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Spatial Variations in Water Beetle Communities in Arid and Semi-Arid Patagonian Wetlands and Their Value as Environmental Indicators

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Luis B. Epele and Miguel Archangelsky (2012) Spatial variations in water beetle communities in arid and semi-arid Patagonian wetlands and their value as environmental indicators. *Zoological Studies* **51**(8): 1418-1431. To evaluate spatial variations in aquatic beetle assemblages, 26 Patagonian ponds were sampled during late spring (Dec.). The hydroperiod, hydrology, abiotic features, precipitation, aridity, and aquatic plant richness of the study sites differed. Fifteen physicochemical features were measured, and aquatic plants were collected to determine taxonomic richness. Sampling of the 26 ponds produced 21 aquatic beetle taxa in 6 families. All aquatic beetles (adults and larvae) were assigned to functional feeding groups. A canonical correspondence analysis (CCA) was run to assess relationships between aquatic beetle assemblages and environmental variables. Of the variance in aquatic beetle taxa abundances, 23% was accounted for by the 1st 3 ordination axes. Moreover, the 1st 2 canonical axes respectively accounted for 38.2% and 28.4% of the variations attributable to environmental variables (i.e., annual precipitation, elevation, pond area, aquatic plant richness, pH, and conductivity), with conductivity and elevation being the most important. A parsimony analysis was performed to establish which species could define and/or group some of the communities (with sampling sites treated as taxa and species treated as characters). Results of the parsimony analysis suggested that some taxa (*Haliplus subseriatus*, *Gymnochthebius* sp., *Enochrus darwini*, *Cyphon* sp., *Luchoelmis* sp., and *Rhantus validus*) were useful in defining some ponds or groups of ponds. These species can be used as indicators since beetle distributions are not considered to randomly occur. Our findings show that aquatic beetle assemblages can be utilized for wetland conservation planning since in arid and semiarid Patagonia, they are important as water reservoirs and for cattle rearing. http://zoolstud.sinica.edu.tw/Journals/51.8/1418.pdf

Key words: Mallines, Ponds, Coleoptera, Indicator species, Parsimony analysis.

Wetlands are transitional zones between terrestrial and aquatic environments and constitute a dynamic link between the 2 systems (Mitsch and Gosselink 2007). Wetlands in Patagonia are called "mallines", an aboriginal (Mapuche) word, which means swampy area or low area where water accumulates. On a local scale, previous analyses had indicated that small aquatic systems were spatially unimportant, yet small waterbodies dominate the global area covered by continental waters (Downing et al. 2006), so that studies emphasizing the global role and contribution of wetlands are necessary. This is the situation with Patagonian wetlands (Malvárez 1999, Perotti et al. 2005) for which only some basic studies have been carried out.

Wetlands can be subdivided into 2 major groups (Mitsch and Gosselink 2007), "connected" and "disconnected" ones. Connected wetlands are often located between dry terrestrial systems and permanently flooded deepwater aquatic systems (e.g., rivers, lakes, estuaries, or oceans). Disconnected wetlands are isolated basins with little outflow and no adjacent deepwater system,

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where the only nearby aquatic system is often a groundwater aquifer. Although we use the term "disconnected", it is understood that they are usually hydrologically connected to groundwater (Mazzoni and Vázquez 2004) and biologically through the movement of mobile organisms.

Aquatic invertebrates have long been used as bioindicators of water quality in streams (Rosenberg and Resh 1993, Barbour et al. 1999), and recent studies proposed the use of invertebrate-based metrics to evaluate the water quality of ponds (King and Richardson 2002). Aquatic Coleoptera are often excluded from such metrics because compared to most invertebrate groups, distributions of water beetles are considered to be more influenced by chance colonization than by habitat suitability (Galewsky 1971). A growing number of studies, however, have shown strong environmental influences on beetle assemblage structure (Larson et al. 2000, Fairchild et al. 2003, Eyre 2006, Eyre et al. 2006, Gioria et al. 2010, Touaylia et al. 2011), implying their potential use as bioindicators of anthropogenic disturbances. Water-beetle assemblages typically include a wide range of predators (e.g., Dytiscidae and larval Hydrophilidae) but also generalized algivores and detritivores (e.g., adult Hydrophilidae), consumers of filamentous algae (e.g., Haliplidae), and herbivores of vascular plants (e.g., Curculionidae and Chrysomelidae). An array of changes in the availability of food resources is thus likely to influence beetle species compositions (Fairchild et al. 2000).

Continental wetlands of southern South America are very diverse and include meadows, marshes, bogs, perilacustrine communities, forests, and salt marshes. The structure and species composition of these environments vary according to the relief, substrate, water period, pH, salinity, alkalinity, mesoclimatic conditions, and land-use patterns. These ecosystems are threatened by a number of human activities, of which the most important include increased nutrient loading, contamination, overgrazing, and invasion by exotic species (Brönmark and Hansson 2002). Grassland wetlands are areas that receive more grazing pressure since they have the best forage (Collantes and Faggi 1999), which in turn increases land-degradation processes (Brönmark and Hansson 2002).

Is known that despite their isolation and small size, water bodies in arid and semiarid regions often include numerous endemics and can be biological hotspots that contribute to regional aquatic biodiversity (Williams 2006, Box et al. 2008). They may also be important areas for terrestrial animals and plants (Mitsch and Gosselink 2007). In Patagonia, wetlands are important for water supplies, but also sustain most of the livestock in arid and semiarid areas (Mazzoni and Vázquez 2004, Gaitán et al. 2011). Several authors showed that land-use patterns and the introduction of exotic species are having the greatest impacts on original communities in Patagonian wetlands (del Valle 1998, Iglesias and Pérez 1998, Macchi et al. 1999, Pascual et al. 2002). One of the main environmental problems affecting Patagonian biomes is the phenomenon of desertification (del Valle et al. 1998), which is defined as land degradation in arid, semi-arid, and subhumid areas resulting from various factors, including climate variations and human activities (UNCCD 2012). Increases in desertification processes (induced in part by overgrazing) have resulted in low productive lands, forcing landowners to change extensive livestock practices for intensive use on more productive areas such as pastures on wetlands. This greater pressure has resulted in loss of wetland habitats (del Valle 1998), loss of biodiversity, and increased salinization of remaining wetlands (Steinman et al. 2003). Currently, it is also important to evaluate the land-use effects on wetlands of arid and semiarid Patagonia within a climate-change scenario (Paruelo et al. 1998, Sala et al. 2000).

