

COMPOSITIONAL FIDELITY OF SUBFOSSIL MOLLUSK ASSEMBLAGES IN STREAMS AND LAKES OF THE SOUTHEASTERN PAMPAS, ARGENTINA

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ABSTRACT

The compositional fidelity of dead assemblages—the extent to which subfossil remains reflect the composition, structure, and scale of the original living community—is an indispensable component of studies assessing the quality of the fossil record and the effects of taphonomic biases on species composition and diversity. The aim of the present study is to evaluate (1) how faithfully abundances of subfossil freshwater mollusk shells deposited in dead assemblages correspond to their abundances in the local living assemblages, (2) how reliably diversity of living assemblages is captured by dead assemblages, (3) whether spatial variation in species composition in living assemblages is captured by dead assemblages in the southeastern Pampas, Argentina. Twenty sites corresponding to five lotic and five lentic sites from two geographic areas were analyzed in terms of taxonomic composition and diversity, and homogeneity of multivariate dispersions. We find that (1) living and dead assemblages occupy similar portions of multivariate space and do not significantly differ in composition within an area, (2) living and dead assemblages show similar richness and evenness, and (3) between-environment differences in among-site variation in composition (beta diversity) captured by living assemblages are preserved by dead assemblages. Thus, the results highlight the potential these environments have to enhance the preservation of mollusks and result in fossil assemblages that are suitable for paleoecological and paleoenvironmental studies of freshwater ecosystems.

INTRODUCTION

Compositional fidelity, which focuses on the reliability of species composition, richness, and abundance measures, can be addressed using live-dead assemblage (LD) comparisons. Many of the works conducted in marginal marine environments (estuaries, lagoons, tidal flats, bays) have demonstrated that most taxa with preservable hard parts are represented in the dead assemblage, commonly in correct rank order, and without significant out-of-habitat transportation (Kidwell and Bosence, 1991; Kidwell and Flessa, 1995; Kidwell, 2001, 2002; Lockwood and Chastant, 2006). Marine mollusk dead assemblages (DAs) can also capture environmental gradients in the same way as living assemblages (LAs), despite showing lower spatial and temporal variation in composition between sites (beta diversity) than their counterpart LAs (Tomašových and Kidwell, 2009). In addition, quantitative disagreements between living and dead mollusk assemblages can indicate anthropogenic impacts on ecosystems, providing a useful tool for recognizing strong, recent change in ecological systems (Kidwell, 2007, 2008; Terry, 2010a; Erthal et al., 2011). As seen, compositional fidelity is a powerful tool; however, many methodological and conceptual uncertainties still affect live-dead fidelity studies.

Despite these significant advancements, our understanding of fidelity is still limited because most studies conducted to date have been primarily restricted to marine or estuarine mollusks (Kidwell, 2001, 2002, 2008; Kowalewski et al., 2003; Zuschin and Oliver, 2003;

Lockwood and Chastant, 2006; Olszewski and Kidwell, 2007), corals (Pandolfi and Minchin, 1996; Pandolfi and Greenstein, 1997; Pandolfi and Jackson, 2001; Pandolfi, 2001; Edinger et al., 2001), brachiopods (Carroll et al., 2003; Kowalewski et al., 2003; Tomašových, 2004; Krause et al., 2010), and mammals (Behrensmeier and Chapman, 1993; Davis, 2005; Terry, 2010a, 2010b; Miller, 2011). Recently, compositional fidelity of dead terrestrial mollusks was also evaluated (Yanes et al., 2008, 2011). The predictive ability of modern land mollusk assemblages to estimate local environmental factors based on their species composition highlighted their potential to draw inferences about paleoenvironmental gradients on the basis of dead assemblages (Horsák, 2011). Freshwater systems have also received little attention, having at present limited knowledge regarding even the most basic questions on fossilization processes and preservation of shelly organisms. Some preliminary studies conducted on freshwater mollusks demonstrated that the live-dead agreement can be high (Cummins, 1994; Martello et al., 2006) or low (Briggs et al., 1990), depending on the type of organism and the environment setting studied. For instance, Cummins (1994) focused solely on unionid bivalves from streams and reservoirs of east-central Ohio, United States, while Briggs et al. (1990) and Martello et al. (2006) analyzed the whole malacofauna (bivalves + gastropods) occupying lotic fluvial systems from Austria and Brazil, respectively. Consequently, the taphonomic knowledge on freshwater environments is presently biased toward particular habitats and taxa, and lacks information on how fidelity in composition and diversity varies between lotic and lentic environments.

The present study evaluates the fidelity of subfossil mollusk shells in lotic and lentic freshwater environments in the southeastern Pampas, Argentina. In particular, the present contribution aims to evaluate: (1) how faithfully abundances of subfossil freshwater mollusk shells deposited in dead assemblages correspond to their abundances in the local living assemblages, (2) how reliably diversity of living assemblages is captured by dead assemblages, (3) whether spatial among-site variation in species composition, measured by dispersion in multivariate space, is captured by dead assemblages.

MATERIAL AND METHODS

Data

The Pampas are a vast grassy plain that covers central Argentina, characterized by a quite uniform relief except for the existence of two ranges of low mountains (Tandilia and Ventania) situated toward the southeast. Overall, the climate is temperate humid or subhumid with a mean annual temperature of 15 °C and a mean annual precipitation of 1100 mm (Feijoó and Lombardo, 2007). Due to the gentle slope of the region, the Pampas plains are characterized by numerous permanent and temporary shallow lakes, called *lagunas pampeanas*, which are very shallow (2 m) and lack thermal stratification except for short periods of time (Quirós and Drago, 1999). Running waters are represented by streams that originate in the southern mountains and have slow current velocity (between 6 and 25 cm s⁻¹). Streambeds are characterized by having hard and homogeneous substrata with fine sediments (primarily

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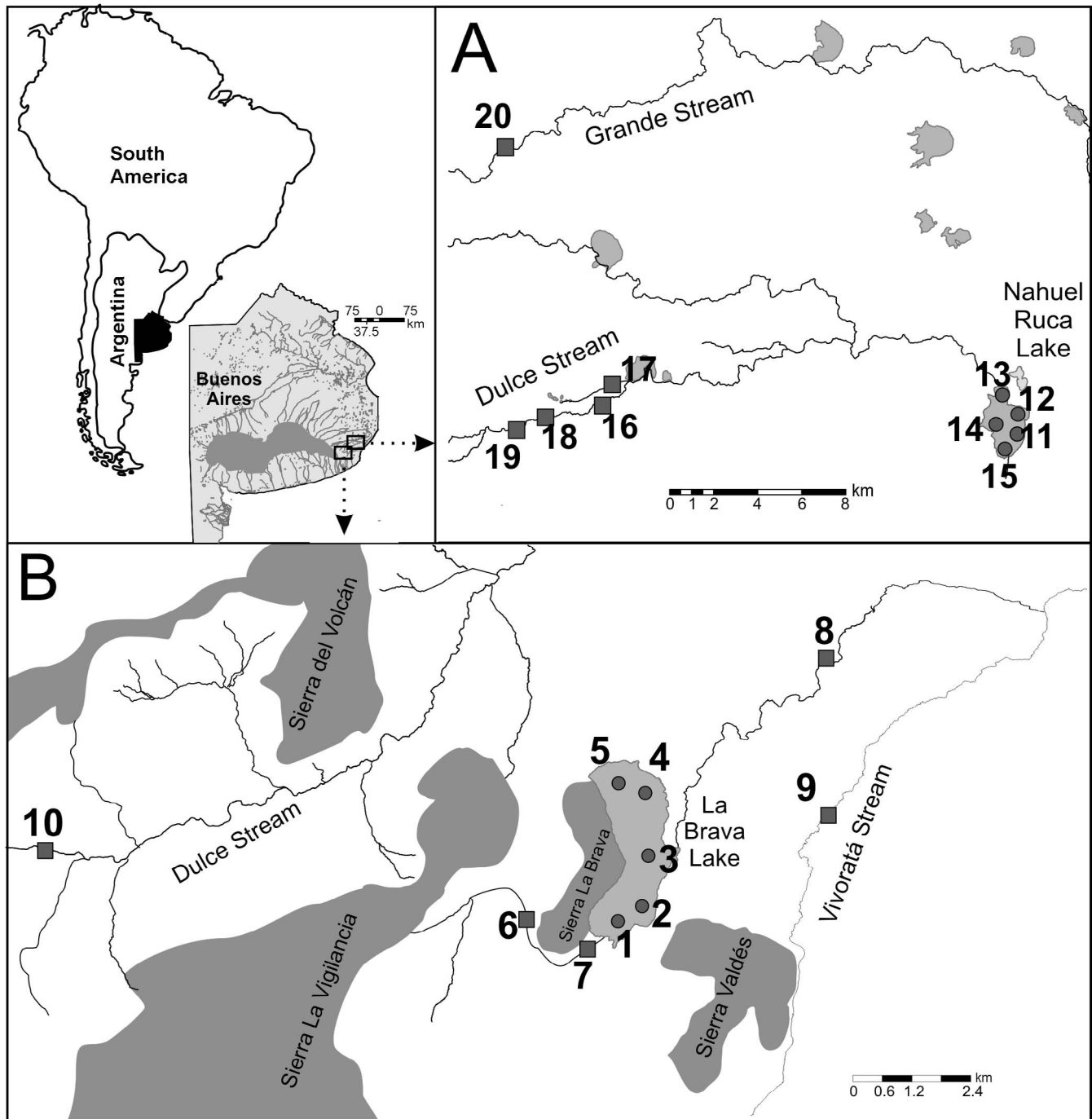


FIGURE 1—Location of the study area. A) Nahuel Rucá (NR) B) La Brava (LB). Circles and squares represent lentic sites and lotic sites respectively.

silt and clay) and high calcium content that forms superficial tufa layers (Feijoó and Lombardo, 2007).

