

LANDSCAPE FACTORS MODULATING PATTERNS OF SALMONID DISTRIBUTION DURING SUMMER IN NORTH PATAGONIAN RIVERS

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INTRODUCTION

Physical habitat conditions in aquatic systems determine the distributions of organisms, availability of food (Frissell *et al.*, 1986; Schlosser & Kallemeyn, 2000), mediate predation processes and affect the roles of competition among organisms (Peckarsky & Dodson 1980; Schlosser, 1991). For example, structurally complex habitats typically support more species and individuals than less complex habitats and may reduce predation rates and the intensity of competitive interactions (Bell *et al.*, 1991; Taniguchi & Tokeshi 2004). Thus, defining which

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habitat variables and spatial scales have the most influence on fish communities is key to effective and efficient management (Matthews, 1998; Gido *et al.*, 2006).

In lotic systems, local habitats and processes have traditionally been considered from a hierarchical perspective of stream networks (Frissell *et al.*, 1986), relating fish densities to habitat features, and intending to capture both local morphology and the influence of larger scale features and biotic interactions (Binns & Eiserman 1979; Stoneman & Jones 2000; Camara *et al.*, 2019). Indeed, general patterns in fish distributions across watersheds result from a combination of historical (e.g., post-glacial dispersion) and extrinsically regulated environmental processes acting at different scales (Ricklefs, 2004; Camara *et al.*, 2019). Although use of such hierarchical approach is limited by the fact that it predicts patterns that cannot be distinguished from those produced at finer scale by other mechanisms, such as competition (Kraft *et al.*, 2015), there are good reasons to explore how patterns of trait or phylogenetic dispersion change in response to the environment (Cadotte & Tucker, 2017).

Several studies have indicated that regional scale processes are important determinants of local variation in fish assemblage structure (Gorman, 1986; Pusey & Kennard, 1996; Watson & Hillman, 1997; Poizat & Corivelli, 1997) and can be summarized by relatively few landscape variables such as hydrogeological traits (Wiley *et al.*, 1997; Zorn *et al.*, 2002), and drainage area (Zorn *et al.* 2002, Creque *et al.*, 2005). These factors can explain patterns of fish distribution as well as abundance even without information at the local habitat scale (Hughes *et al.*, 1987; Lyons, 1996; Wiley *et al.*, 1997; Zorn *et al.*, 2002), usually proposed as the appropriate scale for

fisheries management (Lewis *et al.*, 1996). However, assessments for the role of landscape drivers on fish assemblages are still lacking for important regions of the world such as the neotropics, despite the fact that ongoing land use conversion has already impacted numerous natural ecosystems (Machado *et al.*, 2004, Strassburg *et al.*, 2017).

In Patagonia (southern South America), distribution of fishes across large watersheds has been influenced mainly by the Andean mountain range uplift and subsequent Quaternary glacial cycles. After glacier retreat during the Pleistocene, differential ability of Patagonian fish species to re-colonize post-glacial water bodies – constrained by climate, specially temperature – determined their present-day distribution (Cussac *et al.*, 2004; Ruzzante *et al.*, 2006). However, in more recent times, species introduction brought additional non-native fish stocks. Six native species and four introduced now coexist within Patagonian watersheds (Macchi *et al.*, 1999). Many of the introduced species have established stable populations at several large lakes that have been intensively studied in the past years (Cussac *et al.*, 2014, Macchi & Vigliano, 2014). Nevertheless, after more than sixty years of introductions and restocking practices in the upper Limay River watershed, little is yet known about fish assemblages in rivers and streams (Aigo *et al.*, 2008; Pascual *et al.*, 2002; 2007; Barriga *et al.*, 2013). Evidence from the literature suggests that the importance of landscape environmental variables on stream assemblages tend to be stronger in degraded catchments (Daniel *et al.*, 2014), but little is known about their role in structuring near-pristine habitats like those from North Patagonia. The short and well-known

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history of fish species introductions in Patagonia shows that salmonids have high dispersive capabilities and found practically no biological resistance to invasion (Pascual *et al.*, 2007).

Under the hypothesis that drivers of salmonid distribution are similar in native and introduced ranges, we expect that current distribution of salmonids in Patagonia will be mainly affected by environmental filtering at the landscape scale. The objective of this study was to examine landscape patterns distribution of salmonid species in North Patagonian breeding streams, studying the influence of landscape characteristics that we derived from remote sensing and topography data across the main environmental gradient in the region. More specifically, we aimed to test how much do landscape variables (geomorphology and climatic) explain salmonid assemblage conformation and regional dominance in streams of the Northern Patagonia.

METHODS

Study Area

The Upper Limay river watershed is located across the Argentinean provinces of Río Negro and Neuquén (40°63' S and 71° 70' W) within the Nahuel Huapi National Park and drains an area of 6.980 km²(Figure 1). Originating in the eastern slopes of the Andes mountain range, it presents a complex hydrological network characterized by a series of large interconnected deep oligotrophic lakes of varying size, to which all streams and a myriad of small lakes, ponds and wetlands drain. Westerly winds from the Pacific Ocean are forced to rise along the western

slopes of the Andes, losing most water as precipitation over the mountains and valleys, so that little humidity is left as they move over the eastern Patagonian steppe. Due to this rain shadow effect, the eastern Andean slopes experience a strong precipitation gradient going from over 3000 mm/yr over the mountain peaks to less than 600 mm/yr 60 km farther East (Paruelo *et al.*, 1998). Moreover, the precipitation regime shows marked seasonality, with contrasting periods (Paruelo *et al.* 1998). This climatic gradient results in a vegetation shift that grades from a west temperate Valdivian rainforest through mixed southern beech (*Nothofagus* spp.) and southern cedar (*Austrocedrus chilensis*) forests to the shrub lands typical of the Patagonian steppe towards the East. This whole range of climates and vegetation are present within the Upper Limay river watershed. Nahuel Huapi lake, with an area of 529 km² and a maximum depth of 464 m, is the main water collector that serves as the headwater to the Limay river's Atlantic drainage (Figure 1).

Watershed delimitation

For each watershed, we used the Hydrology toolset of the ArcGIS v.10.1 Spatial Analyst to delineate catchment boundaries and hydrological network using a flow accumulation model based on a digital elevation model. We derived our working DEM from the Shuttle Radar Topography Mission (SRTM) data (Farr *et al.*, 2007). Elevation data with a resolution of 1 arc-second, or about 30 meters, was downloaded as a series of tiles covering the region of interest from the USGS EROS Data Center. We used a flow accumulation model and discharge point method, which calculates for each pixel in the map, the number of other pixels that would drain

into it. To define a pixel as a part of a stream, we required it to have 7000 pixels or more draining to it.

Watershed selection

Thirty-five representative watersheds covering the complete climatic gradient were selected. Representative habitats were chosen in each watershed based on size, stream order (2nd or higher), recorded physiographic changes, tributary junctions, presence of lagoons or waterfalls and accessibility (Bain & Stevenson, 1999) (Figure 1). Stream order was assigned using Strahler's method (Strahler, 1973), by which the order of the stream increases when two streams of the same order converge. When two streams of different orders converge, the lower order stream is considered a tributary and the resulting effluent keeps the same order as the higher order converging stream.

A reach was defined as a stream section at least 20 times longer than its average width (Flosi and Reynolds 1994) that maintains its morphology, flow, physical-chemical, and biological characteristics. Location and number of sections sampled by stream was determined by channel shape pattern, area, and accessibility, thus determining that watersheds with the largest area had the largest number of sampled sections.

Environmental variables

A total of 32 environmental variables were chosen based on previous work (Angermeier & Winston, 1998; Oakes *et al.*, 2005; Smith & Kraft, 2005). We grouped them into four categories:

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climatic, morphologic, land use and vegetation (Table 1). Values for each variable were calculated for all 35 watersheds using either theoretical formulas (Bain & Stevenson, 1999), or digital geoprocessing tools. Summer air temperatures (°F) were calculated from satellite images during the summer season of 2014 (Landsat 6TM +). Average annual precipitation (mm) was calculated based on a map interpolating averages of daily measures from 25 meteorological stations located within from 38°46'S-41°30'S and 70°03'W -71°45'W (Barros *et al.*, 1983). Morphologic variables were calculated based on the same DEM used to delimit watersheds (see above). Land Use and Vegetation categories were obtained from existing base maps (National Geographic Institute, National Institute of Agricultural Technology (INTA) and Biodiversity Information System from Administration of National Parks), aerial photographs (Administration of National Parks) and available satellite imagery (Google Earth ®). Normalized Differential Vegetation Index (NDVI) was extracted from a Landsat thematic product derived from Landsat 6TM + images captured during the summer season of 2014. Geoprocessing and zonal statistics were computed using QGIS (version 2.6) and digital map data.

Fish assemblages

Different stream reaches that presented a succession of pool-riffle-pool were sampled during the austral summer of 2014 (from December to March). The number of sampled reaches and minimum sampled area depended on channel shape pattern, watershed area, presence of barriers and accessibility of the selected reach. In addition, in the largest watersheds (i.e. Machete, Gutiérrez, Ñireco, Ñirihauau and Chacabuco) some of the tributaries were also sampled to better

capture altitudinal variability along the extent of the basin. Each section and reach were electrofished performing three upstream 50 m passes with one Smith-Root mod.12B equipment and three netters following a zigzag trajectory and exploring all habitat types. Relative abundance data were expressed as capture per unit effort (CPUE in $n\ 100\ h^{-1}\ m^{-2}$); since we did not place nets along the whole channel at the downstream limit of the passes, CPUE values should be considered a lower bound estimate of abundance. For those watersheds sampled at several sections, we averaged CPUE from those sections. Caught fish were determined to species, weighed, measured, and sexed through examination of their gonads. Fish age was estimated by examination of scale growth rings (Wootton, 1998)

Data Analysis

Initial exploration of relationships between relative abundances (CPUE) and environmental variables ($n = 32$) was done by computing Spearman-Rank nonparametric correlation coefficients. Then, we used hierarchical cluster analysis (Everitt, 2007), first to group watersheds by similarity in environmental traits, and second to group watersheds by similarity in fish assemblage (using each species' CPUE divided total catch CPUE as group forming variable). The cluster analysis allocates each watershed to a cluster (group); a categorical variable was defined to hold the identity of the allocated group for each watershed. In order to relate the types of fish assemblages with the environmental characteristics of the watersheds, we constructed a classification and regression tree (Breiman *et al.*, 2017; Therneau & Atkinson, 2011). In the tree analysis, the response variable was group allocation resulting for the previous cluster analysis,

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and the predictor variables were abiotic and biotic factors. For this analysis, all watershed variables were included. In the first step of the process, the algorithm divides the whole set of watersheds into two groups according to a question involving one of the explanatory variables (for example, “is precipitation ≥ 1500 mm?”). Allowable questions involve one predictor x : if x is ordered, the question has the form “is $x \geq c$?”, for a given value c ; if x is categorical the question has the form “is x in S ?” where S is any subset of categories of x . The question that defines the partition is automatically selected among all allowable questions based on a rule that maximizes a measure of the improvement caused by the new partition. In this study, we used the Gini measure of improvement (Therneau & Atkinson, 2011). This process is repeated for each subgroup until all the subgroups reach a minimum size. Each step results in subgroups that are more homogeneous than the groups at the previous step; that is, there is less diversity in terms of number of groups. The last step of the tree growing algorithm selects an appropriate tree size (pruning) (Therneau & Atkinson 2011). The resulting model can be represented as a binary tree whose leaves or terminal nodes correspond to the partition of the data. All analyses were performed within the R 3.1.1 computing environment. The classification and regression tree analysis were performed using the package rpart3.1-54 (Therneau & Atkinson 2011).

