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Holocene (~4.5–1.7 cal. kyr BP) paleoenvironmental conditions in central Argentina inferred from entire-shell and intra-shell stable isotope composition of terrestrial gastropods

Yurena Yanes,[1] Andrés D Izeta,[2] Roxana Cattáneo,[2] Thiago Costa[2] and Sandra Gordillo[3]

Abstract
The isotopic fingerprint of terrestrial gastropods has been increasingly used as a credible natural paleoenvironmental archive. Most published work has used this proxy at tropical and temperate latitudes of the Northern Hemisphere, and focused on entire-shell analysis. The present study provides entire-shell and intra-shell isotopic profiles to infer average and seasonal late Holocene environmental conditions in central Argentina (30°S). Shells of *Plagiodontes daedaleus* (Gastropoda: Odontostomidae) were retrieved from the Alero Deodoro Roca–Sector B site, one of the few archaeological sites in central Argentina rich in shells collected by pre-Hispanic hunter-gatherer groups. Ancient entire shells exhibited values that were ~2.5‰ higher in $\delta^{13}C$ and ~1.8‰ higher in $\delta^{18}O$ than modern individuals, pointing to higher abundance of C_4 plants and overall drier conditions (lower relative humidity and/or higher rain $\delta^{18}O$) during 4.5–1.7 cal. kyr BP than today, in agreement with published regional proxies. Intra-shell isotopic profiles suggest that modern and fossil specimens deposited their shells throughout two-to-three summer/winter cycles. Intra-shell $\delta^{18}O$ values varied ~5‰, matching with the seasonal variation of rain $\delta^{18}O$ values. The extent of seasonality was similar during 4.5–1.7 cal. kyr BP and today. Intra-shell $\delta^{13}C$ values varied ~2–3‰ and did not portray distinct seasonal cycles, depicting minimal seasonal variations in the snail diet. This work illustrates that South American terrestrial gastropods have great potential for paleoenvironmental studies.

Keywords
Argentina, Holocene, Ongamira, paleoenvironment, stable isotopes, terrestrial gastropods

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Introduction

The carbonate shell of terrestrial gastropods, which is made of aragonite for the majority of species, exhibits high preservation potential in many archaeological sites worldwide. Carbon and oxygen stable isotopes recorded in fossil shells are often used as paleoenvironmental proxies of terrestrial systems in which snails lived (e.g. Balakrishnan et al., 2005a; Colonese et al., 2007, 2010, 2011, 2013; Goodfriend, 1992; Yanes et al., 2011, 2012, 2013). The carbon isotope composition ($\delta^{13}C$) of the shell reflects the $\delta^{13}C$ values of consumed foods. The majority of terrestrial gastropods are primary consumers that feed upon both living and decayed plant matter (Speiser, 2001). Accordingly, the shell $\delta^{13}C$ values mirror the $\delta^{13}C$ values of assimilated plants, as demonstrated in laboratory studies (Metref et al., 2003; Stott, 2002). Plants that follow different photosynthetic pathways (e.g. C_3 and C_4), which, in turn, are associated with different types of environments, also show distinctive $\delta^{13}C$ values in their tissues (O'Leary, 1981). The $\delta^{13}C$ values of the gastropod shell are, thus, commonly used to estimate variations in the relative abundance of C_4 against C_3 plants in past ecosystems (e.g. Balakrishnan et al., 2005a; Goodfriend and Ellis, 2000; Yanes et al., 2011). The oxygen isotope composition ($\delta^{18}O$) of the shell is primarily influenced by local rain $\delta^{18}O$ values, as revealed in several field studies that observed a positive correlation between the $\delta^{18}O$ values of the shell and the rainfall (Lécolle, 1985; Yanes et al., 2009; Zanchetta et al., 2005). Yet, other important atmospheric variables (e.g. relative humidity (RH), water vapor $\delta^{18}O$ values and temperature), besides input liquid water $\delta^{18}O$ values, appear to also control the $\delta^{18}O$ values of the shell (Balakrishnan and Yapp, 2004; Balakrishnan et al., 2005a, 2005b; Yapp, 1979; Yanes et al., 2011). Balakrishnan and Yapp (2004) developed an evaporative steady-state flux balance-mixing model in which these four variables are mathematically related to explain the environmental meaning of the oxygen isotopic signature of the shell. So far, this is the most complete model available to quantitatively interpret oxygen

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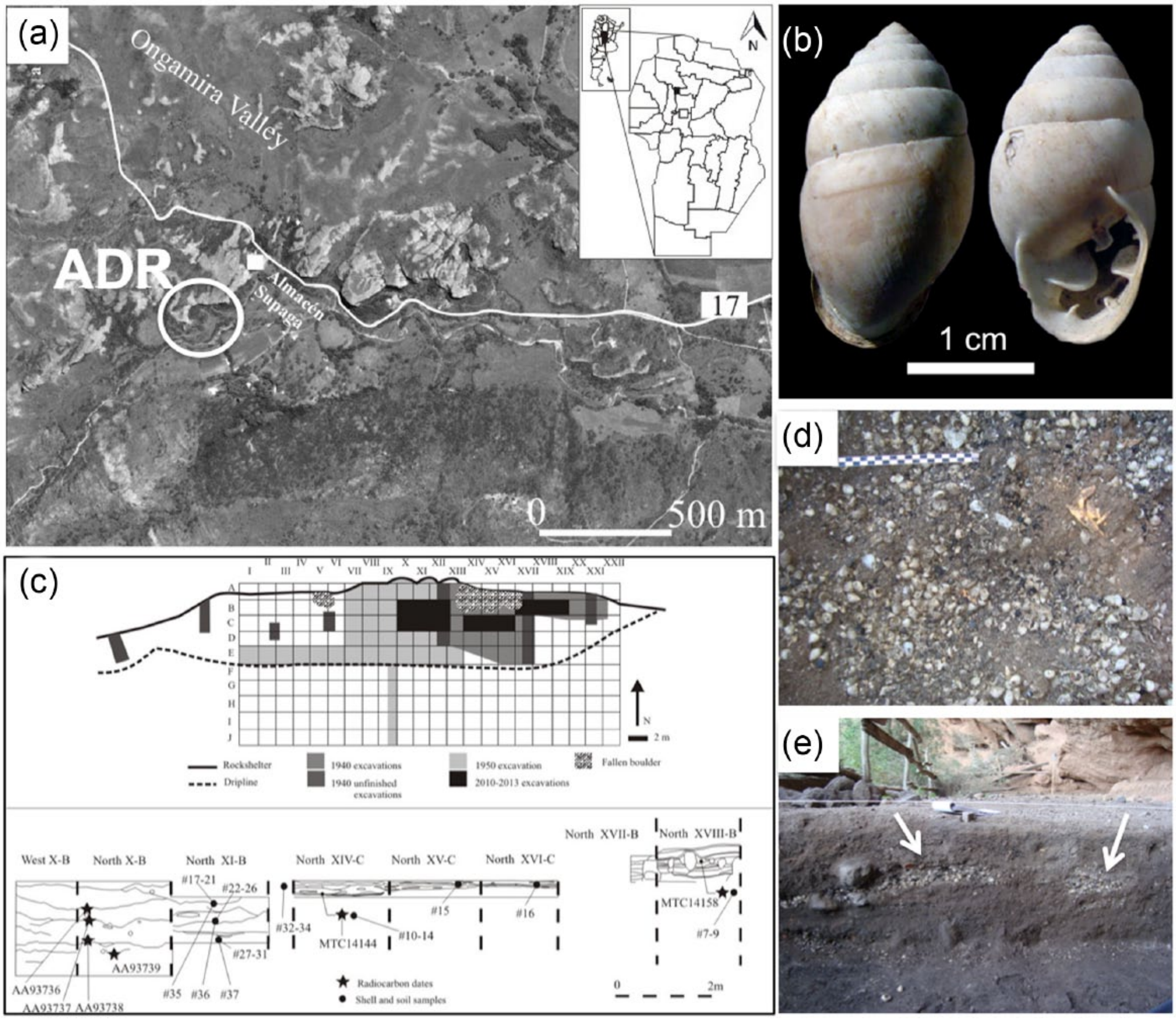