The present study evaluated spatial variations in beetle assemblages within 26 Patagonian ponds which differed in their hydroperiod, hydrology, water chemistry, and precipitation. All studied wetlands were used for livestock grazing. We addressed the following questions: (1) which variables determine spatial variations in beetle assemblages in Patagonian wetlands?; (2) can the distribution of aquatic beetles be used to evaluate the status of wetland ponds?; and (3) does connectivity affect the spatial distribution of beetles?

MATERIALS AND METHODS

Study area

The Patagonian climate is generally dry, cold, and windy. The strong west-to-east rainfall gradient has created 2 main phytogeographical provinces: the Sub-Antarctic Forest and Patagonian Steppe (Tell et al. 1997). In Chubut

Province, across a strip 50 km wide, precipitation ranges from > 3000 to 600 mm. On the steppe, precipitation is concentrated in winter and declines from 300 mm in the west to < 150 mm in the east, increasing slowly toward the Atlantic coast (Barros et al. 1979). The region studied exhibits quite a rich spectrum of vegetation types, from true desert to shrub and grassy steppe. The initial colonization of the Patagonian region, in 1880-1920, was impelled by extensive sheep farming. Since then,

the region has been subjected to intense grazing by sheep (del Valle et al. 1998) and cattle farming in areas with better grasses and water availability.

In the present study, 26 wetlands (11 disconnected and 15 connected ones) located in a 110-km west-to-east gradient and covering an area of at least 28.600 km² were sampled (Fig. 1). Disconnected wetlands were visited in Dec. 2006 and connected ones in Dec. 2007. For site selection, we looked at different conditions of
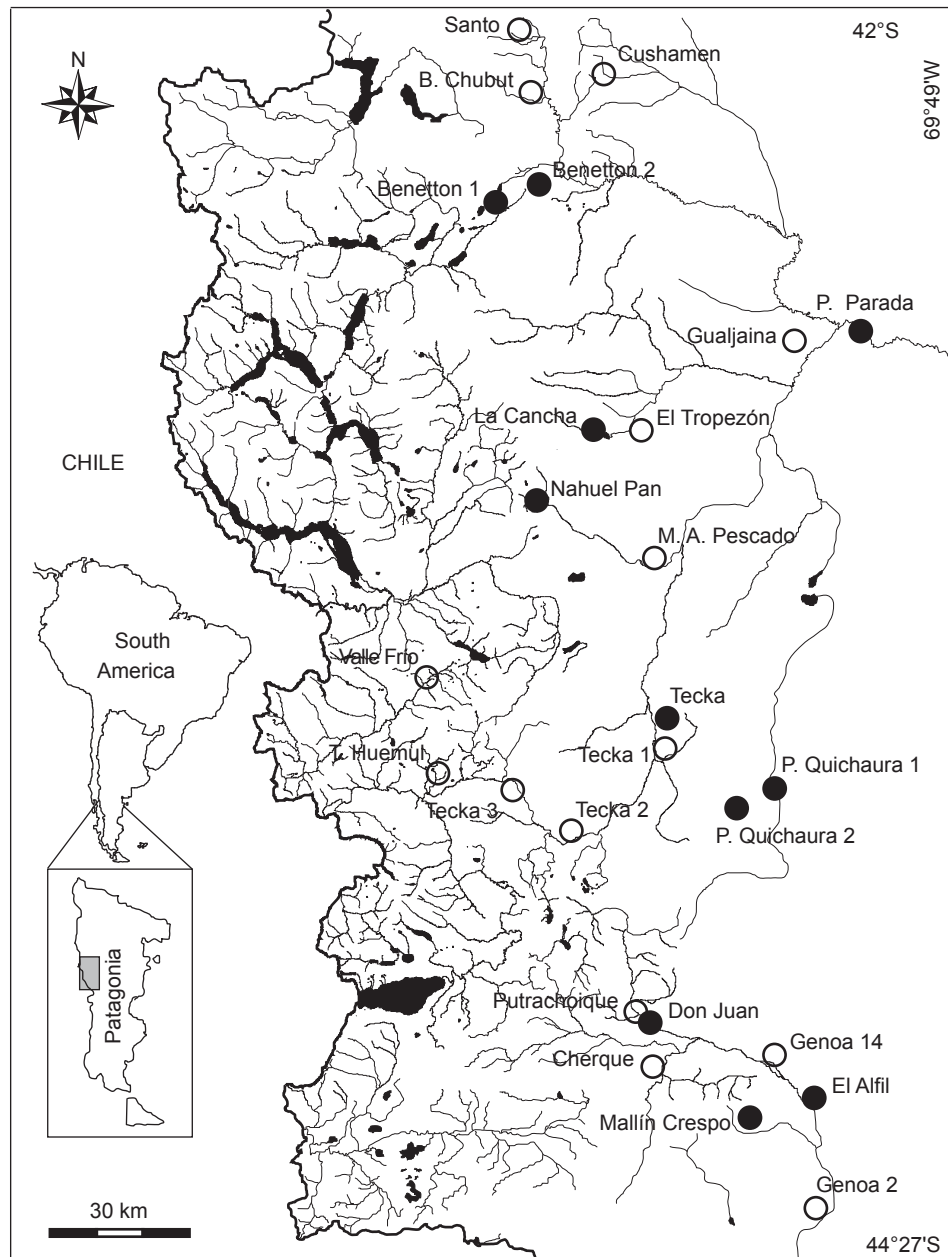

Fig. 1. Locations of the 26 studied wetlands, Chubut Province, Patagonia, Argentina. Black points indicate disconnected wetlands (11) and white ones indicate connected wetlands (15).

wetlands within the geographical range (Table 1), but also evaluated accessibility to the study area. Data on the permanency and connectivity of each studied wetland were obtained through LandSat 7 images RGB 123 (from 2003, with a mapping resolution of 30 × 30 m) and field data. We also revised existing data sources (e.g., fish presence and flooding regime) from various governmental administration offices (Dirección General de Bosques y Parques (DGByP) and Instituto Nacional de Tecnología Agropecuaria (INTA)). Bioclimatic zones of the studied wetlands (Table 1) were assigned based on Le Houérou (1996), and the aridity index was estimated using Paruelo et al. (1998).

