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Ecological variation in invasive brown trout (*Salmo trutta*) within a remote coastal river catchment in northern Patagonia complicates estimates of invasion impact

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Abstract

Salmonids were first introduced into the Chilean fresh waters in the 1880s, and *c.* 140 years later, they are ubiquitous across Chilean rivers, especially in the southern pristine fresh waters. This study examined the brown trout (*Salmo trutta*) and native taxa ecology in two adjacent but contrasting rivers of Chilean Patagonia. During spring 2016 and spring–fall 2017 we examined the variation in benthic macroinvertebrate and fish community composition and characterized fish size structure, stomach contents, and stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) to understand population structure, fish diet, and trophic interactions between *S. trutta* and native taxa. The native *Galaxias maculatus* (puye) dominated the fish community (74% of abundance). *S. trutta* was less abundant (16% of survey catch) but dominated the fish community (over 53%) in terms of biomass. *S. trutta* showed distinct diets (stomach content analysis) in the two rivers, and individuals from the larger river were notably more piscivorous, consuming native fish with a relatively small body size (<100-mm total length). Native fishes were isotopically distinct from *S. trutta*, which showed a wider isotopic niche in the smaller river, indicating that their trophic role was more variable than in the larger river (piscivorous). This study provides data from the unstudied pristine coastal rivers in Patagonia and reveals that interactions between native and introduced species can vary at very local spatial scales.

KEYWORDS
community structure, invasive fish species, native fish species, Patagonia, salmonids, spatial variation, trophic ecology

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1 | INTRODUCTION

Freshwater ecosystems cover less than 1% of the earth's surface but play critical roles in supporting life and human development, providing access to drinking water, food, employment, recreation, and transport (Schlesinger & Bernhardt, 2020). These essential habitats face many threats, including global change, habitat modification and degradation, and invasion by invasive species. Invasive species are recognized as one of the five principal threats to fresh waters (Dudgeon et al., 2006; Strayer & Dudgeon, 2010). Of particular concern in freshwater ecosystems are the impacts of the introduction of fishes that feed at higher trophic levels and/or become strong or superior competitors: these species are also among the most successfully introduced species globally (Francis, 2012). The introduction of invasive fishes can lead to competition with native ecologically analogous fishes or predation on native taxa, disrupting ecosystem function (Soto et al., 2006).

Chile is a long (>4200 km), geographically, and biologically diverse country, with many diverse freshwater ecosystems. Although extensive, these systems support a highly endemic (>80%) but depauperate (*n* species = 43) native freshwater fish fauna (Vila & Quezada-Romegialli, 2018), resulting in a high conservation value. Furthermore, Chilean native freshwater fishes are characteristically small bodied (<20-cm total length; Vila et al., 1999; Soto et al., 2006) and are often adapted to live in high-flow rivers (Dyer, 2000).

Since the 19th century, the Chilean freshwater fish fauna has been augmented by the successful introduction of multiple fish species for the development of aquaculture and fisheries, especially those belonging to the family Salmonidae. These include members of the *Salmo*, *Oncorhynchus*, and *Salvelinus* genera. Today, naturalized (i.e., self-sustaining) populations of Chinook salmon (*Oncorhynchus tshawytscha*), rainbow trout (*Oncorhynchus mykiss*), and brown trout (*Salmo trutta*) are common in catchments across the southern part of Chile (Arismendi et al., 2014; Soto et al., 2006), including Patagonia, the geographical region that forms the southern extreme of continental South America.

The impacts of invasive salmonids on Chilean ecosystems and taxa have been considerable, from local extinction to reduced ecological performance (e.g., growth) of native organisms (Arismendi et al., 2014; Soto et al., 2006). Given their often large biomass in a system, consumption by salmonids is likely to influence invertebrate population size and structure (Buria et al., 2007), as well as changes in behavior, or life histories and fitness of benthic macroinvertebrates (Peckarsky et al., 2002). However, little research has been conducted on the effects of invasive salmonids on native invertebrates.

Patagonian fresh waters have lower native species richness than the already-depauperate Chilean taxa. However, they support high levels of endemic taxa, for example, the region's ichthyofauna is characterized by a high level of endemicity (Dyer, 2000; Vila et al., 1999). Habit et al. (2006) determined that 77% of freshwater fish species (*n* = *c*. 44) are listed in elevated conservation categories, including at risk of extinction (39%), vulnerable (30%), and rare (9%). Not enough information is available for an additional 14% of the native fishes to be adequately categorized. Threats to native Chilean fishes include competition and predation from established wild populations of invasive fishes introduced into freshwater and/or marine ecosystems (Arismendi et al., 2014; Soto et al., 2006). At the population level, extirpations and catchment-wide extinctions, particularly among galaxiid fishes, have been recorded in Chile, as well as from similar habitats in New Zealand, Australia, and Argentina, for example, following the establishment of brown trout (McDowall, 2006). Still, information on ecological interactions between native and invasive species is lacking for the Patagonian ichthyofauna. However, studies have shown that salmonids not only are strong predators but also shift the ecology of native fish in lakes (Correa et al., 2012; Ortiz-Sandoval et al., 2017) and influence the habitat use of native species (Penaluna et al., 2009).

Gathering new information regarding this topic is difficult in regions like Chilean Patagonia where many rivers are remote and unexplored. Data related to the biodiversity of these systems are very limited. This extends to the relative status of both the native and invasive fishes that have been repeatedly reported elsewhere to modify the ecology of native taxa, altering natural ecological and biological processes (Habit et al., 2014). An added complication is that coastal catchments in Patagonia are characteristically heterogeneous and can include rivers in sub-catchments that are fed from distinct sources (e.g., fed by glacier/snow melt and/or rainfall) and drain different landscapes, resulting in rivers often displaying markedly different physicochemical, habitat, and ecological properties within a given wider catchment (Astorga et al., 2018).

As mentioned earlier, very few studies have examined how impacts of invasive species can vary across apparently similar ecosystems, for example, in rivers draining adjacent catchments, but as we mentioned before, it could vary significantly across a few kilometers. This is important as policymakers and ecosystem managers need advice to allow the conservation of native taxa and ecosystem function, and such advice must reflect local reality rather than a spurious model of an invaded ecosystem. Coastal Patagonian rivers provide a valuable opportunity to examine this issue. Here we examine the presence and trophic relationships of native taxa and invasive trout, tracking changes in the amount and types of prey consumed by *S. trutta*, and examine the extent of competition with or predation on native fish in contrasting sub-catchments. We aimed to (1) compare biodiversity (macroinvertebrate and fish) and (2) ecological variation (size structure, relative condition, and diet) in native fishes and brown trout, in two contrasting sub-catchments (one glacier fed and one spring fed) of a putatively pristine, remote coastal watershed in northern Chilean Patagonia.

2 | METHODOLOGY

2.1 | Study site and experimental design

The remote study area is in the fjords of the north-west part of the Aysén region of Chilean Patagonia (Figure 1). We examined the aquatic community structure and trophic ecology of two contrasting rivers, the

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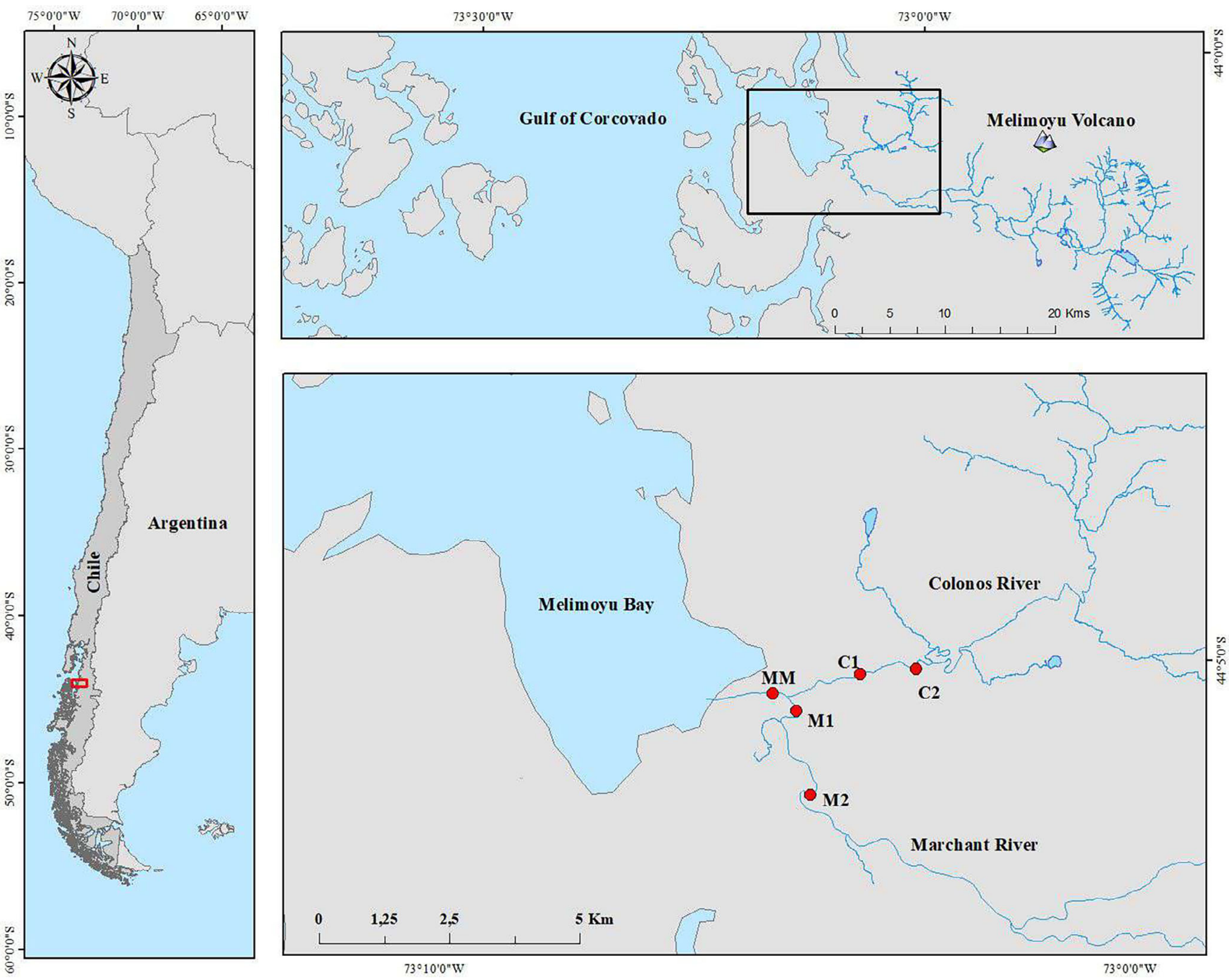

