

Benthic macroinvertebrate community patterns of Mediterranean forested wetlands and their relation to changes in the hydroperiod

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ABSTRACT

Benthic macroinvertebrate community patterns of Mediterranean forested wetlands and their relation to changes in the hydroperiod

The macroinvertebrate community of Mediterranean forested wetlands (FW) in Southern Chile was studied to determine their temporary distribution patterns in relation to changes in the hydroperiod. A total of 540 samples were collected over a period of one year using three complementary techniques. The results indicated a total of 80 taxa dominated by Chironomidae, Oligochaeta and *Hyallolela araucana*. These communities presented significant differences among wetlands with different water regimes (ANOSIM Global $R = 0.45$, $p = 0.001$) and between different seasons ($p < 0.05$). The seasonal differences were clearer in temporary wetlands, which were directly related to depth changes ($r > 0.64$, $p < 0.05$). These differences were primarily due to the following taxa: Asellidae, Chironomidae, *Hyallolela araucana*, *Littoridina* sp. and Oligochaeta. An important number of exclusive and rare taxa were also determined according to the different regimes. The clear influence of the hydroperiod on the community patterns of the benthic macroinvertebrates (BMI) and the importance of conserving these ecosystems as reservoirs of a unique diversity that distinguish these types of wetlands are discussed.

Key words: Mediterranean forested wetlands, hydroperiod, macroinvertebrates, temporary variation, conservation.

RESUMEN

Patrones de la comunidad de macroinvertebrados bentónicos de humedales boscosos mediterráneos y su relación con cambios en el hidropériodo

Se estudió la comunidad de macroinvertebrados de los humedales boscosos Mediterráneos del sur de Chile, con el fin de determinar su patrón de distribución temporal y su relación con los cambios en el hidropériodo. Se recolectaron un total de 540 muestras durante un período de un año, por medio de tres técnicas complementarias. Los resultados mostraron un total de 80 taxones, dominados por Chironomidae, Oligochaeta y *Hyallolela araucana*. La comunidad presentó diferencias significativas entre humedales con diferentes regímenes hídricos (ANOSIM Global $R = 0.45$, $p = 0.001$) y entre diferentes épocas ($p < 0.05$). Las diferencias estacionales fueron más claras en humedales temporales y se relacionaron directamente con los cambios de profundidad ($r > 0.64$, $p < 0.05$). Estas diferencias fueron determinadas principalmente por Asellidae, Chironomidae, *Hyallolela araucana*, *Littoridina* sp. y Oligochaeta. Se determinó un importante número de taxones raros y grupos exclusivos de acuerdo a los distintos regímenes. La influencia del hidropériodo sobre los patrones comunitarios de los macroinvertebrados bentónicos (MIB) fue clara y se discute la importancia de conservar estos ecosistemas como reservorios de una diversidad única, que representa las características distintivas de este tipo de humedales.

Palabras clave: Humedales boscosos mediterráneos, hidropériodo, macroinvertebrados, variación temporal, conservación.

INTRODUCTION

In wetlands, the hydroperiod is primarily defined by variations in both depth and volume and it mainly depends on the rainfall pattern, which influences the monthly and annual variability of the water resources (Pizarro *et al.*, 2006; Little *et al.*, 2009). In Mediterranean zones (MZ), which are characterised by the seasonality of rainfall (Di Castri & Hajek, 1976), water contributions are crucial to maintain a natural hydrological regime of these ecosystems. However, as a product of the decrease in rainfall during the summer season, these ecosystems present a marked decrease in both depth and volume. Several authors have noted that different soil covers are also important variables in the hydrological cycle (Lara *et al.*, 2009). Recent studies have shown that non-native forest cover can exacerbate the decrease of water resources in the summer season (Lara *et al.*, 2009; Little *et al.*, 2009), implying the absence of water during several months of the year (Tavernini, 2008).

Variation in the hydroperiods either from natural causes or by human action determines most of the physicochemical characteristics of the water (i.e., pH, conductivity, and dissolved oxygen) and is fundamental for the development of the biological communities and sustained ecosystem processes (i.e., decomposition) (Nicolet *et al.*, 2004; Tavernini, 2008). In this regard, Talling (2003) described the effects on the algal community, and Ferreira *et al.* (2009) and Correa-Araneda *et al.* (2012) described the wetland woody vegetation. The influence on zooplankton communities (*e.g.*, Tavernini, 2008; Sahuquillo & Miracle, 2010), vertebrates (*e.g.*, Rowe & Dunson, 1995; Spencer *et al.*, 1999) and macroinvertebrates (*e.g.*, Bazzanti *et al.*, 1997) was also examined.

Thus, the condition of intermittence is one of the most influential aspects on the structure of vegetal and animal communities in wetlands (Tavernini, 2008). These ecosystems are varied, and among them, FW present important characteristics that differentiate them from the rest. They are dominated by woody vegetation, primarily from the Myrtaceae family (Correa-Araneda *et al.*,

2011), of approximately 10 to 15 m in height (Correa-Araneda *et al.*, 2012), mainly those located in the Chilean MZ. This vegetation originates from a low penetration of the light to the water, thus decreasing evaporation and directly influencing the hydroperiod. The submerged portion of the forest allows the formation of islets (Duberstein & Conner, 2009), creating a highly heterogeneous environment that provides a great diversity of microhabitats, which are ideal for the development of BMI (Correa-Araneda *et al.*, 2011). These organisms are very sensitive to all types of perturbations, including changes in the hydroperiod (Williams, 2006). They have been frequently used as water quality bioindicators and widely used in all types of freshwater ecosystems (Rosenberg & Resh, 1993). However, the information in Chilean wetlands is restricted to a few studies (*e.g.*, Villagrán-Mella *et al.*, 2006; Figueroa *et al.*, 2009). Based on the abovementioned issues, the aim of this study was to describe the BMI community in Chilean FW and its distribution patterns in relation to changes in the hydroperiod.

