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Distribution of diatoms and mollusks in shallow lakes from the semiarid Pampa region, Argentina: Their relative paleoenvironmental significance

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ABSTRACT

The aim of this study was to assess the potential of diatoms and mollusks as paleoenvironmental indicators in semiarid lakes of the Argentinean Pampas. At each lake, physical and chemical variables were quantified, and diatoms and mollusks collected. The relationships between environmental variables and biological assemblages were explored through ordination techniques. Lakes were highly alkaline (pH 9.5–10.5), and varied significantly in conductivity (0.2–15.7 mS/cm) and hardness (120–1874 mg/l $CaCO_3$). A total of 79 diatom and two mollusk species were identified. The highest percentage variance in diatom data was explained by hardness, conductivity, and mud percentage. Mollusk variability was significantly related to conductivity, hardness, and vegetation cover. Diatom-based ordination of sites accurately reflected the main environmental gradients characteristic of the region, while the resolution provided by mollusk-based ordinations was lower, mainly as consequence of the wide ranges of tolerance to hardness and conductivity exhibited by the two species represented. Hence, while the use of mollusks as paleoenvironmental indicators is only valid at a large, regional scale, diatoms allow discriminating local conditions and subtle environmental differences. As a consequence, the results emphasize the use of mollusks as qualitative and semi-quantitative indicators, while the strong statistical relationship between diatoms and climate-driven environmental parameters highlights their potential use as quantitative indicators of Quaternary climatic changes in the semiarid Pampas.

1. Introduction

The semi-arid region of central Argentina, located between latitudes 32° and 38° S, is situated within the domain of the South American Arid Diagonal, a region considered to have been climatically sensitive to the latitudinal shift of the Pacific and Atlantic anticyclonic centres during the late Pleistocene and the Holocene (Abraham de Vazquez et al., 2000). Although several contributions refer to the Quaternary glacial geology and tree-ring records of the Andes Cordillera at this latitude (Villalba et al., 2009), scarce information is available on the paleoclimatic and paleoenvironmental dynamic of the eastern plains. This is mainly a consequence of the lack of robust paleoclimate data series at an adequate quality (e.g., deep lakes, trees).

In recent years, big efforts have been conducted in the Southern Hemisphere in order to clarify paleoclimatic tendencies from a regional point of view (Villalba et al., 2009). In this context, the advance in the knowledge of past climatic changes in the scarcely studied Central Argentina would provide information of relevance for the climate reconstruction of southern South America. Hence, the area has recently become the focus of a series of paleoclimatic and paleoenvironmental studies, based mainly in the analysis of sedimentary and biological proxies recovered from aeolian and alluvial successions (De Francesco et al., 2007; De Francesco and Hassan, 2009; Páez et al., 2010; Tripaldi and Forman, 2007; Zárate and Mehl, 2008). Studies on lacustrine records were, conversely, very scarce (González and Maidana, 1998). However, a high variability of closed-basin shallow lakes, ranging from freshwater to saline conditions, can be found in this region. Many of these lakes are subjected to significant fluctuations in salinity and water level, as consequence of the great losses of water produced by high evaporation rates and rain seasonality in this semiarid area (Drago and Quirós, 1996). Besides the relevance of these lakes for paleoenvironmental purposes, the paleoclimatic and paloecological

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significance of the biological record preserved in their sediments remains unexplored.

The development of accurate paleoenvironmental reconstructions based on biological remains relies on a complete knowledge of modern communities and their relationship with the physical and chemical environment. The changes in salinity that occur in closed-basin lakes from arid and semi-arid regions are clearly reflected in the composition of lacustrine diatom assemblages. Hence, diatoms are potential climate tracers in arid and semi-arid regions where lakes may respond to changes in the precipitation-evaporation balance by large variations in water volume and ionic concentration (Fritz, 2007). Freshwater mollusks, on the other hand, are less tolerant to saline waters, with most species distributed exclusively in oligohaline waterbodies. One exception is provided by hydrobioid snails of the family Cochliopidae, which have some species capable to tolerate increased salinity. In southern South America the Cochliopidae are represented exclusively by *Heleobia*, with *H. parchappii* usually recorded in saline lakes of semiarid regions (De Francesco and Hassan, 2009). Although diatoms are among the most ubiquitous biological remains preserved in continental Quaternary successions from central Argentina, no studies intending to assess their patterns of distribution and relationship with the main environmental factors have been performed in semiarid environments of this region. In addition, only one work focusing on mollusk distribution has been carried out in the Andean piedmont (De Francesco and Hassan, 2009). Hence, the paleoenvironmental significance of diatoms and mollusks is still limited, restricting the strength and reaches of the paleoclimatic inferences that could lead to the recognition of arid and semiarid environments in the past.

In the present paper, we analyzed the distribution of diatoms and mollusks and their relationship with environmental variables in ten shallow lakes from the semiarid Pampa, Central Argentina. Our main aims were: (1) to identify the main environmental factors that control the distribution of both indicators in semiarid environments, and (2) to identify diatom and mollusk assemblages indicators of semiarid conditions. Results of this contribution will increase our knowledge on diatom and mollusk communities from semiarid environments in Southern South America, allowing for the identification of possible analogous of past semiarid conditions and the future development of accurate environmental reconstructions in shallow lakes of the region.

