

# Top predator fish assemblages in Northern Patagonia, Argentina. What factors regulate their patterns of distribution and abundance?

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**Abstract** According to assemblage theory, three factors regulate fish biogeography: restriction of dispersion, environmental restrictions and biotic interactions. The first two factors act on a regional scale and delimit the area of action of the third, which operates on a local scale. Salmonid introductions began in Patagonia in 1904, and this has led to a restructuring of trophic webs and an increase in the number of top predators. This situation allowed us to evaluate, in a natural setting, how communities are formed on different geographic scales. We studied two large basins in Patagonia, situated close to each other but with different assemblages of top predatory fish. We hypothesized that differences in the structuring of the top predator assemblages between and within the basins are due to 1) environmental factors and dispersion processes facilitated by connectivity on a regional scale; and 2) biotic interaction (internal dynamics) between native perch and salmonids, the former acting as a modulator of the top predator assemblages on a local scale. To test these hypotheses, we analysed the top predator assemblages of 16 lakes and one reservoir, as well as their environmental characteristics. We performed a cluster analysis and related the resulting assembly groups to environmental factors by means of a tree model. We also analysed fish diets, using a similarities test to study biotic interactions. On regional and local scales, water basin, degree of connectivity, area, temperature and Zoogeographic integrity coefficient (ZIC) were important factors in the structuring of top predator assemblages. On a local scale, creole perch modulates the salmonid populations through feeding and the consequent distribution of resources. Our work showed that the structure of top predator assemblages was determined by a combination of local and regional factors acting in synergy, as postulated by the assemblage theory.

**Key words:** connectivity, environmental factors, exotic species, native species, salmonids.

## INTRODUCTION

A central topic in community ecology is whether assemblages are a stochastic or deterministic set of species. If they were a stochastic set, community composition would depend only on random or historical effects. On the other hand, if they were deterministic, it would depend on general ecological principles (Colorado-Zuluaga 2015). The theory of species assemblage attempts to explain how ecological processes shape the biological diversity of the earth and how complex communities assemble over time from a regional group of species (Booth & Swanton 2002). Belya and Lancaster (1999) proposed three determining factors that operate on community assemblages: restriction of dispersion, environmental restrictions and internal dynamics (biotic interactions). 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 2002).

The biogeography of freshwater fish, regulated by the three aforementioned factors (Olden *et al.* 2008), has been reorganized drastically on repeated occasions by the introduction of new species (Jackson *et al.* 2001; Olden *et al.* 2008, 2010; Weiher *et al.* 2011). The consequences of these introductions differ according to the trophic level of the introduced species (Olden *et al.* 2010). Salmonids, top predators, have been widely introduced in the world, modifying trophic chains by predation and competition (Crowl *et al.* 1992; Townsend 1996; Mc Dowall 2003; McDowall 2006; Soto *et al.* 2006; Macchi *et al.* 2007; Habit *et al.* 2010; Correa *et al.* 2012), changing the distribution and abundance of native species (McDowall 2006) and reorganizing the structure of communities. In Patagonia in particular, the biogeography of native fish has been marked by the

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Accepted for publication March 2018.

Andean uplift, marine incursions and glaciations (Moyle & Cech 1982; Nelson 1994; Menni 2004; Hubert & Renno 2006). After the glacial retreat during the Pleistocene, the ability of Patagonian fish to colonize post-glacial water bodies determined their present distribution (Cussac *et al.* 2004; Ruzzante *et al.* 2006), clearly constrained by climate and, in particular, by temperature. Nevertheless, the introduction of salmonids, which began in 1904, was the most recent modulating event that occurred in the region in terms of community structuring, increasing the number of top predators (Macchi *et al.* 2008; Macchi & Vigliano 2014). All these events resulted in a group of 26 species, including 15 native species, which are organized in fish communities that vary between and within each basin. All these communities are characterized by a low number of species and short trophic chains, where the mayor native predator is *Percichthys trucha* (creole perch) (Macchi *et al.* 1999; Pascual *et al.* 2002; Baigún & Ferriz 2003; Aigo *et al.* 2008).

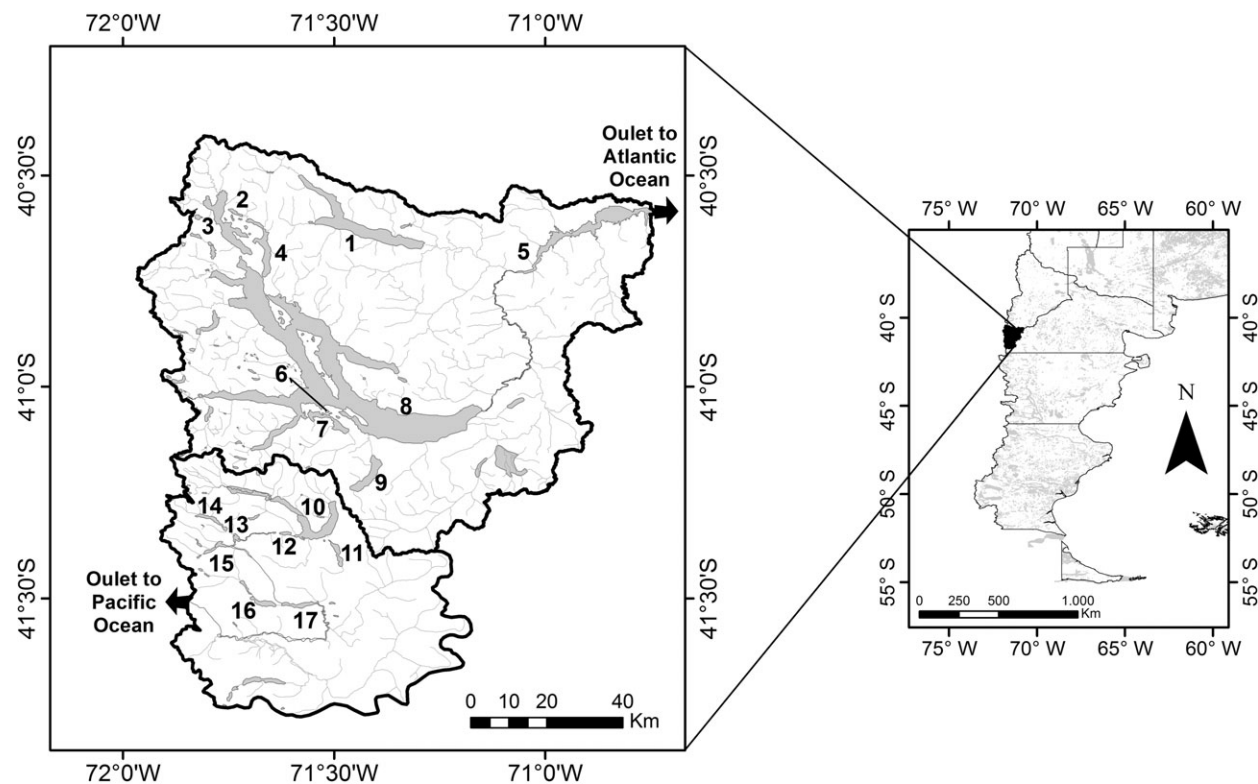
Considering the three factors mentioned in the species assemblage theory, and the current situation of the top predator fish communities of Argentine Patagonia, we hypothesized that differences in the structuring of the top predator assemblages between and within the basins are due to (i) environmental

