



## Null models for study Rotifers and Crustaceans Zooplankton species richness in Chilean Patagonian lakes

Modelos nulos para o estudo de riqueza de espécies de Rotíferos e Crustáceos Zooplancônicos na Patagônia Chilena

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**Abstract: Aims:** The Patagonian lakes are characterized by their oligotrophy that is the cause of low species number in their zooplankton assemblage. The aim of the present study is to analyze the crustacean and rotifers species number pattern in Patagonian lakes among a latitudinal gradient (40-51 °S). **Results:** The results revealed that there are direct significant correlations between total species with rotifer species, and chlorophyll concentration with crustacean species number, and an inverse association between latitude with total species. **Conclusion:** The results of co-occurrence species null model revealed presence of regulator factors in one of three simulations, that would be due to the presence of many species repeated in studied sites. Similar patterns were observed in Argentinean Patagonian lakes.

**Keywords:** crustacean; rotifers; zooplankton; species number.

**Resumo: Objetivo:** Os lagos da Patagônia são caracterizados pela sua oligotrofia que é a causa do baixo número de espécies em sua comunidade zooplancônica. O objetivo do presente estudo é analisar o padrão de espécies de crustáceos e rotíferos em lagos da Patagônia em um gradiente latitudinal (40-51 °S). **Resultados:** Os resultados revelaram que existem correlações significativas diretas entre o total de espécies com espécies de rotíferos, e concentração de clorofila com o número de espécies de crustáceos, e uma associação inversa entre a latitude com total de espécies. **Conclusão:** Os resultados de modelo nulo de co-ocorrência de espécies revelaram a presença de fatores de regulação em uma das três simulações, que seria devido à presença de muitas espécies repetidas nos locais estudados. Padrões semelhantes foram observados nos lagos da Patagônia Argentina.

**Palavras-chave:** crustáceo; rotíferos; zooplâncton; número de espécies.



## 1. Introduction

The use of models for understand ecological patterns can involve the random presence in some determined cases for populations and community scales (Hilborn & Mangel 1997), that can be applied for statistical applications (Zar 1999; Gotelli & Ellison, 2013). At community ecology scale is proposed the null models that involve the absence of regulator factors in community structures (Harvey et al., 1983; Gotelli & Graves, 1996; Gotelli, 2000, 2001). The aim of the null models view point is based in randomization or absence of process and regulator factors on community ecology, and the null hypothesis is based that community is random or without defined structure (Harvey et al., 1983; Gotelli & Graves, 1996). On these null models one of the most applied in community ecology is the co-occurrence species that involves a presence-absence species matrix for a defined sites list with the aim of determine if the species associations are random or structured (Gotelli & Graves, 1996; Gotelli, 2000). These models are based mainly in terrestrial environments (Tondoh, 2006; Tiho & Josens, 2007) and in freshwater environments (De los Ríos, 2008; De los Ríos-Escalante et al., 2011). This kind of model has been applied mainly in field crustacean zooplankton studies on Chilean Patagonian lakes for understand the random or structuration in zooplankton species associations, unfortunately there are not other similar studies for other lakes (De los Ríos, 2008; De los Ríos-Escalante et al., 2011).

The Patagonian lakes are characterized by their oligotrophy and low species number in their zooplankton assemblages (Soto & Zúñiga, 1991; De los Ríos-Escalante, 2010). Similar pattern has been observed for Argentinean Patagonian lakes (Modenutti et al., 1998). The literature has been focused mainly in Crustacean species number (Soto & Zúñiga, 1991; Modenutti et al., 1998; De los

Ríos-Escalante, 2010), but there are not detailed descriptive studies for rotifers assemblages, there are only basic descriptions about presence/absence rotifers species (Campos et al., 1989, 1992, 1988, 1990, 1994a, b; Villalobos, 1999). The aim of the present study is to analyze the crustacean and Rotifera zooplankton assemblages in Chilean Patagonian lakes with the aim of determine if the assemblages are random or structured.