RESULTS

Watershed Variables

The overall pattern at the landscape scale was determined by the west to east environmental gradient resulting from the shadow effect of the Andean range and by the geomorphological

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spatial gradient. As a result, three different clusters of watershed were identified (Figure 2A). Variables as precipitations, NDVI values, stream valley characteristics and size of drainage networks varied from one end of the gradient to the other. Western watersheds presented the highest annual rainfall and NDVI values, large drainage areas, low relief rates and the lowest maximum heights. They were dominated by closed forests, rocky outcrops and High Andean vegetation (i.e; Acantuco, Pireco, Gallardo, Machete, Bravo and Blest). Central watersheds were characterized by intermediate rainfall and NDVI where rainfall and NDVI values were intermediate and low average summer temperatures (Supporting Data Information). These watersheds had small drainage and networks areas, large relief rates and valleys with the highest elevation. They were also dominated by closed forests, high Andean vegetation and rocky outcrops (i.e. Blanco, Bonito, Casa de Piedra, Coluco, Estacada, Frey, Huemul, Lluvuco, Millaqueo, Neuquenco, Patiruco, Ragintuco y Uhueco). Eastern watersheds showed the lowest rainfall and NDVI values and highest average summer temperatures. These watersheds presented the largest and most variable average drainage and network areas, and were characterized by steppe environments and open forests, though wetlands along their valleys were also important (Figure 2A). Eastern watersheds were the only group that included urban areas within their drainage area (i.e: Gutierrez, Cascada, Castilla, Chacabuco, Challhuaco, de la Quebrada, del Medio, Las Minas and Manzano-Jones, Newbery, Pedregoso, Quintriquenco, Torrontegui, Ñireco, Tristeza and Ñirihuau).

Fish Catches

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Out of 4533 fish caught, 4531 were introduced salmonids. We caught salmonids ranging from 0 to 3 years old at all but four watersheds; older specimens (up to 8 years old) were caught only in some eastern watersheds. No fish were caught in the Newbery, Blanco, Bravo and Uhueco watersheds (Figure 2B). Only two specimens of native species were caught: one of *Galaxias maculatus* (Jennyns, 1842) in the Frey watershed and another of *Hatcheria macraei* (Girard, 1885) in Ñirihuau. *Oncorhynchus mykiss* (Walbaum, 1792), was found in all watersheds where fish were caught. Additionally, this species dominated catches of almost all the streams, except for those in the Machete, Gallardo, Gutiérrez, Castilla and Chacabuco watersheds, where *Salmo trutta* (Linnaeus, 1758) dominated the assemblages (Figure 2B). This species was found in 67.74% of the watersheds, and usually was the second most abundant species in the catches. *Salvelinus fontinalis* (Mitchill, 1814), was captured in just 48.39% of the watersheds, and was usually found at low abundance (Figure 2B). The assemblages were composed by either just one species (*O. mykiss* n = 7), two species (*S. trutta* + *O. mykiss*, n = 10; *S. fontinalis* + *O. mykiss*, n = 4) or the three species together (n = 10). In the watersheds with two species, the combination *S. trutta* and *S. fontinalis* never occurred.

Species abundances and Environmental variables.

Total catch of salmonids in the streams showed increasing values of CPUE from West to East ($R = 0.56$, $p = 0.001$) and from North to South ($R = -0.629$, $p = 0.0001$) in the upper Limay river watershed (Table 2). This increase in relative abundances was related to environments belonging to low reliefs and steppe zones, characterized by low rainfall and NDVI, zones of walkable

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forests and rocky outcrops (Table 2). The relative abundance for *O. mykiss* presented the same pattern as the total catch (greater catches in the watersheds located towards the East and South). Higher abundance of *S. trutta* was more linked with low reliefs, presence of water bodies, high temperatures and steppe environments in the watersheds and towards the east of the watershed (Table 2). For *S. fontinalis*, with low catches in all watersheds, no significant correlations were found with any environmental variable.

Cluster Analysis

Clustering based on similarity patterns of species dominance across watersheds yielded four groups (Figure 3) with no clear pattern of geographical distribution (Figure 2C). The four groups were determined mostly by variation in the proportion of the two dominant species, *O. mykiss* and *S. trutta* (Figure 3). *S. fontinalis* was poorly represented in all groups, with proportions below 17.39% (Patiruco). The most numerous group (group A, 18 watersheds) had assemblages formed almost exclusively by *O. mykiss*. In group B (4 watersheds), abundance of *O. mykiss* was lower while that of *S. trutta* was higher. In group C (5 watersheds) both species co-dominated, whereas in group D (4 watersheds) *S. trutta* was the dominant species.

Main watershed characteristics associated with fish groups types.

A classification tree analysis was used to identify the main abiotic and biotic characteristics associated to the watershed clusters defined by catch effort by species (Figure 4.I). Groups were discriminated by 6 variables: precipitation, average height of the watershed (Zav), basin relief (BR), watershed shape (kc), drainage network (DD) and presence of water bodies (WB). The

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first split was based on precipitations, and most watersheds were partitioned to the branch with precipitations under 2.524 mm. Group A watersheds in which *O. mykiss* dominated were all located in the same terminal node (T1), characterized by higher average watershed elevation and moderate relief gradients (relief <1542). Watersheds from groups B and D had greater geophysical heterogeneity, so each group was located in different nodes within the regression tree (B: T3 and T6, D: T2, T4 and T7). On the other hand, Group C, was located almost completely in the same node (T8), characterized by sites with high precipitation and marked relief gradients.

A second classification tree was computed considering only groups B, C and D, to remove the bias generated by the influence of the large number of watersheds belonging to group A (Figure 4.II). Here, it was possible to observe that abundance patterns in watersheds from those groups were discriminated by area, NDVI and minimum elevation. Three terminal nodes (nodes T1, T3 and T4) had each member of only one group, while a fourth node (T2) showed a mix of members of groups B and C. Node T1 concentrated small watersheds of group B. Node T3 concentrated large watersheds from group D with lower elevation and little vegetation cover (Figure 4.II). Node T4 concentrated large watersheds from group C watersheds with abundant vegetation cover (Figure 4.II). Node T2 included large, tall and sparsely vegetated watersheds and two different types of fish assemblages (groups B and C).

DISCUSSION

The findings of this study suggest that fish relative abundances among streams in the upper Limay river are associated with landscape characteristics. Stream location, precipitation regime, altitude and air temperature were important predictors of salmonid abundance. However, factors influencing how each species is grouped within the assemblage were not so clear. Fish–environment relationships are expected to derive both from common ancestry (promoting the dominance of a species but inhibiting the occurrence of others) as well as evolutionary convergence in response to a common set of environmental filters in the region. Although influence on fish communities by landscape-scale features have been reported previously (Marchetti *et al.*, 2004, Stanfield *et al.*, 2006, Barbosa *et al.*, 2018), this is the first report of such dynamics in North Patagonia. We discuss the implication of fish abundance and distribution patterns, the way assemblages are structured and potential drivers of *O. mykiss* trout dominance in the region.

Streams located towards the southeast of the environmental gradient presented the highest relative abundances of fish. These patterns of abundance can be explained by the interaction of two physical filters at the landscape scale: rainfall and geomorphology. On the one hand, the west-east precipitation regime changes from 3000 to 600 mm in just 60 km, determining a switch in dominant vegetation from tall and dense to low and sparse (Paruelo *et al.*, 1998). As a consequence, eastern reaches have riverbanks that are more exposed to solar irradiation and have higher air temperatures, two important factors for the primary production of periphyton and sustainability of large macroinvertebrates biomass in these systems (Miserendino, 2007;

Modenutti *et al.*, 2010). On the other hand, changes in geomorphological factors along the environmental gradient result in northwestern streams basins with small areas, higher slopes draining through narrow and steep valleys. In contrast, southeastern basins are larger in area, have gentler slopes and drain through wider valleys, consequently having less variability in water flow regime through the year. This combination of factors might be driving variation in fish abundance, similar to what has been reported in Chile (Soto *et al.*, 2006) and North America (Chapman, 1966; Stanfield *et al.*, 2006; Lusardi *et al.*, 2018).

Our analysis revealed that fish–environment associations differed across the most abundant species in the assemblages. *O. mykiss*, the species with the widest distribution at landscape scale mirrored the overall pattern of total salmonid abundance, whereas, *S. trutta* had a more restricted distribution and an abundance conditioned by environmental filters imposed by variables such as maximum watershed height, basin relief and presence of water bodies within the watersheds. All these variables are important in determining hydrological conditions of a watershed (Naiman & Bilby, 1998). This situation is different at the Chilean side of the Andes, where Soto *et al.*, (2006) found that *O. mykiss* had the most restricted distribution in terms of watershed characteristics (including a strong affinity with their more eastern streams) related to longitude and water discharge. Finally, in our study area abundance of *S. fontinalis* was low and this diminished our ability to explore the role of landscape features for this species. However, its abundance does not seem to be delimited by basin-scale variables.

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Given that the abundance of the two dominant species (*O. mykiss* and *S. trutta*) was mainly conditioned by the climatic gradient, it is not surprising that precipitation was the first variable that determined the conformation of the assemblages in the regression tree model. Abiotic factors such as rainfall, geology of an area, relief shape and slope are factors that directly influence stream discharge, thus conditioning distribution of salmonid species through their direct influence on one or more early developmental stages of the fish life cycles (Nehring & Anderson, 1993). The highest watersheds, which do not have water bodies in their headwaters, presented assemblages formed almost exclusively by *O. mykiss* (group A). In contrast, streams that presented some type of regulation at their headwaters (i.e wetlands or lakes), had assemblages dominated by *S. trutta* (group D). For groups B, C and D, each having a different degree of importance of *S. trutta*, there was no unique combination of environmental variables that determined their structure. Insufficient control by landscape variables on *S. trutta* abundance could also explain observed distribution patterns of this species in Chilean Patagonia (Soto *et al.*, 2006, Arismendi *et al.*, 2019). While *O. mykiss* was dominant in the upper watersheds of several Chilean rivers, *S. trutta* was dominant in the lower parts of the watersheds where flow regime is more stable.

The relative importance of environmental variables is usually dependent on spatial scale (Junqueira *et al.*, 2016). Our study allowed us to see the influence of the environmental gradient only for the two more abundant species of salmonids, which supports previous suggestions that landscape variables complement the understanding of the factors affecting stream fish in north

Patagonian communities (Quirós, 1991; Aigo, et al., 2008). Therefore, more studies with higher spatial resolution information, such reach scale variables throughout an entire watershed are required for a better insight into the distribution patterns of less abundant species such as brook trout.

