

The devil is in the details: landscape features are insufficient to explain distribution patterns of non-native fishes in north Patagonian streams

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Abstract

Ecological communities are structured by a combination of factors known as habitat templates. These templates work as a ‘filter’ that permits some species with particular traits or phenotypes to establish and persist while excluding others. Defining which habitat variables and spatial scales have the stronger influence on freshwater communities is key to effective and efficient management of fluvial ecosystems. We took advantage of the relatively recent and well-studied history of salmonid introductions to Patagonia to evaluate if patterns of association of non-native species with abiotic factors vary between different spatial scales of the environmental filter. We characterized environmental variables at the basin and reach scale to assess their influence on the presence, abundance and structure of the salmonid assemblages in breeding streams. We found no evidence supporting that presence/absence patterns of salmonid distribution were strongly driven by landscape variables, except for basins with physical barriers to migration. However, we did find support for some climatic and geomorphological variables (e.g., precipitation and relief) influencing relative abundances. Our results do not support a scenario in which the distribution of any of the species affects the distribution of the other species, and suggest interference has played only a minor role in determining current fish distribution in the region. Instead, current patterns of presence and abundance of salmonids are best explained as the product of environmental filters. Our findings contribute to our understanding of the ecology of individual species and provide insight into mechanisms structuring fish assemblages in Southern Hemisphere’s lotic systems.

Introduction

Ecological communities are structured by combinations of factors defined as habitat templates (Southwood, 1977). These habitat templates mold evolutionary forces and structure ecological strategies for each of the species within the community. In other words, both the presence of a species at a particular site and its life history strategy are the result of environmental filtering (i.e., the tolerance of the species to a particular subset of biotic and abiotic characteristics) and trade-offs met during habitat adaptation.

Fluvial ecosystems are characterized by a physical habitat strongly influenced by the inherent hierarchical structure and patchiness that determine the distribution of organisms, food availability, predation and competition (Frissell et al., 1986, Schlosser & Kallemeyn, 2000). Fine-scaled variability results from the interaction between large-scale landscape variables (e.g., basin area, slope profile of stream-associated valleys and other geomorphological traits) and smaller scale variables (e.g., local structure and condition) (Frissell et al. 1986; Schlosser & Kallemeyn 2000). Because of that, defining which habitat variables and spatial scales have the most influence on freshwater communities is key to effective and efficient management of fluvial ecosystems (Matthews, 1998, Gido et al., 2006).

Environmental filtering is considered a major structuring mechanism of communities (Weiher & Keddy 1995). It is dominated by three ecological factors: dispersal restriction, abiotic environment and biotic interactions (Belyea & Lancaster, 1999). The first two act on a regional scale and delimit the area of action of the third,

which operates on a local scale (Booth & Swanton, 2006). While the utility of the environmental filtering concept has been argued on the basis that it predicts patterns that cannot be distinguished from those produced 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). Therefore, if the relative effects of these general classes of factors in streams could be disentangled, then we would gain a comprehensive view of how each factor drives community composition.

In Patagonia, particularly at the scale of large drainage basins, fish distribution has been strongly influenced by the Andean uplift and the Quaternary glacial cycles (Hubert & Renno, 2006). After the retreat of glaciers during the Pleistocene, the ability of Patagonian fish to colonize post-glacial water bodies determined their present distribution, clearly constrained by climate, especially by temperature (Cussac et al., 2004, Ruzzante et al., 2006). In recent times, native freshwater fish communities have been altered on repeated occasions by the introduction of non-native species to generate sport fisheries, resulting in communities where up to six native species and four introduced salmonid species coexist within the watershed (Macchi et al., 1999). Many of these species have stable populations at several large lakes that have been intensively studied (Cussac et al., 2014). In contrast, relatively little is known about fish assemblages in streams or about the environmental filters that structure riverine communities (Aigo et al., 2008, Pascual et al., 2002, 2007, Barriga et al. 2013, Lallement et al. 2020).

Of the four species introduced since 1904, rainbow trout (*Onchorhynchus mykiss*, Walbaum 1792), brown trout (*Salmo trutta*, Linnaeus 1758) and brook trout (*Salvelinus fontinalis*, Mitchill 1814) are currently the most widely distributed and abundant species. The rapid adaptation of these salmonid species to the new environment enabled them to establish self-sustaining populations, obviating the need for continuous import of eggs and ensuring of a steady supply of fish from local reproducers. The short and well-known history of introductions in the region shows that these species have high dispersive capabilities and found practically no biological resistance to invasion (Pascual et al. 2007). Thus, it can be posited that their current distribution in Patagonia is the result of environmental filtering at different scales. Although the influence of the landscape scale factors has been evaluated for the two most abundant species of salmonids in previous works (Quirós, 1991, Aigo, et al., 2008; Lallement et al. 2020), it is not known whether these factors alone explain the richness of non-native species in the watershed.

The objective of this work was to examine watershed and reach-level patterns of introduced salmonid species in North Patagonian rivers and their association with watershed characteristics derived from remote sensing and topography data across an environmental gradient. We compared the relative variation in salmonid density across different kind of watersheds expecting that some environmental characteristics at a landscape and reach scale conditioned i) the presence of salmonids, ii) the abundance of each species, iii) the assemblage conformation and iv) the dominance of a species at a regional level. We characterized environmental variables at the basin and reach scale to assess their influence on the presence, abundance and structure of the salmonid assemblages in breeding streams of the Upper Limay river basin. Our findings contribute to our understanding of the ecology of individual species and provide insight into mechanisms structuring fish assemblages in Southern Hemisphere's stream systems. Such information not only contributes to knowledge of the ecological processes structuring aquatic communities, but also helps direct conservation and management activities.

Methods

Study Area

The Upper Limay River basin is located between the provinces of Río Negro and Neuquén (~40°63' S, 71° 70' W), Argentina, and drains an area of 6.980 km², most of it within the boundaries of Nahuel Huapi National Park (Figure 1). Originating in the eastern slopes of the Andes mountain range, the basin presents a complex hydrological network, with many streams, rivers and lentic water bodies. Due to rain-shadowing effects by the Andes, the area experiences a steep longitudinal climatic gradient going from 3000 mm of yearly precipitation in the West to less than 600 mm to the East in about 60 km (Paruelo et al., 1998). This climatic gradient results in an eastward transition from a cold-temperate rainforest to shrubby dry steppes. The watershed has a highly connected, complex hydrologic network characterized by deep oligotrophic lakes of varying size, interconnected by streams, ponds and wetlands. The main hub of the network is Nahuel Huapi Lake, with

an area of 529 km² and a maximum depth of 464 m, which collects most waters from the basin, and drains through the Limay River towards the Atlantic Ocean (Figure 1).

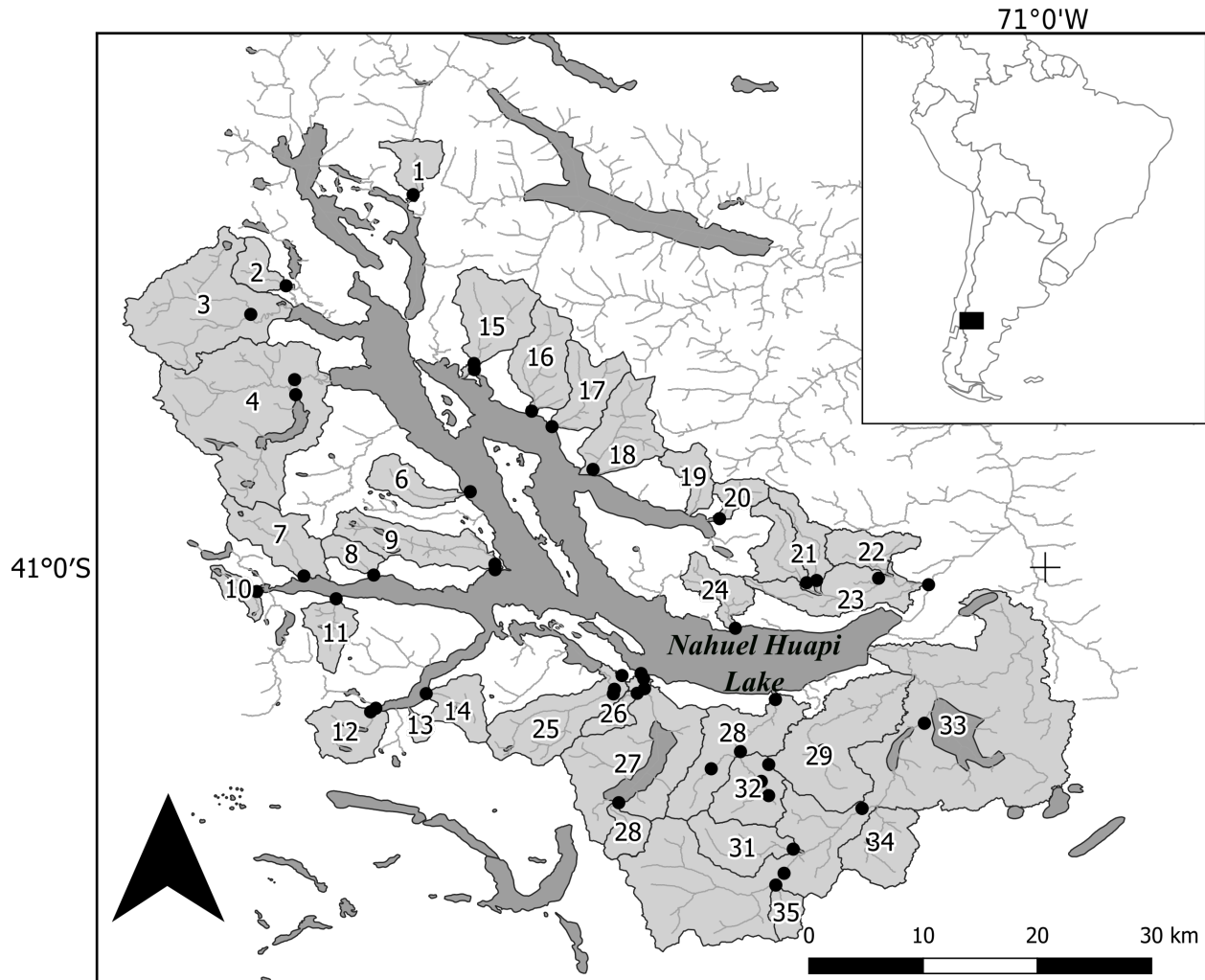


Figure 1: Figure 1

Selection of watersheds

Thirty-five basins fully representing the environmental gradient of the watershed were selected for this study (Figure 1). For each basin, one or more sections of 2nd order or higher were selected; selection criteria were size, registered physiographic changes, existence of natural or anthropic barriers and the accessibility to each section (Bain & Stevenson, 1999). Based on these criteria, some basins were represented by a single section, while others had two or more representative sections. On larger basins with enough altitudinal range (e.g., Machete, Gutiérrez, Ñireco, Ñirihauau and Chacabuco), additional sections on tributary streams were sampled.

Watershed variables

A total of 32 watershed attributes were chosen following the available literature (Angermeier & Winston, 1999, Oakes et al., 2005, Smith & Kraft, 2005), and were grouped into four distinct categories (Geomorphological, Climatological, Land Use and Vegetation) based on the general aspect of the environment measured by each variable (Table A-Appendix section). All categories were calculated using GIS tools (version 2.6) under the QGIS environment (QGIS Development Team, 2014), or using specific formulas following Bain and Stevenson

(1999). Land Use and Vegetation data were obtained from existing digital map layers available from the National Geographic Institute, the National Institute of Agricultural Technology (INTA) and National Parks Administration's Biodiversity Information System; these maps were complemented with satellite imagery from Google Earth. Watershed morphological variables were calculated based on a digital elevation model with a resolution of 30 m (Landsat 6TM+). Average annual precipitation (mm) and temperature were calculated based on a map interpolating averages of daily measures from 25 meteorological stations located within from 38°46'0S–41°30'0S and 70°03'0W–71°45'0W (Barros et al., 1983). The Normalized Differential Vegetation Index (NDVI) was calculated from Landsat 6TM+ satellite images during the summer season of 2014. Geoprocessing and zonal statistics were computed using Quantum Gis (QGIS) (version 2.6) and digital map data. All the variables are available in the Appendix section (Table A).