Figure 1. Geographical and stratigraphic setting. (a) Geographical location of the archaeological site of the Alero Deodoro Roca (ADR) site, Ongamira, Argentina. (b) Photograph of the studied species *Plagiodontes daedaleus*. (c) Stratigraphic sketch of the sampled profiles at ADR-Sector B site. Stars denote depths at which samples were collected. (d) and (e) General and detailed view of the sample ADR XIV-C UE34 (3.1–3.4 cal.kyr BP).

isotopic data extracted from terrestrial gastropod shells. Even though fossil terrestrial gastropods are often used as paleoenvironmental archives, the majority of published studies, however, have been performed in localities of the Northern Hemisphere, whereas studies from the Southern Hemisphere are rather rare (but see Abell and Plug, 2000; Bonadonna et al., 1999). Moreover, the bulk of published work has generally focused on entire-shell (average annual) samples instead of intra-shell (seasonal) analyses (see references cited above). The present study investigates both entire-shell and intra-shell isotopic profiles from fossil and modern terrestrial gastropods recovered from an archaeological site in central Argentina. The Alero Deodoro Roca (ADR) site is located in the valley of Ongamira, at the latitude of 30°46′S and the longitude of 64°26′W (Figure 1). This locality is rich in native continental malacofaunas that lived in the north-center of Argentina during the late Holocene (e.g. Costa et al., 2012; Menghin and González, 1954). This area is also interesting from a paleoenvironmental perspective because (1) several photosynthetic pathways coexist; (2) atmospheric conditions are of continental nature, as opposed to coastal sites; and (3) the orography is rather complex, in which several mountain chains with maximum elevation between 1979 and 1260 m surround the area (Figure 1). In the present study, well-preserved fossil shells of terrestrial gastropods recovered from a multi-layered pre-Hispanic archaeological site were analyzed for $^{13}C/^{12}C$ and $^{18}O/^{16}O$ ratios to infer the paleoenvironmental conditions during an important cultural period in central Argentina, in which human hunter-gatherer societies interacted with organisms and the environment. Modern samples of gastropods, plants, soils, and rainwaters were also analyzed to calibrate the environmental significance of the shell isotopic composition of this system, which has never been studied before isotopically. This work presents a yet minimally explored environmental proxy in South America (i.e. terrestrial gastropods) and provides new paleoenvironmental data that complement other proxies in the region.

Archaeological background

Archaeological studies in Córdoba (Argentina) first started at the end of the 19th century (e.g. Outes, 1911; Frenguelli, 1924). After more than a century of archaeological research, it is now broadly accepted that pre-Hispanic hunter-gatherer societies from central Argentina were well established since 11,000 yr BP (Rivero and Berberián, 2011). However, based on available age data, the first human occupation in Ongamira Valley took place not before than 6550 yr BP ago (Vogel and Lerman, 1969). Hunter-collector human groups developed a lifestyle that included societal and

Table 1. Radiocarbon results from the Alero Deodoro Roca–Sector B archaeological site, Ongamira, Córdoba, central Argentina (data adapted from Cattáneo and Izeta, 2011; Cattáneo et al., 2013).

Sample ID	Stratigraphy	Laboratory code	Laboratory	Sample	^{14}C yr BP	Cal. yr BP (2σ)
ADR 614 UE23	XVIII-B	MTC14158	University of Tokyo	Bone (camelid)	1920 ± 45	1730–1950
ADR 405 UE34	XIV-C	MTC14144	University of Tokyo	Charcoal	3040 ± 40	3140–3360
ADR-1	X-B	AA93736	University of Arizona	Charcoal	3390 ± 40	3560–3720
ADR-2	X-B	AA93737	University of Arizona	Charcoal	3520 ± 40	3690–3890
ADR-3	X-B	AA93738	University of Arizona	Charcoal	3980 ± 40	4340–4520

spatial organization, diversification of dietary habits, and intergroup connections that led to complex social relationships (Laguens and Bonnin, 2009; Rivero et al., 2010). Towards the final stages of human occupation in the area, these societies developed sophisticated technologies for food production (Berberián et al., 2011; Medina et al., 2009; Pastor et al., 2013). According to bioanthropological evidence, the human gene pool of the aboriginal people changed significantly around 1200 yr BP (Nores et al., 2011).

Even though ancient human groups in central Argentina were primarily hunter-gatherers, mollusk collection was not a common activity. Out of the more than 1800 archaeological sites known in Córdoba, only 41 contained shell remains, and of them, merely four included dense accumulations of shells that were collected and manipulated by pre-Hispanic people (Cattáneo et al., 2013; Izeta et al., 2013). The present work investigates one of these sites, the Alero Deodoro Roca (ADR)-Sector B site (Figure 1), a mid-to-late Holocene multi-layered deposit that includes important cultural accumulations of terrestrial gastropod shells. Initial work on this site did not focus on the shell material, and only identified one mollusk species: *Plagiodontes* sp. (Gastropoda: Odontostomidae). Numerous camelid and deer remains were recovered from the deepest layers, whereas mollusks and ratites were the dominant taxa in the uppermost horizons (Montes, 1943; Menghin and González, 1954). Subsequent work since 2010, which investigated new areas within the ADR site, have found dense accumulations of shells of several species associated with combustion areas (Cattáneo and Izeta, 2011; Cattáneo et al., 2013; Izeta et al., 2013). The air-breathing gastropod *Plagiodontes daedaleus* (Deshayes, 1821) was the dominant taxon. Up to six terrestrial gastropod species have been catalogued in this site, including, apart from *Plagiodontes daedaleus, Bulimulus apodemetes* (Orbigny, 1835), *Spixia alvarezii* (d'Orbigny), *Epiphragmophora* sp., *Megalobulimus oblongus* (Müller, 1774), and *Austroborus cordillerae* (Doering, 1876). The former five species are extant in the area, whereas the latter is extinct (Costa et al., 2012; Gordillo et al., 2013; Izeta et al., 2013). *Plagiodontes* shells are particularly abundant in this site and are often associated with combustion areas, suggesting that they were consumed by the aboriginal people. Larger body size species like *Megalobulimus oblongus* and perhaps *Austroborus cordillerae*, very common in other archaeological sites in Córdoba, were also used for ornamentation purposes.

Several AMS radiocarbon analyses of bone and charcoal samples were carried out by Cattáneo et al. (2013) in the radiocarbon laboratories of the University of Tokyo (Japan) and the University of Arizona (US). Their results indicate that shelly accumulations studied here range in age from 4.5 to 1.7 cal. kyr BP (Table 1).