METHODOLOGY

Study area

The study area is located in the Chilean MZ, specifically in the Araucanía Region (37°-40°S), in which five forested wetlands (FW) were studied (Fig. 1). The preponderant climate in this zone is a wet-Mediterranean type, that is characterised by dry summers and rainy winters and has an annual precipitation between 1200 mm and 1600 mm. The summer temperatures fluctuate between 14-23 °C, and the winter temperatures fluctuate between 7-13 °C (Di Castri & Hajek, 1976).

Sampling method

The study was conducted by bi-monthly sampling from April 2011 to March 2012. The sampling of BMI was conducted using three complementary techniques to capture the greatest possible variability of available habitats in these

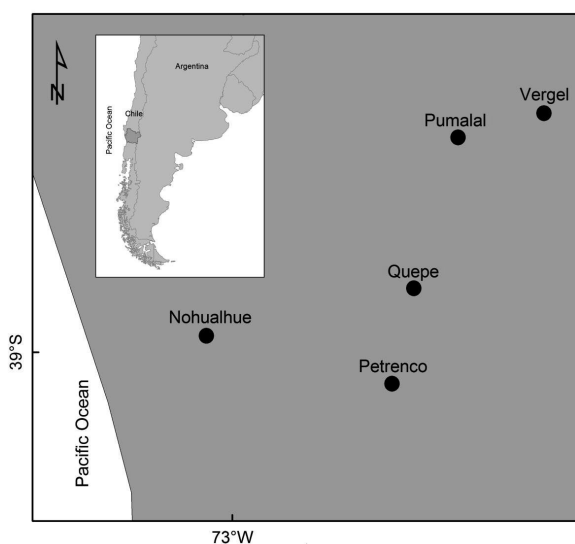


Figure 1. General location of the study area and the considered FW. *Ubicación general del área de estudio y los humedales boscosos considerados.*

systems (*e.g.*, water column, substrate, islets and roots) and seasonality (winter and summer seasons) within ecosystems. These techniques consisted of 1) a 400 cm³ metallic coring device with a cutting edge to penetrate substrates and a closed system that prevented material loss, 2) litter substrates for colonisation, which are basically 5 mm grid bags with 6 g of dehydrated leaves from the dominant woody species (*Blepharocalyx cruckshanksii* (Hook. & Arn.) and *Myrceugenia exsucca* (DC) Berg), that were submerged

for two months so that they could be colonised by the organisms (Ramseyer & Marchese, 2009), and 3) a hand net (250 µm), which was used while wading around the available habitats during a period of 5 minutes using the catch-per-unit-effort (CPUE). All of the techniques were randomly applied in the five studied wetlands ($n = 6$ for each technique). The obtained samples were stored in ethanol (95 %) and labelled for their later taxonomic and functional feeding group identification by means of specialised literature (*e.g.*, McCafferty, 1998; McLellan *et al.*, 2005; Domínguez & Fernández *et al.*, 2009).

Water regime and physicochemical variables

The hydroperiod of the wetlands was determined using autonomous water level sensors (HOBO U20-001-02), which were calibrated to take measurements at one-hour intervals over one year (April, 2011-March, 2012). From the previous measurements, the maximum depth (cm), minimum depth (cm) and average depth (cm) were determined.

The height of the water table (WT) was measured by means of scuttled drilling, which allowed the determination of the percentage of time in which the wetlands remained flooded (depth > 0 cm), saturated (0 > WT > -30 cm) and dry (WT < -30 cm), according to Cole *et al.* (2006).

To characterise the aquatic component and establish possible relations in the distribution pat-

Table 1. Characterisation based on geographical, biological, morphometric and hydrological aspects of the selected FW. *Caracterización basada en aspectos geográficos, biológicos, morfométricos e hidrológicos de los humedales boscosos seleccionados.*

	Petrengo	Quepe	Nohualhue	Vergel	Pumalal
Coordinate South	39°9'20.29"	38°52'26.36"	38°58'0.72"	38°3'43.64"	38°35'55.34"
Coordinate West	72°39'45.27"	72°36'56.02"	73°4'34.59"	72°19'27.93"	72°30'59.57"
Vegetational Association	Temu-Pitra	Temu-Pitra	Temu-Pitra	Temu-Pitra	Temu-Pitra
Wetland Surface (Ha)	269	346	107	138	192
Basin Surface (Ha)	3630	1642	2778	2840	3344
Elevation (m.o.s.l.)	94	95	26	182	158
Hydric Regime	Permanent	Permanent	Permanent	Temporary	Temporary
Hydroperiod (days)	365	365	365	199	215
Non-flooded Phase (days)	0	0	0	166	150
Maximum Depth (cm)	69.7	59.9	83.5	82.4	51.5
Minimum Depth (cm)	30.8	15.7	22.1	0	0
Flooded (%)	100	100	100	54.5	58.9
Saturated (%)	0	0	0	45.5	41.1
Dry (%)	0	0	0	0	0

terns of the invertebrate communities, physico-chemical variables such as pH, conductivity, dissolved oxygen, temperature and turbidity were measured *in situ* from the water column. Samples were also collected for their subsequent laboratory analysis (ammonia, calcium, total organic carbon, chlorides, sulphate, total phosphorous, nitrates, nitrites, total nitrogen, potassium, total solids and biological oxygen demand).

Statistical analyses

The data of taxa richness (S'), abundance (N') and Shannon-Wiener's diversity index (H') were standardised to determine whether there were differences at spatial (wetlands) and temporal (months) scale using a univariate index; the one-way ANOSIM index was performed using a distance matrix based on the Euclidian distance.