#TABLE 1 - Basin-level variables

```
basins <- read_csv("basins.csv")
```

```
## Rows: 35 Columns: 33
```

```
## -- Column specification -----
```

```
## Delimiter: ","
```

```
## chr (1): Basin
```

```
## dbl (32): lat, lon, area, perimeter, length, drain_net, drain_area, shape, K...
```

```
##
```

```
## i Use `spec()` to retrieve the full column specification for this data.
```

```
## i Specify the column types or set `show_col_types = FALSE` to quiet this message.
```

```
gt(basins)
```

Basin	lat	lon	area	perimeter	length	drain_net	drain_area	shape	Kc	relief	Z
Acantuco	-40.6870	-71.8259	18.76	21.67	6.64	8.80	0.47	0.0106	1.40	1165	1
Blanco	-40.9863	-71.7269	14.52	17.75	4.72	4.72	0.32	0.0146	1.30	1241	1
Blest	-41.0244	-71.8452	12.50	20.48	6.80	10.39	0.83	0.0180	1.62	1031	1
Bonito	-40.7357	-71.5788	56.72	39.23	13.24	22.74	0.40	0.0023	1.46	1147	1
Bravo	-40.9687	-71.8035	46.91	38.84	10.38	12.61	0.27	0.0025	1.59	1132	1
Casa de Piedra	-41.1604	-71.5157	64.78	44.05	19.77	34.13	0.53	0.0013	1.53	1457	1
Cascada	-41.1561	-71.4530	12.53	20.42	7.67	7.67	0.61	0.0104	1.62	1355	1
Castilla	-41.0226	-71.3418	25.76	31.00	10.27	21.49	0.83	0.0079	1.71	654	9
Chacabuco	-40.9954	-71.2287	134.94	70.89	25.73	68.23	0.51	0.0008	1.71	1189	10
Challhuaco	-41.2366	-71.3091	41.62	28.95	9.56	12.92	0.31	0.0034	1.26	1289	1
Coluco	-40.9123	-71.6688	25.15	25.93	9.26	9.26	0.37	0.0043	1.45	1182	1
De la Quebrada	-41.3616	-71.2715	14.31	18.53	5.22	5.22	0.36	0.0134	1.37	969	10
Del Medio	-41.1808	-71.2129	108.07	60.25	24.52	35.20	0.33	0.0005	1.62	935	1
Estacada	-40.7830	-71.5257	49.06	35.55	13.87	27.06	0.55	0.0029	1.42	1205	1
Frey	-41.1712	-71.7300	36.59	26.23	7.49	9.84	0.27	0.0048	1.21	1391	1
Gallardo	-40.8701	-71.8212	97.32	52.24	17.38	32.01	0.33	0.0011	1.48	1160	1
Gutierrez	-41.2067	-71.4326	160.17	63.17	28.73	60.57	0.38	0.0005	1.40	1614	1
Huemul	-40.8569	-71.4419	54.14	36.52	12.80	34.12	0.63	0.0038	1.39	1371	1
Las Minas	-41.2928	-71.1703	44.40	31.58	10.59	15.21	0.34	0.0031	1.33	563	1
LLuvuco	-41.1457	-71.6111	27.19	24.98	6.40	9.01	0.33	0.0081	1.34	1389	1
Machete	-40.8373	-71.8332	193.67	72.96	26.40	88.88	0.46	0.0007	1.47	1190	1
Manzano-Jones	-40.9812	-71.2790	30.49	37.40	13.10	13.38	0.44	0.0026	1.90	1038	1
Millaqueo	-40.9743	-71.6598	52.00	42.31	16.96	35.64	0.69	0.0024	1.64	1252	1
Neuquenco	-40.5768	-71.6595	21.94	26.31	6.96	7.42	0.34	0.0070	1.57	1088	1
Newbery	-40.9801	-71.1867	27.83	29.27	6.56	12.97	0.47	0.0108	1.55	660	10
Nireco	-41.2078	-71.3215	113.16	62.83	19.74	37.55	0.33	0.0009	1.65	1455	1
Nirihuau	-41.2253	-71.1863	723.80	193.38	58.07	278.58	0.38	0.0001	2.01	1469	1
Patiruco	-41.0652	-71.7491	24.43	24.84	6.53	13.00	0.53	0.0125	1.41	1224	1

Pedregoso	-40.9034	-71.3690	20.53	25.35	7.22	8.52	0.41	0.0080	1.57	1415	1
Pireco	-40.7283	-71.8834	125.48	61.19	21.53	59.93	0.48	0.0010	1.53	1183	1
Quintriqueuco	-40.9248	-71.3206	15.26	20.80	5.47	5.48	0.36	0.0120	1.49	1147	1
Ragintuco	-40.8126	-71.4787	38.76	34.24	11.62	22.04	0.57	0.0042	1.54	1304	1
Torrontegui	-41.2788	-71.4390	17.47	20.03	6.16	6.16	0.35	0.0093	1.34	1342	1
Tristeza	-41.2894	-71.3209	41.29	32.45	12.16	15.88	0.38	0.0026	1.41	1164	1
Uhueco	-41.1671	-71.6557	5.44	10.82	3.42	3.42	0.63	0.0537	1.30	1212	1

Local Variables

Physicochemical variables were collected in 42 reaches. Variables included geomorphological, substrate type, hydrological and water quality (Table B-Appendix section). Location and number of sections sampled by stream were determined by the pattern shape of channels, covered area and accessibility, which determined that streams with the largest area have a greater number of sections sampled. Thus, sections were selected based on particular characteristics of each stream such as changes in the relief or riverine vegetation, tributary unions and presence of ponds or waterfalls.

#TABLE 2 - Reach-level variables

```
reach <- read_tsv("reaches.tsv")
```

```
## Rows: 42 Columns: 36
```

```
## -- Column specification -----
```

```
## Delimiter: "\t"
```

```
## chr (1): reach
```

```
## dbl (35): order, chanwidth, chandepth, bank_depth, bank_width, sinuosity, sl...
```

```
##
```

```
## i Use `spec()` to retrieve the full column specification for this data.
```

```
## i Specify the column types or set `show_col_types = FALSE` to quiet this message.
```

```
gt(reach)
```

reach	order	chanwidth	chandepth	bank_depth	bank_width	sinuosity	slo
Acantuco	2	16.00	1.50	3.00	22.00	1.046320	0.0558301
Blest Arriba	2	12.40	1.45	2.90	19.00	1.186652	0.0718759
Bonito Toma de agua	2	15.00	1.40	2.80	15.00	1.342516	0.0289773
Bonito trampa	2	30.00	1.22	2.44	50.00	1.342516	0.0379817
Casa de Piedra Ab	3	30.70	0.80	1.60	39.00	1.198908	0.0319890
Casa de Piedra Ar	3	19.00	0.75	1.50	27.00	1.198908	0.0758541
Castilla Abajo	4	5.76	0.93	1.86	6.17	1.202576	0.0039999
Castilla Medio	2	4.26	0.93	1.86	78.00	1.202576	0.0039999
Chacabuco Arriba	3	8.20	0.80	1.60	20.40	1.634708	0.0019999
Chacabuco Des	3	7.00	0.50	1.00	50.00	1.180275	0.0119994
Chacabuco Superior (ex manzano)	2	8.50	0.73	1.46	50.00	1.195238	0.0159986
Challhuaco Abajo	2	11.00	0.60	1.20	80.00	1.174447	0.0319890
Challhuaco Arriba	1	4.60	0.85	1.70	5.00	1.174447	0.0519532
De la Quebrada	1	7.80	0.80	1.60	7.80	1.115385	0.0579350
Del Medio	2	42.50	1.15	2.30	15.00	1.298729	0.0059999
Estacada	3	12.00	1.90	3.80	18.00	1.130399	0.0519532
Frey Abajo	2	14.00	1.50	3.00	20.00	1.044630	0.0778423
Frey Arriba	2	16.00	1.50	3.00	20.00	1.044630	0.0996686
Gallardo	2	31.00	1.60	3.20	31.00	1.203846	0.0279926
Gutierrez municipalidad (ruta)	3	14.00	1.20	2.40	100.00	1.166378	0.0059999
Gutierrez Usina (gendarmes)	3	16.00	1.30	2.60	100.00	1.166378	0.0119994

Gutierrez Virgen	3	67.00	1.80	3.60	100.00	1.166378	0.0019999
Huemul pcpal	3	72.00	1.50	3.00	1000.00	1.123793	0.0439716
Huemul secundario	3	72.00	1.50	3.00	1000.00	1.123793	0.0439716
Jones	1	5.00	0.70	1.40	12.00	1.539197	0.0039999
Las Minas	2	7.00	0.55	1.30	20.43	1.127796	0.0139990
Llucuco	2	16.06	1.04	2.08	16.06	1.056106	0.1115351
Machete	3	50.00	1.30	2.60	51.00	1.877667	0.0059999
Millaqueo abajo (1)	3	2.70	0.72	1.14	45.00	1.493333	0.0079998
Millaqueo arriba (2)	3	31.50	0.60	1.20	31.50	1.195760	0.0079998
Nireco Alto	1	6.60	0.77	1.54	8.00	1.208818	0.0877738
Nireco arriba	2	8.80	0.45	0.90	40.00	1.208818	0.0119994
Nireco Urbano	3	15.00	1.25	2.50	175.00	1.208818	0.0099996
Nirihuau Aerop	4	75.00	2.00	4.00	150.00	1.192892	0.0059999
Nirihuau alto	3	23.00	1.90	3.80	300.00	1.192892	0.0339869
Nirihuau Superior Br1	3	23.60	1.50	3.00	160.00	1.192892	0.0219964
Nirihuau superior Br2	3	13.03	1.00	2.00	160.00	1.192892	0.0219964
Nirihuau Vado	3	65.00	1.60	3.20	500.00	1.192892	0.0099996
Patiruco	2	15.40	1.27	2.54	17.40	1.070492	0.0519532
Pireco	3	33.00	1.50	3.00	70.00	1.218449	0.0099996
Ragintuco	2	15.00	1.30	2.60	15.00	1.136986	0.0918220
Tristeza	2	6.20	0.30	0.60	7.20	1.209559	0.0199973

