

Inland water microcrustacean assemblages in an altitudinal gradient in Aysen region (46° S, Patagonia Chile)

Patricio De los Ríos-Escalante^{a,b*}, Esteban Quinán^a and Patricio Acevedo^{c,d}

^aLaboratorio de Ecología Aplicada y Biodiversidad, Escuela de Ciencias Ambientales, Facultad de Recursos Naturales, Universidad Católica de Temuco - UCTemuco, Casilla 15-D, Temuco, Chile

^bNúcleo de Estudios Ambientales UCTemuco, Avenida Alemania nº 0211, Casilla 15-D, Temuco, Chile

^cDepartamento de Física, Facultad de Ciencias e Ingeniería, Universidad de la Frontera - UFRO, Casilla 54-D, Temuco

^dCenter for Optics and Photonics, Universidad de Concepción - UdeC, Casilla 4012, Concepción, Chile

* e-mail: prios@uct.cl

Received: January 8, 2013 – Accepted: June 4, 2013 – Distributed: February 28, 2014
(With 1 figure)

Abstract

The Chilean Patagonia has numerous kinds of inland water ecosystems such as lakes, ponds, wetlands and rivers that have been poorly studied due to access difficulties. This study was carried out in Aysen region, in southern Chile, and it included different kinds of water bodies such as rivers, streams, ponds, lagoons and lakes distributed along an altitudinal gradient at 46° S. It was found a low species number, essentially cladocerans, copepods and amphipods. A null model was applied in order to determine the existence of regulator factors of species associations, and the results revealed that they are not random. The patterns would be influenced by geographical and limnological characteristics of the studied sites. Our results would agree with regional studies on habitat heterogeneity such as in Torres del Paine National Park and other zones in Tierra del Fuego island.

Keywords: microcrustaceans, *Boeckella*, *Hyalella*, null models, Patagonia

Crustáceos zooplâncton de águas continentais litorais na gradiente de altitude na região de Aysén (46 ° S, Patagônia Chile)

Resumo

A Patagônia chilena apresenta numerosos tipos de ecossistemas aquáticos, como lagos, lagoas, pântanos e rios, os quais tem sido pouco estudados devido a dificuldades de acesso. Este estudo foi feito na região de Aysén, no sul do Chile, e inclui diferentes tipos de corpos d'água, tais como rios, córregos, lagos, lagoas e lagos distribuídos ao longo de um gradiente de altitude a 46° S. Constatou-se baixo número de espécies que inclui, essencialmente, cladóceros, copépodos e anfípodos. Um modelo nulo foi aplicado para determinar a existência de fatores reguladores das associações de espécies os resultados indicam que estes não são aleatórios. Os padrões poderiam ser influenciados pelas características geográficas e limnológicas do locais estudados. Os resultados expostos concordariam com estudos regionais sobre com habitats heterogeneidade como Torres del Paine Parque Nacional e outras zonas na ilha de Tierra del Fuego.

Palavras chave: microcrustaceans, *Boeckella*, *Hyalella*, modelo nulo, Patagonia

1. Introduction

The microcrustacean assemblages in lakes and ponds in central and southern Patagonia (44-53° S) have different characteristics (De los Ríos-Escalante, 2010) due the heterogeneity of water bodies. For example, large lakes, small lakes and shallow ponds of Torres del Paine microcrustacean species associations are regulated by conductivity and the trophic status (Soto and De los Ríos, 2006; De los Ríos and Soto, 2009). This pattern is similar to the one described for lakes and ponds in Argentinean Patagonia (Modenutti et al. 1998) and also with descriptions for New Zealand lakes (Jeppesen et al. 1997, 2000). From this point of view microcrustacean assemblages are not random,

regulatory, or deterministic factors exists to explain the community structure. The absence of regulatory factors and the random distribution in species co-occurrence are the basis of the null models.