2. Materials and methods

2.1. Study area

The study was carried out in the northeast of La Pampa province (Appendix 1, electronic version only), a semiarid area of climatic transition between the humid Pampas and the Patagonian steppe (Paoloni et al., 2003). The semiarid climate characteristic of this region prevent the development of an autochthonous hydrographic net. Therefore, it is characterized by many shallow and saline lakes (<2.5 m deep), usually associated to lowlands without drainage (INTA, 1980). The chemical composition of the water in these lakes is very variable, and depends on the relief, climate and composition of the parental material of each hydrological system (Drago and Quirós, 1996).

Sampling included a total of 10 shallow lakes distributed into two physiographic regions with different hydrological regimes: the Oriental region (sites 1–4, 6–8), located on the east side of La Pampa province, and characterized by a subhumid-dry climate (mean annual precipitation: 700–500 mm; mean annual temperature: 16 °C) and the Central region (sites 5, 9 and 10), located westwards from the former region, and characterized by a semiarid climate with a mean annual precipitation of 400 mm, and a mean annual temperature of 15 °C (INTA, 1980).

The 10 lakes sampled in the present work were chosen to reflect the whole variability of lakes in the region, mainly related to geomorphology and substrate type. Three lakes (2 = Monte Nievas, 4 = Bajo Las Palomas, 5 = Telén) are located in caliche plains, over a substrate that consists of sandy sediment of variable thickness, overlying tertiary muddy sediments. Among them, Bajo Las Palomas is a temporary pond formed in an elongated concave area where pluvial water accumulates during rainy periods. The substrate consists of a thin sandy layer with high carbonate content. Two lakes (1 = El Cañadón, 3 = Lonco May) are located in sandy plains; the substrate being composed of sandy sediments with calcretes interbedded near the surface. These lakes develop in lowlands, where soils display variable salinity and support halophytic and paludal vegetation. Three lakes (8 = La Verde, 9 = El Bote, 10 = La Brava) are located in dune fields, developed within interdunes depressions. The thickness of the sand cover is rather uniform (>6 m). Soils are excessively drained, highly permeable, and with a very low humidity retention potential. Finally, two lakes (6 = Chapalcó, 7 = El Camino) are saline lakes formed in the border of old interfluves that constitute today plateaus extended in SW-NE direction (Relictual Central Valleys), in contact with the plateaus, influenced by a very high saline groundwater inflow, on saline soils (INTA, 1980).

2.2. Field and laboratory methods

2.2.1. Environmental parameters

Conductivity, pH, temperature and Secchi transparency were measured *in situ* with mobile instruments during spring 2004. Aquatic vegetation cover at each sampling site was estimated visually, and a nominal variable erected for statistical purposes: 0 = no vegetation (<5%), 1 = low vegetation cover (between 5 and 10%), and 2 = intermediate vegetation cover (between 10 and 20%). One subsurface water sample (1 l) was taken at each site to assess chemical parameters. Water samples were collected in polyethylene bottles and stored in ice until they were transported to the laboratory. Water samples were analyzed within fifteen days of collection for concentrations of nitrate (NO_3^-), sulfate (SO_4^{2-}), chloride (Cl^-), fluoride (F^-), sodium (Na^+), potassium (K^+), carbonate (CO_3^{2-}), bicarbonate (HCO_3^-), magnesium (Mg^{2+}), calcium (Ca^{2+}) and hardness. Chemical analyses were performed applying standard methods (APHA, 1992). In order to characterize the substrate, sediment grain size was analyzed by dry sieving. Categories of grain size included gravel (>2 mm), very coarse sand (1–2 mm), coarse sand (500 μm–1 mm), medium sand (250–500 μm), fine sand (125–250 μm), very fine sand (63–125 μm) and mud (silt and clay, <63 μm). Additionally, the organic content of each sample was estimated using the loss on ignition method (LOI, 4 h at 550 °C; Heiri et al., 2001). In each lake, perimeter and surface were estimated from Landsat TM satellite images using the DivaGis 7.1.7.2 program (Hijmans et al., 2009).

2.2.2. Diatom samples

Since most sites were shallow, the uppermost 1 cm of superficial sediment was sampled by hand by carefully scrapping the surface sediment with spatula and placed in 100 ml plastic vials. In the laboratory, 5 g of dry sediment were oxidized with hydrogen peroxide (30%) and hydrochloric acid (10%), washed 3 or 4 times with distilled water, and diluted to a total volume of 100 ml. After complete homogenization, a subsample was transferred to a coverslip and air-dried. Permanent drop slides were mounted with Naphrax®. On each slide at least 300 diatom valves were counted in random transects at 1000× magnification. Diatom species were identified according to standard and local floras (e.g. Lange-Bertalot, 2011; Maidana and Romero, 1995; Romero, 1993, 1995).

2.2.3. Mollusk samples

Three randomly quadrats (25 × 25 cm) were delimited in the littoral zone and the uppermost 2 cm of the sediment collected. In the laboratory, mollusks were separated from the sedimentary matrix with the aid of sieves (1 mm mesh size) and counted under stereoscopic microscope. Living mollusks were also searched for among the submerged vegetation and under stones in order to sample species that may not be present in sediments.