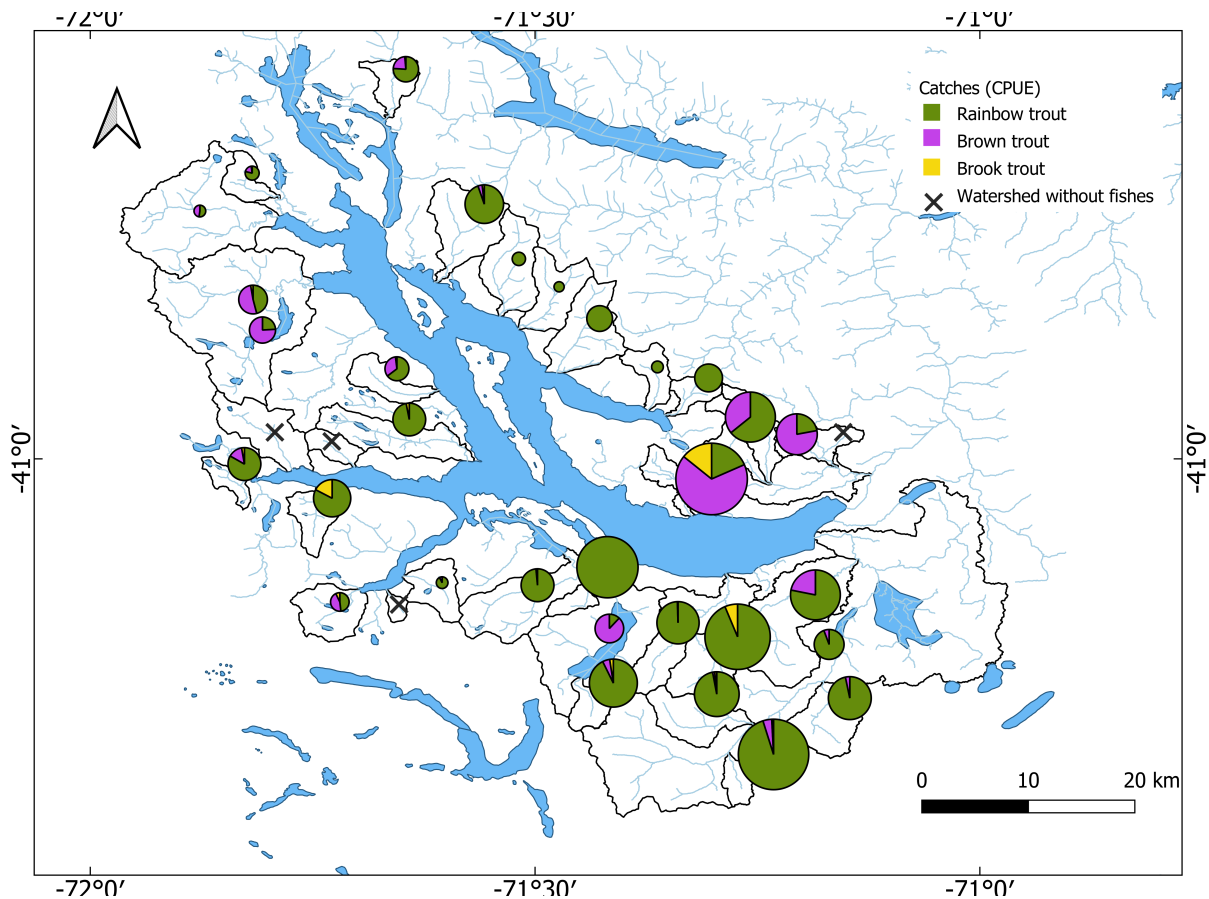
Fish Capture

Different stream segments that presented a succession of pool-riffle-pool habitats were sampled during the austral summer (from December to March) of 2013-2014. The minimum sampled area depended on the size of the selected reach. In each section, presence-absence data were collected by three-pass electrofishing with a Smith-Root mod 12B equipment along 50-m reach. Relative abundance, expressed as catch per unit effort (CPUEN), was standardized based on actual length of each sweep to number of fish caught per 100 m². Electrofishing was conducted from downstream to upstream following a zigzag trajectory and exploring all habitat types. The extremes were not blocked with nets. For basins sampled in more than one section, an average of the CPUEN of all fished sections was used as basin-level fish abundance. The Administration of Nahuel Huapi National Park and San Carlos de Bariloche Town Council approved our protocols and procedures and granted permission to collect fish samples (APN project n° 1173 and S.C de Bariloche Council note n° 412/SSMA/15).

Results

Introduced salmonid species are unevenly distributed among basins

Only two specimens of native species were caught: one of *Galaxias maculatus* (Jennyns, 1842) in the Frey basin and another of *Hatcheria macraei* (Girard, 1885) in the Nirihuau basin. In contrast, a total of 4531 salmonids were caught. We found individuals aged between 0 and 3 years old at all sites, but older specimens (up to 8 years old) were caught only in some of the Eastern basins. No fish were captured in the Newbery, Blanco, Bravo and Uhueco basins; these streams present physical barriers (large waterfalls) restricting upstream movement of fish from the rest of the system (Figure 2).



Oncorhynchus mykiss was present in all basins where fish were caught. This species was also the most abundant in almost all basins (31/35); *Salmo trutta*, though present in 21/35 basins, was dominant in only 4 of them (Figure 2). *Salvelinus fontinalis*, was captured in 15/35 basins, but never dominated the assemblage (Figure 2).

Co-occurrence of introduced salmonid species varied among basins. The three species were found together in 10 basins. Only two out of three possible bispecific assemblages were found: rainbow trout with brown trout (*S.trutta* + *O. mykiss*, $n = 10$) and brown trout with brook trout (*S.fontinalis* + *O.mykiss*, $n = 4$). Monospecific assemblages were found only for rainbow trout (*O. mykiss*, $n = 7$).

No interspecific reciprocal influences on presence are evidenced by salmonid species distribution

Independence of species presence was tested using a contingency table approach, asking whether the probability of a species being present was contingent on the presence of other species. We calculated the expected frequency of each combination of species under the assumption that species distributions are independent of each other, based on the frequency each species was found. We then calculated the expected counts of all combinations, and compared them to the observed counts using a Fisher's exact Test for contingency tables.

####Contingency test on joint species presence####

#Field data: number of basins in which a given species is present

Ntotal <- 35 #Total basins

NOm <- 31 #Basins in which rainbow trout *Oncorhynchus mykiss* (Om) is present

NSf <- 15 #Basins in which brook trout *Salvelinus fontinalis* (Sf) is present

NSt <- 21 #Basins in which brown trout *Salmo trutta* (St) is present

```

#Counts of basins in which each combination of species occur
NOb <- c(4,7,0,0,4,10,0,10)
names(NOb)<-c("none","Om","Sf","St","Om.Sf","Om.St","St.Sf","Om.Sf.St")

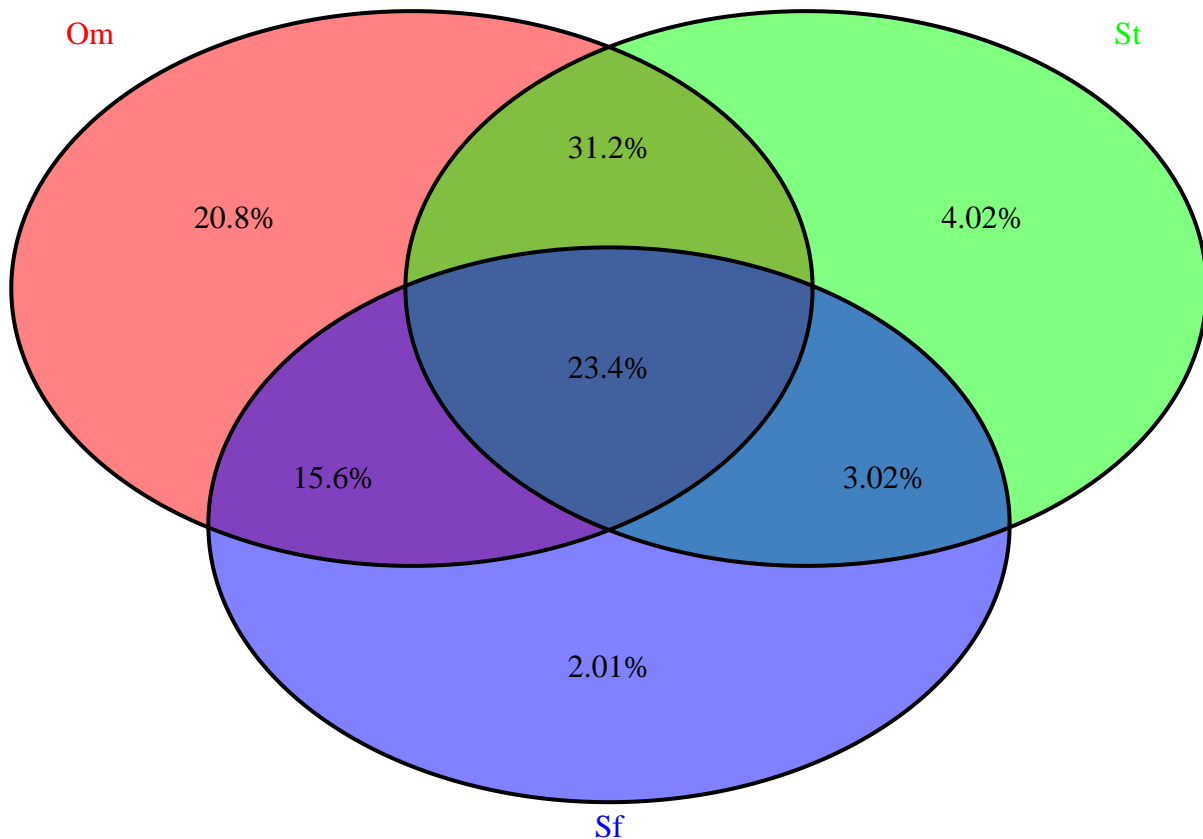
#Marginal probabilities
pOm <- NOm/Ntotal
pSf <- NSf/Ntotal
pSt <- NSt/Ntotal

#Calculate expected frequencies as joint probabilities
cOm <- pOm - pOm*pSf*pSt - (pOm*pSf - pOm*pSf*pSt) - (pOm*pSt - pOm*pSf*pSt)
cSf <- pSf - pOm*pSf*pSt - (pOm*pSf - pOm*pSf*pSt) - (pSt*pSf - pOm*pSf*pSt)
cSt <- pSt - pOm*pSf*pSt - (pOm*pSt - pOm*pSf*pSt) - (pSt*pSf - pOm*pSf*pSt)
cOm.Sf <- pOm*pSf - pOm*pSf*pSt
cOm.St <- pOm*pSt - pOm*pSf*pSt
cSt.Sf <- pSt*pSf - pOm*pSf*pSt
cOm.Sf.St <- pOm*pSf*pSt
none <- 1-sum(cOm,cSf,cSt,cOm.Sf,cOm.St,cSt.Sf,cOm.Sf.St)

#Build a vector of expected frequencies
frExp <- c(none,cOm,cSf,cSt,cOm.Sf,cOm.St,cSt.Sf,cOm.Sf.St)
names(frExp)<-c("none","Om","Sf","St","Om.Sf","Om.St","St.Sf","Om.Sf.St")

#Plot a Venn diagram
col.scheme <- c("red","green","blue")
draw.triple.venn(pOm,pSt,pSf,pOm*pSt,pSt*pSf,pSf*pOm,pOm*pSt*pSf, c("Om","St","Sf"), fill=col.scheme, c

```




```
## (polygon[GRID.polygon.11], polygon[GRID.polygon.12], polygon[GRID.polygon.13], polygon[GRID.polygon.14])
#Calculate vector of expected frequencies
NExp <- frExp*Ntotal

#Build a table of expected and observed occurrences.
expvsobs <- cbind(round(NExp),NOb)
colnames(expvsobs)<-c("Expected","Observed")
expvsobs <- as_tibble(expvsobs, rownames = "Species")
gt(expvsobs)
```

