guiding effective conservation approaches (e.g., Simberloff 2009; Britton et al. 2011; Piczak et al. 2023). In Colombia, adopting a preventive approach to address non-native fish is paramount. This involves implementing guidelines and agreements established through government institutions dedicated to environmental protection, such as the Ministry of Environment and regional autonomous corporations.

In conclusion, our study highlights the trophic niche partitioning among non-native fish species in a high Andean reservoir in the Magdalena basin. The specific feeding strategies and observed differences in dietary composition among the non-native species suggest niche differentiation, which facilitates their coexistence in the reservoir. However, our data did not allow us to determine how much of the coexistence of these three species is due to niche differentiation among only these three species and what the contribution of niche differentiation is in relation to native species. Therefore, we consider that interpretations regarding these three non-native species should be approached with caution, as they may involve apparent or non-genuine interactions. Additionally, this study underscores the importance of understanding trophic interactions in aquatic environments for achieving effective conservation of native biodiversity. Knowledge of these interactions allows for the identification of predators and prey, which is crucial for assessing the balance of aquatic ecosystems. Furthermore, by understanding the effects of these invasive species on the local biota, more effective strategies can be developed to preserve native populations and maintain the health of aquatic ecosystems. Further research should focus on the long-term ecological impacts of these non-native species and evaluate the effectiveness of management strategies to mitigate their negative effects on native fish communities and ecosystem functioning. The results of this study should be validated with the implementation of new methodologies, such as the use of stable carbon and nitrogen isotopes, which would provide information on the assimilation of the diet of prey and aid in the determination of niche partitioning or the possible competition for resources, in addition to contributing to understanding the properties and function of the trophic network of the ecosystem (Márquez-Velásquez et al. 2019; Black and Armbruster 2021).

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Author contributions DRS, DVR and LJS developed the ideas and designed the methodology; LMMT, DVR and DRS collected the data; JDN analyzed the samples in the lab; JDN, JSO, DVR, and DRS analyzed the data; DRS and DVR directed manuscript composition; JDN, LMMT and JSO reviewed and edited the manuscript. All authors contributed to the various drafts of the manuscript and gave their final approval for publication.

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Data availability The data used and derived from this research are available in Supplementary Material Online. The R scripts and the.csvfiles are available upon request from the corresponding author (L. Martinez-Toro).

Declarations

Conflict of interest The authors declare no conflict of interest.

Consent to participate All authors consented to participate.

Consent for publication All authors consented to the publication of the manuscript.

Ethical approval This study was conducted with the recommendations and approval of the Ethics Committee on Animal Testing of the Universidad de Antioquia (CEEA). The protocol was reviewed and approved on November 14, 2017 by CEEA, and the study was approved on December 7, 2017. Specimens were collected under collection permit number 0524 of May 27, 2014.

References

Albert JS, Tagliacollo VA, Dagosta F (2020) Diversification of neotropical freshwater fishes. Annu Rev Ecol Evol Syst 51(1):27–53. https://doi.org/10.1146/annurev-ecolsys-011620-031032

Amundsen P (1996) A new approach to graphical analysis of feeding strategy from stomach contents data—modification of the Costello (1990) method. J Fish Biol 48:607–614. https://doi.org/10.1006/jfbi.1996.0060

Angulo-Valencia MA, Peláez O, Alves DC et al (2023) Ecological traits and range size determine the occurrence of non-native fish species in a Neotropical floodplain. Biol Invas 25:1197–1210. https://doi.org/10.1007/s10530-022-02974-5

Araújo MS, Bolnick DI, Layman CA (2011) The ecological causes of individual specialization. Ecol Lett 14:948–958. https://doi.org/10.1111/j.1461-0248.2011.01662.x

Bezerra LAV, Angelini R, Vitule JRS et al (2018) Food web changes associated with drought and invasive species in a tropical semiarid reservoir. Hydrobiologia 817:475–489. https://doi.org/10.1007/s10750-017-3432-8