The abundance data were processed using a similarity matrix from the Bray-Curtis distance measurement that allowed the use of a non-

parametric multidimensional scaling analysis (NMDS). This was performed to graphically visualise the relationship among previously defined groups. The significance of the groups formed was tested by running the one-way ANOSIM analysis.

The physicochemical variables were normalised to identify the possible relationships with the biological variables, and the BIOENV analysis was applied through the Spearman's coefficient. This allowed the assessment of statistically significant relationships between biota structure and environmental variables. With the same objective, correlations between univariate indices and the duration of the hydroperiod were conducted. These were considered significant when $p < 0.05$. Finally, SIMPER analysis was utilised to identify the most influential taxa on the obtained community patterns. All analyses and graphics were performed using the Primer®v.6 (Clarke & Gorley, 2006) and SigmaPlot v.11.0 (Systat Software, Inc) software packages.

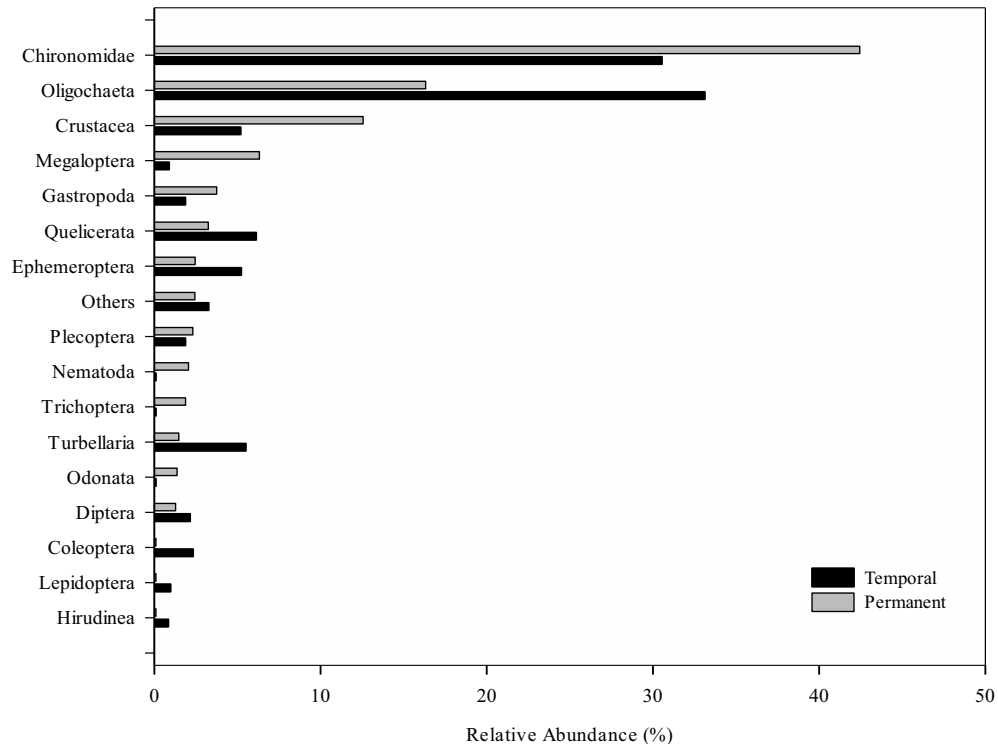


Figure 2. Relative abundance (%) of the major groups of BMI in relation to permanent and temporary hydric regimes. *Abundancia relativa (%) de los principales grupos de BMI en relación a los regímenes hidricos permanente y temporal.*

RESULTS

A decrease in water depth was observed in all wetlands during the summer season, but the Peltreco, Quepe and Nohalhue wetlands presented permanent floods, with depths that varied between 6 and 44 cm, whereas Pumalal and Vergel wetlands presented temporary regimes. Although they presented permanent floods with saturated soils, they only remained flooded for 199 and 215 days, respectively, during the year of study, varying between 0 and 83 cm (Table 1).

Overall, 32 308 macroinvertebrates spread across 80 taxa were counted in the total samples. Seventeen of these taxa were present only in permanent wetlands, and 13 occurred only in temporary wetlands. However, the remaining 50 taxa were common to both types of wetlands (Table 2). Chironomidae and Oligochaeta were dominant in permanent and temporary wetlands, representing 71 % and 69 % of the total abundance, respectively (Fig. 2). The taxa that presented a major occurrence in temporary wetlands were Oligochaeta (81 %), Chironomidae (70 %), *Hyallolela araucana* (58 %) and Acari (39 %). A similar pattern was found in permanent wetlands, where Chironomidae (95 %), Asellidae (90 %), *Hyallolela araucana* (83 %), Oligochaeta (58 %) and *Smicridea* sp. (42 %) had greater occurrence. The dominant functional feeding groups were predators (44 %), followed by shredders (17 %) and collectors (15 %) (Table 2).

Regarding the community indices, the maximum richness in the different samples varied between 13 and 16 taxa, showing a significant differences among wetlands of different hydrological regimes and the Shannon's diversity ($p < 0.001$). The average abundance presented no significant variation among wetlands of different regimes. A significant variation ($p < 0.05$) of the total abundance was observed at the timescale level in all wetlands, and the great majority presented significant differences ($p < 0.05$) in the community indices, with the exception of the Shannon's diversity in the Nohalhue wetland (Fig. 3).

Strong positive correlations were found ($p < 0.05$) between depth and the total abun-

dance of BMI in Vergel ($r = 0.75$) and Pumalal ($r = 0.82$) wetlands and regarding richness in the same wetlands (Vergel $r = 0.64$, Pumalal $r = 0.74$). The Shannon's diversity also presented a strong relationship with depth in the temporary wetlands such as Vergel ($r = 0.74$) and Pumalal ($r = 0.75$). These relationships were not recorded in any of the permanent wetlands (Fig. 3).