Two areas separated by a distance of approximately 55 km (Fig. 1) were chosen for the study. One area, La Brava (LB) is located close to the Tandilia mountain, where most streams originate, while the other, Nahuel Rucá (NR), is situated close to where these streams debouch into the sea. Because of the general homogeneity of the Argentinean Pampas, environments (streams and lakes) display similar physico-chemical characteristics, with only subtle differences related to their relative position along the course. In fact, in both areas (LB and NR) the two environments (streams and lakes) are small and shallow, with low conductivities (between 0.3 and 5 mS/cm) and alkaline waters (pH = 8–10). The transparency is rather variable (mainly in lakes) with turbid and clear periods varying from year to year (González Sagrario

et al., 2009). However, most of the time it is predominantly turbid (Secchi disk transparency ranging from 10 to 40). Sediments are dominated by mud (44%–63%) and very fine sand (21%–43%) (for more information see Tietze and De Francesco, 2010). The two areas are subjected to distinct land use. LB is located in an agricultural area whereas NR is placed in a dominantly cattle-raising zone (although in recent times some agricultural activities have also initiated here). Consequently, the former is a little bit more impacted with possible implications for mollusk distributions.

In each area (i.e., microbasins), 10 sites (5 lentic sites and 5 lotic sites) were sampled in each area seasonally during 2008. At each site, living and dead mollusks from the littoral zone were collected both manually (picking up by hand) and with the aid of sieves (0.5 mm mesh size), using quadrats with sampling area of 5 m² and a penetration depth of

TABLE 1—Total number of specimens (n) of living assemblages.

Mollusk species	LB lentic sites					LB lotic sites					NR lentic sites					NR lotic sites				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Heleobia parchappii</i>	405	1222	28	40	74	19	36	3	60	98	60	32	251	219	348	154	173	279	540	92
<i>Biomphalaria peregriana</i>	14	10	31	2	10	35	1	0	1	0	50	16	9	8	34	16	14	29	18	3
<i>Musculium argentinum</i>	0	0	0	0	0	50	136	1	4	55	15	16	10	24	2	4	33	14	5	38
<i>Physa acuta</i>	0	0	2	0	0	0	0	0	0	0	8	5	4	6	29	2	0	2	0	13
<i>Stenophysa marmorata</i>	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Chilina parchappii</i>	0	0	0	0	0	0	0	0	0	26	0	0	0	0	0	11	33	79	83	105
<i>Uncancylus concentricus</i>	7	4	2	8	2	0	124	11	0	2	2	1	1	16	10	11	2	1	3	16
<i>Pomacea canaliculata</i>	1	0	0	0	0	0	4	0	0	0	2	1	3	1	1	1	0	1	0	4
<i>Succinea meridionalis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	1	0	0
<i>Antillorbis nordestensis</i>	0	0	0	0	0	0	0	0	0	0	30	5	0	5	1	0	0	0	0	0
<i>Omalonyx</i> sp.	1	0	0	0	0	0	0	0	0	0	2	2	0	0	1	0	0	0	0	0
Total (n)	428	1236	65	50	86	104	302	15	65	181	169	78	278	279	426	199	263	405	650	271

approximately 5 cm. According to Cummins (1994) and Martello et al. (2006), this sampling area is adequate to the low abundance of mollusks in freshwater habitats. Living mollusks were searched for among the submerged vegetation, under stones, and on the substratum. Dead specimens were sampled only on the substratum. Sampling was standardized by time of effort (number of snails caught per hour) following Martín et al. (2001), and conducted by the same person to avoid sampling bias. Live-collected specimens and shells or shell fragments representing dead specimens were transported to the laboratory and identified to species, whenever possible, and counted. For bivalves, each disarticulated valve was classified as left or right. The total number of bivalves per sample

corresponded to that of the most abundant valve. Shell fragments were taken into account when identification was possible. Mollusk identification was based on de Castellanos and Fernández (1976), Gaillard and de Castellanos (1976), de Castellanos and Gaillard (1981), Fernández (1981a, 1981b), Rumi (1991), and de Castellanos and Landoni (1995).

Mollusk Ecology

The freshwater malacofauna of the Pampean Region has low taxonomic diversity, i.e., it is characterized by small numbers of families (6), genera (12), and species (23). *Heleobia parchappii* is

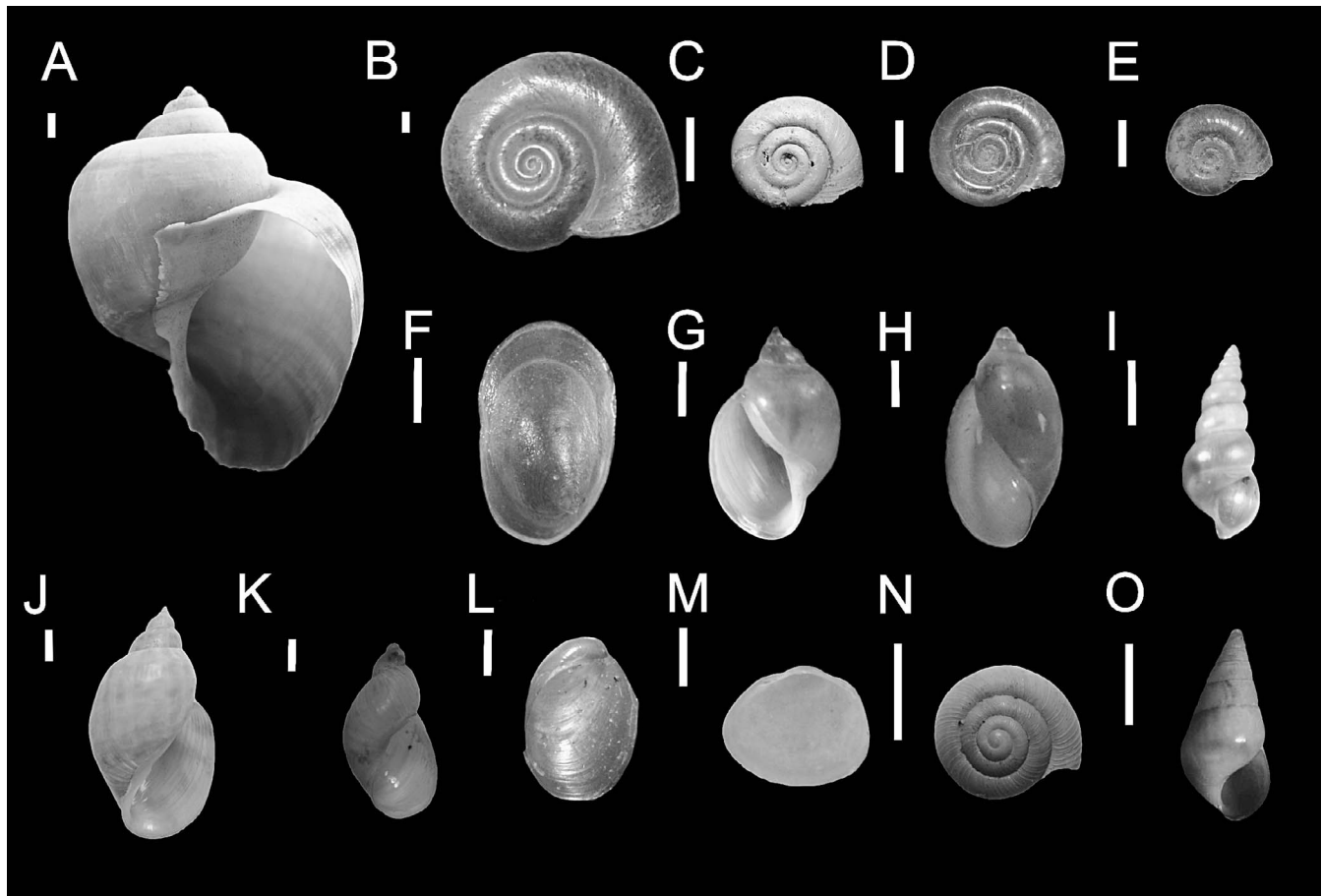


FIGURE 2—Mollusks found in living and dead assemblages. A) *Pomacea canaliculata* (DA), B) *Biomphalaria peregriana* (LA), C) *Drepanotrema lucidum* (DA), D) *D. heloicum* (DA), E) *Antillorbis nordestensis* (DA), F) *Uncancylus concentricus* (LA), G) *Physa acuta* (DA), H) *Stenophysa marmorata* (DA), I) *Heleobia parchappii* (LA), J) *Chilina parchappii* (LA), K) *Succinea meridionalis* (DA), L) *Omalonyx* sp. (LA), M) *Musculium argentinum* (DA), N) Charopidae (DA), O) *Heleobia australis* (DA). Scale bar 2 mm.

