



Drivers of macroinvertebrate metacommunity structure in Tierra del Fuego rivers



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ABSTRACT

Among the different mechanisms that shape metacommunity structure, species sorting and mass effects are the most studied and reported mechanisms. Species sorting is related to environmental filtering, while mass effects are related to high dispersal between communities, which ultimately overrides environmental controls. In this paper, we aimed at studying metacommunity patterns of stream macroinvertebrates on Tierra del Fuego Island at different spatial scales (province, ecoregion and catchment) and at different positions along the river network (upstream, mid-stream and downstream segments) to understand the mechanisms driving metacommunity structure. For this purpose, we used complementary approaches based on the analysis of beta diversity index as well as its turnover and nestedness components, which are associated with the two main underlying mechanisms of metacommunity structure (species sorting and mass effect). Our results indicate that species sorting is the preponderant mechanism structuring these macroinvertebrate metacommunities at larger spatial scales, with an increased importance of mass effects at smaller scales (e.g., catchment). Metacommunities at different positions on the river network exhibit similar total beta diversity values, turnover and nestedness components. On the other hand, turnover and total beta diversity increased with spatial extent, while nestedness remained constant. Those results suggest that at the catchment scale and along the longitudinal axis of the rivers other mechanisms, like randomness and species dispersal, are more important in shaping the macroinvertebrate metacommunity.

1. Introduction

Metacommunities are defined as a group of local communities interacting through the dispersal of multiple species (Leibold et al., 2004). Metacommunity structure (i.e. species distribution patterns at large scale) is mostly explained by environmental controls and spatial processes (Cottenie, 2005; Heino et al., 2015a). Therefore, the focus is set on two main ecological mechanisms, species sorting and mass effects (after Leibold et al., 2004), which structure the majority of the metacommunities (Cottenie, 2005; Grönroos et al., 2013). From a species sorting perspective, environmental gradients are thought to cause local differences in the demography of species, thus determining local community composition (Heino, 2011; Leibold et al., 2004). In contrast, mass effect occurs when good dispersal decouples the effects of environmental conditions (Heino, 2011; Leibold et al., 2004).

The relative importance of these two mechanisms is associated with connectivity among localities and species dispersal (Heino et al., 2015b). High dispersal or connectivity among localities increases the

importance of mass effect while, in contrast, species sorting prevails at moderate dispersal abilities or connectivity (Heino et al., 2015a, 2015b; Tonkin et al., 2015a). When dispersal is low, species are unable to reach all environmentally suitable localities (i.e. dispersal limitation, Heino et al., 2015b). Spatial extent and topography also affect the importance of these mechanisms (Heino et al., 2015b; Tonkin et al., 2018), since larger distances as well as natural barriers can have negative effects on dispersal and connectivity. In relation to spatial extent, it is believed that increased scale enhances environmental filtering due to farther dispersal distances and greater environmental gradients (Heino et al., 2015b; Soininen et al., 2018). On the contrary, mass effect is more likely to override environmental filtering when spatial extent and dispersal distance are shorter (Heino, 2011; Heino et al., 2015b).

The nature of fluvial systems, characterised by dendritic morphology together with flow directionality, creates a unique condition (Altermatt, 2013; Liu et al., 2013) that influences dispersal abilities and metacommunity structure (Tonkin et al., 2018). These systems usually depict longitudinal variations in connectivity, with more isolated

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headwater systems and more connected downstream segments. It has been suggested that such variation in connectivity promotes a longitudinal shift in the prevailing mechanisms shaping metacommunities (Brown and Swan, 2010). Recent studies support this statement, as they have found species sorting as the underlying mechanism in headwater systems and the increasing importance of mass effect in downstream segments (Brown and Swan, 2010; Finn et al., 2011; Sarremejane et al., 2017; Tonkin et al., 2015b).

The concept of beta diversity was first introduced by Whittaker (1960), and it has been used in many community studies ever since. It describes the variation of communities across space and time and can be further broken down in two indexes: turnover and nestedness (Baselga, 2010). The former refers to beta diversity, attributable to species replacement whereas the latter indicates species loss or gain (Baselga, 2010). It is generally thought that turnover reflects species sorting, whereas nestedness is related to ordered extinction-colonization dynamics (Soininen et al., 2018). Thus, by studying beta partitioning, it is possible to obtain more insights than when using beta diversity alone (Soininen et al., 2018) and to infer the mechanisms shaping metacommunity structure (e.g., Tonkin et al., 2016, 2015a). Understanding the underlying mechanisms that drive metacommunity structure is useful to conservation to help design protected areas that effectively preserve biodiversity, but its formal implementation has yet to be done (Gouhier et al., 2013). If mass effect prevails, prioritization should be set at the most species rich sites. On the other hand, if species sorting prevails, the goal should be to preserve large numbers of environmentally different sites within an area (Baselga, 2012; Datry et al., 2016).

Tierra del Fuego Island is characterised by high environmental and topographical diversity; it is located at a high latitude and is geographically isolated from continental Patagonia. On this island, the ecology of stream macroinvertebrate metacommunities remains poorly known. Some studies have described community diversity responses to environmental alteration at the reach scale (e.g., Simanonok et al., 2011) and community diversity in one (mountain range) of the island's four ecoregions (steppe, transition, mountain range and moorland) of the island (Moorman et al., 2006), but there is a relative lack of information concerning community diversity among different ecoregions and at larger spatial extents. By the study of beta diversity patterns, we aimed at understanding what mechanisms structure macroinvertebrate communities in Tierra del Fuego at different spatial scales (three nested scales: province, ecoregion and catchment) and along the river network at upstream, midstream and downstream segments. We analysed total beta diversity and its turnover and nestedness components, as well as variance partitioning of metacommunity diversity. Our general hypothesis was that beta diversity is strongly influenced by spatial scale. We predicted that because environmental gradients increase with spatial extent, turnover and total beta diversity should increase with spatial scale, while nestedness -which is more influenced by complex colonization and extinction dynamics-would remain constant (Soininen et al., 2018). In addition, we further predicted that along the longitudinal axis, given that isolation decreases towards the lowland segments, headwaters should have higher total beta diversity and turnover (i.e. species sorting mechanisms), compared to downstream segments.