Species	Expected	Observed
none	1	4
Om	7	7
Sf	1	0
St	1	0
Om.Sf	5	4
Om.St	11	10
St.Sf	1	0
Om.Sf.St	8	10

```
#Performs Fisher's exact test for testing the null of independence of rows and columns in a contingency table
ftest_all_basins <- fisher.test(expvsobs %>% select(Expected, Observed))
ftest_all_basins
```

```
##
## Fisher's Exact Test for Count Data
##
## data: expvsobs %>% select(Expected, Observed)
## p-value = 0.7537
## alternative hypothesis: two.sided

## Now repeat all of the above, but dropping those basins where no fish was caught.
## This explores that those basins are categorically different due to insurmountable obstacles for dispersal
##Field data: number of basins in which a given species is present
Ntotal <- 31
NOm <- 31
NSf <- 15
NSt <- 21

#Counts of basins in which each combination of species occur
NOb <- c(7,0,0,4,10,0,10)
names(NOb)<-c("Om", "Sf", "St", "Om.Sf", "Om.St", "St.Sf", "Om.Sf.St")

#Marginal probabilities
pOm <- NOm/Ntotal
pSf <- NSf/Ntotal
pSt <- NSt/Ntotal

#Calculate expected frequencies as joint probabilities
cOm <- pOm - pOm*pSf*pSt - (pOm*pSf - pOm*pSf*pSt) - (pOm*pSt - pOm*pSf*pSt)
cSf <- pSf - pOm*pSf*pSt - (pOm*pSf - pOm*pSf*pSt) - (pSt*pSf - pOm*pSf*pSt)
cSt <- pSt - pOm*pSf*pSt - (pOm*pSt - pOm*pSf*pSt) - (pSt*pSf - pOm*pSf*pSt)
cOm.Sf <- pOm*pSf - pOm*pSf*pSt
```

```

cOm.St <- pOm*pSt - pOm*pSf*pSt
cSt.Sf <- pSt*pSf - pOm*pSf*pSt
cOm.Sf.St <- pOm*pSf*pSt
none <- 1-sum(cOm,cSf,cSt,cOm.Sf,cOm.St,cSt.Sf,cOm.Sf.St)

#Build a vector of expected frequencies
frExp <- c(cOm,cSf,cSt,cOm.Sf,cOm.St,cSt.Sf,cOm.Sf.St)
names(frExp)<-c("Om","Sf","St","Om.Sf","Om.St","St.Sf","Om.Sf.St")

#Plot a Venn diagram
col.scheme <- c("red","green","blue")
#draw.triple.venn(pOm,pSt,pSf,pOm*pSt,pSt*pSf,pSf*pOm,pOm*pSt*pSf, c("Om","St","Sf"), fill=col.scheme,

#Calculate vector of expected frequencies
NExp <- frExp*Ntotal

#Build a table of expected and observed occurrences.

expvsobs.2 <- cbind(round(NExp),NOb)
colnames(expvsobs.2)<-c("Expected","Observed")
expvsobs.2 <- as_tibble(expvsobs.2, rownames = "Species")
gt(expvsobs.2)

```

Species	Expected	Observed
Om	5	7
Sf	0	0
St	0	0
Om.Sf	5	4
Om.St	11	10
St.Sf	0	0
Om.Sf.St	10	10

```

#Performs Fisher's exact test for testing the null of independence of rows and columns in a contingency
ftest_no_empty_basins <- fisher.test(expvsobs.2 %>% select(Expected, Observed))
ftest_no_empty_basins

```

```

##
## Fisher's Exact Test for Count Data
##
## data:  expvsobs.2 %>% select(Expected, Observed)
## p-value = 0.9378
## alternative hypothesis: two.sided

```

Fisher's exact test failed to reject the hypothesis of independence ($p = 0.753685$), suggesting that species interactions are not needed to explain the frequency of each combination. Expected and observed counts are even more similar when basins without fish captures are excluded from the calculations ($p = 0.9377599$).

Salmonid abundances varied with environmental variables.

We then used generalized linear models (GLMs) on presence/absence and relative abundance data to assess the filtering influence of landscape and local variables. For each level and response variable type, we tried two approaches: 1) reducing the dimensionality of the independent variables through a principal components analysis (PCA), and then using the principal components explaining most variance as predictor variables in

the GLM; and 2) by selecting independent variables that were not significantly correlated and using them as predictor variables in the GLM. While these two approaches are expected to yield qualitatively similar results, the second approach lends to more straightforward interpretations. All analyses were run using the function `glm` from the `base` package of the R computing environment R Core Team, version 3.5.1 (2018). To regress environmental variables using presence/absence as a response variable, we used a binomial logistic regression with a logit link. When the response variable was the logarithm of relative abundance, we used a Gaussian regression with an identity link.

```
#### Basin-level correlation analysis ####
basin.cpue.cor <- cor(basins[,-1], use="pairwise.complete.obs", method="spearman")[,18:21]
basin.cpue.cor.test <- rcorr(as.matrix(basins[,-1]), type="spearman")
basin.cpue.cor.test$r[,29:32] %>%
  as_tibble(rownames = "variable")
```

```
## # A tibble: 32 x 5
##   variable      TAI      TAM      TAR      Total
##   <chr>      <dbl>    <dbl>    <dbl>    <dbl>
## 1 lat        -0.512  -0.109  -0.198  -0.538
## 2 lon         0.434   0.0728 -0.182   0.475
## 3 area       -0.0271  0.248   -0.221  0.0772
## 4 perimeter -0.0273  0.304   -0.243  0.104
## 5 length      0.0842  0.331   -0.207  0.213
## 6 drain_net   0.0430  0.267   -0.131  0.178
## 7 drain_area -0.0321 -0.141   0.104  0.0311
## 8 shape       -0.0847 -0.345   0.213 -0.191
## 9 Kc          0.0955  0.187   -0.187  0.204
## 10 relief     -0.124  -0.350  -0.129 -0.178
## # ... with 22 more rows
```

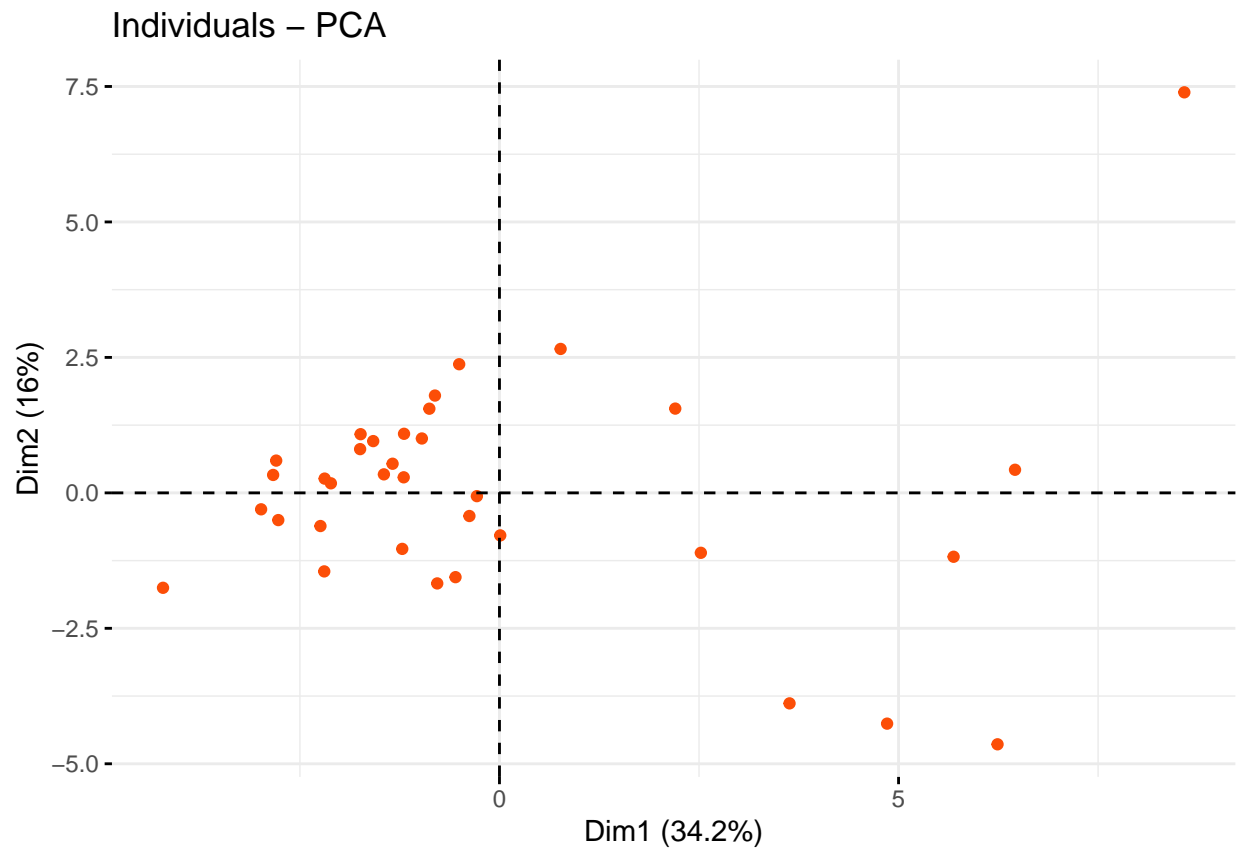
Total catch of salmonids in streams from the upper Limay basin increased along a NW-SE gradient (Table 2). This gradient in relative abundance was associated to basins having a larger proportion of lowland, shrubby environments characterized by low rainfall, open woodlands and fewer rocky outcrops. This pattern in total catch was likely driven by dominance of rainbow trout, since its relative abundances presented the same pattern as the total catch (with the addition that abundance was higher at lower basins).

In contrast, brown trout abundances were not clearly associated with geographic gradients (Table 2). Instead, higher abundances were associated with lower, warmer and flatter basins, with fewer High-Andean habitat and more wetlands. Brook trout abundance showed no significant correlations with any environmental variable. However, spotty occurrence and low overall abundance of this species resulted in very low statistical power to detect any existing correlations.

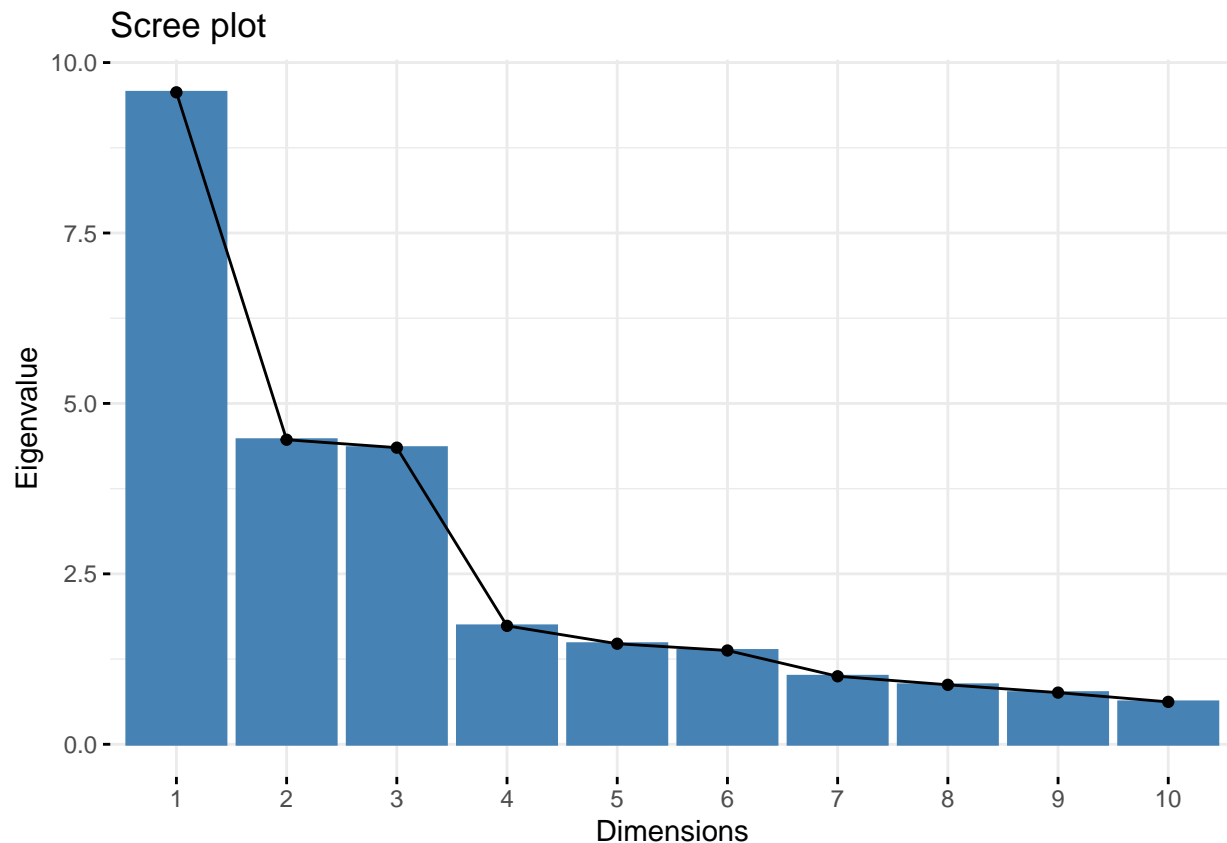
Patterns of salmonid distribution are not strongly driven by landscape variables