Local scale variables, like water velocity and habitat structural complexity have been reported to function as universal environmental filters, producing similar assemblage trait distributions in streams across different regions (Bower & Winemiller, 2019). Studies conducted on a wider spatial scale found instead a greater effect of landscape variables over local ones (Esselman & Allan, 2010). In our study, sampled streams are mostly headwaters encompassing a narrow range of the landscape gradient. This limited range could be the reason why landscape variables explained comparatively less variation than reported elsewhere (Stanfield *et al.*, 2006, Barbosa *et al.*, 2018). Nonetheless, our findings suggest that some landscape traits are important enough to produce responses in fish assemblages along a landscape scale environmental gradient.

Habitat template theory posits that spatial and temporal variation of habitat features selects for certain traits and, therefore, influences the structure of local communities (Poff, 1997). Although we did not characterize year-round discharge regimes, such regimes are strongly modulated by basin geomorphology (Rosgen, 1997), so that even under a common climatic regime, adjacent basins can have contrasting dynamics driven by differing topographic factors (Sosnovsky *et al.*, 2020). Thus, landscape-scale traits drive structuring of fish assemblages through their modulation of stream flow regimes (Poff, 1997b). Because hydrologic extremes are important

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constraints for lotic biota, streams with similar flow regimes should share certain ecological features, including the invasion success of certain life history types (Poff *et al.*, 1997b; Perkin *et al.*, 2017). In our study area, most streams respond to two contrasting flow regimes: a more irregular regime with sudden environmental changes and quick responses to rain events (a “flashy” stream *sensu* Baker *et al.*, 2004 and other one with a much more stable hydrogram (Sosnovsky *et al.*, 2019). The first one, similar to that of the region where *O. mykiss* evolved (Fausch, 2008) has probably been determinant for the current abundance of the species in the upper Limay river watershed. This results are consistent with those of Fausch *et al.* (2001) in Japan where the success of *O. mykiss* was best explained by a match between timing of fry emergence and months of low flood probability. For the contrary, and due to the scarce number of regulated streams in the Upper Limay river basin (streams with stable flow regimes during a year), *S. trutta* dominates over *O. mykiss* only in a small number of streams.

We believe that our findings expand our understanding of the factors that influence the distribution and density of abundant species within Patagonia and can be used to strategically guide future management actions. For example, to develop more robust models that link critical life history events with the timing of disturbances to explain the complex interactions in communities that will inevitably drive invasion success. Considering the pristine (or near-pristine) condition of the streams sampled here, the relationships observed between fishes and landscape variables this study can be used as a baseline to assess the effects of human modifications on aquatic biodiversity of North Patagonia and to predict invasion success.

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CONTRIBUTIONS

Author contribution for this manuscript were: Conceptualization and Methodology: M.E.L, P.M, P.V; Data curation; M.E.L, P.M, P.V, M.A, G.L, M.R; Investigation: M.E.L, A.S; Visualization: M.R, Z.E, M.V.F and M.E.L; Software and Data Analysis; G.G and M.E.L; Resources: A.M, M.P, V.P; Writing-original draft; M.E.L; Writing- review & editing: M.E.L, E.Z, P.M, M.V.F, M.R, A.S and Funding acquisition and Project administration: P.V, P.M, L.M.E.

SIGNIFICANCE STATEMENT

Salmonids were deliberately introduced to Patagonia from the Northern Hemisphere during the 20th century and have since colonized almost every environment they had access to, but not always thriving. Through field captures and landscape analysis, we found that differential distribution and abundance may result from the interplay between the evolutionary fingerprint left by each species' native environment and the availability of those conditions in new environments to which they have been translocated.

REFERENCES

Aigo, J., Cussac, V., Peris, S., Ortubay, S., Gómez, S., López, H., Gross, M., Barriga, J. and Battini, M. (2008) Distribution of Introduced and Native Fish in Patagonia (Argentina): Patterns and Changes in Fish Assemblages. *Reviews in Fish Biology and Fisheries* **18**, 387–408.

Angermeier, P. L. and Winston, M. R. (1998) Local vs. Regional Influences on Local Diversity in Stream Fish Communities of Virginia. *Ecology* **79**, 911–927.

Arismendi, I, Penaluna, B, Gomez-Uchida, D, Di Prinzio, C, Rodríguez-Olarte, D, Carvajal-Vallejos, F. M., Mojica, J.I., Mazzoni, R, Cussac, V., Maldonado, M, Caramaschi, E.P., Zeballos, A.J., Villalba, A., Van Damme, P.A., Córdova, L., Iglesias-Rios, R., Cañas-Rojas, D., Cañas-Merino, M., Benavente, J.N, Núñez-Flores, M., Musleh, S.S., Savaria, P. (2019). Trout and Char of South America. In: Kershner, J.L, Williams, J.E., Gresswell, R.E., and Lobón-Cerviá, J. (Eds). Trout and Char of the World (pp.1-33). American Fisheries Society

Bain, M.B. and Stevenson, N.J. (1999) *Aquatic Habitat Assessment :Common Methods*. Bethesda: American Fisheries Society.

Baker, D.B., Richards, R.P., Loftus, T.T. and Kramer, J.W. (2004) A New Flashiness Index: Characteristics and Applications to Midwestern Rivers and Streams. *Journal of the American Water Resources Association* **40**, 503–522.

Barbosa, H.O., Borges, P.P., Dala-Corte, R.B., Martins, P.T.A., and Teresa, F.B. (2018) Relative importance of local and landscape variables on fish assemblages in streams of Brazilian savanna. *Fisheries Management and Ecology* **26**(2): 1–12.

Barriga, J. P., Espinós, N. A., Chiarello-Sosa, J. M. and Battini, M. A. (2013) The Importance of Substrate Size and Interstitial Space in the Microhabitat Selection by the Stream-Dwelling Catfish *Hatcheria Macraei* (Actinopterygii, Trichomycteridae). *Hydrobiologia* **705**, 191–206.

Barros, V., Cordon, V., Moyano, C., Mendez, R., Forquera, J. and Pizzio, O. (1983) *Cartas de Precipitación de La Zona Oeste de Las Provincias de Rio Negro y Neuquén: Primera Contribución*. Buenos Aires.

Bell, S.S., McCoy, E.D. and Mushinsky, H.R. (Eds) (1991). *Habitat structure: the physical arrangement of objects in space*. Chapman and Hall.

Binns, N. A., and F. M. Eiserman. (1979). Quantification of fluvial trout habitat in Wyoming. *Transactions of the American Fisheries Society* **108**:215–228.

Breiman, L., Friedman, J.H., Olshen, R. A. and Stone, C.J. (2017) *Classification and Regression Trees*. CRC Press.

Bower, L.M., and Winemiller, K.O. (2019). Fish assemblage convergence along stream environmental gradients: an intercontinental analysis. *Ecography*. **42**,1–13

Cadotte, M and Tucker, C. (2017). Should Environmental Filtering be Abandoned?. *Trends in Ecology and Evolution*. **32**,429-437

Camara, E. M., Costa de Azevedo, M. C., Franco, T. P. and Araújo, F. G. (2019) Hierarchical Partitioning of Fish Diversity and Scale-Dependent Environmental Effects in Tropical Coastal Ecosystems. *Marine Environmental Research* **148**, 26–38.

Chapman, D. W. (1966) Food and Space as Regulators of Salmonid Populations in Streams. *The American Naturalist* **100**, 345–357.

Creque, S.M., Rutherford, E.S. and Zorn, T.G. (2005) Use of GIS-Derived Landscape-Scale Habitat Features to Explain Spatial Patterns of Fish Density in Michigan Rivers. *North American Journal of Fisheries Management* **25**, 1411–1425.

Cussac, V. E., Ortubay, S., Iglesias, G., Milano, D., Lattuca, E., Barriga, J. P., Battini, M. and Gross, M. (2004) The Distribution of South American Galaxiid Fishes : The Role of Biological Traits and Post-Glacial History. *Journal of Biogeography* 103–121.

Cussac, V., Becker, L., Aigo J., Conte-Grand C., Blasetti G., Cordero, P., Crichigno S., and

Nabaes, D.(2014). Abundance of native fishes, wild-introduced salmonids and escaped farmed Rainbow Trout in a Patagonian reservoir. *Lakes and Reservoirs, Research and Management* **19**,1–12.

Daniel, W.M., Infante, D.M., Hughes, R.M., Esselman, P.C., Tsang, Y.P., Wieferich, D., and Taylor, W.W. (2014). Characterizing coal and mineral mines as a regional source of stress to stream fish assemblages.*Ecological Indicators* **50**, 50–61.

Esselman, P.C., and Allan, J.D. (2010). Relative influences of catchment-and reach-scale abiotic factors on freshwater fish communities in rivers of northeastern Mesoamerica. *Ecology of Freshwater Fish* **19**, 439–454.

Everitt B. (2007) An R and S-Plus companion to multivariate analysis. Springer-Verlag, New York, NY.

Farr, T.G., et al. (2007). The Shuttle Radar Topography Mission, *Reviews Geophysics.*, 45, RG2004, doi:10.1029/2005RG000183.

Fausch, K. D. (2008) A Paradox of Trout Invasions in North America. *Biological Invasions* **10**, 685–701.

Fausch, K. D., Taniguchi, Y., Nakano, S., Grossman, G. D. and Townsend, C. R. (2001) Flood Disturbance Regimes Influence Rainbow Trout Invasion Success among Five Holartic Regions. *Ecological Applications* **11**, 1438–1455.

Frissell, C. A., Liss, W. J., Warren, C. E. and Hurley, M. D. (1986) A Hierarchical Framework for Stream Habitat Classification: Viewing Streams in a Watershed Context. *Environmental Management* **10**, 199–214.

Gido, K. B., Falke, J. A., Oakes, R. M. and Hase, K. (2006) Fish-Habitat Relations across Spatial Scales in Prairie Streams. *American Fisheries Society Symposium* **48**, 265–285.

Gorman, O. T. (1986) Assemblage Organization of Stream Fishes: The Effect of Rivers on Adventitious Streams. *The American Naturalist* **128**, 611–616.

Hughes, R. M., Rexstad, E. and Bond, C.E. (1987) The Relationship of Aquatic Ecoregions, River Basins, and Physiographic Provinces to the Ichthyogeographic Regions of Oregon. *Copeia* **2**, 423–432.

Junqueira, N.T., Macedo, D.R., Souza, R. C.R., Hughes, R.M., Callisto, M., and Pompeu, P.S. (2016). Influence of environmental variables on stream fish fauna at multiple spatial scales. *Neotropical Ichthyology* **14**, 1–12.

Kraft, N.J.B, Adler P.B., Godoy, O., James, E.C., Fuller, S., and Levine, J.M. (2015) Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology* **29**: 592–599.

Lewis, C.A., Lester N.P., Bradshaw A.D., Fitzgibbon J.E., Fuller K., Hakanson L., and Richards C. (1996). Considerations of scale in habitat conservation and restoration. *Canadian Journal of Fisheries and Aquatic Sciences* **53**(Supplement 1):440–445.

Lusardi, R.A., Jeffres, C.A. and Moyle, P.B. (2018) Stream Macrophytes Increase Invertebrate Production and Fish Habitat Utilization in a California Stream. *River Research and Applications* **34**, 1003–1012.

Lyons, J. (1996) Patterns in the Species Composition of Fish Assemblages among Wisconsin Streams. *Environmental Biology of Fishes* **45**, 329–341.