FIGURE 1 Map of the river's location in northern Patagonia: the Marchant River and the Colonos River. The red dots indicate the sampling sites within the Colonos River (C1 and C2), the Marchant River (M1 and M2), and the Marchant Mouth (MM).

Marchant River and the Colonos River, which together form the wider Marchant River basin. The system originates from waters draining glaciers located on the slopes of the Melimoyu Volcano (1200 m a.s.l.) and extends from east to west for *c.* 50 km, where it enters the sea at Melimoyu Bay as a fifth-order river. In total, the Marchant basin drains an area of *c.* 265 km^2 (not including the sub-catchment area of the Colonos River), largely consisting of old-growth Patagonian rainforest. The Marchant River is braided with a maximum channel wetted width of 170 m, with limited (2.4%–3.5%) riparian canopy cover. High flows and elevated concentrations of glacial silt imply that habitats and refuges for invertebrates and fish are largely restricted to areas adjacent to the riverbank. The Colonos River subbasin drains *c.* 43-km^2 area of lower-altitude rainforest. The Colonos River is a third-order river that extends for *c.* 15 km and enters the main stem of the Marchant River *c.* 1.5 km upstream of the point where the latter enters the sea at Melimoyu Bay. In contrast to the Marchant River, the Colonos River is not highly colored with glacial silt or heavily braided and has a much smaller channel wetted width (maximum = 50 m) and more developed canopy cover (10%–15%).

Each river section (Figure 1) was sampled during austral spring 2016 and fall/spring 2017 for 10–15 days of fieldwork for each season (years 1 and 2). The Colonos River had two sampling sites, and the Marchant River had two sampling sites upstream. A third section, the Marchant Mouth, was sampled to assess the saline influence of the tides.

2.1.1 | Biota collection

Benthic macroinvertebrates were collected at each location at random sites using Surber samplers (250 μm, 30 × 30 cm) or by hand from submerged rocks/wood, upstream and downstream the pools and in the riffles, and identified to order/family and counted under a stereoscope (Celestron LABS S10-60). The identification was based on specialized literature on the taxonomy of each group: Plecoptera (Caamaño, 1985; Illies, 1963), Trichoptera (Flint, 1979; Flint et al., 1999; Holzenthal, 2004), Megaloptera (Flint, 1983), Ephemeroptera (Dominguez et al., 2006), and neotropical macroinvertebrates, in general (Fernández & Domínguez, 2002). In addition, the functional

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trophic group was defined for each of the taxa based on Merrit and Cummins (1996) and Miserendino (2007).

Fish were collected at each site using a combination of electrofishing and gillnets. Electrofishing was conducted using a backpack electrofishing unit (Halltech Aquatic Research Inc., HT-2000), covering an area of 150 ± 30 m^2 per site. Gillnets (5 cm) were fished overnight from dusk to dawn (*c.* 8 h) at one of the edges of the rivers (average depth, 3 m). Captured fish were identified to species level and weighed (±0.01 g), and the total length was measured (±1 mm). All salmonid fishes captured were retained, but all native fishes beyond a small subset of adult fish were returned to the river live. The care and use of experimental animals complied with Subsecretaría de Pesca y Acuicultura animal welfare laws, guidelines, and policies of the American Fisheries Society (UFR Committee, 2013) approved by the Departamento Pesquero de Subsecretaría de Pesca y Acuicultura under license SubPesca R.Ex.No. 348, February 2016.

Fish were dissected, and samples of dorsal muscle were taken from some native and invasive fishes for analysis of C and N stable isotope ratios, stored on ice, and then frozen at -20°C. Stomachs were preserved in 75% ethanol solution until subsequent analysis of stomach contents in the laboratory. Invertebrate prey were identified to the same resolution as those collected from the environment using the same identification. Where possible, fish prey were identified to species.

2.1.2 | Stable isotope analysis

Frozen fish muscle samples (stored at -20°C) were freeze dried for 48 h and ground to a fine powder using a ceramic mortar. Tin capsules (8×5 mm) containing *c.* 1.5 mg of homogenized tissue were weighed for analysis using a high-precision (repeatability $= 0.0008$ mg) microbalance (model XS 3DU, Mettler Toledo, Greifensee, Switzerland). We estimated the elemental percentages for carbon and nitrogen and stable isotope ratios (δ^{13}C and δ^{15}N) using a Pyrocube (Elementar, Langenselbold, Germany) elemental analyser linked to a visION (Elementar) continuous-flow isotope ratio mass spectrometer. Stable isotope ratios were expressed in δ units for Vienna Pee Dee Belemnite for carbon and air for nitrogen as isotopic standards. Different international standards were used in each batch run to calibrate and assess analytical error using the ionOS software package (Elementar). Certified reference material USGS40 and USGS41 were used for carbon and nitrogen. Repeated analysis of standards showed that analytical errors (±1 SD [standard deviation]) were ±0.05‰ for δ^{13}C and ±0.1‰ for δ^{15}N. We used two calibration standards, (1) sulfonamide (Elementar) and (2) an in-house, matrix-matched standard (rainbow trout) to correct for machine drift.

2.2 | Statistical analysis

2.2.1 | Community composition

We examined variation in macroinvertebrate and fish community composition between and within the two catchments using distance-based, multivariate ordination (nMDS; Legendre & Legendre, 2012) and permutational multivariate analysis of variance (PERMANOVA/adonis, Anderson, 2001; SIMPER, Clarke, 1993) in the R package *vegan* (Oksanen et al., 2020). Briefly, invertebrate and fish community data were first recalculated as percentage contribution for each sampling event at each site. Data were then square-root transformed to balance the contributions from dominant and less-abundant taxa, and Bray–Curtis similarity matrices were generated. We used nMDS to graphically show variation in the data (within and between rivers) and PERMANOVA/adonis ($N_{\text{permutations}} = 9999$) to test for differences in macroinvertebrate (relative abundance) and fish (relative abundance and relative biomass) community composition. Post hoc differences were examined using the R package *RVAideMemoire* using the false discovery rate to adjust for multiple comparisons (Hervé, 2021). We then used similarity percentage (SIMPER) to examine which taxa drove patterns in similarity.

2.2.2 | Fish size structure

We compared differences in size structure in the overall fish community across the different sectors of the Marchant/Colonos system. We focused on differences between the native fish community and the dominant member of the invasive salmonid community *S. trutta*. We examined whether, on average, members of the native fish ensemble had a different size (total length in cm) compared to invasive *S. trutta* and tested if size differed between each of the river sections. Given the positive skew in the data, we fitted a generalized linear model (GLM, gamma family with a log link) using the base R function *glm* to examine the variation in fish total length associated with origin Status (native vs. *S. trutta*) and River, and the interaction between these two factors (formula: Length $\sim$ Status $\times$ River). We then ran individual models for *S. trutta* and the most numerous native fish (*G. maculatus*) to examine the intraspecific differences in fish length in the three river sections. We used the *Anova* function of the *car* package (Fox & Weisberg, 2019) to report the results of the analysis of deviance (type III) associated with the factors Status and River.

2.2.3 | Fish condition

To examine the variation in relative growth performance between the different river sections, we examined the relative mass for length (condition) of (1) *S. trutta* and (2) *G. maculatus* (the only native fish captured in all three sections). We used a two-way GLM of $\log_{10}$-transformed mass and total length values via the *lm* function in base R, with results reported using type III sum of squares via the package *car* (Fox & Weisberg, 2019). This linear model approach is more robust than the commonly used Fulton condition index, which can vary with fish size (Froese, 2006). First, for each of the two species, ANCOVA (analysis of covariance) was run including an interaction term (lm($\log_{10}$mass – $\log_{10}$Length $\times$ River)), which examines the assumption of common slopes. Then, in both cases, the non-

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significant interaction term was excluded, and the model was run again (lm($\log_{10}$mass ~ $\log_{10}$Length + River)). We used the *emmeans* package (Lenth, 2022) to compare the relative mass for a fixed length (the marginal mean value) in each of the river sections.