TABLE 2—Richness (=S), Shannon-Weiner (=H'), and Simpson (=1-D) indices of living and dead assemblages of LB and NR based on nonrarefied and rarefied samples.

Samples	La Brava						Nahuel Rucá							
	Nonrarefied samples			Rarefied samples			Nonrarefied samples			Rarefied samples				
	S	H'	1-D	S	H'	1-D	S	H'	1-D	S	H'	1-D		
LAs	Lentic	1	5	0.26	0.10	2	0.08	0.03	8	1.55	0.74	5	1.43	0.73
		2	3	0.07	0.02	2	0.08	0.03	8	1.57	0.74	8	1.59	0.74
		3	5	1.04	0.58	5	1.06	0.59	6	0.45	0.18	4	0.43	0.19
		4	3	0.60	0.33	-	-	-	7	0.84	0.37	5	0.82	0.39
		5	3	0.46	0.25	3	0.47	0.24	8	0.70	0.32	4	0.63	0.32
	Lotic	6	3	1.03	0.62	3	0.97	0.59	7	0.87	0.39	6	1.07	0.50
		7	6	1.07	0.61	4	1.08	0.61	6	1.09	0.53	5	0.97	0.48
		8	3	0.73	0.42	-	-	-	7	0.93	0.48	3	0.70	0.40
		9	3	0.31	0.14	3	0.33	0.15	6	0.58	0.29	4	0.67	0.36
		10	4	1.02	0.59	3	0.99	0.60	7	1.43	0.71	6	1.34	0.69
DAs	Lentic	1	6	0.51	0.26	2	0.42	0.25	9	1.56	0.75	7	1.56	0.76
		2	5	0.48	0.26	3	0.53	0.30	8	1.28	0.59	8	1.28	0.60
		3	4	0.71	0.48	2	0.60	0.40	8	1.42	0.71	5	1.23	0.69
		4	5	0.54	0.26	4	0.64	0.32	6	1.39	0.68	6	1.36	0.67
		5	4	0.63	0.35	4	0.72	0.40	8	1.54	0.73	8	1.57	0.74
	Lotic	6	5	0.93	0.50	4	0.79	0.42	9	0.65	0.26	3	0.47	0.24
		7	5	0.99	0.53	4	1.00	0.54	11	1.21	0.51	9	1.24	0.52
		8	4	0.87	0.49	3	0.71	0.40	8	1.19	0.53	7	1.24	0.55
		9	10	1.23	0.58	6	1.04	0.51	9	1.25	0.56	6	1.17	0.55
		10	7	1.10	0.57	6	1.02	0.54	8	0.56	0.23	4	0.31	0.13

frequently the dominant species, living in waters with conductivity values ranging between 0.46 and 35 mS/cm associated to submerged vegetation, pebbles, or mud (De Francesco and Isla, 2004; Tietze and De Francesco, 2010). This species, and the rest of the species present in the region, are found in both lotic and lentic environments. The only exception is *Chilina parchappii* that occurs only in streams with hard substrata (Tietze and De Francesco, 2010). The planorbids *Drepanotrema heloicum*, *D. lucidum*, *Biomphalaria peregrina*, and *Antillorbis nordestensis*, together with the apple snail *Pomacea canaliculata*, and the physids *Stenophysa marmorata* and *Physa acuta* prefer vegetated microhabitats located in shallow parts of water bodies as well as in streams with stagnant waters (Tietze and De Francesco, 2010; Tietze et al., 2011). The limpet *Uncancylus concentricus* prefers clear waters and is usually found in habitats with hard substrata (macrophytes, boulders, artificial substrates) (Tietze et al., 2011). *Succinea meridionalis* is a terrestrial gastropod that is associated with aquatic environments (Landoni, 1992). In this study *S. meridionalis* is associated with emergent macrophytes, and commonly occurs in fossil freshwater assemblages in this region. *Omalonyx* sp. lives on macrophytes and adjacent vegetation in swamps, marshes and floodplains (Arruda and Thomé, 2008).

Musculium argentinum is an infaunal bivalve that lives buried within the first few centimeters below the sediment–water interface (Peredo et al., 2009). *Heleobia australis* and Charopidae sp. are allochthonous species that belong to estuarine and land environments.

Analysis of Fidelity of Diversity within Sites and within Areas

In order to evaluate fidelity of diversity and composition (i.e., presence/absence of species and proportional abundances) between living (LAs) and dead assemblages (DAs), the following measures were extracted from absolute counts at each sampling site: (1) total number of shells (n) per site, (2) relative abundance of species, (3) richness (S), and (4) two alpha-diversity indices: Shannon-Wiener index (H'; Magurran, 1988) and Simpson index (1-D; Simpson, 1949). Samples were standardized to the same sample size n (n = 60) by rarefaction, i.e., random resampling of n individuals drawn without replacement from all individuals present in the assemblages (Hurlbert, 1971; Heck et al., 1975), in order to avoid sample size effects. Diversity indices and rarefaction were performed using Vegan package (Oksanen et al., 2011) in R.

TABLE 3—Total number of specimens (n) of dead assemblages.

Mollusk species	LB lentic sites					LB lotic sites					NR lentic sites					NR lotic sites				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Heleobia parchappii</i>	559	904	408	459	141	73	61	101	625	451	38	1	33	38	28	410	309	190	313	1627
<i>Biomphalaria peregrina</i>	86	146	237	30	32	303	10	17	245	17	37	36	45	19	27	7	5	23	53	13
<i>Musculium argentinum</i>	2	0	0	3	2	68	198	1	29	40	2	12	1	4	1	18	44	25	38	55
<i>Physa acuta</i>	1	0	0	0	0	0	0	0	17	29	7	1	3	2	7	0	16	5	4	17
<i>Stenophysa marmorata</i>	0	0	0	0	0	0	0	0	0	0	1	0	2	0	3	0	1	0	0	0
<i>Chilina parchappii</i>	0	2	0	0	0	2	0	0	61	239	0	0	0	0	0	27	34	22	32	120
<i>Uncancylus concentricus</i>	8	12	6	45	4	7	37	31	31	10	34	4	43	9	11	7	5	12	43	18
<i>Pomacea canaliculata</i>	3	2	1	0	0	0	0	0	17	0	0	2	1	0	1	1	15	5	6	5
<i>Drepanotrema heloicum</i>	0	0	0	0	0	0	0	0	7	0	1	0	0	0	0	4	3	2	1	7
<i>Drepanotrema lucidum</i>	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	4	7	0	0	0
Charopidae	6	1	0	0	1	0	0	0	2	2	0	0	0	0	0	0	0	0	0	5
<i>Succinea meridionalis</i>	0	0	0	0	0	0	0	0	10	1	0	0	0	0	0	1	11	0	3	0
<i>Heleobia australis</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0
<i>Antillorbis nordestensis</i>	0	0	0	0	0	0	0	0	0	0	6	3	5	6	2	0	0	0	0	0
<i>Omalonyx</i> sp.	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Total (n)	665	1067	652	538	180	453	307	150	1046	789	127	60	133	78	80	479	450	284	494	1867