The NMDS analysis from the biological matrix clearly showed the formation of two defined groups according to the hydrological regime in the wetlands (Fig. 4A), which presented highly significant differences (ANOSIM Global $R = 0.45$, $p = 0.001$). In agreement with Simper's analyses, the most influential taxa on these differences were Asellidae, Chironomidae, *Hyallolela araucana* and Oligochaeta (Table 4).

The BMI community from temporary wetlands presented the formation of two groups associated with the summer and winter season (Fig. 4 Ve and Pu). These groups are also significantly different in both wetlands (Ve: ANOSIM Global $R = 0.33$, $p = 0.001$; Pu: ANOSIM Global $R = 0.32$, $p = 0.001$). The differences were primarily explained by Oligochaeta (Collector), Chironomidae and *Hyallolela araucana* (Shredder/Gathering Collector). Specifically for the Vergel wetland, Limnephilidae (Predator) was relevant, and Elmidae (Gathering Collector) was similarly relevant in Pumalal. In permanent wetlands, the same grouping was also observed, as were significant differences (No: ANOSIM Global $R = 0.11$, $p = 0.001$; Que: ANOSIM Global $R = 0.17$, $p = 0.001$; Pe: ANOSIM Global $R = 0.32$, $p = 0.08$), though this was not as clear as in the temporary wetlands because the sites tend to overlap (Fig. 4 No, Que and Pe). These differences were mostly influenced by the following taxa: Asellidae (Shredder), Chironomidae, *Hyallolela araucana* (Shredder/Gathering Collector), *Littoridina* sp. (Scraper) and Oligochaeta (Collector) (Table 4).

Regarding the physicochemical variables (Table 5), significant differences between temporary and permanent wetlands (ANOSIM Global $R = 0.34$, $p = 0.01$) were observed. The Bioenv analysis identified that the environmental variables that better explained the multivariate

Table 2. Frequency of the occurrence matrix (%) of identified BMI. OFT = Frequency of occurrence (%) in all samples of temporary wetlands. OFP = Frequency of occurrence in all samples of permanent wetlands. *= rare species (frequency of occurrence and relative abundance in all samples <1 %). FFT = Functional feeding group (S = Shredder, SC = Scraper, C = Collector, FC = Filtering Collector, GC = Gathering Collector, P = Predator, PI = Piercer). *Matriz de frecuencia de ocurrencia (%) de BMI identificados.* OFT = Frecuencia de ocurrencia en todas las muestras de humedales temporales. OFP = Frecuencia de ocurrencia en todas las muestras de humedales permanentes. *= especie rara (frecuencia de ocurrencia y abundancia relativa en todas las muestras <1 %). FFT = Grupo funcional de alimentación (S = Triturador, SC = Raspador, C = Colector, FC, Filtrador Colector, P = Predador, PI = Perforador).

	OFT	OFP	FFG		OFT	OFP	FFG
Oligochaeta	80.56	57.6	C	Trichoptera			
Polichaeta*	0.69	0	—	<i>Smicridea sp.</i>	18.06	41.94	C
Hirudinea	3.47	0	—	Limnephilidae	0	13.82	P
Nematoda	6.25	3.23	—	Leptoceridae	2.08	2.76	S
Turbellaria				<i>Brachysetodes sp.</i>	2.78	1.84	S
<i>Dugesia sp.</i>	17.36	2.76	—	<i>Triplectides sp.*</i>	0.69	0.46	S
Gastropoda				Hydroptilidae*	0.69	0	P
Ancylidae	17.36	28.57	SC	Stenopshychidae*	0.69	0	S
<i>Chilina sp.</i>	2.78	2.76	SC	<i>Polycentropus sp.</i>	2.08	0	FC
<i>Littoridina sp.</i>	15.97	35.48	SC	Megaloptera			
<i>Physa sp.</i>	2.08	6.91	SC	Megaloptera Indet.	1.39	1.84	P
<i>Biomphalaria sp.</i>	0	11.06	SC	<i>Prosisalis sp.</i>	3.47	21.66	P
Sphaeriidae	4.17	9.22	FC	Odonata			
Crustacea				Odonata Indet.	0	1.84	P
<i>Hyallole araucana</i>	58.33	82.49	S/GC	Coenagrionidae	5.56	11.06	P
Asellidae	18.06	89.86	S	Libellulidae	1.39	10.14	P
<i>Parastacus pugnax</i>	1.39	23.96	—	Lestidae	1.39	3.69	P
<i>Aegla araucanioensis</i>	5.56	0	P	Aeshnidae	2.08	2.3	P
Collembola	8.33	5.53	—	Calopterygidae*	0	0.92	P
Hymenoptera*	0	0.46	—	Hemiptera			
Diptera				Veliidae	0	9.22	P
Chironomidae	70.14	94.93	—	Gerridae	0	3.23	PI
Culicidae	13.19	4.61	P	Mesoveliidae	2.08	0	—
Limoniidae	1.39	2.3	P	Notonectidae*	0	0.46	P
Ephydriidae	1.39	4.61	SC	Belostomatidae*	0	0.92	P
Ceratopogonidae	17.36	4.61	C	Corixidae	1.39	0	SC
Simuliidae	1.39	2.76	C	Hebridae	2.08	0.92	P
Tipulidae	9.03	8.29	P	Plecoptera			
Psychodidae	0	3.69	P	Plecoptera indet.*	0.69	0	—
Empididae	4.17	0.92	P	<i>Antarctoperla michaelsini</i>	11.81	7.37	S/ GC
Athericidae	0.69	4.15	P	<i>Perlugoperla personata</i>	1.39	2.3	S/ GC
Coleoptera				Perlidae	10.42	0	P
<i>Hydrochus stolpi</i>	8.2	1.6	P	<i>Neonemura barrosi</i>	2.78	14.75	S
<i>Berosus sp.</i>	0.7	1.1	P	Ephemeroptera			
<i>Tropisternus setiger*</i>	0	0.5	P	Ephemeroptera indet.*	0.69	0	—
Coleoptera indet. a	4.8	1.7	—	Coloburiscidae	4.86	0	C
Staphylinidae	4.8	3.8	P	Leptophlebiidae	27.08	20.74	C
<i>Cyphon sp</i>	25.9	6.6	—	<i>Nousia crena</i>	6.94	5.99	C
<i>Lancetes sp.*</i>	0	0.5	—	<i>Caenis sp.</i>	5.56	3.23	C
<i>Phantus sp</i>	5.4	2.2	—	Mecoptera			
Coleoptera indet. b	1.4	0.5	—	Nannochoristidae*	0	0.92	—
<i>Luchoelmis sp.*</i>	0.7	0	—	Neuroptera			
<i>Austrelmis*</i>	0.7	0	—	Osmylidae	3.47	0	P
Elmidae indet.	5.4	3.3	GC	Lepidoptera			
Carabidae	1.4	0	P	Pyralidae	6.25	1.84	C/S
Hydraenidae	1.4	1.1	—	Quelicerata	2.08	0	—
Coleoptera indet. c	3.4	0.5	—	Acari	38.89	22.58	—