factors and dispersion processes facilitated by connectivity on a regional scale; and (ii) biotic interaction (internal dynamics) between the native perch and salmonids, the former species acting as modulator of the top predator assemblages on local scale. To evaluate the influence of these factors at both scales, we took advantage of the existence of two basins due to their origins, geological history and different degree of connectivity, present water bodies with different fish assemblages (mainly presence-absence of the Creole perch).

## METHODS

### Study area

For the present study, we considered the Limay and Manso River Basins in Northern Argentine Patagonia. These basins, which drain to the Atlantic and Pacific oceans respectively, were selected because they have different composition of top predator assemblages, are spatially close, show a common spatial environmental gradient with large topographic differences and landscapes and have different degrees of connectivity between water bodies. The basins are located between 40°63'S and 41°30'S, and 71° 70'W and 71° 00'W, respectively, (Fig. 1) and include 16 post-glacial lakes and one reservoir. The water bodies sampled



**Fig. 1.** Location of study lakes. Limay River basin: Trafal (1); Espejo Chico (2); Espejo (3); Correntoso (4); Alicura (5); Morenito (6); Moreno (7); Nahuel Huapi (8); Gutiérrez (9) Manso River basin: Mascardi (10); Guillermo (11); Los Moscos (12); Hess (13); Fonck (14); Roca (15); Martin (16); Steffen (17).

from the Limay River basin were: Traful, Espejo Chico, Espejo, Correntoso, Morenito, Moreno, Nahuel Huapi and Gutiérrez lakes and the Alicura reservoir. The lakes sampled from the Manso River basin were: Mascardi, Guillermo, Los Moscos, Hess, Fonck, Roca, Martin and Steffen. Classified as oligotrophic (Pedrozo *et al.* 1993), these lakes vary morphometrically, their chemical characteristics lying within the ranges of typical Andean Patagonian lakes (Diaz *et al.* 2007). Climate in the region is cold temperate, and fall/winter precipitation varies from 500 to 2700 mm year<sup>-1</sup> (Modenutti *et al.* 1998; Paruelo *et al.* 1998).

The Limay River basin (Fig. 1) in Neuquén and Río Negro provinces covers 63 700 km<sup>2</sup> up to the river's confluence with the Neuquén River, where it becomes the Negro River, which drains into the Atlantic Ocean. The upper drainage basin of Limay River comprises a complex hydrological network of innumerable streams that originate mostly in the eastern slopes of the Andean range and form major rivers and shallow and deep lakes of glacial origin. The Limay River originates in Nahuel Huapi Lake at an altitude of 769 m.a.s.l., descending 500 m to its confluence with the Neuquén River.

The Nahuel Huapi Lake serves as the main headwater collector of the Limay River basin, as well as intermediate lakes and an undetermined number of small lakes and ponds. Major natural barriers such as waterfalls exist only in some headwater lake drainages, while five hydroelectric dams have altered the lower reaches of the Limay River. In general, the marked hydrological regime is characterized by two peak floods, one caused by autumn rains and the other by spring snowmelt. Precipitation amounts to around 3000 mm per year in the west and 600 mm per year 60 km towards the east, thus determining a marked climatic gradient. This strong precipitation gradient influences the vegetation, characterized by dense *Nothofagus* sp., *Austrocedrus chilensis* and *Chusquea culeou* temperate forests in the west, and the Patagonian xerophile-shrubland steppe in the east.

The Manso River basin (Fig. 1) covers 2800 km<sup>2</sup> in Río Negro province. The river is divided into upper, middle and lower basins due to the complexity of its course, consisting of stretches of river interspersed with various lake subdrainages. The Upper Manso River originates in the Ventisquero Negro glacier on Mount Tronador, and drains into Mascardi Lake. The headwater Guillermo Lake also drains into Mascardi Lake through a stream whose connectivity was interrupted in the 1940s by the construction of a small hydroelectric dam. The Middle Manso River extends westward from the outlet of Mascardi Lake, forming Los Moscos Lake. This lake drains into a stretch of river that flows into Hess Lake, which in turn collects the water from the headwater Fonck Lake. From the outlet of Hess Lake, another stretch of the river going southwards collects the waters of the headwater Roca Lake and then flows southeasterly for 20 km before draining into Steffen Lake. This lake also receives waters from the headwater Martin Lake and drains on its Eastern shore, giving rise to the Lower Manso basin which continues in a southeasterly direction until the point of confluence with the Villegas River, where it turns sharply west and after 34 km crosses the Andes and drains into the Pacific Ocean. Two annual peak floods define the hydrological regime along all Manso River

subbasins, one caused by autumn precipitations and the other by spring snowmelt. Precipitation amounts to around 1500 mm per year (De Aparicio & Difrieri 1958; Drago 1974). *Nothofagus* sp., *Fitzroya cupresoides* and *Austrocedrus chilensis* (Dimitri 1972) dominate the basin's vegetation.