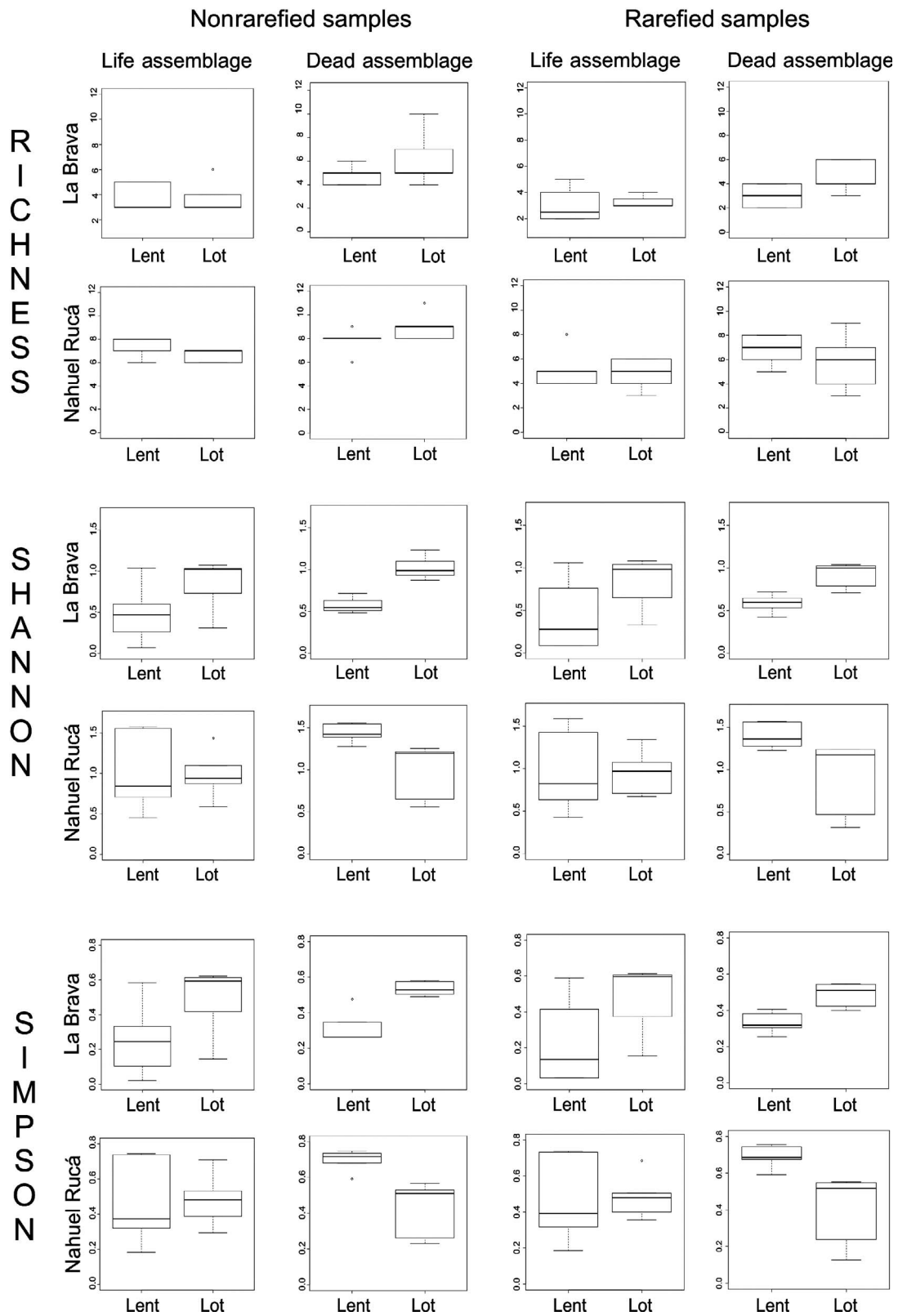


FIGURE 3—Box-plot of richness, Shannon-Wiener and Simpson indices comparing lotic and lentic environments in LAs and DAs of LB and NR.

Differences in diversity between LAs and DAs at area scale (i.e., sites within areas were pooled) were evaluated with two-sample permutation tests through Monte Carlo calculation using permTS function in Perm package (Fay and Shaw, 2010) in rarefied and nonrarefied samples. This function performs two-sample permutation tests wherein the null hypothesis states that there is no difference between means of diversity

in LAs and DAs. An increase in time-averaging of DAs is generally associated with an increase in sample size, assuming some positive rate of shell preservation. Therefore, size standardization also partly reduces the effects of time-averaging that can be expected to increase the diversity of DAs. We thus report results of analyses based on both raw (nonstandardized) data and sample size-standardized data.

TABLE 4—Monte Carlo calculation mean differences and associated *p*-values comparing LAs and DAs assemblages and lotic and lentic environments of LB and NR. Significant values are in boldface.

Comparisons	Nonrarefied samples						Rarefied samples (n = 60)						
	S		H'		I-D		S		H'		I-D		
	Dif mean	<i>p</i> -value	Dif mean	<i>p</i> -value	Dif mean	<i>p</i> -value	Dif mean	<i>p</i> -value	Dif mean	<i>p</i> -value	Dif mean	<i>p</i> -value	
LAs vs. DAs	LB	1.500	0.050	0.144	0.360	0.063	0.476	0.675	0.342	0.113	0.428	0.052	0.548
	NR	1.400	0.024	0.200	0.230	0.081	0.318	1.300	0.140	0.177	0.328	0.064	0.446
Lotic vs. lentic	LAs LB	0.000	1.000	-0.346	0.152	-0.221	0.134	-0.250	1.000	-0.420	0.238	-0.268	0.176
	DAs LB	-1.400	0.354	-0.449	0.010	-0.214	0.010	-1.600	0.128	-0.328	0.014	-0.151	0.020
	LAs NR	0.800	0.248	0.040	0.922	-0.009	0.946	0.400	0.874	0.027	0.964	-0.012	0.918
	DAs NR	-1.200	0.294	0.464	0.010	0.274	0.010	1.000	0.504	0.513	0.034	0.294	0.010

Analysis of Fidelity of Environmental Differences in Diversity

Differences in diversity between lotic and lentic environments (separately for LB and NR) were also compared with two-sample permutation tests through Monte Carlo calculation in rarefied and non-rarefied samples. The permutation test was performed using Perm package (Fay and Shaw, 2010) in R.

Analysis of Fidelity in Abundances and Presence/Absence at Site Scale

The Sørensen index of similarity was used to quantify compositional similarity on the basis of presence/absence between LAs and DAs at site scale, according to the formula: $S = 2C/(A + B)$, where S = index of similarity, A = number of species in one assemblage, B = number of species in the other assemblage, and C = number of species common to both assemblages. This index ranges from a value of 0 where there is no species overlap between living and dead assemblages, to a value of 1 when exactly the same species are found in both assemblages (Odum, 1971).

Proportional abundances between pairs of LAs (x-axis) and DAs (y-axis) were compared in bivariate plots. They are presented separately for lotic and lentic environments from LB and NR.

TABLE 5—Sørensen indices show that compositional fidelity at site scale is higher in the NR area than in the LB area. The values as LB lent or LB lot are indices based on one single comparison based on data pooled from five sites.

Sites	Sørensen index
1	0.73
2	0.50
3	0.67
4	0.75
5	0.86
LB lent	0.67
6	0.75
7	0.80
8	0.86
9	0.46
10	0.73
LB lot	0.71
11	0.82
12	1.00
13	0.86
14	0.92
15	0.87
NR lent	0.89
16	0.75
17	0.71
18	0.93
19	0.80
20	0.93
NR lot	0.84

Analysis of Fidelity in Abundance and Presence/Absence at Area Scale

The Sørensen index of similarity was also used to quantify the fidelity in presence/absence at area scale between LAs and DAs, as described above.

The use of multivariate-based analyses on dissimilarities among samples and their centroid is the preferred way to test between-group (here, live-dead) differences in multivariate dispersions in order to compare habitat- or regional-scale compositions that are autocorrelated rather than fully independent (Anderson, 2006; Tomašových and Kidwell, 2009). We used a modified analysis of homogeneity in multivariate dispersions (HMD) following Tomašových and Kidwell (2011), which is appropriate for the autocorrelated samples that characterize most LD studies, i.e., individuals occurring in LAs are partly descendants of individuals preserved in DAs. This approach differentiates between the effects of premortem and postmortem processes on time-averaged assemblages. Two dissimilarity measurements were used: (1) Jaccard dissimilarity, based on presence/absence data, reflects the probability that two randomly chosen species from two assemblages do not belong to any of the species shared by the two assemblages, and (2) Horn-Morisita dissimilarity, based on untransformed proportional species abundances, reflects the probability that two randomly drawn individuals from two assemblages do not belong to the same species.