Material and methods

Present climate

Ongamira (latitude: 30°46′S, longitude: 64°26′W) is located in the northern edge of 'Sierras Chicas' mountain chains. The region, with a maximum altitude of 1979 m above sea level (a.s.l.) in 'Uritorco' peak, and located over 1000 km from the coast (Figure 1), exhibits a temperate continental climate, with warm and wet summers and dry and cold winters. Between June–July, snow occasionally falls at elevations above 1100 m (a.s.l.). Climatic data for the recording period 1961–1990 from the meteorological stations of Córdoba and Villa de María de Río Seco, situated to the south and the north of Ongamira, respectively, were available at the *Servicio Meteorológico Nacional de Argentina* (http://www.smn.gov.ar). Climatic data indicate that monthly average air temperature ranges from 9°C in June–July to 25°C in January–December (Figure 2). Average annual air temperature is 17–18°C. The rainfall exhibits a marked seasonal pattern, probably in response to seasonal fluctuations of the Atlantic and South Pacific anticyclones and the sea surface temperature (SST) along the coast of southern Brazil and Buenos Aires (Bonadonna et al., 1999; González et al., 2012). Precipitation ranges from 10 mm during winter (dry) months to 150 mm in the summer (wet) months (Figure 2). The total annual precipitation in the region is about 870 mm. RH can be relatively high and, based on data from 2011, monthly average values range from 64% in September to 93% in June. The average annual RH is 85%.

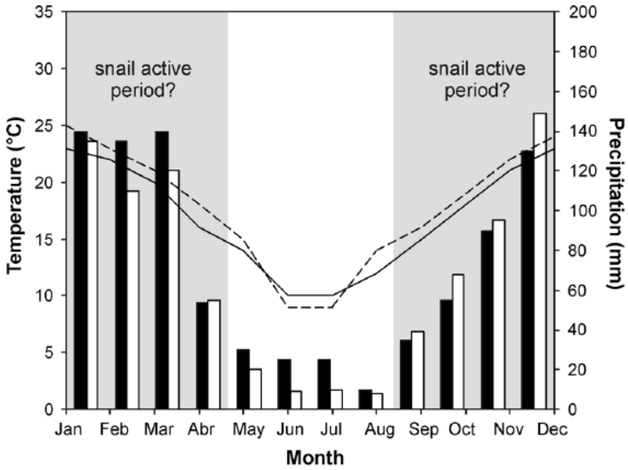

Figure 2. Present climate on central Argentina. Data adapted from the Servicio Meteorológico Nacional de Argentina (http://www.smn.gov.ar) for the recording period 1961–1990.
Lines depict mean temperature data whereas bars represent precipitation. Dashed line and black bars depict data from Villa de María de Río Seco (the northernmost meteorological station of Córdoba province). Continuous line and white bars represent data from Córdoba meteorological station. Gray bands mark the possible months at which snails are thought to be more active (i.e. warmer and wetter months).

Target species and sampling protocol

The genus *Plagiodontes* includes nine species geographically distributed among three mountain systems: the sierras of central Argentina, the sierras of southern Buenos Aires province, and the

Uruguayan *cuchillas* (Pizá and Cazzaniga, 2003). These three mountain groups are separated by extensive flat areas of grasslands (so-called 'pampas') and are considered as 'faunistic islands' (Cabrera and Willink, 1972). The gastropod taxon investigated in this study is *Plagiodontes daedaleus* (Gastropoda: Orthalicidae: Odontostominae). *Plagiodontes daedaleus* is the most variable and abundant species of the genus, widely distributed across eastern Córdoba (Pizá and Cazzaniga, 2010). It is a medium size (about 23–25 mm of maximum shell length) air-breathing terrestrial gastropod that mainly feeds upon living and decayed vegetation (Figure 1b).

Six shells of modern *Plagiodontes* specimens were collected for stable isotope analysis to establish the first isotopic baseline for this species in the study area. Modern shells represent recently dead individuals that were on the soil surface about 20 m to the north from the archaeological site. Fresh leaves of seven native and introduced plant species and soil samples were collected to constrain the isotopic signature of the present terrestrial ecosystem in Ongamira. Analyzed plant species included *Lithrea molleoides* (Anacardiaceae), *Croton* sp. (Euphorbiaceae), *Salix* sp. (Salicaceae), *Ligustrum lucidum* (Oleaceae), *Boccharis flabellata* (Asteraceae), *Rubus ulmifolius* (Rosaceae), and one undetermined Bromeliaceae. These plant species were selected because they were the most abundant in the study site and because gastropods likely fed upon them (personal field observations, 2011–2012).

Fossil specimens and the bulk sediment matrix were excavated from multiple layers of known ^{14}C age (Figure 1c–e). Several specimens per layer were randomly selected for stable isotope analyses. A total of 28 fossil shells and three bulk sediment samples in which shells were preserved were used for this study. X-ray diffraction analyses of two fossil shells studied in the Instituto Andaluz de Ciencias de la Tierra (CSIC – Universidad de Granada) confirmed that fossil material preserved the original aragonitic composition, and therefore, they were suitable for geochemical analyses.

Stable isotope analysis

All samples were prepared and analyzed in the Stable Isotope Laboratory of the Department of Earth and Environmental Sciences, University of Kentucky. Water samples were measured in a Picarro instrument. Organic matter samples (plants and soil organic matter) were analyzed in a Costech Elemental Analyzer (ESC 4010) connected to a continuous flow isotope ratio mass spectrometer (IRMS) Finnigan Delta^{PLUS} XP. Carbonate samples (shells and sediment carbonates) were analyzed in a GasBench II connected to the IRMS. All stable isotope results are reported in δ notation relative to the international standard Pee Dee Belemnite (PDB) for organic matter and carbonate samples, and Standard Mean Ocean Water (SMOW) for water samples. The δ values are defined as:

$$\delta^{13}\mathrm{C} \text{ or } \delta^{18}\mathrm{O} = \left[\left(R_{\text{sample}} / R_{\text{standard}}\right) - 1\right] \times 1000(‰)$$

where $R = {}^{13}\mathrm{C}/{}^{12}\mathrm{C}$ or ${}^{18}\mathrm{O}/{}^{16}\mathrm{O}$

Rainwater samples

Several rainwater samples (n = 9) were collected during rain events in October and June–July of 2011. Water samples were collected in plastic bottles that were rapidly sealed after collection to prevent evaporation. Data were calibrated using several international standards (SMOW, GISP) placed throughout the run sequence in a Picarro device. Analytical uncertainty was ±0.1‰ for $\delta^{18}O$ and ±1‰ for δD.

Organic matter samples

A total of seven modern fresh leave samples of dominant plants of seven species were rinsed with deionized water, oven-dried at 40°C overnight, and homogenized using an electric blender. About 1.5 mg of each plant sample was weighed in a tin capsule, crimped, and combusted in an Elemental Analyzer (EA). The CO_2 and N_2 produced after combustion were analyzed using the IRMS. Analytical uncertainty was ±0.1‰ based on the recurrent measurements of in-house standards dispersed periodically throughout each run sequence. One sample of bulk soil organic matter was also analyzed isotopically for comparison with plants.

Carbonate samples

Shells were cleaned in distilled water and ultrasonication and subsequently oven-dried at 40°C overnight. Entire shells (n = 34 total) were finely ground manually using an agate mortar and pestle. About 150 µg of carbonate was placed in a 6 mL Exetainer™ vial that was subsequently flushed with helium. The carbonate was then converted to CO_2 gas by adding 0.1 mL of 100% H_3PO_4 at 25°C. The resulting CO_2 was analyzed after 24 h using the GasBench II connected to the IRMS. Analytical uncertainty was ±0.1‰ for both carbon and oxygen isotopes based on the repeated measurements of in-house and international (NBS-19) standards throughout each run sequence.