One of these models used the presence and absence of species to determine the absence of deterministic factors as regulators of species co-occurrence or guild structure, these null models are more robust in comparison with deterministic models (Gotelli, 2000, 2001). The aim of the present study is to apply a null model analysis based on presence-absence of species matrix using of non-random test procedures in order to contribute to the understanding

of community ecology in inland water microcrustaceans along an altitudinal gradient in Aysen region inland waters

2. Material and methods

The studied region is located at 46° S (Aysen region, Chile, Figure 1), and it is characterized by the presence of a variety of landscapes, valleys, mountains, lakes, rivers and ponds (Niemeyer and Cereceda, 1984). Within the inland water bodies there are large and deep lakes, small

lakes, shallow permanent and ephemeral pools, and rivers (Niemeyer and Cereceda, 1984; De los Ríos-Escalante, 2010). This region is difficult to access due to the marked isolation that is an advantage because these ecosystems are practically pristine but the disadvantage is that it is difficult to carry out systematic field works due to geographical and climatic features (De los Ríos, 2008).

Information from 22 sites was obtained during field works in February 2012 (Table 1). The geographical location and altitude were obtained using a GPS Garmin, pH, temperature,

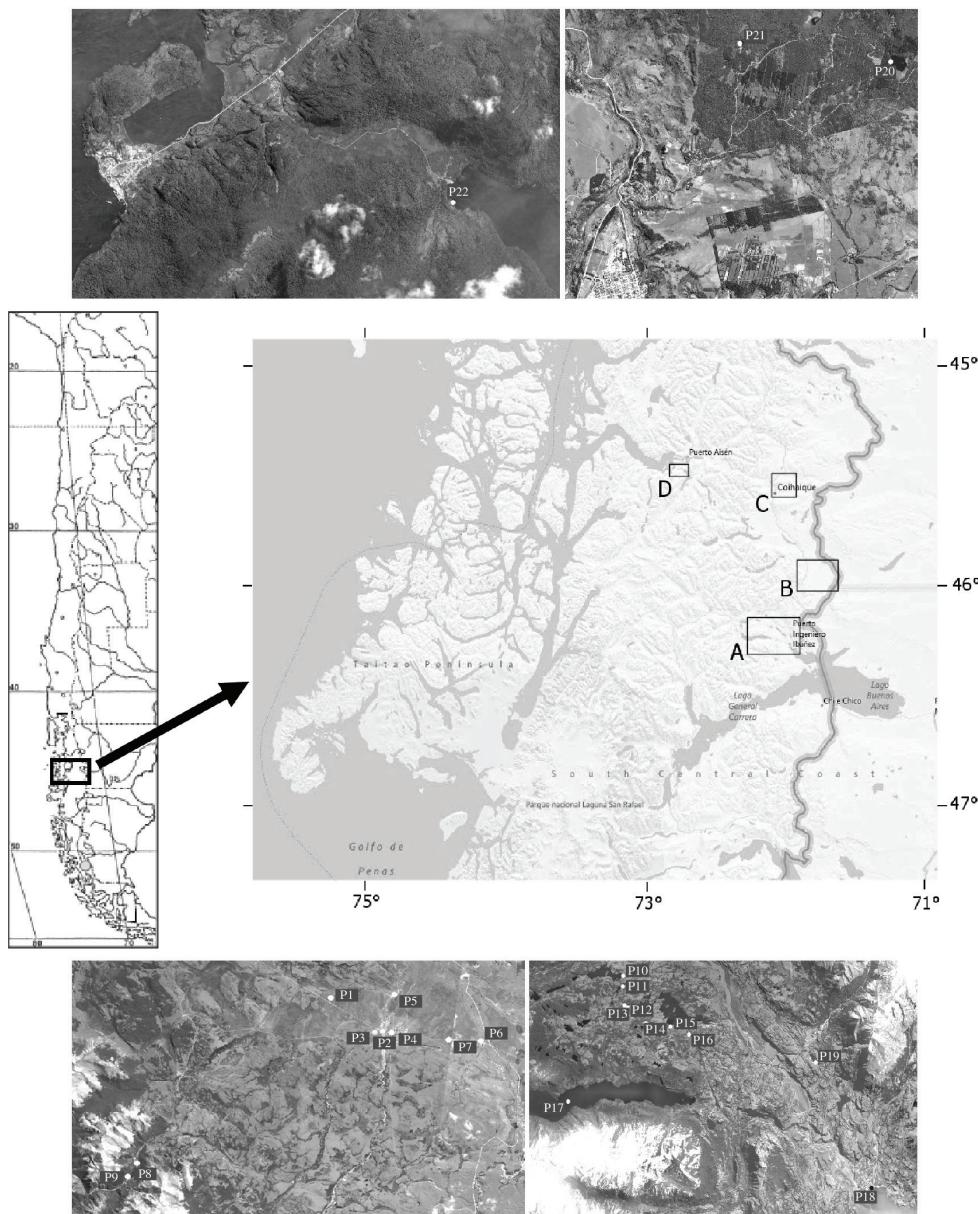


Figure 1. Sampled sites: P1(Balmaceda 1); P2 (Balmaceda 2); P3 (Balmaceda 3); P4 (Balmaceda 4); P5 (Balmaceda 5); P6 (Balmaceda 6); P7 (Balmaceda 7); P8 (Verde 1); P9 (Chiguay); P10 (Ardilla); P11 (Chacano); P12 (Lagoon 1); P13 (Lagoon 2); P14 (Lagoon 3); P15 (Tamango); P16 (Lagoon 4); P17 (Laparent); P18 (General Carrera); P19 (Venus); P20 (Verde 2); P21 (De los Sapos); P22 (Riesco).

Table 11 Geographical location, altitude, temperature, conductivity, total dissolved solids, pH and species reported at the studied sites.

Kind	Balmaceda 1		Balmaceda 2		Balmaceda 3		Balmaceda 4		Balmaceda 5		Balmaceda 6		Balmaceda 7	