Black CR, Armbruster JW (2021) New method of isotopic analysis: baseline-standardized isotope vector analysis

shows trophic partitioning in loricariids. Ecosphere. https://doi.org/10.1002/ecs2.3503
Braun C, Walser C (2011) Distribution and diet of Largemouth bass (*Micropterus salmoides*) in the lower boise river, Idaho. West North Am Nat 71:316–326. https://doi.org/10.3398/064.071.0315
Britton JR, Gozlan RE, Copp GH (2011) Managing non-native fish in the environment. Fish Fish 12:256–274. https://doi.org/10.1111/j.1467-2979.2010.00390.x
Cárdenas-Mahecha LP, Vitule JRS, Padial AA (2022) Prey selectivity of the invasive largemouth bass towards native and non-native prey: an experimental approach. Neotrop Ichthyol. https://doi.org/10.1590/1982-0224-2021-0123
Chao A, Gotelli NJ, Hsieh TC et al (2014) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecol Monogr 84:45–67. https://doi.org/10.1890/13-0133.1
Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Aust J Ecol 18:117–143. https://doi.org/10.1111/j.1442-9993.1993.tb00438.x
Clarke KR, Gorley RN, Sommerfield PJ, Warwick RM (2014) Change in marine communities-statistical analysis, 3rd edn. PRIMER-E, Plymouth
Clavero M, Garcia Berthou E (2005) Invasive species are a leading cause of animal extinctions. Trends Ecol Evol 20:110–110. https://doi.org/10.1016/j.tree.2005.01.003
Colautti DC, Freyre LR (2001) Alimentación de la carpa (*Cyprinus carpio* Linnaeus 1758) en la laguna de Lobos, Provincia de Buenos Aires, Argentina. Ecol Austral 11:69–78. http://www.scielo.org.ar/scielo.php?script=sci_arttext&pid=S1667-782X2001000200003&lng=es
Costantini ML, Carlino P, Calizza E et al (2018) The role of alien fish (the centrarchid *Micropterus salmoides*) in lake food webs highlighted by stable isotope analysis. Freshw Biol 63:1130–1142. https://doi.org/10.1111/fwb.13122
Cucherousset J, Olden JD (2011) Ecological impacts of non-native freshwater fishes. Fisheries 36:215–230. https://doi.org/10.1080/03632415.2011.574578
de Carvalho DR, de Castro DMP, Callisto M et al (2019) Stable isotopes and stomach content analyses indicate omnivorous habits and opportunistic feeding behavior of an invasive fish. Aquat Ecol 53:365–381. https://doi.org/10.1007/s10452-019-09695-3
Di Prinzio CY, Miserendino ML, Casaux R (2013) Feeding strategy of the non-native rainbow trout, *Oncorhynchus mykis*s, in low-order Patagonian streams. Fish Manag Ecol 20:414–425. https://doi.org/10.1111/fme.12028
DoNascimiento C, Bogotá Gregory JD, Albornoz Garzón JG, et al (2023). Lista de especies de peces de agua dulce de Colombia / Checklist of the freshwater fishes of Colombia. Version 2.15. Asociación Colombiana de Ictiólogos. Checklist dataset https://doi.org/10.15472/numrso accessed via GBIF.org on 2023–06–03
García-Alzate C, DoNascimiento C, Villa-Navarro FA et al (2020) Diversidad de peces de la cuenca del río Magdalena. In: Jiménez-Segura LF, Lasso CA (eds) Peces de la cuenca del río Magdalena, Colombia: diversidad, conservación y uso sostenible. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, pp 85–114. https://doi.org/10.21068/B2020RRHHXIX02