The total species composition based on multiple assemblages inhabiting one environment or one region, using a full Euclidean multivariate space defined by principal coordinates, can be separated into two parts: the centroid location of assemblages (mean assemblage composition) and the dispersion of assemblages around their centroid location (Anderson, 2006; Anderson et al., 2006). In the modified approach, total LD variation is expressed as the average distance among individual DAs and the centroid of LAs, because the centroid of LAs define the mean composition of living assemblages that represents a baseline against which DAs are compared. The premortem variation, due to biological and sampling variation, is estimated as the average compositional distance of spatially replicate LAs from their centroid. The postmortem variation unexplained by variation among LAs, is expressed as the average distance between LAs and their centroid (i.e., premortem variation) subtracted from the average distance among DAs and the centroid of LAs. The average distance among DAs and the centroid of LAs thus measures over- or underdispersion of DAs relative to the composition of LAs. Underdispersion of DAs corresponds to a loss of variation compared with that of LAs, but DAs are still embedded within the multivariate space defined by those LAs. Overdispersion of DAs signifies that DAs occupy portions of multivariate space outside those occupied by LAs.

The F-statistic for the HMD is

$$F = (SS_A / (n - 1)) / (SS_W / (N - p))$$

Where: SS_A = among-group sum of squared distances (refers to the sum of squared deviations between the grand distance (i.e., among all assemblages and the centroid of LAs) and the average group distances

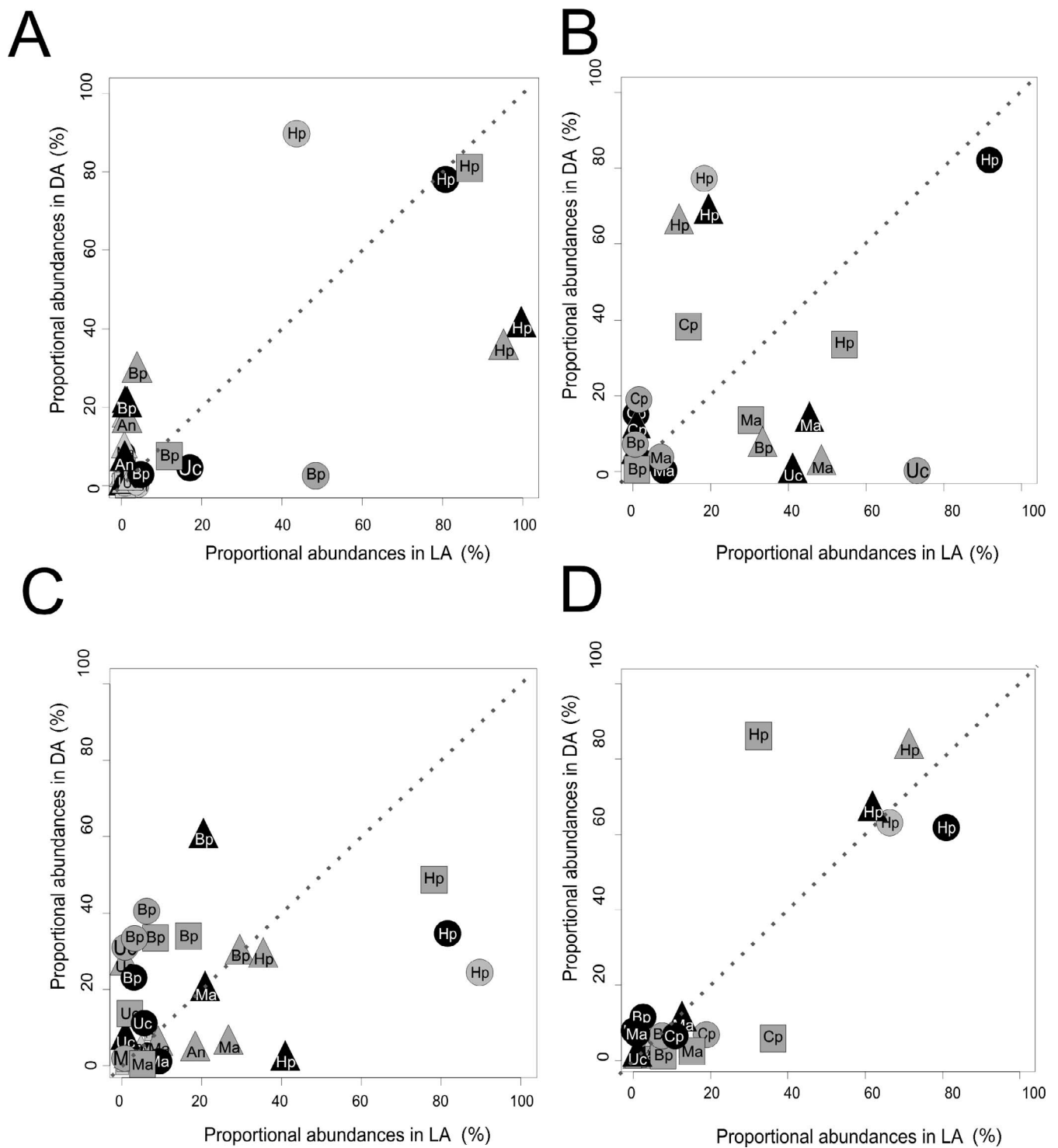


FIGURE 4—Bivariate plots of species proportional abundances of LAs (x-axes) and of DAs (y-axes). The gray triangle, black triangle, gray circle, dark circle and gray square represents in **A**) LB lentic: sites 1 to 5, **B**) LB lotic: sites 6 to 10, **C**) NR lentic: sites 11 to 15 and **D**) NR lotic: sites 16 to 20 respectively. The letters represent: Hp = *Heleobia parchappii*, Bp = *Biomphalaria peregrina*, Ma = *Musculium argentinum*, Cp = *Chilina parchappii*, An = *Antillorhis nordestensis*, Sm = *Stenophysa marmorata*, Pc = *Pomacea canaliculata*, O = *Omalonyx* sp., S = *Succinea meridionalis*, Pa = *Physa acuta*, Dh = *Drepanotrema heloicum*, Dl = *D. lucidum*.

of LAs (i.e., among LAs and their centroid) and DAs (i.e., among DAs and the centroid of LAs) and SS_w = within-group sum of squared distances (refers to the sum of squared distances between individual DAs and LAs and their average group distance from the LA centroid). The HDM approach developed by Tomašových and Kidwell (2011) was implemented using the statistical programming environment R, version 2.14.0 (R Development Core Team, 2009).

Analysis of Fidelity of Environmental Differences in Among-Site Variation in Composition

To test whether dispersion among living assemblages within environments (i.e., average dissimilarity between the environment centroid and assemblages—a measure of beta diversity) is preserved among DAs, separately for LB and NR, we used a test for homogeneity

TABLE 6—Results showing: ratio (premortem variation/total LD variation), the estimates of premortem and postmortem variation, the significance values of modified test of multivariate dispersions, which indicates whether variation among DAs and the centroid of LAs is larger (overdispersion) or smaller (underdispersion) than variation among LAs and their centroid. NS = not significant at $\alpha = 0.05$.

HMD results	La Brava		Nahuel Rucá	
	Jaccard	Horn-Morisita	Jaccard	Horn-Morisita
Ratio (premortem variation/total LD variation)	0.84	1.37	0.56	0.23
Premortem variation	0.55	0.31	0.41	0.13
Postmortem variation (total LD variation: premortem variation)	0.05	-0.05	0.13	0.11
Test of homogeneity in dispersions: <i>p</i> -value	0.17	0.48	0.06	0.15
LD change in composition	NS	NS	NS	NS

of multivariate dispersions. Dispersions are represented by distances of samples to their environment centroid (i.e., centroid of lentic and lotic sites) in multivariate space (Anderson et al., 2006). The principal coordinate analysis (PCoA) of a dissimilarity matrix (based on Horn-Morisita Index) that places the multivariate observations into a Euclidean space defined by PCoA axes that completely preserves the original between-sample dissimilarities (Anderson, 2006). This test is equivalent to the univariate Levene's test for homogeneity of variance. A *p*-value is obtained by computing the number of permuted *F*-values that do not exceed the observed *F*-value. We used 999 permutations. This analysis was performed using betadisper function in Vegan package (Oksanen et al., 2011) in R.

RESULTS

Overall Composition of Living Assemblages

A total of 5550 individuals belonging to 11 molluscan species were recorded in the LAs (Table 1). The bivalve fauna was represented by 407 individuals of *Musculium argentinum*, while the remaining individuals ($n = 5143$) corresponded to the gastropods *Heleobia parchappii*, *Pomacea canaliculata*, *Chilina parchappii*, *Biomphalaria peregrina*, *Antillorbis nordestensis*, *Uncancylus concentricus*, *Stenophysa marmorata*, *Physa acuta*, *Succinea meridionalis*, and *Omalonyx* sp. (Fig. 2). Most of the sites were dominated by *H. parchappii*. The richness per site varied between 3 and 8 in nonrarefied samples and between 2 and 8 in rarefied samples (Table 2).