Carbonates from bulk sediment samples in which shells were preserved (n = 3) were also analyzed isotopically for comparison with shells. Bulk sediment samples contain carbonates that represent a mixture of detrital carbonate derived from the shells themselves and pedogenic carbonate. Soil organic matter was removed using 5% H_2O_2 overnight and subsequently rinsing with DI water. Carbonate sediments were then treated as gastropod shells for successive isotopic analysis.

Three additional shells were selected for intra-shell isotopic analyses (n = 145 total). Aliquots of 150 µg were milled manually using a dremel drill with a 0.5 mm bit. Samples were collected from the lip, which depicts the last growth episode closest to organism death, and sequentially every ~1 mm along shell world spires up to the protoconch, which depicts the youngest part of the shell. Each intra-shell sample was analyzed as indicated above for entire shells.

Results

Rainwater

The rainwater $\delta^{18}O$ values (n = 9) ranged from −6.1‰ to +2.0‰, with an average value of −1.8 ± 2.9‰, whereas δD values ranged from −30‰ to +10‰, with an average value of −5.1 ± 12.8‰ (Table 2). Rainwater data were plotted jointly with the Global Meteoric Water Line (GMWL) by Craig (1961), which is defined as $\delta D = 8\delta^{18}O + 10‰$ (Figure 3a). Samples that plot to the right of the GMWL curve likely underwent evaporation processes. Rainwater samples collected in October 2011 (n = 5) showed an average $\delta^{18}O$ and δD value of −4.0 ± 1.4‰ (Figure 3b) and −11 ± 14‰, respectively. In contrast, samples collected in June–July 2011 (n = 4) displayed respective average $\delta^{18}O$ and δD values of +1 ± 1.2‰ (Figure 3b) and +3 ± 6‰ (Figure 3b). All evaporated rainwaters were collected during June–July (=cool/dry season), whereas samples from October (=warm/wet season) do not seem to have been fractionated (Figure 3a). The weighted average annual $\delta^{18}O$ value of rainwater from central Argentina is around −4.0‰ (e.g. Bonadonna et al., 1999; Rozanski et al., 1993), which agrees with the measured average value of rainwater samples from Ongamira valley collected in October 2011 for

Table 2. Oxygen and hydrogen stable isotope values of local rainwater samples from Ongamira, Córdoba, central Argentina.

Sample ID	Sample type	Collection date	δ18O‰ (SMOW)	δD‰ (SMOW)
ONG-rain-1	Rainwater	1 October 2011	−4.3	−12
ONG-rain-2	Rainwater	14 October 2011	−3.3	−12
ONG-rain-3	Rainwater	22 October 2011	−2.3	+9
ONG-rain-4	Rainwater	13 October 2011	−6.1	−30
ONG-rain-5	Rainwater	20 October 2011	−3.9	−12
ONG-rain-6	Rainwater	27 July 2011	+1.5	−5
ONG-rain-7	Rainwater	27 July 2011	+2.0	+6
ONG-rain-8	Rainwater	27 July 2011	+1.0	+0
ONG-rain-9	Rainwater	1 June 2011	−0.7	+10

SMOW: Standard Mean Ocean Water.

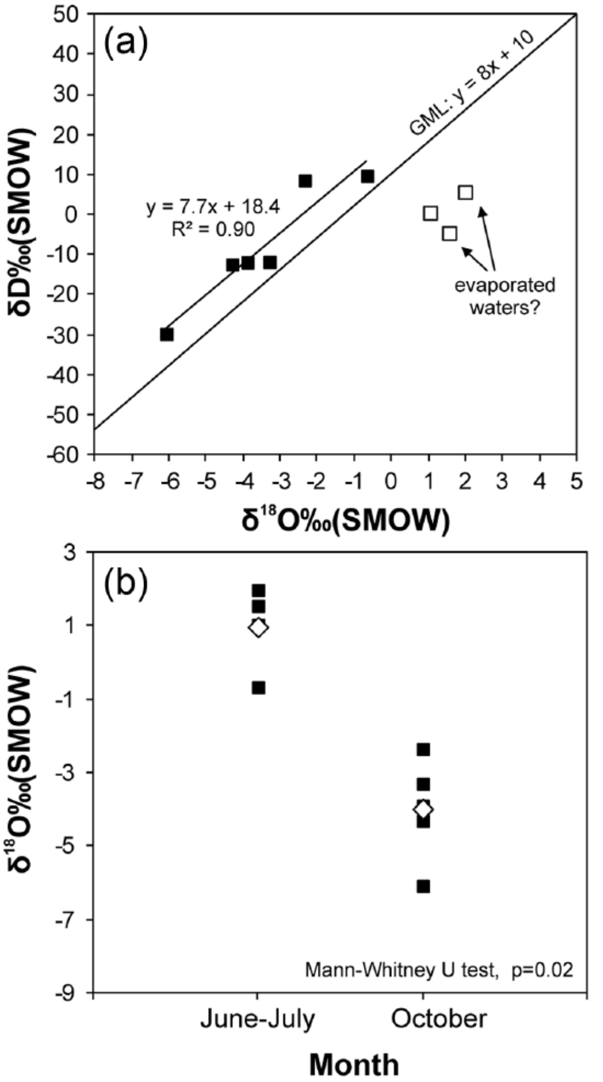

Figure 3. Present rainwater collected in Ongamira valley (Córdoba, Argentina). (a) Hydrogen and oxygen stable isotope values of rainwater samples compared with the global meteoric line (GML). White quadrates depict possible evaporated waters. (b) Oxygen stable isotope values of rainwater samples plotted by month. White diamonds depict average values. Note that the coldest and driest season (June–July) is characterized by significantly higher rain δ18O values.
SMOW: Standard Mean Ocean Water.

the present study. Such value is adopted here as the δ18O value of input liquid water by modern *Plagiodontes* gastropods from the study area.

Plant and soil organic matter

Bulk foliar δ13C values of analyzed plants (n = 7) varied from −33.1‰ to −29.1‰, with an average value of −31.0 ± 1.4‰ (Table 3). The measured bulk soil organic matter sample (n = 1) exhibited a δ13C value of −25.5‰. Thus, soil organics was 5.5‰ higher in δ13C values than surrounding fresh plants (Figure 4a), as expected for decayed plant matter (Melillo et al., 1989).

Carbonate sediment

Carbonates from the sediment matrix in which shells were preserved (n = 3) ranged from −19.6‰ to −8.6‰ for δ13C values, with an average value of −13.8 ± 5.5‰; and from −12.1‰ to −5.1‰ for δ18O values, averaging −8.0 ± 3.7‰ (Table 4). Isotopic values of carbonates from the sediment are significantly different than those from fossil shells (Figure 4b), which suggest that measured fossil shells were not contaminated by carbonates from the sediment and exhibit distinctive isotopic populations. Modern soil samples did not contain carbonates.

Entire shells

The δ13C values of entire shells of modern *Plagiodontes* shells from Ongamira (n = 6) ranged from −13.1‰ to −10.8‰ (Table 4; Figure 5a). In contrast, the δ13C values of fossil specimens (n = 28) ranged from −10.7‰ to −7.6‰ (Table 4; Figure 5a). Fossil specimens did not significantly differ in δ13C values across age intervals (Kruskal–Wallis, $p > 0.05$), but they all differed notably from modern shells (Mann–Whitney U test, $p < 0.001$). Thus, fossil specimens were, on average, 2.5‰ higher in shell δ13C values than modern counterparts.