2. Materials and methods

2.1. Study area

The study was conducted in the Argentine portion of Tierra del Fuego Island (between 52°5' - 55°03' S and 65°05' - 72°04' W), which represents 47% of the island's total surface area (the rest is part of Chile). The climate is cool temperate in the south and oceanic temperate in the north with a mean annual temperature of 5 °C (Tuhkanen, 1992). Annual precipitation is low and decreases from 600 mm yr⁻¹ in the southwest to 300 mm yr⁻¹ in the northeast (Tuhkanen, 1992). The

area is divided into four ecoregions differing in their climatic, vegetational and hydrological settings: Steppe, Transition, Mountain Range and Moorland. This study mainly focused on the Transition and Mountain Range ecoregions, as they cover the largest area (67% of the island's surface) and are the most accessible logistically. Transition is mostly hilly terrain (influenced by glaciation) with grasslands in lowland areas and *Nothofagus* forests (southern beeches) in mountainous upland areas (Oliva et al., 2001). The Mountain Range area is characterised by the Fuegian Andes, which have been intensively eroded by Late Cenozoic glaciers, developing deep valleys and rugged mountains (Rabassa et al., 2000). The Mountain Range ecoregion has *Nothofagus* forests, high alpine vegetation above 700 m a.s.l. and peat bogs in lowland glacial valleys (Premoli et al., 2006). The Steppe is characterised by an undulating landscape covered by grasslands and low shrubs. The Moorland has extensive peat bogs and evergreen (*N. betuloides*) forest patches.

2.2. Sampling design

We studied three spatial scales: province, ecoregion and river. For the largest spatial scale (province), five main fluvial systems were studied (range of drainage areas: 135–1023 km²). These rivers also were used to represent the ecoregion scale, two belonging to Transition and three to Mountain range ecoregions. For the catchment scale, each river was represented by three main sections, which also served for assessing differences within the river system: upstream, midstream and downstream (Table 1). Within each section, we selected one representative segment with a length ≥ 10 times its wet width, based on a combination of satellite images, technical advice from the Provincial Water Bureau and our own field inspection. The downstream segment was located near the sea but far enough to avoid marine influences (i.e. direct tide effects). At each segment, two reaches, separated by at least two pools, were selected and invertebrates samples were taken. However, for simplicity in the analysis, we averaged invertebrate samples and environmental parameters from the two reaches at the same segment. All segments were sampled once in summer. For analysing beta diversity at the province scale, we additionally selected one representative river at the Steppe and one at the Moorland ecoregions. Due to logistic reasons, the Moorland river was sampled at the downstream segment, whereas the Steppe river at the mid-stream and downstream segments (Table 1). Such a sampling design was uneven, limiting the use of those rivers in the ecoregion analysis. For these two rivers, we followed the same sampling and analysis protocols to obtain data that was comparable to the rivers of Transition and Mountain Range ecoregions for analysing beta diversity at the province scale. Catchment areas in the Mountain range Ecoregion are in general smaller than those in Transition, due to contrasting geomorphologic settings determining that river networks are shorter in length and smaller in drainage area. Because of this, our sampling design focused on dividing river networks in three main sections (see details above), which were comparable in the relative distance to the sources or to the river mouth.

Table 1
Drainage area (km²) upstream of each river segment per ecoregion.

Ecoregion	River	Upstream	Mid-stream	Downstream
Steppe	Cullen	–	763	862
Transition	Ewan	38	568	1023
	San Pablo	27	93	469
Mountain Range	Lasifashaj	3	133	420
	Olivia	4	98	197
	Valdez	37	120	135
Moorland	Moat	–	–	435

2.3. Environmental and spatial variables

Conductivity, pH and temperature were measured with a HI9820 multiparameter (Hanna Instruments, Inc., Woonsocket, Rhode Island, USA). Water samples for chemical analysis were collected in acid washed bottles (Butturini et al., 2009) filtered with MG-F filters (Munktell Co) and stored at -20°C . Nitrate, nitrite and soluble reactive phosphorous concentrations were quantified by an Autoanalyzer Technicon II, following standard protocols (see Eberlein and Kattner, 1987; Grasshoff et al., 1983; Treguer and Le Corre, 1975). Before freezing, a filtered water sample was used to measure light absorption at 440 nm (Pace and Cole, 2002) for estimating water colour associated to dissolved organic substances. Periphyton abundance was estimated as Chlorophyll *a* concentration (mg m^{-2}) from single cobbles collected randomly on the stream bottom (3 cobbles per reach). Chlorophyll *a* extraction was performed with ethanol and assessed following Biggs and Kilroy (2000). Benthic particulate organic matter (BPOM) was collected together with the macroinvertebrate samples (section 4.4). In the laboratory, BPOM was classified into coarse and fine particulate organic matter ($\geq 1,000 \mu\text{m}$ and $< 1,000 \mu\text{m}$, respectively), oven dried until constant mass and weighed. Percentages of boulder, cobble, pebble, gravel and sand were estimated by the Wolman pebble count method on 100 randomly selected substrates at each segment (Wolman, 1954). The relative abundance of each substrate category was used to compute new variables (i.e. PC-S1 and PC-S2) from a principal component analysis (Kenkel et al., 2002; Quinn and Keough, 2002). Water flow was assessed by timing a spherical floating object along a 14 m length distance (5 measures). In each study segment, four transects were established to measure channel width and depth at regular intervals.

The Euclidean distance between pairs of sites (i.e. segments) was used as substitute of environmental difference (hereafter environmental distance). The most relevant predictor variables were selected by performing a Principle Components Analysis (PCA) and keeping those highly correlated with any of the two first axes. Selected variables were: temperature, Chlorophyll *a* concentration, water colour, soluble reactive phosphorous, BPOM fine, mean depth and mean width.

Latitude, longitude and altitude of each segment studied were obtained with a Garmin GPS. Spatial distance between each pair of segments was measured as the distance in a straight line.

2.4. Macroinvertebrate samples

Three quantitative macroinvertebrate samples were taken with a Surber sampler (0.06 m^2 ; $200 \mu\text{m}$ mesh size) in one riffle habitat per reach ($n = 3$ per reach and $n = 6$ per segment). Samples were fixed with 80% alcohol until sorting and identification in the laboratory. Macroinvertebrate individuals were identified to the lowest possible taxonomic level using available keys (e.g. species, genus or family; Domínguez and Fernández, 2009; Nieto, 2004) and counted to determine abundance per sampling unit. Average taxa number per segment was 19 ± 4 (mean \pm standard deviation).