Overall Composition of Dead Assemblages

A total of 9899 individuals belonging to 15 molluscan species were recorded in the DAs (Table 3). Similarly to LAs, the bivalve fauna was represented by 543 individuals of *Musculium argentinum* (no significant difference was found between the proportion of left and right valves), and the rest of the individuals ($n = 9356$) were represented by gastropods assigned to *Heleobia parchappii*, *H. australis*, *Pomacea canaliculata*, *Chilina parchappii*, *Biomphalaria peregrina*, *Drepanotrema heloicum*, *Drepanotrema lucidum*, *Antillorbis nordestensis*, *Uncancylus concentricus*, *Stenophysa marmorata*, *Physa acuta*, *Succinea meridionalis*, *Omalonyx* sp., and a terrestrial species of the family Charopidae (Fig. 2). *Heleobia australis* and Charopidae sp. were thus excluded from all analyses because they are allochthonous species in freshwater habitats. Most sites were also dominated by *H. parchappii*. The richness per site was higher than in LAs varying between 4 and 11 in nonrarefied samples and between 2 and 9 in rarefied samples (Table 2, Fig. 3). Similarly, the total abundance per site was higher in DAs than in LAs, with the only exception of NR lentic sites that presented the opposite pattern.

Fidelity of Diversity within Sites and within Areas

When richness, Shannon-Wiener, and Simpson indices were compared between LAs and DAs, significant differences were only found in

richness (*S*) in nonrarefied samples (mean difference = 1.5 and 1.4; *p*-values = 0.05 and 0.02, in LB and NR respectively, Fig. 3). However, this difference was not significant in rarefied samples (Table 4).

Fidelity of Environmental Differences in Diversity

Diversity indices were significantly different between lotic and lentic environments in DAs, separately in LB and NR (differences in Shannon-Wiener and Simpson indices with *p*-values < 0.05 in nonrarefied and rarefied samples) but no significant differences were found between environments in LAs (Table 4, Fig. 3). Lentic environments were more diverse (higher values of Shannon-Wiener and Simpson indices), and significant differences were found in nonrarefied and rarefied samples with one exception (NR rarefied samples, where the lentic environment presented higher values of the indices) (Table 4, Fig. 3).

Fidelity in Abundance and Presence/Absence at Site Scale.—All sites exhibited a relatively high fidelity in species presence/absence (Sørensen indices between 0.46 and 1) (Table 5). When proportional abundances of species in the LAs are plotted against proportional abundances of the same species in the DAs, considerable scatter is evident at site scales (Fig. 4). Most of the points fall near the 0 and some points fall on the line where abundances in LAs and DAs are equal for all species. The species that have abundances higher than 20% are commonly *Heleobia parchappii*, and occasionally *Biomphalaria peregrina*, *Musculium argentinum*, *Chilina parchappii*, and *Uncancylus concentricus*, the remaining species have lower abundances (<20%).

Fidelity in Abundance and Presence/Absence at Area Scale

The presence/absence fidelity (Sørensen index) was similar in lotic and lentic environments but differed between the two study areas. NR presented higher Sørensen indices (0.76–0.88) than LB (0.60) (Table 5).

The HMD test indicated that total LD variation was not significantly larger than premortem variation in both areas, demonstrating that DAs occupy the same portions of multivariate space and thus have the same composition as LAs (*p*-values of LB = 0.17, 0.48; *p*-values of NR = 0.06, 0.15; on the basis of Jaccard and Horn-Morisita respectively, Table 6). The total LD variation values were higher when Jaccard index was used (Total LD variation = 0.60, 0.54, in LB and NR respectively, Table 6) compared with the values obtained using Horn-Morisita index (Total LD variation = 0.26, 0.24, in LB and NR respectively, Table 6). Despite this difference, the total LD variation was similar in both areas when the results obtained with each index were compared. Nahuel Rucá presented lower ratios of LD variation explained by premortem variation (0.56 and 0.23 based on Jaccard index and Horn-Morisita respectively) compared with LB (0.84 and 1.37 based on Jaccard index and Horn-Morisita respectively) (Fig. 5). Bivariate plots (Fig. 6) shows that the sites fall along the expected line of correlation for good agreement, or in a band slightly above that line as expected from within-habitat time-averaging (modeled with neutral community dynamic) in both LB and NR (Tomašových and Kidwell, 2011). Most of the sites that do not fall in this expected line, fall into the lower portion of the plots, i.e., are

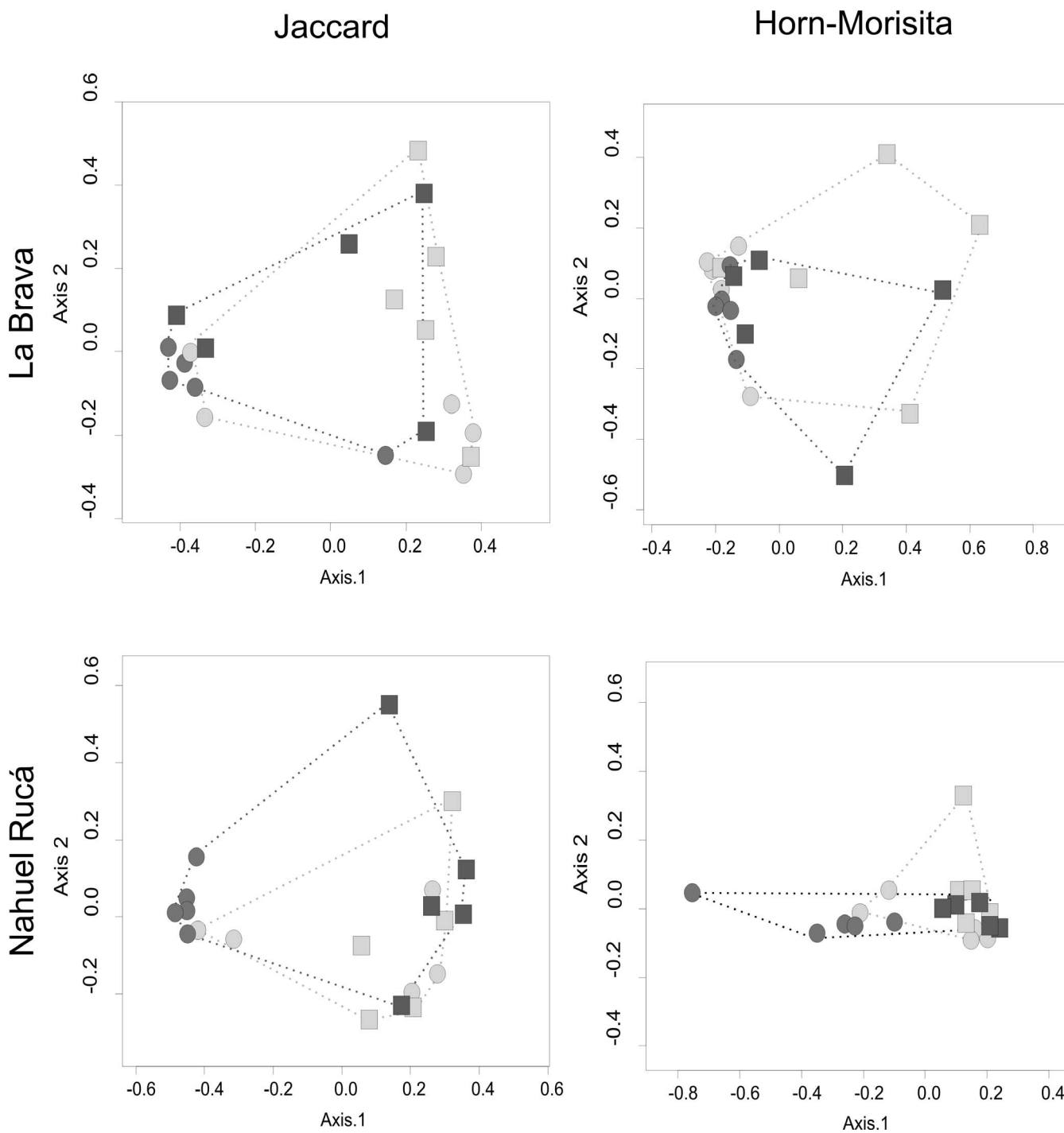


FIGURE 5—Multivariate space visualized by the two principal coordinates analysis (PCoA, axes 1–2) of LB and NR based on Jaccard and Horn-Morisita dissimilarities. Circles are lentic sites, squares lotic ones. LAs are in light gray and DAs in dark gray.

underdispersed because the variation among DAs and centroid of LAs is smaller than variation among LAs (but no significant underdispersion was found). This shows that LD differences can be explained entirely by within-habitat time-averaging, not being affected significantly by postmortem bias and/or between-habitat time-averaging.