Having ruled out a role for the interaction between species in their joint distribution (see above), we evaluated the influence of basin characteristics on individual species presence and abundances. We derived 28 watershed variables from remote sensing and topographical data sources.

```
#### Basin-level PCA and GLM analysis ####
basin.pca <- prcomp(basins[,2:29],center = TRUE, scale. = TRUE)
summary_basin.pca <- summary(basin.pca)
biplot(basin.pca)
```

```
fviz_screplot(basin.pca, choice="eigenvalue")
```



```
basins <- cbind(basins, basin.pca$x[,1:3])
```

```
total.glm<-glm(Total~PC1+PC2+PC3, data=basins)
summary(total.glm)
```

```
##
## Call:
## glm(formula = Total ~ PC1 + PC2 + PC3, data = basins)
##
## Deviance Residuals:
##      Min       1Q   Median       3Q      Max
## -32.526  -6.982  -1.672   4.607  33.232
##
## Coefficients:
##              Estimate Std. Error t value Pr(>|t|)
## (Intercept)  13.8917     2.2405   6.200 6.95e-07 ***
## PC1           1.3951     0.7351   1.898  0.0671 .
## PC2          -2.1101     1.0755  -1.962  0.0588 .
## PC3           2.1466     1.0898   1.970  0.0578 .
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for gaussian family taken to be 175.6907)
##
##      Null deviance: 7437.3  on 34  degrees of freedom
## Residual deviance: 5446.4  on 31  degrees of freedom
```

```
## AIC: 285.98
##
## Number of Fisher Scoring iterations: 2
p.tai.glm<-glm(p.TAI~PC1+PC2+PC3, data=basins, family="binomial")
summary(p.tai.glm)

##
## Call:
## glm(formula = p.TAI ~ PC1 + PC2 + PC3, family = "binomial", data = basins)
##
## Deviance Residuals:
##      Min       1Q   Median       3Q      Max
## -2.4523   0.1155   0.2870   0.4394   0.8824
##
## Coefficients:
##              Estimate Std. Error z value Pr(>|z|)
## (Intercept)   3.13791    1.07382   2.922 0.00348 **
## PC1           0.43453    0.31319   1.387 0.16530
## PC2           1.03896    0.56752   1.831 0.06715 .
## PC3          -0.04685    0.24091  -0.194 0.84579
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for binomial family taken to be 1)
##
##      Null deviance: 24.877  on 34  degrees of freedom
## Residual deviance: 19.421  on 31  degrees of freedom
## AIC: 27.421
##
## Number of Fisher Scoring iterations: 7
tai.glm<-glm(TAI~PC1+PC2+PC3, data=basins)
summary(tai.glm)

##
## Call:
## glm(formula = TAI ~ PC1 + PC2 + PC3, data = basins)
##
## Deviance Residuals:
##      Min       1Q   Median       3Q      Max
## -19.3260  -6.5525   0.1208   5.3114  27.9262
##
## Coefficients:
##              Estimate Std. Error t value Pr(>|t|)
## (Intercept)  10.6617    1.8193   5.860 1.83e-06 ***
## PC1           0.5367    0.5969   0.899 0.37549
## PC2          -1.1018    0.8733  -1.262 0.21646
## PC3           3.1618    0.8849   3.573 0.00118 **
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for gaussian family taken to be 115.8403)
##
##      Null deviance: 5348.1  on 34  degrees of freedom
```

```
## Residual deviance: 3591.1 on 31 degrees of freedom
## AIC: 271.41
##
## Number of Fisher Scoring iterations: 2
tai.glm<-glm(TAI~PC1+PC2+PC3, data=basins)
summary(tai.glm)

##
## Call:
## glm(formula = TAI ~ PC1 + PC2 + PC3, data = basins)
##
## Deviance Residuals:
##      Min       1Q   Median       3Q      Max
## -19.3260  -6.5525   0.1208   5.3114  27.9262
##
## Coefficients:
##              Estimate Std. Error t value Pr(>|t|)
## (Intercept)  10.6617     1.8193   5.860 1.83e-06 ***
## PC1           0.5367     0.5969   0.899  0.37549
## PC2          -1.1018     0.8733  -1.262  0.21646
## PC3           3.1618     0.8849   3.573  0.00118 **
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for gaussian family taken to be 115.8403)
##
##      Null deviance: 5348.1 on 34 degrees of freedom
## Residual deviance: 3591.1 on 31 degrees of freedom
## AIC: 271.41
##
## Number of Fisher Scoring iterations: 2
log.tai.glm<-glm(log(TAI+0.00001)~PC1+PC2+PC3, data=basins)
summary(log.tai.glm)

##
## Call:
## glm(formula = log(TAI + 1e-05) ~ PC1 + PC2 + PC3, data = basins)
##
## Deviance Residuals:
##      Min       1Q   Median       3Q      Max
## -11.6393  -0.2021   1.3702   2.5841   3.6290
##
## Coefficients:
##              Estimate Std. Error t value Pr(>|t|)
## (Intercept)   0.3574     0.7689   0.465   0.645
## PC1           0.1810     0.2523   0.717   0.478
## PC2           0.4053     0.3691   1.098   0.281
## PC3           0.1480     0.3740   0.396   0.695
##
## (Dispersion parameter for gaussian family taken to be 20.69327)
##
##      Null deviance: 680.34 on 34 degrees of freedom
## Residual deviance: 641.49 on 31 degrees of freedom
```



```
## AIC: 211.12
##
## Number of Fisher Scoring iterations: 2
```

```
p.tam.glm<-glm(p.TAM~PC1+PC2+PC3, data=basins, family="binomial")
summary(p.tam.glm)
```

```
##
## Call:
## glm(formula = p.TAM ~ PC1 + PC2 + PC3, family = "binomial", data = basins)
##
## Deviance Residuals:
##      Min       1Q   Median       3Q      Max
## -1.7402  -1.1886   0.7392   1.0056   1.4048
##
## Coefficients:
##              Estimate Std. Error z value Pr(>|z|)
## (Intercept)   0.5059     0.3826   1.322   0.186
## PC1           0.2536     0.1640   1.546   0.122
## PC2           0.1758     0.2411   0.729   0.466
## PC3          -0.1049     0.1706  -0.615   0.539
##
## (Dispersion parameter for binomial family taken to be 1)
##
##      Null deviance: 47.111  on 34  degrees of freedom
## Residual deviance: 43.254  on 31  degrees of freedom
## AIC: 51.254
##
## Number of Fisher Scoring iterations: 4
```

```
tam.glm<-glm(TAM~PC1+PC2+PC3, data=basins)
summary(tam.glm)
```

```
##
## Call:
## glm(formula = TAM ~ PC1 + PC2 + PC3, data = basins)
##
## Deviance Residuals:
##      Min       1Q   Median       3Q      Max
## -11.4313  -2.5794  -0.9743   1.8485  25.0488
##
## Coefficients:
##              Estimate Std. Error t value Pr(>|t|)
## (Intercept)   2.7591     0.9938   2.776 0.00924 **
## PC1           0.8081     0.3261   2.478 0.01885 *
## PC2          -0.7949     0.4771  -1.666 0.10575
## PC3          -0.9194     0.4834  -1.902 0.06650 .
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for gaussian family taken to be 34.57034)
##
##      Null deviance: 1505.0  on 34  degrees of freedom
## Residual deviance: 1071.7  on 31  degrees of freedom
## AIC: 229.08
```

```
##
## Number of Fisher Scoring iterations: 2
log.tam.glm<-glm(log(TAM+0.00001)~PC1+PC2+PC3, data=basins)
summary(log.tam.glm)

##
## Call:
## glm(formula = log(TAM + 1e-05) ~ PC1 + PC2 + PC3, data = basins)
##
## Deviance Residuals:
##      Min       1Q   Median       3Q      Max
## -10.422   -5.904    2.523    4.789    8.267
##
## Coefficients:
##              Estimate Std. Error t value Pr(>|t|)
## (Intercept)  -4.3252     1.0037  -4.309 0.000154 ***
## PC1           0.6148     0.3293   1.867 0.071378 .
## PC2           0.1230     0.4818   0.255 0.800167
## PC3          -0.4896     0.4882  -1.003 0.323693
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for gaussian family taken to be 35.26049)
##
##      Null deviance: 1253.7  on 34  degrees of freedom
## Residual deviance: 1093.1  on 31  degrees of freedom
## AIC: 229.77
##
## Number of Fisher Scoring iterations: 2
p.tar.glm<-glm(p.TAR~PC1+PC2+PC3, data=basins, family="binomial")
summary(p.tar.glm)

##
## Call:
## glm(formula = p.TAR ~ PC1 + PC2 + PC3, family = "binomial", data = basins)
##
## Deviance Residuals:
##      Min       1Q   Median       3Q      Max
## -1.7296  -1.0883  -0.5299   1.1070   1.4891
##
## Coefficients:
##              Estimate Std. Error z value Pr(>|z|)
## (Intercept)  -0.42512    0.39038  -1.089  0.2762
## PC1          -0.31573    0.17710  -1.783  0.0746 .
## PC2          -0.25317    0.25557  -0.991  0.3219
## PC3          -0.08613    0.17121  -0.503  0.6149
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for binomial family taken to be 1)
##
##      Null deviance: 47.804  on 34  degrees of freedom
## Residual deviance: 42.691  on 31  degrees of freedom
```

```
## AIC: 50.691
##
## Number of Fisher Scoring iterations: 5
tar.glm<-glm(TAR~PC1+PC2+PC3, data=basins)
summary(tar.glm)

##
## Call:
## glm(formula = TAR ~ PC1 + PC2 + PC3, data = basins)
##
## Deviance Residuals:
##      Min       1Q   Median       3Q      Max
## -1.7754  -0.5585  -0.2577   0.1115   5.9613
##
## Coefficients:
##              Estimate Std. Error t value Pr(>|t|)
## (Intercept)  0.46686    0.23242   2.009  0.0533 .
## PC1          0.05132    0.07625   0.673  0.5059
## PC2         -0.21428    0.11156  -1.921  0.0640 .
## PC3         -0.09477    0.11305  -0.838  0.4083
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for gaussian family taken to be 1.89062)
##
##      Null deviance: 67.769  on 34  degrees of freedom
## Residual deviance: 58.609  on 31  degrees of freedom
## AIC: 127.37
##
## Number of Fisher Scoring iterations: 2
log.tar.glm<-glm(log(TAR+0.00001)~PC1+PC2+PC3, data=basins)
summary(log.tar.glm)
```

```
##
## Call:
## glm(formula = log(TAR + 1e-05) ~ PC1 + PC2 + PC3, data = basins)
##
## Deviance Residuals:
##      Min       1Q   Median       3Q      Max
## -7.005  -4.859  -2.265   5.253   8.996
##
## Coefficients:
##              Estimate Std. Error t value Pr(>|t|)
## (Intercept)  -6.9855    0.9037  -7.730 1.02e-08 ***
## PC1          -0.4800    0.2965  -1.619  0.116
## PC2          -0.3564    0.4338  -0.822  0.418
## PC3          -0.1365    0.4396  -0.311  0.758
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for gaussian family taken to be 28.5864)
##
##      Null deviance: 983.14  on 34  degrees of freedom
```

```
## Residual deviance: 886.18 on 31 degrees of freedom
## AIC: 222.43
##
## Number of Fisher Scoring iterations: 2
```

We found that many of the variables were highly correlated; thus, we used a principal component analysis (PCA) to reduce the dimensionality of variable space. The first three principal components (PC) explained 65.651 % of the total variance (PC1 34.155%; PC2 15.956%, PC3 15.54%).

We used these three PCs to test if basin characteristics influenced the presence of each species by fitting a logistic regression using GLMs (see Methods), but found no significant influence of either PC on presence for any of the species. We then repeated the same analysis using relative abundance (individuals caught per unit effort; CPUEN) as a dependent variable instead. We found that rainbow trout abundance was significantly influenced by PC3 ($p=0.001$, loaded mainly by Latitude and Zmin), while brown trout abundance was instead, significantly influenced by PC1 ($p=0.002$, loaded mainly by Steppe and precipitations). Brook trout was not influenced by any PCs (Table 3). Repeating the analyses using the logarithm of relative abundance as response variable yielded no significant results for any species or PCs.