Environmental variables

The surface area, permanency, and connectivity of each studied wetland were obtained through LandSat images ETM (from 2000 and 2001, with a mapping resolution of 15 m) and field data. The mean annual precipitation was estimated using a regression analytical model (Jobbágy et al. 1995), based on the distance to the Andes. The depth in shallow areas was measured with a calibrated stick in 5 places.

At each sampling site, the water temperature, specific conductance, salinity, total dissolved solids (TDS), pH, and dissolved oxygen (DO) were measured with a Hach sensION 156 multi-parameter probe (Hach Company, Loveland, CO, USA). For nutrient analyses, water samples were collected below the water surface and kept at 4°C prior to analysis. In the laboratory, total nitrogen (TN), total phosphorus (TP), nitrate plus nitrite nitrogen (NO_3-NO_2), ammonia (NH_4), and soluble reactive phosphate (SRP) (± 0.01 mg/μL) were analyzed following methods of the APHA (1994).

Invertebrate and aquatic plant collection

Aquatic macroinvertebrates were sampled using a D-frame net (with a 1-mm mesh). At each site, the net was swept 8 times from the margins to the middle part of the pond, removing invertebrates

Table 1. Site names, codes, connectivity, presence/absence of fishes, aridity, and flooding regime

Site name	Site code	Connectivity	Fish	Aridity	Flooding regime
Santo	SAN	C	A	SA	I
Cushamen	CUS	C	P	SA	I
B. Chubut	BCH	C	A	SA	I
Benetton 2	MB2	D	A	SA	I
Benetton 1	MB1	D	A	SA	P
P. Parada	PiP	D	A	Ar	I
Gualjaina	GUJ	C	A	SA	I
La Cancha	LaC	D	A	SA	I
El tropezón	ElT	C	A	SA	I
Nahuel Pan	NhP	D	A	SA	I
M.A. Pescado	MAP	C	P	SA	P
Valle Frío	VFr	C	A	SA	P
Tecka 1	TK1	C	A	Ar	I
Tecka 3	TK3	C	P	Ar	P
Tecka 2	TK2	C	P	SA	P
Tecka	MTe	D	A	Ar	I
T. Huemul	TrH	C	A	SA	I
P. Quichaura 1	PQ1	D	A	Ar	I
P. Quichaura 2	PQ2	D	A	SA	P
Putrachoique	PCh	C	A	Ar	P
Don Juan	DoJ	D	A	Ar	I
Genoa 14	Ge1	C	P	Ar	P
Cherque	CHE	C	A	Ar	I
El Alfil	ElA	D	A	Ar	I
Mallín Crespo	MCr	D	A	Ar	I
Genoa 2	Ge2	C	P	Ar	I

C, connected; D, disconnected; A, absence; P, presence; SA, semi-arid; Ar, arid; I, intermittent; P, permanent.

associated with the water column and aquatic plants. This was repeated 3 times in each pond (n = 3).

Macroinvertebrates were fixed in the field in 4% formalin. In the laboratory, samples were sorted under 5x magnification and then stored in 70% ethyl alcohol. Water beetles were identified using a Leica MZ6 stereomicroscope (Wetzlar, Germany). Adults were identified to species, while larvae were identified to either the genus or species level, depending on the available literature (van-Vondel 2001, Oliva et al. 2002, Alarie et al. 2007 2009, Michat and Archangelsky 2007, Michat et al. 2008, Archangelsky et al. 2009).

At each site, samples of plant material were collected and packaged in plastic bags, and specimens were herborized at the end of the day, in the laboratory. Species were observed in a Leica MZ6 stereomicroscope, and identified using general and regional bibliographies (Correa 1978-1999).

Data analysis

All aquatic beetles (adults and larvae) were assigned to functional feeding groups (FFGs). For this purpose, we used an available bibliography (White and Roughley 2008). Adults and larvae were treated as separate entities when their diets differed. A canonical correspondence analysis (CCA) was run using CANOCO (ter Braak and Smilauer 1999) to assess relationships between aquatic beetle assemblages and environmental variables. All environmental variables included in table 2 were initially included to evaluate the response of species and sites to environmental gradients. We used all species of adults and genera of larvae as taxa. Variables (except pH) were log (x+1)-transformed prior to the analysis. Variables that were strongly intercorrelated with others (i.e., those with an inflation factor of > 20) in the initial analysis were removed (including latitude, longitude, salinity, PRS, TDS, and wetland width and length), and a further analysis was carried out with the remaining environmental variables. The forward selection option provided by CANOCO was applied, and those variables with $p < 0.05$ (according to the Monte Carlo permutation test with 999 permutations) were retained for the analysis (after omission of water temperature, mean depth, DO, TP, TN, NH_4, and NO_3). The final CCA was run using a set of independent and significant environmental variables (ter Braak and Smilauer 1998).