Fidelity of Environmental Differences in Among-Site Variation in Composition

The test for homogeneity of multivariate dispersions found that in LB area, lotic and lentic environments differ in dispersion, i.e., lentic sites are

clearly much more similar to each other in La Brava than lotic sites (based on Fig. 7) in LAs (F-value = 7.08; $p = 0.02$, Table 7) and in DAs (F-value = 7.79; $p = 0.04$, Table 7) (Fig. 7). In contrast, in the Nahuel Rucá area, lentic and lotic environments have comparable among-site variation in species composition both in LAs and DAs. Lentic living communities had higher abundances of *Heleobia parchappii*, *Biomphalaria peregrina*, and *Physa acuta* while lotic communities had higher abundances of *Musculium argentinum* and *Chilina parchappii*. In DAs *Biomphalaria peregrina* and *Uncancylus concentricus* were more abundant in lentic sites while *Heleobia parchappii*, *Musculium argentinum*, and *Chilina parchappii* were more abundant in lotic ones.

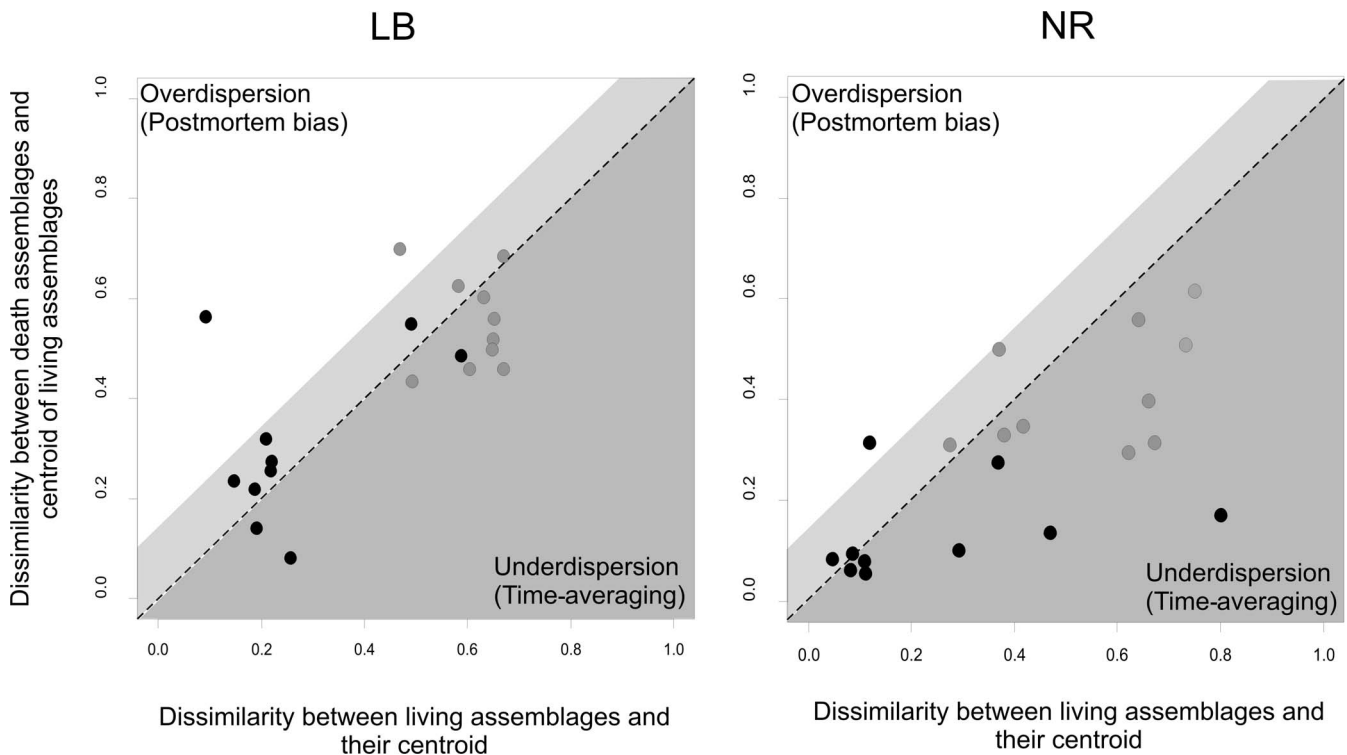


FIGURE 6—Relationship between premortem variation among LAs (x-axis) and total live-dead (LD) variation (y-axis) when using either Jaccard (gray circles) or Horn-Morisita (dark circles) dissimilarity.

DISCUSSION

The mollusk assemblages recorded in the present study were relatively similar in species composition at all sites, with a clear dominance of gastropods (bivalve/gastropod relationship = 1/12). Spatial autocorrelation is an inevitability of the natural world, making ecological variables more similar the nearer they are measured along spatial gradients (spatial autocorrelation; Legendre, 1993); species composition is not an exception (Jiménez-Valcerde et al., 2009).

However, even when presence/absence data can show that most species are widespread, we find that individual assemblages markedly differ in species abundances. Most species present in the Pampean region display a wide range of ecological tolerance, i.e., most species are found in different kinds of water bodies (low beta diversity), but subtle differences in specific microhabitats (which occur in different water bodies as well) can be reliably recognized from the presence of some species (Tietze and De Francesco, 2010). Therefore, one can argue that high live-dead correspondence can be expected in communities with generalistic species because spatial mixing can have negligible effects if most species have broad ranges. Nevertheless, fidelity studies are still necessary in systems with low beta diversity because we can expect that taphonomic processes can affect composition of DAs. For example, DAs can be affected by the origins of the water bodies, time-averaging, or differential species preservation.

The higher abundance of shells in DAs than in LAs generally implies the accumulation of multiple generations of mollusks (time-averaging) in surface sediments, which is in agreement with previous studies (see Briggs et al., 1990; Cummins, 1994 for freshwater environments; Kidwell and Bosence, 1991; Kidwell and Flessa, 1995; Best and Kidwell, 2000; Kowalewski et al., 2003 for marine environments). In fact, DAs are usually time-averaged; with their magnitude varying in relation to the influence of intrinsic factors (abundance and durability of the original population) and extrinsic environmental (physical, chemical, and biological) processes operating over a wide range of scales (Kidwell and Flessa, 1995; Kowalewski, 1996; Behrensmeier et al., 2000). The exception to this general pattern was found in the Touro Passo River, in

South Brazilian Pampas (Martello et al., 2006). There, the slightly acidic pH (6–8) determined the rapid destruction of dead shells, diminishing the abundance in DAs (Kotzian and Simões, 2006). In the present study NR Lake also showed lower abundances in DAs than in LAs. However, the pH is alkaline in Argentinean Pampas. Thus, the lower abundances in DAs can be related to lower shell input rates which can be related either to a recent decrease in dead-shell production rates (e.g., low shell density correspond to times of low productivity, which decreases the proportion of recently dead cohorts), or/and to a recent increase in shell destruction rates. The first scenario may be possible due to the regional drought conditions that characterized the sampling year, which probably differentially affected LB and NR (in fact, during 2007–2008 most water bodies from NR dried out completely). Both are shallow lakes, but they present differences in their hydrologic regime, which depends on the pluvial regime, the interaction between groundwater and the morphometric characteristics of the basin. In a classification based on these parameters, LB is defined as a permanent lake, whereas NR is classified as a semipermanent lake (Dangavs, 2005). The second scenario is also possible but observations suggesting a stronger influence of taphonomic conditions in these environments are currently not available.

Analysis of Fidelity of Diversity within Sites and within Areas

Sample size standardization by rarefaction eliminated the differences in diversity between LAs and DAs, mainly by removal of rare species that occur in DAs only. This either implies that temporal turnover in species composition over the course of time-averaging was not very extensive (because it should generate higher diversity in dead assemblages even after rarefaction, Tomašových and Kidwell, 2011). In contrast, the Shannon-Wiener and Simpson indices, where abundances come into play, did not show significant differences between the living and the dead, neither before nor after the rarefaction. These results broaden to the freshwater realm the previous conclusions obtained in marine environments about the accuracy of DAs to reflect the composition and structure of the source community in marine mollusks (Kidwell, 2001, 2002).