2.3. Data analyses

2.3.1. Environmental data and water chemistry

Principal Component Analysis (PCA) was used for the ordination of sampling sites based on the total set of environmental variables measured. Environmental data were log transformed, as log $(x+1)$. The analysis was carried out with the computer program PAST v 1.81 (Hammer et al., 2008).

In order to compare the hydrochemistry of lakes and define the water type, the ionic composition was analyzed following a general statistical characterization and Piper diagram (Hem, 1992). In the plot, major ions are plotted in the two base triangles as cation and anion percentages of milliequivalents per liter, respectively. Total cations and total anions are each considered as 100%. The cation and anion locations for analysis are projected into a diamond graph that represents the total ion relationships, which can be used to characterize the water type. The mechanism that controls the chemical composition of water was evaluated using Gibbs's plots (Gibbs, 1970), which represents the ratio Na^+/($Na^+ + Ca^{2+}$) versus salinity. This diagram was used to identify the main process responsible for the ionic composition of each sample (*i.e.* atmospheric precipitation, rock dominance or evaporation–crystallization).

2.3.2. Biological data

Detrended correspondence analyses (DCA) were applied to biological data (diatom and mollusk) to estimate species turnover (Eilertsen et al., 1990). DCA calculates the length of the species gradients (DCA axis 1 scores), which describe the degree of species turnover, with half change in species composition occurring at approximately 1.0–1.4 standard deviation (SD) units, and gradient lengths more than 4 SD indicating a complete turnover of species (Heino and Soininen, 2005). DCA was also used to assess whether a unimodal method or linear method would be appropriate for interpreting the environmental and biological data. A gradient length higher than ~2 SD indicates a relatively long gradient, and, in this case, unimodal species models are more appropriate. Linear methods are more appropriated when the gradient lengths are short (<2 SD).

DCA results showed that the gradient length for the first two axes of diatom ordination were 3.6 and 2.1 SD, indicating unimodal responses of the diatom data. Consequently, Canonical Correspondence Analyses (CCA, focused on inter-species distances, rare taxa down-weighted) were employed to explore the relationship between diatom composition and environmental variables. CCA is a multivariate method with the main advantage, compared with indirect gradient analyses such as PCA and CA, that it can elucidate the relationships between biological assemblages of species and known variations in environments (ter Braak, 1986). The resulting ordination diagrams of CCA show the main pattern of variation in compositions of the biological assemblages as accounted by the environmental variables and, in an approximate way, the distributions of the species along each environmental variable.

The mollusk data set yielded a gradient length of 1.4 SD according to DCA, indicating a linear relationship between environmental and biological data. Therefore, Redundancy Analysis (RDA), a constrained ordination technique based on linear (Euclidean distance) relationships between variables, was used to relate environmental and mollusk data. RDA is an enhancement of the commonly applied principal component analysis (PCA) but in contrast to PCA, it allows a direct analysis of the biotic- environment components (ter Braak, 1994).

Ordination techniques based either on linear or unimodal distributions were applied to the diatom and mollusk dataset using the program CANOCO version 4.5 (ter Braak and Smilăuer, 1998). The statistical significance was assessed by applying Monte Carlo tests (reduced model) involving 999 permutations.

2.3.3. Comparison of the environmental information provided by diatoms and mollusks

In order to compare the ability of diatom and mollusk datasets to differentiate between sites with different environmental characteristics, a series of MDS (Multidimensional Scaling) were applied. MDS is a statistical technique that allows one to map the similarities between points in a high dimensional space into a lower dimensional space. For a given set of observed similarities between every pair of N items, MDS finds a representation of the items in as few dimensions as possible, such that the similarities in the lower dimension match as closely as possible the original similarities (Johnson, 1998). Unlike such traditional approaches as cluster analysis or discriminant function analysis, MDS does not rigidly define species associations, and, consequently, the approach is biologically more realistic. A numerical measure of the closeness between the similarities in the lower dimensional and the original spaces is called stress. The stress has a value between 0 and 1, with 0 indicating perfect fit and 1 indicating worst possible fit. MDS plots of sites derived from environmental variables, diatoms and mollusks were constructed based on similarities of Euclidean distances matrices. Analysis of similarity (ANOSIM) were used to test for significant differences between the groups observed in the different plots using the program PAST v 1.81 (Hammer et al., 2008).

3. Results

3.1. Environmental data and water chemistry

The sampled lakes were characterized by highly alkaline (pH 9.5–10.5) and very hard (120–1874 mg/l $CaCO_3$) waters (Appendix 1, electronic version only). Conductivity was highly variable, ranging from 0.2 to 15.7 mS/cm. Vegetation, when present, was always restricted to small patches of macrophytes (*Schoenoplectus californicus*) located near the littoral zone. However, most of the lakes showed no vegetation or very low vegetation cover. According to grain size, two main groups were differentiated: (1) lakes dominated by very fine sand and mud, and (2) lakes dominated by medium and fine sands (Appendix 1, electronic version only).