## 2. Material and methods

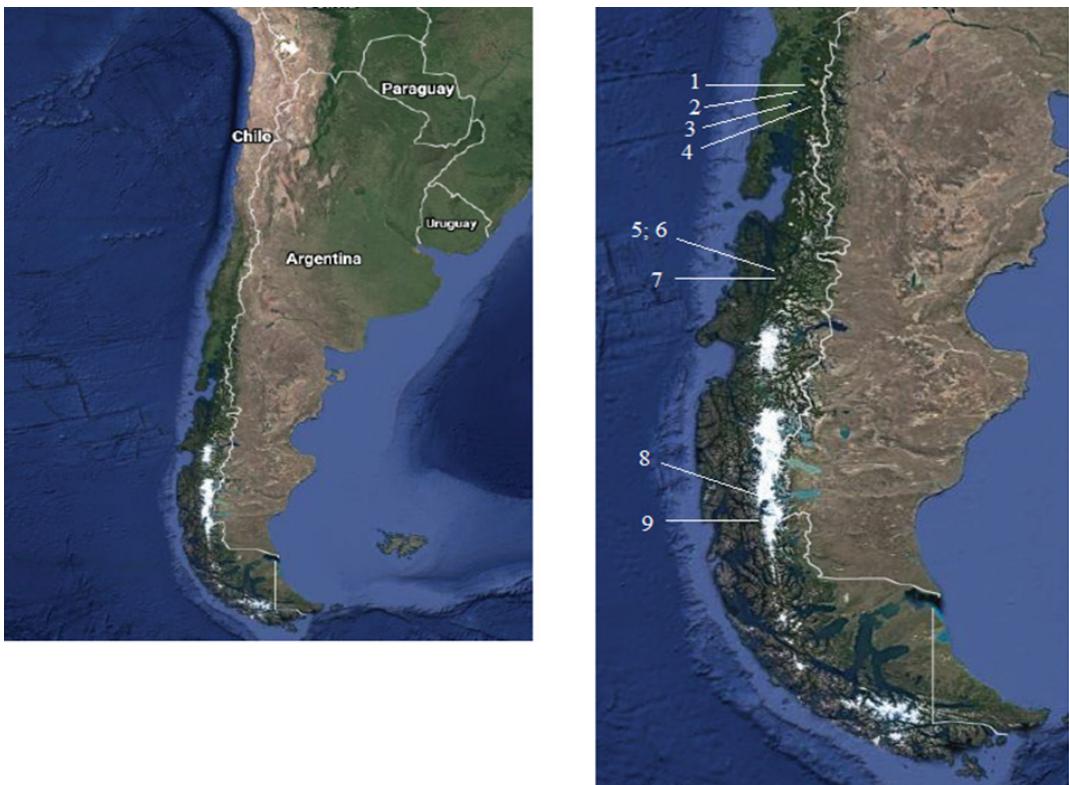
Data of geographical location, surface, maximum depth, mean chlorophyll, rotifer, crustacean species number were obtained from literature, (Campos et al., 1989, 1992, 1988, 1990, 1994a, b; Villalobos, 1999) (Table 1, Figure 1), it was selected these variables, because: these are available for all studied sites; some trophic variables have wrong in some lakes due methodological procedures (Woelfl et al., 2003), and these variables are considered in many zooplankton studies in Chilean lakes (Soto & Zúñiga, 1991; De los Ríos & Soto, 2005, 2006; De los Ríos-Escalante, 2010, 2013).

Data was analyzed in three steps: a first step is determine if the rotifer, crustacean and total zooplankton species was associated with the mentioned parameters, for this purpose, it was previously verified the normality using a Shapiro test, and as this condition was not found, it was applied a Spearman non parametric correlation test using software "R" (R Development Core Team, 2009).

In the following steps a species absence/ presence matrix was constructed, with the species in rows and the sites in columns (Table 2). As second step consisted, it was applied a UPGMA cluster analysis using Neighbour-joining method for determine potential similarities between sites on the basis of species associations using the R package Phangorn (Schliep, 2011). Thirdly we calculated

**Table 1.** Geographical location, maximum depth (Zmax in m), surface (km<sup>2</sup>), chlorophyll "a" concentration (µg/L), and rotifer and crustacean species number for sites considered in the present study.

	Lat. S, Long W.	Zmax	Surface	Chlorophyll "a"	Rotifer	Crustacean
Puyehue	40°40' 72°30'	123	165.4	2.1	6	7
Rupanco	40°50' 72°30'	272	235.0	1.2	9	4
Todos los Santos	41°08' 72°50'	335	178.5	0.4	9	4
Llanquihue	41°08' 72°50'	317	870.5	0.5	12	3
Los Palos	45°19' 72°42'	59	5.0	0.8	12	4
Riesco	45°39' 72°20'	130	14.7	0.9	9	4
Escondida	45°49' 72°40'	43	7.0	0.5	9	5
Del Toro	51°03' 72°38'	312	86.0	0.3	2	5
Sarmiento	51°12' 72°37'	300	196.0	0.4	5	4



**Figure 1.** Map with sites included in the present study (1: Puyehue; 2: Rupanco; 3: Llanquihue; 4: Todos los Santos; 5: Los Palos; 6: Escondida; 7: Riesco; 8: Sarmiento; 9: Del Toro). Source: Google Earth (2016).

a Checkerboard score (“C-score”), which is a quantitative index of occurrence that measures the extent to which species co-occur less frequently than expected by chance (Gotelli, 2000). A community is structured by competition when the C-score is significantly larger than expected by chance (Gotelli, 2000; Tondoh, 2006; Gotelli & Entsminger, 2007; Tiho & Josens, 2007; Ehouman et al., 2009). Thirdly we compared co-occurrence patterns with null expectations via simulation. Gotelli & Ellison (2013) suggested the as statistical null models 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). The null model analyses were performed using the package EcosimR version 7.0 (Gotelli & Ellison, 2013; Carvajal-Quintero et al., 2015).