Machado, R. B., Neto, M. B. R., Pereira, P. G. P., Caldas, E. F., Gonçalves, D. A., Santos, N. S., ... Steininger, M. (2004). Estimativas de perda da área do Cerrado brasileiro. Relatório técnico não publicado. Conservação Internacional, Brasília.

Macchi, P. J. and Vigliano, P. H. (2014) Salmonid Introduction in Patagonia: The Ghost of Past, Present and Future Management. *Ecología austral* **24**, 162–172.

Macchi, P.J., Cussac, V.E., Alonso, M.F., and Denegri, M.A. (1999) Predation Relationships between Introduced Salmonids and the Native Fish Fauna in Lakes and Reservoirs in Northern Patagonia. *Ecology of Freshwater Fish* **8**, 227–236.

Marchetti, M. P., Moyle, P. B. and Levine, R. (2004) Alien Fishes in California Watersheds: Characteristics of Successful and Failed Invaders. *Ecological Applications* **14**, 587–596.

Matthews, W. (1998) *Patterns in Freshwater Ecology*. Hall, C. and, ed. New York.

Miserendino, M. L. (2007) Macroinvertebrate Functional Organization and Water Quality in a Large Arid River from Patagonia (Argentina). *Annales de Limnologie - International Journal of*

Limnology **43**, 133–145.

Modenutti, B., Albariño, R., Navarro, M. B., Villanueva, V. D., Sol Souza, M., Trochine, C., Laspoumaderes, C., Cuassolo, F., Mariluán, G., Buria, L., et al. (2010) Structure and Dynamic of Food Webs in Andean North Patagonian Freshwater Systems: Organic Matter, Light and Nutrient Relationships. *Ecologia Austral* **20**, 95–114.

Naiman, R. and Bilby, R. E. (1998) River Ecology and Management in the Pacific Coastal Ecoregion. In *Ecology and Management: Lessons from the Pacific Coastal Ecoregion* (Naiman, R. J., Bilby, R. E., eds), pp. 1–10 New York: Springer-Verlag.

Nehring, R.B. and Anderson, R.M. (1993) Determination of Population-Limiting Critical Salmonid Habitats in Colorado Streams Using the Physical Habitat Simulation System. *Rivers* **4**, 1–19.

Oakes, R.M., Gido, K.B., Falke, J.A., Olden, J.D. and Brock, B.L. (2005) Modelling of Stream Fishes in the Great Plains, USA. *Ecology of Freshwater Fish* **14**, 361–374.

Paruelo, J.M., Beltrán, A., Jobbágy, E., Sala, O. E. and Golluscio, R. (1998) The Climate of Patagonia: Gneral Patterns and Control Son Biotic Processes. *Ecología Austral* **8**, 85–102.

Pascual, M., Macchi, P., Urbanski, J., Marcos, F., Riva Rossi, C., et al. (2002) Evaluating Potential Effects of Exotic Freshwater Fish from Incomplete Species Presence-Absence Data. *Biological Invasions* **4**, 101–113.

Pascual, M. A., Cussac, V., Dyer, B., Soto, D., Vigliano, P., Ortubay, S. and Macchi, P. (2007) Freshwater Fishes of Patagonia in the 21st Century after a Hundred Years of Human Settlement, Species Introductions, and Environmental Change. *Aquatic Ecosystem Health & Management* **10**, 212–227.

Peckarsky, B.L and Dodson, S.I. (1980) An experimental analysis of biological factors contributing to stream community structure. *Ecology* **61**,1283–1290.

Perkin, J. S., Knorp, N. E., Boersig, T. C., Gebhard, A. E., Hix, L. A. and Johnson, T. C. (2017) Life History Theory Predicts Long-Term Fish Assemblage Response to Stream Impoundment. *Canadian Journal of Fisheries and Aquatic Sciences* **74**, 228–239.

Poff, N. L. (1997)a Landscape Filters and Species Traits: Towards Mechanistic Understanding and Prediction in Stream Ecology. *Journal of the North American Benthological Society* **16**, 391–409.

Poff, N.L., Allan J.D., Bain M.B., Karr J.R., Prestegard K.L., Richter B.D., Sparks R.E. and Stromberg J.C.(1997)b. The Natural Flow Regime. *Bioscience*, 47 (11): 769-784.

Poizat, G. and Corivelli, A.J. (1997) Use of Seasonally Flooded Marshes by Fish in a Mediterranean Wetland: Timing and Demographic Consequences. *Journal of Fish Biology* **51**, 106–119.

Pusey, B.J. and Kennard, M.J. (1996) Species Richness and Geographical Variation in Assemblage Structure of the Freshwater Fish Fauna of the Wet Tropics Region of Northern

Queensland. *Marine and Freshwater Research* **47**, 563–573.

Quirós, R. (1991). Factores que afectan la distribución de salmónidos en Argentina. COPESCAL, FAO, Documento Técnico **9**, 163-173

Ricklefs, R. E. (2004) A Comprehensive Framework for Global Patterns in Biodiversity. *Ecology Letters*. **7**, 1–15.

Rosgen, D.L. (1997) A Geomorphological Approach to Restoration of Incised Rivers. *Proceedings of the Conference on Management of Landscapes Disturbed by Channel Incision*, 1997 **1**, 12–29.

Ruzzante, D.E., Walde, S. J., Cussac, V.E., Dalebout, M.L., Seibert, J., Ortubay, S. and Habit, E. (2006) Phylogeography of the Percichthyidae (Pisces) in Patagonia: Roles of Orogeny, Glaciation, and Volcanism. *Molecular Ecology* **15**, 2949–2968.

Schlosser, I.J. and Kallemeyn, L.W. (2000) Spatial Variation in Fish Assemblages across a Beaver-Influenced Successional Landscape. *Ecology* **81**, 1371.

Schlosser, I.J. (1991) Stream fish ecology: A landscape perspective. *Bioscience* **41**, 704–712

Smith, T.A. and Kraft, C.E. (2005) Stream Fish Assemblages in Relation to Landscape Position and Local Habitat Variables. *Transactions of the American Fisheries Society* **134**, 430–440.

Sosnovsky, A., Lallement, M.E., Rechencq, M., Zattara, E., Fernández, M.V., Daga, R. Suarez, J., Leiva, S. and Cantet, R.J.C. (2019) Topography and Land Use Modulate Hydrological and

Nutrient Export Dynamics in Andean Streams. *bioRxiv* 742411. doi:
<https://doi.org/10.1101/742411>.

Sosnovsky, A., Rechencq, M., Fernández, M.V, Suarez M.J and Cantet, R.J.C. (2020). Hydrological and Physico-chemical dynamics in two Andean streams. *Limnetica*, **39** (1): 17-33.

Soto, D., Arismendi, I., González, J., Sanzana, J., Jara, F., Jara, C., Guzman, E. and Lara, A. (2006). Southern Chile, Trout and Salmon Country: Invasion Patterns and Threats for Native Species. *Revista chilena de historia natural* **79**, 97–117.

Stanfield, L.W., Gibson, F. and Borwick, J.A. (2006) Using a Landscape Approach to Identify the Distribution and Density Patterns of Salmonids in Lake Ontario Tributaries. *American Fisheries Society Symposium* **48**, 601–621.

Strahler, A.N. and Strahler, A.H. (1973). Environmental geoscience, Hamilton Pub., New York.

Taniguchi, H. and M. Tokeshi, (2004). Effects of habitat complexity on benthic assemblages in a variable environment. *Freshwater Biology* **49**: 1164–1178.

Therneau, T. and Atkinson, E. (2011) R Port Brian Ripley, Rpart: Recursive Partitioning.R Package Version. 2011, 1–50.

Strassburg, B.B.N., Brooks, T., Feltran-Barbieri, R., Iribarrem, A., Crouzeilles, R., Loyola, R. and Balmford, A. (2017). Moment of truth for the *Cerrado* hotspot. *Nature Ecology & Evolution*, **1**: 1–3.

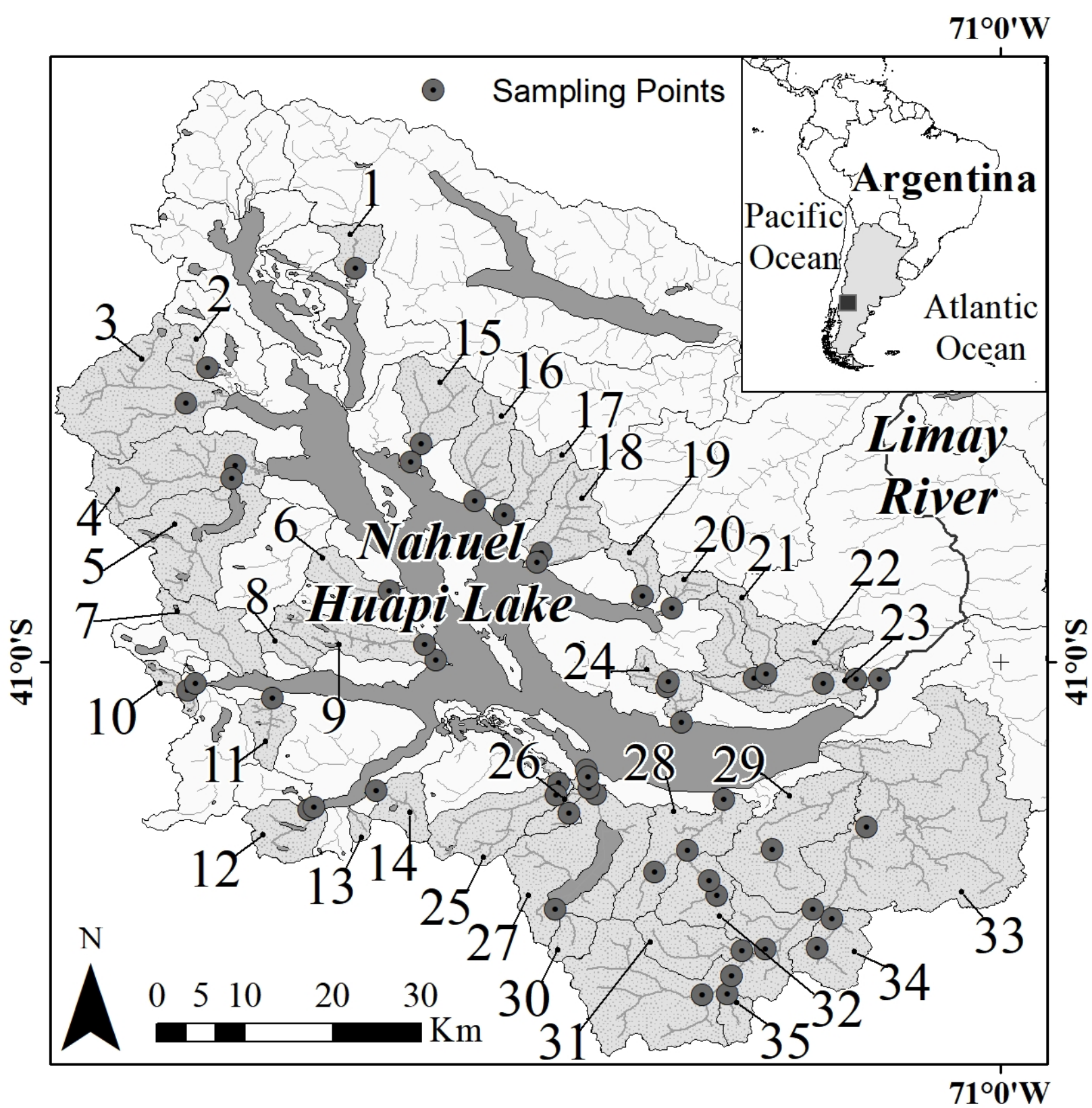
Stoneman, C. L., and Jones M.L. (2000). The influence of habitat features on the biomass and distribution of three species of southern Ontario stream salmonids. *Transactions of the American Fisheries Society* **129**:639–657.