The first two components of the PCA ordination accounted for 49.9% of the variation in the data. The first axis explained 29.1% of the total variation and exhibited a positive correlation with sedimentary variables (coarse sand $r = 0.45$; medium sand, $r = 0.7$; mud, $r = 0.52$; and LOI $r = 0.56$), and negative with hardness (r = -0.94), gravel (r = -0.85), Mg^{2+} ($r = -0.80$), SO_4^{-2} ($r = -0.76$), Cl^- ($r = -0.73$), and conductivity ($r = -0.73$). The second axis, which explained 20.7% of total variation, was positively correlated with very fine sand ($r = 0.85$) and mud ($r = 0.77$), and negatively with fine sand ($r = -0.76$). The first axis represented a gradient of ionic strength, while the second represented a gradient of grain size. Sites 1 and 7 displayed the highest hardness as well as the highest concentrations of Mg^{2+}, Cl^{-}, and SO_4^{2-} (Appendix 1, electronic version only).

Four water-type groups were identified in the Piper plot (Fig. 1A). The first group (lakes 2, 3, 6, and 7) was located on the right side of the main plot (diamond) and characterized as Cl^{-}/Na^{+} water type. The second group (lakes 5, 8, 9 and 10) was plotted towards the lower corner of the diamond, indicating that Na^{+} and HCO_3^{-} are among the dominant ions. The third group, which was only represented by site 1, was located towards the top of the diamond, and characterized as Cl^{-}/Ca^{2+} type. The fourth group was only represented by site 4, and characterized as $HCO_3^{-}/Cl^{-}/Ca^{2+}$ type. According to the Gibbs's plot (Fig. 1B), evaporation is the mechanism that control water chemistry in all sites except Bajo Las Palomas (site 4). The main process that defines the water composition of site 4 appears to be rock dominance.

3.2. Diatoms

A total of 79 diatom species were identified (Appendix 2, electronic version only). Average richness was 20, with a range of 8–37. The most abundant species were represented by *Amphora copulata*, *Cyclotella meneghiniana*, *Hantzschia amphyoxis*, *Hippodonta hungarica* and *Planothidium delicathulum* (Fig. 2).

According to the DCA gradient lengths, many sites showed complete species turnover along the major axis of variation. In six sites, DCA scores remained relatively constant and ranged between 0 and 1, indicating that diatom assemblages were fairly similar among them. The remaining four sites, which corresponded to shallow lakes characterized by sandy sediments, showed extreme values that indicated strong species shifts (>2 SD, Fig. 2).

In a first step, a series of partial CCAs, run with one explanatory variable at a time was applied in order to separate total variation in diatom data into components that represent the unique contributions of individual environmental variables. Hence, the environmental data set was reduced to the most powerful variables explaining the highest amount of variance in the diatom data set (Bigler et al., 2006). After variable selection 6 chemical and physical variables accounted for significant specific portions of the total variance in species composition: conductivity, LOI, fine sand ($p < 0.05$), hardness, transparency and mud ($p < 0.01$). However, as water transparency, LOI and fine sand were significantly correlated with mud ($r > 0.75$, $p < 0.01$), these variables were removed from further analyses.

Hardness was identified as the strongest variable explaining 19.2% of the variance within the diatom data set, followed by conductivity (17.6%), and mud (16.6%). The reduced set of environmental variables explained 48.5% of the variation in diatom distribution. The species-environment correlations of CCA axis 1 (0.982) and axis 2 (0.971) were high and indicated a strong relationship of diatom relative frequencies to environmental variables (Table 1). The first axis of CCA plot (19.9% of the explained variance) showed a positive correlation with hardness ($r = 0.93$) and conductivity ($r = 0.75$), and a negative correlation with mud ($r = -0.67$), while the second axis (15.1% of the variance explained) was positively correlated with conductivity ($r = 0.53$). Accordingly, sites were ordinated following hardness, conductivity and grain size gradients along axis 1, while the second axis allowed plotting sites according to the conductivity gradient (Fig. 4A).

3.3. Mollusks

Eight of the 10 shallow lakes had live mollusks. Only two species were represented: *Biomphalaria peregrina* and *Heleobia parchappii*. Whereas the former was present in 7 sites, the later was restricted to only 2 sites located on the easternmost part of the study area. These two species only coexisted in the largest lake (El Cañadón). In addition, the highest abundance of *H. parchappii* was recorded here. On the other hand, the highest abundance of *B. peregrina* was recorded at site 3 (Fig. 3).