### Fish collection and environmental characteristics

We selected the fish data collection methods and environmental variables due to their importance in the structuring of fish assemblages (Naiman & Bilby 1998; Bain & Stevenson 1999). For this study, we used a subset of the data collected as part of an intensive fishing program carried out in the region during the years 1997–2009 (we used only the data collected during the austral summer). In all cases, fish were sampled with gill nets (60 m long; 2 m high). Each gill net consisted of six 10-m-long panels with randomly located bar mesh sizes (15, 20, 30, 50, 60 and 70 mm), placed at 2, 10, 30 and 50 m bottom depths, following Vigliano *et al.* (1999). Gillnets were set parallel to the shore and left in place overnight. We considered five top predator species (Juncos *et al.* 2011): rainbow trout *Oncorhynchus mykiss*, brown trout *Salmo trutta*, brook trout *S. fontinalis* and Atlantic salmon *S. salar*, which coexist with creole perch, *Percichthys trucha*.

For all the species of each lake, we estimated relative abundance as catch per unit effort (CPUE), effort being defined as the product of soak time multiplied by the total area of each gill net used, and standardized to 15 h and 100 m<sup>2</sup> of gill net.

To test whether the differences in the top predator assemblages were due to environmental characteristics, we recorded the following variables at each site: water temperature (WT), Secchi Disc Transparency (m) and maximum depth (Z; m). We obtained soluble reactive phosphorus (PRS) data from the literature (Pedrozo *et al.* 1993; Diaz *et al.* 2007). Using Google Earth™ maps and field observations, we calculated lake altitude (m.a.s.l) and area (Km<sup>2</sup>). We established coastline development (km) and aquatic vegetation as 1: cover <10 % of coastline perimeter; 2: cover from 10 to 30% of coastline perimeter and 3: cover over 30 % of coastline perimeter. We established connectivity range as 1: headwater lake; 2: intermediate lake (lakes which the river flows into and out of) and 3: lake connected to two or more lakes. Zoogeographic integrity coefficient (ZIC) refers to the ratio between the number of native species and the total number of species recorded. The ZIC index is an indicator of the degree to which fish populations have been invaded by introduced species. We extracted mean summer air temperatures (MSAT) and precipitation data from the WorldClim global climate database ([www.worldclim.org](http://www.worldclim.org)).

To test whether trophic interactions between species determine top predator composition assemblages, we examined the stomach contents of all fish. We identified prey items to the lowest possible taxon level under a dissecting microscope. For food category (i), we determined the weight contribution as  $P = P_i * P_t^{-1}$ , where  $P_i$  is the total wet weight of the item's prey and  $P_t$  is the total prey wet weight. Then, we grouped these data into four categories for simplicity: benthic food (insect larvae and pupae,

aquatic adult insects, molluscs, Crustacea, Hirudinea, Oligochaeta and Acari); fish (*Galaxias maculatus* (small puyen), *G. platei* (big puyen), *P. trucha* and salmonid species); allochthonous food (terrestrial insects and rodents) and zooplankton.

### Statistical analysis

We performed a Mann–Whitney U test (*MW*) to compare the collective relative abundance of top predator species, the relative abundance of salmonid species, and of salmonids plus creole perch between the basins. Relative abundance was expressed as a CPUE proportion.

To determine whether each species fulfils the same trophic role in different lakes, we analysed the weight proportion of each prey category (grouped as mentioned above) for each top predator species and lake, using the statistical package PRIMER. We square root transformed the weight value proportions, and ran a hierarchical agglomerative cluster analysis to define lake groups with top predators with similar diets, using the Bray–Curtis coefficient of similarity (multiplied by 100) based on a similarity matrix and the group-average linking method (Clarke & Warwick 2001). We applied a similarity profile (SIMPROF) test ( $\alpha = 0.05$ ; 999 permutations) to distinguish significant groups in the cluster analysis, in order to test the null hypothesis of no meaningful structure within samples (Clarke *et al.* 2008). We performed an ANOSIM (analysis of similarities) test to search for differences in diet between possible lake groups. This permutation test analyses differences between replicates within groups, in contrast to differences between groups, computing an R statistic under the null hypothesis ( $H_0$ ): there are no differences between groups. R may fall between  $-1$  and  $1$ ; R is close to 0 if the null hypothesis is true and  $R = |1|$  if all replicates within groups are more similar to each other than any replicates from different groups. We assessed the importance of prey

category in different trophic groups by the SIMPER (percentage similarity analysis) procedure, which determines the prey categories responsible for the resulting grouping in terms of Bray–Curtis mean similarity.

We performed a hierarchical cluster analysis to uncover clusters of lakes with similar top predator relative abundance proportions. Following this, we performed a classification and regression tree analysis (Breiman *et al.* 1984; Therneau & Atkinson 2011) to characterize lake groups in terms of their geographical traits and top predator assemblages. The complete linkage based on Euclidean distance was used to measure intercluster dissimilarity (Everitt 2007). For the regression tree analysis, the response variable considered was a categorical variable indicating the cluster where lakes were located in the first stage of the analysis, and predictor variables were the biotic and abiotic factors described above. In the first step of the process, the algorithm divided the entire set of lakes into two groups according to a question involving one of the explanatory variables. The resulting model can be represented as a binary tree whose leaves or terminal nodes correspond to the partition of the data. For each terminal node, we reported the predicted cluster and proportions of top predator fish species from the lakes. Statistical analyses were carried out in two stages using R 3.1.1 software.