Finally, it was applied a correspondence analysis with the presence-absence data with the aim of determine the potential groups of lakes and their respective zooplankton components. This analysis was performed using the R-package CA (Nenadic & Greenacre, 2007).

### 3. Results

The correlation results revealed the absence of significant associations between studied parameters (Table 3). The results of cluster analysis revealed for total species and Rotifera the presence of three main groups, the first joined by Sarmiento and Del Toro lakes, the second joined by Los Palos, Escondida and Riesco lakes, and the third joined by Llanquihue, Todos los Santos, Rupanco and Puyehue lakes (Figure 2), whereas for crustacean the groups observed were first joined by Sarmiento, Del Toro, Llanquihue and Todos los Santos lakes, the second joined by Los Palos, Escondida and Riesco lakes, and the third group joined by Rupanco and Puyehue lakes (Figure 2).

The results of co-occurrence null model species revealed the presence of regulator factors for total, crustaceans and rotifer species (Table 4), that is confirmed by respective simulation graphs (Figure 3).

The results CA analysis agree with UPGMA about the presence of three main groups joined the first with Sarmiento and Del Toro lakes, the second joined by Riesco, Los Palos and Escondida lakes, and the third joined by Todos Los Santos, Rupanco, Puyehue and Llanquihue lakes (Table 5, Figure 4).

**Table 2.** Rotifera and crustacean species reported for sites considered in the present study.

	Del Toro	Sarmiento	Escondida	Riesco	Los Palos	Llanquihue	Todos Los Santos	Rupanco	Puyehue
<b>Crustacea</b>									
<i>Daphnia pulex</i> (Leydig 1860)	0	0	0	0	0	0	1	1	0
<i>Ceriodaphnia dubia</i> (Richard 1894)	0	0	1	1	1	0	0	1	1
<i>Neobosmina chilensis</i> (Daday 1902)	0	1	1	1	1	1	1	1	1
<i>Diaphanosoma chilense</i> (Daday 1902)	0	0	0	0	0	0	0	1	1
<i>Tumeodiaptomus diabolicus</i> (Brehm 1935)	0	0	0	0	0	0	0	1	1
<i>Boeckella gracilipes</i> (Daday 1901)	1	1	1	1	1	1	1	0	0
<i>Boeckella michaelensi</i> (Mrazek 1901)	1	1	0	0	0	0	0	0	0
<i>Parabroteas sarsi</i> (Ekman 1905)	0	0	1	1	1	0	0	0	0
<i>Tropocyclops prasinus meridionalis</i> (Kiefer 1927)	1	1	1	1	1	0	0	0	1
<i>Mesocyclops araucanus</i> (Löffler 1962)	1	1	1	1	1	1	1	0	1
<b>Rotifera</b>									
<i>Ascomorpha</i> sp. (Perty 1850)	0	0	0	0	0	1	1	0	0
<i>Asplanchna</i> (Gosse 1850)	0	0	1	1	1	0	0	0	0
<i>Collotheaca pellagica</i> (Rousselet 1893)	0	0	1	1	1	1	1	1	1
<i>Conochilooides coenobastis</i> (Hudson 1885)	0	0	0	0	0	0	0	0	1
<i>Conochilus unicornis</i> (Rousselet 1892)	0	1	1	1	1	1	1	1	1
<i>Euchalanis</i> sp. (Ehrenberg 1832)	1	1	0	0	0	0	0	0	0
<i>Filinia longiseta</i> (Ehrenberg 1834)	0	0	1	1	1	0	0	0	0
<i>Gastropus</i> sp. (Inhof 1898)	0	0	1	1	1	0	0	0	0
<i>Keratella cochlearis cochlearis</i> (Gosse 1851)	0	0	1	1	1	1	1	1	1
<i>Keratella gracilenta</i> Alstrom	0	0	0	0	0	0	0	1	0
<i>Lecane luna</i> (Müller 1776)	0	0	1	1	1	0	0	0	0
<i>Monostyla lunaris</i> (Ehrenberg 1832)	1	1	0	0	0	1	0	0	0
<i>Notholca caudata</i> (Carlin 1943)	0	1	0	0	0	0	0	0	0
<i>Polyartha dolichoptera</i> (Idelson 1925)	0	0	0	0	0	1	1	1	1
<i>P. vulgaris</i> (Carlin 1943)	0	1	1	1	1	1	0	0	0
<i>Pompholyx sulcata</i> (Hudson 1855)	0	0	0	0	0	1	1	0	0
<i>Synchaeta</i> sp. (Ehrenberg 1832)	0	0	1	1	1	0	0	0	0
<i>S. stylata</i> (Wierzejski 1893)	0	0	0	0	0	1	1	1	0
<i>Tricocerca</i> (Lamarck 1801)	0	0	0	0	0	0	0	0	1
<i>T. porcellus</i> (Gosse 1851)	0	0	0	0	0	1	1	1	0
<i>T. similis</i> (Wierzejski 1893)	0	0	0	0	0	0	0	1	0
Phylodina indet.	0	0	1	1	1	0	0	0	0
Rotatoria indet.	0	0	0	0	0	0	0	1	0
Bdelloidea indet.	0	0	0	0	0	1	1	0	0