García-Berthou E (2001) Size- and depth-dependent variation in habitat and diet of the common carp (*Cyprinus carpio*). Aquat Sci 63:466–476. https://doi.org/10.1007/s00027-001-8045-6
Gozlan RE, Britton JR, Cowx I, Copp GH (2010) Current knowledge on non-native freshwater fish introductions. J Fish Biol 76:751–786. https://doi.org/10.1111/j.1095-8649.2010.02566.x
Green SJ, Grosholz ED (2021) Functional eradication as a framework for invasive species control. Front Ecol Environ 19(2):98–107. https://doi.org/10.1002/fee.2277
Haubrock PJ, Bernery C, Cuthbert RN et al (2022) Knowledge gaps in economic costs of invasive alien fish worldwide. Sci Total Environ 803:149875. https://doi.org/10.1016/j.scitotenv.2021.149875
Herbold B, Moyle PB (1986) Introduced and native species. Am Nat 128:751–760
Hill MO (1973) Diversity and evenness: a unifying notation and its consequences. Ecology 54:427–432. https://doi.org/10.2307/1934352
Hodgson JR, Hansen EM (2005) Terrestrial prey items in the diet of Largemouth Bass, *Micropterus salmoides*, in a Small North temperate lake. J Freshw Ecol 20:793–794. https://doi.org/10.1080/02705060.2005.9664809
Howick GL, O'Brien WJ (1983) Piscivorous feeding behavior of largemouth bass: an experimental analysis. Trans Am Fish Soc 112:508–516. https://doi.org/10.1577/1548-8659(1983)112%3c508:PFBOLB%3e2.0.CO;2
Hsieh TC, Ma KH, Chao A (2016) iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods Ecol Evol 7:1451–1456. https://doi.org/10.1111/2041-210X.12613
Huser B, Bartels P (2015) Feeding ecology of carp. In: Pietsch C, Hirsch P (eds) Biology and ecology of carp. CRC Press LLC, BocaRaton, pp 217–243
Hyslop EJ (1980) Stomach contents analysis-a review of methods and their application. J Fish Biol 17:411–429. https://doi.org/10.1111/j.1095-8649.1980.tb02775.x
Jackson DA (2002) Ecological effects of Micropterus introductions: the dark side of black bass. Am Fish Soc Symp 2002:221–232
Javahery S, Nekoubin H, Moradlu AH (2012) Effect of anaesthesia with clove oil in fish (review). Fish Physiol Biochem 38:1545–1552. https://doi.org/10.1007/s10695-012-9682-5
Jeschke JM, Bacher S, Blackburn TM et al (2014) Defining the impact of non-native species. Conserv Biol 28:1188–1194. https://doi.org/10.1111/cobi.12299
Jiménez Segura L, Restrepo Santamaría D, López Casas S et al (2014) Ictiofauna y desarrollo del sector hidroeléctrico en la cuenca del río Magdalena-Cauca, Colombia. Biota Colomb 15:3–25. https://www.redalyc.org/articulo.oa?id=49140782002
Jiménez-Segura LF, Galvis-Vergara G, Cala-Cala P et al (2016) Freshwater fish faunas, habitats and conservation challenges in the Caribbean river basins of north-western South America. J Fish Biol 89:65–101. https://doi.org/10.1111/jfb.13018
Jost L (2006) Entropy and diversity. Oikos 113:363–375. https://doi.org/10.1111/j.2006.0030-1299.14714.x