A parsimony analysis using TNT (Goloboff et al. 2008) was performed in order to establish which species could define and/or group some of the communities. As in any cladistic analysis, a matrix was constructed; sampling sites were treated as taxa, and species were treated as characters (presence/absence). This resulted in a matrix of 27 stations by 19 taxa, which was analyzed with TNT using the implicit enumeration algorithm (which finds the shortest tree by analyzing all possible combinations). To root the tree, a hypothetical site with all taxa represented by absences was included. To establish support for the groups, Jackknife values were calculated with 2000 replicates and P (the removal probability) = 36. A parsimony analysis was preferred over a clustering (phenetic) analysis since it is more informative. With clustering analyses, tree branches are not supported by particular taxa but are generated by algorithms working on pairwise distances which estimate the overall similarity among sites (Pellens et al. 2005, Wenzel and Luque 2008). The parsimony analysis was not expected to yield a fully resolved tree since the number of taxa (19) was smaller than the number of sites (27 including the outgroup). Some taxa were excluded (*Lancetes* spp. and *Berosus* sp.) since they represented larvae that could not be assigned to any particular species (more than 1 species of *Lancetes* and *Berosus* were recorded in the area of study).

RESULTS

Environmental characterization

For the studied wetlands, the mean annual precipitation showed a strong west-to-east gradient, with a mean value of 333 mm (Table 2), being significantly higher at semiarid sites (Kruskal-Wallis test, $p < 0.001$). The minimum of 86 mm at Piedra Parada (arid) and the maximum of 794 at Valle Frío (semiarid) respectively corresponded to eastern and western wetlands (Table 2, Fig. 1). Water temperatures ranged from 10.5°C at Pocitos de Quichaura 1 to 26.5°C at Santo. The size of the assessed wetlands varied from small pools (3.14 m² at El Tropezón) to large ponds (248,000 m² at Nahuel Pan). Moreover, the area of disconnected wetlands was significantly smaller than that of connected ponds (Kruskal-Wallis test, $p < 0.001$). Most ponds were shallow (< 0.6 m in mean depth) with the exception of Nahuel Pan

(1.5 m in mean depth).

As to chemical conditions, DO contents ranged 5.6 (at Benetton 1) to 18.27 mg/L (at Cushamen). The pH was almost neutral at sites such as Benetton 1, Valle Frío (pH 6.79), and Tributario Huemules (6.93), whereas La Cancha (9.45), Don Juan (9.25), and Cherque (9.11) contained extremely alkaline waters. Water conductivity ranged from 28 to 6610 μS/cm with a mean value of 640 μS/cm (Table 2). Moreover, disconnected wetlands had significantly higher salinities than connected ones (Kruskal-Wallis test, $p < 0.01$). Maximum values of TN and ammonia were recorded at disconnected sites such as Don Juan, La Cancha, and Piedra Parada, whereas lower values of TN occurred at a connected site on the Chubut River (153 μg/L). Extreme TP values were recorded at La Cancha (3922 μg/L), Don Juan (1951 μg/L), and Gualjaina (982 μg/L), but most sites had values of < 130 μg/L. TN was significantly higher in disconnected wetlands (Kruskal-Wallis test, $p < 0.001$). The presence of fish was positively correlated with both permanent (Kruskal-Wallis test, $p < 0.02$) and connected ponds (Kruskal-Wallis test, $p < 0.02$).

Aquatic beetles and plants

A total of 21 aquatic beetle taxa were identified from the sampling of the 26 ponds. Two families were the most relevant in terms of taxon richness: Dytiscidae (8; 7 species and *Lancetes* spp. larvae) and Hydrophilidae (6 species) (Table 3). Beetles represented a substantial portion of the total invertebrate taxon richness (mean 24.2%, range 9.42%-50%).

According to the functional feeding group (FFG) characterization, we found 5 FFGs, among which predators were the most important FFG (10 taxa), followed by collector-gatherers (7 taxa) (Table 3). Nonetheless, predators were much more abundant than the other FFGs (92%) (Fig. 2). Moreover, predators were dominant (more than 50%) in 23 ponds, with the exception of Cushamen, Gualjaina, and La Cancha (Fig. 2).

Forty-nine aquatic plant species were recorded in the studied wetlands. The best represented groups of plants were the dicotyledons (Magnoliopsida, 45.2%), monocotyledons (Liliopsida, 47.2%), and algae (5.7%). According to our results, 77.1% of species were native, and of these, 6 species are endemic to Chilean and Argentinean Patagonia; however 22.9% of the total inventory were exotics.

Beetle assemblage structure and environmental relationships

Results of the CCA ordination for the 21 beetle taxa, 26 ponds, and 20 environmental variables showed that 23% of the variance in species abundances was accounted for by the 1st 3 ordination axes (Table 4). The 1st 2 canonical axes respectively accounted for 38.2% and 28.4%

Table 2. Physicochemical characteristics of 26 wetlands studied in Dec. 2006 and Dec. 2007 in Chubut Province, Patagonia, Argentina

Variable	Media	Standard deviation	Minimum	Maximum	Median
Annual precipitation (mm)	333.88	194.42	86	794	280
Elevation (m)	708.50	104.69	448	918	720
Mean depth (m)	0.34	0.27	0.04	1.50	0.27
Area (m^2)	148	49,602	3.14	248,971	88.36
Water temperature (°C)	17.06	4.13	10.50	26.5	17.60
Dissolved O_2 (mg/L)	10.86	2.44	5.60	18.27	10.53
pH	8.01	0.85	6.79	9.45	8.09
Conductivity (μS/cm)	640.12	1442.50	28	6610	200.50
TDS (mg/L)	308.6	852.45	17.8	4430	120.9
Salinity (‰)	0.40	0.98	0	4.6	0.10
TN (μg/L)	1251.70	2263.80	153	10,514	509
NO_3 (μg/L)	21.63	65.92	2.50	316	2.50
NH_4 (μg/L)	126	444.01	4	2269	8
TP (μg/L)	323.12	841.62	17	3922	47.50
SRP (μg/L)	177.81	618.53	1	3062	3