**Table 3.** Results of correlation between studied parameters with Rotifera, crustacean and total species number.

	Rho	P
Latitude – Rotifera	-0.386	0.304 n.s
Zmax – Rotifera	-0.131	0.736 n.s
Surface – Rotifera	0.043	0.911 n.s
Chlorophyll – Rotifera	0.321	0.398 n.s
Latitude – crustacea	-0.036	0.925 n.s
Zmax – crustacea	-0.477	0.194 n.s
Surface – crustacea	-0.477	0.194 n.s
Chlorophyll – crustacea	0.106	0.785 n.s
Latitude – total	0.362	0.337 n.s
Zmax – total	-0.391	0.297 n.s
Surface – total	-0.226	0.558 n.s
Chlorophyll – total	0.381	0.310 n.s

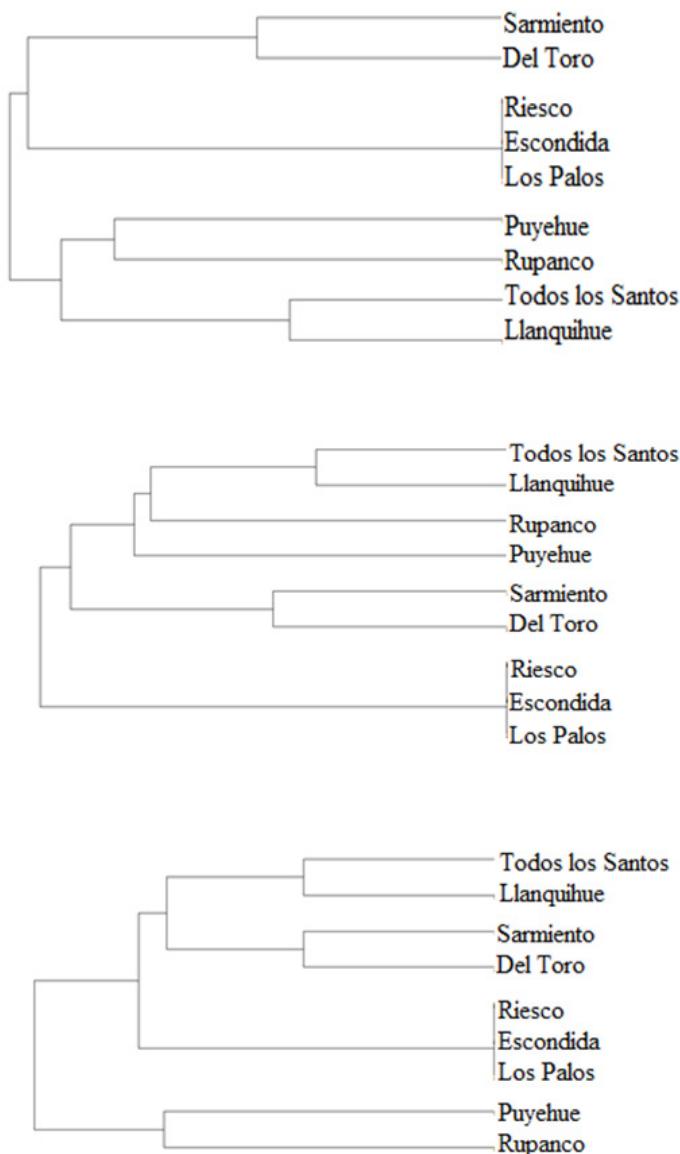
"P" values lower than 0.05 denotes significant association.

#### 4. Discussion

The results revealed that the zooplankton species associations are not random, this mean the existence of regulator factors, this is supported first by marked significantly of co-occurrence species null models, that would avoid the presence of type I and type II errors (Gotelli, 2000; Veech, 2012). Although the correlation analysis does not denote significant associations, the literature mentioned an inverse relation between species richness latitude, and a direct association between species richness and chlorophyll a (De los Ríos-Escalante, 2010, 2013). This is because, there is an inverse association between chlorophyll and latitude in large and deep

lakes due mixing depth increasing, that generate an strong physical stressor for phytoplankton activity (Soto, 2002; De los Ríos-Escalante, 2010).