Lasso CA, Escobar MD, Herrera J, et al (2020) Peces introducidos en el río magdalena y cuencas vecinas, Colombia. In: Jiménez-Segura L, Lasso C (eds) Peces de la cuenca del río Magdalena, Colombia: diversidad, conservación y uso sostenible. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt. https://doi.org/10.21068/B2020RRHHXIX02.

Liu C, Comte L, Olden JD (2017) Heads you win, tails you lose: life-history traits predict invasion and extinction risk of the world's freshwater fishes. Aquatic Conserv Mar Freshw Ecosyst 27:773–779. https://doi.org/10.1002/aqc.2740

Luo D, Ye M, Yang D (2022) Predator-prey interactions between Nonnative Juvenile Largemouth Bass (*Micropterus salmoides*) and local candidate prey species in the pearl river delta: predation capacity. Prefer Growth Perform Life 12:295. https://doi.org/10.3390/life12020295

Luque FJ, González-Trujillo JD (2019) Auto-ecological responses of rainbow trout populations to ecoregional differences in a neotropical andean river. Limnetica 40(1):43–55. https://doi.org/10.23818/limn.40.04

Magalhães MF (1993) Feeding of an Iberian stream cyprinid assemblage: seasonality of resource use in a highly variable environment. Oecologia 96:253–260. https://doi.org/10.1007/BF00317739

Márquez-Velásquez V, Rosa RS, Galindo E, Navia AF (2019) Feeding habits and ecological role of the freshwater stingray Potamotrygon magdalenae (Duméril 1865) (Myliobatiformes: Potamotrygonidae), combining gut-content and stable isotope analysis. Environ Biol Fishes 102:1119–1136. https://doi.org/10.1007/s10641-019-00897-0

Martínez Arbizu P (2020) pairwiseAdonis: Pairwise multilevel comparison using adonis. In: R Packag. version 0.4

Martínez-Toro LM, Restrepo-Santamaría D, Valencia-Rodríguez D, Jiménez-Segura LF (2022) Ensamblajes de peces en embalses altoandinos: El caso de los embalses Quebradona y Riogrande II en la cuenca Magdalena. Caldasia 43:1–27. https://doi.org/10.15446/caldasia.v44n2.93495

Mazo-B D, Ramírez-Restrepo JJ, Díaz-C A (2015) Caracterización física y química del embalse Riogrande II (Antioquia) Colombia. Actual Biol 37:155–168. https://doi.org/10.17533/udea.acbi.328995

McKnight E, García-Berthou E, Srean P, Rius M (2017) Global meta-analysis of native and nonindigenous trophic traits in aquatic ecosystems. Glob Change Biol 23:1861–1870. https://doi.org/10.1111/gcb.13524

Milardi M, Gavioli A, Soininen J et al (2019) Exotic species invasions undermine regional functional diversity of freshwater fish. Sci Rep 9:17921. https://doi.org/10.1038/s41598-019-54210-1

Musseau C, Vincenzi S, Jesenšek D et al (2018) Dietary niche expansion and niche shift in native marble trout (*Salmo marmoratus*) living in sympatry with introduced rainbow trout (*Oncorhynchus mykiss*). Ecol Freshw Fish 27:720–731. https://doi.org/10.1111/eff.12387

Nakano S, Miyasaka H, Kuhara N (1999) Terrestral-Aquatic linkages: Riparian arthropod inputs alter throphic cascades in a stream food web. Ecology 80:2435–2441. https://doi.org/10.1890/0012-9658(1999)080[2435:TALRAI]2.0.CO;2

Oksanen J, Simpson G, Blanchet F, et al (2022) vegan: Community Ecology Package. In: R Packag. version 2.6–2. https://cran.r-project.org/web/packages/vegan/index.html

Ortega JCG, Júlio HF, Gomes LC et al (2015) Fish farming as the main driver of fish introductions in Neotropical reservoirs. Hydrobiologia 746:147–158. https://doi.org/10.1007/s10750-014-2025-z

Pelicice FM, Agostinho AA (2009) Fish fauna destruction after the introduction of a non-native predator (*Cichla kelberi*) in a neotropical reservoir. Biol Invas 11:1789–1801. https://doi.org/10.1007/s10530-008-9358-3

Pennock CA, Ahrens ZT, McKinstry MC et al (2021) Trophic niches of native and nonnative fishes along a river-reservoir continuum. Sci Rep 11(1):1–12. https://doi.org/10.1038/s41598-021-91730-1

Pereira FW, Vitule JRS (2019) The largemouth bass *Micropterus salmoides* (Lacepède, 1802): impacts of a powerful freshwater fish predator outside of its native range. Rev Fish Biol Fish 29:639–652. https://doi.org/10.1007/s11160-019-09570-2