3. Data analysis

3.1. Drivers of metacommunity structure

To examine the mechanisms structuring metacommunities, we followed the methodology developed by Baselga (2010), which computes multiple-site beta diversity (or total beta diversity) and partitions this value in two additive components. This components are related with the different phenomena explaining beta diversity: nestedness, where poor species sites are subsets of rich species sites, and turnover, where species are replaced among sites due to environmental constraints or spatial barriers (Baselga, 2010; Tonkin et al., 2015a). We used Sørensen dissimilarity index to account for total beta diversity (hereafter call

β_{SOR}) and the nestedness (β_{NES}) and turnover (β_{SIM}) indexes to account for its components ($\beta_{\text{SOR}} = \beta_{\text{NES}} + \beta_{\text{SIM}}$). We computed all these beta diversity indexes for each study scale using the *betapart* package (Baselga et al., 2013). In some occasions, we calculated average pair-wise biodiversity indexes (hereafter pairwise- β) instead of the multi-site to accomplish specific statistical approaches. Although multiple site diversity accounts overall heterogeneity in communities better than mean pairwise diversity (Baselga et al., 2013), it gives only one value thus constraining further analyses.

First, at the province scale (Argentine Tierra del Fuego) beta diversity index was obtained considering all study segments as single localities regardless of their catchment. A total of seven rivers, representing the four ecoregions of the province, were considered. Secondly, at the Ecoregion scale, beta diversity index was obtained separately for Transition and Mountain range ecoregions. As Transition and Mountain range ecoregions were represented by a different number of sites (more sites in Mountain range), beta diversity in Mountain range was obtained with a resampling procedure (Baselga, 2010), which allows a weighed comparison between indexes. This method consisted of taking 100 random samples of 6 segments in Mountain range ecoregion (same number of segments as in Transition), then obtaining beta diversity indexes for each sample and finally computing the mean indexes. Last, at the catchment scale, beta diversity index was obtained for each river considering their three study segments (within-catchment diversity). We also explored the correlation between spatial and environmental distances and between turnover or nestedness components of beta diversity, and spatial or environmental distance. We calculated pairwise beta diversity indexes (function *beta.pair* of *betapart* package), which allowed us to compare the relationship between the indexes and both distances by a Mantel test. Analyses were run with the *mantel* function of the *vegan* package (Oksanen et al., 2016), with 999 permutations, and rivers were set as *strata* within that function in order to eliminate catchment effect.

At the province scale, the large number of replicated locations ($n = 18$) allowed us to complement the partition analysis of beta diversity with a partial redundancy analysis (p-RDA). This method enables obtaining the percentage of community variability explained by environmental, spatial or both types of variables. All segments within a river system were considered independent of each other since the distance between them was longer than 3 km. The macroinvertebrate abundance matrix was modified with Hellinger's transformation (Legendre and Gallagher, 2001), employing the *decostand* function of the *vegan* package (Oksanen et al., 2016). Principal coordinates of neighbor matrices (PCNM) were used to transform latitude, longitude and altitude with the *pcnm* function in the *vegan* package, to be used in this constrained ordination method, following Tonkin et al. (2015a). Prior to running the partial RDA analysis, a preliminary analysis was done with *rda* (of the *vegan* package) and *step* functions in order to eliminate correlated and non significant variables. Percentages of explained, shared and unexplained variation were computed following Zuur et al. (2007).

Pairwise indexes (function *beta.pair* of *betapart* package) for each beta diversity component were computed for each segment along the river (upstream, mid-stream and downstream) to investigate contributions of nestedness and turnover in the different segments of the rivers. The relationship between pairwise- β_{SOR} and environmental or spatial distance was explored with a Mantel correlation test, as no relationship was found between environmental and spatial distances in any segment (Mantel test: upstream $r = 0.37$, $p = 0.2$; midstream $r = 0.42$, $p = 0.1$; and downstream $r = 0.08$, $p = 0.38$). Pearson coefficient was used as well as 199 permutations (i.e. the maximum number possible of permutations).

3.2. Comparison among different spatial scales and positions along the river network

To analyze the relationship of spatial scale and metacommunity beta diversity, we performed a general comparison of all beta diversity indexes obtained across the different spatial scales of the study. As the smallest spatial scale (catchment) was represented by three segments, we conducted a resampling procedure to compute the three diversity indexes (β_{SOR} , β_{SIM} and β_{NES}) at the ecoregion and province scales. The resampling procedure was described in the previous section, following Baselga (2010), and used to eliminate sample size effect on beta diversity. We analysed the correlation between beta diversity indexes and spatial extent (measured as mean distance between locations), using Pearson correlation, after the normality of variable distribution was confirmed. Correlation was assessed with Infostat software (Di Rienzo et al., 2016).

Finally, to determine if total beta diversity varied among positions in the river network and if it had different contributions of the turnover and nestedness component, we calculated pairwise beta diversity indexes (i.e. pairwise- β_{SOR} , pairwise- β_{SIM} and pairwise- β_{NES}) among the three river positions. Differences were tested by PERMDISP2 analysis, using the *betadisper* function to compute distances to group centroid and a permutation test, *permutest*, to assess differences in dispersion among positions along the river, following (Tonkin et al., 2016). Both analysis are from the *vegan* package (Oksanen et al., 2016), *permutest* was carried with 999 permutations.

All analyses, except otherwise indicated, were performed using R version 3.1.1 (R Core Team, 2016). When applicable, the results of these analysis were considered significant if p values were lower than 0.05.

4. Results

4.1. Beta diversity and drivers of beta diversity at different spatial scales

At the province scale, β_{SOR} was 0.82, and beta partitioning indicated that metacommunity was mostly structured by turnover ($\beta_{\text{SIM}} = 0.77$) while nestedness component was more than tenfold lower ($\beta_{\text{NES}} = 0.05$). The variance partitioning analysis (p-RDA) revealed that environmental variables account for almost twice as much community structure variation (34%) as spatial variables (18%), with shared variation explaining 26%. The p-RDA showed more importance of the environmental gradient, reflecting the prevalence of the turnover component, though the difference was smaller than when beta diversity was partitioned.