The role of rotifers and crustacean zooplankton is important because they are main grazers in Patagonian lakes (Woelfl, 2007; Woelfl et al., 2010;

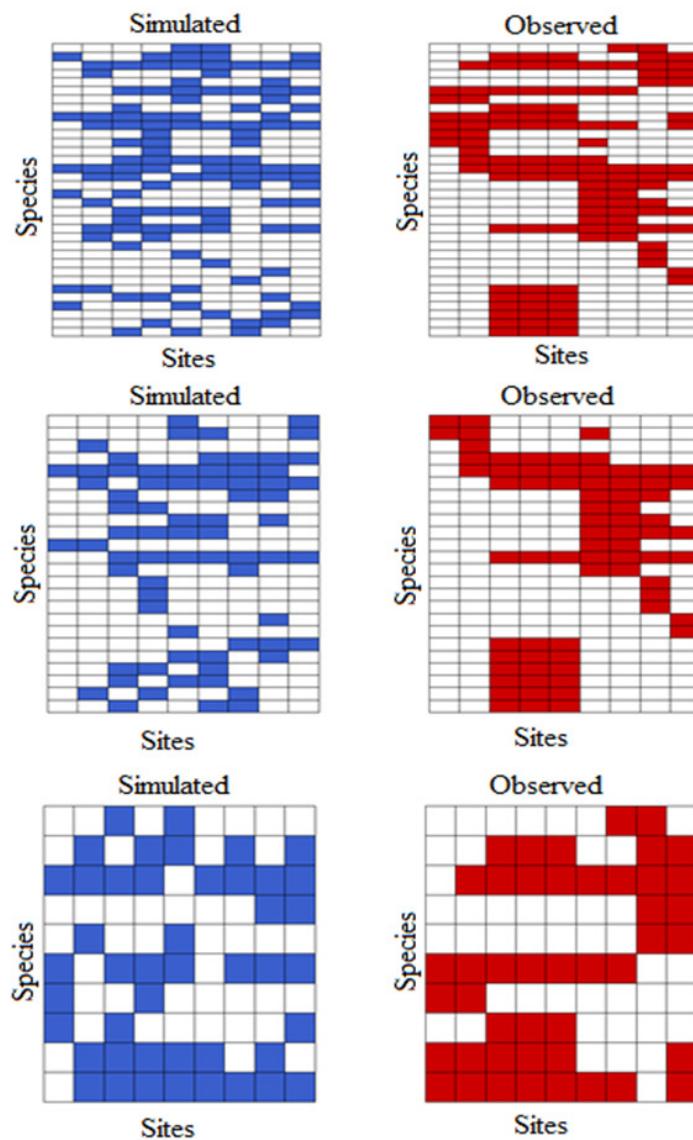


**Figure 2.** UPGMA based on neighbour-joining method for total species (up), rotifer species (center) and crustacean species (down).

**Table 4.** Results of null model co-occurrence species for total species number, rotifer and crustacean species for studied sites.

Models	Total species				
	Observed index	Mean index	Standard effect size	Variance	P
Fixed-fixed Total species: 34	3.019	2.667	10.444	0.002	<0.001 *
Fixed-fixed Rotifer species: 24	3.511	3.064	3.663	0.014	0.004 *
Fixed-fixed Crustacean species: 10	2.858	2.526	7.586	0.001	<0.001 *

\* "P" values lower than 0.05 denotes the presence of regulator factors.



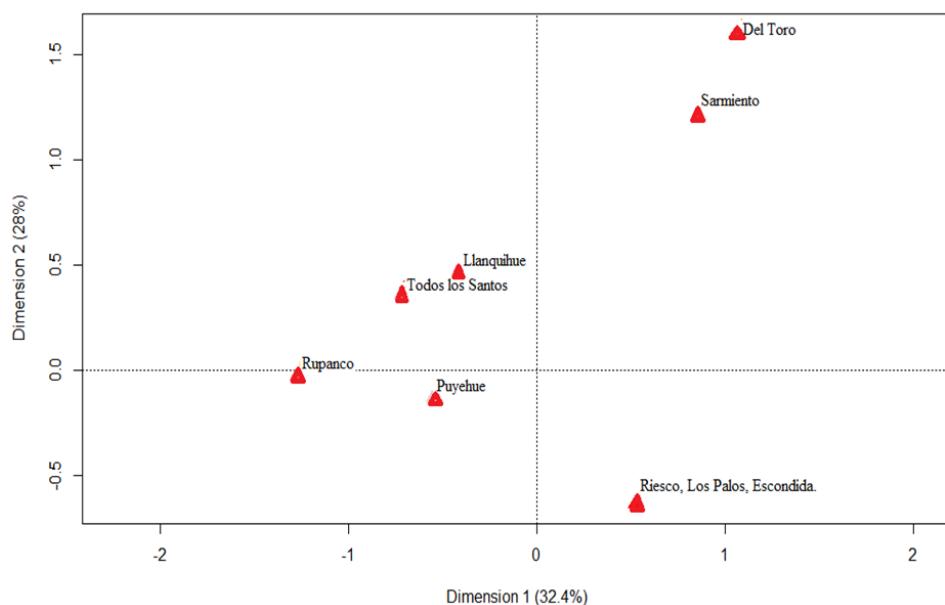
**Figure 3.** Graphs with simulated and observed species associations based on null model co-occurrence analysis for total species (up), rotifer species (center) and crustacean species (down).