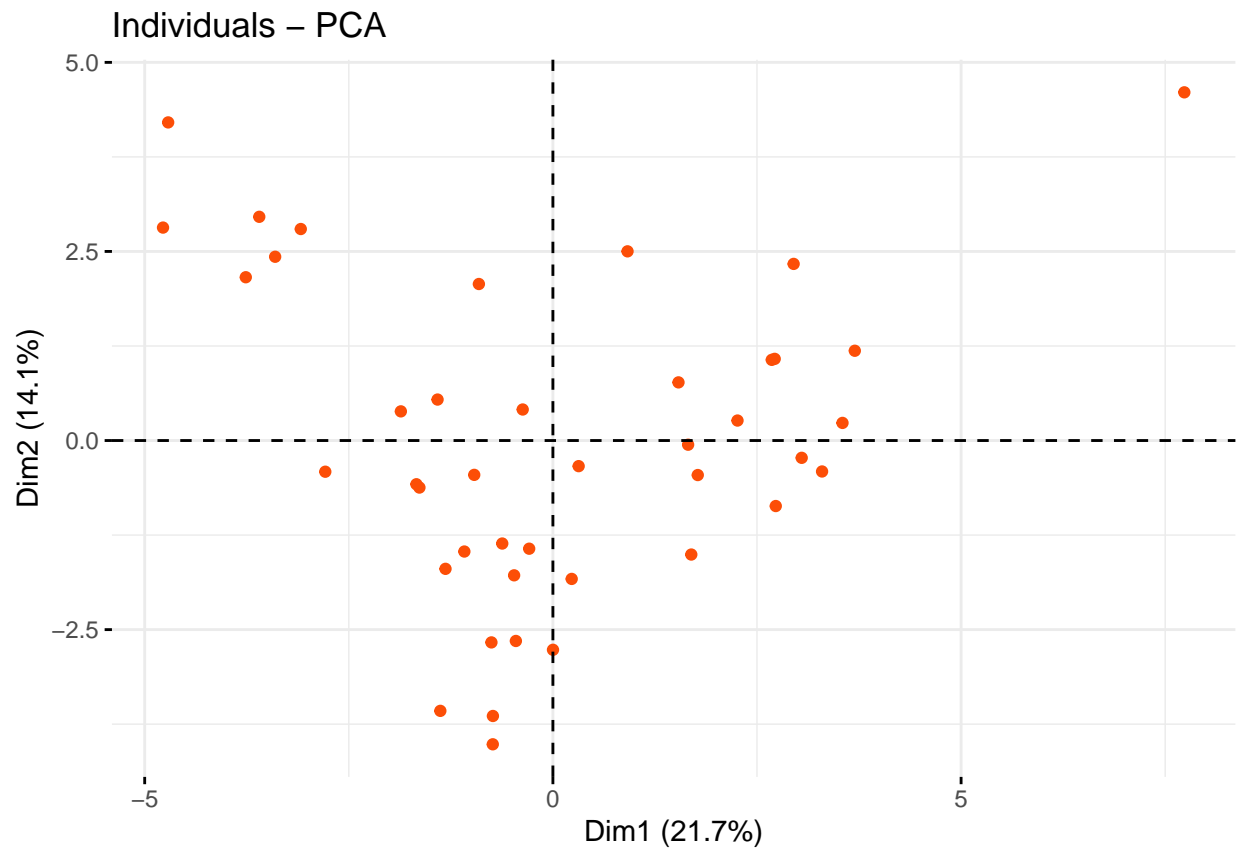
Hence, for all three species, we found that the probability of a species being present in a basin was not explained by any of the basin characteristics we used in this analysis. However, we detected evidence that the abundance of rainbow trout and brown trout (but not brook trout) is influenced by different combinations of basin traits. Thus, the three species differ in their response to landscape level filtering variables.

Local variables influence weakly but differentially the abundance of each species

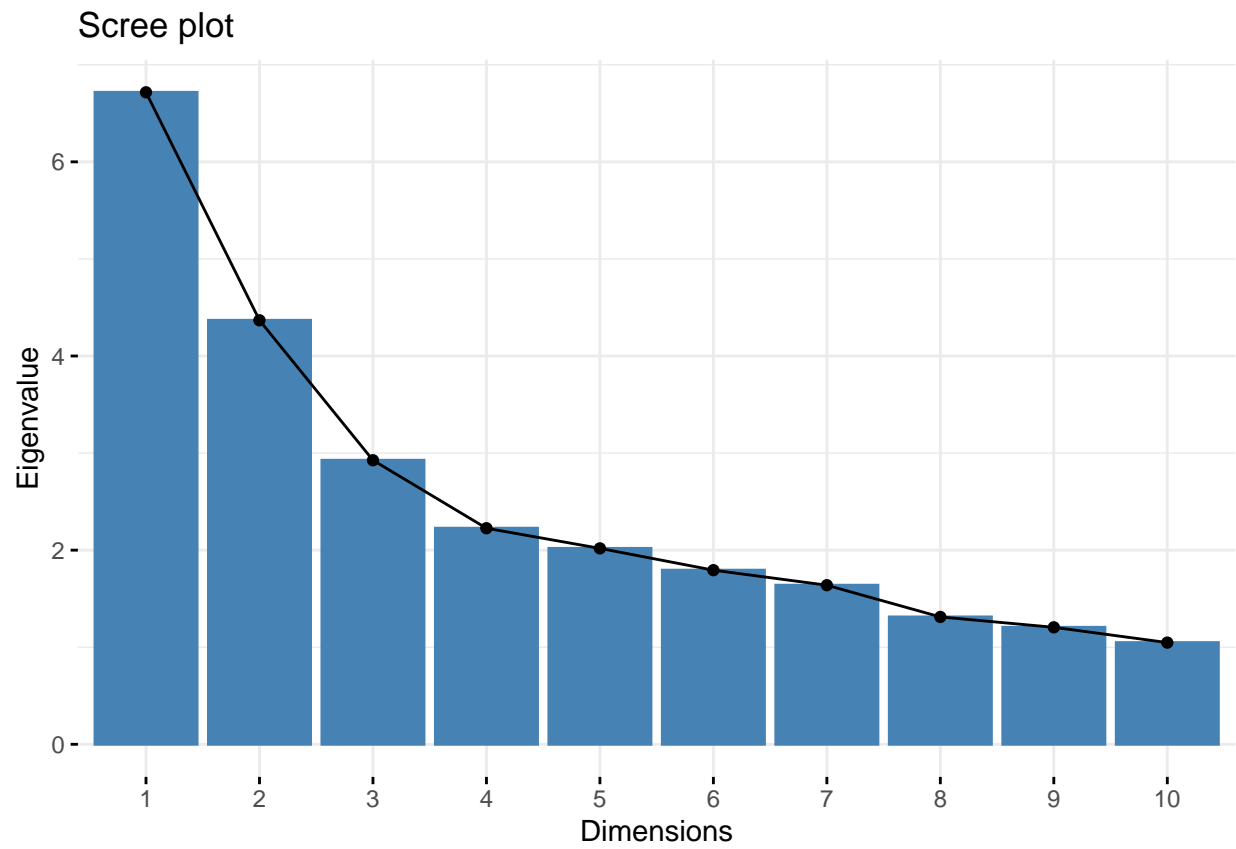
To evaluate the influence of local characteristics on species presence we estimated 31 variables using local data records (see Table 3). Since several local-scale variables presented significant correlations, we used PCA to reduce the dimensionality of the variable space.

```
#### Reach-level PCA and GLM analysis ####
reach<-read.table("reaches.tsv", header=TRUE, sep="\t")
reach$p.TAI <- ifelse(reach$TAI==0,0,1)
reach$p.TAR <- ifelse(reach$TAR==0,0,1)
reach$p.TAM <- ifelse(reach$TAM==0,0,1)

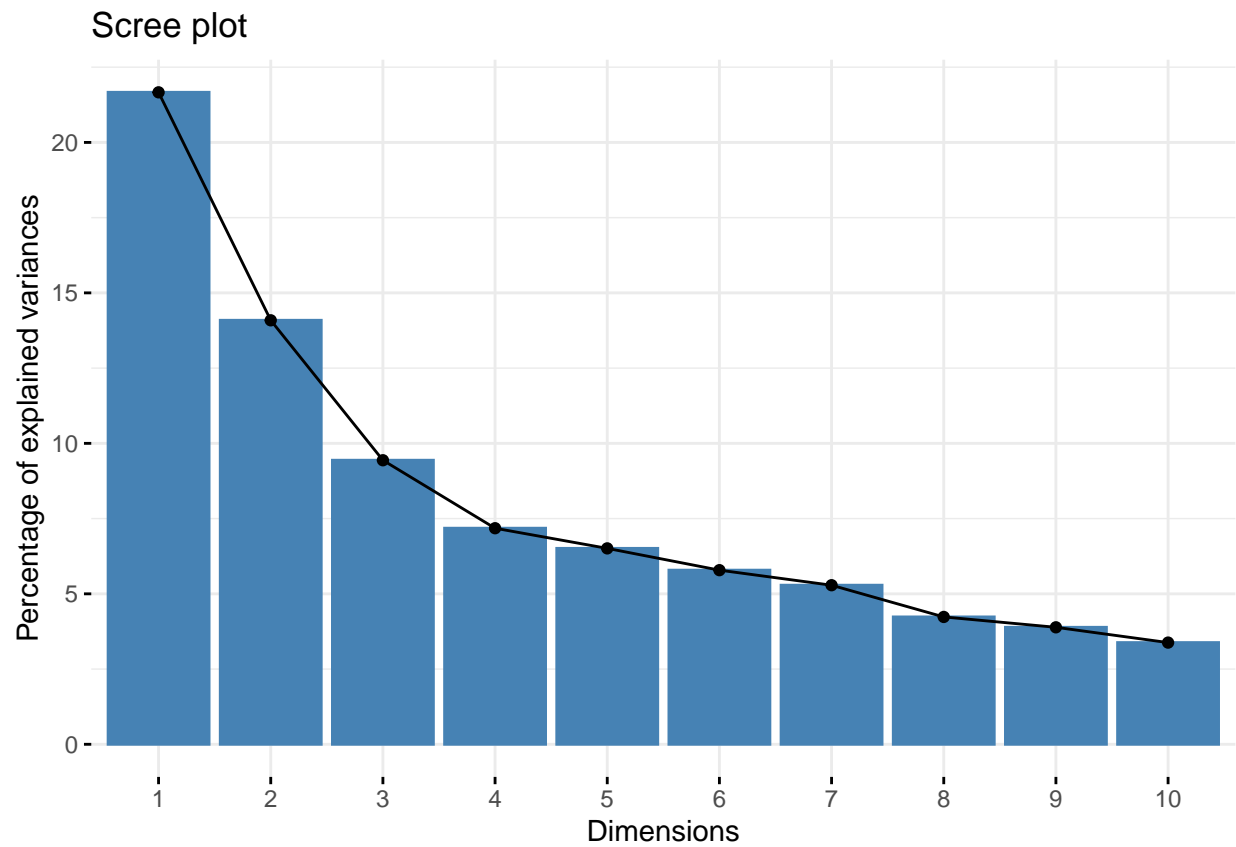
reach.pca <- prcomp(na.omit(reach[,2:32]),center = TRUE, scale. = TRUE)
summary_reach.pca <- summary(reach.pca)
biplot(reach.pca)
```

```
fviz_screepplot(reach.pca, choice="eigenvalue")
```