## RESULTS

### Fish species and top predators present in the Limay and Manso Basins

We found differences in the top predator species present in each lake and in their relative abundances (CPUE) between lakes within a basin (Table 1). The Limay Basin presented nine species, five of which are

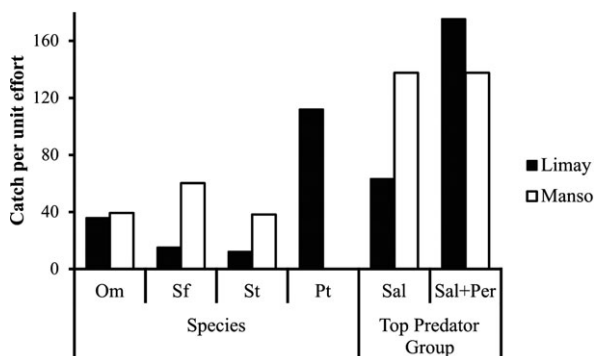
**Table 1.** Top predator species relative abundance (CPUE) and native species presence in lakes (G.m: *Galaxias maculatus*, G.p: *Galaxias platei*; O.v: *Olivachthys viedmensis*; O.h: *Odontesthes hatcheri*).

Lake	Basin	<i>Oncorhynchus mykiss</i>	<i>Salvelinus fontinalis</i>	<i>Salmo trutta</i>	<i>Salmo salar</i>	<i>Perchichthys trucha</i>	Other species
Trafal	Limay	1,69	0,46	0,57	0,11	–	<i>G.m, G.p, O.v</i>
Espejo Chico	Limay	0,65	–	0,16	–	1,64	<i>G.m, G.p</i>
Espejo	Limay	4,41	6,72	1,79	–	4,65	<i>G.m, G.p, O.v</i>
Correntoso	Limay	1,62	0,12	0,25	–	1,25	<i>G.m, G.p, O.v</i>
Alicura	Limay	10,69	–	7,70	0,59	75,86	<i>G.m, G.p, O.v, O.h</i>
Morenito	Limay	–	–	–	–	14,25	<i>G.m, O.h</i>
Nahuel Huapi	Limay	0,98	0,07	0,66	–	1,07	<i>G.m, G.p, O.v, O.h</i>
Moreno	Limay	4,54	3,63	0,47	–	12,63	<i>G.m, G.p, O.v, O.h</i>
Gutierrez	Limay	12,07	4,28	1,17	–	–	<i>G.m, G.p, O.v</i>
Fonck	Manso	7,41	16,85	1,50	–	–	<i>G.m, G.p</i>
Hess	Manso	4,21	0,76	4,00	–	–	<i>G.m</i>
Roca	Manso	3,17	6,59	0,79	–	–	<i>G.m</i>
Mascardi	Manso	4,90	5,17	6,97	–	–	<i>G.m, G.p</i>
Martin	Manso	5,05	1,77	7,32	–	–	<i>G.m, G.p</i>
Los moscos	Manso	5,08	2,97	2,96	–	–	<i>G.m, G.p</i>
Guillermo	Manso	6,62	25,34	–	–	–	<i>G.m</i>
Steffen	Manso	2,92	0,73	14,62	–	–	<i>G.m, G.p</i>

considered in this study as top predators (rainbow trout, brown trout, brook trout, Atlantic salmon and native creole perch). Five species were present in the Manso River Basin, three of which are top predators (rainbow, brown and brook trout). The high relative abundance of *Percichthys trucha* in the lakes of the Limay basin and its absence in the Manso basin was an important difference. Nevertheless, when we considered total relative abundance of overall top predators (i.e. salmonids + creole perch), we found no significant differences between basins (*MW*;  $N = 17$ ;  $P = 0.56$ ; Fig. 2). In the Manso River basin, the total relative abundance of salmonids was significantly higher than that recorded for the Limay River basin (*MW*;  $N = 17$ ;  $P = 0.02$ ). When salmonid relative abundance was compared, only brook trout relative abundance was significantly different between basins, being lower in the Limay River Basin (*MW*;  $N = 17$ ;  $P = 0.009$ ). This was not the case for rainbow trout (*MW*;  $N = 17$ ;  $P = 0.199$ ) or brown trout relative abundance (*MW*;  $N = 17$ ;  $P = 0.074$ ) between basins (Fig. 2). *Salmo salar* was found only in the Limay River Basin, and in very low numbers.

### Top predator assemblages

Hierarchical cluster analysis separated four significantly different groups at a cutoff distance of 1.1, based on the relative abundance proportions of the five top predators in the 17 water bodies studied (Fig. 3). Morenito, Alicura, Espejo Chico, Moreno, Correntoso and Nahuel Huapi Lakes, all belonging to Limay basin, formed Group A. A high proportion of creole perch characterized this group. Group B included only Steffen Lake, belonging to the Manso River Basin, and was characterized by a high proportion of brown trout. Espejo, Guillermo, Roca and



**Fig. 2.** Fish species abundance (catch per unit effort) in Limay and Manso River Basins. Fish species: *Oncorhynchus mykiss* (Om); *Salvelinus fontinalis* (Sf); *Salmo trutta* (St); *Percichthys trucha* (Pt). Top predator Groups: Salmonids (Sal); Salmonids and *P. trucha* (Sal+Per).

Fonck Lakes formed group C, characterized by a high proportion of brook trout. Finally, Gutiérrez, Traful, Hess, Martin, Mascardi and Los Moscos Lakes formed group D, characterized by a mixture of salmonids. Groups C and D were formed by lakes belonging to both river basins.