**Table 5.** Results of correspondence analysis for presence-absence species matrix.

	Masses	Total quality	Inertia value
<b>Crustacea</b>			
<i>D. pulex</i>	17	575	34
<i>C. dubia</i>	43	630	15
<i>N. chilensis</i>	68	120	3
<i>D. chilense</i>	17	446	36
<i>T. diabolicus</i>	17	446	36
<i>B. gracilipes</i>	60	762	16
<i>B. michaelensi</i>	17	876	70
<i>P. sarsi</i>	26	961	22
<i>T. prasinus meridionalis</i>	51	638	23
<i>M. araucanus</i>	68	690	10
<b>Rotifera</b>			
<i>Ascomorpha</i> sp.	17	290	34

**Table 5.** Continued...

	<b>Masses</b>	<b>Total quality</b>	<b>Inertia value</b>
<i>Asplanchna</i>	26	961	22
<i>C. pellagica</i>	60	857	6
<i>C. coenobastis</i>	9	68	45
<i>C. unicornis</i>	68	120	3
<i>Euchalanis</i> sp.	17	876	70
<i>F. longisetata</i>	26	961	22
<i>Gastropus</i> sp.	26	961	22
<i>K. cochlearis cochlearis</i>	60	857	6
<i>K. gracilenta</i>	9	413	38
<i>L. luna</i>	26	961	22
<i>M. lunaris</i>	26	890	52
<i>N. caudata</i>	9	418	55
<i>P. dolichoptera</i>	34	894	25
<i>P. vulgaris</i>	43	439	17
<i>P. sulcata</i>			
<i>Synchaeta</i> sp.	26	733	29
<i>S. stylata</i>	26	961	22
<i>Tricocerca</i>	9	69	45
<i>T. porcellus</i>	26	733	29
<i>T. similis</i>	9	413	38
Phylodina indet.	26	991	22
Rotatoria indet.	9	413	38
Bdelloida indet.	17	290	34
Sites			
Puyehue	103	131	153
Rupanco	120	612	193
Todos los Santos	111	413	105
Llanquihue	120	316	89
Los Palos	137	980	57
Riesco	137	980	57
Escondida	137	980	57
Del Toro	51	783	147
Sarmiento	85	787	142

**Figure 4.** Results of correspondence analysis for sites in the presence-absence species matrix.

Montecino et al., 2011; Modenutti, 2014). In this scenario, the literature described a direct relation between chlorophyll concentration and crustacean species richness for Patagonian lakes (De los Ríos-Escalante, 2010, 2013), but the chlorophyll concentration is inversely related with latitude for these lakes (Soto, 2002, De los Ríos-Escalante, 2010). It was not found significant associations between crustacean zooplankton species richness with surface and depth (Soto & Zúñiga, 1991; De los Ríos-Escalante, 2010, 2013). These results would agree partially with observations for northern hemisphere lakes where it was found the direct association between crustaceans species number with chlorophyll concentration, nevertheless in northern hemisphere lakes it was found a direct association between crustacean species number with surface (Dodson, 1992; Karataev et al., 2008; Dodson et al., 2009; Van Egeren et al., 2011).

In the present study, the lacks of coincidences between correlation test with null models would support the literature descriptions about null models because these are statistically robust (Tondoh, 2006; Tiho & Josens, 2007; Gotelli & Ulrich, 2012). The present study would suggest compare null model analysis with traditional statistical null hypothesis for improve the data analysis.

