

Verónica Díaz Villanueva · Gustavo Mariluan
Ricardo Albariño

Disturbance disrupts the relation between community similarity and environmental distance at small spatial scale

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Abstract Aquatic invertebrate distribution within a fluvial network is affected both by dispersal capabilities of the species and changes in the environment along spatial gradients. Disturbance that affects part of the network may represent an abrupt change in environmental gradients, which should be reflected on its communities. We analysed whether the composition of benthic insect communities is associated to environmental and geographic distances in a small catchment, partially disturbed by a wildfire (non burned forest-control: C, moderate impacted: I and burned zones: B). We postulated that changes in main resource availability differently affect certain functional feeding groups. We found that taxonomic differences were related to the disturbance condition but not to the distance among streams and that the effect of disturbance targeted mostly on shredders. Environmental differences were larger among C sites than among B sites, but community taxonomic composition was more similar among C than B sites. As a result, neither environmental nor geographic distances explained community similarity. When the analysis was scaled up by incorporating new data from a larger area, community similarity was explained both by environmental and geographic distance, independently (i.e. geographic and environmental distances did not correlate). Our results highlight the influence of a disturbance on the riparian vegetation on the benthic community composition and functional structure of forested streams, and showed the effect of scale in habitat asso-

ciation, as environmental and geographic distance together explained community similarity when the spatial scale was enlarged.

Keywords Species distribution · Functional groups · Benthic community · Stream network · Riparian vegetation

Introduction

Studies on stream invertebrate distribution within a network have revealed that community similarity among stream reaches depends both on the dispersal capability of species that conform the community (Clarke et al. 2008; Altermatt et al. 2013) and environmental gradients along the network (Mykrä et al. 2007; Heino and Mykrä 2008). These two features, environmental gradient and dispersal ability, were taken individually to explain the decrease of community similarity with increasing spatial distance by two opposing theories: niche and neutral, respectively (Tilman 1982; Hubbell 2001). However, both forces shape communities differentially, depending on species traits, e.g. the trophic habits (Thompson and Townsend 2006). For aquatic insects, adults would have the capacity to colonize neighbour streams within a catchment and among catchments greatly depending on their longevity, the number of generations per year which may increase the opportunity to disperse farther (Saito et al. 2015), and dispersal capability of the individuals (e.g. flying) (Hughes 2007). Although dispersal ability depends on a great variety of species traits (for example some small species may passively disperse via wind currents and get far away from the site they emerged), mean maximum dispersal distance is usually less than half the distance among adjacent streams (Clarke et al. 2008). As a consequence, the distribution of insect species with weak dispersal ability may be more constrained by geographical distance than by environmental gradients (Astorga et al. 2012) resulting in higher

V. Díaz Villanueva (✉) · G. Mariluan
Laboratory of Limnology, Instituto de Investigaciones en Biodiversidad y Medioambiente, Consejo Nacional de Investigaciones Científicas y Técnicas, Universidad Nacional del Comahue, Bariloche, Río Negro, Argentina
E-mail: diazv@comahue-conicet.gov.ar
Tel.: +54-294-4428505 (105)

R. Albariño
Laboratory of Photobiology, Instituto de Investigaciones en Biodiversidad y Medioambiente, Consejo Nacional de Investigaciones Científicas y Técnicas, Universidad Nacional del Comahue, Bariloche, Río Negro, Argentina

community similarities among neighbour sites (Altermatt et al. 2013).

Spatial and temporal variations in community composition are also influenced by ecological disturbances. However, the effects of disturbance on diversity may have opposite results. On one hand, disturbance may create new opportunities for species colonization (increasing species diversity) (Hutchinson 1953; Townsend and Scarsbrook 1997; Hawkins et al. 2015), while on the other hand, it may exclude species that lack the adaptations to the new conditions (decreasing species diversity) (Death 2002). Moreover, if ecosystems are characterized by low resilience or if disturbances provoke long lasting structural and functional changes, the new community may persist for years. Summarizing, the effects of disturbances depend both on the spatiotemporal scale of observation (Lepori and Hjerdt 2006; Myers et al. 2015) and on the productivity of the disturbed ecosystem (Cardinale et al. 2009; Sircom and Walde 2011; Tonkin et al. 2012).

Wildfires and logging are well known disturbances in forests, with strong effects also on aquatic environments. Certain effects immediately reach streams, such as altered run-off (Benavides-Solorio and MacDonald 2001), with increasing discharge pulses, soil erosion, sediment and nutrient loading and sedimentation (Sabater et al. 2000; Bladon et al. 2008). Others, as when surrounding plants die, might be long lasting, resulting in higher sunlight incidence, higher temperature fluctuation (Studinski et al. 2012) and reduction in allochthonous organic matter inputs to streams (Pettit and Naiman 2007; Straka et al. 2012). These latest factors would have a positive effect on algal production (Stevenson et al. 1996), so a shift from heterotrophic energy sources to autotrophic ones would be expected (Sabater et al. 2000; Spencer et al. 2003). This shift on the availability of trophic resources at the base of the food web would affect the communities of primary consumers (Benstead and Pringle 2004; Mellon et al. 2008; Díaz Villanueva et al. 2010), depending on trophic habits.

If a disturbance affects species independently of their functional role, as usually do high intensity disturbances, then it is likely that functional diversity remains unaltered and functional redundancy assures the maintenance of ecosystem functioning (Loreau et al. 2001; Giller et al. 2004). On the contrary, disturbances that target all the species of certain functional trophic role would have greater impact on ecosystem functioning (Díaz and Cabido 2001; Schmera et al. 2012). For instance, studies on invertebrate biota in streams affected by fire or deforestation found that collector-gatherer and scraper species were able to take advantage of increased primary production in biofilms, while species with other feeding habits were unable to track resource availability and declined in biomass (Benstead and Pringle 2004; Kasangaki et al. 2008; Mellon et al. 2008; Rugenski and Minshall 2014).

Fire constitutes the main large-scale disturbance factor in Andean–Patagonian forests (Veblen et al. 1992). Our study analysed stream insect community structure within a catchment primarily immersed in a deciduous forest of *Nothofagus pumilio* (Poepp. & Endl.) Krasser in the North Patagonian Andes. The catchment was partially affected by a wildfire 9 years before the survey, but by the time of sampling the forest had not recovered in heavily burned areas. Instead, it became replaced by a shrubby-herbaceous and sparse plant community of *Diostea juncea* (Gillies & Hook.) Miers, *Schinus patagonica* (Phil.) I.M. Johnst. & *Vicia nigricans* Hook. & Arn., among other species (Mermoz et al. 2005). Many of the effects associated with fire (e.g. ash and fine sediment inputs and rapid changes in organic matter inputs and standing stock) would have taken place in the short-term and likely affected aquatic communities detrimentally. Those effects are not attempted to be covered here; instead, we focus on the residual consequences for stream communities associated to the slow-recovery ability characteristic of *Nothofagus* mountain forests (Mermoz et al. 2005) and rapid-recovery potential of invertebrate communities (Fritz and Dodds 2004).