2.2.4 | Fish diet: Stomach content analysis

Fish stomach contents were analysed for the large-bodied native *Aplochiton* zebra ($n = 27$) in the Colonos River (as a species under likely trophic or space competition with *S. trutta*) and for *S. trutta* across the three river sections ($n = 59$). The macroinvertebrates in the stomachs were identified up to family level, and their relative contribution to each fish was calculated (%*N*), as relative volume (%*V*) and by frequency of occurrence (%*F*) (Hyslop, 1980). We compared the diet of *S. trutta* across the three river sections. Comparisons of the diet of native fishes and *S. trutta* were limited due to sample sizes. To understand the scope for trophic competition between native and invasive fishes, we compared the stomach contents of the relatively large-bodied native fish *A. zebra* (mean total length = 220 mm) with the invasive *S. trutta* in the Colonos River.

To examine the variation in trophic niche breadth, we calculated Levins's (Levins, 1968) niche breadth index (*B*) on %*N* and %*V* data ($B = 1/(\Sigma p_i^2)$, where p_i is the mean proportion of individuals consuming resource *i*). Due to differences in the number of food resources consumed between species/rivers, we also calculated the standardized form of Levins's index (B') to allow direct comparisons of niche width ($B' = (B - 1)/(n - 1)$, where *B* is Levins's index and *n* is the number of food resources used).

To provide an indication of dietary preference for invertebrate prey, we calculated Ivlev's (Ivlev, 1961) electivity index *E*. This index compares the relative contribution of a prey category in the diet (r_i) with its frequency in the environment (p_i) via the following equation $E_i = (r_i - p_i)/(r_i + p_i)$. Values of Ivlev's *E* vary between −1 for prey that are avoided and +1 for prey that are preferred: the value 0 indicates prey are randomly consumed. We used the R package *Electivity* to estimate the values of *E* (Quintans, 2019). Analysis of trophic preference (Ivlev's *E*) shown by *A. zebra* (Colonos River) and *S. trutta* (all three river sections) was limited to macroinvertebrate prey as the estimation of their abundance in the environment sampling was more comparable. Therefore, this provides a broad indication of food preferences that do not consider spatial or temporal variation within each river. We plotted the relationship between individual length in *S. trutta* and the relative contribution of fish to stomach contents (by volume) using LOESS (locally estimated scatterplot smoothing) smoothing (Cleveland, 1979) to provide a comparative measure of the scale of piscivory and the size at which it was initiated.

We studied variance in the stomach contents of individual fish between and within the two catchments using a multivariate technique similar to that used to study invertebrate and fish community composition. Data were first recalculated as a percentage contribution to the stomach of each fish. Data were then square-root transformed to balance the contributions from dominant and less-abundant taxa, and Bray–Curtis similarity matrices were generated. Variation in (1) *S. trutta* stomach contents across the three river sections and (2) in *S. trutta* and *A. zebra* stomach contents in the Colonos River was graphically represented using nMDS and tested using PERMANOVA/adonis. SIMPER was used to identify which taxa drove patterns in stomach contents.

2.2.5 | Fish stable isotope analysis

Prior to statistical analyses, fish $\delta^{13}C$ data were arithmetically lipid corrected based on Kiljunen et al. (2006) as more than 50% of the fish analysed had C:N values >3.5. Stable isotope data were used to examine several questions. First, we used summary statistics and scatterplots to examine how stable isotope values differed by river section and between *S. trutta* and native fishes. We used Pearson's correlation to examine relationships between individual length and $\delta^{13}C$ and $\delta^{15}N$ in each taxon–river section combination.

Given the limited sample sizes for some native fishes, we restricted formal statistical comparisons of isotopic overlap to between the native fish community as a whole (pooling species) and *S. trutta*. We used a two-way PERMANOVA to examine the variation in $\delta^{15}N$–$\delta^{13}C$ centroids associated with Status (native vs. *S. trutta*) and River section, and the potential interaction between the two factors. A PERMANOVA ($N_{\text{permutations}} = 9999$) based on Euclidean distances was used to test for differences in $\delta^{15}N$–$\delta^{13}C$ centroid location via the *adonis* routine in *vegan*. Post hoc differences were examined using the R package *RVAideMemoire* using the false discovery rate to adjust for multiple comparisons (Hervé, 2021). We further used a Bayesian approach to characterize the isotopic niche (relative variation in $\delta^{15}N$–$\delta^{13}C$ isotope space), calculating the sample-corrected standard eclipse area (SEA_C) and its Bayesian counterpart (SEA_B) in the *SIBER* (version 2.1.6) R package (Jackson et al., 2011). *SIBER* was run using default settings for the number of iterations, burn-in, thinning, and Markov chain Monte Carlo chains.

More detailed statistical analyses were restricted to comparisons between the invasive fishes and the dominant invasive salmonid *S. trutta*. We examined the effects of both Status and River on fish muscle lipid-corrected $\delta^{13}C$ and $\delta^{15}N$ using two-way ANOVA/linear models (formulae: $\delta^{13}C \sim \text{Status} \times \text{River}$; $\delta^{15}N \sim \text{Status} \times \text{River}$). For both $\delta^{13}C$ and $\delta^{15}N$, the Status × River interaction was not significant ($p > 0.140$), so the models were rerun by including only the main terms. Stable isotope sample sizes were more robust for the Colonos River, allowing robust comparisons of $\delta^{15}N$–$\delta^{13}C$ values between native fishes and *S. trutta*.

For all statistical analyses we used R version 4.1.2 (R Core Team, 2021) managed through the RStudio (2022.02.0) integrated development environment (RStudio Team, 2022). $\alpha = 0.05$ was used to indicate statistical significance. Wherever errors are presented, they refer to ±1 SD, unless otherwise indicated. The R packages *ggplot2* (Wickham, 2016) and *ggridges* (Wilke, 2021) were used to generate figures.

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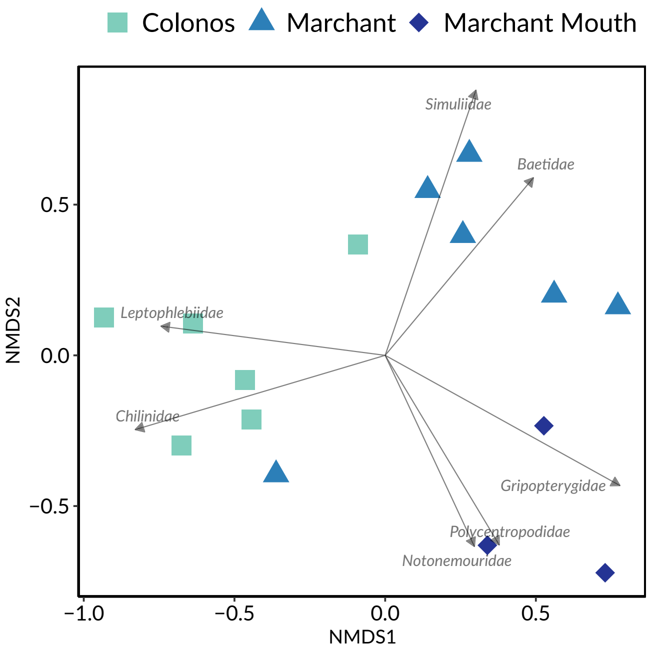

FIGURE 2 MDS (2D stress = 0.11) ordination showing variation in benthic macroinvertebrate community structure (Bray–Curtis dissimilarity of square-root-transformed relative abundance data) between the three different sampling zones in the Marchant–Colonos system. Vectors (selected using a threshold of $r \geq 0.4$) reflect the relative strength and direction of correlations between the abundance of certain taxa and ordination scores.

3 | RESULTS

3.1 | Macroinvertebrate and fish community structure

A detailed list of macroinvertebrate families and abundance is provided by site in Supplementary Table S1, and the Bray–Curtis dissimilarities (up to 80% of cumulative dissimilarity) in invertebrate community structure between the three different sampling areas are provided in Supplementary Table S2. Macroinvertebrate community composition differed between the three river sections (Figure 2; PERMANOVA: $F_{2,12} = 5.14$, $p = 0.0001$, $R^2 = 0.46$). Macroinvertebrate communities were statistically distinct in each of the three different river sections ($p \leq 0.014$ in all cases). Communities from the Colonos River were characterized by the increased relative abundance of Chilinidae (Gastropoda) and Leptophlebiidae (Ephemeroptera), whereas macroinvertebrate from Marchant River included more Simuliidae (Diptera) and Baetidae (Ephemeroptera). The macroinvertebrate community of the Marchant Mouth included more Gripopterygidae (Plecoptera), Notonemouridae (Plecoptera), and Polycentropodidae (Trichoptera) (Figure 2).

Eight fish species (Table 1) as well as one nonidentified *Oncorhynchus* sp. were identified during the surveys. Overall, fish community composition (Table 1) was dominated by invasive species (*S. trutta*, *O. mykiss*, *Oncorhynchus* sp., and *Salmo salar*) in terms of biomass (61%) but by native fishes (*A. zebra*, *G. maculatus*, *Basilichthys microlepidotus*, *Eleginops maclovinus*, and *Geotria australis*) in terms of abundance (86%). Fish community composition varied based on both biomass (Figure 3a, PERMANOVA: $F_{2,12} = 6.99$, $p = 0.0001$, $R^2 = 0.54$) and abundance (Figure 3b, $F_{2,11} = 5.78$, $p = 0.0003$, $R^2 = 0.51$: one sample was excluded from the analysis due to marked dissimilarity with other samples). Fish community composition was distinct in each of the three river sections (biomass: all $p \leq 0.013$; abundance: $p \leq 0.03$), and the relative influence of each species on the separation of the three river sections differed considerably depending on whether the analysis was based on biomass or abundance (Supplementary Table S3).