Three environmental variables explained significant portions of the variability of mollusk abundances. In order of importance, these were: conductivity, hardness, and vegetation cover ($p < 0.05$;

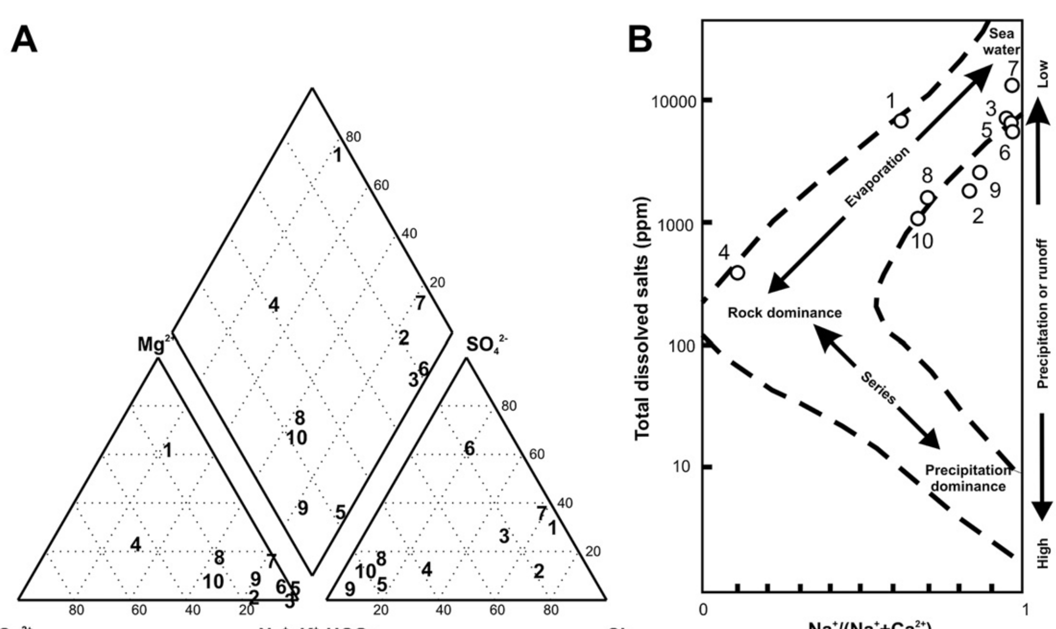

Fig. 1. (A) Piper diagram showing hydrochemistry of water samples from La Pampa lakes; (B) Variation of the weight ratio $Na^{+}/(Na^{+} + Ca^{2+})$ as a function of the total dissolved salts of La Pampa lakes waters. The boomerang shape envelope (dashed line) was observed by Gibbs (1970) for surface waters from various regions of the world.

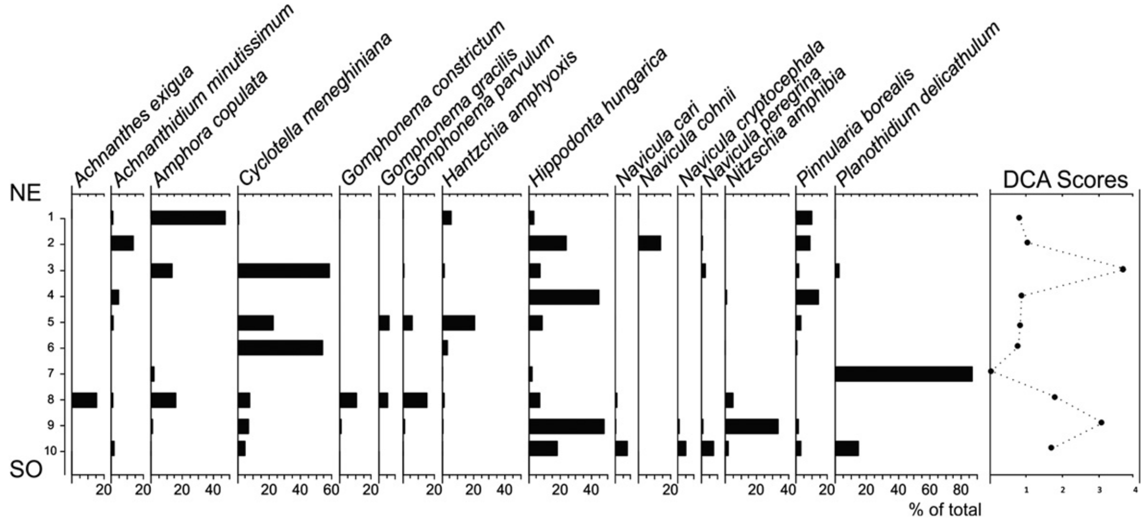

Fig. 2. Relative frequency diagram of dominant diatom taxa and DCA scores in La Pampa sites.

Table 1). The 85% of the overall variability was explained by the first two axes. The RDA1 × RDA2 plot (Fig. 4B) showed that *H. parchappii* dominated in lakes characterized by fine sediments, high hardness and high conductivity. On the other hand, *B. peregrina* was restricted to oligohaline lakes characterized by high vegetation cover and coarser sediments.

3.4. Comparison of the environmental information provided by diatoms and mollusks

The MDS ordination plot of sites based on environmental variables (Fig. 5A; Table 2) allowed defining five groups that differed significantly from each other (ANOSIM, $R = 1$; $p = 0.0002$). These groups were represented by (I) site 7, (II) site 1, (III) sites 3 and 6, (IV) site 5, and (V) sites 2, 4, 8, 9, 10. Overall, differences between groups were based on conductivity, hardness and grain size, and sites were ordinated along axis 1 following a gradient from higher conductivity and hardness (site 7) to fresh water (group V).