Our aims were to assess if the similarities of the assembly of stream insect communities within a disturbed catchment were more affected by environmental differences or by the distance among sites. Also, we investigated if the disturbance targeted a particular functional feeding group. We assumed that 9 years was enough time to ensure reasonable dispersal and settlement of individuals across the catchment. For this purpose, we examined stream insect species abundance and distribution along a spatial gradient of wildfire intensity. Our hypothesis is that disturbance disrupts the association between community similarity and geographic distance, so that local environmental characteristics are more important in shaping the composition of benthic insect assemblages. On the other hand, spatial scale may strongly affect the patterns of habitat association (Garzon-Lopez et al. 2014). Chase (2014) hypothesized that as scale decreases, stochasticity (geographic distance) is more important than environment in the community structure, and viceversa. Thus, we also assessed the effects of geographic distance and environmental characteristics on community similarity among sites of streams at a larger scale, using published data (Mauad et al. 2015). We expect to find (a) shifted pattern in the proportion of functional feeding groups within communities varying from one dominated by shredder/collector-gatherer guilds at the unburned forest area to one dominated by scraper/collector-filterer guilds at the burned forest catchment, (b), that disturbance plays a drastic role in disrupting the relation between community similarities and geographic distance, and (c) community similarities associated more to environmental characteristics than to geographic distance in a larger scale survey.

Materials and methods

Study area

The study was performed in Chall-Huaco catchment (47 km²), in the Nahuel Huapi National Park (41° 13' S; 71° 20' W, Fig. 1), which represents the easterly driest limit of the *Nothofagus* temperate rain forest in North-Patagonian Andes (Albariño et al. 2009). Headwaters in Patagonia are located in the Andes above 1000 m a.s.l., where streams are canopied by the deciduous endemic mountain beech *Nothofagus pumilio*. Chall-Huaco stream runs from 1500 m a.s.l. to its outlet into Ñireco stream at 950 m a.s.l. Human activity above 1000 m a.s.l. is restricted to hiking.

The studied area covered ca. 4 km² of subalpine forests in the mid valley with different intensities and extension among subcatchments (Kitzberger et al. 2005). Sampling was carried out in nine first to second-order streams, covering a straight distance of 6 km between the farthest sites, covering three contrasting impact degrees (Fig. 1): three streams in an unburned forest area (Control sites: C1, C2, C3), three in marginally affected areas (i.e. Intermediate burned streams, I1, I2, I3); and three in the intense burned area (B1, B2, B3). The Control streams are sub-catchments totally covered by old-growth monospecific forest of *N. pumilio*; the burned streams are sub-catchments with a shrubby-herbaceous vegetation; and the intermediate streams belong to sub-catchments that were partially burned and where small isolated forest fragments and most riparian vegetation remained (I1 and I2), or sub-catchments where only the downstream area was affected (I3). Sites I2 and B1 are

neighbor sub-catchments but strong differences in forest degradation were recorded.

Sampling procedure

Sampling was carried out in February (summer) 2006. Temperature and conductivity were measured at each site with a multiprobe instrument (YSI 85, Yellow Spring, Ohio) and pH with pHmeter (HANNA, HI 8424). Water samples were taken to measure nutrient concentration (phosphorus and nitrate), and fine particulate organic matter in transport (TFPOM). Five cobbles were collected at each site to estimate periphyton biomass.

In the laboratory, soluble reactive phosphorus (SRP) and nitrate (NO₃) concentrations were determined from water subsamples filtered through Whatman GF/F filters. Phosphorus was determined by the ascorbate-reduced molybdenum blue method (APHA 2005). Nitrate was measured as NO₂ after reduction through a cadmium-copper column (Wood et al. 1967) and quantified spectrophotometrically.

Periphytic algal biomass was estimated as chlorophyll *a* concentration (Chl *a*) and periphyton organic matter (OM) as ash free dry mass (AFDM). Cobbles were carried to the laboratory in individual containers in dark and refrigerated. Periphyton was scraped from individual substrates with a nylon brush and washed with distilled water. The obtained sample was homogenised and an aliquot of 1 ml was used for chlorophyll *a* estimation. Extraction was done with hot 90% ethanol (Nusch 1980) and measurements were carried out in a fluorometer (Turner designs 10-AU). Periphyton OM was deter-

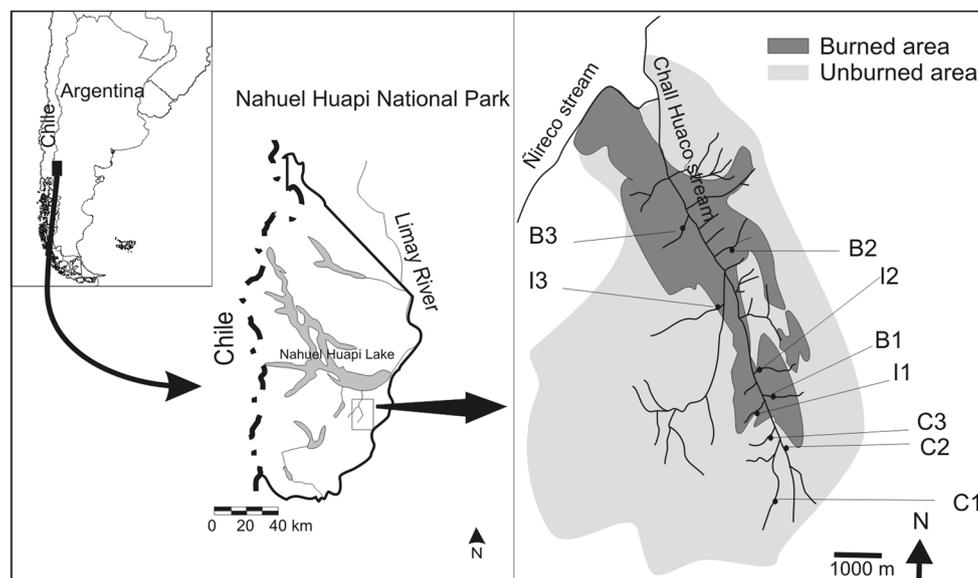


Fig. 1 Map shows the study area, located in the Nahuel Huapi National Park, in the northern Patagonian Andean region of Argentina, and the study sites in the Chall-Huaco catchment, three

in the burned area (B1, B2 and B3), three in the marginal area (intermediate disturbance, I1, I2 and I3) and three in the unburned area (C1, C2 and C3)

mined by filtering a 5-ml aliquot onto pre-weighed and pre-combusted Whatman GF/C filters and dried at 80 °C for 48 h. The filters were weighed, combusted at 550 °C for 1 h and re-weighed, considering that OM was the difference in mass before and after incineration, i.e. AFDM (APHA 2005). The total surface of each sampled stone was estimated from the length of its three main axes.

Benthic leaf litter was sampled together with insect samples (see below). In the laboratory, leaves were separated from woody debris and fine organic fragments to quantify leaf litter mass. Dry mass was obtained by oven-dried at 60 °C for 48 h and weighed to the nearest 0.1 mg.