3.2 | Fish size structure

Across the three river sections fish size varied considerably, ranging between a total length of 45 mm and a mass of 0.23 g in the native *G. maculatus* up to 560 mm and 1520 g in *S. trutta*. The mean (±SD) total lengths of native fishes and *S. trutta* were 70 ± 39 and 146 ± 81 mm, respectively. The mean (±SD) masses of native fishes and *S. trutta* were 7.4 ± 52 and 60 ± 152 g, respectively (Figure 4).

Differences in fish size were associated with both Status (*S. trutta* vs. native fishes: $F_{1,962} = 60.9$, $p < 0.0001$) and River section ($F_{2,962} = 23.3$, $p < 0.0001$). The interaction term was also significant ($F_{2,962} = 6.7$, $p = 0.001$), showing that the differences between *S. trutta* and native fishes differed across the three different river sections. The model's intercept, corresponding to Status = Native and River = Colonos, was 4.39 (95% confidence limits [4.34–4.45], $t_{962} = 148.8$, $p < 0.001$).

S. trutta were on average considerably larger than native fishes ($\beta = 0.56$, 95% confidence limits 0.41–0.72, $t_{962} = 7.32$, $p < 0.001$). Overall fish from the Marchant River were smaller than those from the Colonos ($\beta = -0.29$, 95% confidence limits -0.38 to -0.21, $t(962) = -6.78$, $p < 0.001$), as were those from the Marchant Mouth ($\beta = -0.16$, 95% confidence limits -0.25 to -0.08, $t_{962} = -3.90$, $p < 0.001$).

Subsequent examination of the variation in the total length of *S. trutta* showed an overall effect of River section ($F_{2,122} = 5.0$, $p = 0.008$); however, its explanatory power was poor (Nagelkerke's $R^2 = 0.10$; Figure 4). *S. trutta* captured from the Colonos and Marchant Rivers were statistically indistinguishable (Tukey's post hoc comparison, $Z = -0.63$, $p = 0.80$) in terms of total length. However, *S. trutta* from Marchant Mouth were larger than those from both the Colonos ($Z = 2.54$, $p = 0.029$) and Marchant Rivers ($Z = 3.0$, $p = 0.008$). Native fish from the Colonos River were larger on average than those from the Marchant River ($Z = 6.8$, $p < 0.001$) and the Marchant Mouth ($Z = 3.9$, $p < 0.001$). Native fish from the Marchant Mouth were larger on average than those from the Marchant River ($Z = 3.0$, $p = 0.008$; Figure 4).

3.3 | Fish condition

The $\log_{10}$Length ($F_{1,120} = 14{,}174.2$, $p < 0.0001$) and River ($F_{2,120} = 5.6$, $p = 0.005$) had a significant effect on fish biomass

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TABLE 1 Relative contribution to survey catch by fish species in the three sections of the Marchant catchment.

	Colonos (%)	Marchant (%)	Marchant Mouth (%)
(A) Biomass species			
Aplochiton zebra	42.2	0.2	–
Basilichthys microlepidotus	–	0.8	–
Eleginops maclovinus	–	–	37.1
Galaxias maculatus	7.6	7.7	2.7
Geotria australis	0.3	–	–
Oncorhynchus mykiss	–	4.5	23.6
Oncorhynchus sp.	–	–	9.2
Salmo salar	27.9	–	–
Salmo trutta	22.0	86.8	27.4
Native species	50.1	8.7	39.8
Invasive species	49.9	91.3	60.2
Total biomass (g)	5197	2664	8884
(B) Abundance species			
A. zebra	8.3	0.3	–
B. microlepidotus	–	2.8	–
E. maclovinus	–	–	7.7
G. maculatus	72.4	77.0	86.5
G. australis	4.0	–	–
O. mykiss	–	0.9	0.3
Oncorhynchus sp.	–	–	0.6
S. salar	0.9	–	–
S. trutta	14.5	18.9	4.8
Native species	84.6	80.2	94.2
Nonnative species	15.4	19.8	5.8
Total abundance (*n*)	351	318	310

Note: Data are shown as (A) biomass and (B) abundance and are pooled across sites and sampling dates within each section. Several measures of α diversity are shown based on fish abundance.

(Figure 5a,c). *S. trutta* from Marchant River were in a better condition (higher relative mass for a given length) than conspecifics, from both the Colonos ($p = 0.017$) and Marchant Mouth ($p = 0.028$) when estimated marginal means were compared by post hoc analysis (Figure 5b). Overlap in the estimated marginal means for *S. trutta* from the Marchant River and Marchant Mouth ($p = 0.697$) indicated that fish from these sections were in similar condition. Estimated values for the slope and intercept parameters of the $\log_{10}$ mass – $\log_{10}$ total length relationship are provided in Supplementary Table S4.

Body condition of the *G. maculatus* relationship was similar in the three river sections (Figure 5c: $F_{2,761} = 0.30$, $p = 0.724$). Both $\log_{10}$total length ($F_{1,763} = 1839.7$, $p < 0.001$) and River section ($F_{2,763} = 5.78$, $p = 0.003$) affected *G. maculatus* $\log_{10}$mass. *G. maculatus* from the Colonos River were heavier for a given length relative to those from both the Marchant River ($p = 0.015$) and the Marchant Mouth ($p = 0.005$, Figure 5d). There was no measurable difference in the condition of *G. maculatus* captured from the Marchant River and the Marchant Mouth ($p = 0.976$). Estimated values for the slope and intercept parameters of the $\log_{10}$ mass – $\log_{10}$ total length relationship are provided in Supplementary Table S4.

3.4 | Fish diet

Assessing the diet of *S. trutta* across the three river sections was partly complicated by the contribution of indeterminate digested material (range: 6%–39%; Supplementary Table S5). Although the relative importance of different taxa varied based on the dietary index used, *S. trutta* diet included a mix of macroinvertebrate and fish prey (27%–88% by volume). *S. trutta* trophic niche width varied considerably between river sections, with the standardized measure Levins's B′ varying between 0.11 and 0.48 (based on %*N*) and 0.02 and 0.18 (based on %*V*). Although complicated by large volumes (55%) of indeterminate digested material, each dietary measure indicated that *A. zebra* captured from the Colonos River was entirely composed of macroinvertebrates (Supplementary Table S6). The relative importance of each taxon consumed differed between the measures used. Helicophidae (Trichoptera) and Simuliidae (Diptera) contribute most based on %*N* and %*V*. Use of %*F*, which simply measures the presence of a particular prey taxon in the diet, showed that a number of different taxa were consumed by more than 20% of individuals examined (Chironomidae, Elmidae, Gripopterygidae, Helicophidae, Leptophlebiidae, and Simuliidae).

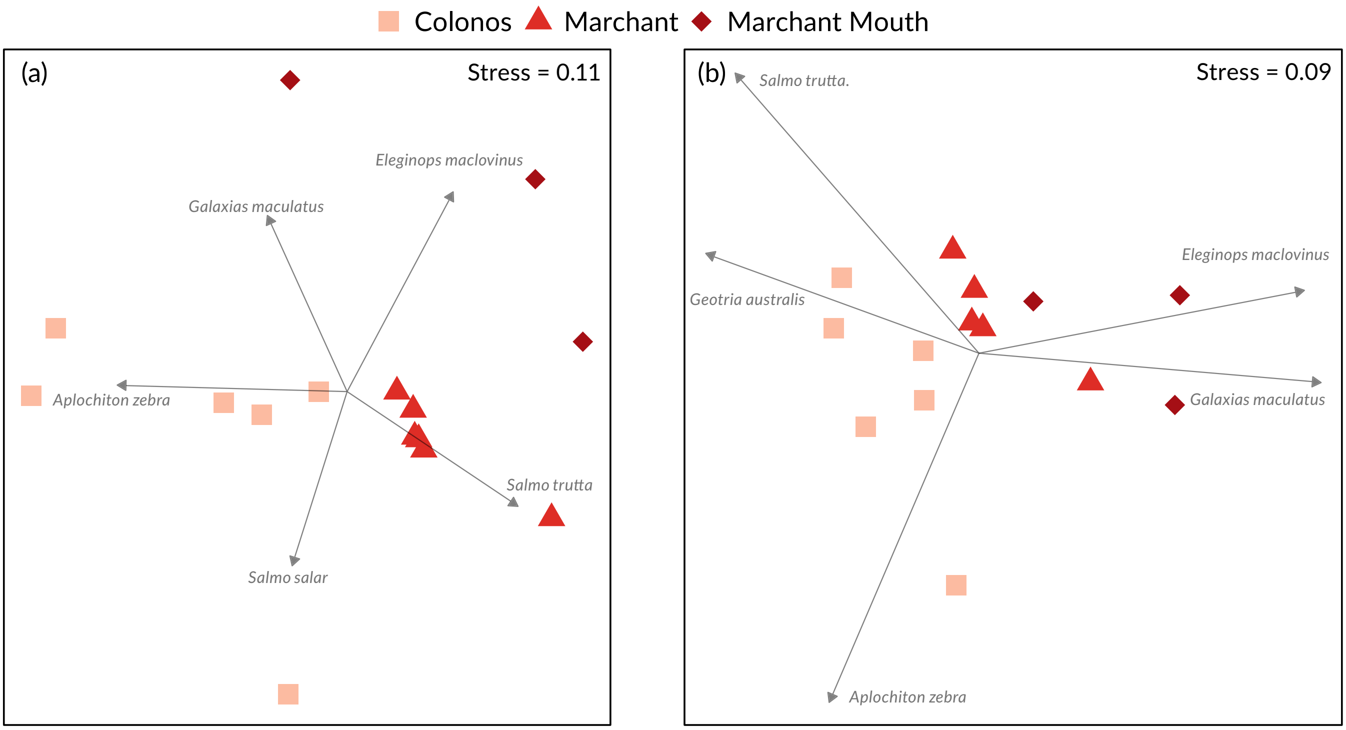

FIGURE 3 MDS ordinations showing variation in fish community structure between the three different sampling zones in the Marchant–Colonos system as (a) percentage biomass (stress = 0.11) and (b) percentage abundance (stress = 0.09). Ordinations are based on Bray–Curtis dissimilarities of square-root-transformed data. Vectors (selected using a threshold of $r \geq 0.4$) reflect the relative strength and direction of correlations between the abundance of different species and ordination scores.