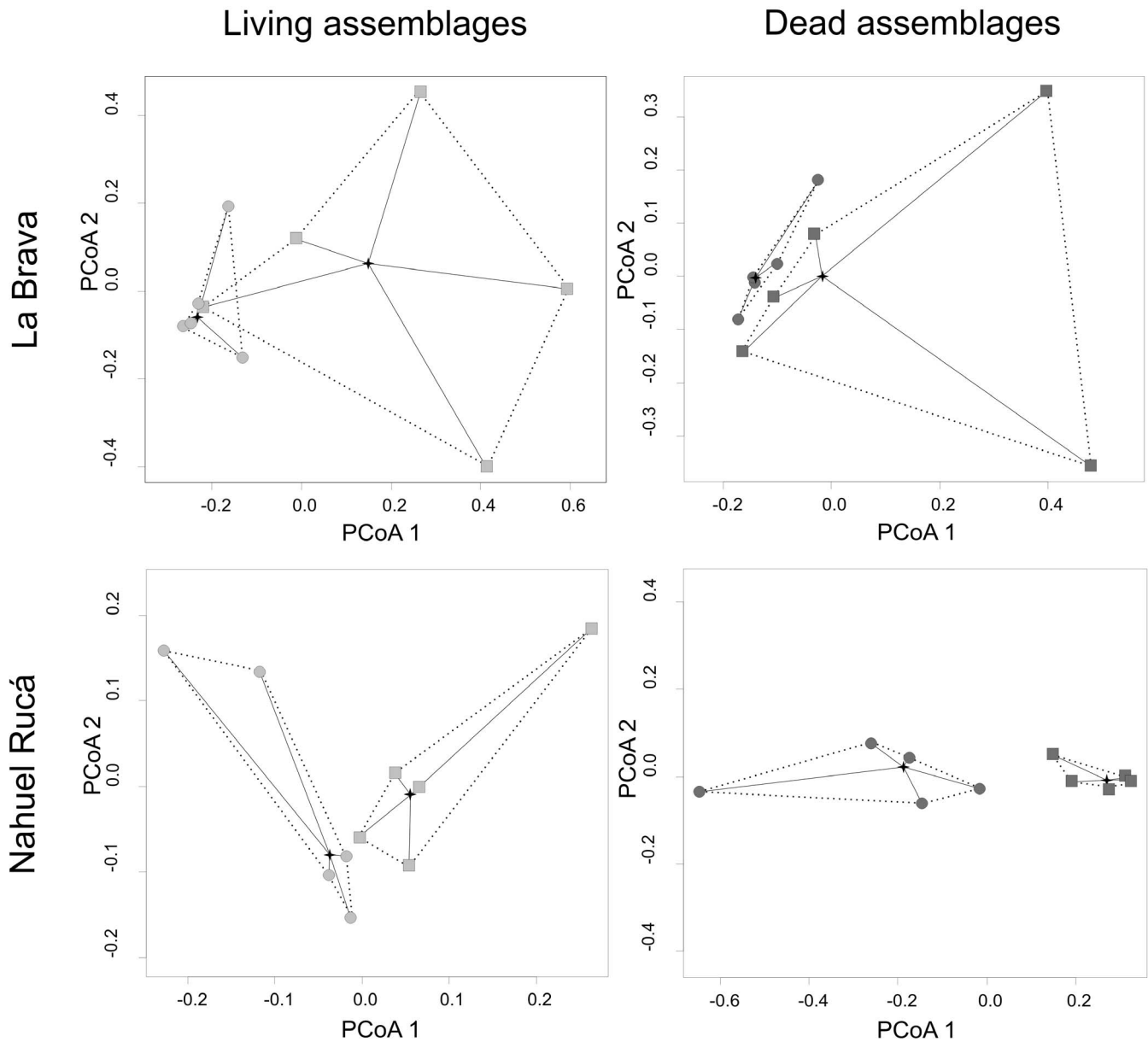


FIGURE 7—Principal Coordinates Analysis based on Horn-Morisita dissimilarity shows that lentic sites are more variable in composition than lotic sites in the La Brava area and that this difference in variation (beta diversity) is equally captured by LAs and DAs. Lentic and lotic sites do not differ in their dispersion in the Nahuel Rucá area. Circles represent lentic sites and squares lotic sites. Light gray correspond to living assemblages and dark gray to dead assemblages.

Analysis of Fidelity of Environmental Differences in Diversity

Diversity differed among environments in DAs, but no differences were observed in LAs. Two possible explanations for this pattern are: (1) an increase in temporal scale due to time-averaging, affecting all site/environments equally, but with some environments being characterized by higher temporal turnover in species composition; or (2) differences in time-averaging or in other aspects of preservation dynamic among DAs from

different environments. In the first case, DAs originated in environments with different temporal rate of change in species composition. The environment with higher variability or higher temporal rate of change in species composition can become more diverse than DAs from other environments. In the second case, an artifactual difference in diversity of DAs between environments can occur when DAs from one environment are more time-averaged than DAs from another environment. Hence, the differences may reflect the distinct sedimentary/taphonomic processes that operate in each environment (Pip, 1988; Briggs et al., 1990; Martello et al., 2006), e.g., environments with higher energy and/or winnowing or slower net sedimentation rates should be more time-averaged.

TABLE 7—F-values and *p*-values of HMD test used to compare lotic and lentic dispersions. Significant values are in boldface.

HMD results	La Brava		Nahuel Rucá	
	Live	Dead	Live	Dead
F-value	7.08	7.79	0.02	2.16
Test of homogeneity in dispersions: <i>p</i> -value	0.02	0.04	0.91	0.11

Analysis of Fidelity in Abundances and Presence/Absence at Site Scale

Most sites show relatively high fidelity, both in terms of presence/absence and proportional abundance of individual species suggesting that dead mollusk assemblages are not under significant alteration by stochastic and biostratigraphic processes or are not affected by

postmortem transport in these freshwater environments. A high preservation of species abundances have also been recorded in other freshwater environments (Cummins, 1994; Martello et al., 2006), highlighting the overall reliability of species dominance information in freshwater mollusk dead assemblages.

Analysis of Fidelity in Abundance and Presence/Absence at Area Scale

A relatively high live/dead agreement is seen in both areas (LB and NR), and there are no significant differences in mean species composition on the basis of the modified HMD test. Premortem variation can be produced by the stochastic variability of the system and by sampling biases, so variation in composition among LAs represents a null expectation for the amount of variation that can exist among LAs and DAs in the absence of postmortem bias from differential turnover and preservation of species and in the absence of scaling (time-averaging) (Tomašových and Kidwell, 2011). On one hand, total live-dead variation is expected to increase with increased time-averaging because LAs and DAs become less autocorrelated, allowing the DA centroid to move away from the LA centroid owing to true drift in mean composition of LAs. On the other hand, acting at the same time but with an opposite effect, increased time-averaging tends to reduce variation among DAs and their centroid because temporal fluctuations in species abundances are averaged out. This effect reduces total LD variation. In the case of LB, premortem variation was larger than total LD variation, resulting in negative values of postmortem variation. The higher premortem values also produced a ratio larger than one when sum of squares are used ($SSL/SST = 1.37$), meaning that 100 percent of total-live dead variation is explained by premortem variation in species composition, and DAs are underdispersed relative to LAs. The difference in composition between LAs and DAs is thus probably caused by time-averaging (generating underdispersion of DAs). Additional (postmortem) effects on the composition of DAs were likely minor. In the case of NR, even when premortem variation explains a smaller amount of total-live dead variation (0.13–0.41), mean species composition of LAs does not differ from mean species composition of DAs.

Analysis of Fidelity of Environmental Differences in Among-Site Variation in Composition

Lentic environments show higher among-site variation in species composition than lotic environments in the La Brava area. The fact that this difference is equally captured by LAs and DAs also implies, in accord with other findings, that time-averaging was not extensive. LAs and DAs in the Nahuel Rucá area do not show such difference among lentic and lotic environments. It is possible that this outcome depends on the environmental conditions and the microhabitat availability that differ among these areas. *Musculium argentinum* and *Chilina parchappii* were more abundant in lotic communities. The coexistence of these two species can be explained by the spatial heterogeneity of the sites, where accumulation of soft sediments, presence of hard substrates, and patchy vegetation are common (Tietze and De Francesco, 2010). The species that were more abundant in lentic communities (i.e., *Biomphalaria peregrina*, *Heleobia parchappii*) were also highly abundant in lotic communities.

CONCLUSION

Subfossil mollusk dead assemblages preserved in freshwater environments of the Pampean Region exhibit a relatively high compositional fidelity reflecting the taxonomic composition (richness) and relative abundance of species. These results suggest that (1) living and dead assemblages occupy similar portions of multivariate space and do not significantly differ in composition within an area, (2) show similar richness and evenness, and (3) between-environment differences in

multivariate dispersion (beta diversity) captured by living assemblages are preserved by dead assemblages. This indicates that ecological information can be extracted from the fossil deposits with a high degree of confidence, which is good news for paleoenvironmental reconstructions that demonstrate that dead mollusk assemblages from freshwater environments constitute hugely informative records of past life. For this reason, dead mollusk assemblages can be a particularly suitable target for paleoecological and biostratigraphic studies.

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