Piczak ML, Bzonek PA, Pratt TC et al (2023) Controlling common carp (*Cyprinus carpio*): barriers, biological traits, and selective fragmentation. Biol Invas 25:1317–1338. https://doi.org/10.1007/s10530-022-02987-0

R Core Team (2022) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.r-project.org

Rahman MM, Kadowaki S, Balcombe SR, Wahab MA (2010) Common carp (*Cyprinus carpio* L.) alters its feeding niche in response to changing food resources: direct observations in simulated ponds. Ecol Res 25:303–309. https://doi.org/10.1007/s11284-009-0657-7

Restrepo Santamaria D, Navia AF, Palacio J, Jiménez-Segura LF (2022a) Feeding strategy of fish that colonize reservoirs in the Magdalena river basin. Univ Sci 27:234–252. https://doi.org/10.11144/Javeriana.SC273.fsof

Restrepo Santamaria D, Valencia-Rodríguez D, Herrera-Pérez J et al (2022b) Contribution to the knowledge of non-native fishes in reservoirs in the Magdalena River basin: the study case Piedras blancas reservoir. Neotrop Biodivers 8:292–296. https://doi.org/10.1080/23766808.2022.2104971

Shelton JM, Bird MS, Samways MJ, Day JA (2017) Non-native rainbow trout (*Oncorhynchus mykiss*) occupy a different trophic niche to native Breede River redfin (*Pseudobarbus burchelli*) which they replace in South African headwater streams. Ecol Freshw Fish 26:484–496. https://doi.org/10.1111/eff.2017.26.issue-3

Simberloff D (2009) We can eliminate invasions or live with them. Successful management projects. Biol Invas 11:149–157. https://doi.org/10.1007/s10530-008-9317-z

Toussaint A, Charpin N, Beauchard O et al (2018) Non-native species led to marked shifts in functional diversity of the world freshwater fish faunas. Ecol Lett 21:1649–1659. https://doi.org/10.1111/ele.13141

Turbelin AJ, Diagne C, Hudgins EJ et al (2022) Introduction pathways of economically costly invasive alien species. Biol Invas 24:2061–2079. https://doi.org/10.1007/s10530-022-02796-5

Valencia-Rodríguez D, Herrera-Pérez J, Restrepo-Santamaría D et al (2022) Fish community turnover in a dammed

Andean river over time. Neotrop Ichthyol 20:1–19. https://doi.org/10.1590/1982-0224-2021-0091

Valencia-Rodríguez D, Herrera-Pérez J, Botero-Escalante D et al (2023) Distribution of diversity of fishes in an Andean fluvial network. Rev Biol Trop. https://doi.org/10.15517/rev.biol.trop..v71i1.52183

Villéger S, Blanchet S, Beauchard O et al (2015) From current distinctiveness to future homogenization of the world's freshwater fish faunas. Divers Distrib 21:223–235. https://doi.org/10.1111/ddi.12242

Vitule JRS, Freire CA, Simberloff D (2009) Introduction of non-native freshwater fish can certainly be bad. Fish Fish 10:98–108. https://doi.org/10.1111/j.1467-2979.2008.00312.x

Vitule JRS, Skóra F, Abilhoa V (2012) Homogenization of freshwater fish faunas after the elimination of a natural barrier by a dam in neotropics. Divers Distrib 18:111–120. https://doi.org/10.1111/j.1472-4642.2011.00821.x

Vitule JRS, Occhi TVT, Kang B et al (2019) Intra-country introductions unraveling global hotspots of alien fish species. Biodivers Conserv 28:3037–3043. https://doi.org/10.1007/s10531-019-01815-7

Weber MJ, Brown ML (2009) Effects of common carp on aquatic ecosystems 80 Years after "Carp as a dominant": ecological insights for fisheries management. Rev Fish Sci 17:524–537. https://doi.org/10.1080/10641260903189243

Wickham H (2016) ggplot2: Elegant graphics for data analysis. Springer, New York