Watson, G. and Hillman, T.W. (1997). Factors Affecting the Distribution and Abundance of Bull Trout: An Investigation at Hierarchical Scales. *North American Journal of Fisheries Management* **17**: 237–252.

Wiley, M. J., Kohler, S. L. and Seelbach, P. W. (1997) *Reconciling Landscape and Local Views of Aquatic Communities: Lessons from Michigan Trout Streams*. Vol. 37.

Wootton, R.J. (1998) *Ecology of Teleost Fishes*. Kluwer Academic Publishers.

Zorn, T. G., Seelbach, P. W. and Wiley, M. J. (2002) Distributions of Stream Fishes and Their Relationship to Stream Size and Hydrology in Michigan's Lower Peninsula. *Transactions of the American Fisheries Society* **131**: 70–85.



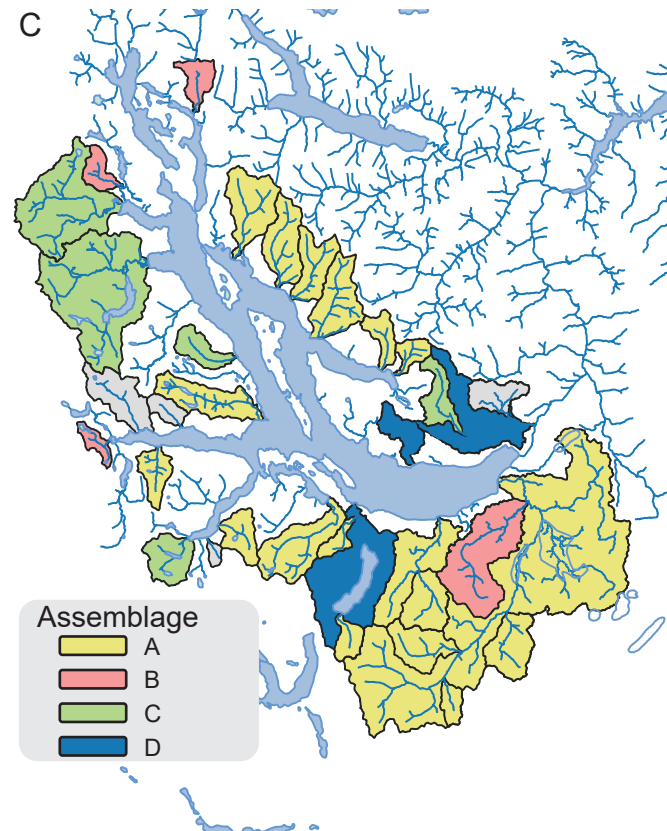
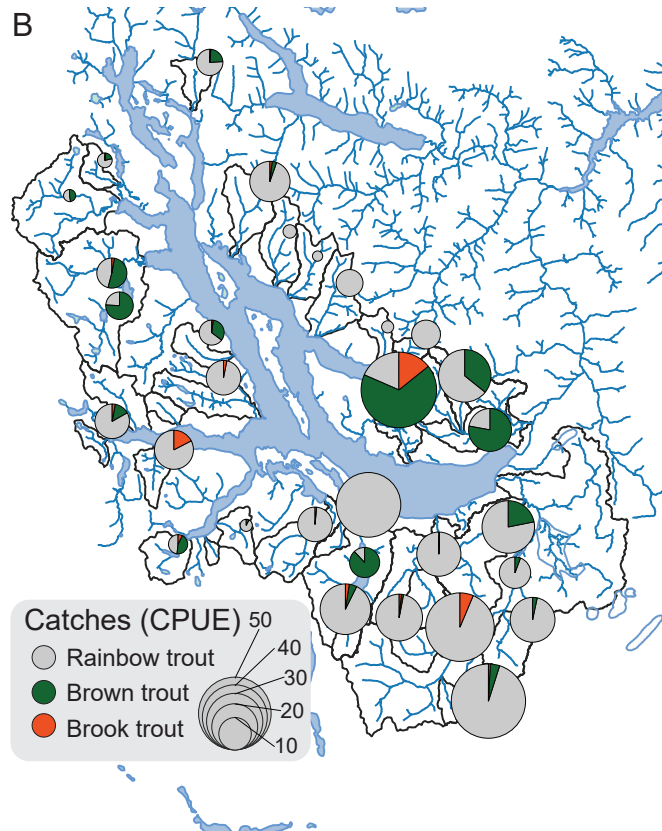
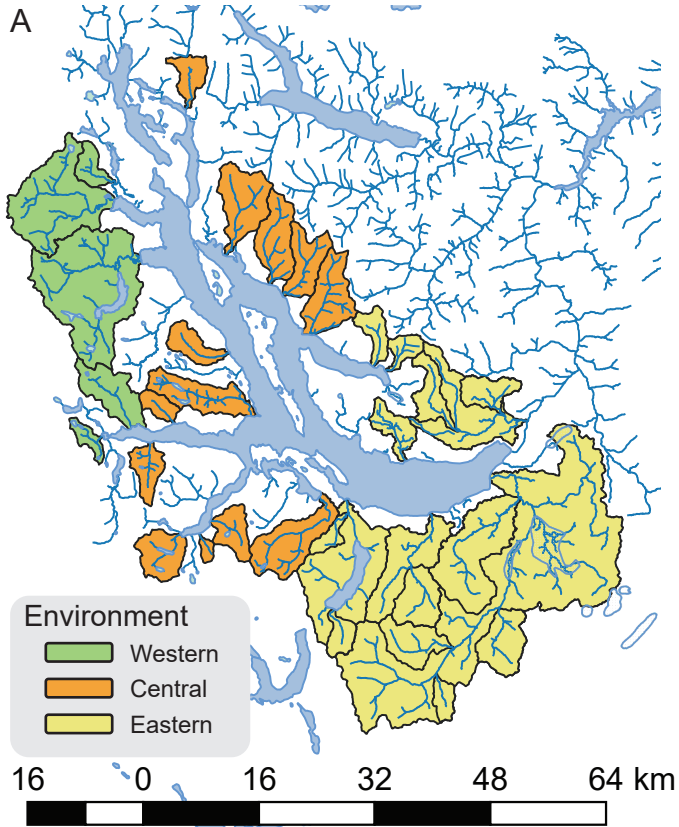


Figure Captions Lallement et al. 2020

Figure 1 Sampling sites in each watershed in the Upper Limay river Basin; 1- Neuquenco, 2-Acantuco, 3-Pireco, 4-Machete, 5-Gallardo, 6-Coluco, 7-Bravo, 8- Blanco, 9-Millaqueo, 10-Blest, 11-Patiruco, 12-Frey, 13-Uhueco, 14-Lluvuco, 15- Bonito, 16- Estacada, 17- Ragintuco-, 18-Huemul, 19-Pedregoso, 20-Quintriquenco, 21- Manzano-Jones, 22-Newbery, 23- Chacabuco, 24-Castilla, 25-Casa de Piedra, 26- Cascada, 27-Gutierrez, 28-Ñireco, 29-del Medio, 30-Torrontegui, 31-Tristeza, 32- Challhuaco 33-Ñirihuau, 34-Las Minas, 35-de las Quebradas.

Figure 2A. Watershed clusters formed based on environmental characteristics after hierarchical cluster analysis. **2.B** Proportion of Salmonid Species captured in sampled streams. The size of the pie chart is proportional to the total density of fish caught in each watershed. The crosses indicate watershed without fishes. Rainbow trout (*Oncorhynchus mykiss*), Brown trout (*Salmo trutta*), Brook trout (*Salvelinus fontinalis*). **2.C.** Clustering based on similarity patterns of species dominance across watersheds. Cluster A: assemblages formed almost exclusively by *Oncorhynchus mykiss*, Cluster B: assemblages with *Oncorhynchus mykiss* in higher proportion than *Salmo trutta*, Cluster C: *Oncorhynchus mykiss* and *Salmo trutta* co-dominated, Cluster D: assemblages dominated by *Salmo trutta*.

Figure 3 Cluster analysis dendrogram based on Euclidean distance, showing stream groups (dashed boxes: A, B, C, D of fish assemblages (upper) and CPUE composition (%) of salmonid species for each stream (lower). Species: *Salmo trutta* (gray in bars); *Salvelinus fontinalis* (black in bars); *Oncorhynchus mykiss* (white in bars).

Figure 4 I. Regression tree analysis showing stream groups based on capture effort and basin variables. Variables: Precipitation (mm^3); Zav (Average basin height, m.a.s.l); BR (Highest basin point – Lower basin point); Kc ($0.28 (P/\sqrt{A})$); DD (Drainage network/area, Km/km^2); WB (presence of lakes or wetlands-mallines). Clusters of Salmonid assemblages (A, B, C, D). **4.II.** Regression tree without Cluster A. Variables: BA (Basin area, km^2); NDVI (Normalized Differential Vegetation Index); Zmin (Lower basin point, m.a.s.l).

Table 1 Basin variables measured with QGIS. Land Use and Vegetation variables correspond to % of basin occupied with that specific category.

