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Null models for explaining macroinvertebrate communities in northern Patagonian Cautín river (39° S, Araucania region, Chile)

David Figueroa & Patricio De los Ríos-Escalante

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The Cautín river is closely related to the economic development of Temuco city, Chile, and this river has along its course different kinds of human intervention. The present study aims to characterise the benthonic macroinvertebrate communities using species co-occurrence and niche sharing null models to understand the presence of a random or structured pattern in species assemblages for ten stations throughout the main course of the Cautín river from its origin to its low zones. The results of co-occurrence null model revealed that species associations are structured in one of three models, whereas two models revealed that species associations are random, whereas the results of the niche sharing null model revealed the absence of niche sharing, which would indicate the lack of interspecific competition. The obtained results provide information about the ecological structure and function in the benthos of the Cautín river, which would be similar to other descriptions for other Argentinean and Chilean Patagonian rivers.

David Figueroa, Facultad de Recursos Naturales, Departamento de Ciencias Ambientales, Universidad Católica de Temuco, Casilla 15 D, Temuco, Chile; e-mail: dfiguero@uct.cl

Patricio De los Ríos-Escalante, Facultad de Recursos Naturales, Departamento de Ciencias Biológicas y Químicas, Universidad Católica de Temuco, Casilla 15 D, Temuco, Chile; and Núcleo de Estudios Ambientales UC Temuco

Introduction

The benthic communities in rivers are affected by different kinds of human intervention in their surrounding basins, because these have a crucial role in primary ecological processes in rivers and lakes and they can be used as water quality bioindicators (Hellawell 1986, Rosenberg & Resh 1993, Pinel-Alloul et al. 1996, Figueroa et al. 2003, 2007). In this context, the distribution of benthic macroinvertebrates in fluvial systems reflects the quality of environmental conditions of these systems because these animals have a strong relation with both, physico-chemical parameters of their habitats (Bronmark et al. 1984, Grubaugh et al. 1995, Rice et al. 2001), and biotic parameters such as food availability and diversity and areas that are habitats for littoral flora and fauna (Malmqvist & Bronmark 1985, Malmqvist & Hoffsten 2000). On this basis, Cummings & Klug (1979) proposed that benthic community structure and composition is markedly related to littoral zones of the river, indicating changes in functional feeding groups in the river. Also, Vannote et al. (1980) formulate a hypothesis that suggests predictable changes in the structure and function of the benthic communities among fluvial system according to energy inputs.

Many aspects of South American benthic communities in rivers and fluvial systems in general are poorly studied (Habit et al. 1998, Figueroa et al. 2003, 2007). Some benthic community taxonomy, distribution, ecology, and bioindicators have been studied for Argentinean Patagonia (Miserendino & Pizzolon 2000, Miserendino 2001, 2004, 2005). In Chile, a few studies were performed in Patagonia

(Figueroa et al. 2003, 2007, Moya et al. 2009, Fierro et al. 2012, 2015). Also, some benthos studies are based on stomach contents analyses (Vila et al. 1999, Palma et al. 2002, Figueroa et al. 2010, Vargas et al. 2010). Nevertheless, these descriptions are based on taxonomic categories other than species level. In this context, Biobio river is the only fluvial system that was studied considering benthic and fish communities (Arenas 1993, 1995), being the unique reference for Chilean fluvial systems. Moreover, with respect to Cautín river, there are only preliminary reports about species occurrence and distribution, and these are restricted to medium zones in the course of this river. The present research aims to characterise the taxonomy and distribution of macroinvertebrate benthic communities along the main course of Cautín river considering co-occurrence of species and niche sharing null models.

Material and methods

The Cautín river is the principal affluent of the Imperial river (Niemeyer & Cereceda 1984). It is 174 km long, and its sedimentary composition makes it a rhithral zone (Rivera et al. 2004, Fernández et al. 2018, Acuña 2020). It rises to the south of the Lonquimay river and draws waters from the Sierra Nevada and Cordillera de las Raíces, which limit the Bíobío basin (Rivera et al. 2004, Figueroa & De los Ríos-Escalante 2022). The main water inputs into the Cautín river are precipitations and snowmelt brought down by streams that drain the higher part of the sub-basin where snow lies in winter, above approximately 1400 m a.s.l. The Cautín river sub-basin is inhabited by at least 236 000 inhabitants in the city of Temuco, which is approximately 40 % of the total human population of the Imperial river basin. In this section of the river, it receives its main pollution load in the form of wastewater from Temuco (Rivera et al. 2004, Fernández et al. 2018, Acuña 2020).