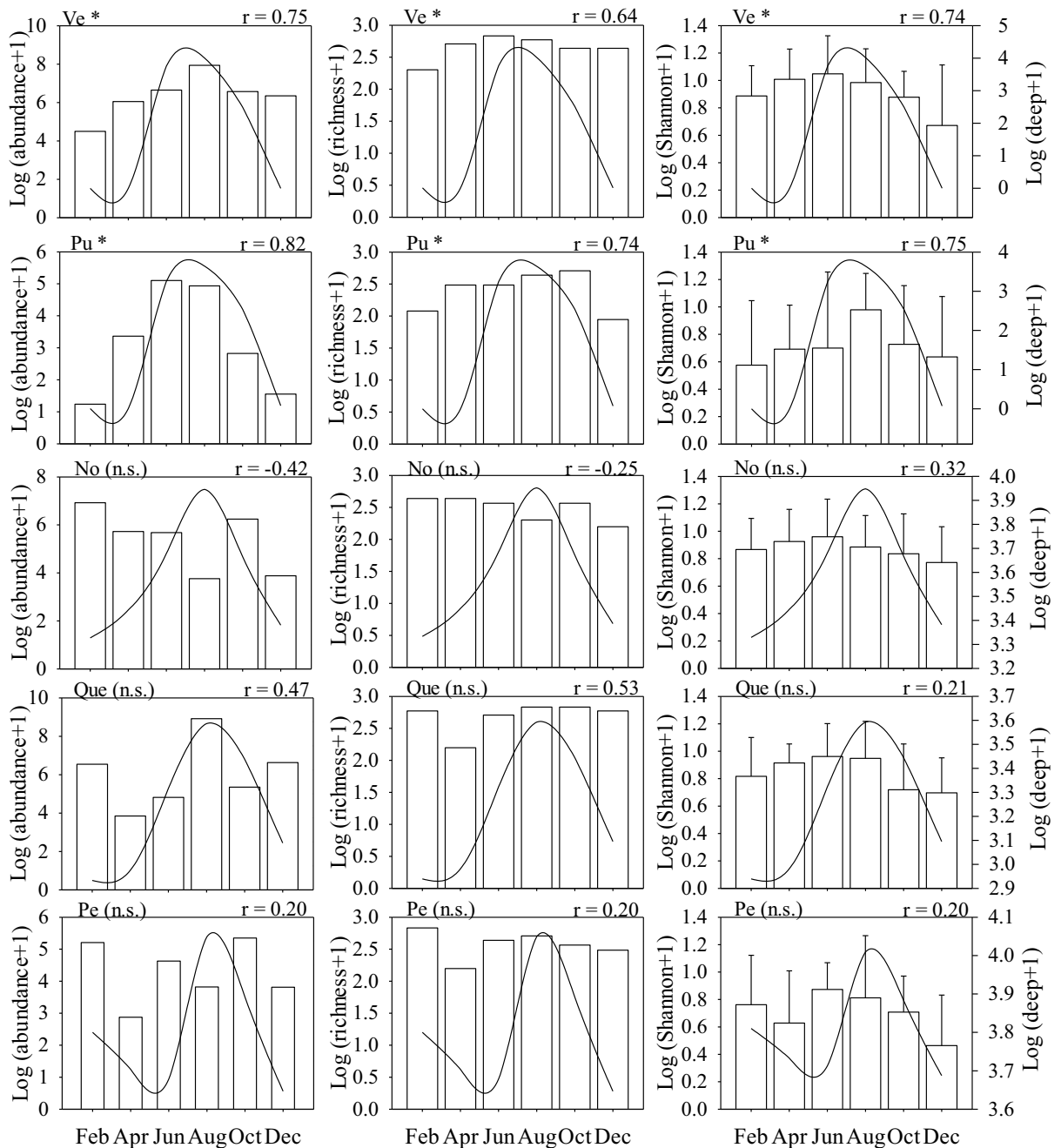


Figure 3. Timescale variation ($\log(x + 1)$) of the total abundance, maximum richness and Shannon diversity index (H') (box) and their relation to the depth of the wetlands (line). All showed significant differences in temporary scale ($p < 0.01$) except the Shannon diversity in Nohualhue (n.s.). The r -values show the relationship between community indices and water depth based on the Pearson correlation coefficient (*= $p < 0.05$). Ve (Vergel), Pu (Pumalal), No (Nohualhue), Pe (Petrenco), Que (Quepe). *Variación temporal ($\log(x + 1)$) de la abundancia total, riqueza máxima y el índice de diversidad de Shannon (H') (caja) y su relación con la profundidad de los humedales (línea). Todas muestran diferencias significativas a escala temporal ($p < 0.01$), excepto la diversidad de Shannon en Nohualhue (n.s.). Valores de r muestran la relación entre los índices comunitarios y la profundidad del agua basados en el coeficiente de correlación de Pearson (*= $p < 0.05$). Ve (Vergel), Pu (Pumalal), No (Nohualhue), Pe (Petrenco), Que (Quepe).*