Benthic aquatic invertebrates were collected from riffles with a Surber sampler (0.09 m⁻², 250 µm mesh size, $n = 5$ per site). Although we did not survey pools, a recent study in the catchment reported that pools cover < 40% of stream bottoms and have no exclusive taxa compared to riffles (Mariluan 2017). Thus our sampling procedure had a good representation of species richness. Samples were preserved in 5% formalin until processing. In the laboratory samples were washed through 1.00, 0.50 and 0.25 mm sieves to facilitate invertebrate sorting. Invertebrates were separated and preserved in 90% ethanol until counting. Identification of insect larvae was carried out under a stereomicroscope to the lowest possible taxonomic level. Oligochaetes and Platyhelminthes were also present but they were not taken into account in the analysis, as they greatly differ in their dispersal capacities due to the lack of a terrestrial winged stage. For insect larvae, individuals of each taxa were counted and dried at 80 °C for 24 h and weighed to the nearest 0.01 mg to obtain abundance and biomass, respectively. Each Surber sample was quantified separately.

Insect larvae were assigned to five functional feeding groups (FFGs): collector-gatherers (CG), collector-filterers (CF), shredders (Sh), scrapers (S) and predators (P), following general literature (Merritt and Cummins 1996), and specific works from the area (Díaz Villanueva and Albarino 1999; Velásquez and Miserendino 2003; Díaz Villanueva et al. 2004; Albariño and Díaz Villanueva 2006).

Data analysis

Principal Component Analysis (PCA) on seven environmental variables (water temperature, conductivity, SRP, NO₃, periphytic OM and Chl *a* concentration, and TFPOM) was performed after normalizing variables to identify those most responsible for the spatial variation among streams, using PRIMER v.6.1.6 (Primer-E Ltd 2006., Plymouth, UK). Differences among stream types (three levels of fire intensity: Control, Intermediate and Burned) were analyzed with one way-ANOVA (Quinn and Keough 2002) using SigmaPlot v.12.5.

Community similarity (CS) between pair of streams was calculated with Bray–Curtis index using mean taxa abundance [after log ($x + 1$) transformation] per stream. Although five samples per site were quantified separately, we used mean stream values as replicates (three streams per disturbance level, 3 × 3) to avoid pseudo-replication within each stream (i.e. Surber samples). Environmental distance (ED) between each pair of streams was obtained from the Euclidean distance matrix on environmental data. We performed these matrix analyses using the statistical package PRIMER (version 6.1.6, PRIMER-E Ltd 2006). Geographic distance (GD) was measured as the straight length between stream sites for each pair of stream combinations. We preferred this measurement instead of the distance between sites along the watercourse, because instream connectivity between sites should assume upstream movement, which is less likely to occur than terrestrial dispersal by insect adults. Simple linear distance has been used as a proxy for physical constraints to stream invertebrate movement between streams (Finn et al. 2006).

To test the relationships between community dissimilarity, environmental distance and geographic distance, matrix correlation was assessed using permutation Mantel tests (Legendre and Legendre 2012). While Mantel test analyses significant correlation between two matrices, partial-Mantel test do the same for three or more matrices. Essentially, it allows a comparison between two matrices while controlling for (or removing the effect of) a third one. Therefore, when strong correlation between matrices was detected (Mantel $R > 0.5$ and $P < 0.01$), partial Mantel tests were used to assess correlation between community dissimilarity and the matrix of interest, while controlling for the second matrix (Legendre and Legendre 2012).

The effect of spatial scale was assessed using a database from a recent study which described stream invertebrate communities in the Ñireco catchment (Mauad et al. 2015). The study included sites with similar and higher stream order and a more diverse canopy cover; we excluded from the analysis sites under urban development to avoid incorporating a new human-driven impact. Such study did not include sites within the fire-impacted area, and differences in vegetation cover were related to natural gradients (from forest to open vegetation). The catchment has an area of 74 km² and the maximum distance between further streams was 11 km. Data on Mauad et al. (2015) was analysed using the same indexes (community similarity, environmental and spatial distances), and the relation among matrices was analysed with Mantel test.

Aquatic invertebrate assemblages were compared using analysis of similarities (one way-ANOSIM with 1000 iterations, (Clarke and Warwick 2001)), which assesses the differences among invertebrate assemblages based on the rank similarities from the Bray–Curtis similarity matrices, with fire intensity as factor (three levels). Non-metric Multidimensional scaling (nMDS) was applied to visualize the ordination of sites according

Table 1 Physical and chemical characteristics, and resource abundance of sampled streams

	C1	C2	C3	I1	I2	I3	B1	B2	B3
Burning severity	Unburned (control)			Intermediate			High (burned)		
Catchment area (km ²)	0.14	0.35	0.12	0.26	0.16	0.46	0.21	0.24	0.26
T (°C)	8.5	9	9.8	13	8.8	16	10.2	14	17
pH	6.98	7.20	7.44	7.40	7.40	7.60	7.30	7.56	7.30
Conductivity (µS cm ⁻¹)	50	71	81	68	87	93	72	85	52
SRP (µg L ⁻¹)	< 2	7.47	8.62	3.69	2.5	4.19	< 2	< 2	< 2
NO ₃ (µg L ⁻¹)	4.52	23.42	85.01	82.60	28	9.55	1.7	2.00	9.41
TFPOM (mg L ⁻¹)	1.70 ± 0.30	2.00 ± 0.30	2.80 ± 0.90	1.20 ± 0.10	0.87 ± 0.04	1.23 ± 0.01	0.67 ± 0.12	1.05 ± 0.02	1.54 ± 0.07
Chlorophyll <i>a</i> (µg cm ⁻²)	9.2 ± 2.1	51.5 ± 13.5	11.2 ± 1.9	33.5 ± 7.4	16.1 ± 3.7	35.8 ± 5.5	41.3 ± 21.6	24.5 ± 3.7	37.8 ± 5.6
Periphytic organic matter (mg cm ⁻²)	18.7 ± 3.0	40.0 ± 5.5	41.3 ± 12.5	37.0 ± 6.0	31.7 ± 3.3	65.0 ± 12.1	57.7 ± 3.9	36.1 ± 4.9	44.7 ± 5.9
Leaf litter (g m ⁻²)	0.76 ± 0.13	1.30 ± 0.40	0.69 ± 0.40	0.64 ± 0.40	0.34 ± 0.06	0.27 ± 0.08	0.09 ± 0.09	0.00	0.03 ± 0.03

Some data of phosphorus concentration was below detection value (< 2 µg L⁻¹)
 C control, I intermediate, B burned, SRP soluble reactive phosphorus, TFPOM fine particulate organic matter in transport