TDS, total dissolved solids; TN, total nitrogen; TP, total phosphorus; SRP, soluble reactive phosphate.
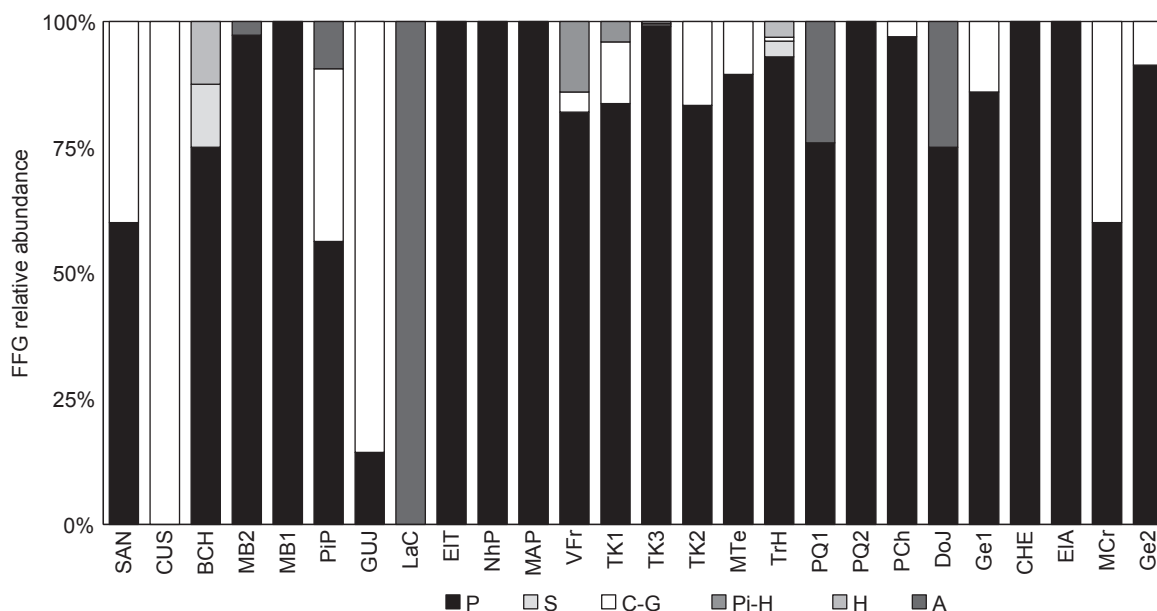
Fig. 2. Relative abundances of aquatic beetle functional feeding groups in 26 Patagonian wetlands, Chubut Province, Argentina. P, predator; S, scraper; C-G, collector-gatherer; Pi-H, piercer-herbivore; H, herbivore; A, algivore. Site codes are given in table 1.

Table 3. Aquatic beetle taxon list with codes and functional feeding groups (FFGs) collected in 26 wetlands in Chubut Province, Patagonia, Argentina

Taxon	Taxa code	FFG
Adephaga		
Haliplidae		
Haliplus subseriatus	HaS	A
Dytiscidae		
Desmopachria punctatissima	Des	P
Lancetes sp.	Lsp	P
Lancetes arauco	LaA	P
Lancetes varius	LaV	P
Liodessus patagonicus	Lio	P
Rhantus antarcticus	RhA	P
Rhantus signatus	RhS	P
Rhantus validus	RhV	P
Polyphaga		
Hydrochidae		
Hydrochus stolpi	Hyd	H
Hydrophilidae		
Enochrus (*H.*) *darwini*	EnD	Pi-H; P[a]
Hemiosus dejeanii	HeD	C-G
Berosus sp.	Bsp	P
Berosus alternans	BeA	C-G
Berosus chalcocephalus	BeC	C-G
Tropisternus lateralis	TrL	
Tropisternus setiger	TrS	C-G; P[a]
Hydraenidae		
Gymnochthebius sp.	Gym	H
Scirtidae		
Cyphon sp.	Cyp	S
Prionocyphon sp.	Pri	S
Elmidae		
Luchoelmis sp.	Luc	C-G

P, predator; S, scraper; C-G, collector-gatherer; Pi-H, piercer-herbivore; H, herbivore; A, algivore. [a]indicates a larval FFG.

of the variation attributable to environmental variables. The CCA produced a significant model as shown by the Monte Carlo test. The 1st ordination axis reflected a gradient mostly related to pH, pond area, and conductivity (Fig.

3A). These variables decreased from the positive to the negative end of the axis. Moreover, all disconnected wetlands were placed at the positive end of the 1st axis, and most connected wetlands (with the exception of M.A. Pescado, Cherque,
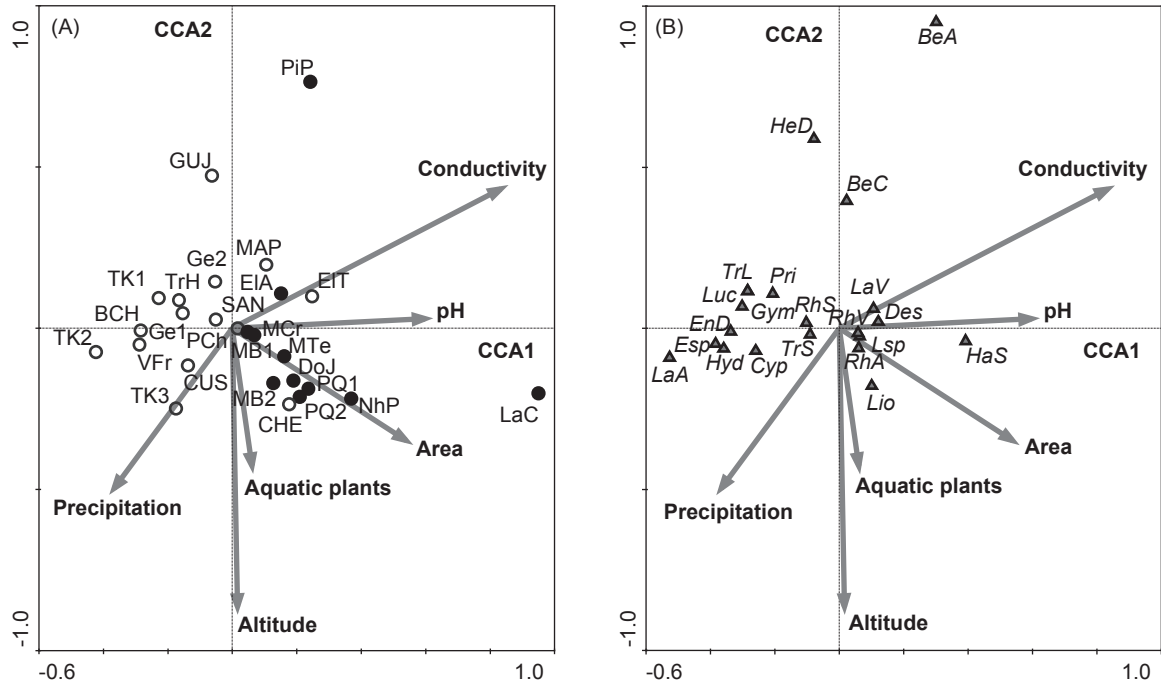