Table 3. Community index (mean \pm standard deviation) of BMI in each wetland. *R*-values are the result of one-way ANOSIM. Significance levels: *** $p < 0.001$, ns = $p > 0.05$. *Índices comunitarios (promedio \pm desviación estandar) de BMI en cada humedal. Valores de R son el resultado de ANOSIM de una vía. Niveles de significancia: *** $p < 0.001$, ns = $p > 0.05$.*

	Maximum Richness (S')	Abundance (N)	Shannon (H')
Vergel	16	107.1 \pm 161.7	1.5 \pm 0.4
Pumalal	14	27.3 \pm 33.8	1.1 \pm 0.6
Nohualhue	13	78.5 \pm 55.1	1.4 \pm 0.3
Quepe	16	126.3 \pm 148.5	1.3 \pm 0.4
Petrenco	16	110.2 \pm 141.8	1.0 \pm 0.5
Global <i>R</i>	0.082	0.076	0.064
<i>P</i>	***	***	***
Temporary	16	67.2 \pm 123.1	1.3 \pm 0.6
Permanent	16	105.0 \pm 123.8	1.3 \pm 0.4
Global <i>R</i>	0.055	0.015	0.053
<i>P</i>	***	ns	***

pattern of the macroinvertebrate community in permanent wetlands were turbidity, calcium and depth ($\rho = 0.508$, $p = 0.04$), whereas in temporary wetlands, these variables were pH, temperature, nitrites and depth ($\rho = 0.502$, $p = 0.05$).

DISCUSSION

In the current study, all wetlands presented a significant decrease in both depth and water volume during the summer season. This phenomenon is mostly associated with the normal distribution of the rainfall in this season (Pizarro *et al.*, 2006; Little *et al.*, 2009). However, this can be incremented due to the growing replacement of native forest cover by forest plantations in the studied zone (Lara *et al.*, 2009; Little *et al.*, 2009). This was the case for the Vergel and Pumalal wetlands, where the decrease was more critical, with the absence of the water mirror lasting for more than five months, though there was always a saturated substrate.

In general, the taxonomic richness of BMI (80 taxa) was greater than that registered in the semi-arid zones (Figuerola *et al.*, 2009) and the Chilean MZ (Villagrán-Mella *et al.*, 2006), where 12 and 24 taxa were identified, respectively. Our results were similar to those reported by Della Bella and Mancini (2009) and Bazzanti *et al.* (2010), who described a total of 63 and 67 taxa (gen-

era/species) in temporary and permanent wetlands in Central Italy, respectively, and 57 taxa in five FW in North America. However, this variable was lower than wetlands from other MZ, in which Florencio *et al.* (2009) identified 123 taxa in 22 temporary wetlands from Doñana National Park, which is explained by the sampling effort and the amount of wetlands considered in the respective studies. Similarly, it has been reported that richness and abundance is normally higher in permanent wetlands (Della Bella *et al.*, 2005), which are mostly dominated by Diptera, Amphipoda and Hemiptera (Della Bella & Mancini, 2009). However, temporary wetlands tend to be dominated by Chironomidae larvae (Bazzanti *et al.*, 1997). Our results are in agreement with the above because the permanent wetlands presented greater richness and abundance than did temporary wetlands, although Amphipoda and Chironomidae were important in both types of wetlands.

Many authors have also described that wetlands with temporary regimes present exclusive taxa or they are scarce in permanent environments (*e.g.*, Della Bella *et al.*, 2005; Williams, 2006). This has also been observed in the studied wetlands, where 13 taxa were only registered in temporary wetlands and 17 were exclusive to permanent wetlands. However, most of them were common to both types of environment, in agreement with studies conducted in temperate regions (*e.g.*, Bazzanti *et al.*, 2000).

Table 4. Similarity percentages analysis (SIMPER) between season (summer and winter) and hydrological regime (permanent = P and temporary = T). The most important contributions of taxa for the differences in each wetland are highlighted in bold. *Análisis de porcentajes de similitud (SIMPER) entre época (estival e invernal) y entre régimen hídrico (permanente = P y temporal = T). En negrita se destaca la contribución más importante de los taxones a las diferencias en cada humedal.*

	Ve	Pu	No	Que	Pe	P-T
Acari		7.65				3.32
Ancylidae	4.03			4.75	6.48	2.82
Asellidae	4.57		12.14	11.01	18.92	15.8
Chironomidae	7.65	12.37	9.6	11.36	11.54	10.9
<i>Dugesia</i> sp.	5.45					
Elmidae		13.69				3.94
<i>Hyallole araucana</i>	9.88	10.74	13.84	9.52	11.8	10.56
Leptophlebiidae	8.09		3.44			3.73
Limnephilidae			3.15			
<i>Littoridina</i> sp.	4.29		3.79	11.3	7.14	4.61
Neonemura barrosi			5.12			
Oligochaeta	8.44	18.61	8.92	8.77	5.92	8.76
<i>Parastacus pugnax</i>			3.59			
<i>Smicridea</i> sp.			7.32			3.17

These patterns correspond to the stress generated by the absence of water and the adaptation of the organisms to the physical characteristics of the environment (e.g., extreme temperatures or low levels of dissolved oxygen) that generate an important influence on the composition of the community (Wellborn *et al.*, 1996). To face this situation, organisms must develop several physiological adaptations to survive (Williams, 2006; Florencio *et al.*, 2009). However, permanent wetlands offer a more stable environment in comparison to temporary environments. Furthermore, these are regulated by higher predators (e.g., fishes) that contribute to maintain greater diversity thresholds and imply the existence of specialist taxa, with higher mobility (e.g., Isopoda) or other strategies to counteract predation (Wellborn *et al.*, 1996; Williams, 2006).