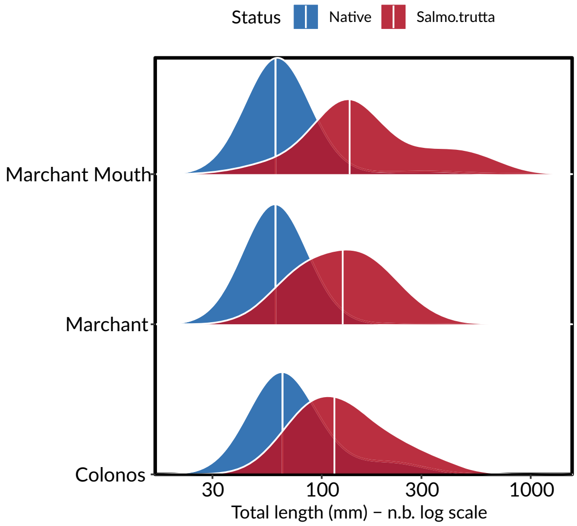

FIGURE 4 Distribution of fish total length (mm) values in native fish (blue) and the dominant invasive fish *Salmo trutta* (red) in the three different sampling areas. The solid vertical line represents the mean value for each group. Note that that the *x*-axis is shown using a $\log_{10}$ scale. Figures were produced using the ggridges R package, with a common bandwidth value of 0.15.

Diet of *S. trutta* (based on %*V*) varied between the three river sections (PERMANOVA: $F_{2,56} = 8.2$, $p = 0.0001$) but explained only a moderate amount of variation in stomach contents ($R^2 = 0.23$). *S. trutta* consumed distinct prey in each of the three river sections ($p \leq 0.02$ in all cases). There was a considerable variation in individual stomach contents in *S. trutta* captured in each of the river sections (Figure 6a), with multiple clusters particularly apparent from the Marchant River and the Marchant Mouth, likely reflecting individuals with distinct trophic strategies (e.g., piscivory vs. invertivory). *SIBER* analysis indicated that the difference between the Colonos and Marchant Rivers was driven by increased consumption of invertebrates (e.g., Leptophlebiidae, Odontoceridae, Baetidae, and Helicophidae) in fish captured from the Colonos River, whereas individuals from the Marchant River consumed more fish and some invertebrates (Gripopterygidae). Compared to conspecifics from the Marchant Mouth, *S. trutta* from the Colonos River consumed relatively more Leptophlebiidae and less *Galaxias* and several macroinvertebrate taxa (Blephariceridae, Gripopterygidae, Polycentropodidae, Baetidae, Glossosomatidae, and Simuliidae). *S. trutta* from the Marchant Mouth consumed less *Galaxias* and Gripopterygidae compared to those captured in the Marchant River, which also consumed more Leptophlebiidae, Blephariceridae, Polycentropodidae, Glossosomatidae, and Simulidae.

Native *A. zebra* and invasive *S. trutta* had distinct diets in the Colonos River (Supplementary Table S5, Figure 6b; PERMANOVA: $F_{1,47} = 12.2$, $p = 0.0001$). These differences were driven by increased consumption of Helicophidae, Simuliidae, Gripopterygidae, and Chironomidae in *A. zebra*, and of Odontoceridae, *Galaxias* sp., Baetidae, and Leptoceridae in *S. trutta*.

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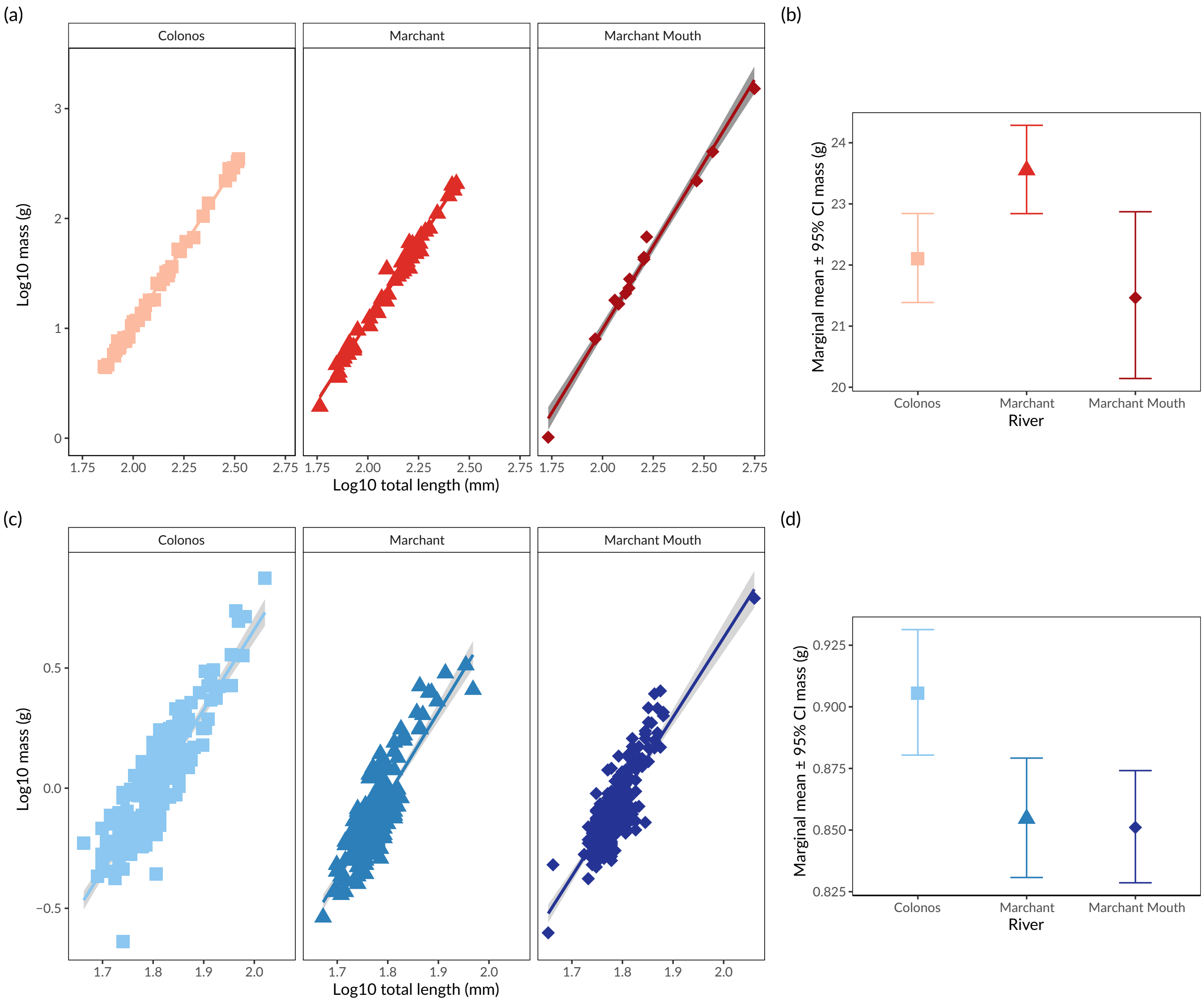

FIGURE 5 Variation in $\log_{10}$ transformed mass–length relationships and back-transformed estimated marginal mean (±95% CI) mass for a standardized length for (a, b) the invasive *Salmo trutta* and (c, d) the native *Galaxias maculatus* in three river sections of the Colonos–Marchant system. *Salmo trutta* from the Marchant and *Galaxias maculatus* from the Colonos were heavier for a given length than conspecifics from the other two river sections.

Ivlev's electivity index for *A. zebra* showed a preference for ($E > 0.5$) 18 prey taxa and avoided ($E < -0.5$) 16 taxa relative to their abundance in the environment (Figure 7a). *S. trutta* differed notably in the Colonos River, showing preference for 8 prey taxa and avoiding 17 (Figure 7b). *S. trutta* in the Marchant River selectively consumed 12 taxa and avoided 11 taxa (Figure 7c), and finally, *S. trutta* captured from the Marchant Mouth showed a preference for and avoided nine different prey taxa (Figure 7d).