Fig. 3. Canonical correspondence analysis ordination plot for (A) sites and environmental variables and (B) aquatic beetle taxa and environmental variables. The ordination was performed on data of 26 wetlands and 21 coleopteran taxa from Chubut Province, Patagonia, Argentina (in Dec. 2006 and Dec. 2007). Full sampling sites names are in given in table 1. Aquatic beetle taxon codes are given in table 3. In A, black points indicate disconnected wetlands, and white ones indicate connected wetlands.

Table 4. Eigenvalues and intra-set correlations of environmental variables with 3 axes of a canonical correspondence analysis (CCA) of aquatic beetle taxon data. The study was carried out in 26 wetlands of northwestern Chubut Province, Patagonia, Argentina (in Dec. 2006 and Dec. 2007)

Axis	CCA1	CCA2	CCA3
Eigenvalue	0.314	0.233	0.090
Species-environmental correlation	0.830	0.808	0.651
Cumulative percentage variance			
Of species data	11.5	20.0	23.2
Of species-environmental relation	38.2	66.6	77.6
Correlations			
Elevation	0.013	-0.698	-0.116
pH	0.497	0.024	0.014
Conductivity	0.692	0.349	-0.025
Aquatic plants	0.050	-0.345	-0.125
Area	0.447	-0.281	0.294
Precipitation	-0.305	-0.401	-0.292
Test of significance of the 1st canonical axis: $F = 2.46$, $p < 0.04$			
Test of significance of all canonical axes: $F = 1.35$, $p < 0.03$			

and El Tropezón) were at the negative end (Fig. 3A). The 2nd ordination axis indicated that elevation, aquatic plants, and precipitation had the next largest effect on the occurrence of species. Thus, the highest and wettest ponds occurred at the negative extreme correlated with a higher richness of aquatic plants. The ordination of beetle taxa on the 1st 2 axes is presented in figure 3B. Taxa occurring in larger ponds with high levels of annual rainfall, low conductivity, and alkaline waters were positioned in the lower left quadrant. Beetles associated with lowland areas, and lower conductivity and aquatic plant richness occurred in the upper left quadrant.

Indicator species

Results of the parsimony analysis generated 1219 equally parsimonious trees; the strict consensus is depicted in figure 4. The strict consensus shows all groups that were present in all equally parsimonious trees. As expected, the resolution was not perfect since the number of taxa was smaller than the number of sampling stations, but several sites or groups of sites were well defined by 1 or more taxa.

Desmopachria punctatissima characterized a group including stations El Tropezón and Benetton 1 (with a jackknife value of 49). A 2nd group including stations Tributario Huemul, Tecka 3, and Brazo Chubut was defined by the presence of larvae of *Cyphon* sp. (with a jackknife value of 34). The 3rd group, supported by the presence of *Gymnochthebius* sp., included 4 stations Genoa 2, Tecka 1, Tecka 2, and Valle Frío (with a jackknife value of 46); within this group Tecka 1, Tecka 2, and Valle Frío were characterized by the presence of 2 species, *Enochrus darwini* and *Tropisternus setiger* (with a jackknife value of 60). The last group, including stations Don Juan, Pocitos de Quichaura 1, La Cancha, Piedra Parada, and Benetton 2, was supported by the presence of *Haliplus subseriatus* (with a jackknife value of 37).

As for individual stations, the following taxa were unique to just 1 station: *Hemiosus dejeanii* to Gualjaina, *Rhantus validus* to Benetton 1, larvae of *Prionocyphon* to Tributario Huemul, *Lancetes arauco* to Tecka 2, *Luchoelmis* sp. and *Tropisternus lateralis* to Tecka 1, *Hydrochus stolpi* to Valle Frío, and *Berosus alternans* to Piedra Parada.

DISCUSSION

Environmental and biological features

Given the broad geographic and climatic gradients that were evaluated in this study, environmental water features were quite variable (Table 2). However, in the CCA, only annual precipitation, elevation, pond area, aquatic plant richness, pH, and conductivity determined the aquatic beetle assemblages. Effects of abiotic conditions on water-beetle communities (and also on other aquatic insects) were addressed by many studies (Fairchild et al. 2003, Menetrey et al. 2005, Gioria et al. 2010, Touaylia et al. 2011,
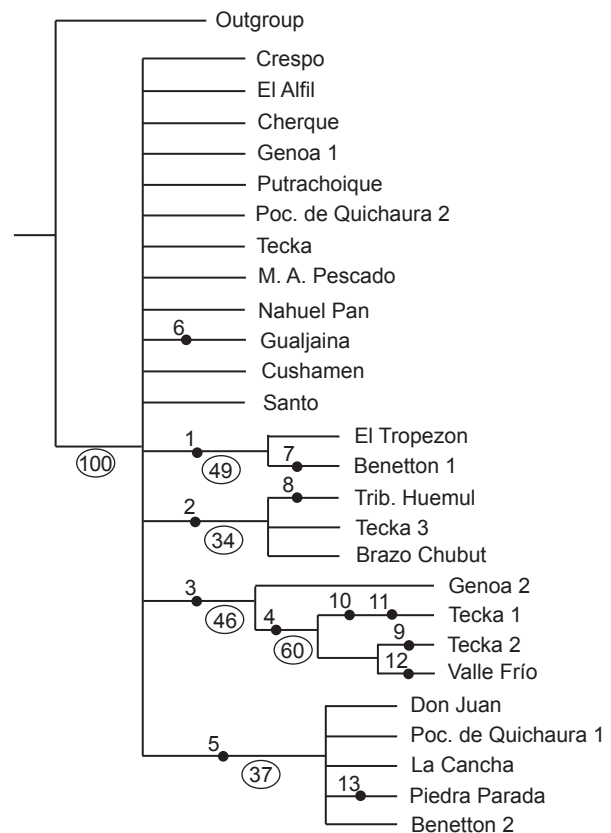