The δ18O values of entire shells of modern individuals ranged from −2.0‰ to −0.4‰ (Table 4; Figure 5b), with an average value of −1.2 ± 0.6‰ (n = 6). Late Holocene entire shells exhibited an average δ18O value of +0.7 ± 0.9‰ (n = 28). Fossil shells from different age intervals did not differ significantly in δ18O among them (Kruskal–Wallis, $p > 0.05$) (Figure 5b). However, fossil shells differed significantly in δ18O values from modern specimens (Mann–Whitney U test, $p < 0.001$). Like this, fossil shells were, on average, 1.8‰ higher in shell δ18O values than modern individuals.

Intra-shell samples

The δ13C values of samples collected sequentially throughout ontogeny from a modern specimen (n = 49) varied between −13.1‰ and −11.4‰ (Table 5; Figure 6a), with an average value of −12.2 ± 0.3‰. Intra-shell δ13C values of a 1.7–1.9 cal. kyr BP individual (n = 45) ranged from −9.3‰ to −6.3‰ (Table 5; Figure 6b), averaging −8.0 ± 0.9‰. Finally, a 3.6–3.7 cal. kyr BP

Table 3. Carbon stable isotope values of modern plants and soil organic matrix from Ongamira, Córdoba, central Argentina.

Sample ID	Sample type	Family	Species	$\delta^{13}C$‰ (PDB)
ONG-plant-1	Fresh foliar sample	Anacardiaceae	*Lithrea molleoides*	−29.6
ONG-plant-2	Fresh foliar sample	Euphorbiaceae	*Croton* sp.	−31.9
ONG-plant-3	Fresh foliar sample	Salicaceae	*Salix* sp.	−29.1
ONG-plant-4	Fresh foliar sample	Oleaceae	*Ligustrum lucidum*	−30.6
ONG-plant-5	Fresh foliar sample	Asteraceae	*Boccharis flabellata*	−32.2
ONG-plant-6	Fresh foliar sample	Bromeliaceae	undetermined	−33.1
ONG-plant-7	Fresh foliar sample	Rosaceae	*Rubus ulmifolius*	−30.8
ONG-soil-1	Bulk soil organic matter			−25.6

PDB: Pee Dee Belemnite.

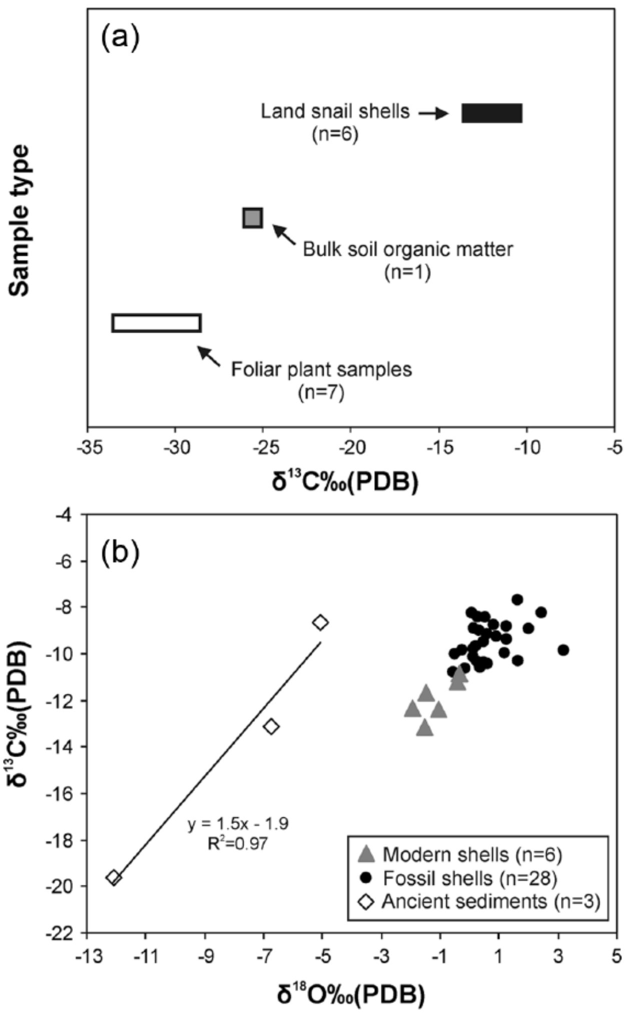

Figure 4. Stable isotope results. (a) Carbon stable isotope results of modern foliar plants (white symbol), bulk soil organic matter (gray symbol), and modern terrestrial gastropod shells (black symbol). (b) Comparison of the carbon and oxygen stable isotope values of ancient bulk carbonate sediments (open symbols) and terrestrial gastropod shells (filled symbols).
PDB: Pee Dee Belemnite.

specimen (n = 51) showed intra-shell $\delta^{13}C$ values ranging from −8.6‰ to −6.6‰ (Table 5; Figure 6c), with an average value of −7.6 ± 0.4‰.

A modern specimen exhibited intra-shell $\delta^{18}O$ values (n = 49) that varied between −3.4‰ and +2.2‰ (Table 5; Figure 6d), averaging −1.1 ± 1.3‰. A specimen collected from a layer dated at 1.7–1.9 cal. kyr BP showed intra-shell $\delta^{18}O$ values (n = 45) ranging from −1.3‰ to +4.3‰ (Table 5; Figure 6e), averaging +0.7 ± 1.4‰. Finally, a 3.6–3.7 cal. kyr BP shell (n = 51) varied between −2.1‰ and +2.9‰ (Table 5; Figure 6f), averaging −0.1 ± 1.3‰.

Discussion

Carbon stable isotopes

Because carbonates are negligible on modern soils on which gastropods live, it is considered that the $\delta^{13}C$ values of *Plagiodontes* shells should primarily represent the $\delta^{13}C$ values of assimilated vegetation (Metref et al., 2003; Stott, 2002). Modern individuals showed a rather narrow range (from −10.8‰ to −13.1‰) of shell $\delta^{13}C$ values that suggests that gastropods followed a C_3 plant diet only. Modern shells were up to 19.2‰ and 13.7‰ higher in $\delta^{13}C$ values than analyzed plants and bulk soil organic matter, respectively. Considering the unusually large $\delta^{13}C$ offset between fresh plants and shells, it is likely that *Plagiodontes* consumed large quantities of decayed plant matter, which is enriched in ^{13}C (Melillo et al., 1989) as indicated by the soil organic matter sample analyzed here. In contrast, all measured archaeological shells (from 4.5 to 1.7 cal. kyr BP) exhibited $\delta^{13}C$ values that were, on average, 2.5‰ higher than modern individuals. This suggests that gastropods during the late Holocene in central Argentina consumed significant amounts of C_4 plants, whereas today, gastropods only consumed C_3 plants. Even if modern specimens are corrected by the *Suess effect* (+1.5‰), they still show significantly lower shell $\delta^{13}C$ values than archaeological specimens, reinforcing that C_4 vegetation was probably more abundant during the late Holocene than today. An alternative hypothesis is that ancient individuals could have consumed only C_3 plants that were water-stressed during 4.5–1.7 cal. kyr BP and, consequently, were enriched in ^{13}C as a consequence of drier conditions, for example, lower mean annual precipitation (Diefendorf et al., 2010; Kohn, 2010), with respect to the present.