This finding is also reinforced by the presence of islets that dominate these environments and are formed by adventitious roots and coarse particulate organic matter (Correa-Araneda *et al.*, 2012), thus providing a greater amount of microhabitats and increasing the surface available for colonisation. Experimental and field studies (e.g., Vivian-Smith, 1997; Koponen *et al.*, 2004) have indicated that these morphometric characteristics imply a great richness of rare species in comparison to other types of wetlands. This is consistent

with the results obtained from this study because approximately 19 % of the taxa are scarcely represented despite the high sampling effort in terms of techniques and the number of samples.

In addition, seasonal differences were observed in the FW studied, although these differences were more important in temporary wetlands, where the flooding and non-flooding phases are particularly relevant. In the non-flooded period, the most characteristic invertebrates are those that inhabit the substrate (Gerard, 2001). This finding explains why Oligochaeta and Chironomidae were important in the recorded seasonal differences and why the *Hyallole araucana* survive in small isolated ponds that are kept during the summer season. This is facilitated in FW by the presence of evergreen woody vegetation, which implies a low penetration of light toward the water mirror, thereby minimising evaporation and allowing preservation of the humidity of the substrate during that season. In permanent wetlands, the same organisms were also relevant in seasonal differences, indicating that these taxa are fundamental for the community patterns of BMI in both types of wetlands.

The registered seasonal differences are a consequence of the changes experienced by the aquatic habitats, which present optimal environ-