	45° 53' 35,5"S; 71° 44' 44,5"W	45° 54' 36,0"S; 71° 42' 38,3"W	45° 54' 37,5"S; 71° 43' 00,6"W	45° 54' 38,3"S; 71° 42' 19,3"W	45° 54' 38,2"S; 71° 42' 14,0"W	45° 53' 28,2"S; 71° 42' 14,0"W	45° 54' 51,7"S; 71° 38' 46,6"W	45° 54' 50,2"S; 40° 01,0"W	45° 54' 51,7"S; 71° 38' 46,6"W	45° 54' 50,2"S; 40° 01,0"W				
Altitude	513	525	519	523	502	498	499							
Temperature	10.3	10.1	10.8	10.3	10.9	10.1	11.1							
Conductivity	0.02	0.02	0.14	0.02	0.03	0.04	0.12							
Total dissolved solids	0.02	0.02	0.14	0.02	0.03	0.04	0.12							
pH	7.80	7.87	8.70	8.27	8.40	8.63	8.17							
<i>D. pulex</i>		x												
<i>D. ambiguua</i>														
<i>C. dubia</i>														
<i>S. expinifera</i>														
<i>S. serrulata</i>			x											
<i>C. sphaericus</i>			x											
<i>L. leydigii</i>														
<i>A. pulchella</i>														
<i>B. michaelseni</i>					x									
<i>M. araucanus</i>	x		x		x		x							
<i>Harpacticoida</i>														
<i>Ostracoda</i>														
<i>H. chiloensis</i>			x		x		x							
<i>H. patagonica</i>					x		x							
<i>H. simplex</i>						x								

Table 1. (Continued).

Kind (and map location)	Verde 1		Chiguay		Ardilla		Chacano		Lagoon 1		Lagoon 2		Lagoon 3	
	Lagoon (B)	Lagoon (B)	Lagoon (B)	Lagoon (B)	Lagoon (A)	Lagoon (A)	Lagoon (A)	Lagoon (A)	Lagoon	Lagoon	Lagoon	Lagoon	Lagoon	Lagoon
Altitude	962	961	961	501	501	514	540	539	539	539	539	539	539	606
Temperature	14.6	13.0	16.4	20.1	19.4	20.1	19.4	24.8	24.8	24.8	24.8	24.8	24.8	17.2
Conductivity	0.03	0.02	0.06	0.04	0.04	0.04	0.04	0.03	0.03	0.03	0.03	0.03	0.03	0.03
Total dissolved solids	0.06	0.04	0.14	0.09	0.09	0.09	0.09	0.09	0.09	0.09	0.09	0.09	0.09	0.09
pH	8.19	8.33	8.40	8.92	8.68	8.68	8.68	9.08	9.08	9.08	9.08	9.08	9.08	9.21
<i>D. pulex</i>	x													
<i>D. ambiguua</i>	x													
<i>C. dubia</i>														
<i>S. expinifera</i>			x		x		x		x		x		x	
<i>S. serrulata</i>			x		x		x		x		x		x	
<i>C. sphaericus</i>			x		x		x		x		x		x	
<i>L. leydigii</i>														
<i>A. pulchella</i>														
<i>B. michaelseni</i>	x		x		x		x		x		x		x	
<i>M. araucanus</i>	x		x		x		x		x		x		x	
<i>Harpacticoida</i>	x													
Ostracoda					x		x		x		x		x	
<i>H. chiloensis</i>	x				x		x		x		x		x	
<i>H. patagonica</i>					x		x		x		x		x	
<i>H. simplex</i>			x		x		x		x		x		x	

Table 1. (Continued).