In terms of natural resources, the Cautín river basin can be divided into two main areas: one in the Andes mountains and the other in the intermediate depression or central valley. The higher zone is characterised by steppe, mountain shrub plant formations, and *Araucaria* and *Nothofagus* forests. The intermediate depression has a marked degree of anthropogenic intervention through agricultural activities (Rivera et al. 2004, Fernández et al. 2018, Acuña 2020). The main uses of the Cautín river are associated with towns lying close to the river, predominantly drinking water, irrigation, recreation, and discharge of wastewater and liquid industrial waste (Rivera et al. 2004, Fernández et al. 2018, Acuña 2020).

Data of geographical parameters (Table 1) and benthic invertebrate fauna (Table 2) were obtained from Figueroa (2000) and Figueroa & De los Ríos-Escalante (2022) from ten different sites: upper sector: Volcán Lonquimay (Site 1), Malalcahuello (Site 2) and Curacautín (Site 3); middle sector: Agua Fría (Site 4), Cajón (Site 5), Temuco-San Antonio (Site 6) and Temuco-Amanecer (Site 7); low sector: Reñalil (Site 8), Boroa (Site 9) and Almagro (Site 10) (Fig. 1). Biological data correspond to an average southern summer (December–March) between 1997–2000 (Figueroa & De los Ríos-Escalante 2022)

A community is structured by competition when the C-score is significantly larger than expected by chance (Gotelli 2000, Tondoh 2006, Tiho & Josens 2007). Consequently, we compared co-occurrence patterns with null expectations via simulation using statistical null models fixed-fixed (Gotelli & Ellison 2013). In this model, the row and column sums of the matrix are preserved. Thus, each random community contains the same number of species as the original community (fixed column), and each species occurs with the same frequency as in the original community (fixed row). The null model analyses were performed using the software R (R Development Core Team 2009) and the package EcosimR (Gotelli & Ellison 2013, Carvajal-Quintero et al. 2015).

For niche overlap analysis, an individual matrix was built in which rows and columns represented species and sites, respectively. This matrix was used to test if the niche overlap significantly differed from the corre-

Table 1. Geographical location, altitude and classification of the sampling sites on the main course of the Cautín river (cf. Figueroa & De los Ríos-Escalante 2022).

Name	Site	Latitude (S) / Longitude (W)	Altitude (m a.s.l.)	Section	Human alteration
Volcan Lonquimay	Site 1	38°26'13'' / 71°30'33''	1160	High	Non-human altered
Malacahuello	Site 2	38°28'38'' / 71°35'092''	892	High	Non-human altered
Curacautín	Site 3	38°28'32'' / 71°56'52''	445	High	Non-human altered
Agua Fria	Site 4	38°28'16'' / 72°19'15''	280	Middle	Agriculture/Town
Cajón	Site 5	38°40'54'' / 72°30'15''	120	Middle	Agriculture/Town
Temuco (San Antonio)	Site 6	38°47'03'' / 72°23'57''	104	Middle	Town
Temuco (Amanecer)	Site 7	38°45'23'' / 72°36'53''	97	Middle	Town
Reñalil	Site 8	38°46'48'' / 72°47'33''	79	Low	Agriculture
Boroa	Site 9	38°46'22'' / 72°52'20''	77	Low	Agriculture
Almagro	Site 10	38°46'48'' / 72°56'54''	44	Low	Agriculture