Fig. 4. Parsimony analysis depicting relationships among sampling sites based on distributions of beetle species. Black circles with numbers represent particular species which can be considered indicators. Numbers below the lines (within clear circles) represent support values (jackknife) for groups of interest. Numbers correspond to the following species: (1) *Desmopachria punctatissima*, (2) *Cyphon* sp., (3) *Gymnochthebius* sp., (4) *Enochrus darwini*, (5) *Hapliplus subseriatus*, (6) *Hemiosus dejeanii*, (7) *Rhantus validus*, (8) *Prionocyphon* sp., (9) *Lancetes arauco*, (10) *Luchoelmis* sp., (11) *Tropisternus lateralis*, (12) *Hydrochus stolpi*, (13) *Berosus alternans*.

Picazo et al. 2012). Influences of conductivity on macroinvertebrate and microinvertebrate community composition and diversity are well documented (Biggs et al. 2005, De Jonge et al. 2008, Küppers and Claps 2012). We found that conductivity was one of the most important variables determining beetle assemblages and was also negatively correlated with beetle taxon richness. Such a finding is in line with a number of previous studies which pointed to the importance of conductivity in shaping macroinvertebrate distributions (Picazo et al. 2012). High conductivities were associated with a decline in the diversity of freshwater macroinvertebrates, which largely operates through osmotic challenges of high ion concentrations (Blasius and Merritt 2002).

We found an inverse relation between the annual rainfall and the conductivity of water ponds, which was expected (Perotti et al. 2004), because on the steppe, scanty rainfall, high summer temperatures, and the drying effect of wind conditions increase wetland evapotranspiration, causing salinization due to rising salts concen-trations (Luque 1997).

Moreover, overgrazing causes soil crusting and compaction (del Valle et al. 1998) and can remove substantial amounts of vegetation through herbivory, diminishing water retention and exposing soils to erosion. So, grazing may have directly affected the composition of water beetles, via increases in nutrient levels due to deposition of cow dung, either in the marginal vegetation or in the water, and via increases in water conductivity, salinity, and alkalinity (Perotti et al. 2005, Gioria et al. 2010). pH values were quite variable among sites (6.79-9.45), and high values were due to the effects described above. Arnott et al. (2006) found that pH had little or no influence on aquatic beetles. Nevertheless, our findings revealed that it was important in aquatic beetle regional distribution, which was concordant with Juliano's findings (1991). Finally, elevation could be considered among the physical factors that affected the distribution of wetland beetle taxa. In accordance with Touaylia et al. (2011), beetle taxon richness significantly decreased with increasing elevation.

Even though our study was conducted during late spring and early summer, DO values were very high (mean 10.86 mg/L), and did not seem to affect water beetle distributions. Most ponds were shallow (only 1 pond reached a mean depth of 1.5 m), and wind action in Patagonia is an important generator of turbulence in the water column, thus mixing oxygen concentrations (Perotti et al. 2004). Additionally, differences in DO are less important, since most aquatic beetles use atmospheric oxygen and temporary subelytral air stores (de Szalay and Resh 2000).

Several ecological aquatic beetle studies found that the area of the water body was a determinant variable of community assemblages (Oertli et al. 2002, Arnott et al. 2006, Gioria et al. 2010). We found significant differences in areas between connected and disconnected ponds, of which connected ones were significantly smaller. In the CCA, disconnected sites had higher area-vector values. According to Oertli et al. (2002), the biogeographic principle of a larger area supporting more species seems to have limitations when applied to ponds. For example, Nilsson and Svensson (1995) reported a positive relationship between area and richness for the Dytiscidae, but Oertli et al. (2002) found a species (*Agabus bipustulatus*) associated with smaller ponds.

Despite environmental variables showing a higher predictive capacity compared to that of plant taxon richness, this variable was also significant in the CCA. Plants are known to affect the stability of the substratum and the cycling of nutrients (Keddy 2000), which may also affect the composition of water beetles (Fairchild et al. 2000, Menetrey et al. 2005). Gioria et al. (2010) also reported that the positive predictive strength of environmental variables is the result of both regional and local factors, and they may affect water beetle assemblages directly or indirectly via changes in vegetation.

Pond hydrology

Hydrology and particularly the hydroperiod play critical roles in wetland ecology (Steinman et al. 2003). Wetland hydroperiods are known to influence invertebrate richness and community composition (Tarr et al. 2005, Williams 2006), and their abundance and reproductive success (Leeper and Taylor 1998). Moreover, there is evidence that temporary water communities are somewhat less diverse than are permanent water bodies (Nilsson and Svensson 1995, Gioria et al. 2010), because the physicochemical environment is harsher in temporary waters. However, the concept of temporary waters constraining their faunas is based more on human conceptions than on facts (Williams 1996 2006). The hydroperiod, at least in the way we measured it (permanent and intermittent categories), did not seem to be

a key factor driving assemblage compositions, since many water beetles typical of lentic waters only need a few weeks to colonize temporary sites (Picazo et al. 2012). Fairchild et al. (2003) found that during late spring, temporary and permanent sites supported similar beetle richness levels, a finding that agrees with our results. The convergence between temporary and permanent ponds during late spring may have resulted from extensive opportunities for dispersal among ponds, promoted by winter precipitation which in turn increased pond areas and replenished dry ones.