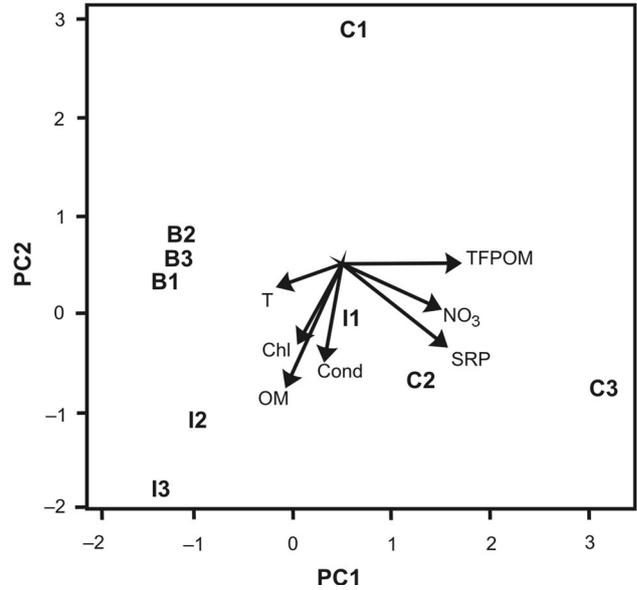


Fig. 2 Distribution of study sites in the control area (C1, C2 and C3), in the marginal area (I1, I2 and I3) and in the burned area (B1, B2 and B3) based on environmental (*T* temperature, *Cond* conductivity, *NO₃* nitrate and *SRP* soluble reactive phosphorus), and biological (*Chl* chlorophyll *a* concentration, *OM* periphyton organic matter, *TFPOM* fine particulate organic matter in transport) variables according to a principal component analysis (PCA)

to insect species and functional feeding group abundance. Insect abundance data was transformed by log (*x* + 1) to down-weight high abundances. When there were significant differences, post hoc Tukey tests were used to account for multiple comparisons among stream types. When ANOSIM revealed significant differences, we used the species contributions to similarity (SIMPER) to identify which taxa were responsible for the observed differences in assemblages. We performed these multivariate analyses using the statistical package PRIMER (version 6.1.6, PRIMER-E Ltd 2006, PML Luton, England).

Results

Local habitat conditions

Although some environmental variables varied among streams, when data was analysed according to stream type there was little variation (Table 1). However, the ordination of sites based exclusively on these characteristics showed segregation in PC1 between Control and Burned sites, while Intermediate streams distributed near to Control sites (ANOVA, *P* = 0.027, Fig. 2). The first two PCs explained 62.8% of the variation. Control sites distributed in the positive values of the PC1 (which explained 35.2% of the variation) and Burned sites in the negative side. PC1 was positively correlated with TFPOM (linear combination coefficient = 0.56) and nutrient concentrations (linear combination coefficient

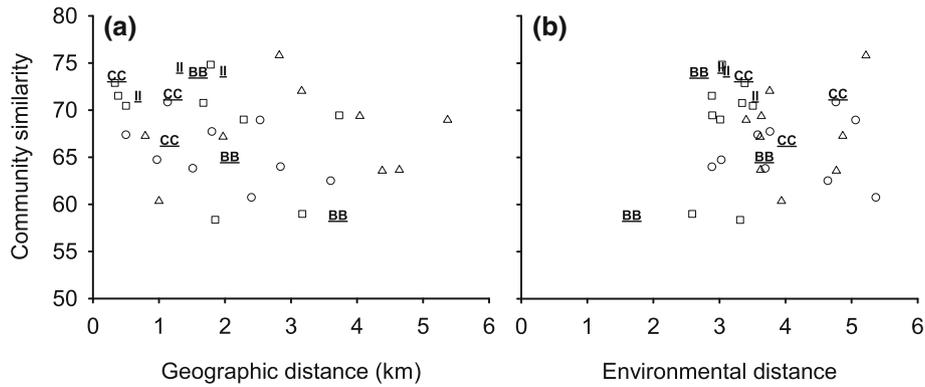


Fig. 3 Community similarity index (Bray-Curtis) of sites based on taxonomic composition of insect in Chall-Huaco catchment, plotted against **a** geographic linear distance, and **b** environmental distance (Euclidean distance) for all pairwise comparisons. Comparisons between sites with the same impact (*CC* Control-Control,

II Intermediate-Intermediate, and *BB* Burned-Burned) are underlined; comparisons between Control-Intermediate sites are represented with circles, between Burned-Intermediate sites with squares and between Control-Burned sites with triangles

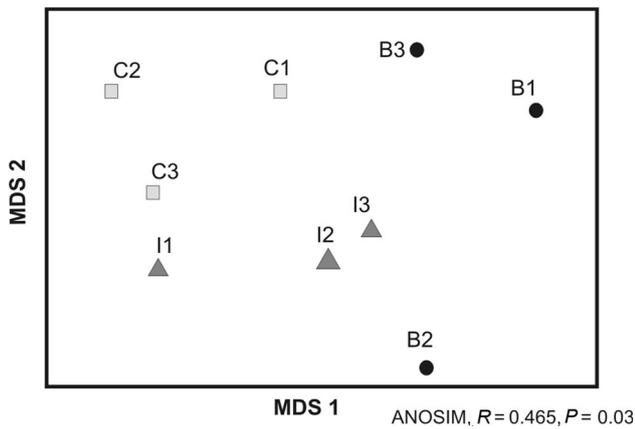


Fig. 4 Multidimensional scaling (MDS) ordinations of sites in the control area (C1, C2 and C3), in the intermediate area (I1, I2 and I3) and in the burned area (B1, B2 and B3) based on insect species abundance

SRP = 0.50 and $\text{NO}_3 = 0.46$). The PC2 (which explained 27.6% of the variation) did not discriminate among sites (ANOVA $P = 0.350$) and was negatively related to periphyton OM (0.61) and conductivity (0.49).

Taxonomic composition

Total insect abundance did not differ among stream types (KW, $H = 1.16, P = 0.56$), but total community biomass was lower in Burned streams than in the other two stream types, which did not differ (KW, $H = 13.12, P = 0.001$, Table 2). A total of 27 insect taxa were recorded, belonging to 19 families of 5 orders (Table 2). All taxa found corresponded to larval stages of terrestrial adults.

Community similarity among sites was $> 58\%$ and it was neither correlated to GD nor ED (partial-Mantel tests, $P = 0.064, P = 0.382$ for each independent variable, respectively). In particular, there were three pairs of sites very close to each other (i.e. low GD: C2-

B1, C3-B1 and I1-B1) with highly dissimilar communities, which were responsible for this lack of relation (Fig. 3). When this analysis was applied to the dataset of Ñireco catchment, CS among sites was significantly explained by GD and ED (partial-Mantel tests, $P = 0.005, P = 0.009$ respectively).

Eight taxa were common to all streams and 15 out of 27 taxa (55%) were common to all stream types. Despite this similarity, MDS ordination analyses showed a gradient from impacted to not impacted streams (Fig. 4), that significantly differed in community composition (ANOSIM, Global Rho: 0.465, $P = 0.032$, Tukey post hoc $P < 0.05, C = I, I = B, C \neq B$). According to SIMPER analysis, differences were higher between Control and Burned streams than either between Intermediate-Control and Intermediate-Burned streams (Table 3), and taxa that most contributed to the differences were Tipulidae sp. 3 and the caddisflies *Myotrichia murina* and *Smicridea frequens*, which were more abundant in Control streams. Intermediate streams were more similar to Control than to Burned streams (Table 3), and the species that contributed to this difference were Tipulidae sp. 1 and sp. 2 and *M. murina* (5.93%), which were more abundant in Control streams. The species that most contributed to the differences between Burned-Intermediate were *M. murina* and the caddisfly *Reochorema* sp., more abundant in Intermediate streams, and the plecopteran *Austronemoura* sp., more abundant in Burned streams (Tables 2 and 3). Eight taxa were absent in Burned streams and three species were absent in Control streams, two Baetidae and one Ephyridae species (Table 2). Only one species (the large-sized scraper larvae of *Notoperla archiplatae*) was absent at intermediate impacted streams.