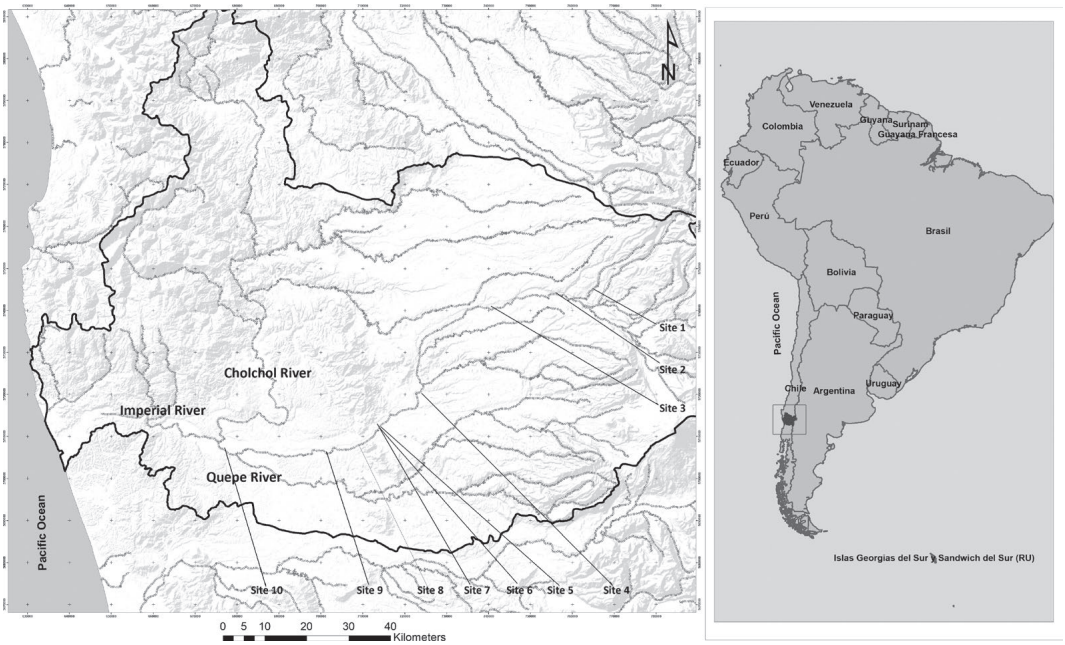

Fig. 1. Map with sites on the Cautín river included in the present study (cf. Figueroa & De los Ríos-Escalante 2022).

sponding value under the null hypothesis (random assemblage). These analyses were applied to data from the second field period and were based on Pianka index. The models show the probability of niche sharing compared to the niche overlap of the theoretically simulated community (Gotelli & Ellison 2013). The niche amplitude can be retained or reshuffled, when it is retained it preserves the specialization of each species.

In contrast, when it is reshuffled, it uses a wide utilization gradient of specialisation. Furthermore, zero participation in the observed matrix can be maintained or omitted. In the present study, we used the RA3 algorithm (Gotelli & Ellison 2013, Carvajal-Quintero et al. 2015). This algorithm retains the amplitude and reshuffles the zero conditions (Gotelli & Ellison 2013). This null model analysis was carried out using the software R (R Development Core Team 2009) and the package EcosimR (Pfeifer et al. 2006, Gotelli & Ellison 2013, Carvajal-Quintero et al. 2015).

Table 2. Distribution and average abundance (ind/m^2) of the macrozoobenthos and community parameters along the Cautín river during study period in sampling sites (cf. Figueroa & De los Ríos-Escalante 2022).

	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8	Site 9	Site 10
Annellida										
Tubifex sp.	–	–	–	1	–	56	15	28	24	6
Mesobdella gemmata (Blanchard, 1849)	–	–	–	–	–	–	4	1	–	–
Mollusca										
Chilina dombeyana (Brugière, 1789)	–	–	–	–	–	–	–	207	264	490
Physa chilensis Clessin, 1886	–	–	–	–	–	–	–	39	24	13
Lymnaea viator (D'Orbigny, 1835)	–	–	–	–	–	–	–	1	–	–
Gundlachia gayana (D'Orbigny, 1895)	–	–	–	–	–	–	–	6	296	6
Crustacea, Decapoda										
Aegla araucaniensis Jara, 1980	–	–	2	–	–	–	–	–	–	–
A. abtao Jara, 1977	–	–	12	–	3	67	2	–	–	–
Insecta, Ephemeroptera										
Chiloporter penai Demoulin, 1955	–	1	–	–	–	–	–	–	–	–