The MDS ordination plot of sites based on diatom composition (Fig. 5B; Table 2) revealed the existence of seven groups (ANOSIM, $R = 1$; $p = 0.0002$). These groups coincided with those previously recognized from the environmental variables alone with the only difference that the previously named group V, characterized by freshwater conditions, was subdivided here into three groups: (V-a) sites 2, 4 (V-b) sites 8, 10 and (V-c) site 9. This difference was mostly related to shifts in the relative abundances of the species that dominate in each lake.

On the other hand, the MDS ordination plot of sites based on mollusk composition (Fig. 5C; Table 2) only allowed differentiating four groups (ANOSIM, $R = 1$; $p = 0.018$). Two of these groups coincided with those previously defined as groups I and II. The third group coincided partially with group III because included site 3 but excluded site 6 which did not contain any mollusk at all. The remaining sites were grouped all together and included the sites previously defined as groups IV and V. This difference was mostly related to the abundance and richness of snails in each lake.

Table 1
Summary statistics for the first two axes of CCA and RDA, performed on diatoms and mollusks, respectively.

Ordination results	Axis	
	1	2
Diatoms (CCA)		
Eigenvalues (λ)	0.748	0.569
Species-environment correlation	0.982	0.971
Cumulative % variation of species data	19.9	35.0
Species-environment relationship	40.9	72.0
Sum of all λ	3.767	
Sum of all canonical λ	1.829	
Test of significance of the first canonical axis $p \leq 0.05$		
Test of significance of all canonical axis $p \leq 0.001$		
Mollusks (RDA)		
Eigenvalues (λ)	0.789	0.062
Species-environment correlation	0.980	0.590
Cumulative % variation of species data	78.9	85.1
Species-environment relationship	92.7	100.0
Sum of all λ	1.00	
Sum of all canonical λ	0.85	
Test of significance of the first canonical axis $p < 0.05$		
Test of significance of all canonical axis $p < 0.05$		

The significance of canonical axes is indicated based on 999 unrestricted Monte Carlo permutations.

4. Discussion

4.1. Diatoms

Diatom assemblages were diverse and dominant taxa were strongly related to the environmental characteristics of the waterbodies. *H. hungarica, H. amphyoxis* and *N. amphibia* were highly abundant in lakes with low conductivity (<1 mS/cm) and hardness (<200 mg/l $CaCO_3$). These are cosmopolitan taxa, very frequent in the benthos of temperate fresh waterbodies of neutral to alkaline pH (De Wolf, 1982; Van Dam et al., 1994). They are also frequent in surface sediments of lakes and streams from the Humid Pampas (Hassan et al., 2009). On the other hand, lakes with highest salinities (3–15 mS/cm) were mainly dominated by *P. delicathulum*, *C. meneghiniana* and *A. copulata*. These taxa are widely distributed in brackish and alkaline waters (Van Dam et al., 1994). Particularly *P. delicathulum*, which tolerated the highest hardness values (>1800 mg/l $CaCO_3$), is almost exclusively restricted to hard and

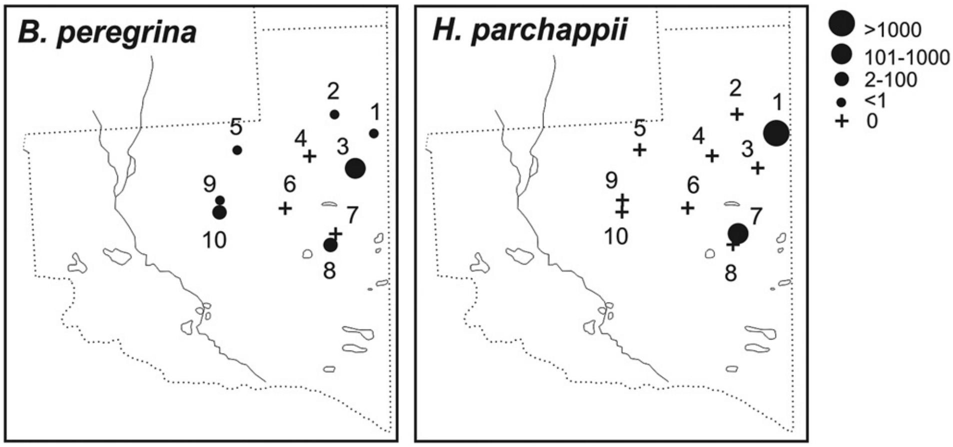

Fig. 3. Distribution and abundance of the two mollusk species represented in lakes from La Pampa province.

alkaline waters (Van Dam et al., 1994). Overall, these two diatom assemblages allow a clear distinction between fresh and brackish lakes of the semiarid Pampas. As most of these taxa are common in Holocene successions of the region (Hassan et al., 2004; Stutz et al., 2010), they constitute potential indicators of past conductivity fluctuations.