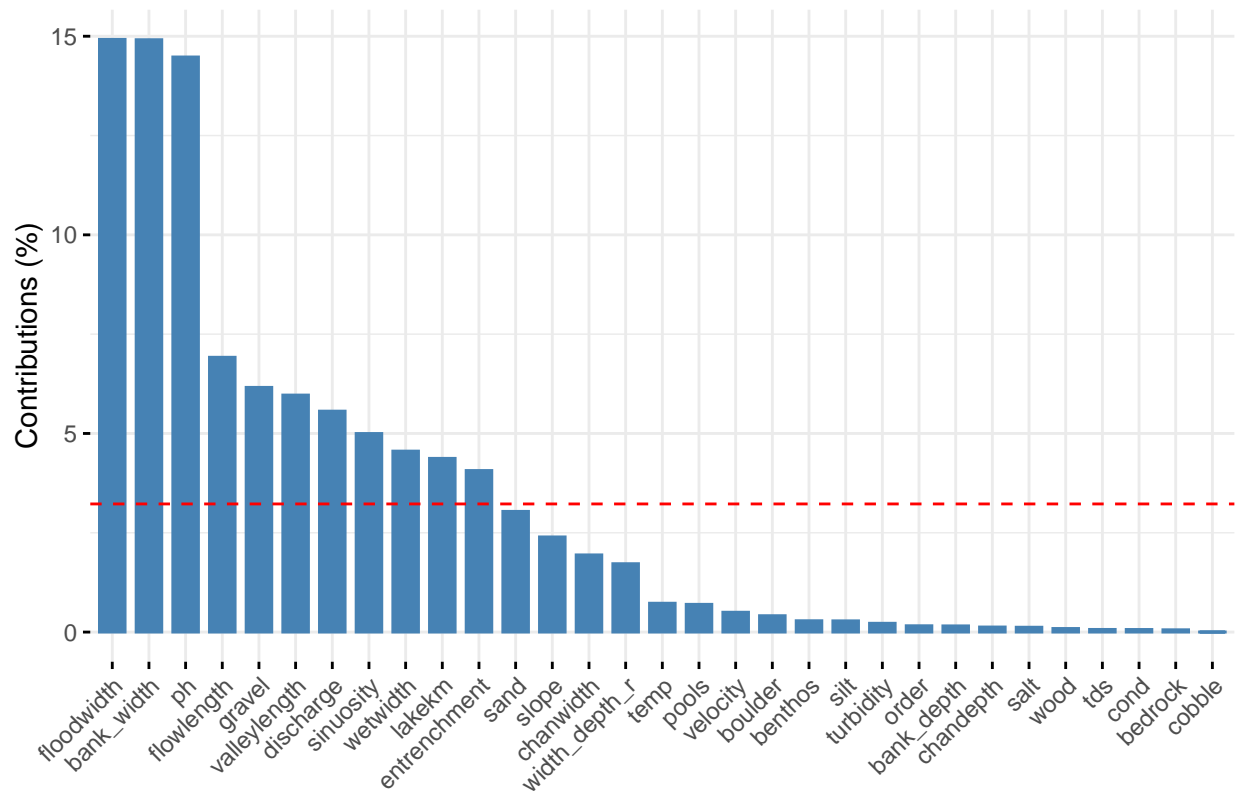


```
fviz_screplot(reach.pca, choice="variance")
```



```
fviz_contrib(reach.pca, choice="var", axes=3)
```


Contribution of variables to Dim-3



```
reach <- cbind(reach, reach.pca$x[,1:3])
```

```
r.total.glm<-glm(Total~PC1+PC2+PC3, data=reach)
summary(r.total.glm)
```

```
##
## Call:
## glm(formula = Total ~ PC1 + PC2 + PC3, data = reach)
##
## Deviance Residuals:
##      Min       1Q   Median       3Q      Max
## -18.893   -6.282   -2.203    2.488   47.972
##
## Coefficients:
##              Estimate Std. Error t value Pr(>|t|)
## (Intercept)  16.6030     2.0181   8.227 5.75e-10 ***
## PC1           3.9703     0.7882   5.037 1.18e-05 ***
## PC2           1.0609     0.9774   1.085  0.285
## PC3          -0.2520     1.1941  -0.211  0.834
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for gaussian family taken to be 171.0609)
##
##      Null deviance: 11049.8  on 41  degrees of freedom
## Residual deviance: 6500.3  on 38  degrees of freedom
```

```
## AIC: 340.95
##
## Number of Fisher Scoring iterations: 2
```

```
r.p.tai.glm<-glm(p.TAI~PC1+PC2+PC3, data=reach, family="binomial")
summary(r.p.tai.glm)
```

```
##
## Call:
## glm(formula = p.TAI ~ PC1 + PC2 + PC3, family = "binomial", data = reach)
##
## Deviance Residuals:
##      Min       1Q   Median       3Q      Max
## 2.409e-06  2.409e-06  2.409e-06  2.409e-06  2.409e-06
##
## Coefficients:
##              Estimate Std. Error z value Pr(>|z|)
## (Intercept)  2.657e+01  5.495e+04      0      1
## PC1          -1.717e-16  2.146e+04      0      1
## PC2           2.082e-10  2.661e+04      0      1
## PC3          -6.497e-11  3.251e+04      0      1
##
## (Dispersion parameter for binomial family taken to be 1)
##
##      Null deviance: 0.0000e+00  on 41  degrees of freedom
## Residual deviance: 2.4367e-10  on 38  degrees of freedom
## AIC: 8
##
## Number of Fisher Scoring iterations: 25
```

```
r.tai.glm<-glm(TAI~PC1+PC2+PC3, data=reach)
summary(r.tai.glm)
```

```
##
## Call:
## glm(formula = TAI ~ PC1 + PC2 + PC3, data = reach)
##
## Deviance Residuals:
##      Min       1Q   Median       3Q      Max
## -21.076    -6.200    -1.187     3.473    49.760
##
## Coefficients:
##              Estimate Std. Error t value Pr(>|t|)
## (Intercept)  11.9807      1.8374   6.520 1.1e-07 ***
## PC1           2.7704      0.7176   3.861 0.000426 ***
## PC2           0.6754      0.8899   0.759 0.452562
## PC3          -0.7988      1.0872  -0.735 0.467007
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for gaussian family taken to be 141.7978)
##
##      Null deviance: 7659.9  on 41  degrees of freedom
## Residual deviance: 5388.3  on 38  degrees of freedom
## AIC: 333.07
```

```
##
## Number of Fisher Scoring iterations: 2
r.log.tai.glm<-glm(log(TAI+0.00001)~PC1+PC2+PC3, data=reach)
summary(r.log.tai.glm)

##
## Call:
## glm(formula = log(TAI + 1e-05) ~ PC1 + PC2 + PC3, data = reach)
##
## Deviance Residuals:
##      Min       1Q   Median       3Q      Max
## -3.0062  -0.7251   0.3885   0.8647   1.9106
##
## Coefficients:
##              Estimate Std. Error t value Pr(>|t|)
## (Intercept)  1.82758    0.18479   9.890 4.64e-12 ***
## PC1          0.21254    0.07217   2.945  0.00549 **
## PC2          0.10634    0.08949   1.188  0.24208
## PC3         -0.05795    0.10934  -0.530  0.59918
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for gaussian family taken to be 1.434127)
##
##      Null deviance: 69.363  on 41  degrees of freedom
## Residual deviance: 54.497  on 38  degrees of freedom
## AIC: 140.13
##
## Number of Fisher Scoring iterations: 2
r.p.tam.glm<-glm(p.TAM~PC1+PC2+PC3, data=reach, family="binomial")
summary(r.p.tam.glm)

##
## Call:
## glm(formula = p.TAM ~ PC1 + PC2 + PC3, family = "binomial", data = reach)
##
## Deviance Residuals:
##      Min       1Q   Median       3Q      Max
## -1.7358  -1.2681   0.7601   0.8739   1.2453
##
## Coefficients:
##              Estimate Std. Error z value Pr(>|z|)
## (Intercept)  0.73545    0.34421   2.137  0.0326 *
## PC1          0.09223    0.14663   0.629  0.5293
## PC2          0.11422    0.16897   0.676  0.4991
## PC3         -0.30266    0.21264  -1.423  0.1546
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for binomial family taken to be 1)
##
##      Null deviance: 53.467  on 41  degrees of freedom
## Residual deviance: 50.270  on 38  degrees of freedom
```

```

## AIC: 58.27
##
## Number of Fisher Scoring iterations: 4
r.tam.glm<-glm(TAM~PC1+PC2+PC3, data=reach)
summary(r.tam.glm)

##
## Call:
## glm(formula = TAM ~ PC1 + PC2 + PC3, data = reach)
##
## Deviance Residuals:
##      Min       1Q   Median       3Q      Max
## -12.344   -3.251   -1.789    1.620   39.693
##
## Coefficients:
##              Estimate Std. Error t value Pr(>|t|)
## (Intercept)   3.9785     1.2848   3.097 0.00367 **
## PC1           0.9957     0.5018   1.984 0.05447 .
## PC2           0.3825     0.6222   0.615 0.54238
## PC3           0.3544     0.7602   0.466 0.64378
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for gaussian family taken to be 69.3289)
##
##      Null deviance: 2948.8  on 41  degrees of freedom
## Residual deviance: 2634.5  on 38  degrees of freedom
## AIC: 303.02
##
## Number of Fisher Scoring iterations: 2
r.log.tam.glm<-glm(log(TAM+0.00001)~PC1+PC2+PC3, data=reach)
summary(r.log.tam.glm)

##
## Call:
## glm(formula = log(TAM + 1e-05) ~ PC1 + PC2 + PC3, data = reach)
##
## Deviance Residuals:
##      Min       1Q   Median       3Q      Max
##  -9.702   -6.654    2.851    4.018    6.707
##
## Coefficients:
##              Estimate Std. Error t value Pr(>|t|)
## (Intercept)  -3.4370     0.9120  -3.769 0.000557 ***
## PC1           0.3985     0.3562   1.119 0.270279
## PC2           0.3307     0.4417   0.749 0.458589
## PC3          -0.6849     0.5396  -1.269 0.212100
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for gaussian family taken to be 34.93458)
##
##      Null deviance: 1447.1  on 41  degrees of freedom

```

```
## Residual deviance: 1327.5 on 38 degrees of freedom
## AIC: 274.23
##
## Number of Fisher Scoring iterations: 2
```

```
r.p.tar.glm<-glm(p.TAR~PC1+PC2+PC3, data=reach, family="binomial")
summary(r.p.tar.glm)
```

```
##
## Call:
## glm(formula = p.TAR ~ PC1 + PC2 + PC3, family = "binomial", data = reach)
##
## Deviance Residuals:
##      Min       1Q   Median       3Q      Max
## -1.8308  -0.7637  -0.3839   0.9686   2.2445
##
## Coefficients:
##              Estimate Std. Error z value Pr(>|z|)
## (Intercept)  -1.1141     0.5261  -2.118  0.03421 *
## PC1           0.1992     0.2207   0.903  0.36670
## PC2          -0.7662     0.2922  -2.622  0.00875 **
## PC3          -0.6633     0.4834  -1.372  0.17003
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for binomial family taken to be 1)
##
##      Null deviance: 54.748 on 41 degrees of freedom
## Residual deviance: 42.257 on 38 degrees of freedom
## AIC: 50.257
##
## Number of Fisher Scoring iterations: 6
```

```
r.tar.glm<-glm(TAR~PC1+PC2+PC3, data=reach)
summary(r.tar.glm)
```

```
##
## Call:
## glm(formula = TAR ~ PC1 + PC2 + PC3, data = reach)
##
## Deviance Residuals:
##      Min       1Q   Median       3Q      Max
## -2.0393  -0.8905  -0.4877   0.1706  13.9396
##
## Coefficients:
##              Estimate Std. Error t value Pr(>|t|)
## (Intercept)  0.642742   0.392217   1.639   0.110
## PC1          0.204868   0.153183   1.337   0.189
## PC2          0.002313   0.189950   0.012   0.990
## PC3          0.193184   0.232069   0.832   0.410
##
## (Dispersion parameter for gaussian family taken to be 6.461028)
##
##      Null deviance: 261.55 on 41 degrees of freedom
## Residual deviance: 245.52 on 38 degrees of freedom
```

```
## AIC: 203.35
##
## Number of Fisher Scoring iterations: 2
r.log.tar.glm<-glm(log(TAR+0.00001)~PC1+PC2+PC3, data=reach)
summary(r.log.tar.glm)

##
## Call:
## glm(formula = log(TAR + 1e-05) ~ PC1 + PC2 + PC3, data = reach)
##
## Deviance Residuals:
##      Min       1Q   Median       3Q      Max
## -7.8960  -4.0011  -0.9523   3.9675  11.6834
##
## Coefficients:
##              Estimate Std. Error t value Pr(>|t|)
## (Intercept)  -7.7087     0.7528 -10.241 1.76e-12 ***
## PC1           0.1362     0.2940   0.463  0.64590
## PC2          -1.0812     0.3646  -2.966  0.00519 **
## PC3          -0.2874     0.4454  -0.645  0.52270
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for gaussian family taken to be 23.7996)
##
##      Null deviance: 1128.75  on 41  degrees of freedom
## Residual deviance:  904.38  on 38  degrees of freedom
## AIC: 258.11
##
## Number of Fisher Scoring iterations: 2
```

The first three principal components (PC) explained 45.192 % of the total variance (PC1 21.664 %; PC2 14.089%, PC3 9.439%).