Based on laboratory experiments, shells are about 13‰ higher in $\delta^{13}C$ values than assimilated foods (Metref et al., 2003; Stott, 2002). If we assume that shell $\delta^{13}C$ values of *Plagiodontes* are only influenced by the $\delta^{13}C$ values of consumed plants, then, a two-source input mass balance model may be used to calculate the proportion of C_4 plants during the late Holocene using the measured $\delta^{13}C$ values of fossil shells. For model calculations, it is considered that individuals that followed a C_3 plant diet only exhibit an average shell $\delta^{13}C$ value of −11.9‰. In contrast, it is assumed that gastropods that incorporated C_4 plants only should have shown a shell $\delta^{13}C$ value of +1.7‰, on average (Stott, 2002; Yanes et al., 2008). Accordingly, the $\delta^{13}C$ values of archaeological shells (average value of −9.4‰) suggest that gastropods possibly incorporated around 20% of C_4 plants in their diet, ranging from as much as 30% (for a shell value of −7.6‰) to a minimum of 10% (for a shell value of −10.7‰). Thus, during the late Holocene in Ongamira valley, C_4 vegetation was not only present but was relatively abundant, possibly forming around 20% of the total plant cover. These patterns derived from terrestrial gastropods

Table 4. Carbon and oxygen stable isotope values of modern and fossil terrestrial gastropod shells, and bulk carbonate sediments, from the Alero Deodoro Roca–Sector B archaeological site, Ongamira, Córdoba, central Argentina.

Sample #	Sample ID	Stratigraphy	^{14}C age (years)	2σ cal. BP	$\delta^{18}O$‰ (PDB)	$\delta^{13}C$‰ (PDB)
Shell samples						
1	ONG-mod-1		Modern		−1.5	−11.6
2	ONG-mod-2		Modern		−0.4	−11.2
3	ONG-mod-3		Modern		−2.0	−12.3
4	ONG-mod-4		Modern		−1.6	−13.1
5	ONG-mod-5		Modern		−0.4	−10.8
6	ONG-mod-6		Modern		−1.1	−12.3
7	ADR 614 UE32	XVIII-B	1920 ± 45	1730–1950	+0.1	−10.1
8	ADR 647 UE37	XVIII-B	1920 ± 45	1730–1950	+1.6	−7.6
9	ADR 647 UE37	XVIII-B	1920 ± 45	1730–1950	+1.2	−8.8
10	ADR 1363 UE43	XIV-C	3040 ± 40	3140–3360	−0.5	−9.9
11	ADR 338 UE62	XIV-C	3040 ± 40	3140–3360	+0.6	−10.4
12	ADR 539 UE7	XIV-C	3040 ± 40	3140–3360	−0.2	−10.6
13	ADR 405 UE34	XIV-C	3040 ± 40	3140–3360	+0.3	−10.5
14	ADR 566 UE7	XIV-C	3040 ± 40	3140–3360	+0.5	−8.4
15	ADR 543 UE7	XV-C	3040 ± 40	3140–3360	+0.3	−8.9
16	ADR 597 UE7	XVI-C	3040 ± 40	3140–3360	+2.0	−8.9
32	ADR 5354 UE77	XIII-C	3040 ± 40	3140–3360	+0.1	−9.7
33	ADR 5356 UE77	XIII-C	3040 ± 40	3140–3360	+1.2	−9.3
34	ADR 5354 UE77	XIII-C	3040 ± 40	3140–3360	+3.2	−9.8
17	ADR-1	X-B	3390 ± 40	3560–3720	+2.4	−8.2
18	ADR-1	X-B	3390 ± 40	3560–3720	+0.1	−8.8
19	ADR-1	X-B	3390 ± 40	3560–3720	+0.2	−8.4
20	ADR-1	X-B	3390 ± 40	3560–3720	+0.4	−9.4
21	ADR-1	X-B	3390 ± 40	3560–3720	+0.8	−8.7
22	ADR-2	X-B	3520 ± 40	3690–3890	+0.2	−10.3
23	ADR-2	X-B	3520 ± 40	3690–3890	+0.9	−9.2
24	ADR-2	X-B	3520 ± 40	3690–3890	−0.6	−10.7
25	ADR-2	X-B	3520 ± 40	3690–3890	+0.2	−9.6
26	ADR-2	X-B	3520 ± 40	3690–3890	−0.3	−9.8
27	ADR-3	X-B	3980 ± 40	4340–4520	+0.0	−8.2
28	ADR-3	X-B	3980 ± 40	4340–4520	+0.5	−9.1
29	ADR-3	X-B	3980 ± 40	4340–4520	+0.4	−10.3
30	ADR-3	X-B	3980 ± 40	4340–4520	+1.6	−10.2
31	ADR-3	X-B	3980 ± 40	4340–4520	+1.1	−9.9
Sediment samples						
35	ADR-sed-1	X-B	3390 ± 40	3560–3720	−5.1	−8.6
36	ADR-sed-2	X-B	3520 ± 40	3690–3890	−6.8	−13.1
37	ADR-sed-3	X-B	3980 ± 40	4340–4520	−12.1	−19.6

PDB: Pee Dee Belemnite.

agree with other published studies of the region that used different proxy data. Silva et al. (2011) measured the $\delta^{13}C$ values of Holocene soil organic matter in central Argentina and concluded that C_4 species were more abundant in the past, and gradually, C_3 species increased numerically in a significant manner. They associated the gradual replacement of C_4 by C_3 plants with a progressive climate change from warmer/drier during the Holocene to colder/wetter at present.

For comparison, our late Holocene data here were plotted jointly with gastropod data collected by Bonadonna et al. (1999) from the last glacial and early Holocene in Argentina (Figure 7a). The $\delta^{13}C$ values of gastropod shells from Argentina suggest a higher proportion of C_4 plants during the last glacial and, from there, the proportion of C_4 plants gradually declined to present negligible values. Overall, previously published terrestrial gastropod data from Argentina combined with the present study suggest that the vegetation has shifted significantly over the last 30,000 years and that C_4 plants in the past showed notably higher abundance, which gradually dropped to present levels. This Quaternary regression of C_4 plants is probably best explained by climate change (Silva et al., 2011).

The intra-shell $\delta^{13}C$ values are used to evaluate seasonal variations in gastropod diet, which, in turn, should reflect seasonal variations in the surrounding vegetation. The three individuals analyzed exhibited generally higher $\delta^{13}C$ values during the initial growth episodes and gradually fluctuated thereafter (Figure 6a–c). However, the dietary habits seem to have been relatively comparable throughout the gastropod lifespan and did not show distinctive seasonal cycles. The modern shell (Figure 6a) showed the smallest seasonal variation in $\delta^{13}C$ values ($\delta^{13}\Delta = 1.7$‰), whereas the specimen recovered from the 1.7–1.9 cal. kyr BP layer (Figure 6b) exhibited the largest variation in intra-shell $\delta^{13}C$ values ($\delta^{13}\Delta = 3.0$‰). As inferred from entire-shell analyses, both late Holocene shells were, on average, about 4‰ higher in intra-shell $\delta^{13}C$ values than the values from the modern individual (Figure 6a–c), reinforcing that gastropods consumed substantially higher proportions of C_4 plants during the late Holocene (between 3.7 and 1.7 cal. kyr BP) than at present, whereas today, C_4 plants seem to be negligible in the study area. The fluctuation in intra-shell $\delta^{13}C$ values may depict (1) slight seasonal variations in the proportion of C_3 versus C_4 plants, (2) variations in foliar $\delta^{13}C$ values of C_3 plants associated with seasonal shifts in water availability, (3) or both.