Hardness, conductivity and grain size have been reported as important factors influencing diatom distribution in continental settings (Bigler et al., 2006; Rosén et al., 2000; Schönfelder et al., 2002), even in lakes and streams of the adjacent Humid Pampa

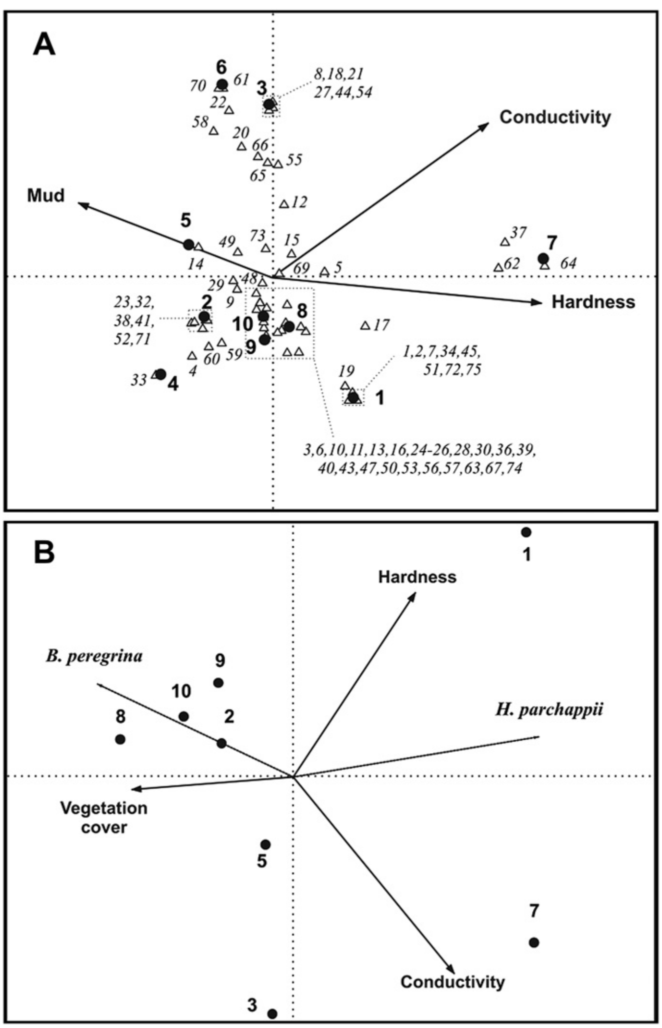

Fig. 4. (A) Canonical correspondence analysis (CCA) of surface sediment diatom taxa against selected environmental variables from the sampled sites. Diatom species numbers corresponding to those listed in Appendix 1. (B) Redundancy analysis (RDA) of mollusk species against selected environmental variables from the sampled sites.

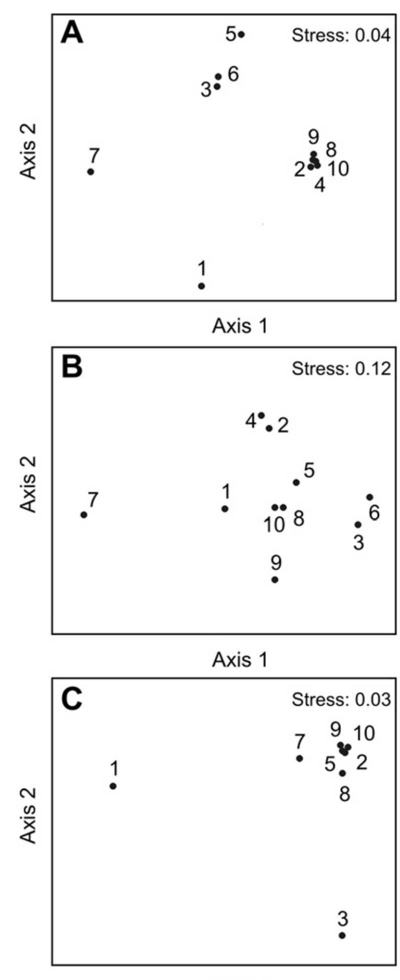

Fig. 5. MDS plot of sites based on (A) environmental variables, (B) diatoms, and (C) mollusks.

Table 2
Groups of sites defined by MDS ordination based on environmental variables and their corresponding dominant diatom and mollusk taxa.

Group	I	II	III		IV	V			
						a		b	c
Sites	7	1	3	6	5	2	4	8, 10	9
Diatoms	*P. delicathulum*	*A. copulata*	*C. meneghiniana*		*C. meneghiniana* *H. amphioxys*	*H. amphioxys* *P. borealis* *A. minutissima*		*H. hungarica* *Gomphonema* spp. *Navicula* spp.	*H. hungarica* *N. amphibia*
Mollusks	*H. parchappii*								
		B. peregrina			*B. peregrina*			*B. peregrina*	

Region (Hassan et al., 2009). The main observed difference between Semiarid and Humid Pampa was related to diatom diversity, which was lower in the present study (Hassan et al., 2009). This is probably related to the higher hardness and conductivities exhibited by lakes developed in the semiarid Pampa, which poses limitations to the development of many freshwater taxa. Moreover, it has been pointed out that the diversity of continental diatoms decreases as salinity increases (Fritz, 2007).

The 51.5% of the total variation of species data remained unexplained. Whether this is due to some overlooked factor or to a large amount of stochastic variation remains unclear. Aquifers in La Pampa province have been reported to contain high concentrations of arsenic (up to 5300 μg/l), mainly as a consequence of the evaporation under semiarid climatic conditions (Smedley et al., 2002). As arsenic stress can induce shifts in diatom species dominance (Sanders and Cibik, 1985), arsenic concentration might be one of the “overlooked” factors responsible for the unexplained variance in CCA. Nevertheless, the explained percentage is considerably greater than those found in many other similar biological datasets, which have a large number of samples with many zero values, and have been used to develop transfer functions (Gasse et al. , 1997; Jones and Juggins, 1995).