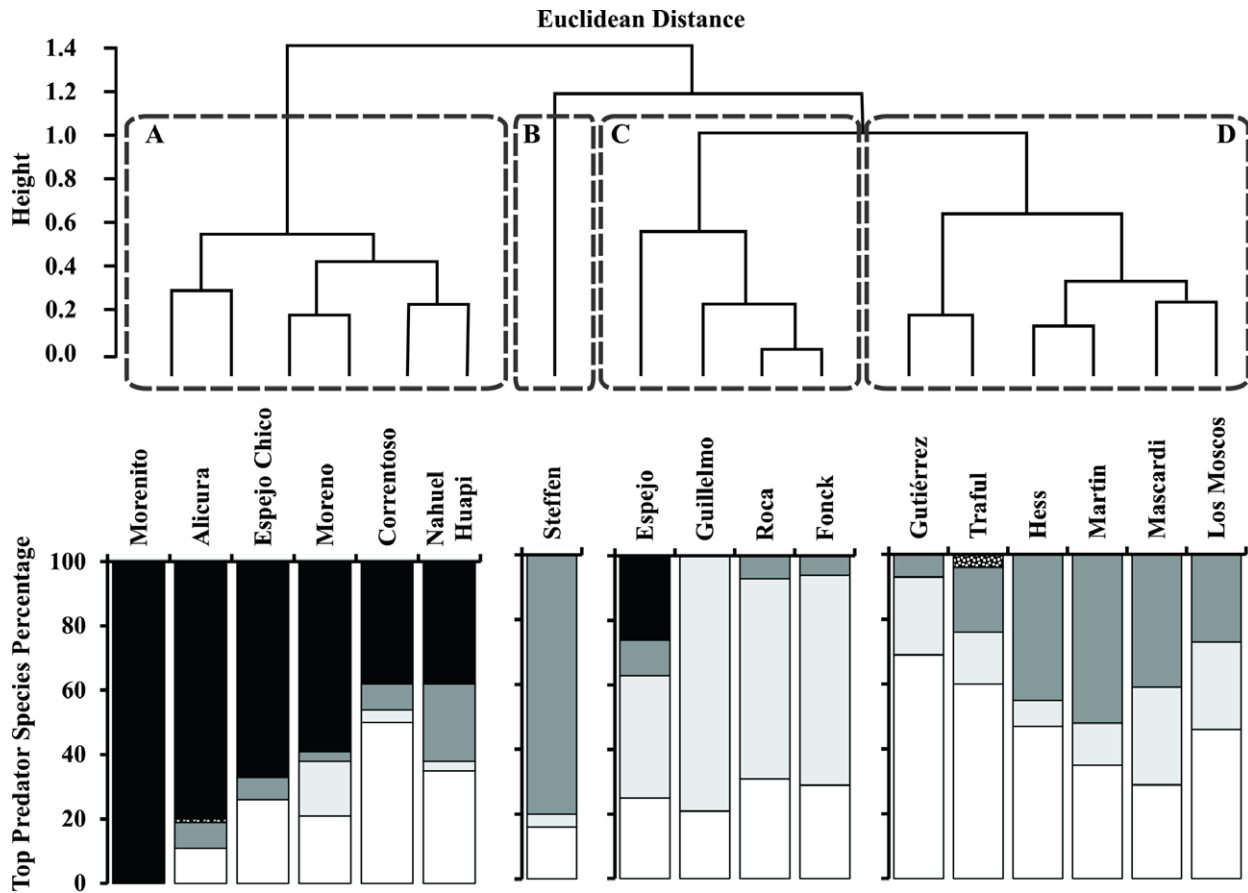
### Relationship between top predator assemblages and environmental factors

We used a classification tree analysis to identify the main abiotic and biotic characteristics associated with the lake groups defined by top predator proportions (Table 2, Fig. 4). Six predictor variables explained top predator assemblage: basin, connectivity range, lake area, ZIC, water temperature and average summer air temperature. The model correctly classified 82.35 % of top predator assemblages, all labelled as pure terminal nodes (Fig. 4). In the multivariate regression tree, the first predictor variable was basins (Limay vs. Manso). Within the Limay River Basin lake groups, the division was made according to connectivity range; header lakes were separated from lakes crossed by a river or connected by two or more lakes (Alicura, Correntoso, Espejo Chico, Moreno and Nahuel Huapi Lakes).

Headwater lakes were separated into those with higher ZIC values ( $>53.55$ ; Morenito and Espejo Lakes) and those with low ZIC values ( $<53.55$ ; Gutiérrez and Traful Lakes). In addition, lakes with higher ZIC were separated by summer water temperatures, into Morenito Lake ( $>18.7^{\circ}\text{C}$ ) and Espejo Lake ( $<18.7^{\circ}\text{C}$ ). The Manso River Basin lake groups were also divided according to connectivity range: Intermediate lakes or lakes connected to two or more lakes (Steffen, Hess; Mascardi and Los Moscos Lakes) were separated from headwater lakes (Guillermo, Roca, Fonck and Martin Lakes). Headwater lakes were separated by area: lakes with  $<7.5\text{ km}^2$  (Guillermo, Roca and Fonck) and lakes with a greater area (Martin Lake). Lakes with two and three ranges of connectivity were divided by MSAT into lakes with high average air temperatures ( $<13.6^{\circ}\text{C}$ ; Hess, Mascardi and Los Moscos Lakes) and those with lower than  $\geq 13.6^{\circ}\text{C}$  (Steffen Lake).

### Top predator diet

In all the lakes studied, the diet of all predator species was similar except for rainbow trout. Stomach content analysis revealed that top predators feed primarily upon benthic macroinvertebrates, fish, allochthonous and planktonic prey. Planktonic prey occurred only in fish samples from Alicura reservoir. The cluster analysis and SIMPROF test carried out



**Fig. 3.** Cluster analysis dendrogram based on Euclidean distance, showing lake groups (dashed boxes: A, B, C, D) of top predator fish assemblages (upper) and CPUE composition (%) of top predator species for each lake (lower). Species: *Percichthys trucha* (Pt, black); *Salmo salar* (Ss, dotted); *Salmo trutta* (St, dark grey); *Salvelinus fontinalis* (Sf, light grey); *Oncorhynchus mykiss* (Om, white).