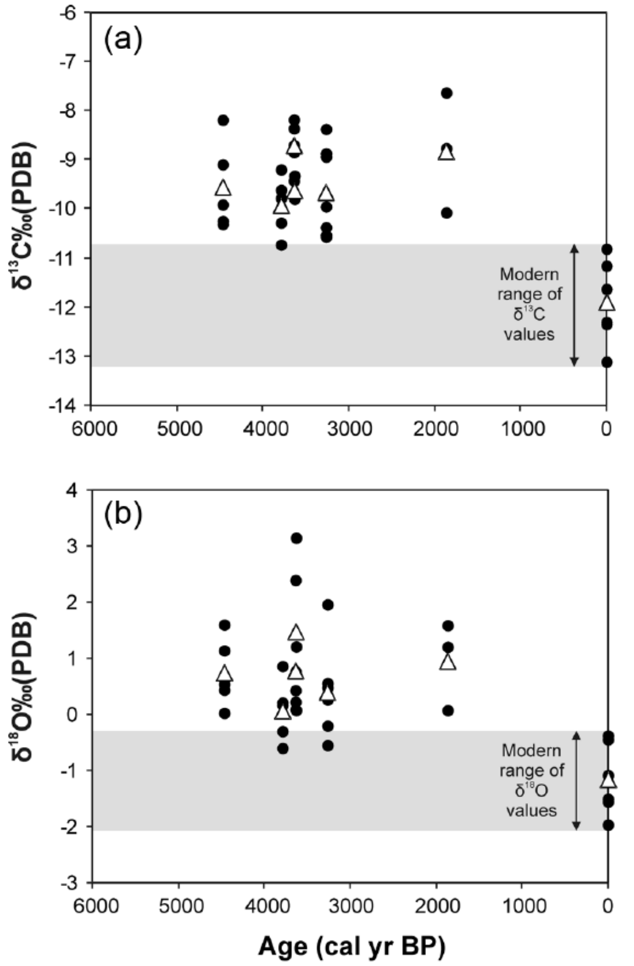

Figure 5. Stable isotope results of modern (gray band) and fossil *Plagiodontes* shells from the Alero Deodoro Roca archaeological site, Ongamira valley (Córdoba, central Argentina). (a) Carbon stable isotope values through time. (b) Oxygen stable isotope values through time.
PDB: Pee Dee Belemnite.

Oxygen stable isotopes

The $\delta^{18}O$ values of modern shells are 2.8‰ higher than measured local rainwaters. The evaporative steady-state flux balance-mixing model by Balakrishnan and Yapp (2004) is used here to calculate the value of RH during calcification. This model predicts that the $\delta^{18}O$ value of the shell is mainly influenced by air temperature, rainwater, and water vapor $\delta^{18}O$ values and RH during the gastropod active period. Model calculations here assume that water loss occurred through evaporation and that rainwater and water vapor were in isotopic equilibrium. If the shell precipitates at present average environmental conditions, that is, average air temperatures of 17°C and rainwater $\delta^{18}O$ values of −4‰, then, modern shells, with an average $\delta^{18}O$ value of −1.2‰, should have precipitated at RH values of around 94%. This predicted value from the shell is very similar to the observed maximum value of RH today in the study area (93%, on average). The predicted value of RH suggests that *Plagiodontes* specimens are currently mostly active and grow shell at considerably moist conditions. Interestingly, all measured late Holocene shells exhibited comparable values among them, but, on average, they were 1.8‰ higher than modern counterparts. If air temperature and rainwater $\delta^{18}O$ values were similar during the late Holocene than at present, then, the model by Balakrishnan and Yapp (2004) predicts that ancient shells deposited shell at RH values of around 90%, on average. Model calculations suggest that late Holocene shells grew under significantly lower RH values than today, if all other environmental variables are held constant. Alternatively, a combination of higher rain $\delta^{18}O$ values as a result of lower rainfall or increased summer precipitation and lower RH during the late Holocene could also explain the observed patterns. The inferred drier scenario during the late Holocene in Ongamira valley here agrees with published proxy data from the region (e.g. Silva et al., 2011). Based on eolian deposit and paleosol evidence, the Holocene in the Pampean Region has been considered as a wet period during the early Holocene, from 8.5 to 3.5 kyr BP, and a dry interval during the late Holocene, from 3.5 to 1.4 kyr BP (Iriondo and García, 1993). Carignano (1999) studied the Quaternary climate in Córdoba Province and, based on geomorphological evidence, he also concluded that a widespread eolian deposition during the mid-to-late Holocene depicts a drier scenario. These published studies from the region that used different proxy data agree with the terrestrial gastropod results reported in the present work.

Shell $\delta^{18}O$ values from late Holocene specimens from Ongamira generally overlapped with published terrestrial gastropod values by Bonadonna et al. (1999) from the early Holocene (8.2–10.8 cal. kyr BP) and the Late Glacial period (28.0–35.3 cal. kyr BP) of Argentina (Figure 7b). This overlap of values suggests that gastropods recorded somewhat drier conditions at those age intervals. However, they all differ significantly from values of modern specimens collected in Ongamira (Figure 7b), supporting that gastropods grew their shells at times when RH was lower and/or rain $\delta^{18}O$ values were higher (e.g. lower rainfall totals or increased summer precipitation) in the past than at present. The inferred trend from drier conditions during the late Holocene towards wetter conditions at present may have affected the aboriginal resource selection and exploitation. An increase in land snail consumption during the late Holocene could be linked to a decline in other resources affected by the drought period. Moreover, this change in the natural moisture regime during the late Holocene, which caused changes in the vegetation cover (as revealed by the shell $\delta^{13}C$ values), may have affected the distribution and abundance of native vertebrate fauna in the study site.

Intra-shell $\delta^{18}O$ values of a modern specimen (n = 49) varied up to 5.5‰, in agreement with the range of measured rain $\delta^{18}O$ values in the study site (Figure 6d). This suggests that intra-shell $\delta^{18}O$ values likely mimic the seasonal variation of local rain $\delta^{18}O$ values. Archaeological shells showed similar magnitude of variation in the intra-shell $\delta^{18}O$ values (Figure 6e and f), pointing to a similar degree of seasonality during the late Holocene and today. The three analyzed individuals showed from two to three marked seasonal cycles, suggesting that they exhibited a lifespan of around 2–3 years. Even though the degree of seasonality seems to have been comparable throughout the late Holocene in central Argentina, intra-shell $\delta^{18}O$ values of archaeological individuals were, on average, significantly higher than those from the modern shell, as observed in entire-shell data reported above. This finding reinforces that gastropods during late Holocene in Ongamira valley grew their shells when conditions were rather drier than today at all seasons.

Conclusion

Well-preserved *Plagiodontes* shells (Gastropoda: Orthalicidae: Odontostominae) from the Alero Deodoro Roca–Sector B archaeological site in Ongamira valley (Córdoba province) were analyzed isotopically to infer the paleoenvironment in central Argentina during the late Holocene. The carbon stable isotope values indicate that C_4 plants were notably more abundant during ~4.5–1.7 cal. kyr BP, pointing to a temporal decline in the local C_4 plant cover to present negligible values. The oxygen stable isotope composition of the shell suggests that environmental conditions at ~4.5–1.7 cal. kyr BP were drier (e.g. lower RH and/or

Table 5. Intra-shell oxygen and carbon stable isotope values of *Plagiodontes daedaleus* shells from the Alero Deodoro Roca–Sector B archaeological site, Ongamira, Córdoba, central Argentina.