At the Ecoregion scale, both Transition and Mountain Range had similar β_{SOR} values (0.58 and 0.59, respectively), with a dominance of the β_{SIM} component (0.44 and 0.52, respectively). Interestingly, β_{NES} was two-fold higher in Transition (0.14) than in Mountain range (0.07).

At the catchment scale, pairwise- β_{SOR} varied substantially within each catchment (between 0.23 and 0.49), and it correlated with spatial (Mantel test, $r = 0.48$, $p = 0.02$) but not with environmental distance (Mantel test, $r = 0.22$, $p = 0.41$, Fig. 1 A and B). In each river, the pairwise- β_{SIM} was dominant ($73 \pm 11\%$ of pairwise- β_{SOR}) over pairwise- β_{NES} ($26 \pm 11\%$ of pairwise- β_{SOR}). The exception was Valdez, the smallest river sampled, where pairwise- β_{SIM} and pairwise- β_{NES} had similar values (0.12 and 0.10 respectively). Besides pairwise- β_{SOR} , pairwise- β_{SIM} was related with spatial (Mantel test, $r = 0.50$, $p = 0.01$) but not with environmental distance (Mantel test, $r = 0.18$, $p = 0.52$, Fig. 1 C and D), while pairwise- β_{NES} showed no relationship with predictor variables (Mantel test, $p > 0.05$ in both cases, Fig. 1 E and F). Environmental and spatial distances did not correlate (Mantel test, $r = 0.03$, $p = 0.93$).

When analyzing the relationship with spatial extent across scales, we found a significantly positive relationship with β_{SOR} (Pearson correlation $r = 0.78$, $p = 0.02$). β_{SIM} showed a marginal relationship

(Pearson correlation $r = 0.66$, $p = 0.07$), while β_{NES} had no significant relationship with spatial extent ($p = 0.80$).

4.2. Different positions along the longitudinal axis of the river

None of the beta diversity indexes differed among studied positions (permutation test, pairwise- β_{SOR} : $F = 0.57$, $p = 0.58$; pairwise- β_{SIM} : $F_{(2,12)} = 0.38$, $p = 0.69$; pairwise- β_{NES} : $F_{(2,12)} = 1.52$, $p = 0.26$). It is worth noting that pairwise- β_{SIM} represented the largest contribution to pairwise- β_{SOR} . Pairwise- β_{SOR} was not correlated with environmental distance in any segment (Fig. 2 A, C and E, Mantel test, $p > 0.05$ in all cases). However, pairwise- β_{SOR} was positively correlated with spatial distance at the upstream and mid-stream (Fig. 2 B and D, $p < 0.05$) but not at the downstream segments (Fig. 2 F).

5. Discussion

Our analysis of the beta diversity of the benthic invertebrate community in the rivers of Tierra del Fuego Island indicates that turnover is the dominant structuring component. This result was consistent across the three spatial scales analysed: province, ecoregion and catchment. As predicted, total and turnover beta diversities increased with spatial extent, while nestedness beta diversity remained constant. When analyzing beta diversity at different positions along the river network we found that, contrary to our expectations, neither total, turnover or nestedness beta diversity indexes differed among positions.

Considering that beta diversity turnover component generally reflects species sorting (Soininen et al., 2018), our results indicate a dominance of species sorting processes at the province, ecoregion and catchment scales. This is in agreement with several studies that have previously found the same process shaping macroinvertebrate metacommunities (Göthe et al., 2013; Grönroos et al., 2013; Landeiro et al., 2012; Padial et al., 2014; Soininen et al., 2018), even at different spatial scales (Cottenie, 2005). For example, in continental Patagonia at 40° S latitude, beta diversity (measured as invertebrate community similarity) was studied within the detritivore trophic guild and showed a positive correlation with environmental but not with spatial distance (Boyer et al., 2015). In that survey the lack of spatial signaling in addition to longer distances among study localities (mean distance 167 km) suggests species sorting as the mechanism shaping the metacommunity. Similarly, when we partitioned the effects that environmental and spatial drivers had on metacommunity structure, environmental variables explained much more variation (two-fold) than spatial variables. In a more recent meta-analysis across a large range of latitudes and involving communities from freshwater, marine and terrestrial realms as well as a variety of life forms, Soininen et al. (2018, appendix S3) found highly variable turnover component values. For instance, turnover diversity at latitudes similar to those in our study (50 - 60°) fluctuated between 0 and 0.9. Therefore, our measured turnover for benthic stream macroinvertebrates at the province scale ($n = 15$, $\beta_{\text{SIM}} = 0.75$) is among the highest when compared with different community types at high latitude.

Dispersion of overland colonizers can be constrained by topographic heterogeneity (for a review see Tonkin et al., 2018), as when communities in different river branches are separated by large overland barriers (e.g. high and pronounced hillslopes, see Tonkin et al., 2017). Therefore, we expected a higher contribution of species sorting to the structuring of metacommunities in the Mountain Range ecoregion than in the Transition ecoregion because landscapes in the former are characterised by isolated steep valleys in contrast with the low hills found in Transition. Our results indicate that while β_{SIM} dominated beta diversity in both ecoregions, β_{NES} component was two-fold higher in Transition. This might reflect more accessible stream reaches within Transition landscapes facilitating individual dispersal and increasing the probability for nested metacommunity structure.