Morphology	
Basin Area	BA (Km ²)
Basin Perimeter	BP (Km)
Main Stream Length	MSL (Km)
Drainage Network	DN=Σ stream length(Km)
Drainage Density	DD=RD/A (Km/Km ²)
Basin Shape	BS=DD/(main channel lenght) ²
Compacity Coefficient	Kc=0.28(P/√A)
Basin Relief	BR=Highest basin point – Lower basin point
Basin Relief Ratio	BRR=RC – stream lenght
Maximum heigth	Zmax= Highest basin point (m.a.s.l)
Average heigth	Zav= Average basin height (m.a.s.l)
Minimum heigth	Zmin=Lower basin point (m.a.s.l)
Climate	
Summer Mean Temperature	T (F)
Mean Annual Precipitation	Precipitation (mm)
Normalized Differential Vegetation Index	NDVI
Land Use (%)	
Rocky outcrop	
Gravel	
Closed Forest	
Open woodlands	
Rocky summit	
Water Bodies (WB)	
Urban	
Plantation	
Clearing	
Vegetation (%)	
<i>Fitzroya cupressoides</i>	(Alerce)
<i>Austrocedrus chilensis</i>	(Cipres de la cordillera)
<i>Nothofagus dombeyi</i>	(Coihue)
<i>Nothofagus pumilio</i>	(Lenga)

Nothofagus antarctica

(Ñire)

Steepe

Wetland

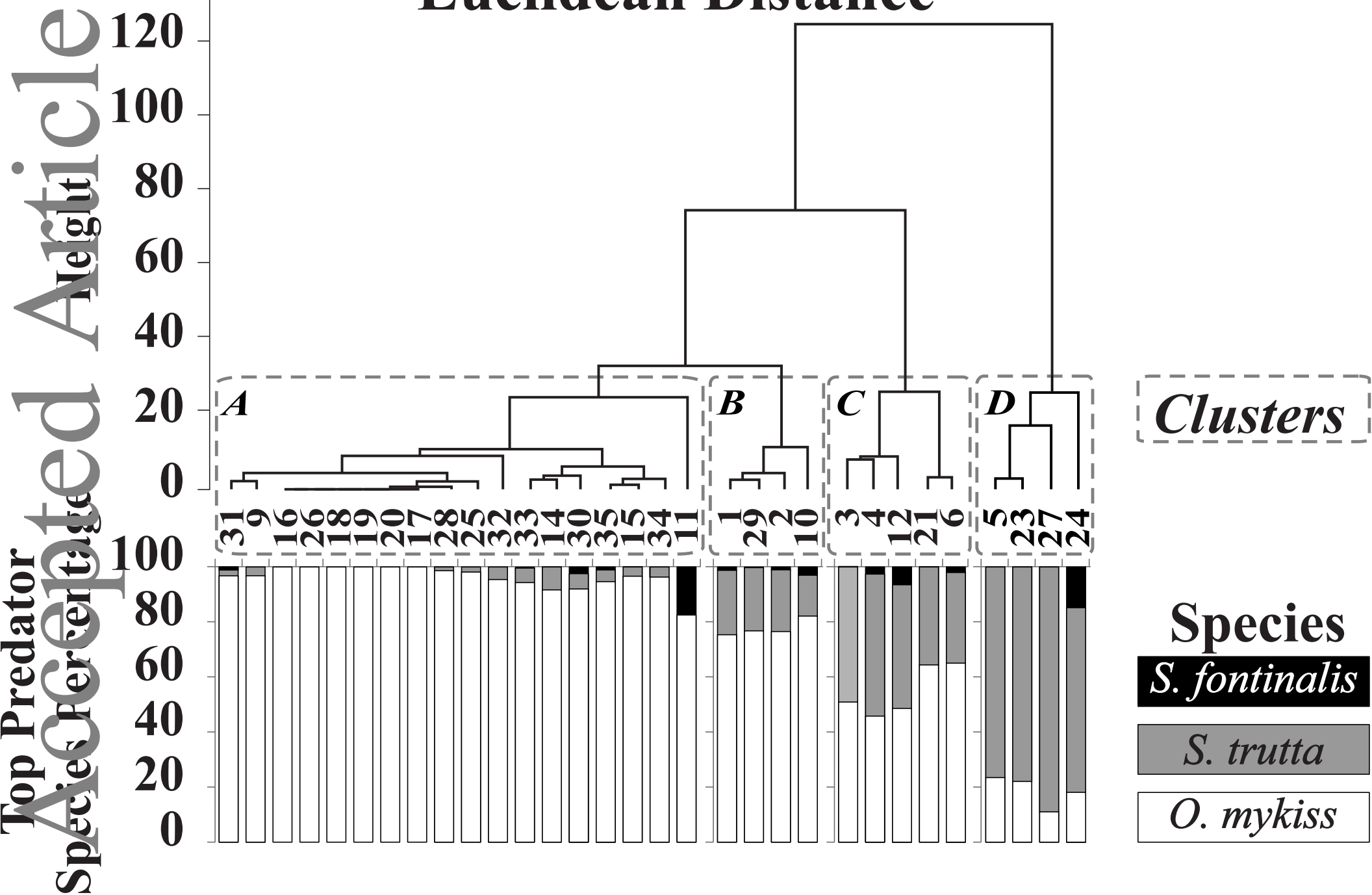
High-Andean

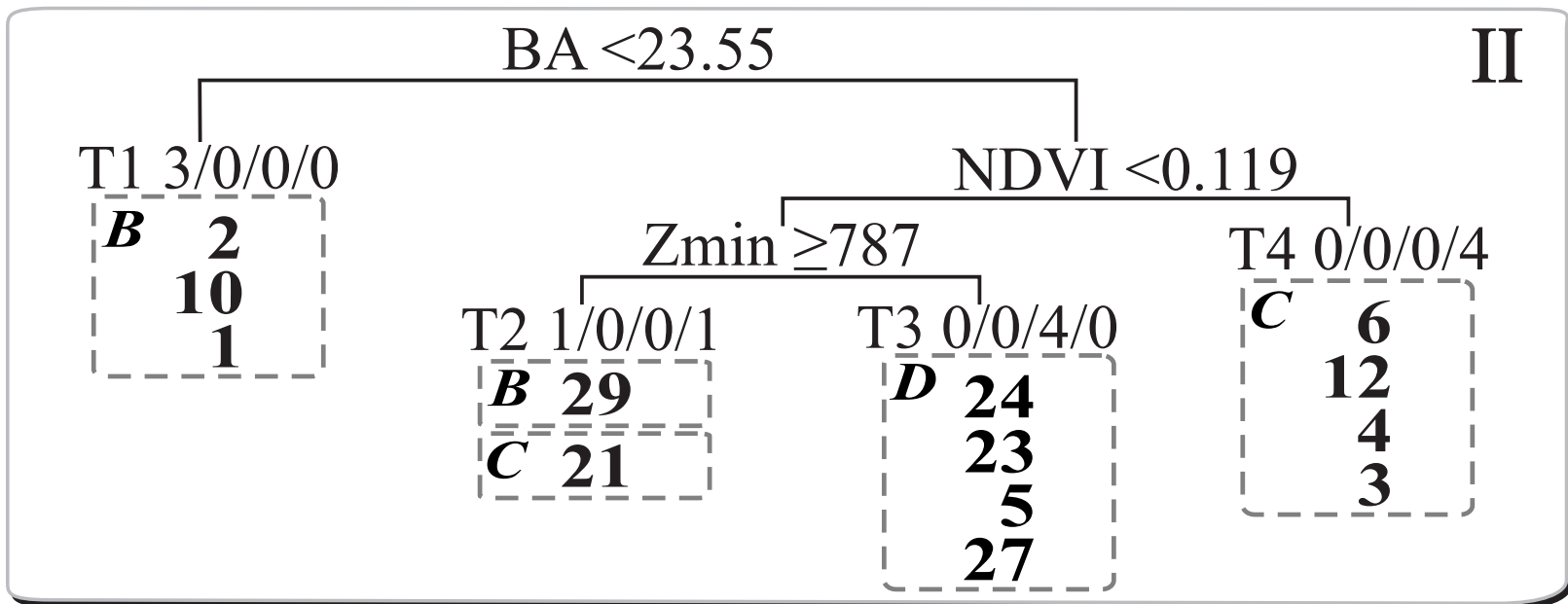
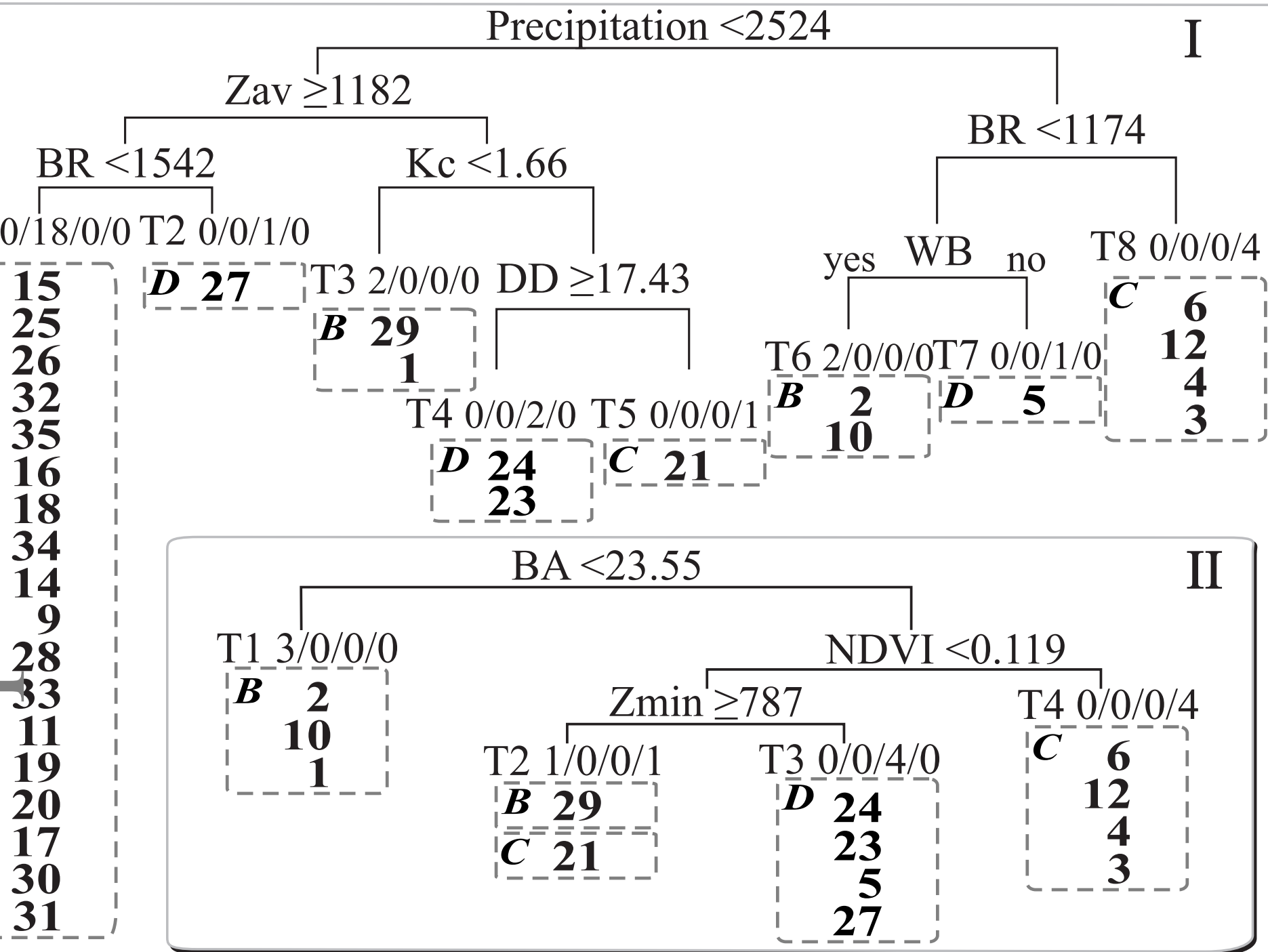
Table 2 Spearman Rank Correlations for total and per specie catch of salmonid per unit effort (CPUE) in relation to basin variables (n = 31). Only statistically significant differences were included in the table (p-value <0.005).