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## References

- CAMPOS, H., SOTO, D., STEFFEN, W., AGÜERO, G., PARRA, O. and ZÚÑIGA, L. Limnological studies in lake del Toro, Chilean Patagonia. *Archiv für Hydrobiologie*, 1994a, 99(1/2), 199-215.
- CAMPOS, H., SOTO, D., STEFFEN, W., AGÜERO, G., PARRA, O. and ZÚÑIGA, L. Limnological studies in lake Sarmiento, a subsaline lake from Chilean Patagonia. *Archiv für Hydrobiologie*, 1994b, 99(1/2), 217-234.
- CAMPOS, H., STEFFEN, W., AGÜERO, G., PARRA, O. and ZÚÑIGA, L. Limnological study of lake Llanquihue (Chile): morphometry, physics, chemistry and primary productivity. *Archiv für Hydrobiologie*, 1988, 81(1), 37-67.
- CAMPOS, H., STEFFEN, W., AGÜERO, G., PARRA, O. and ZÚÑIGA, L. Estudios limnológicos en el lago Puyehue (Chile): morfometría, factores físicos y químicos, plancton y productividad primaria. *Medio Ambiente*, 1989, 10, 36-53.
- CAMPOS, H., STEFFEN, W., AGÜERO, G., PARRA, O. and ZÚÑIGA, L. Limnological study of lake Todos los Santos (Chile): morphometry, physics, chemistry and primary productivity. *Archiv für Hydrobiologie*, 1990, 117(4), 453-484.
- CAMPOS, H., STEFFEN, W., AGÜERO, G., PARRA, O. and ZÚÑIGA, L. Limnological studies of lake Rupanco (Chile): Morphometry, physics, chemistry and primary productivity. *Archiv für Hydrobiologie*, 1992, 90, 85-113.
- CARVAJAL-QUINTERO, J.D., ESCOBAR, F., ALVARADO, F., VILLA-NAVARRO, F.A., JARAMILLO-VILLA, U., and MALDONADO-OCAMPO, J.A. Variation in freshwater fish assemblages along a regional elevation gradient in the northern Andes, Colombia. *Ecology and Evolution*, 2015, 5(13), 2608-2620. <http://dx.doi.org/10.1002/ece3.1539>.
- DE LOS RÍOS, P. A null model for explain crustacean zooplankton species associations in central and southern Patagonian inland waters. *Anales del Instituto de la Patagonia*, 2008, 36(1), 25-33.
- DE LOS RÍOS, P. and SOTO, D. Survival of two species of crustacean zooplankton under to two chlorophyll concentrations and protection or exposure to natural ultraviolet radiation. *Crustaceana*, 2005, 78(2), 163-169. <http://dx.doi.org/10.1163/1568540054020613>.
- DE LOS RÍOS, P. and SOTO, D. Structure of the zooplanktonic crustaceous chilean lacustre assamblages: role of the trophic status and protection resources. *Crustaceana*, 2006, 79(1), 23-32. <http://dx.doi.org/10.1163/156854006776759716>.
- DE LOS RÍOS-ESCALANTE, P. Crustacean zooplankton communities in Chilean inland waters. *Crustaceana Monographs*, 2010, 12, 1-109.
- DE LOS RÍOS-ESCALANTE, P. Crustacean zooplankton species richness in Chilean lakes and ponds (23°-51 °S). *Latin American Journal of Aquatic Research*, 2013, 41(3), 600-605.
- DE LOS RÍOS-ESCALANTE, P., HAUENSTEIN, E. and ROMERO-MIERES, M. Microcrustacean assemblages composition and environmental variables in lakes and ponds of the Andean region - South of Chile (37-39 °S). *Brazilian Journal of Biology = Revista Brasileira de Biologia*, 2011, 71(2), 353-358. PMid:21755151.
- DODSON, S.I. Predicting crustacean zooplankton species richness. *Limnology and Oceanography*, 1992, 37(4), 848-856. <http://dx.doi.org/10.4319/lo.1992.37.4.0848>.
- DODSON, S.I., NEWMAN, A.M., WILL-WOLF, S., ALEXANDER, M.L., WOODFORD, M.P. and VAN EGREN, S. The relationship