4.2. Mollusks

Mollusk assemblages exhibited a very low diversity. Only two species were represented, which contrasts significantly with the higher diversity usually found in water bodies from adjacent regions, such as the humid Pampa and Mendoza Province, located eastward and westward from the study area, respectively (De Francesco and Hassan, 2009; Tietze and De Francesco, 2010). In the present study, we found a correlation between *B. peregrina* and vegetation cover. It is known that *B. peregrina* develops abundant populations in freshwater vegetated shallow lakes, living attached to macrophytes (Tietze and De Francesco, 2010). Therefore, the presence of this species in the fossil record may be indicative of vegetated freshwater shallow lakes. On the other hand, *H. parchappii* is very widespread in freshwater environments but can also develop and maintain stable populations in brackish waters (De Francesco and Hassan, 2009). It has been recorded at conductivities between 8 and 19 mS/cm and hardness between 598 and 3764 mg/l in lakes from the semiarid region of Mendoza (Ciocco and Scheibler, 2008; De Francesco and Hassan, 2009). Moreover, it is the unique species represented in lakes with conductivity levels higher than 6 mS/cm and hardness higher than 687 mg/l in the southern Humid Pampas (Tietze and De Francesco, 2010). In the present work, *H. parchappii* was only present in sites with very high values of conductivity and hardness. Therefore, the presence of this taxon without any other coexisting species appears to be indicative of very hard and saline waters. The reason why this species is absent from freshwater lakes in the semiarid Pampa remains unknown.

4.3. Paleoenvironmental and paleoclimatic significance

Our results showed that shallow lakes from La Pampa province exhibit a significant variability in hardness and conductivity, which strongly affects the distribution of diatoms and mollusks. Overall, waters are very hard and saline, with scarce vegetation; conditions that pose osmotic restrictions to the establishment of most freshwater organisms. These conditions are driven by evaporative processes, and, consequently, linked to climate. Hence, lakes in the semiarid Pampas have the potentiality to be good archives of the climatic variations occurred during the Quaternary in the region. These climatic variations can be indirectly inferred by reconstructing conductivity and hardness fluctuations on the basis of diatom and mollusk studies. According to the results obtained here it is, thus, expectable that fossil assemblages dominated by the diatoms *P. delicathulum*, *C. meneghiniana* and *A. copulata* and the snail *H. parchappii* would be indicative of high conductivities related to dry climatic conditions. Conversely, assemblages dominated by the diatoms *H. hungarica, H. amphyoxis, N. amphibia*, and the mollusk *B. peregrina* would be indicative of low conductivity conditions associated to wetter climates. Although it is not possible at present to consider the regional or temporal generality of these ideas with the scattered observations presented here, the study of a higher number of lakes would bring support to this preliminary interpretation. Paleoclimatic inferences based on diatoms or mollusks have proven to be successful in similar semiarid and arid regions of the world subjected to strong evaporative forcing (e.g. Abell and Hoelzmann, 2000; Fritz, 2007).

An important paleoecological distinction should be made between the two biological proxies analyzed in the present work. The low environmental resolution provided by mollusks is consequence of the wide ranges of tolerance to hardness and conductivity exhibited by the two species represented here, which represents an adaptation to semiarid environments where these variables fluctuate greatly. This circumstance has also been observed in other snails such as *Melanoides tuberculata*, which occurs abundantly in a wide range of water habitats throughout Asia and Africa, but is the only mollusk present in highly evaporated saline lakes (Pointier et al., 1992). Therefore, while the use of mollusks as paleoenvironmental indicators is valid at a large, regional scale, they have a limited importance as indicators of local conditions within semiarid regions. Instead, local conditions can be accurately assessed through diatom analyses, as they demonstrated to be useful for discriminating between sites with subtle environmental differences. Moreover, the strong statistical relationship between diatoms and climate-driven environmental parameters emphasizes their potential use as quantitative indicators of Quaternary climatic changes in the semiarid Pampas.

5. Conclusion

Diatoms and mollusks are useful indicators of past environmental conditions in shallow lakes from semiarid Central

Argentina, in particular of changes in conductivity and hardness associated to fluctuations in the evaporation/precipitation ratios. As is usual in most semiarid and arid regions of the world (Fritz, 2007), these lakes often provide the best, and maybe the unique, archives of long-term continental climate change. Although their record may be discontinuous, core samples collected from these lakes may serve as reliable proxies to understand how Holocene climate was in this semiarid region, which remains at present as "terra incognita". Hence, modern data presented in this work should be contrasted with fossil assemblages in order to establish the temporal resolution of the paleoclimatic inferences that can be done from the sedimentary record in these lakes. This would be of great importance in order to resolve the paleoclimatic history of this largely unexplored region of South America.

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Appendix. Supplementary data

Supplementary data associated with this article can be found in the online version, at doi:10.1016/j.jaridenv.2011.11.002.

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