Kind (and map location)	Tamango	Lagoon 4	Laparent	General Carrera	Venus	Verde 2	De los Sapos	Riesco
	46° 11' 37.6" S; 72° 08' 19.5" W	46° 11' 56.0" S; 72° 07' 11.8" W	46° 14' 31.0" S; 72° 14' 31.0" W	46° 17' 42.4" S; 71° 56' 02.4" W	46° 12' 58.4" S; 71° 59' 29.2" W	45° 32' 11.1" S; 72° 01' 05.0" W	45° 32' 03.0" S; 72° 02' 49.4" W	45° 28' 09.4" S; 72° 43' 56.4" W
Altitude	550	661	559	202	476	608	586	22
Temperature	16.0	17.2	19.7	18.0	19.7	14.3	11.5	13.3
Conductivity	0.07	0.07	0.04	0.05	0.09	0.02	0.02	0.01
Total dissolved solids	0.05	0.17	0.11	0.12	0.19	0.05	0.06	0.01
pH	8.72	8.63	9.14	9.01	9.09	9.28	9.56	8.91
<i>D. pulex</i>	x	x	x	x	x	x	x	x
<i>D. ambiguus</i>								
<i>C. dubia</i>							x	x
<i>S. expinifera</i>							x	x
<i>S. serrulata</i>							x	x
<i>C. sphaericus</i>	x	x	x	x	x	x	x	x
<i>L. leydigii</i>	x	x	x	x	x	x	x	x
<i>A. pulchella</i>					x			
<i>B. michaelseni</i>					x	x	x	x
<i>M. araucanus</i>	x	x	x	x	x	x	x	x
<i>Harpacticoida</i>	x	x	x	x	x	x	x	x
<i>Ostracoda</i>	x	x	x	x	x	x	x	x
<i>H. chiloensis</i>	x	x	x	x	x	x	x	x
<i>H. patagonica</i>								
<i>H. simplex</i>					x			

Table 2. Results of null model analysis for co-occurrence of species at the studied sites ($P < 0.05$ denotes random absence).

	C-score		V-ratio	
	Fixed-Fixed	Fixed-proportional	Fixed-Equiprobable	Fixed-proportional
Observed index	10.676	10.676	10.676	1.548
Mean of simulated index	10.728	10.981	9.807	1.963
Standard effect size	0.044	0.505	0.951	0.194
Variance of simulated index	-0.250	-1.835	0.890	-0.941
P	0.586	0.955	0.193	0.843
				0.049

Table 3. Correlation matrix between altitude, total dissolved solids, conductivity, temperature and pH with species number at the studied sites (*= significant correlation).

	R	P
Species number-altitude	0.444	0.038*
Species number- total dissolved solids	0.176	0.432
Species number-conductivity	-0.127	0.570
Species number-temperature	0.447	0.037*
Species number-pH	0.345	0.114

total dissolved solids and conductivity were measured in situ with a Hanna sensor, the microcrustaceans were collected in rivers using a 25 * 25 cm and 100 µm mesh size surber net (Domínguez and Fernandez, 2009), whereas in lakes the samples were collected using horizontal hauls with a plankton net of 25 cm diameter and 100 mm mesh size (De los Ríos et al. 2010). Microcrustacean species were fixed in absolute ethanol and identified using specialized literature (Araya and Zúñiga, 1985; Reid, 1985; Bayly, 1992; González, 2003; Dos Santos et al. 2008).