Variables	Spearman R	Statistic	P-values
<u>Salmonids CPUE</u>			
Latitude	-0.63	-4.36	0.0001
Longitude	0.56	3.64	0.0010
Rocky outcrop	0.45	2.70	0.0115
Open woodland	0.47	2.90	0.0070
Rocky summit	-0.63	-4.34	0.0002
Coihue Forest	-0.66	-4.76	0.0001
NDVI	-0.45	-2.68	0.0121
Precipitation	-0.59	-3.92	0.0005
Steppe	0.49	3.01	0.0054
<u><i>Oncorhynchus mykiss</i> CPUE</u>			
Latitude	-0.61	-4.19	0.0002
Longitude	0.49	3.06	0.0047
Rocky outcrop	0.45	2.69	0.0116
Rocky summit	-0.44	-2.64	0.0133
Coihue Forest	-0.56	-3.63	0.0011
Precipitations	-0.48	-2.94	0.0064
<u><i>Salmo trutta</i> CPUE</u>			
Relief	-0.42	-2.47	0.0198
Z max.	-0.40	-2.40	0.0238
Rocky summit	-0.45	-2.70	0.0115
Mallin	0.63	4.41	0.0001

Steppe	0.37	2.32	0.0274
Wetland	0.40	2.35	0.0256
High-Andean	-0.48	-2.93	0.0065
Air Temperature	0.47	2.83	0.0083

Figure 3





Clusters

Supporting Information

Table A Basin morphology variables calculated for the 35 watersheds.

Basin name	Latitude	Longitude	BA	BP	MSL	DN	DD	BS	Kc	BRR	BR	Elevation	Z av	Zmax	Zmin
Acantuco	-40.6870	-71.8259	18.76	21.67	6.64	8.80	0.47	0.0106	1.40	175.34	1165.00	1351.50	1286.18	1934.00	769.00
Blanco	-40.9863	-71.7269	14.52	17.75	4.72	4.72	0.32	0.0146	1.30	263.11	1241.00	1393.00	1410.95	2014.00	773.00
Blest	-41.0244	-71.8452	12.5	20.48	6.80	10.39	0.83	0.0180	1.62	151.63	1031.00	1281.50	1227.72	1797.00	766.00
Bonito	-40.7357	-71.5788	56.72	39.23	13.24	22.74	0.40	0.0023	1.46	86.65	1147.00	1342.50	1384.99	1916.00	769.00
Bravo	-40.9687	-71.8035	46.91	38.84	10.38	12.61	0.27	0.0025	1.59	109.08	1132.00	1333.00	1263.73	1901.00	769.00
Casa de Piedra	-41.1604	-71.5157	64.78	44.05	19.77	34.13	0.53	0.0013	1.53	73.70	1457.00	1477.50	1473.44	2206.00	749.00
Cascada	-41.1561	-71.4530	12.53	20.42	7.67	7.67	0.61	0.0104	1.62	176.58	1355.00	1487.50	1256.49	2149.00	794.00
Castilla	-41.0226	-71.3418	25.76	31	10.27	21.49	0.83	0.0079	1.71	63.67	654.00	1099.00	925.18	1426.00	772.00
Chacabuco	-40.9954	-71.2287	134.94	70.89	25.73	68.23	0.51	0.0008	1.71	46.20	1189.00	1359.00	1054.93	1954.00	765.00
Challhuaco	-41.2366	-71.3091	41.62	28.95	9.56	12.92	0.31	0.0034	1.26	134.85	1289.00	1779.50	1450.07	2228.00	939.00
Coluco	-40.9123	-71.6688	25.15	25.93	9.26	9.26	0.37	0.0043	1.45	127.71	1182.00	1362.00	1438.06	1953.00	771.00
De la Quebrada	-41.3616	-71.2715	14.31	18.53	5.22	5.22	0.36	0.0134	1.37	185.57	969.00	2000.50	1635.22	2103.00	1134.00
Del Medio	-41.1808	-71.2129	108.07	60.25	24.52	35.20	0.33	0.0005	1.62	38.14	935.00	1217.00	979.40	1727.00	792.00
Estacada	-40.7830	-71.5257	49.06	35.55	13.87	27.06	0.55	0.0029	1.42	86.87	1205.00	1373.50	1447.21	1976.00	771.00
Frey	-41.1712	-71.7300	36.59	26.23	7.49	9.84	0.27	0.0048	1.21	185.76	1391.00	1465.50	1363.49	2159.00	768.00
Gallardo	-40.8701	-71.8212	97.32	52.24	17.38	32.01	0.33	0.0011	1.48	66.76	1160.00	1362.00	1273.73	1942.00	782.00
Gutierrez	-41.2067	-71.4326	160.17	63.17	28.73	60.57	0.38	0.0005	1.40	56.18	1614.00	1576.00	1261.34	2383.00	769.00
Huemul	-40.8569	-71.4419	54.14	36.52	12.80	34.12	0.63	0.0038	1.39	107.09	1371.00	1446.50	1416.06	2140.00	769.00
Las Minas	-41.2928	-71.1703	44.4	31.58	10.59	15.21	0.34	0.0031	1.33	53.14	563.00	1322.50	1190.42	1503.00	940.00
LLuvuco	-41.1457	-71.6111	27.19	24.98	6.40	9.01	0.33	0.0081	1.34	216.94	1389.00	1497.00	1537.49	2190.00	801.00
Machete	-40.8373	-71.8332	193.67	72.96	26.40	88.88	0.46	0.0007	1.47	45.07	1190.00	1350.00	1279.72	1945.00	755.00
Manzano-Jones	-40.9812	-71.2790	30.49	37.4	13.10	13.38	0.44	0.0026	1.90	79.23	1038.00	1336.00	1174.19	1892.00	854.00
Millaqueo	-40.9743	-71.6598	52	42.31	16.96	35.64	0.69	0.0024	1.64	73.81	1252.00	1392.00	1353.28	2018.00	766.00
Neuquenco	-40.5768	-71.6595	21.94	26.31	6.96	7.42	0.34	0.0070	1.57	156.24	1088.00	1323.00	1128.61	1871.00	783.00

Supporting Information

Table A. Continuation

Basin name	Latitude	Longitude	BA	BP	MSL	DN	DD	BS	Kc	BRR	BR	Elevation	Z_{av}	Z_{max}	Z_{min}
Newbery	-40.9801	-71.1867	27.83	29.27	6.56	12.97	0.47	0.0108	1.55	100.62	660.00	1183.50	1066.44	1454.00	794.00
Ñireco	-41.2078	-71.3215	113.16	62.83	19.74	37.55	0.33	0.0009	1.65	73.69	1455.00	1500.50	1292.83	2228.00	773.00
Ñirihuau	-41.2253	-71.1863	723.8	193.38	58.07	278.58	0.38	0.0001	2.01	25.30	1469.00	1499.50	1191.72	2234.00	765.00
Patiruco	-41.0652	-71.7491	24.43	24.84	6.53	13.00	0.53	0.0125	1.41	187.55	1224.00	1392.50	1271.24	2001.00	777.00
Pedregoso	-40.9034	-71.3690	20.53	25.35	7.22	8.52	0.41	0.0080	1.57	195.93	1415.00	1478.50	1567.94	2186.00	771.00
Pireco	-40.7283	-71.8834	125.48	61.19	21.53	59.93	0.48	0.0010	1.53	54.94	1183.00	1345.50	1258.26	1937.00	754.00
Quintriqueuco	-40.9248	-71.3206	15.26	20.8	5.47	5.48	0.36	0.0120	1.49	209.61	1147.00	1358.00	1526.57	1932.00	785.00
Ragintuco	-40.8126	-71.4787	38.76	34.24	11.62	22.04	0.57	0.0042	1.54	112.25	1304.00	1423.00	1460.31	2075.00	771.00
Torrontegui	-41.2788	-71.4390	17.47	20.03	6.16	6.16	0.35	0.0093	1.34	217.84	1342.00	1980.00	1622.19	2145.00	803.00
Tristeza	-41.2894	-71.3209	41.29	32.45	12.16	15.88	0.38	0.0026	1.41	95.75	1164.00	1899.50	1648.61	2234.00	1070.00
Uhueco	-41.1671	-71.6557	5.44	10.82	3.42	3.42	0.63	0.0537	1.30	354.38	1212.00	1427.00	1530.51	2024.00	812.00

Supporting Information

Table B. Land use in streams basins. Data expressed in% of the watershed occupied for each land use.

Basin name	Rocky outcrop	Gravel	Closed forest	Open woodland	Rocky summit	Water body	Mallin	Urban	Plantation	Clearance
Acantuco	0.00	0.66	70.76	0.00	28.56	0.00	0.00	0.00	0.00	0.00
Blanco	0.00	0.00	43.92	0.00	54.10	1.98	0.00	0.00	0.00	0.00
Blest	0.00	0.00	77.32	0.00	17.29	5.35	0.00	0.00	0.00	0.00
Bonito	0.00	0.00	73.58	0.00	26.42	0.00	0.00	0.00	0.00	0.00
Bravo	0.00	0.00	68.04	0.00	31.95	0.02	0.00	0.00	0.00	0.00
Casa de Piedra	0.00	0.00	58.11	10.50	30.75	0.64	0.00	0.00	0.00	0.00
Cascada	0.00	0.00	54.93	20.67	24.37	0.00	0.00	0.00	0.00	0.00
Castilla	0.00	0.00	52.79	47.02	0.00	0.00	0.209	0.00	0.00	0.00
Chacabuco	19.55	7.40	33.13	22.48	0.00	0.00	17.45	0.00	0.00	0.00
Challhuaco	20.04	0.00	54.40	21.40	4.16	0.00	0.00	0.00	0.00	0.00
Coluco	0.00	0.00	60.19	0.00	39.50	0.29	0.00	0.00	0.00	0.00
De la Quebrada	39.39	0.00	59.59	0.00	0.00	0.00	1.00	0.00	0.00	0.00
Del Medio	0.00	64.63	0.00	25.64	1.91	0.00	1.00	0.00	0.00	0.00
Estacada	0.00	0.00	67.66	0.00	32.33	0.00	7.82	0.10	0.00	0.00
Frey	0.00	0.00	74.71	0.00	21.06	4.23	0.00	0.00	0.00	0.00
Gallardo	0.00	0.00	63.91	0.00	26.78	8.61	0.704	0.00	0.00	0.00
Gutiérrez	0.00	0.00	60.22	10.85	17.55	11.31	0.00	0.00	0.00	0.00
Huemul	0.00	0.00	64.29	0.00	35.72	0.00	0.00	0.00	0.00	0.00
Las Minas	53.93	0.00	17.67	28.10	0.00	0.00	0.31	0.00	0.00	0.00
LLuvuco	0.00	0.00	71.01	0.00	27.95	1.04	0.00	0.00	0.00	0.00
Machete	0.00	0.00	63.42	0.00	28.57	4.78	3.23	0.00	0.00	0.00
Manzano-Jones	7.37	0.00	77.96	4.13	0.00	0.00	10.55	0.00	0.00	0.00
Millaqueo	0.00	0.00	63.32	0.00	36.67	0.01	0.00	0.00	0.00	0.00
Neuquenco	0.00	0.00	53.04	36.24	10.73	0.00	0.00	0.00	0.00	0.00

Supporting Information

Table B. Continuation

Basin name	Rocky outcrop	Gravel	Closed forest	Open woodland	Rocky summit	Water body	Mallin	Urban	Plantation	Clearance
Newbery	60.25	0.54	0.00	19.38	0.00	0.00	19.84	0.00	0.00	0.00
Ñireco	11.90	0.00	37.37	38.55	8.73	0.04	0.00	1.58	0.80	1.02
Ñirihuau	41.89	15.72	18.99	9.30	3.60	0.01	8.94	0.02	0.41	0.00
Patiruco	0.00	0.00	80.76	0.00	18.38	0.87	0.00	0.00	0.00	0.00
Pedregoso	0.00	0.00	45.62	7.32	47.06	0.00	0.00	0.00	0.00	0.00
Pireco	0.00	2.38	65.65	0.00	21.35	0.96	3.83	0.00	0.00	0.00
Quintriqueuco	23;17	0.00	68.78	5.04	3.03	0.00	0.00	0.00	0.00	0.00
Ragintuco	0.00	0.00	57.67	0.00	42.34	0.00	0.00	0.00	0.00	0.00
Torrontegui	0.00	0.00	61.19	0.00	38.27	0.55	0.00	0.00	0.00	0.00
Tristeza	32.36	0.00	63.47	4.19	0.00	0.00	0.00	0.00	0.00	0.00
Uhueco	0.00	0.00	70.47	0.00	29.16	0.42	0.00	0.00	0.00	0.00

Supporting Information

Table C Vegetation strata (data expressed in%) and climatic variables in the sub-basins of the streams of Limay river basins.