Although complicated by differences in fish length, there were clear differences in the relative importance of piscivory and the size at which it occurred in the different river sections (Supplementary Figure S1). *S. trutta* were not only more piscivorous in the Marchant River compared to the other river sections, but it started at a very small size (total length: 80 mm). However, not all individuals larger than this size were piscivorous in the Marchant River.

3.5 | Stable isotopes

Carbon and nitrogen stable isotope data (Table 2) were available from seven different fish taxa, including native (*A. zebra*, *E. maclovinus*, *G. australis*, and *G. maculatus*) and invasive taxa (*O. mykiss*, *Oncorhynchus* sp., and *S. trutta*). However, sample sizes were variable and often small, limiting formal statistical comparisons.

At a whole catchment level, lipid-corrected δ^{13}C (referred to as δ^{13}C from hereon) varied by 20.1‰, ranging between −35.5‰ (an 80-mm-long *S. trutta* in the Marchant River) and −15.4 ‰ (a 330-mm-long *Oncorhynchus* sp. from the Marchant Mouth). Variation in δ^{15}N was considerable (14.6‰) but less marked than δ^{13}C, ranging between 1.7‰ (in a 100-mm *G. australis* from the Colonos River) and 16.3‰ (the ^{13}C-enriched *Oncorhynchus* sp. from the Marchant Mouth).

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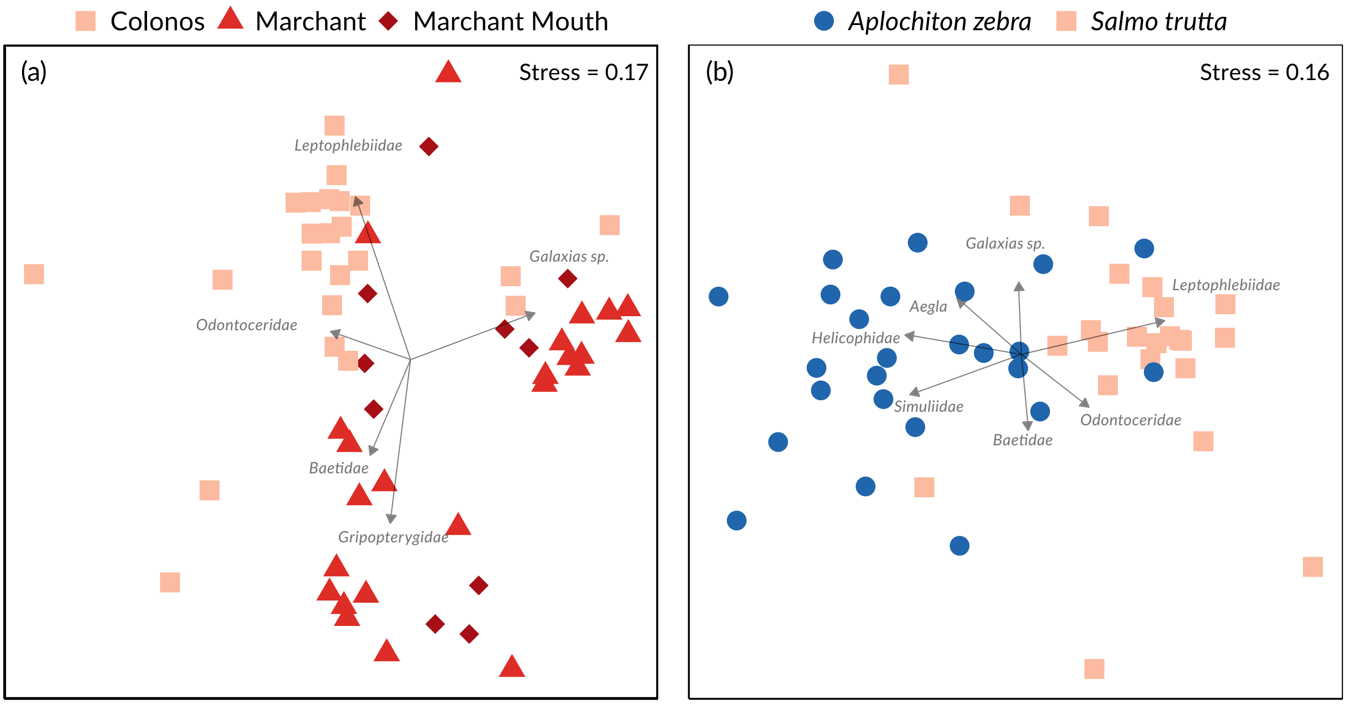

FIGURE 6 Nonmetric MDS ordination showing variation in (a) individual *Salmo trutta* stomach contents in three different capture zones during the current study and (b) stomach contents of the native fish *Aplochiton zebra* and the invasive *S. trutta* in the Colonos River. Ordinations are based on Bray–Curtis dissimilarities of square-root-transformed data. Vectors (selected using a threshold of $r \geq 0.4$) reflect the relative strength and direction of correlations between the abundance of certain prey species and the ordination scores.

Fish $\delta^{13}C$ was affected by both Status ($F_{1,53} = 11.98$, $p = 0.001$) and River section ($F_{2,53} = 11.68$, $p < 0.0001$). Overall, native fishes were enriched in ^{13}C by 3.0‰ compared to *S. trutta*. $\delta^{13}C$ values were similar in fish from the Colonos and Marchant Rivers ($p = 0.93$), but Marchant Mouth fish were $\delta^{13}C$ enriched relative to those from the Colonos (5.3‰, $p < 0.001$) and Marchant (5.7‰, $p < 0.001$) Rivers (Table 2). Fish $\delta^{15}N$ was similar in native fishes and *S. trutta* ($F_{1,53} = 0.09$, $p = 0.77$), but $\delta^{15}N$ differed between the three river sections ($F_{2,53} = 22.11$, $p < 0.0001$). Fish from the Colonos and Marchant Rivers had similar $\delta^{15}N$ ($p = 0.856$); however, fish were $\delta^{15}N$ enriched in the Marchant Mouth ($p < 0.0001$) compared to both the Colonos (3.7‰) and Marchant Rivers (4.1‰).

When data were pooled to include all native fishes and *S. trutta* (Supplementary Figure S2), there were moderate positive correlations between individual size (total length) and both $\delta^{13}C$ ($r = 0.30$, $n = 55$, $p = 0.02$) and $\delta^{15}N$ ($r = 0.37$, $n = 55$, $p = 0.004$). Native fishes showed no statistical support for relationships between length and $\delta^{13}C$ ($r = 0.22$, $n = 29$, $p = 0.23$) or $\delta^{15}N$ ($r = 0.34$, $n = 29$, $p = 0.06$). *S. trutta* however showed strong positive relationships in both $\delta^{13}C$ ($r = 0.73$, $n = 24$, $p < 0.0001$) and $\delta^{15}N$ ($r = 0.57$, $n = 24$, $p = 0.002$). There was no evidence of overall relationships between fish total length and $\delta^{13}C$ or $\delta^{15}N$ in any of the three river sections ($p = 0.07$–0.96).

When comparing the relative contribution of river and fish species status (native vs. *S. trutta*) to variation in $\delta^{15}N$ and $\delta^{13}C$, the Status × River interaction was not significant ($F_{2,51} = 1.39$, $p = 0.255$). This indicated that $\delta^{15}N$–$\delta^{13}C$ centroids varied with both Status ($F_{1,53} = 18.09$, $p = 0.0002$) and River ($F_{2,53} = 13.89$, $p = 0.0001$) but that River had the largest explanatory power (cf. R^2 River $= 0.28$, R^2 Status $= 0.18$). $\delta^{15}N$–$\delta^{13}C$ values were statistically similar in fish collected in the Colonos and Marchant Rivers ($p = 0.21$), but these fish differed from those captured from the Marchant Mouth ($p = 0.0003$ in both cases). Comparisons of native fishes and *S. trutta* showed that the two groups of fish had distinct $\delta^{15}N$–$\delta^{13}C$ centroids in the Colonos River (PERMANOVA: $F_{1,27} = 3.91$, $p = 0.03$, $R^2 = 0.13$). Statistical comparisons between the two groups of fish in the Marchant River and the Marchant Mouth were not possible due to limited sample sizes.

However, significant variation was associated with River stretch ($F_{2,23} = 4.27$, $p = 0.026$, $R^2 = 0.27$), and $\delta^{15}N$–$\delta^{13}C$ values were similar in *S. trutta* captured in the Colonos and Marchant Rivers ($p = 0.145$) and the Colonos River and Marchant Mouth ($p = 0.132$), but they varied between the Marchant River and Marchant Mouth ($p = 0.047$; Table 3). There was a small (Table 2) but significant ($F_{1,27} = 3.91$, $p = 0.03$, $R^2 = 0.12$) difference between the two groups.