for each species led to the identification of two significant diet groups in relation only to rainbow trout ( $\pi = 3.37$ ;  $P = 0.002$ ). For this species (Fig. 5a), two significant (ANOSIM;  $R = 0.777$ ;  $P = 0.001$ ) lake groups were recognized due to differences in diet. One group, which showed 86.94% similarity (SIMPER), included Moreno, Correntoso, Espejo and Nahuel Huapi lakes, associated with fish (58.96%) and benthic prey (30.58%). A second lake group was conformed by Alicura, Trafal, Espejo Chico, Gutiérrez, Mascardi, Los Moscos, Hess, Roca, Fonck, Steffen, Martín and Guillermo lakes (SIMPER Similarity 77.97%). This group was related through a fish diet of benthic prey (60.98%). In contrast, we did not observe dietary differences between lakes for brown trout (SIMPROF;  $\pi = 3.29$ ;  $P = 0.326$ ), brook trout (SIMPROF;  $\pi = 4.09$ ;  $P = 0.144$ ) or creole perch (SIMPROF;  $\pi = 0.72$ ;  $P = 0.824$ ) (Fig. 5b-d). Atlantic salmon was not considered in the analysis because it was caught only in Trafal Lake, where it consumed 71% fish and 29% allochthonous prey.

doi:10.1111/aec.12610

## DISCUSSION

On a regional scale and in accordance with our first hypothesis, the determining factors of the assemblies of top predators were basin, area, temperature and degree of connectivity between water bodies. On a local scale, and in line with our second hypothesis, top predator assemblages were modulated by the proportion of native and exotic species indicated by the zoogeographic index (ZIC). In the two water basins studied, the top predator assemblage differed between and within each basin, and the studied lakes could be divided into four groups according to the composition of their assemblages. Although it was not possible to associate these assemblies with a fixed combination of variables on a regional scale, it was possible to identify the main factors affecting the structure of the top predator assemblies. Watershed, connectivity, lake area and temperature acted as filters on a regional scale and ZIC on a local scale.

At a regional level, there were four factors that synergistically affected the conformation of the

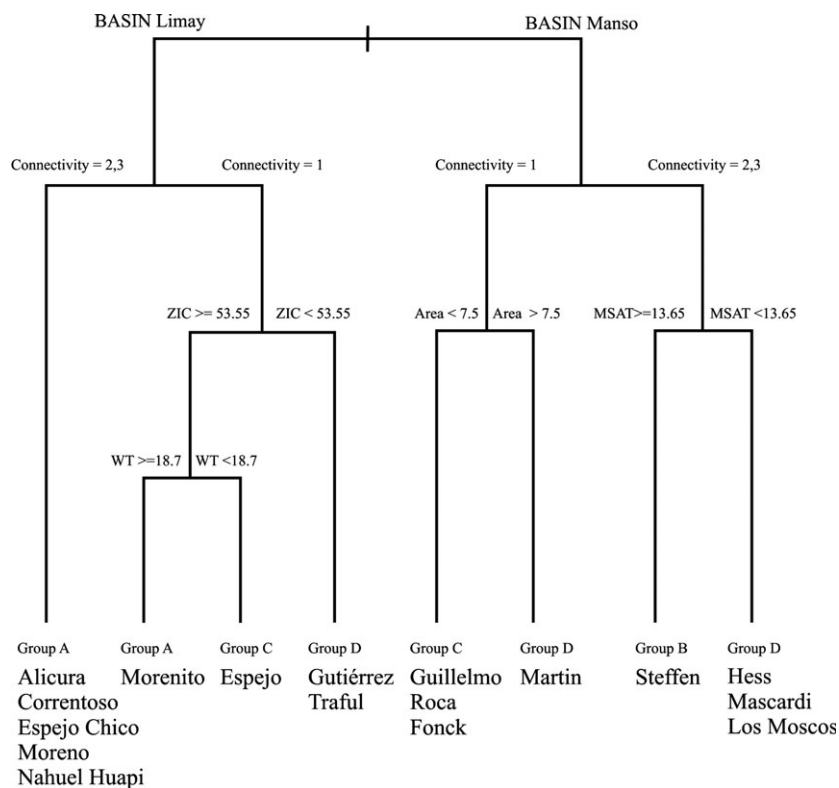
**Table 2.** Lake characteristics. Coastline development (CLD); Zoogeographic integrity coefficient (ZIC); Mean summer air temperatures (MSAT).

Basin	Lake	Latitude	Longitude	Altitude (m.a.s.l.)	Temperature (°C)	Area (km <sup>2</sup> )	Depth (m)	Connectivity range	Aquatic vegetation	CLD (km)	ZIC	MSAT (°C)	Secchi disc (m)	Top predator groups
Limap	Traful	-40.54	-71.50	805	12	78.8	339	1	1	2.91	50	12.8	15	D
	Espejo	-40.60	-71.70	788	13.7	0.4	100	2	3	2.05	60	13.8	15	A
	Chico													
	Espejo	-40.64	-71.70	790	16.6	38.8	245	1	2	3.29	57.1	13.8	16	C
	Correntoso	-40.66	-71.66	776	16	20.05	87.2	2	2	2.78	57.1	13.5	10	A
	Alicura	-40.66	-71.00	577	16.2	67.5	110	3	1	7.40	62.5	15.4	7	A
	Morenito	-41.03	-71.53	771	20.8	0.29	12	1	3	1.38	1	14	7	A
	Moreno	-41.06	-71.55	770	18.2	11.34	112	2	2	2.79	62.5	13.8	19.5	A
	Nahuel	-41.06	-71.40	769	14.8	557	464	3	1	4.27	62.5	14.1	18	A
	Huapi													
Manso	Gutiérrez	-41.17	-71.41	808	18.3	16.4	111.2	1	1	1.74	57.1	14.1	18	D
	Mascardi	-41.26	-71.64	807	17.4	39.26	218	2	2	2.52	40	9.3	10	D
	Guillelmo	-41.37	-71.50	835	16.2	6.5	107.1	1	2	2.17	33.3	12.5	11	C
	Los	-41.34	-71.61	804	16.6	2.3	50	2	2	1.08	40	12.7	12	D
	Moscós													
	Hess	-41.22	-71.43	760	18.5	1.34	29	2	3	2.14	25	13.2	14	D
	Fonck	-41.19	-71.45	777	19.5	4.07	88	1	3	2.03	40	12.4	9	C
	Roca	-41.23	-71.55	762	18.2	3.5	38	1	3	1.08	25	13.2	12	C
	Martin	-41.30	-71.40	546	17.2	7.56	88	1	3	2.51	40	14	11	D
Steffen	-41.51	-71.55	539	18.4	5.39	77	2	2	2.12	40	14.1	13	B	