The obtained information was analyzed in two steps. The first step included firstly the information on species co-occurrence (only adult stages) which was ordered using an absence/presence matrix. Secondly, a Checkerboard score ("C-score"), a quantitative index of occurrence, was applied, which measures the extent to which species co-occur less frequently than expected by chance alone (Gotelli 2000, 2001). Gotelli and Entsminger (2009), Tiho and Johens (2007), and Tondoh (2006) suggested that the following robust statistical models should be used in a co-occurrence analysis. First, the matrix layout needs to include the species names in the rows and the sites in the columns. Second, the following models should be used: (1) Fixed-Fixed. 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). (2) Fixed-Equiprobable. In this algorithm only the row sums are fixed and the columns are treated as equiprobable. This null model considers all the sites (columns) as equally available for all species, which occur in the same proportions as in the original communities. (3) Fixed-Proportional. This

model maintains the species occurrence as in the original community and the probability that a species occurs at a site (column) is proportional to the column total for that sample. The variance ratio of the column sum to the sum of the row variances. Unlike C-score index, the variance ratio does not measure patterns of co-occurrence within the matrix, but it is determined exclusively by row and column sums of the matrix (Gotelli, 2000). Therefore, this model is not valid for the fixed-fixed null model. For this reason, the variance ratio was not tested with this null model. The variance ratio measures the variability in the number of species by sample. If species richness is regulated by biological interactions, communities should converge to a relatively constant number of species per sample (Gotelli, 2000). In a competitively structured community the observed variance ratio should be significantly smaller than expected by chance (Tiho and Johens, 2007). All null model analyses were carried out using the software Ecosim version 7.0 (Tondoh, 2006; Tiho and Johens, 2007; De los Ríos 2008; De los Ríos et al. 2008b; Gotelli and Entsminger, 2009).

As second step, it was applied a correlation analysis between species number with temperature, pH, total dissolved solids, conductivity and altitude, using the software Prisma 5.0.

3. Results

The results revealed a relatively low species number, and notable cladocerans and amphipods occurrence (Table 1). The cladoceran and copepod species *Chydorus sphaericus* and *Mesocyclops araucanus* were widespread, whereas the most frequent species of amphipods, *Hyalella chiloensis* and *H. simplex*, were frequent in central and southern Patagonia (Table 1). For Balmaceda streams (Table 1), a zone located in semi-arid plain, the most frequent species were *C. sphaericus*, *M. arauanus*, *H. chiloensis* and *H. patagonica*. For lagoons Verde I, Chiguay, Ardilla, Chacano, Lagoon 1, Lagoon 2, Lagoon 3, Tamango, Laparent, Lagoon 4 and General Carrera, that are located within and in the surroundings of Cerro Castillo National Reserve in a mountain zone, it was found a higher species richness with Daphniids cladocerans, *C. sphaericus*, *B. michaelensi*, *M. araucanus*, *H. chiloensis*, *H. patagonica* and *H. simplex* (Table 1). For ponds located in Coyhaique National Reserve, in a mountain zone close to Coyhaique

town (Venus, Verde 2 and De los Sapos), were found cladocerans mainly *C. sphaericus* and *M. araucanus* (Table 1). Finally, for Riesco coastal mountains close to Puerto Chacabuco, it was found only *D. ambigua* and *B. michaelseni* (Table 1).

The results of null model co-occurrence analysis revealed that the species associations are random in practically all simulations with exception to fixed-equivprobable model of the V-ratio (Table 2).

The correlation analysis revealed significant association between species number with temperature and altitude with species number (Table 3).

4. Discussion

It is reported species that are widespread in Patagonia (38-51° S) such as *Daphnia ambigua*, *D. pulex*, *Scapholeberis exspinifera*, *Simsa serrulata*, *Chydorus sphaericus*, *Leydigia leydi*, *Alona pulchella*, *Mesocyclops araucanus*, *Hyalella chiloensis* and *Hyalella patagonica* (Table 1; González, 2003; De los Ríos-Escalante, 2010).

Two species from central and southern Patagonia (46-54° S) were reported: *Boeckella michaelseni*, and *Hyalella simplex* (Table 1; González, 2003; De los Ríos-Escalante, 2010). These results would agree partially with first descriptions for zooplanktonic crustaceans in Aysen region that reported a kind of a transitional pattern where it is possible to found species from northern and southern Patagonia (Menu-Marque et al. 2000; De los Ríos, 2008). An example can be the presence of three amphipods species: *H. chiloensis* that is found between 36°-45° S, *H. simplex* that is found between 38-55° S and *H. simplex* between 39-53° S (De los Ríos-Escalante et al., 2012).