3.6 | Stable isotope niche

When examined at the scale of the wider Colonos–Marchant system (Table 3), native fishes had a larger modal isotopic niche (modal $SEA_B = 24.7‰^2$) compared to *S. trutta* ($18.0‰^2$); however, the 95% credibility intervals overlapped, suggesting that they were similar

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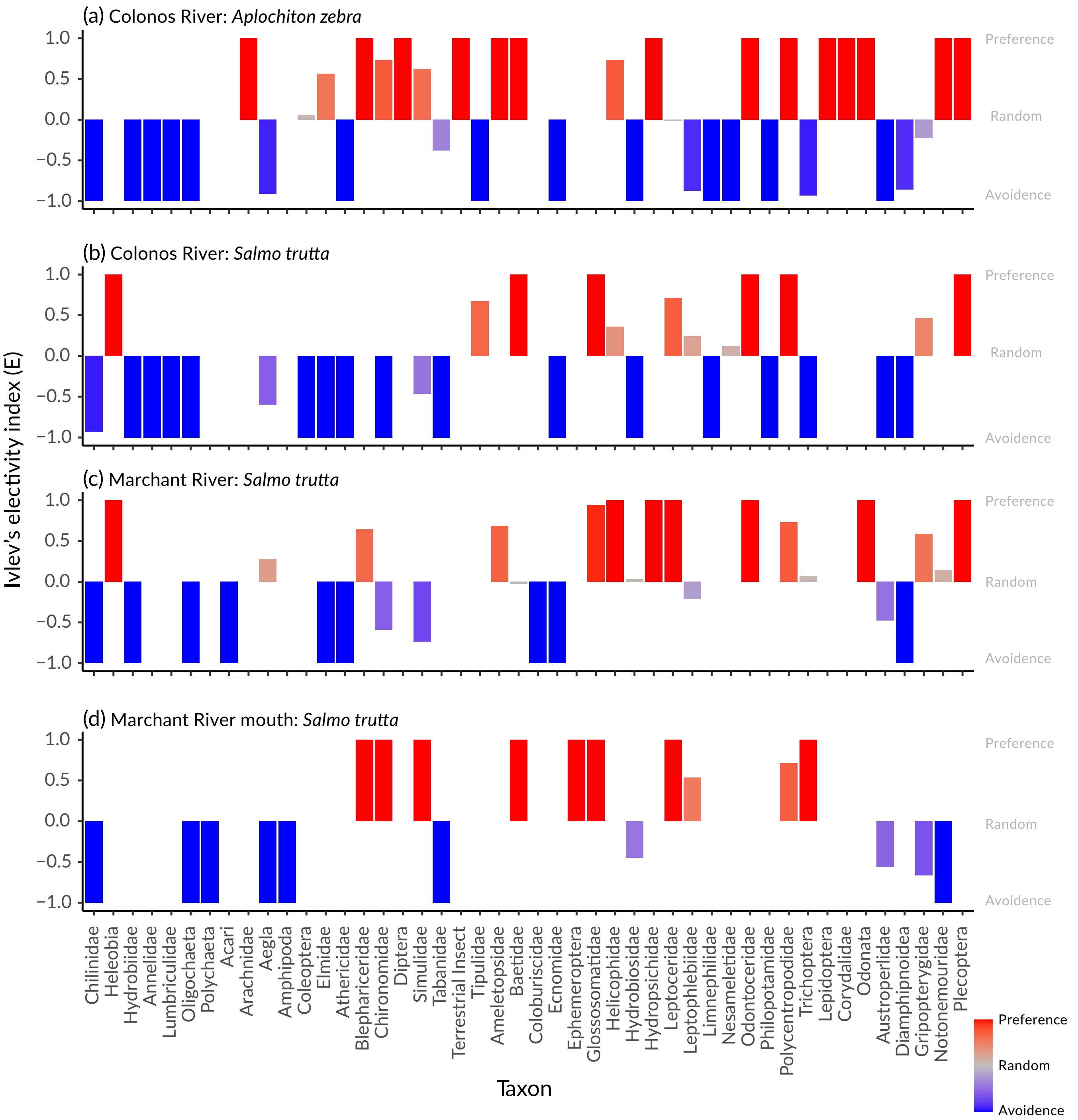

FIGURE 7 Variation in estimated trophic preference (Ivlev's *E*) for different macroinvertebrate prey shown by (a) the native fish *Aplochiton zebra* in the Colonos River and (b–d) the invasive *Salmo trutta* in the three different river sections of the Colonos–Marchant River system. Values vary between 1 (preference) and −1 (avoidance). Macroinvertebrates are ordered taxonomically (largely by order).

generally. The Colonos River was the only river section where sufficient data were available to make a robust, within-river comparison of the isotopic niche of native fishes and *S. trutta*. Here native fishes had a modal SEA$_B$ of 9.3‰, *c*. 40% smaller than that of invasive *S. trutta* (15.6‰). However, again, there was overlap in the 95% credibility intervals, suggesting that they were not markedly different.

4 | DISCUSSION

The presence of several salmonid fishes and their distribution across different sections of the system studied here provide another example of the successful colonization by these species of a remote region of Chilean Patagonia. In this area, *S. trutta* dominates streams and lakes, and can contribute to more than 95% of the total fish biomass, with

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TABLE 2 Mean (±SD) carbon and nitrogen stable isotope ratios and C:N in fish muscle captured in the three different river sections of the Marchant–Colonos system.

River section	Species (*n*)	Status	δ^{13}C	Lipid-corrected δ^{13}C	δ^{15}N	C:N
Colonos River	*Aplochiton zebra* (*n* = 7)	Native	−27.8 (1.5)	−27.2 (1.4)	7.1 (0.5)	3.3 (0.1)
Colonos River	*Geotria australis* (*n* = 2)	Native	−25.1 (0.1)	−22.2 (1.7)	5.3 (5.1)	5.5 (2.3)
Colonos River	*Galaxias maculatus* (*n* = 8)	Native	−27.7 (1.7)	−26.0 (2.0)	6.3 (0.7)	3.9 (0.3)
Colonos River	*Salmo trutta* (*n* = 12)	Invasive	−29.3 (3.8)	−28.5 (3.7)	7.3 (1.9)	3.4 (0.2)
Marchant River	*G. maculatus* (*n* = 4)	Native	−25.8 (3.5)	−24.0 (3.7)	7.2 (2.5)	4.0 (0.3)
Marchant River	*Oncorhynchus mykiss* (*n* = 2)	Invasive	−31.6 (2.1)	−30.3 (1.5)	4.6 (1.5)	3.7 (0.3)
Marchant River	*S. trutta* (*n* = 10)	Invasive	−31.1 (2.3)	−30.3 (2.1)	6.1 (0.7)	3.4 (0.2)
Marchant Mouth	*Eleginops maclovinus* (*n* = 6)	Native	−22.6 (4.4)	−21.1 (4.5)	10.9 (2.4)	3.9 (0.7)
Marchant Mouth	*G. maculatus* (*n* = 4)	Native	−20.9 (4.2)	−19.5 (3.8)	11.2 (1.7)	3.7 (0.4)
Marchant Mouth	*O. mykiss* (*n* = 1)	Invasive	−18.4 (–)	−18.0 (–)	11.7 (–)	3.4 (–)
Marchant Mouth	*Oncorhynchus* sp. (*n* = 1)	Invasive	−16.4 (–)	−15.4 (–)	16.3 (–)	3.5 (–)
Marchant Mouth	*S. trutta* (*n* = 4)	Invasive	−25.5 (6.6)	−23.6 (7.6)	9.6 (3.2)	4.1 (0.7)

Abbreviation: SD, standard deviation.

TABLE 3 Variation in estimated isotopic niche associated with the native fish community and the dominant salmonid in the Colonos–Marchant Rivers.

River	Taxon	*N*	Mode SEA$_C$ ‰^{2}	Mode SEA$_B$ ‰^{2}	2.5% CI ‰^{2}	97.5% CI ‰^{2}
Combined (all)	Native fishes	31	25.3	24.7	16.9	35.3
Combined (all)	*Salmo trutta*	26	17.5	18.0	12.2	26.8
Colonos	Native fishes	17	10.3	9.3	5.8	15.6
Colonos	*S. trutta*	12	17.4	15.6	8.8	30.0
Marchant	Native fishes	*4*	*28.0*	*20.2*	*5.8*	*69.0*
Marchant	*S. trutta*	10	4.6	5.3	2.9	9.9
Marchant Mouth	Native fishes	10	9.9	12.9	6.7	26.1
Marchant Mouth	*S. trutta*	*4*	*33.3*	*47.7*	*12.1*	*109.4*

Note: Values shown are modal estimates of sample-corrected standard ellipse area (SEA$_C$) and the Bayesian estimate (SEA$_B$), including 95% credibility intervals. Combined samples represent the values for fish combined from the three different river sections. Values in italics are based on small sample sizes (*n* = 4).

very few or no other fish, either introduced or native being encountered (Soto et al., 2006). Our data show that such observations now extend to the Colonos–Marchant system. Invasive salmonids dominated the fish community at study sites in terms of biomass, with *S. trutta* making by far the largest contribution of this group. Numerically, the fish community composition was dominated by native fishes (e.g., *G. maculatus*), but only five native freshwater fishes were encountered, highlighting both the depauperate nature of the ichthyofauna in the region and the impacts that the establishment of invasive species can have (species number has increased by at least three after salmonid invasion). Galaxiids such as *G. maculatus* and *A. zebra* are restricted to the Southern Hemisphere and have not coevolved with salmonid predators that have been deliberately introduced from the Northern Hemisphere (Correa & Hendry, 2012; McDowall, 2006).