assemblages historically regulated by the geology, topography and climate of the region (Cussac *et al.* 2004, 2009; Ruzzante *et al.* 2006; Pascual *et al.* 2007; Aigo *et al.* 2008; Aigo 2010). During the Pleistocene, the study area was covered by ice. As the ice retreated, it shaped the drainage areas, basins and connectivity between the water bodies, and delimited the temperature ranges for the species, establishing the original top predator assemblage (Cussac *et al.* 2004; Ruzzante *et al.* 2008, 2011). However, the current assemblages were modified after the introduction of salmonids in 1904. Moreover, seeding policies have allowed the dispersion of these introduced species (Habit *et al.* 2012; Macchi & Vigliano 2014). Both the original assemblages of top predators and the current ones have been influenced by the connectivity between water bodies. This is an important factor in the maintenance of populations because it facilitates the dispersal of fish throughout their life cycle (Crooks & Sanjayan 2006; Buria *et al.* 2007; Habit *et al.* 2015). In this work, we observed a segregated distribution for salmonids, associated with connectivity. Brook trout were found in headwater lakes and brown trout in lakes with an intermediate level of connection, while rainbow trout overlapped in distribution with the other two species, irrespective of the level of connection. Segregated distributions like the ones described here have already been mentioned at basin and river levels in another Patagonian study (Lallement 2017), as well as in other parts of the world (Larson & Moore 1985; Fausch 1988, 1989, 2008; Bozek & Hubert 1992; Flebbe 1994; Magoulick & Wilzbach 1998; Dunham & Rieman 1999; Korsu *et al.* 2007). In the case of the creole perch,

found only in the Limay river basin, connectivity played a key role, enabling this species to access shallow lakes and environments with thermal fluctuations that serve as a refuge for larvae and juveniles (Aigo *et al.* 2014). The importance of connectivity between lakes for this species has already been mentioned for the Moreno-Morenito system, where the creole perch has shown trophic and reproductive migrations (Buria *et al.* 2007). The importance of connectivity for the life cycles of Percichthyidae and migratory behaviour has also been observed in Australian aquatic systems (Koster *et al.* 2013; Tonkin *et al.* 2016).

Other factors that contributed to grouping top predator assemblages at a regional level were area and temperature. These factors have already been mentioned by other authors as structuring factors of Patagonian ichthyofauna (Aigo *et al.* 2008; Cussac *et al.* 2009; Lallement *et al.* 2016). It has been documented that temperature is a key factor for development of the different life cycles of the species in general (Cussac *et al.* 2009), and of the studied species in particular (Aigo 2010; Crichigno *et al.* 2014). Temperature was a determining factor in species distribution for both water basins. In the case of the salmonids, the segregated distribution was related to the thermal preference for colder water of the three species, while the native perch can be found in lakes with warmer temperatures. With regard to area, it is known that a larger area leads to greater diversity of available habitats (Eadiel *et al.* 1986; Amarasinghea & Welcomme 2002), and we can therefore suppose that there is an equitable distribution of resources. If this relationship was direct, and this was the only factor at work in shaping the assemblages, the bigger lakes should



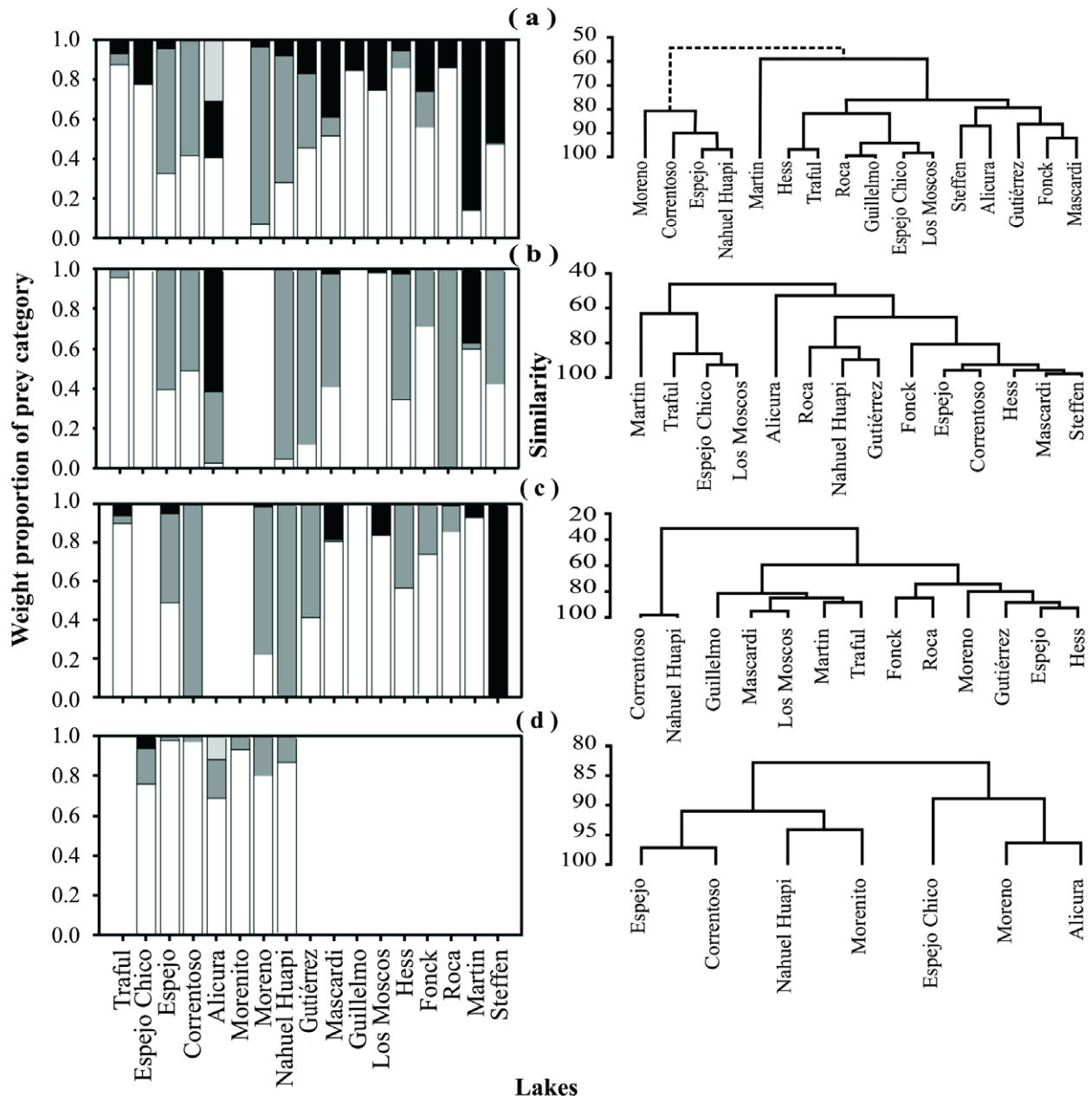
**Fig. 4.** Regression tree analysis showing lake groups based on major top predator fish assemblages and abiotic factors. Variables: Range of connectivity (Connectivity); Zoological integrity coefficient (ZIC); Water temperature (WT, °C); Area (Size, Ha); Mean summer air temperatures (MSAT, °C); Groups of top predator fish assemblages (A, B, C, D).