Functional composition

The five FFGs were found in all the streams (Table 2). Among collector-gatherers, Ephyridae sp. was absent

Table 2 Insect taxa abundance and total insect abundance (mean \pm standar error, ind m⁻²), and their corresponding functional feeding groups (FFG): Predators (P), Collector–gatherers (CG), Collector–filterers (CF), Scrapers (S) and Shredders (Sh)

		0-10	10-50	50-100	100-500	500-1000	>1000				
		FFG	C1	C2	C3	I1	I2	I3	B1	B2	B3
Diptera											
Ahericidae											
	<i>Dasyomma</i> sp.	P	244 ±67	89 ±14	58 ±12	39 ±12	96 ±67	89 ±25	181 ±76	49 ±27	13 ±2
	Ceratopogonidae	P	33 ±11	42 ±21	67 ±25	100 ±48	128 ±29	367 ±192	48 ±23	93 ±39	78 ±42
	Chironomidae	CG	756 ±322	173 ±76	253 ±101	297 ±173	1056 ±274	3324 ±176	501 ±153	1044 ±231	1098 ±186
Empididae											
	<i>Chelifera</i> sp.	P	28 ±17	20 ±10	20 ±4	6 ±6	5 ±	24 ±	0	36 ±	7 ±
	Ephydriidae	CG	0	0	0	3 ±3	5 ±4	89 ±83	0	76 ±22	0
	Simuliidae	CF	433 ±211	11 ±6	480 ±408	139 ±75	187 ±97	780 ±255	187 ±91	453 ±151	78 ±54
Tipulidae											
	Tip sp. 1	Sh	0	0	18 ±7	11 ±11	0	4 ±3	0	7 ±7	2 ±2
	Tip sp. 2	Sh	0	0	13 ±11	0	33 ±10	16 ±8	3 ±3	4 ±4	0
	Tip sp. 3	Sh	561 ±150	11 ±6	727 ±155	8 ±5	0	0	0	0	0
	Tip sp. 4	Sh	6 ±6	0	2 ±2	0	0	0	0	0	0
Ephemeroptera											
Leptophlebiidae											
	<i>Meridialaris chiloensis</i>	S	517 ±328	64 ±44	411 ±69	317 ±36	613 ±148	209 ±48	1125 ±391	193 ±91	67 ±26
Baetidae											
	<i>Andesiops peruvianus</i>	S	0	0	0	0	0	9 ±9	0	0	116 ±76
	<i>Andesiops torrens</i>	S	0	0	0	6 ±6	5 ±4	38 ±21	27 ±19	0	27 ±24
Nesameletidae											
	<i>Metamonius anceps</i>	S	28 ±6	0	2 ±2	6 ±6	0	9 ±9	0	0	0
Plecoptera											
Austroperlidae											
	<i>Klapopteryx kuscheli</i>	Sh	117 ±94	344 ±97	82 ±24	133 ±34	117 ±10	120 ±65	507 ±11	9 ±6	40 ±12
Gripopterygidae											
	<i>Aubertoperla illesi</i>	S	22 ±11	64 ±44	0	42 ±23	11 ±4	229 ±52	11 ±4	29 ±12	642 ±322
	<i>Chilenoperla</i> sp.	Sh	22 ±11	196 ±72	18 ±10	3 ±3	37 ±15	36 ±14	5 ±4	0	13 ±8
	<i>Notoperla archiplatae</i>	S	11 ±6	9 ±4	2 ±2	0	0	0	0	0	36 ±36
	<i>Notoperlopsis femina</i>	S	0	2 ±2	0	3 ±3	0	0	0	0	0
Notonemouridae											
	<i>Austronemoura</i> sp.	Sh	211 ±72	0	2 ±2	0	43 ±4	0	219 ±52	0	24 ±24
	<i>Udamocercia arumifera</i>	Sh	6 ±3	82 ±44	7 ±7	28 ±16	0	107 ±20	11 ±4	0	18 ±6
	<i>Neofulla</i> sp.	Sh	0	0	7 ±7	0	0	4 ±0	0	0	0
Trichoptera											
Hydropsychidae											
	<i>Smicridea frequens</i>	CF	94 ±72	136 ±64	182 ±69	36 ±16	43 ±24	44 ±37	0	27 ±22	24 ±11
Hydrobiosidae											

Table 2 continued

	FFG	C1	C2	C3	I1	I2	I3	B1	B2	B3
<i>Reochorema</i> sp.	P	6 ±3	11 ±6	18 ±8	50 ±46	64 ±17	60 ±28	0	4 ±4	11 ±9
Limnephilidae										
<i>Monocosmoecus</i> sp.	Sh	0	4 ±3	4 ±3	64 ±31	0	0	0	0	0
Limnephilidae sp. 1	Sh	0	0	2 ±2	8 ±8	0	0	0	0	0
Sericostomatidae										
<i>Myotrichia murina</i>	Sh	0	11 ±7	556 ±54	94 ±41	64 ±39	0	0	0	0
<i>Parasericostoma cristatum</i>	Sh	0	0	2 ±2	0	11 ±4	11 ±7	0	0	0
Coleoptera										
Scirtidae	S	33 ±16	4 ±3	11 ±5	36 ±36	0	2 ±2	0	0	0
Elmidae										
<i>Austrelmis</i> sp.	CG	67 ±18	216 ±46	58 ±29	381 ±129	21 ±14	82 ±20	21 ±14	16 ±8	13 ±6
Total abundance (ind. m ⁻²)		3194 ±1019	1488 ±253	2997 ±460	1808 ±540	5728 ±575	2538 ±597	2848 ±661	2300 ±400	2040 ±370
Total biomass (g m ⁻²)		1.70 ±0.60	3.30 ±0.70	2.22 ±0.43	1.15 ±0.40	3.07 ±0.70	0.75 ±0.15	0.57 ±0.17	1.03 ±0.31	0.70 ±0.06
		Control			Intermediate			Burned		
Mean total abundance (ind m ⁻²)		2560±535			3358±1203			2398±238		
Mean biomass (g m ⁻²)		2.22±0.55			1.66±0.55			0.77±0.13		

Grey scale from white to black visually emphasizes abundance-ranges

Table 3 Similarity values according to SIMPER analyses within and among control, intermediate and burned streams, and species that most contributed to the similarities within stream types (to more than 50%) and species that most contributed to dissimilarities among stream sites (to 20%)

Control sites average similarity: 73.97%	%	Intermediate sites average similarity: 72.48%	%	Burned sites average similarity: 66.48%	%
Chironomidae	9.78	Chironomidae	10.40	Chironomidae	17.08
<i>Meridialaris chiloensis</i>	8.84	<i>M. chiloensis</i>	9.30	Simuliidae	12.37
Smicridea	8.67	Simuliidae	8.55	<i>M. chiloensis</i>	12.15
<i>Klapopteryx kuscheli</i>	8.40	<i>K. kuscheli</i>	8.10	Ceratopogonidae	10.70
Athericidae	7.81	Ceratopogonidae	7.97		
Elmidae	7.63	<i>Reochorema</i> sp.	6.77		
Total contribution to similarity	51.13		51.09		52.30
Control-intermediate average similarity: 69.53%	%	Control-burned average similarity: 63.69%	%	Intermediate-burned average similarity: 67.56%	%
Tipulidae sp. 3	7.29	Tipulidae sp. 3	7.73	<i>M. murina</i>	6.63
Tipulidae sp. 2	6.71	<i>M. murina</i>	6.29	<i>Reochorema</i> sp.	6.05
<i>Myotrichia murina</i>	5.93	Smicridea	5.81	<i>Austronemoura</i> sp.	5.71
Total contribution to dissimilarity	19.93		19.82		18.39

in all the control samples. Collector-filterers were represented by Simuliidae and *Smicridea frequens*, which were present in all stream types. Shredders were the best represented FFG, with up to 13 species in C3 and only 3-5 species in the burned sites. There were also more species of scrapers in control and intermediate streams than in burned streams. Four predator species were found and they were present in all sites (Table 2).