Invasive species have several advantages over native fish in Chile, especially when we focus on fish size, but habitat quality and differences in rivers' physical characteristics modulate fish size relationship among native and invasive species. Furthermore, differences in habitat structure and complexity likely affected the availability of refugia for native fish and invertebrates (Correa & Hendry, 2012; Sobenes et al., 2013). Previous studies have shown that the effect of lower-order stream and increased habitat complexity (such as observed in the Colonos River) could be crucial for galaxiid survival and performance, especially due to the higher availability of refugia in the more heterogeneous riverbed as apparent in the Colonos River (Correa & Hendry, 2012; Sobenes et al., 2013). Our results are in agreement with the literature, given that diet differences between the three river sections were not driven by difference in size of the fish but maybe in the development of *S. trutta* and habitat complexity differences between the rivers. *S. trutta* from the Colonos River mostly consumed macroinvertebrates, whereas conspecifics from the Marchant River largely consumed fish (*c.* 90% of diet by volume) and some macroinvertebrates. *S. trutta* in the Marchant River first became piscivorous at 80 mm, with larger individuals showing a combination of trophic strategies (some piscivorous, some invertivorous). These differences in trout diet possibly reflected differences in the availability of prey,

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given that fish and macroinvertebrate communities differed between the three study sections.

S. trutta are successful invaders in Chilean rivers, as they maximize prey consumption by displacing native fish species (Arismendi et al., 2014; Soto et al., 2006). In our case, we observed that *S. trutta* and *A. zebra* largely consumed macroinvertebrates in the Colonos River, but they apparently partitioned this trophic resource. The results of our electivity analysis indicated that *A. zebra* from the Colonos River selectively consumed (i.e., ate them more than expected based on their relative abundance in the environment) more macroinvertebrate taxa ($n = 18$) than *S. trutta* ($n = 8$), even though the two fishes avoided a similar number of taxa (*A. zebra* $= 16$, *S. trutta* $= 17$). *A. zebra* selectively consumed Chironomidae, Simuliidae, Helicophidae, and Gripopterygidae. Most of these families, with the exception of Simuliidae, inhabit protective burrows from which they slowly move their bodies on the bottom of the river to feed on deposited detritus and microalgae from the surrounding sediment (Hölker & Stief, 2005). Simuliidae (or blackflies) are significant components of lotic ecosystems and are often present in varying densities, often attached to the surface of rocks, where they filter-feed on fine particulate organic matter (Malmqvist et al., 1999). In parallel, *S. trutta* largely fed on active macroinvertebrates that swim in the water column, such as Leptophlebiidae, Odontoceridae, and Baetidae. We can provide information only on the trophic niche of *A. zebra* in the presence of *S. trutta*, and it is unclear whether they would consume other prey in the absence of the invasive trout. Previous studies support the hypothesis that behavioral changes in *A. zebra* in the presence of salmonids, such as avoiding jumping out of the water for flying prey (Elgueta et al., 2013), could lead to major changes in diet and a forced displacement to prey other benthic invertebrates that inhabit refuges that we are observing in our study.

On the contrary, in the Marchant River (where piscivorous *S. trutta* dominated) trout preferably selected 12 macroinvertebrate taxa (avoiding 11). Arcagni et al. (2013) showed that small fish such as *G. maculatus* and juveniles of other species contributed most to the diet of rainbow trout (*O. mykiss*) and brook trout (*Salvelinus fontinalis*) introduced in a lake in Patagonia, Argentina. Our dietary analysis and electivity results highlight marked differences in diet preferences within a single fish species but between different sub-catchments of a single river system. The existence of such marked differences in *S. trutta* trophic niches across the three study sections was supported by the results of stable isotope analysis (although based on small sample sizes).

Our data reinforce the evidence that the ecological performance of *S. trutta* can be driven by diet (Eisendle et al., 2022). Trout in the Marchant River also displayed an increased somatic condition factor, likely reflecting a higher metabolic performance relative to the other two river sections. The relatively higher condition factor and abundance of *S. trutta* in the Marchant River compared to conspecifics from the Colonos River reflect the scope of *S. trutta* to adjust to different ecological conditions and maintain their invasive capability in Patagonian rivers (Arismendi et al., 2014; Ortiz-Sandoval et al., 2017; Soto et al., 2006).

To complement stomach content analysis, stable isotope ratios provide a longer-term indication of individual diet than stomach contents. Overall, habitat (i.e., river section) had the greatest effect on fish isotope values, but there were overall differences between native fishes and *S. trutta*, supporting the results from the analysis of stomach contents. Fish from the more saline Marchant Mouth were relatively ^{13}C and ^{15}N enriched. Unfortunately, due to a lack of data for putative prey and isotopic baselines, we were not able to estimate and compare the diet (Phillips, 2012) or trophic position (Quezada-Romegialli et al., 2018) of *S. trutta* and native fish using stable isotopes. Comparisons of stable isotope niches were limited by small sample sizes. Both at the whole catchment level and at the Colonos River scale, the isotopic niche (SEA$_B$) of *S. trutta* and native fish overlapped, suggesting similar levels of isotopic variation in the two groups.

Similar condition factor, a wide trophic niche (C and N stable isotope data), and stomach contents data suggest that *S. trutta* do not necessarily need to prey on fish species cohabiting the Colonos River as the energy cost of living in this smaller river could be lesser and is covered by macroinvertebrates with a high rate of digestion (i.e., Diptera, Sloman et al., 2002; Flodmark et al., 2004). A similar behavior is shown by *G. maculatus*, as they have a smaller, overlapping trophic niche (within the brown trout niche) in the Colonos River, with less energy sources available as *S. trutta* dominates the area and prey over all the present macroinvertebrates. Despite the competition by *S. trutta*, *G. maculatus* are still present and abundant in that river system, with good condition factors and a healthy population size structure (Arcagni et al., 2015).

Galaxiid species develop alternative life histories where some populations are diadromous, whereas others are landlocked (Chapman et al., 2006; Cussac et al., 2004). Lattuca et al. (2008) classified *A. zebra* among the synchronous group, with the spawning season varying from autumn to spring. This spawning season concurs with *S. trutta* spawning season at Patagonia, usually from May to September (Casalinuovo et al., 2017). We did not find YOYs or juveniles of *A. zebra*, showing a minimal abundance of these fish in the area and possibly a more successful development and growth for *S. trutta*. On the contrary, *G. maculatus* has a great plasticity related to seasonality, length of the spawning season, and reproductive strategy (Chapman et al., 2006), but in Patagonia it has been described to spawn from October to February, with its maximum abundance during November and December (Boy et al., 2009). *G. australis* were found in the Colonos River, the river characterized for having higher organic matter, which is food for this species at the macrophthalmia stage, just prior to ocean migration (Renaud, 2011). The data show that this life stage inhabits a "parallel" habitat within the rivers, buried in the sediment and safe from interaction with the rest of the fish species.

This study showed that despite the dominance of trout in the freshwater systems of southern Chile, we were able to find stable native fish species populations in coastal watersheds from Patagonia. More studies on coastal rivers in Patagonia are needed to identify possible areas free from salmonids; as Habit et al. (2012) discussed, most of the presence and abundance of salmonids in Patagonia is

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explained by current habitat connectivity, but not for native fish, and coastal river may play a role in dispersal along the shore of the Aysén region. There are still some unexplored pristine areas that meet the condition (i.e., waterfalls) to be free of salmonid invasion (Habit et al., 2012) to study fish biology under natural condition and to assess the ecological pathways that allow the survival of native fish in such lotic and lentic systems. River systems very similar as these (Colonos River and Marchant River) showed quite different biodiversity and feeding ecology that could be related to the structural differences observed in the rivers. Unfortunately, we were not able to evaluate these factors in our study sites mainly because of logistical reasons, including that most of the fish and macroinvertebrates were captured in the shallow area of both rivers and we were unable to obtain population parameters in the deeper sections of the Colonos and Marchant Rivers. Colonos River is two orders smaller (at least with lower water flow and speed) than Marchant River, which could lead to a lesser energetic cost for brown trout. Finally, there is a pressing need to reassess and update the conservation status of native fish in Chile, as current information on the conservation status of most native Chilean species (and the real scope of threats such as invasive salmonids) is not available. Recently, native species such as *A. zebra* has been assessed as "least concern" by the IUCN and Natural Resources-IUCN (Cussac, 2022), but *E. maclovinus* has not been evaluated by the IUCN, whereas *B. microlepidotus* (IUCN 1996) and the lamprey *G. australis* (Bice, Gorski, et al., 2019) are categorized as data deficient. *G. maculatus* is in the "least concern" category (Bice, Raadik, et al., 2019). However, that information is based on conservation information from Australia and New Zealand. Despite the information, an update on the conservation status from Patagonian ichthyofauna is immediately needed.

In summary, the evidence of our study confirms the ecological plasticity of *S. trutta* and the high capacity to invade and disrupt the food web of Patagonian coastal river systems (as observed by Elgueta et al., 2013, for Patagonian lakes), even in very different (but similar) river systems, in two ways: one indirect, by competing for food resources and space with similar native fish species (*A. zebra*), displacing them and possibly impacting their ability to survive; and a direct impact over native fish species, predating over small fish.

AUTHOR CONTRIBUTIONS

Paulina Andrea Bahamonde: Conceptualization, Investigation, Data analysis, Funding, Writing – original draft. Gustavo Chiang: Conceptualization, Investigation, Data Analysis, Funding, Writing – review & editing. Gabriela Mancilla: Investigation, Data Analysis, Writing – review & editing. Tamara Contador: Investigation, Data Analysis, Writing – review & editing. Caudio Quezada-Romegialli: Investigation, Data Analysis, Writing – review & editing. Kelly Roland Munkittrick: Conceptualization, Writing – review & editing. Chris Harrod: Conceptualization, Data Analysis, Writing – review & editing.

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