Turnover is expected to increase with spatial extent as a

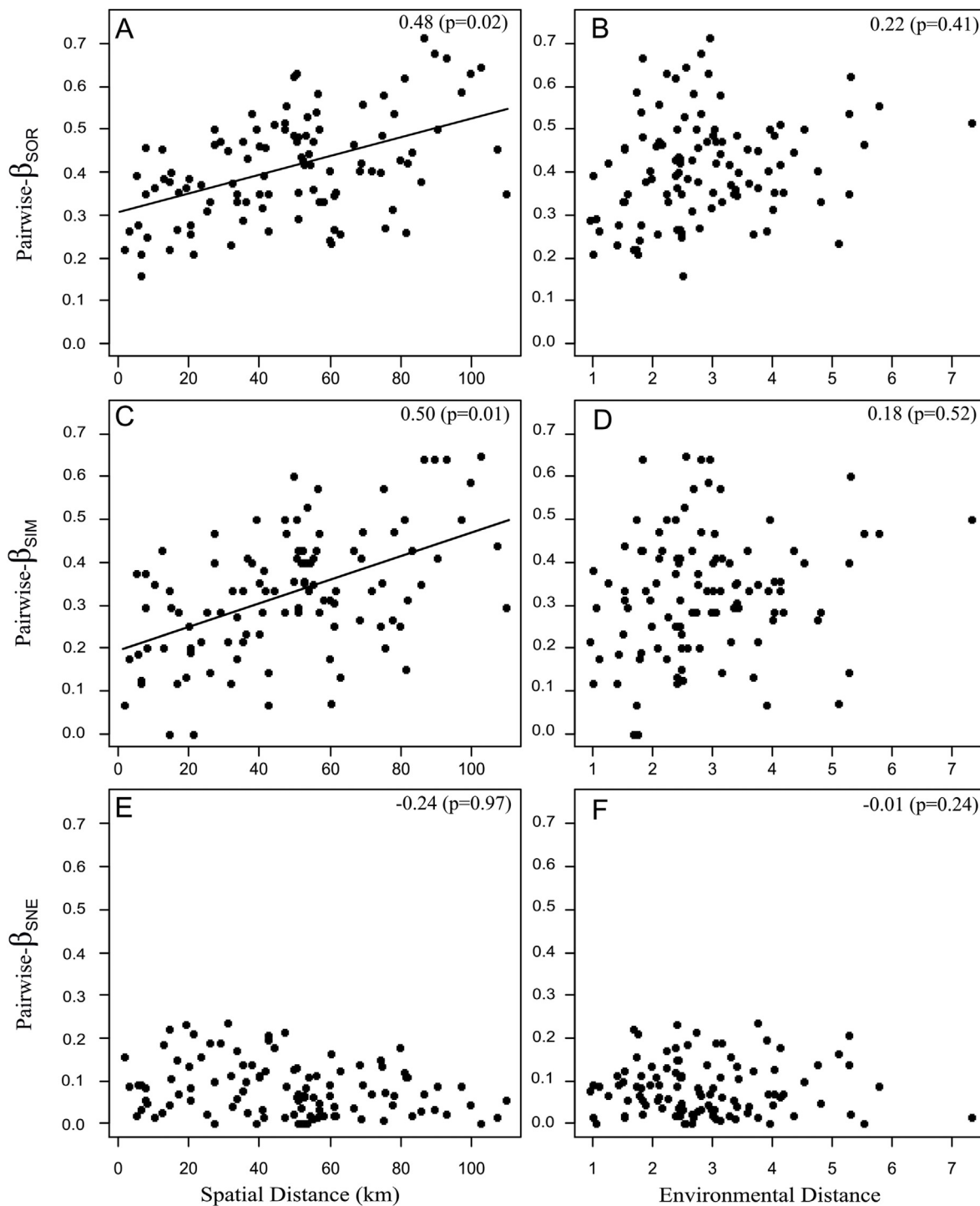


Fig. 1. Beta diversity of benthic invertebrate communities at the catchment scale in five rivers of Tierra del Fuego, Argentina. Pairwise- β_{SOR} as a function of spatial (A) and environmental distance (B); pairwise- β_{SIM} as a function of spatial (C) and environmental distance; (D); pairwise- β_{NES} as a function of spatial (E) and environmental (F) distance. Pearson correlation coefficient and its p value (Mantel test) are shown. The line in A and C represents the significant correlation between variables.

consequence of larger environmental gradients, which in turn results in increased environmental filtering of species (Heino et al., 2015a). Similarly, nestedness is also expected to increase with spatial extent (Soininen et al., 2018) because farther locations are less likely to be reached thus promoting ordered extinction. However, Soininen et al. (2018) found that the nestedness component of beta diversity did not vary with spatial extent. Our results showed that turnover beta diversity increased with spatial extent while the nestedness component remained

invariant. While species sorting and mass effects have been most often identified as the predominant models, metacommunities rarely fit a single model (Logue et al., 2011). We believe that the pattern in the nestedness component is caused by a more complex interaction of processes (Soininen et al., 2018). Although turnover represented the highest contribution of total beta diversity, both indexes (total diversity and turnover component) related with spatial distance at the catchment scale, suggesting the importance of spatial processes over