When analysed in terms of biomass, we found a shift in the dominance of shredders in control streams (ANOVA, $P = 0.001$) to one dominated by scrapers in burned streams (marginally significant, ANOVA, $P = 0.065$) (Fig. 5). The proportions of the other FFGs were similar among stream types (ANOVA, $P_{CG} = 0.077$; $P_{CF} = 0.907$, $P_P = 0.884$).

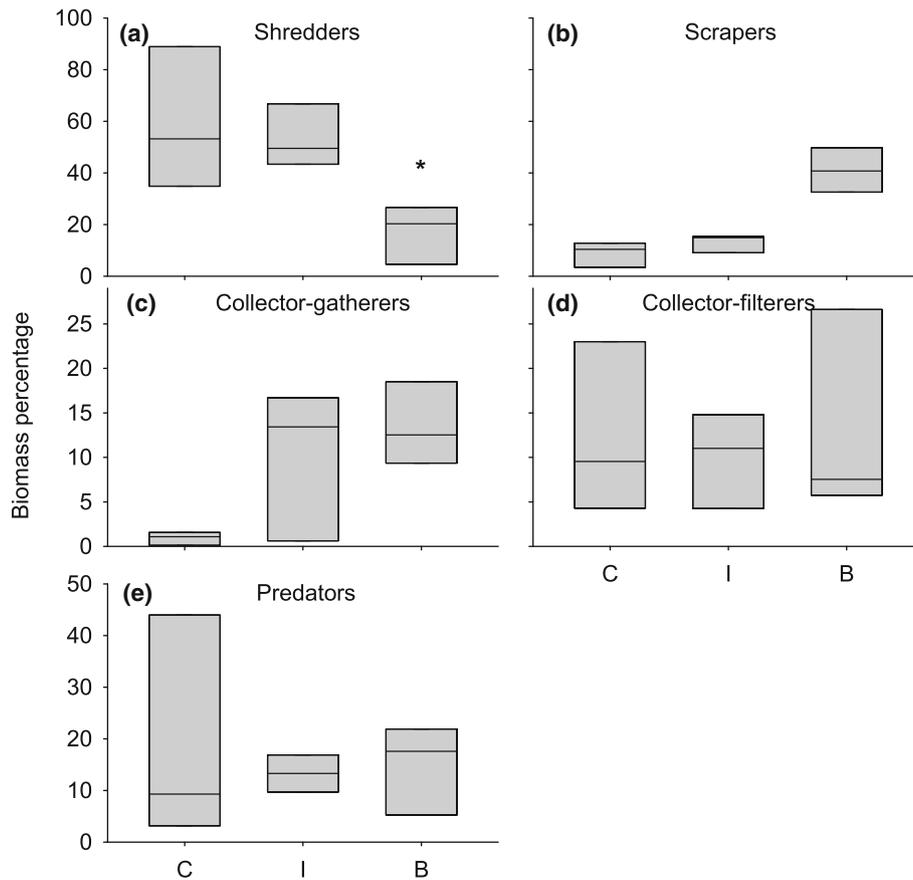


Fig. 5 Percentage of the different functional feeding groups at control (C), intermediate (I) and burned (B) areas calculated in terms of biomass (mg m^{-2}). Asterisk indicates a posteriori significant differences ($P < 0.05$) with the other two sites

Discussion

When environmental and geographic distances are correlated, it is difficult to separate each effect on species distribution (Thompson and Townsend 2006; Astorga et al. 2012; Heino et al. 2015). In our study, ED among streams was not related to GD, as both distant and close sites had either similar or dissimilar environmental features, but ED was related to residual fire disturbance. As a result, community similarity in adjacent sites but with contrasting disturbance history was low. In this sense, our hypothesis of a disruption of the association between community similarity and geographic distance in a disturbed catchment could not be rejected. This result suggests that community recovery, even when species may be good dispersers, was precluded by prevailing environmental conditions. But, at the same time, sites with similar disturbance history (as B1 and B3) had also lower community similarities than expected. The lack of correlation between community similarity and GD or ED might be in part explained by the scale of our study. However, as disturbances by definition are unpredictable alterations with varied spatial intensity and extension over ecosystems, we argue that the legacy of a

wildfire did strongly disrupt environment/community relationships along the spatial landscape.

Interestingly, the scale of study was crucial since when expanded it within the stream network (from 5 km to ~ 20 km), CS was negatively related both to environmental and geographic distances. Garzon-Lopez et al. (2014) found that patterns of habitat association (the association between species distribution and environmental factors) are strongly affected by the choice of sampling scale and location. They generated a conceptual model in which the probability of finding habitat associations increases with spatial scale. Although they worked with tree species, this concept could be applied to other ecosystems. In our study, the disrupting effect of fire disturbance on community structure was observed at small scale study. A recent study in our area covering a much larger scale (mean distances ~ 160 km) which focused exclusively on the shredder guild assemblage colonising leaf litter in pristine forested streams, found no significant relationship between CS and GD, but a negative relation between CS and ED (Boyero et al. 2015). This suggests that regionally, the relationship between CS and ED is held while that between CS and GD may be more complex.

The disturbance affected not only the community taxonomic composition but also its trophic structure, as it targeted one specific FFG reducing shredder biomass. Trophic similarities between communities in some of our intermediate impacted streams with control streams suggest that, as canopy cover recovers, community functional structure does recover too. Burned streams had not only less shredder species richness but also had reduced abundance and biomass, probably attributed to the low resource inputs from the sparse shrubby riparian vegetation. Although in our study leaf litter amount was low in all sites due to the timing of sampling (summer), a recent study showed that leaf litter standing stock in May was three times higher in unburned forest streams than in the burned sites (Mariluan 2017). Thus, the low resilience to wildfires which characterises subalpine forests of *N. pumilio* in xeric and semi-xeric areas (Mermoz et al. 2005) of Patagonia drives strong and long lasting effects on the trophic structure of streams also affecting ecosystem functioning.