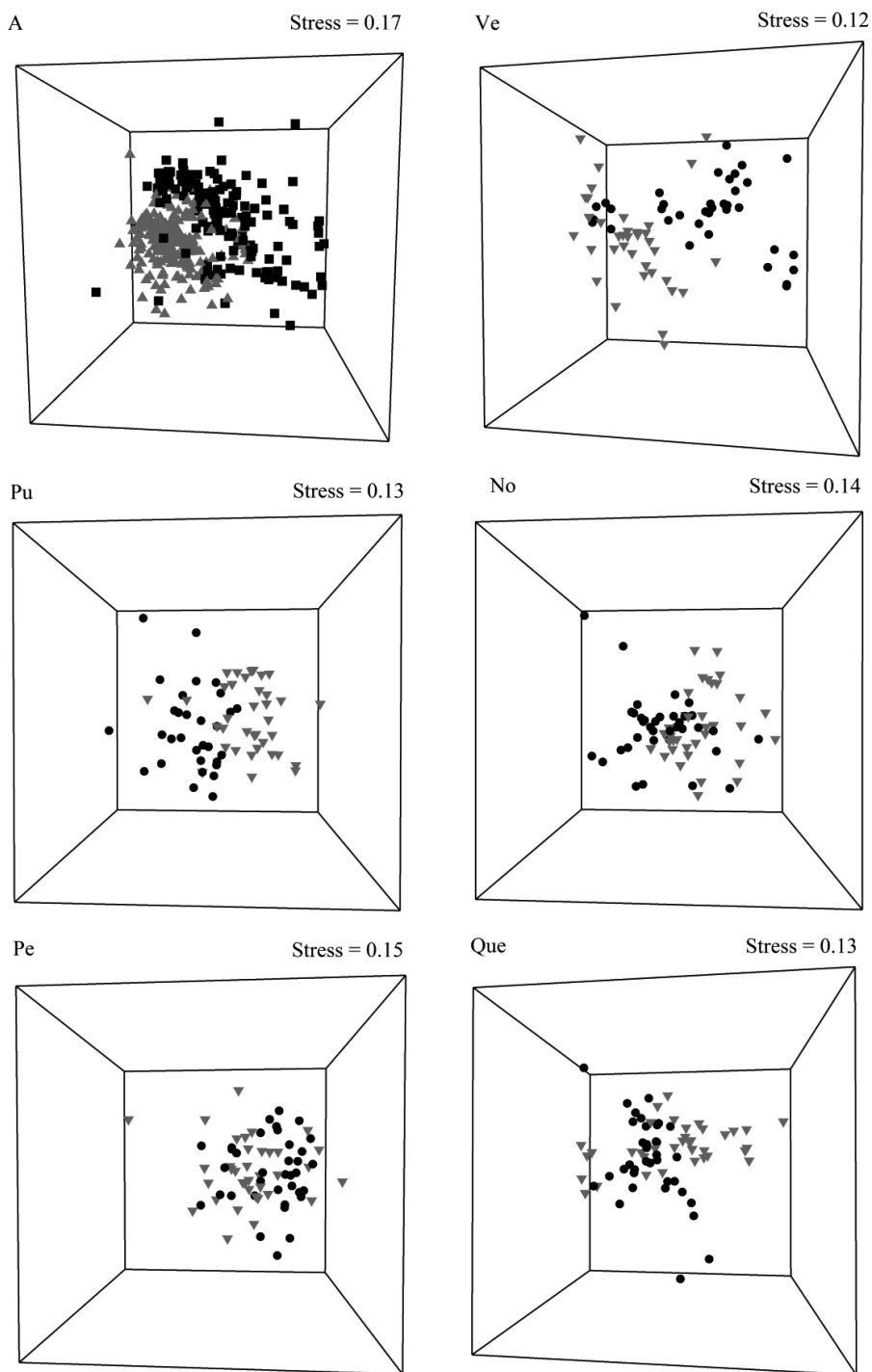


Figure 4. Three-dimensional ordering graph of the non-parametric multi-dimensional scaling (NMDS) based on BMI matrix, using the hydrological regime (■ = temporary, ▲ = permanent; A) and season (● = summer, ▼ = winter) as factors. Ve (Vergel), Pu (Pumalal), No (Nohualhue), Pe (Petrenco), Que (Quepe). *Gráfico de ordenación en tres dimensiones del escalamiento multidimensional no paramétrico (NMDS) basado en la matriz de BMI, usando el régimen hídrico (■ = temporal, ▲ = permanente; A) y la época (● = estival, ▼ = invernal) como factores. Ve (Vergel), Pu (Pumalal), No (Nohualhue), Pe (Petrenco), Que (Quepe).*

Table 5. Physicochemical variables (mean \pm standard deviation) recorded in wetlands with temporary ($n = 12$) and permanent ($n = 18$) hydric regimes. *Variables fisicoquímicas (promedio \pm desviación estándar) registradas en humedales con régimen hídrico temporal ($n = 12$) y permanente ($n = 18$).*

	Unit of measure	Temporary	Permanent
pH	1-14 (H ⁺)	4.40 \pm 2.68	5.85 \pm 1.58
Conductivity	μ S/cm	39.75 \pm 48.10	57.76 \pm 42.91
Dissolved oxygen	mg/L	4.93 \pm 4.93	5.38 \pm 3.83
Temperature	°C	6.67 \pm 4.45	9.96 \pm 4.46
Turbidity	NTU	87.72 \pm 124.31	16.54 \pm 25.33
Ammonium	mg/L	0.28 \pm 0.51	0.04 \pm 0.04
Calcium	mg/L	5.64 \pm 5.65	4.18 \pm 1.85
Total organic carbon	mg/L	3.29 \pm 3.49	3.74 \pm 2.57
Chlorides	mg/L	2.35 \pm 1.91	4.17 \pm 1.79
DBO5	mg/L	2.67 \pm 3.34	1.64 \pm 0.91
Total phosphorus	mg/L	0.51 \pm 1.45	0.05 \pm 0.03
Magnesium	mg/L	2.17 \pm 2.10	1.96 \pm 0.60
Nitrates	mg/L	1179.98 \pm 2221.90	295.99 \pm 585.91
Nitrites	mg/L	0.05 \pm 0.06	0.05 \pm 0.04
Total nitrogen	mg/L	1.73 \pm 2.63	0.53 \pm 0.20
Potassium	mg/L	0.80 \pm 1.14	0.99 \pm 0.56
Total suspended solids	mg/L	198.50 \pm 556.64	10.96 \pm 10.44
Sulfate	mg/L	1.89 \pm 2.27	2.22 \pm 2.02
Depth	cm	19.81 \pm 20.20	28.15 \pm 16.01

mental conditions for different groups of macroinvertebrates. In addition, these seasonal differences implicate variations in macroinvertebrate life strategies such as reproduction, feeding, development and dispersion (Williams, 2006). However, the reduction of the hydroperiod produces the greatest effects on organisms with long life cycles, such that changes in the key environmental variables would impede these organisms' ability to complete their aquatic life. These community differences have also been reflected by a significant increment in both richness and relative abundance (Williams, 2006), which is in agreement with the results presented in the current study, where temporary wetlands presented greater abundance and richness in the summer season.

The relevance of the different factors that influence at different scales on the composition of the aquatic communities is still barely stud-

ied. However, several authors (*e.g.*, Kiflawi *et al.*, 2003; Bilton *et al.*, 2009) have reported that most of the variability in the community of wetlands BMI depends on local physicochemical aspects. On this regard, the hydroperiod has been widely mentioned as a variable strongly related to both physical and chemical dynamics (Escalera-Vazquez & Zambrano, 2010).

This is even more crucial in temporary wetlands, because it implies that from the filing process until desiccation, important variations are experienced by these variable. Studies such as those by Ripley & Simovich (2009) and Escalera-Vazquez & Zambrano (2010) reported that most of the physical and chemicals variables of temporary wetlands, such as dissolved oxygen, nitrogen, pH, temperature and conductivity, fluctuate by seasons. This was also observed in the current study and it may be related to variations in both the composition and abundance of macroinver-

tebrates. Among the abovementioned variables, depth was detected as relevant in the seasonal differences registered in richness and abundance for both temporary and permanent wetlands. Particularly in temporary wetlands, turbidity and calcium also contributed to the seasonal variability, whereas in permanent wetlands, pH, temperature and nitrate also explained the differences recorded in the BMI community.

Nevertheless, this first approach presents the relationship that exists between water availability and the environmental variables that determine the studied biological communities. The high BMI richness observed in these ecosystems provides new background to justify the necessity of conservation, which would be more relevant if the presence of an important number of rare species were added. The existence of taxa adapted to survive in these types of ecosystems, which can sustain fauna of higher trophic levels and a higher degree of specialisation, is also observed. Equally relevant is the morphometry of these ecosystems, which are characterised by the presence of a mosaic of islets that set a highly heterogeneous environment and are particularly different from other wetlands. This has been considered an important factor for both BMI and other aquatic communities, though it has not been sufficiently studied. In general, Chilean FW have not been considered in the strategies or conservation plans of natural areas because they are practically unknown or simply not classified as wetlands and have a high risk of disappearing before their functional dynamics are known.

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