We tested whether local characteristics influenced the presence-absence of each species by fitting a logistic regression using Generalized Linear Models, and found no significant influence of either PCs on presence-absence for rainbow trout and brown trout, while PC2 (loaded mainly by water quality and slope variables) had a significant influence on presence of brook trout (z-value=-2.62, p-value=0.009). We then tested if reach variables influence relative abundances (either absolute values or their logarithms) and found a significant relation between PC1 (loaded mainly by channel morphology and water quality variables) and rainbow trout abundances (absolute – $t=3.86$, $p=0.0004$ and logarithms values – $t=2.94$, $p=0.0055$), but no significant influence on brown trout. We found significant influence of PC2 on the logarithm of brook trout abundance (t -value=-2.97, $p=0.0052$) but not on the absolute values. In summary, our regression analysis showed that the influence of local traits varies across all three salmonid species.

Discussion

One of the most pervasive concepts in the study of community assembly is the metaphor of the environmental filter, which refers to abiotic factors that prevent the establishment or persistence of species in a particular location. However, this concept has been criticized because the evidence used in many studies to assess environmental filtering is insufficient to distinguish filtering from the evolutionary outcome of historical biotic interactions (Kraft et al. 2015). In our work we took advantage of the relatively recent and well-studied history of salmonid introductions to evaluate if non-native species show different patterns of association with abiotic factors at different spatial scales of the filter.

Successful establishment of introduced salmonid species can depend on both biotic resistance (by the native community of organisms) and environmental resistance (habitat suitability), as well as chance events (Moyle & Light, 1996, Karr et al., 1987, Fausch, 2007). The success of its dispersion has been well studied in several environments such as New Zealand (McDowall, 2003), Europe (Korsu, Huusko & Muotka, 2008) and Chile (Arismendi et al., 2014, 2019, Habit, 2015). When salmonids were introduced to Patagonian waters in 1904 (Baigún & Quirós, 1985), they found almost no biotic resistance for the invasion and achieved a wide distribution throughout the region (Pascual et al. 2007). We indeed found widespread presence of salmonid species and almost total absence of native species in our study area. Thus, the only expected source of current biotic interference would be interspecific interaction between the salmonid species themselves. However, the results of our contingency analysis on species distribution does not support a scenario in which any of the species is affecting the distribution of the other species. This suggests that the streams in our study area have not reached carrying capacity for salmonids. Alternatively, salmonid species might be partitioning the riverine habitats to minimize niche overlap, as reported in other parts of the world (Bozek & Hubert, 1992, Reeves, Bisson & Dambacher, 1998, Fausch, 2008, Marchetti et al., 2011).

Interspecific interference among salmonid species has been proposed in previous studies in this region (Juncos, Beauchamp & Vigliano, 2013, Arismendi et al., 2014); we found however no evidence for it. Thus, we can assume that interference has played only a minor role in determining current fish distribution in the region. Instead, current patterns of presence and abundance of salmonids are best explained as the product of environmental filters. Indeed, reasons for the successful invasion reported from southern Chile has been related in part to the excellent abiotic conditions they found in the region (Pascual et al., 2005, Habit et al., 2012, Habit et al., 2015).

Biological invasions are inherently complex. A successful invader must survive a series of events: transport to the invasion site, initial establishment, spread to a broad area, and then integration into the existing biotic community (Moyle & Light, 1996, Kolar & Lodge, 2001). Not surprisingly, most introduced species fail to become established and reach invasive status (Moyle and Light 1996, Arismendi et al., 2014). Our results suggest that in North Patagonia, biotic resistance from native fish species seems to have had little or no influence on the invasion process by introduced salmonid species, and that success of invaders in the face of low odds is related, as we previously suggested, mostly with the presence of favorable environments, such as flow regime (conditioned for the rainfall gradient) and food availability (Lallement et al. 2020).

In contrast to other reports (Marchetti, Moyle & Levine, 2004, Stanfield, Scott & Borwick, 2006), we saw no evidence that presence/absence patterns of salmonid distribution were strongly driven by landscape variables, except for those basins with environmental barriers. However, when analyzing responses of relative abundances (CPUEN), the influence of climatic and geomorphological variables (e.g., precipitation and relief) became more evident. These two types of factors have been mentioned in other systems as determinants of salmonid distribution (Stanfield et al., 2006, Warren, Dunbar & Smith, 2015): rainfall and geology have a direct influence on stream discharge and are thus determinant during early development of salmonid life cycles (Heggenes & Traaen, 1988, Nehring & Anderson, 1993).

Landscape characteristics (e.g., general slope of the valley and geomorphological aspects) determine local river section traits such as substrate composition, pool dimensions and refuge availability, which in turn strongly correlate with the structure and distribution of the assemblages of fish in a basin (Fischer & Paukert, 2008, Rowe, Pierce & Wilton, 2009). For our study area, we found evidence that some local traits modulate rainbow trout abundance but do not explain abundances of brown trout and brook trout, or the presence-absence patterns for all three salmonid species. Low abundances for a species could be causing diminished statistical power to detect the influence of environmental variables; this could be affecting our results for brook trout. Differential abundances are nonetheless likely to result from differential responses to the same environment by each species. Thus, the layered influence of environmental filters was reflected in a weak but differential influence of local traits on abundance of each salmonid species.

Habitat suitability for salmonids is often controlled by local variables as temperature regime (Rahel & Nibbelink, 1999, Harig & Fausch, 2002, Coleman & Fausch, 2007), flow regime (Strange & Foin, 1999, Fausch et al., 2001), stream size (Rahel & Nibbelink, 1999) and habitat factors correlated with stream gradient and channel geomorphology (Fausch, 1989, Montgomery et al., 1999). Due to the steep precipitation

gradient in our study area, several streams originate in wooded areas and cross wide valleys where shrubby vegetation typical of arid steppes predominates. Shrubby riverbanks result in higher solar irradiation and air temperatures, favoring higher primary production of the periphyton and sustaining an important biomass of macroinvertebrates (Miserendino, 2007, Modenutti et al., 2010). It is these streams where we found higher fish abundances.

A hierarchical perspective of stream systems, whereby properties at the site level are constrained by processes occurring in the catchment, provides a useful analytical framework (Vannote et al., 1980, Frissell et al., 1986, Imhol, Fitzgibbon & Annable, 1996). Previous predictive modeling studies have indicated that landscape-scale watershed characteristics are better to explain fish distributions than reach-scale characteristics (Creque, Rutherford & Zorn, 2005, Frimpong et al., 2005). However, this study did not find that watershed-scale variables were significantly better at explaining or predicting fish distributions in North Patagonia. The most likely explanation for this absence of significance can be the lack of habitat saturation by fishes due to temporal variability in fish distributions, unmeasured explanatory (reach- and watershed-scale characteristics) variables in the data set or insufficient sample size. As Stanfield and Gibson (2006), we do not contend that landscape variables are important for salmonids, but suggest that landscape traits condition the range of geomorphological variation inside a watershed that ultimately defines the current densities in a section as we previously observed (Lallement et al. 2020). Results from this study suggest further information is needed to understand how the variability of spatial scale affects the distribution of fishes in streams of Patagonia.

Conservation of stream habitats and their biota requires an understanding of how environmental factors, both natural and human-influenced, structure aquatic assemblages across different scales of space and time (Fausch, Baxter & Murakami, 2010, Grossman, Warnell & Sabo, 2010). Many previous studies have focused on the importance of variables at the local habitat scale or across relatively small study regions. Although not explored in this study, distributions of fishes are variable and may be regulated by seasonal movements and the frequency and duration of stochastic flow cycles. In any case, it is important to bear in mind that the results obtained in regions with different histories of colonization and introduction are not necessarily extrapolated. By including a comprehensive suite of variables at multiple spatial scales in a large region, our study contributes to understanding how these environmental factors may interact to structure invasive fish communities. Moreover, considering the pristine (or near-pristine) condition of the streams sampled here, the relationships observed between fishes and landscape variables can be used as a reference for further studies addressing the effects of human modifications on aquatic biodiversity of North Patagonia.

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Data Availability Statement

The data and code with the analyses supporting our findings are available at https://github.com/ezattara/patagonian_salmonid_distribution

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Session Information

`sessionInfo()`

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## R version 4.0.2 (2020-06-22)
## Platform: x86_64-w64-mingw32/x64 (64-bit)
## Running under: Windows 10 x64 (build 19041)
##
## Matrix products: default
##
## locale:
## [1] LC_COLLATE=English_United States.1252
## [2] LC_CTYPE=English_United States.1252
## [3] LC_MONETARY=English_United States.1252
## [4] LC_NUMERIC=C
## [5] LC_TIME=English_United States.1252
##
## attached base packages:
## [1] grid      stats      graphics  grDevices  utils      datasets  methods
## [8] base
##
## other attached packages:
## [1] factoextra_1.0.7      Hmisc_4.5-0           Formula_1.2-4
## [4] survival_3.2-12       lattice_0.20-44        VennDiagram_1.6.20
## [7] futile.logger_1.4.3    gt_0.3.1              forcats_0.5.1
## [10] stringr_1.4.0          dplyr_1.0.7           purrr_0.3.4
## [13] readr_2.0.1           tidyr_1.1.3           tibble_3.1.3
## [16] ggplot2_3.3.5         tidyverse_1.3.1
##
## loaded via a namespace (and not attached):
## [1] fs_1.5.0              lubridate_1.7.10      bit64_4.0.5
## [4] RColorBrewer_1.1-2    httr_1.4.2            tools_4.0.2
## [7] backports_1.2.1       utf8_1.2.2            R6_2.5.0
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## [13] nnet_7.3-16	withr_2.4.2	tidyselect_1.1.1
## [16] gridExtra_2.3	curl_4.3.2	bit_4.0.4
## [19] compiler_4.0.2	cli_3.0.1	rvest_1.0.1
## [22] formatR_1.11	htmlTable_2.2.1	xml2_1.3.2
## [25] labeling_0.4.2	scales_1.1.1	checkmate_2.0.0
## [28] digest_0.6.27	foreign_0.8-81	rmarkdown_2.10
## [31] rio_0.5.27	base64enc_0.1-4	jpeg_0.1-9
## [34] pkgconfig_2.0.3	htmltools_0.5.1.1	highr_0.9
## [37] dbplyr_2.1.1	htmlwidgets_1.5.3	rlang_0.4.11
## [40] readxl_1.3.1	rstudioapi_0.13	farver_2.1.0
## [43] generics_0.1.0	jsonlite_1.7.2	vroom_1.5.4
## [46] zip_2.2.0	car_3.0-11	magrittr_2.0.1
## [49] Matrix_1.3-4	Rcpp_1.0.7	munsell_0.5.0
## [52] fansi_0.5.0	abind_1.4-7	lifecycle_1.0.0
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