The species that most contributed to the difference between control and burned streams were Tipulidae sp. 3 and the caddisflies *Myotrichia murina* (both shredders) and *Smicridea frequens* (collector-filterer). Although there are detritivores that may display diet plasticity as generalist feeders (Mihuc and Minshall 1995), certain species are highly dependent on leaf litter as food (Hall et al. 2000). An example of this strong trophic interaction in headwater streams of Patagonia Andes is the plecopteran *Klapopteryx kuscheli*, one of the most conspicuous and frequent species, which has been described as strict shredder (Albariño and Díaz Villanueva 2006). In our study, *K. kuscheli* showed a clear distribution pattern with higher biomass in control and intermediate sites. Although it was more abundant in one of the burned sites (B1), the numerous larvae had very low individual biomass, as they were mostly early instars. Because stream B1 is very close to two streams of intermediate impact (I2 and I3), it is possible that females would have been laying eggs back in the stream (i.e. recolonising process). This species in the region has semivoltine life cycles with overlapping cohorts and late instar larvae can be found year round. The absence of late instar larvae in this stream suggests the species is having low recolonisation success.

Contrary to our expectations, we did not find a shift from heterotrophic energy source to a more autotrophic base in the burned sites since algal biomass (periphytic Chl *a* concentration and OM content) was higher in one of the forest sites (C2) and one of the burned sites (B2), without a clear difference among stream types. Higher algal biomass in forested streams than in open sites has been previously described in other reaches of the same network (Díaz Villanueva et al. 2010). Those findings emphasise that algal biomass per se is not be a good indicator of grazer abundance; this is especially true when periphyton is rapidly converted to grazer biomass, instead of resulting in high periphyton standing stock (McIntire et al. 1996). Cooper et al. (2015) showed that

invertebrate diets in streams with burned riparian vegetation were based on higher proportions of algal material than on riparian plant detritus relative to those from streams with unburned vegetation. The increase in scraper abundance in our burned streams (some Chironomidae and the presence of Baetidae species) is a common pattern in post-fire streams (Mellon et al. 2008; Rugenski and Minshall 2014) and may respond to an increase in primary production, which may be immediately transformed into secondary production.

Metacommunity structure is shaped by geographic distance and environmental differences among locations within fluvial (dendritic) networks (Tonkin et al. 2015, 2016). Relationships between community similarity and geographic or environmental distances are not always explained by simple models (e.g. linear relations) especially when long lasting disturbances occur.

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References

- Albariño RJ, Díaz Villanueva V (2006) Feeding ecology of two plecopterans in low order Andean-Patagonian Streams. *Int Rev Hydrobiol* 91:122–135
- Albariño R, Villanueva VD, Buria L (2009) Leaf litter dynamics in a forested small Andean catchment, northern Patagonia, Argentina. In: Oyarzún C, Verhoest N, Boeckx P, Godoy R (eds) *Ecological advances on Chilean temperate rainforests* Academia Press, Ghent, Belgium, pp 183–211
- Altermatt F, Seymour M, Martínez N, Sadler J (2013) River network properties shape α -diversity and community similarity patterns of aquatic insect communities across major drainage basins. *J Biogeogr* 40:2249–2260
- APHA (2005) *Standard methods for the examination of water and wastewater*. American Public Health Association, Washington, DC
- Astorga A, Oksanen J, Luoto M, Soinen J, Virtanen R, Muotka T (2012) Distance decay of similarity in freshwater communities: do macro- and microorganisms follow the same rules? *Global Ecol Biogeogr* 21:365–375
- Benavides-Solorio J, MacDonald LH (2001) Post-fire runoff and erosion from simulated rainfall on small plots, Colorado Front Range. *Hydrol Process* 15:2931–2952
- Benstead JP, Pringle CM (2004) Deforestation alters the resource base and biomass of endemic stream insects in eastern Madagascar. *Freshw Biol* 49:490–501
- Bladon KD, Silins U, Wagner MJ, Stone M, Emelko MB, Mendoza CA, Devito KJ, Boon S (2008) Wildfire impacts on nitrogen concentration and production from headwater streams in southern Alberta's Rocky Mountains. *Can J Forest Res* 38:2359–2371
- Boyero L, Pearson RG, Swan CM, Hui C, Albariño RJ, Arunachalam M, Callisto M, Chará J, Chará-Serna AM, Chauvet E (2015) Latitudinal gradient of nestedness and its potential drivers in stream detritivores. *Ecography* 38:949–955
- Cardinale BJ, Bennett DM, Nelson CE, Gross K (2009) Does productivity drive diversity or vice versa? A test of the multi-variate productivity–diversity hypothesis in streams. *Ecology* 90:1227–1241
- Chase JM (2014) Spatial scale resolves the niche versus neutral theory debate. *J Veg Sci* 25:319–322