- between zooplankton community structure and lake characteristics in temperate lakes (Northern Wisconsin, USA). *Journal of Plankton Research*, 2009, 31(1), 93-100. <http://dx.doi.org/10.1093/plankt/fbn095>.
- EHOUMAN, N.M., TIHO, S. and DAGNOGO, M. Co-occurrence of earthworms in Lam to savanna: a null model analysis of community structure. *European Journal of Soil Biology*, 2009, 53, 40-47. <http://dx.doi.org/10.1016/j.ejsobi.2012.08.007>.
- GOOGLE EARTH. [online]. 2016 [viewed 25 July 2016]. Available from: <https://www.google.cl/maps/@-48.4349816,-78.6138143,1945228m/data=!3m1!1e3>
- GOTELLI, N.J. and ELLISON, A.M. *EcoSimR 1.00*. 2013 [viewed 21 Mar 2016]. Available from: <http://www.uvm.edu/~ngotelli/EcoSim/EcoSim.html>
- GOTELLI, N.J. and ENTSINGER, G.L. *EcoSim: null models software for ecology: VT 05465* [online]. Victoria: Acquired Intelligence, 2007 [viewed 21 Mar 2016]. Available from: <http://garyentsminger.com/ecosim>
- GOTELLI, N.J. and GRAVES, G.R. *Null models in ecology*. Washington: Smithsonian Institution Press, 1996, 357p.
- GOTELLI, N.J. and ULRICH, W. Statistical challenges in null model analysis. *Oikos*, 2012, 121(2), 171-180. <http://dx.doi.org/10.1111/j.1600-0706.2011.20301.x>.
- GOTELLI, N.J. Null model analysis of species co-occurrence patterns. *Ecology*, 2000, 81(9), 2606-2621. [http://dx.doi.org/10.1890/0012-9658\(2000\)081\[2606:NMAOSC\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2000)081[2606:NMAOSC]2.0.CO;2).
- GOTELLI, N.J. Research frontiers in null model analysis. *Global Ecology and Biogeography*, 2001, 10(4), 337-343. <http://dx.doi.org/10.1046/j.1466-822X.2001.00249.x>.
- HARVEY, P.H., COLWELL, R.K., SILVERTOWN, J.W. and MAY, R.M. Null models in ecology. *Annual Review of Ecology and Systematics*, 1983, 14(1), 189-211. <http://dx.doi.org/10.1146/annurev.es.14.110183.001201>.
- HILBORN, R. and MANGEL, M. *The ecological detective, confronting model with data*. Princeton: Princeton University Press, 1997. 315 p. Monographs in Population Biology, no. 28.
- KARATAYEV, A.Y., BURLAKOVA, L.E. and DODSON, S.I. Community analysis of Belarusian lakes: correlations of species diversity with hydrochemistry. *Hydrobiologia*, 2008, 605(1), 99-112. <http://dx.doi.org/10.1007/s10750-008-9323-2>.
- MODENUTTI, B.E. Mixotrophy in Argentina freshwaters. *Advances in Limnology*, 2014, 65, 359-374. <http://dx.doi.org/10.1127/1612-166X/2014/0065-0051>.
- MODENUTTI, B.E., BALSEIRO, E.G., QUEIMALIÑOS, C.P., AÑÓN SUÁREZ, D.A., DIEGUEZ, M.C. and ALBARIÑO, R.J. Structure and dynamics of food webs in Andean lakes. *Lakes and Reservoirs: Research and Management*, 1998, 3(2), 179-189. <http://dx.doi.org/10.1046/j.1440-1770.1998.00071.x>.
- MONTECINO, V., OYANEDEL, J.P., VILA, I. and ZUÑIGA, L. Limnetic zooplankton of Chilean lakes and reservoirs: a tribute to Bernard Dussart. In D. DEFAYE, E. SUÁREZ-MORALES and J.C. VON VAUPEL KLEIN, eds). *Studies on freshwater copepod: a volume in honour of Bernard Dussart*. Leiden: Brill, 2011, pp. 367-382. Crustaceana Monographs, no. 16.
- NENADIC, O. and GREENACRE, M. Correspondence analysis in R, with two- and three-dimensional graphics: the ca package. *Journal of Statistical Software*, 2007 [viewed 21 Mar 2016], 20(3). Available from: <http://www.jstatsoft.org/v20/i03/>
- R DEVELOPMENT CORE TEAM. *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing, 2009.
- SCHLIEP, K.P. phangorn: phylogenetic analysis in R. *Bioinformatics (Oxford, England)*, 2011, 27(4), 592-593. <http://dx.doi.org/10.1093/bioinformatics/btq706>. PMid:21169378.
- SOTO, D. and ZUÑIGA, L.R. Zooplankton assemblages of Chilean temperate lakes: a comparison with North American counterparts. *Revista Chilena de Historia Natural (Valparaíso, Chile)*, 1991, 64(3), 569-581.
- SOTO, D. Oligotrophic patterns in southern Chile lakes: the relevance of nutrients and mixing depth. *Revista Chilena de Historia Natural (Valparaíso, Chile)*, 2002, 75(2), 377-393. <http://dx.doi.org/10.4067/S0716-078X2002000200009>.
- TIHO, S. and JOSENS, G. Co-occurrence of earth worms in urban surroundings: a null model analysis of community structure. *European Journal of Soil Biology*, 2007, 43(2), 84-90. <http://dx.doi.org/10.1016/j.ejsobi.2006.10.004>.
- TONDOH, J.E. Seasonal changes in earthworm diversity and community structure in Central Côte d'Ivoire. *European Journal of Soil Biology*, 2006, 42, s334-s340. <http://dx.doi.org/10.1016/j.ejsobi.2006.09.003>.
- VAN EGEREN, S.J., DODSON, S.I., TORKE, B. and MAXTED, J.M. The relative significance of environmental and anthropogenic factors affecting zooplankton community structure in Southeast Wisconsin Till Plain lakes. *Hydrobiologia*, 2011, 668(1), 137-146. <http://dx.doi.org/10.1007/s10750-011-0636-1>.
- VEECH, J.A. Significance testing in ecological null models. *Theoretical Ecology*, 2012, 5(4), 611-616. <http://dx.doi.org/10.1007/s12080-012-0159-z>.
- VILLALOBOS, L. *Determinación de capacidad de carga y balance de fósforo y nitrógeno de los lagos Riesco, Los Palos*,

y Laguna Escondida en la XI región. Valdivia: Universidad Austral de Chile, 1999. pp. 97-39. Technical Report Fisheries Research Foundation-Chile.

WOELFL, S. The distribution of large mixotrophic ciliates (*Stentor*) in deep North Patagonian lakes (Chile): first results. *Limnologica- Ecology and Management of Inland Waters*, 2007, 37(1), 28-36.

WOELFL, S., GARCIA, P. and DUARTE, C. Chlorella-bearing ciliates (*Stentor*, *Ophrydium*) dominate in an oligotrophic, Deep, North Patagonian lake (Lake Caburgua, Chile). *Limnologica- Ecology and Management of Inland Waters*, 2010, 40(2), 134-139.

WOELFL, S., VILLALOBOS, L. and PARRA, O. Trophic parameters and method validation in Lake Riñihue (North Patagonia: Chile) from 1978 through 1997. *Revista Chilena de Historia Natural (Valparaíso, Chile)*, 2003, 76(3), 459-474. <http://dx.doi.org/10.4067/S0716-078X2003000300010>.

ZAR, J.H. *Biostatistical analysis*. New Jersey: Prentice Hall, 1999. 663 p.

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