The results of null model agree with observations of zooplankton species associations based on null model co-occurrence species for southern Patagonian lakes and/or ponds (De los Ríos et al. 2008a; De los Ríos 2008) and northern Patagonian mountain lakes and shallow ponds (De los Ríos et al. 2008b,c). It is due to the presence of few species repeated in all or practically all sites (De los Ríos et al. 2008a, b, c; De los Ríos 2008). This pattern of species repetition by site in spite of environmental heterogeneity was observed for lakes and ponds in Torres del Paine National Park at 51° S (De los Ríos & Soto, 2009), and in large scale in lakes and ponds in Magallanes region between 51-53°, including Torres del Paine National Park and Tierra del Fuego island (De los Ríos et al., 2010b).

Similar results would occur in terrestrial systems (Ribas and Schoereder 2002; Sanders et al. 2007). Other similar causes what could be related to the homogeneity of the studied habitats (Franca and Araujo 2007), or interactions between species with similar ecological characteristics (Tondoh 2006; Tiho and Johens 2007). In an opposite scenario, the presence of interspecific competition and ecological differentiation denotes the absence of random patterns in species association (Ulrich 2004; Rodríguez-Fernandez et al. 2006). Conversely, the existence of significant effects, expressed in random absence, as it

was observed in two simulations, denoted the existence of habitat segregations and resources partition (Costa de Azevedo et al. 2006).

The lack of correlation between microcrustacean assemblages with conductivity would agree with results observed for inland waters in Southern Patagonia, (Soto and De los Ríos, 2006; De los Ríos et al. 2008; De los Ríos and Soto, 2009; De los Ríos-Escalante, 2010). This condition would be explained due the low variability range of mineral concentrations observed in many Patagonian inland waters (Pedrozo et al., 1993) that probably would not affect the community structure. This scenario is different in the northern Chilean Andean inland rivers where the mineral contents variability is high interfering in the species associations (De los Ríos et al., 2010a).

The obtained results agree with similar observations for Magallanes region inland waters (51-55° S), in terms of biogeographic aspects and community structure. Nevertheless it is necessary more studies in this region for understanding ecological and biogeographical patterns of inland water crustacean species.

Acknowledgements – The present study was financed by projects DID-UACH d2001-11, CONICYT-Chile (Doctoral Fellowship and Grant for support Doctoral Thesis), project MECESUP UCT 0804, and the Research Direction of the Catholic University of Temuco (Fund for Development of Limnology), CEFOP CONICYT FB0824 and DI08-0040 from the Research Direction of the Universidad de la Frontera, former National Environmental Ministry,

References

- ARAYA, JM. and ZÚÑIGA, LR., 1985. Manual taxonómico del zooplancton lacustre de Chile. *Boletín Limnológico*, vol. 8, p. 1-169.
- BAYLY, IAE., 1992. Fusion of the genera *Boeckella* and *Pseudoboeckella* and a revision of their species from South America and Subantarctic islands. *Revista Chilena de Historia Natural*, vol. 65, no. 1, p. 17-63.
- COSTA DE AZEVEDO, MC., ARAUJO, FG., MACHADO, AL. and DE ARAUJO SILVA, M., 2006. Co-occurrence of demersal fishes in a tropical bay in southeastern Brazil: A null model analysis. *Estuarine Coastal and Shelf Science*, vol. 66, no. 1-2, p. 315-322. <http://dx.doi.org/10.1016/j.ecss.2005.09.006>
- DE LOS RÍOS-ESCALANTE, P., 2010. Crustacean zooplankton communities in Chilean inland Waters. *Crustaceana Monographs*, vol. 12, p. 1-109.
- DE LOS RIOS-ESCALANTE, P., MORRONE, JJ. and RIVERA, R., 2012. Distributional patterns of the South American species of *Hyalella* (Amphipoda, Hyalellidae). *Gayana*, vol. 76, p. 153-162. <http://dx.doi.org/10.4067/S0717-65382012000300008>
- DE LOS RÍOS, P., 2008. A null model for explain crustacean zooplankton species associations in central and southern Patagonian inland waters. *Anales del Instituto de la Patagonia*, vol. 36, no. 1, p. 25-33. <http://dx.doi.org/10.4067/S0718-686X2008000100002>
- DE LOS RÍOS, P. and SOTO, D., 2009. Estudios limnológicos en lagos y lagunas del Parque Nacional Torres del Paine (51 S,