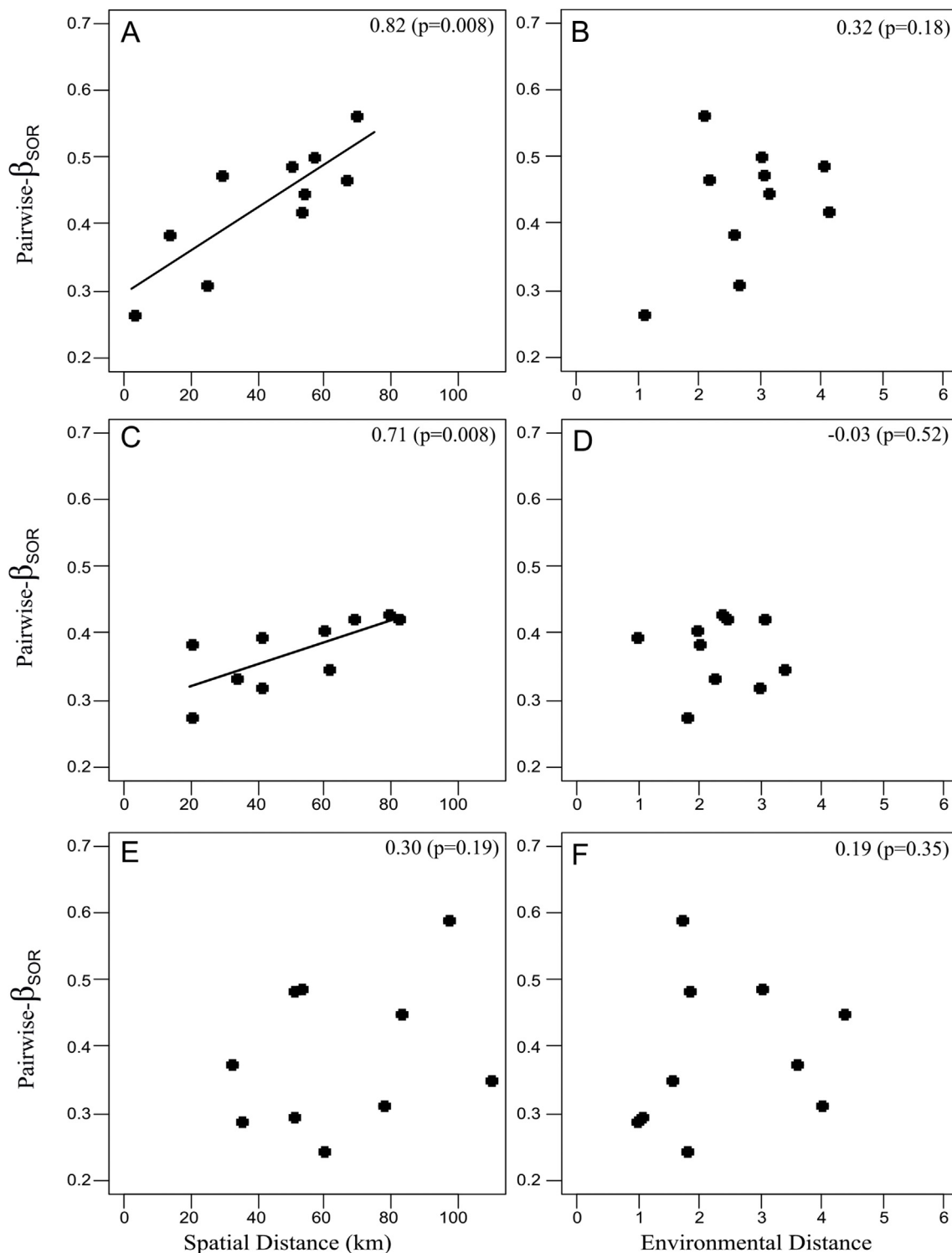


Fig. 2. Beta diversity (pairwise- β_{SOR}) as a function of environmental and spatial distance in upstream (A, B), mid-stream (C, D) and downstream (E, F) river segments. The correlation coefficient and its significance (Mantel test) are shown on each panel. The line in A and C represents the significant correlation between variables.

environmental filtering. In this sense, the significant spatial signal observed at different spatial scales may indicate strong dispersal limitation in shaping macroinvertebrate metacommunity structure (Sarremejane et al., 2017).

The dendritic condition along with flow uni-directionality in fluvial systems (Allan and Castillo, 2007) make headwater areas more isolated in comparison to other fluvial segments within the network. Headwater isolation and higher environmental heterogeneity, in combination with

higher channel density, result in higher beta diversity here than in other segments of the river (Brown et al., 2011; Brown and Swan, 2010; Finn et al., 2011; Gomi et al., 2002). These features should also favor species sorting in headwaters in contrast to the more connected and less heterogeneous downstream extensions where higher dispersal and massive colonization events are likely to occur (Brown and Swan, 2010; Finn et al., 2011; Sarremejane et al., 2017; Tonkin et al., 2015b). Beta diversity in our study rivers showed no relationship with position in the

network, contrary to our expectations. This lack of difference in beta diversity among river segments can be caused by a similar connectivity and dispersal (hence the pattern is real) along the network. In this regard, headwater streams may not necessarily be the most isolated segments in a river network as, due to its dendritic nature, they can be either close to or far from each other (Schmera et al., 2018). On the other hand, we found that total beta diversity did relate to spatial distance in upstream and midstream segments, indicating the importance of spatial factors. Moreover, the relationship between spatial distance and beta diversity in our upstream segments was more pronounced than in midstream ones reflecting higher dispersal limitation among headwaters. In contrast, no spatial relationship was found in downstream segments. Such findings are similar to those of Sarremejane et al. (2017). In their recent study comprising headwater and mid-stream systems, they highlighted that dispersal limitation and randomness also structure beta diversity, with varying importance according to connectivity, ultimately leading to mass effects in more connected mid-size streams. Our results suggest a shift on the prevailing mechanism from dispersal limitation in upstream segments to the predominance of mass effect in downstream ones. However, as beta diversity was similar among river segments (see above) it is likely that other processes not assessed in this study interplay to yield the observed patterns. For example, groups with different dispersal traits may have different associated mechanisms (Grönroos et al., 2013), thus obscuring the patterns of this metacommunity.

The higher importance of turnover at our contrasting spatial scales indicates that conservation efforts should be focused on preserving streams and rivers with different environmental conditions at least at scales larger or equal to the ecoregion. Our results are valuable for management decisions as they provide information to identify valuable streams to protect or restore the biodiversity in river networks. Recent advances in our understanding of community structure across landscapes and riverscapes and their environmental/spatial drivers offer complementary ecological information to help designing protected areas for preserving or restoring ecosystems and their biota (Gouhier et al., 2013). However, the formal implementation of such concepts in conservation biology has yet to be done.

Declaration of interest

None.

Contributions

A. P. Villatarco Vazquez, D. A. Fernández and R. J. Albariño conceived the ideas and the sampling design. A. P. Villatarco Vazquez carried out the sampling and collected the data. A. P. Villatarco Vazquez and R. J. Albariño analysed the data. A. P. Villatarco Vazquez led the writing with contributions of all authors.

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References

Allan, J.D., Castillo, M.M., 2007. *Stream Ecology*. Springer, Dordrecht, Netherlands. <https://doi.org/10.1017/CBO9781107415324.004>.

Altermatt, F., 2013. Diversity in riverine metacommunities: a network perspective. *Aquat.*