Indicator species

Results of the parsimony analysis are depicted in figure 4, which shows those species that are useful for defining some ponds or groups of ponds. These beetles can be used as indicators since species distributions (their absence or presence) are not considered a random situation (Pellens et al. 2005, Rachlin et al. 2008, Wenzel and Luque 2008, Rachlin and Warkentine 2012).

Five wetlands (DoJ, PQ1, LaC, PiP, and MB2) were united by the presence of *Haliplus subseriatus*; haliplids show an affinity for well-vegetated ponds, especially those with filamentous algae and characeans, since they are algivores (Flechtner 1986, van-Vondel 2001); they also like well-oxygenated waters since the larvae breathe by means of tracheal gills. Four of the 5 wetlands in which *H. subseriatus* appeared shared the following characteristics: a relatively large surface area, well-vegetated, located at intermediate elevations, moderately alkaline waters (pH of > 8.0), and being disconnected; the only exception was Piedra Parada, which had few aquatic plants and was located at a low elevation.

Another group of 4 wetlands (Ge2, TK1, TK2, and VFr) was supported by the presence of *Gymnochthebius* sp. All of these wetlands were connected, and this is in agreement with the habitat of other species present in arid or semiarid environments (Perkins and Archangelsky 2002, Delgado and Archangelsky 2005). All of the wetlands in which *Gymnochthebius* sp. appeared shared the following characteristics: an intermediate pH (except Ge2), a relatively small surface area, and intermediate to low conductivity values. *Gymnochthebius* adults and larvae are herbivorous and are usually associated with filamentous algae (Perkins and Archangelsky 2002, Delgado and Archangelsky 2005). Within this group, three of the wetlands (TK1, TK2, and

VFr) were characterized by the presence of 1 hydrophilid, *Enochrus darwini*; the main difference between these 3 stations and Ge2 was that Ge2 had higher values of conductivity, and especially pH and TDS. *Enochrus darwini* is restricted to northwestern Patagonia; so it could be considered a good indicator of environmental characteristics.

Three of the wetlands (TrH, TK3, and BCH) had larvae of the genus *Cyphon* in common; these larvae are associated with decaying plant material, and stations at which they appeared had the following characteristics in common: a low pH, a relatively small surface area, and a low conductivity. Very little is known about the South American Scirtidae, but the larvae are detritivores (scrapers), consuming fine particulate matter, and some genera are known to be habitat specific (Lawrence 2005).

EIT and MB1 had 1 species, *Desmopachria punctatissima*, in common; this is a ubiquitous species and has a very extensive distribution (Michat and Archangelsky 2007). Neither of these 2 stations showed very distinctive environmental variables; therefore we consider that *D. punctatissima* probably is not a good indicator of environmental conditions.

Of the remaining species that were unique to 1 site, very little can be discussed here since their biology is still poorly understood, but some comments on two of those species are worth including. *Luchoelmis* sp. (Elmidae) is typical of well-oxygenated running waters (adult and larval elmids breathe oxygen dissolved in the water); it only appeared at TK1, and its presence there suggests that this connected wetland must be regularly flooded, and the *Luchoelmis* specimens (9 in total) must have been carried to the wetland by a strong flood. *Rhantus validus* is a relatively large species, not very common, and characteristic of waters of intermediate depth (50-80 cm, pers. observ.) in either slowly running waters or small ponds; only two of all the sampled sites shared this characteristic, and *R. validus* appeared in one of them, Benetton 1, suggesting that its presence there could be an indicator of depth. On the other hand, *Rhantus antarcticus*, a related species, is more ubiquitous, being found in a variety of situations (it appeared in 3 different wetlands).

Conservation implications

There are several anthropogenic activities (e.g., grazing by livestock and feral animals, non-native plants, and road construction) and natural

factors (global climate change) that can potentially impact isolated water bodies in Patagonia. These impacts, either singly or jointly, can affect temperature regimes, sedimentation processes, riparian vegetation, chemical concentrations, solar radiation, and evaporation rates, which in turn can potentially make the water bodies unsuitable for animals and/or human usage (Luque 1997, Box et al. 2008). The ecological equilibrium of Patagonia is highly susceptible to human impacts, and the present methods of natural rangeland management are based on the extreme overuse in space and time (del Valle et al. 1998). Identification and protection of areas of biological value in relation to abundances of species or the presence of endemics are necessary in view of high rates of desertification and habitat degradation (du Pisani et al. 1995).

Protective measures designed to retain the diversity of wetlands that span the hydrological gradient are necessary to ensure the long-term persistence of aquatic invertebrate biodiversity (Tarr et al. 2005). Moreover, monitoring invertebrates can provide valuable information to wildlife mangers (Tangen et al. 2003), since invertebrates are an essential food source for many species of birds (Cox et al. 1998) and amphibians (Perotti et al. 2005) that live in and around wetlands. Further, the importance of larger temporary waters (e.g., Nahuel Pan) as habitats and sources of invertebrate food has become widely appreciated (Finlayson and Moser 1991). On the other hand, semi-permanent and permanent wetlands serve as source populations for the re-colonization of more-temporary, nearby water bodies, provide refugia for rare or relict species during prolonged droughts (Williams 2006), and are less sensitive to extinctions. These assemblages, together with the indicator species identified in our analyses, can be utilized for conservation planning in the future (Picazo et al. 2012). Given the wide range of environmental features and the loyalty of some beetles to specific ponds, our findings highlight the need to maintain a range of lentic habitats for effective conservation of the regional fauna, and also point to possible impacts of livestock on the composition of the fauna and flora of wetlands of arid and semi-arid Patagonian region.

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