- Clarke KR, Warwick RM (2001) PRIMER v5: user manual/tutorial. Primer-E Limited, Plymouth, UK
- Clarke A, Mac Nally R, Bond N, Lake PS (2008) Macroinvertebrate diversity in headwater streams: a review. *Freshw Biol* 53:1707–1721
- Cooper SD, Page HM, Wiseman SW, Klose K, Bennett D, Even T, Sadro S, Nelson CE, Dudley TL (2015) Physicochemical and biological responses of streams to wildfire severity in riparian zones. *Freshw Biol* 60:2600–2619
- Death RG (2002) Predicting invertebrate diversity from disturbance regimes in forest streams. *Oikos* 97:18–30
- Díaz S, Cabido M (2001) Vive la différence: plant functional diversity matters to ecosystem processes. *Trends Ecol Evol* 16:646–655
- Díaz Villanueva V, Albarino RJ (1999) Feeding habit of Notoperla archiplatae (Plecoptera) larvae in a North Patagonia Andean stream, Argentina. *Hydrobiologia* 412:43–52
- Díaz Villanueva V, Albariño RJ, Modenutti B (2004) Grazing impact of two aquatic invertebrates on periphyton from an Andean-Patagonian stream. *Arch fur Hydrobiol* 159:455–471
- Díaz Villanueva V, Buria L, Albariño R (2010) Primary consumers and resources: annual variation in two contrasting reaches of a Patagonian mountain stream. *Ann Limnol Int J Limnol* 46:21–28
- Finn DS, Theobald DM, Black WC, Poff NL (2006) Spatial population genetic structure and limited dispersal in a Rocky Mountain alpine stream insect. *Mol Ecol* 15:3553–3566
- Fritz KM, Dodds WK (2004) Resistance and resilience of macroinvertebrate assemblages to drying and flood in a tall-grass prairie stream system. *Hydrobiologia* 527:99–112
- Garzon-Lopez CX, Jansen PA, Bohlman SA, Ordóñez A, Olf H (2014) Effects of sampling scale on patterns of habitat association in tropical trees. *J Veg Sci* 25:349–362
- Giller PS, Hillebrand H, Berninger UG, Gessner M, Hawkins S, Inchausti P, Inglis C, Leslie H, Malmqvist B, Monaghan MT, Morin PJ, O'Mullan G (2004) Biodiversity effects on ecosystem functioning: emerging issues and their experimental test in aquatic environments. *Oikos* 104:423–436
- Hall RO Jr, Wallace JB, Eggert SL (2000) Organic matter flow in stream food webs with reduced detrital resource base. *Ecology* 81:3445–3463
- Hawkins CP, Mykrä H, Oksanen J, Vander Laan JJ (2015) Environmental disturbance can increase beta diversity of stream macroinvertebrate assemblages. *Global Ecol Biogeogr* 24:483–494
- Heino J, Mykrä H (2008) Control of stream insect assemblages: roles of spatial configuration and local environmental factors. *Ecol Entomol* 33:614–622
- Heino J, Melo AS, Siqueira T, Soininen J, Valanko S, Bini LM (2015) Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. *Freshw Biol* 60:845–869
- Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography (MPB-32), vol 32. Princeton University Press, Princeton
- Hughes JM (2007) Constraints on recovery: using molecular methods to study connectivity of aquatic biota in rivers and streams. *Freshw Biol* 52:616–631. <https://doi.org/10.1111/j.1365-2427.2006.01722.x>
- Hutchinson GE (1953) The concept of pattern in ecology. *Proc Acad Nat Sci Phila* 105:1–12
- Kasangaki A, Chapman LJ, Balirwa J (2008) Land use and the ecology of benthic macroinvertebrate assemblages of high-altitude rainforest streams in Uganda. *Freshw Biol* 53:681–697
- Kitzberger T, Raffaele E, Heinemann K, Mazzarino MJ (2005) Effects of fire severity in a north Patagonian subalpine forest. *J Veg Sci* 16:5–12
- Legendre P, Legendre LF (2012) Numerical ecology, vol 24. Elsevier, Oxford, UK
- Lepori F, Hjerdt N (2006) Disturbance and aquatic biodiversity: reconciling contrasting views. *Bioscience* 56:809–818
- Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A, Hooper DU, Huston MA, Raffaelli D, Schmid B, Tilman D, Wardle DA (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294:804–808
- Mariluan GD (2017) Caracterización de arroyos de cabecera temporarios y permanentes del norte de la patagonia andina. Phd, Universidad Nacional del Comahue
- Mauad M, Miserendino ML, Risso MA, Massaferró J (2015) Assessing the performance of macroinvertebrate metrics in the Challhuaco-Nireco System (Northern Patagonia, Argentina). *Iheringia Série Zool* 105:348–358
- McIntire CD, Gregory SV, Steinman AD, Lamberti GA (1996) Modeling benthic algal communities: an example from stream ecology. In: Stevenson RJ, Bothwell ML, Lowe RL, Thorp JH (eds) *Algal ecology: freshwater benthic ecosystem*. Academic Press, San Diego, pp 669–704
- Mellon CD, Wipfli MS, Li JL (2008) Effects of forest fire on headwater stream macroinvertebrate communities in eastern Washington, U.S.A. *Freshw Biol* 53:2331–2343
- Mermoz M, Kitzberger T, Veblen T (2005) Landscape influences on occurrence and spread of wildfires in patagonian forests and shrublands. *Ecology* 86:2705–2715
- Merritt RW, Cummins KW (1996) An introduction to the aquatic insects of North America. Kendall Hunt, Dubuque
- Mihuc T, Minshall GW (1995) Trophic generalists vs. trophic specialists: implications for food web dynamics in post-fire streams. *Ecology* 76:2361–2372
- Myers JA, Chase JM, Crandall RM, Jiménez I, Austin A (2015) Disturbance alters beta-diversity but not the relative importance of community assembly mechanisms. *J Ecol* 103:1291–1299. <https://doi.org/10.1111/1365-2745.12436>
- Mykrä H, Heino J, Muotka T (2007) Scale-related patterns in the spatial and environmental components of stream macroinvertebrate assemblage variation. *Global Ecol Biogeogr* 16:149–159. <https://doi.org/10.1111/j.1466-8238.2006.00272.x>
- Nusch E (1980) Comparison of different methods for chlorophyll and phaeopigment determination. *Arch Hydrobiol* 14:14–36
- Pettit NE, Naiman RJ (2007) Fire in the Riparian Zone: characteristics and ecological consequences. *Ecosystems* 10:673–687. <https://doi.org/10.1007/s10021-007-9048-5>
- Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge
- Rugenski AT, Minshall GW (2014) Climate-moderated responses to wildfire by macroinvertebrates and basal food resources in montane wilderness streams. *Ecosphere*. <https://doi.org/10.1890/es13-00236.1>
- Sabater F, Buttirini A, Martí E, Muñoz I, Romani A, Wray J, Sabater S (2000) Effects of riparian vegetation removal on nutrient retention in a Mediterranean stream. *J N Am Benthol Soc* 19:609–620
- Saito VS, Soininen J, Fonseca-Gessner AA, Siqueira T (2015) Dispersal traits drive the phylogenetic distance decay of similarity in Neotropical stream metacommunities. *J Biogeogr* 42:2101–2111
- Schmera D, Baur B, Erős T (2012) Does functional redundancy of communities provide insurance against human disturbances? An analysis using regional-scale stream invertebrate data. *Hydrobiologia* 693:183–194. <https://doi.org/10.1007/s10750-012-1107-z>
- Sircorn J, Walde SJ (2011) Niches and neutral processes contribute to the resource-diversity relationships of stream detritivores. *Freshw Biol* 56:877–888
- Spencer CN, Gabel KO, Hauer FR (2003) Wildfire effects on stream food webs and nutrient dynamics in Glacier National Park, USA. *Forest Ecol Manag* 178:141–153. [https://doi.org/10.1016/s0378-1127\(03\)00058-6](https://doi.org/10.1016/s0378-1127(03)00058-6)
- Stevenson RJ, Bothwell ML, Lowe RL, Thorp JH (1996) *Algal ecology: Freshwater benthic ecosystem*. Academic press, San Diego, USA
- Straka M, Syrovátka V, Helešic J (2012) Temporal and spatial macroinvertebrate variance compared: crucial role of CPOM in a headwater stream. *Hydrobiologia* 686:119–134. <https://doi.org/10.1007/s10750-012-1003-6>
- Studinski JM, Hartman KJ, Niles JM, Keyser P (2012) The effects of riparian forest disturbance on stream temperature, sedimentation, and morphology. *Hydrobiologia* 686:107–117

- Thompson R, Townsend C (2006) A truce with neutral theory: local deterministic factors, species traits and dispersal limitation together determine patterns of diversity in stream invertebrates. *J Anim Ecol* 75:476–484
- Tilman D (1982) Resource competition and community structure. Princeton University Press, New Jersey, USA
- Tonkin JD, Death RG, Collier KJ (2012) Do productivity and disturbance interact to modulate macroinvertebrate diversity in streams? *Hydrobiologia* 701:159–172
- Tonkin JD, Sundermann A, Jähnig SC, Haase P (2015) Environmental controls on river assemblages at the regional scale: an application of the elements of metacommunity structure framework. *PLoS ONE* 10:e0135450
- Tonkin JD, Stoll S, Jähnig SC, Haase P (2016) Contrasting meta-community structure and beta diversity in an aquatic-floodplain system. *Oikos* 125:686–697
- Townsend C, Scarsbrook MR (1997) The intermediate disturbance hypothesis, refugia, and biodiversity in streams. *Limnol Oceanogr* 42:938–949
- Veblen TT, Kitzberger T, Lara A (1992) Disturbance and forest dynamics along a transect from Andean rain forest to Patagonian shrubland. *J Veg Sci* 3:507–520
- Velásquez SM, Miserendino ML (2003) Habitat type and macroinvertebrate assemblages in low order Patagonian streams. *Arch Hydrobiol* 158:461–483
- Wood ED, Armstrong F, Richards FA (1967) Determination of nitrate in sea water by cadmium-copper reduction to nitrite. *J Mar Biol Assoc UK* 47:23–31