- Ecol.* 47, 365–377. <https://doi.org/10.1007/s10452-013-9450-3>.
- Baselga, A., 2012. The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Glob. Ecol. Biogeogr.* 21, 1223–1232. <https://doi.org/10.1111/j.1466-8238.2011.00756.x>.
- Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. *Glob. Ecol. Biogeogr.* 19, 134–143. <https://doi.org/10.1111/j.1466-8238.2009.00490.x>.
- Baselga, A., Orme, D., Villeger, S., De Bortoli, J., Leprieux, F., 2013. *Betapart: Partitioning Beta Diversity into Turnover and Nestedness Components*.
- Biggs, B.J.F., Kilroy, C., 2000. *Monitoring Manual Stream Periphyton*. NIWA, Christchurch.
- Boyer, L., Pearson, R.G., Swan, C.M., Hui, C., Albariño, R.J., Arunachalam, M., Callisto, M., Chará, J., Chará-Serna, A.M., Chauvet, E., Cornejo, A., Dudgeon, D., Encalada, A.C., Ferreira, V., Gessner, M.O., Gonçalves, J.F., Graça, M.A.S., Helson, J.E., Mathooko, J.M., McKie, B.G., Moretti, M.S., Yule, C.M., 2015. Latitudinal gradient of nestedness and its potential drivers in stream detritivores. *Ecography* 38, 949–955. <https://doi.org/10.1111/ecog.00982>.
- Brown, B.L., Swan, C.M., 2010. Dendritic network structure constrains metacommunity properties in riverine ecosystems. *J. Anim. Ecol.* 79, 571–580. <https://doi.org/10.1111/j.1365-2656.2010.01668.x>.
- Brown, B.L., Swan, C.M., Auerbach, D.A., Campbell Grant, E.H., Hitt, N.P., Maloney, K.O., Patrick, C., 2011. Metacommunity theory as a multispecies, multiscale framework for studying the influence of river network structure on riverine communities and ecosystems. *J. North Am. Benthol. Soc.* 30, 310–327. <https://doi.org/10.1899/10-129.1>.
- Butturini, A., Sabater, S., Romani, A.M., 2009. La química de las aguas. Los nutrientes. In: Elosegi, A., Sabater, S. (Eds.), *Conceptos Y Técnicas En Ecología Fluvial*. Fundación BBVA, Bilbao, Vizcaya, pp. 97–116.
- Cottenie, K., 2005. Integrating environmental and spatial processes in ecological community dynamics. *Ecol. Lett.* 8, 1175–1182. <https://doi.org/10.1111/j.1461-0248.2005.00820.x>.
- Datry, T., Bonada, N., Heino, J., 2016. Towards understanding the organisation of metacommunities in highly dynamic ecological systems. *Oikos* 125, 149–159. <https://doi.org/10.1111/oik.02922>.
- Di Rienzo, J.A., Casanoves, F., Balzarini, M.G., Gonzales, L., Tablada, E., Robledo, C.W., 2016. *InfoStat*.
- Domínguez, E., Fernández, H.R., 2009. *Macroinvertebrados bentónicos sudamericanos: sistemática y biología*. In: *Fundación Miguel Lillo, San Miguel de Tucumán, Primera Ed.*
- Eberlein, K., Kattner, G., 1987. Automatic method for determination of orthophosphate and total dissolved phosphorus in the marine environment. *Fresenius' Z. für Anal. Chem.* 326, 354–357.
- Finn, D.S., Bonada, N., Múrria, C., Hughes, J.M., 2011. Small but mighty: headwaters are vital to stream network biodiversity at two levels of organization. *J. North Am. Benthol. Soc.* 30, 963–980. <https://doi.org/10.1899/11-012.1>.
- Gomi, T., Sidle, R.C., Richardson, J.S., 2002. Understanding processes and downstream linkages of headwater systems. *Bioscience* 52, 905–916.
- Göthe, E., Angeler, D.G., Sandin, L., 2013. Metacommunity structure in a small boreal stream network. *J. Anim. Ecol.* 82, 449–458. <https://doi.org/10.1111/1365-2656.12004>.
- Gouhier, T.C., Guichard, F., Menge, B.A., 2013. Designing effective reserve networks for nonequilibrium metacommunities. *Ecol. Appl.* 23, 1488–1503. <https://doi.org/10.1890/12-1801.1>.
- Grasshoff, K., Erhardt, M., Kremling, K., 1983. *Methods of Seawater Analysis*, second ed. Verlag Chemie, Weinheim, Germany.
- Grönroos, M., Heino, J., Siqueira, T., Landeiro, V.L., Kotanen, J., Bini, L.M., 2013. Metacommunity structuring in stream networks: roles of dispersal mode, distance type, and regional environmental context. *Ecol. Evol.* 3, 4473–4487. <https://doi.org/10.1002/ece3.834>.
- Heino, J., 2011. A macroecological perspective of diversity patterns in the freshwater realm. *Freshw. Biol.* 56, 1703–1722. <https://doi.org/10.1111/j.1365-2427.2011.02610.x>.
- Heino, J., Melo, A.S., Bini, L.M., 2015a. Reconceptualising the beta diversity-environmental heterogeneity relationship in running water systems. *Freshw. Biol.* 60, 223–235. <https://doi.org/10.1111/fwb.12502>.
- Heino, J., Melo, A.S., Siqueira, T., Soininen, J., Valanko, S., Bini, L.M., 2015b. Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. *Freshw. Biol.* 60, 845–869. <https://doi.org/10.1111/fwb.12533>.
- Kenkel, N.C., Derksen, D.A., Thomas, A.G., Watson, P.R., 2002. Multivariate analysis in weed science research. *Weed Sci.* 50, 281–292.
- Landeiro, V.L., Bini, L.M., Sanches Melo, A., Oliveira Pes, A.M., Magnusson, W.E., 2012. The roles of dispersal limitation and environmental conditions in controlling caddisfly (Trichoptera) assemblages. *Freshw. Biol.* 57, 1554–1564. <https://doi.org/10.1111/j.1365-2427.2012.02816.x>.
- Legendre, P., Gallagher, E.D., 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129, 271–280. <https://doi.org/10.1007/s004420100716>.
- Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., Gonzalez, A., 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.* 7, 601–613. <https://doi.org/10.1111/j.1461-0248.2004.00608.x>.
- Liu, J., Soininen, J., Han, B.-P., Declerck, S.A.J., 2013. Effects of connectivity, dispersal directionality and functional traits on the metacommunity structure of river benthic diatoms. *J. Biogeogr.* 40, 2238–2248. <https://doi.org/10.1111/jbi.12160>.
- Logue, J.B., Mouquet, N., Peter, H., Hillebrand, H., Group, M.W., 2011. Empirical approaches to metacommunities: a review and comparison with theory. *Trends Ecol.*