Basin name	Alerce	Ciprés cordillera	Coihue	Lenga	Ñire	Steppe	Wetland	High-Andean	Summer Temperature	NDVI	Precipitation
Acantuco	0.00	0.00	27.56	43.02	0.80	0.00	0.00	28.62	53.94	0.22	2698.29
Blanco	0.00	0.00	13.71	40.63	0.00	0.00	0.00	45.66	48.98	0.11	2386.56
Blest	11.28	0.00	14.08	62.48	0.00	0.00	0.00	0.00	56.30	0.26	3113.83
Bonito	0.00	0.00	20.38	38.10	12.96	0.00	0.00	28.56	50.77	0.22	2001.43
Bravo	32.83	0.00	0.00	30.31	0.00	0.00	0.00	35.96	53.59	0.12	2775.10
Casa de Piedra	0.00	0.00	0.05	35.86	23.37	0.00	0.00	37.17	41.99	0.07	2324.05
Cascada	0.00	0.00	0.00	17.56	47.57	0.00	0.00	20.43	61.77	0.07	1926.90
Castilla	0.00	16.11	0.00	8.85	43.59	31.37	0.00	0.00	75.16	0.11	1439.01
Chacabuco	0.00	0.00	0.00	13.35	0.00	71.03	11.17	4.45	65.27	-0.02	1196.57
Challhuaco	0.00	0.00	0.00	51.83	16.75	0.00	0.00	31.43	45.33	0.06	1834.49
Coluco	0.00	0.00	21.11	38.93	0.00	0.00	0.00	39.72	51.98	0.13	2541.63
De la Quebrada	0.00	0.00	0.00	48.36	6.08	0.00	0.00	45.56	36.31	0.04	1526.00
Del Medio	0.00	0.00	0.00	7.07	15.00	72.01	4.52	1.41	68.12	-0.05	1248.79
Estacada	0.00	0.00	22.85	41.70	0.00	0.00	0.00	35.45	48.62	0.18	1978.71
Frey	0.00	0.00	24.76	53.79	0.00	0.00	0.00	15.63	49.46	0.20	2626.64
Gallardo	0.00	0.00	17.70	45.91	0.00	0.00	0.00	27.51	50.81	0.10	2962.76
Gutiérrez	0.00	10.41	6.07	25.99	18.51	0.00	0.00	20.90	52.12	0.03	1741.80
Huemul	0.00	0.00	26.21	29.63	3.68	0.00	0.00	40.49	44.65	0.12	2112.66
Las Minas	0.00	0.00	0.00	6.58	0.00	93.42	0.00	0.00	62.07	-0.04	1382.30
LLuvuco	0.00	0.00	2.98	51.82	0.00	0.00	0.00	44.21	40.86	0.04	2507.22
Machete	0.00	0.00	19.26	43.64	0.00	0.00	0.00	32.51	52.89	0.13	2942.88
Manzano-Jones	0.00	0.00	0.00	41.52	0.00	49.49	2.33	6.69	62.25	0.10	1426.93
Millaqueo	0.00	0.00	16.13	30.13	15.88	0.00	0.00	35.83	52.01	0.13	2310.23
Neuquenco	0.00	0.00	46.17	21.10	27.21	0.00	0.00	5.52	62.26	0.30	2302.93

Supporting Information

Table C. Continuation

Basin name	Alerce	Ciprés cordillera	Coihue	Lenga	Ñire	Steppe	Wetland	High-Andean	Summer temperat ure	NDVI	Precipitation
Newbery	0.00	0.00	0.00	0.00	0.00	100.00	0.00	0.00	70.76	-0.09	1137.50
Ñireco	0.00	0.00	0.00	30.10	20.46	5.34	0.00	26.90	51.12	0.01	1657.58
Ñirihuau	0.00	0.00	0.00	16.92	3.96	60.04	5.48	13.08	56.12	-0.04	1203.16
Patiruco	0.00	0.00	23.82	58.37	0.00	0.00	0.00	17.81	56.32	0.17	2165.42
Pedregoso	0.00	5.36	0.00	2.19	7.26	0.00	0.00	85.24	39.16	0.00	1796.36
Pireco	0.00	0.00	26.24	41.35	2.66	0.00	0.00	28.80	54.22	0.19	2800.08
Quintriqueuco	0.00	5.57	0.00	55.37	0.00	0.00	0.00	39.06	43.96	0.12	1576.86
Ragintuco	0.00	0.00	14.40	41.51	6.91	0.00	0.00	37.18	46.61	0.15	2132.30
Torrentegui	0.00	6.18	0.00	39.38	6.81	0.00	0.00	47.17	36.65	0.03	1462.27
Tristeza	0.00	0.00	0.00	37.54	9.01	0.48	0.00	52.97	38.22	-0.01	1733.11
Uhueco	0.0	0.00	1.84	72.24	0.00	0.00	0.00	25.92	43.35	0.15	2586.98

Supporting Information

Table D: Average values of environmental variables included in the hierarchical cluster analysis for watersheds. Maximum and minimum values for each cluster are shown in brackets. Only statistically significant variables are considered.

Variables	Watershed Location		
	West	Central	East
N	6	13	16
Morphology			
Basin Area (Km ²)	82,4 (12.5 - 193.8)	36.2 (5.4 - 64.8)	95.7 (12.5 - 723.8)
Drainage Area (Km)	35.4 (8.8 - 88.9)	17.9 (3.4 - 35.6)	37.8 (5.2 - 278.6)
Kc	1.5 (1.4 - 1.6)	1.4 (1.2 - 1.6)	1.7 (1.3 - 2.0)
BR	100.5 (45.1 - 175.3)	156.3 (73.7 - 354.4)	109.5 (25.3 - 217.8)
Zmax (m)	1909.3 (1797-1945)	2041.8 (1871-2206)	1986.1 (1426-2383)
Land Use			
Rocky outcrop (%)	0	0	19.4 (0 - 60)
Closed Forest (%)	68.2 (63.4 - 77.3)	64.5 (43.9 - 80.8)	44.1 (0 - 78.0)
Open Forest (%)	0	3.6 (0 - 36.2)	16.5 (0 - 47.0)
Rocky summit (%)	25.8 (17.3 - 32.0)	31.2 (10.7 - 54.1)	9.3 (0 - 47.1)
WB (%)	1.3 (0 - 3.82)	0	4.1 (0 - 19.8)
Urban (%)	0	0	0.1 (0 - 1.6)
Vegetation			
Coihue (%)	17.5 (0 - 27.7)	18.0 (0.05 - 46.1)	0.4 (0 - 6.1)
Lenga (%)	44.5 (30.3-62.5)	42.6 (21.1 - 72.2)	25.16 (0 - 55.4)
Steppe (%)	0	0	30.2 (0 - 100)
Wetland (%)	0	0	1.5 (0 - 11.2)
High-Andean (%)	25.6 (0 - 36.0)	31.5 (-5.5 - 45.7)	24.7 (0 - 85.2)
Climatics			
Temperature (°C)	12.0 (10.5 - 13.5)	9.5 (4.9 - 16.8)	12.2 (2.4 - 24.0)
NDVI	0.2 (0.1 - 0.3)	0.2 (0.04 - 0.3)	0.02 (-0.09 - 0.1)
Precipitation (mm)	2882.2 (2698-3114)	2305.9 (1979-2627)	1518.1 (1138-1927)

Supporting Information

Table E. CPUE (number of fish / 100m²) in the 31 watersheds of the Limay river basins. Only watersheds where fish were caught are considered.

Watershed	Latitude	Longitude	CPUEN			Total
			<i>O. mykiss</i>	<i>S. trutta</i>	<i>S. fontinalis</i>	
Pireco	-40,7283365	-71,883447	0,76	0,69	-	1,45
Acantuco	-40,6870432	-71,8259462	1,63	0,40	0,04	2,07
Machete	-40,837265	-71,8331876	4,01	4,48	0,24	8,73
Gallardo	-40,8700759	-71,8211752	1,75	5,50	-	7,25
Blest	-41,0243555	-71,8452124	9,50	1,60	0,32	11,43
Patiruco	-41,0651909	-71,7490861	12,13	-	2,55	14,69
Frey	-41,1711721	-71,7299522	1,76	1,63	0,26	3,78
Millaqueo	-40,9742568	-71,6598227	11,01	-	0,35	11,36
Coluco	-40,9123437	-71,6687729	3,93	2,02	0,12	6,07
Neuquenco	-40,5767528	-71,6595039	5,16	1,54	0,09	6,78
Llucuco	-41,145673	-71,611091	1,34	0,11	-	1,45
Casa de Piedra	-41,1604288	-71,5157383	11,27	-	0,17	11,44
Bonito	-40,7356713	-71,5787519	14,88	0,56	0,28	15,73
Estacada	-40,7829627	-71,5257495	1,88	-	-	1,88
Ragintuco	-40,8125503	-71,4787445	1,10	-	-	1,10
Huemul	-40,8569227	-71,4418746	7,00	-	-	7,00
Pedregoso	-40,9034006	-71,3690179	1,45	-	-	1,45
Quintriquenco	-40,9247984	-71,3205718	8,19	-	-	8,19
Castilla	-41,022637	-71,3417586	10,01	36,48	7,72	54,21
Jones-Manzano	-40,9812028	-71,2790299	17,00	9,46	-	26,46
Chacabuco	-40,9954146	-71,2287048	3,91	1378	-	17,69
Tristeza	-41,2894088	-71,3208816	20,56	0,32	0,32	21,19
Cascada	-41,1560917	-71,4530239	39,70	-	-	39,70
Gutiérrez	-41,2066666	-71,4325938	1,05	7,64	-	8,69
Torrontegui	-41,2788083	-71,4389803	22,61	1,19	0,59	24,39
Ñireco	-41,2078291	-71,321543	18,80	0,09	-	18,89
Challhuaco	-41,2365767	-71,3090935	42,43	-	2,86	45,29
Quebradas	-41,3616476	-71,271492	50,00	2,14	0,43	52,56
del Medio	-41,180827	-71,2128754	20,56	5,76	-	26,32
Las Minas	-41,2928298	-71,1703178	18,86	0,64	-	19,50
Ñirihuau	-41,2252532	71,1862508	8,92	0,54	-	9,47