Table 2. continued

	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8	Site 9	Site 10
Meridialaris diguillina (Demoulin, 1955)	19	52	217	151	21	5	–	1	–	1
M. chiloeense (Demoulin, 1955)	9	10	–	–	–	–	–	–	–	–
M. laminata (Ulmer, 1920)	–	1	–	–	–	–	–	–	–	–
Hapsiphlebia anastomosis (Demoulin, 1955)	–	–	1	–	–	–	–	–	–	–
Nousia delicata Návas, 1918	–	16	59	–	6	–	–	–	–	–
N. maculata (Demoulin, 1955)	–	–	67	–	–	–	–	–	–	–
N. minor (Demoulin, 1955)	–	–	10	–	–	–	–	–	–	–
Penaphlebia sp.	–	–	4	3	16	–	–	–	–	–
Deceptiviosa torrens Lugo-Ortiz & McCafferty, 1999	88	7	–	8	3	11	–	1	–	3
Andesiops peruviana (Ulmer, 1920)	40	93	280	136	116	–	–	376	19	14
Dactylobaetis sp.	–	–	–	–	22	–	–	4	–	–
Insecta, Plecoptera										
Klapopteryx armillata Návas, 1928	12	–	–	–	–	–	–	–	–	–
K. kuscheli Illies, 1960	–	6	1	–	–	–	–	–	–	–
Potamoperla myrmidon (Mabille, 1881)	–	2	2	28	–	–	–	–	–	–
Notoperlopsis femina Illies, 1863	1	16	1	76	2	–	–	–	–	–
Senzilloides panguipulli (Navas, 1928)	1	–	–	–	–	–	–	–	–	–
Teutoperla sp.	1	1	–	–	–	–	–	–	–	–
Aubertoperla sp.	9	2	–	154	2	–	–	–	–	–
Limnoperla jaffueli (Navas, 1928)	0	7	14	–	–	–	–	–	–	–
Perlugoperla personata Vera, 2008	19	27	2	–	–	–	–	–	–	–
Ceratoperla schwabei Illies, 1963	–	–	2	–	–	–	–	–	–	–
Antarctoperla michaelseni (Klapácek, 1904)	–	5	53	–	–	–	–	–	–	–
Austronemoura sp.	–	–	–	1	–	–	–	–	–	–
Udamocercia sp.	–	–	4	–	–	–	–	–	–	–
Pictetoperla gayi (Pictet, 1841)	–	–	4	7	3	–	–	–	–	–
Diamphipnoa sp.	1	–	2	–	–	–	–	–	–	–
Insecta, Trichoptera										
Hydrobiosidae	–	1	–	1	–	–	–	–	–	–
Smicridea chilensis Schmid, 1950	10	30	20	150	–	211	104	903	261	1696
Ochrotrichia sp.	1	–	1	–	3	–	–	3	–	6
Glossomatidae	1	25	–	–	21	–	–	–	94	–
Limnephilidae	–	–	25	–	–	–	–	178	79	44
Leptoceridae	–	1	–	3	–	–	–	–	–	–
Helicopsychidae	–	1	–	1	–	–	–	–	–	1
Insecta, Coleoptera										
Amphizoidae	–	–	–	26	–	–	–	–	–	–
Dytiscidae	–	–	–	–	–	–	–	–	47	–
Andogyrus sp.	–	–	–	–	–	–	–	3	–	–
Elmis sp.	–	22	–	285	38	–	–	28	97	19
Hydrophilidae	–	–	–	–	–	–	–	6	3	17
Insecta, Diptera										
Tanypodinae	30	–	1	–	–	–	–	158	222	290
Diamesinae	102	–	57	–	103	–	–	1428	211	153
Chironominae	109	–	157	–	1516	–		513	593	656
Orthocladiinae	212	–	22	–	295	230	559	1875	1410	3496
Rheotanytarsus sp.	–	2	–	24	–	–	–	26	143	392
Limoniinae	–	94	362	164	51	14	–	–	–	–
Simulium sp.	–	–	1	–	–	–	–	–	–	–
Athericidae	5	11	15	3	5	–	–	–	–	1
Edwardsina sp.	4	70	–	–	–	–	–	–	–	–

Results

The benthic invertebrate fauna in the Cautín river comprises 56 taxa, of which 48 were aquatic insects, two were crustaceans, and six taxa were Annellida and Mollusca. The aquatic insects identified to species level were mainly Plecoptera (16 taxa), most of which belonged to the Gripopterygidae (9 taxa, that belong to *Potamoperla*, *Notoperlopsis*, *Senzilloides*, *Teutoperla*, *Aubertoperla*, *Limnoperla*, *Pelurgoperla*, *Ceratoperla*, and *Antarctoperla*); this was followed by the Ephemeroptera (12 taxa), mostly Leptophlebiidae (8 taxa that belong to *Meridialaris*, *Hapsiphlebia*, *Nousia*, and *Penaphlebi*a) (Table 2).