- Chile). *Anales del Instituto de la Patagonia*, vol. 37, no. 1, p. 63-71. <http://dx.doi.org/10.4067/S0718-686X2009000100006>
- DE LOS RÍOS, P., ACEVEDO, P., RIVERA, R. and ROA, G., 2008a. Comunidades de crustáceos litorales de humedales del norte de la Patagonia chilena (38° S): rol potencial de la exposición a la radiación ultravioleta. In VOLPEDO, A. and FERNANDEZ, L. (Eds.). *Efecto de los cambios globales en la diversidad*. Programa CYTED 406RT0285. p. 209-229.
- DE LOS RÍOS, P., ADAMOWICZ, S. and WITT, J., 2010a. Aquatic fauna in the driest desert on earth: first report on the crustacean fauna of the Loa river (Atacama desert, Antofagasta region, Chile). *Crustaceana*, vol. 83, no. 3, p. 257-266. <http://dx.doi.org/10.1163/001121609X12596543952333>
- DE LOS RÍOS, P., MANSILLA, A. and VEGA, M. 2010b. Species co-occurrences base don a presence/absence null model for copepoda and cladocerans in Patagonia and Tierra del Fuego lakes and ponds. *Biología, Bratislava*, vol. 65, no. 6, p. 1019-1027. <http://dx.doi.org/10.2478/s11756-010-0123-6>
- DE LOS RÍOS, P., RIVERA, N. and GALINDO, M., 2008b. The use of null models to explain zooplankton species associations in shallow water bodies of the Magallanes region, Chile. *Crustaceana*, vol. 81, no. 10, p. 1219-1228. <http://dx.doi.org/10.1163/156854008X374540>
- DE LOS RÍOS, P., ROGERS, DC. and RIVERA, N., 2008c. *Branchinecta gaini* (Daday, 1910) (Branchiopoda, Anostraca) as a bioindicator of oligotrophic and low conductivity shallow ponds in southern Chilean Patagonia. *Crustaceana*, vol. 81, no. 9, p. 1025-1034. <http://dx.doi.org/10.1163/156854008X360789>
- DOMINGUEZ, E. and FERNÁNDEZ, HR. (Eds.), 2009. *Macroinvertebrados bentónicos sudamericanos. Sistemática y Biología*. Tucumán: Fundación Miguel Lillo. 654 p.
- DOS SANTOS, A., ARAUJO, P. and BOND-BUCKUP, G., 2008. New species and new reports of *Hyalella* (Crustacea, Amphipoda, Dogielinotidae) from Argentina. *Zootaxa*, vol. 1760, p. 24-36.
- FRANCA, FGR. and ARAÚJO, AFB., 2007. Are there co-occurrence patterns that structure snake communities in Central Brazil? *Brazilian Journal of Biology*, vol. 67, no. 1, p. 33-40. <http://dx.doi.org/10.1590/S1519-69842007000100005>
- GONZÁLEZ, E., 2003. The freshwater amphipods *Hyalella* Smith, 1874 in Chile (Crustacea: Amphipoda). *Revista Chilena de Historia Natural*, vol. 76, no. 4, p. 623-637. <http://dx.doi.org/10.4067/S0716-078X2003000400007>
- GOTELLI, NJ., 2000. Null models of species co-occurrence patterns. *Ecology*, vol. 81, no. 9, p. 2606-2621. <http://dx.doi.org/10.2307/177478>
- , 2001. Research frontiers in null model analysis. *Global Ecology and Biogeography*, vol. 10, p. 337-343. <http://dx.doi.org/10.1046/j.1466-822X.2001.00249.x>
- GOTELLI, NJ. and ENTSINGER, GL., 2009. *EcoSim: Null models software for ecology*. version 7. Acquired Intelligence Inc. and Kesey-Bear. Jericho, VT 05465. Available from: <<http://garyentsminger.com/ecosim.htm>>
- JEPPENSEN, E., LAURIDSEN, TL., MITCHELL, SF. and BURNS, CW., 1997. Do planktivorous fish structure the zooplankton communities in New Zealand lakes? *New Zealand Journal of Marine and Freshwater Research*, vol. 31, no. 1, p. 163-173. <http://dx.doi.org/10.1080/00288330.1997.9516755>