reflect this in their collective relative abundances of top predators. However, some smaller lakes presented higher species diversity and relative abundance of top predators than some larger lakes, suggesting that other factors acting on different scales are contributing to assemblage formation. These four factors have already been cited in other parts of the world and in Patagonia as structuring factors of the fish communities (Horton 1945; Hynes 1970; Larson & Moore 1985; Cussac *et al.* 2004; Aigo *et al.* 2008; Fausch 2008; Lallement 2017).

On a local scale, the proportion of native and exotic species structured the different assemblages of top predators; the low values for ZIC in the Manso basin indicated the high level of invasion experienced in this basin in comparison with the Limay River. Records show that the two galaxiids (*G. maculatus* and *G. platei*) were and still are widely distributed (Cussac *et al.* 2004). Before the introduction of salmonids, the creole perch, *G. platei* and *Odontesthes hatcheri* (Patagonian silverside) fulfilled the same trophic role as top predators (Macchi *et al.* 1999; Ruzzante *et al.* 2003; Macchi 2004; Ortiz-Sandoval 2014; Habit *et al.* 2015). However, the creole perch is currently the only native top predator (Macchi 2004) and is found in only one of the two basins

studied. With the introduction of salmonids, the populations of the native *G. platei* and *O. hatcheri* decreased or were displaced (Macchi *et al.* 1999; Milano 2003). In other parts of the world, the negative effects of salmonid introduction on native fauna have already been registered (Crowl *et al.* 1992; Polis & Strong 1996; Townsend 1996; Post *et al.* 2000; Mc Dowall 2003; McDowall 2006; Soto *et al.* 2006; Ortiz-Sandoval 2014). Among the negative effects of salmonids is competition for space and food resources and the perch could be experienced a reduction in their populations because of that. Nevertheless, when we analysed the trophic role of top predator fish in the two studied water basins, the rainbow trout, with a similar trophic role to creole perch, became more piscivorous in the presence of this native predator, while the other salmonids maintained their trophic role in all the studied lakes independently of the presence of creole perch. Thus, in accordance with our second hypothesis, through the use of resources in the Limay river basin the perch had a modulating effect upon salmonids, structuring the top predator assemblage. Conversely, in the Manso river basin, a system with three top predators, the brook trout found an opportunity to take on more dominance in top predator assemblages.





**Fig. 5.** Top predator diet composition by species: *Oncorhynchus mykiss* (a); *Salmo trutta* (b); *Salvelinus fontinalis* (c); *Percichthys trucha* (d). Left panels show total weight of each prey category by lake. Prey categories: Benthic prey (white); Fish (dark grey); Allochthonous (black); Zooplankton (light grey). Right panels exhibit dendrograms for hierarchical clustering based on the Bray–Curtis similarity matrix constructed on diet composition and contribution percentage similarity (SIMPROF test); dashed lines indicate no diet overlaps.

Diversification in behaviour and habitat use among different top predators in order to reduce competition for resources has already been mentioned in the region (Juncos *et al.* 2015) and other parts of the world (Kobler *et al.* 2009). However, we did not find any other study in which a native top predator modulates the abundance of exotic species widely distributed in the receptor ecosystem, as we have shown here.

On regional and local scales, the water basin, connectivity, area, temperature and ZIC were important factors in the structuring of top predator assemblages. Although the introduction of salmonids has modified fish assemblages, increasing the number of species and the number of top predators, on a local scale, the creole perch modulates salmonid populations through feeding and the resulting distribution of resources. Here, we have shown that top predator

assemblage structure in North Andean Patagonian basins is due to a combination of local and regional factors acting synergistically, as postulated by the assemblage theory.

## ACKNOWLEDGEMENTS

We wish to thank Gilda Garibotti for her advice on statistical analyses, Daniela Milano for the contribution of diet data analysis, and Paula Casanovas and Audrey Shaw for the English revision. The data collection for this work was funded by grants from the Universidad Nacional del Comahue (CRUB; UNCo, B923; B940, B166) and the Agencia Nacional de Promoción de Ciencia y Tecnología, Argentina (PICT 25722, PICT 2959).

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