The results of co-occurrence null model analysis revealed that species associations were structured for fixed-fixed simulation, whereas for fixed-equiprobable and fixed-proportional the species associations were random (Table 3). The results of niche sharing null model analysis revealed the absence of niche sharing, which indicates the lack of interspecific competition (Table 3).

Discussion

In zoogeographical terms, the community studied corresponds to Neotropical fauna of Southern South America, with endemic characteristics due to the marked bio-geographical isolation of Chile (Morrone 2014, 2015). The macroinvertebrates in the Cautín river consisted of dominant groups belonging to Ephemeroptera, Plecoptera, Trichoptera, and Diptera. This fauna has been reported for rhitronic habitats located in the cold-temperate zone (Figueroa et al. 2007, Vega et al. 2020, De los Ríos-Escalante et al. 2020), similar to reports from the northern hemisphere (Hauer & Lamberti 2007).

The results of species co-occurrence null model analysis that revealed the existence of a structured pattern for fixed-fixed simulation, and absence of a structured pattern, i. e., random presence, for fixed-proportional and fixed-equiprobable simulation, can be explained by the presence of many species repeated by studied sites (Tondoh 2006, Tiho & Johens 2007). The obtained results would be similar with observations for Argentinean and Chilean Patagonian rivers where a zonation in benthic macroinvertebrate communities occurs (Arenas 1995, Figueroa et al. 2003, 2007, 2010, 2013, Oyanedel et al. 2008, Moya et al. 2009, Miserendino et al. 2018, Barile et al. 2021). In this scenario, it would be possible to obtain this kind of results in benthic communities in rivers (De los Ríos-Escalante et al. 2020, Solis-Lufí et al. 2022). The possible causes of this community structure are a gradual development of the phytobenthos in the riverbed, allowing the appearance of functional feeding groups (Allan & Del Castillo 2007, Schmid-Araya et al. 2012) or the presence of litter (Lopez-Rojo et al. 2020, see also Miserendino et al. 2018). The decrease in species richness and diversity in the middle and low sectors are explained by the natural transformation of the riverbed and marked human intervention (Marchant et al. 2016).

The result indicating the absence of niche sharing would agree with results on community structure (De los Ríos-Escalante et al. 2022), because in the course of Cautín river, there are marked differences in macroinvertebrate communities. The high zones are dominated by shredders. This group decreases gradually in the medium and low zones, and is replaced by filtering organisms (Figueroa 2000, Li & Zeng 2020, Figueroa & De los Ríos-Escalante 2022). These tendencies could also be enhanced by human alterations in surrounding basins that affect water quality and in consequence also affect the benthic fauna (Figueroa et al. 2003, 2007).

Finally, the results of our null model analysis of invertebrate benthic community ecology in Cautín river would agree with earlier observations (Figueroa 2000, Figueroa & De los Ríos-Escalante 2022), and would explain the structure and function of benthic communities (Gray 2005, Ings et al. 2009, Woodward et al. 2010, Schmid-Araya et al. 2012, Vega et al. 2020). On this basis, it is necessary do more studies on ecology of benthic communities includ-

Table 3. Co-occurrence and niche overlap null model analysis results for all stations in Cautín river.

	Mean index	Observed index	Variance	P
Species co-occurrence				
Fixed-fixed	2.712	2.918	< 0.001	< 0.001
Fixed-equiprobable	2.918	3.358	0.081	0.945
Fixed-proportional	2.918	3.175	0.006	0.999
Niche sharing				
Pianka index	0.215	0.179	< 0.001	< 0.001

ing interactions between native and introduced fishes (salmonids), that would affect the benthic communities' structure and function (Vargas et al. 2010, Vega et al. 2020).

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