- Evol. 26, 482–491. <https://doi.org/10.1016/j.tree.2011.04.009>.
- Moorman, M.C., Anderson, C.B., Gutiérrez, Á.G., Charlin, R., Rozzi, R., 2006. Watershed conservation and aquatic benthic macroinvertebrate diversity in the Alberto D'Agostini National Park, Tierra del Fuego, Chile. *An. Inst. Patagon.* 34, 41–58.
- Nieto, C., 2004. South American Baetidae (Ephemeroptera): a new generic synonymy. *Stud. Neotrop. Fauna Environ.* 39, 95–101. <https://doi.org/10.1080/01650520412331333747>.
- Oksanen, J., Blanchet, G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., Minchin, P.R., Al, E., 2016. *Vegan: community ecology package*.
- Oliva, G., González, L., Rial, P., 2001. El ambiente en la Patagonia Austral. In: Borrelli, P., Oliva, G. (Eds.), *Ganadería Sustentable En La Patagonia Austral*. INTA Reg. Pat. Sur, pp. 17–80.
- Pace, M.L., Cole, J.J., 2002. Synchronous variation of dissolved organic carbon and color in lakes. *Limnol. Oceanogr.* 47, 333–342.
- Padial, A., Ceschin, F., Declerck, S.A.J., De Meester, L., Bonecker, C.C., Lansac-Tôha, F., Rodrigues, L., Rodrigues, L.C., Train, S., Velho, L.F.M., Bini, L.M., 2014. Dispersal ability determines the role of environmental, spatial and temporal drivers of meta-community structure. *PLoS One* 9.
- Premoli, A., Aizen, M., Kitzberger, T., Raffaele, E., 2006. Situación ambiental en los Bosques Andino Patagónicos. In: Brown, A., Martínez Ortiz, U., Acerbi, M., Corcuera, J. (Eds.), *La Situación Ambiental Argentina 2005*. Fundación Vida Silvestre Argentina, Buenos Aires, Argentina, pp. 279–281.
- Quinn, G.P., Keough, M.J., 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press. <https://doi.org/10.1017/CBO9781107415324.004>.
- Rabassa, J., Coronato, A., Bujalesky, G., Salemme, M., Roig, C., Meglioli, A., Heusser, C., Gordillo, S., Roig, F., Borronei, A., Quattrocchio, M., 2000. Quaternary of Tierra del Fuego, Southernmost South America: an updated review. *Quat. Int.* 68–71, 217–240. [https://doi.org/10.1016/S1040-6182\(00\)00046-X](https://doi.org/10.1016/S1040-6182(00)00046-X).
- Sarremejane, R., Mykrä, H., Bonada, N., Aroviita, J., Muotka, T., 2017. Habitat connectivity and dispersal ability drive the assembly mechanisms of macroinvertebrate communities in river networks. *Freshw. Biol.* 62, 1073–1082. <https://doi.org/10.1111/fwb.12926>.
- Schmera, D., Árbá, D., Boda, P., Bódís, E., Bolgovics, Á., Borics, G., Csercsa, A., Déak, C., Krasznai, E.Á., Lukács, B.A., Mauchart, P., Móra, A., Sály, P., Specziár, A., Süveges, K., Szivák, I., Takács, P., Tóth, M., Várbíró, G., Vojtkó, A.E., Erős, T., 2018. Does isolation influence the relative role of environmental and dispersal-related processes in stream networks? An empirical test of the network position hypothesis using multiple taxa. *Freshw. Biol.* 63, 74–85. <https://doi.org/10.1111/fwb.12973>.
- Simanonok, M.P., Anderson, C.B., Martínez Pastur, G.J., Lencinas, M.V., Kennedy, J.H., 2011. A comparison of impacts from silviculture practices and North American beaver invasion on stream benthic macroinvertebrate community structure and function in Nothofagus forests of Tierra del Fuego. *For. Ecol. Manage.* 262, 263–269. <https://doi.org/10.1016/j.foreco.2011.03.031>.
- Soininen, J., Heino, J., Wang, J., 2018. A meta-analysis of nestedness and turnover components of beta diversity across organisms and ecosystems. *Glob. Ecol. Biogeogr.* 27, 96–109. <https://doi.org/10.1111/geb.12660>.
- Tonkin, J.D., Altermatt, F., Finn, D.S., Heino, J., Olden, J.D., Pauls, S.U., Lytle, D.A., 2018. The role of dispersal in river network metacommunities: patterns, processes, and pathways. *Freshw. Biol.* 63, 141–163. <https://doi.org/10.1111/fwb.13037>.
- Tonkin, J.D., Arimoro, F.O., Haase, P., 2016. Exploring stream communities in a tropical biodiversity hotspot: biodiversity, regional occupancy, niche characteristics and environmental correlates. *Biodivers. Conserv.* 25, 975–993. <https://doi.org/10.1007/s10531-016-1101-2>.
- Tonkin, J.D., Shah, R.D.T., Shah, D.N., Hoppeler, F., Jähnig, S.C., Pauls, S.U., 2017. Metacommunity structuring in Himalayan streams over large elevational gradients: the role of dispersal routes and niche characteristics. *J. Biogeogr.* 44, 62–74. <https://doi.org/10.1111/jbi.12895>.
- Tonkin, J.D., Stoll, S., Jähnig, S.C., Haase, P., 2015a. Contrasting metacommunity structure and beta diversity in an aquatic-floodplain system. *Oikos* 125, 686–697. <https://doi.org/10.1111/oik.02717>.
- Tonkin, J.D., Sundermann, A., Jähnig, S.C., Haase, P., 2015b. Environmental controls on river assemblages at the regional scale: an application of the elements of meta-community structure framework. *PLoS One* 10, e0135450. <https://doi.org/10.1371/journal.pone.0135450>.
- Treguer, P., Le Corre, P., 1975. *Analyse des Sels Nutritifs sur AutoAnalyzer II*. Manuel D'Analyse des Sels Nutritifs dans L'Eau de Mer. Université de Bretagne Occidentale, Brest, France.
- Tuhkanen, S., 1992. The climate of Tierra del Fuego from a vegetation geographical point of view and its ecoclimatic counter parts elsewhere. *Acta Bot. Fenn.* 145, 1–64.
- Whittaker, R.H., 1960. Vegetation of the Siskiyou mountains, Oregon and California. *Ecol. Monogr.* 30, 279–338.
- Wolman, M.G., 1954. A method of sampling coarse river-bed material. *Trans. Am. Geophys. Union* 35, 951–956.
- Zuur, A.F., Ieno, E.N., Smith, G.M., 2007. *Analyzing Ecological Data*. Springer Science & Business Media. <https://doi.org/10.1016/B978-0-12-387667-6.00013-0>.