- JEPPENSEN, E., LAURIDSEN, TL., MITCHELL, SF., CHRISTOFFERSEN, K. and BURNS, CW., 2000. Trophic structure in the pelagic of 25 shallow New Zealand lakes: changes along nutrient and fish gradients. *Journal of Plankton Research*, vol. 22, no. 5, p. 951-968. <http://dx.doi.org/10.1093/plankt/22.5.951>
- MENU-MARQUE, S., MORRONE, JJ. and LOCASCIO DE MITROVICH, C., 2000. Distributional patterns of South American species of *Boeckella* (Copepoda, Centropagidae): a track analysis. *Journal of Crustacean Biology*, vol. 20, no 2, p. 262-272. [http://dx.doi.org/10.1651/0278-0372\(2000\)020\[0262:DPOTSA\]2.0.CO;2](http://dx.doi.org/10.1651/0278-0372(2000)020[0262:DPOTSA]2.0.CO;2)
- MODENUTTI, BE., BALSEIRO, EG., QUEIMALIÑOS, CP., SUAREZ, DA., DIEGUEZ, MC. and ALBARÍÑO, RJ., 1998. Structure and dynamics of food webs in Andean lakes. *Lakes and Reservoir Research and Management*, vol. 3, p. 179-186. <http://dx.doi.org/10.1046/j.1440-1770.1998.00071.x>
- NIEMEYER, H. and CERECEDA, P., 1984. Hidrografía. Geografía de Chile. *Chilean Military Geographic Institute*, vol. 8, 320 p.
- PEDROZO, F., CHILLRUD, S., TEMPORETTI, P. and DÍAZ, M., 1993. Chemical composition and nutrient limitation in rivers and lakes of northern Patagonian Andes (39.5-42° S, 71° W) (Rep. Argentina). *Verhandlungen International Vereinung Angewandte Limnologie*, vol. 25, p. 207-214.
- REID, J., 1985. Chave de identificação e lista de referências bibliográficas para as espécies continentais sul-americanas de vida livre da ordem Cyclopoida (Crustacea, Copepoda). *Boletim Zoológico Universidade do São Paulo*, vol. 9, p. 17-143.
- RIBAS, CR. and SCHÖREDER, JH., 2002. Are all ants mosaics caused by competition? *Oecologia*, vol. 131, no. 4, p. 606-611. <http://dx.doi.org/10.1007/s00442-002-0912-x>
- RODRÍGUEZ-FERNANDEZ, JI., BARROS DE CARVALHO, CJ. and MOURA, MO., 2006. Estrutura de assembleias de Muscidae (Diptera) no Paraná: uma análise por modelos nulos. *Revista Brasileira de Entomologia*, vol. 50, no. 1, p. 93-100. <http://dx.doi.org/10.1590/S0085-56262006000100014>
- SANDERS, NJ., CRUTSINGER, GM., MAJER, RR. and DELABIE, JHC., 2007. An ant mosaic revisited: dominant ant species dissemble arboreal ant communities but co-occur randomly. *Biotropica*, vol. 39, no. 3, p. 422-427. <http://dx.doi.org/10.1111/j.1744-7429.2007.00263.x>
- SOTO, D. and DE LOS RÍOS, P., 2006. Trophic status and conductivity as regulators of daphnids dominance and zooplankton assemblages in lakes and ponds of Torres del Paine National Park. *Biología, Bratislava*, vol. 61, no. 5, p. 541-546. <http://dx.doi.org/10.2478/s11756-006-0088-7>
- TIHO, S. and JOHENS, J., 2007. Co-occurrence of earthworms in urban surroundings: a null models of community structure. *European Journal of Soil Biology*, vol. 43, no 2, p. 84-90. <http://dx.doi.org/10.1016/j.ejsobi.2006.10.004>
- TONDOH, JE., 2006. Seasonal changes in earthworm diversity and community structure in central Côte d'Ivoire. *European Journal of Soil Biology*, vol. 42, supplement 1, p. S334-S340. <http://dx.doi.org/10.1016/j.ejsobi.2006.09.003>
- ULRICH, W., 2004. Species co-occurrences and neutral models: reassessing J.M. Diamond's assembly rules. *Oikos*, vol. 107, no. 3, p. 603-609. <http://dx.doi.org/10.1111/j.0030-1299.2004.12981.x>