Sample ID	~Age (kyr)	δ18O‰ (PDB)	δ13C‰ (PDB)	Sample ID	~Age (kyr)	δ18O‰ (PDB)	δ13C‰ (PDB)
ONG-mod-lip	Modern	−3.3	−11.8	ONG-mod-47	Modern	−1.2	−11.6
ONG-mod-1	Modern	−2.5	−12.4	ONG-mod-prot	Modern	−1.0	−11.4
ONG-mod-2	Modern	−2.5	−12.4	ADR 614-lip	1.8	−0.6	−7.2
ONG-mod-3	Modern	−3.4	−12.3	ADR 614-1	1.8	−0.3	−7.3
ONG-mod-4	Modern	−2.0	−12.4	ADR 614-2	1.8	−0.7	−9.3
ONG-mod-5	Modern	−3.0	−12.5	ADR 614-3	1.8	−1.2	−8.8
ONG-mod-6	Modern	−0.4	−12.8	ADR 614-4	1.8	−1.3	−8.9
ONG-mod-7	Modern	0.1	−12.7	ADR 614-5	1.8	−0.5	−8.3
ONG-mod-8	Modern	1.1	−12.6	ADR 614-6	1.8	0.0	−8.9
ONG-mod-9	Modern	0.6	−12.1	ADR 614-7	1.8	0.0	−8.5
ONG-mod-10	Modern	−1.3	−12.1	ADR 614-8	1.8	0.1	−8.6
ONG-mod-11	Modern	−0.6	−12.3	ADR 614-9	1.8	0.6	−9.0
ONG-mod-12	Modern	2.2	−12.1	ADR 614-10	1.8	2.2	−8.8
ONG-mod-13	Modern	2.0	−12.3	ADR 614-11	1.8	1.1	−8.6
ONG-mod-14	Modern	−0.1	−12.2	ADR 614-12	1.8	1.5	−9.2
ONG-mod-15	Modern	0.6	−12.4	ADR 614-13	1.8	0.8	−8.6
ONG-mod-16	Modern	−0.1	−12.3	ADR 614-14	1.8	0.5	−8.9
ONG-mod-17	Modern	0.7	−12.3	ADR 614-15	1.8	0.2	−8.8
ONG-mod-18	Modern	−0.9	−12.3	ADR 614-16	1.8	0.5	−8.4
ONG-mod-19	Modern	−0.4	−12.4	ADR 614-17	1.8	0.3	−8.8
ONG-mod-20	Modern	−0.4	−12.2	ADR 614-18	1.8	0.1	−8.5
ONG-mod-21	Modern	0.5	−12.1	ADR 614-19	1.8	0.7	−9.1
ONG-mod-22	Modern	0.5	−12.4	ADR 614-20	1.8	1.4	−8.5
ONG-mod-23	Modern	0.7	−12.2	ADR 614-21	1.8	2.7	−8.8
ONG-mod-24	Modern	−1.5	−12.0	ADR 614-22	1.8	2.4	−8.6
ONG-mod-25	Modern	−1.1	−11.6	ADR 614-23	1.8	3.1	−8.9
ONG-mod-26	Modern	−1.5	−12.0	ADR 614-24	1.8	3.7	−8.7
ONG-mod-27	Modern	−2.7	−12.1	ADR 614-25	1.8	3.4	−8.4
ONG-mod-28	Modern	−2.2	−12.0	ADR 614-26	1.8	3.8	−8.6
ONG-mod-29	Modern	−1.8	−12.0	ADR 614-27	1.8	4.3	−9.0
ONG-mod-30	Modern	−2.2	−12.0	ADR 614-28	1.8	0.1	−6.6
ONG-mod-31	Modern	−1.8	−12.1	ADR 614-29	1.8	−0.3	−7.3
ONG-mod-32	Modern	−1.6	−13.1	ADR 614-30	1.8	1.3	−7.3
ONG-mod-33	Modern	−2.0	−12.8	ADR 614-31	1.8	1.6	−8.2
ONG-mod-34	Modern	−1.4	−12.7	ADR 614-32	1.8	0.2	−7.3
ONG-mod-35	Modern	−1.0	−12.6	ADR 614-33	1.8	1.0	−7.5
ONG-mod-36	Modern	−1.6	−12.2	ADR 614-34	1.8	0.5	−7.4
ONG-mod-37	Modern	−0.7	−12.5	ADR 614-35	1.8	0.4	−7.3
ONG-mod-38	Modern	−0.7	−12.1	ADR 614-36	1.8	−0.5	−7.0
ONG-mod-39	Modern	−0.8	−12.2	ADR 614-37	1.8	−0.3	−6.9
ONG-mod-40	Modern	−1.4	−12.2	ADR 614-38	1.8	−0.6	−6.8
ONG-mod-41	Modern	−1.2	−12.0	ADR 614-39	1.8	−0.1	−6.7
ONG-mod-42	Modern	−1.1	−11.9	ADR 614-40	1.8	0.2	−6.8
ONG-mod-43	Modern	−2.1	−11.6	ADR 614-41	1.8	0.2	−6.3
ONG-mod-44	Modern	−2.6	−11.9	ADR 614-42	1.8	0.0	−6.3
ONG-mod-45	Modern	−2.2	−11.8	ADR 614-43	1.8	−0.1	−6.8
ONG-mod-46	Modern	−2.1	−11.6	ADR 614-prot	1.8	0.0	−6.6
ADR-1-lip	3.6	−1.4	−6.7	ADR-1-26	3.6	−1.0	−7.6
ADR-1-1	3.6	−0.9	−6.7	ADR-1-27	3.6	−0.8	−7.8
ADR-1-2	3.6	−0.9	−7.1	ADR-1-28	3.6	−1.0	−7.8
ADR-1-3	3.6	−1.1	−7.1	ADR-1-29	3.6	−0.8	−7.5
ADR-1-4	3.6	−2.1	−6.6	ADR-1-30	3.6	0.1	−8.1
ADR-1-5	3.6	−0.3	−7.6	ADR-1-31	3.6	−0.9	−7.9
ADR-1-6	3.6	−1.1	−7.2	ADR-1-32	3.6	−1.8	−7.8
ADR-1-7	3.6	−0.5	−7.2	ADR-1-33	3.6	−1.0	−8.2
ADR-1-8	3.6	−0.8	−7.5	ADR-1-34	3.6	−1.0	−8.4
ADR-1-9	3.6	−0.8	−7.4	ADR-1-35	3.6	−1.1	−8.6
ADR-1-10	3.6	0.2	−7.5	ADR-1-36	3.6	−1.7	−8.0
ADR-1-11	3.6	−0.4	−7.4	ADR-1-37	3.6	−0.8	−8.2
ADR-1-12	3.6	−0.3	−7.1	ADR-1-38	3.6	0.6	−8.0
ADR-1-13	3.6	−0.3	−7.2	ADR-1-39	3.6	2.9	−8.5
ADR-1-14	3.6	0.3	−7.6	ADR-1-40	3.6	1.4	−8.2
ADR-1-15	3.6	0.1	−7.8	ADR-1-41	3.6	1.2	−7.9
ADR-1-16	3.6	−0.5	−7.0	ADR-1-42	3.6	−0.6	−7.5
ADR-1-17	3.6	2.9	−7.8	ADR-1-43	3.6	0.4	−7.9
ADR-1-18	3.6	2.7	−7.3	ADR-1-44	3.6	−1.6	−7.3
ADR-1-19	3.6	2.8	−7.5	ADR-1-45	3.6	−1.1	−8.0
ADR-1-20	3.6	1.5	−7.5	ADR-1-46	3.6	−0.4	−7.6
ADR-1-21	3.6	2.1	−7.5	ADR-1-47	3.6	−0.4	−7.2
ADR-1-22	3.6	1.8	−7.5	ADR-1-48	3.6	−0.2	−7.4
ADR-1-23	3.6	1.1	−7.2	ADR-1-49	3.6	−0.1	−7.3
ADR-1-24	3.6	−0.7	−6.9	ADR-1-prot	3.6	0.0	−7.0
ADR-1-25	3.6	−1.0	−7.6				

PDB: Pee Dee Belemnite.

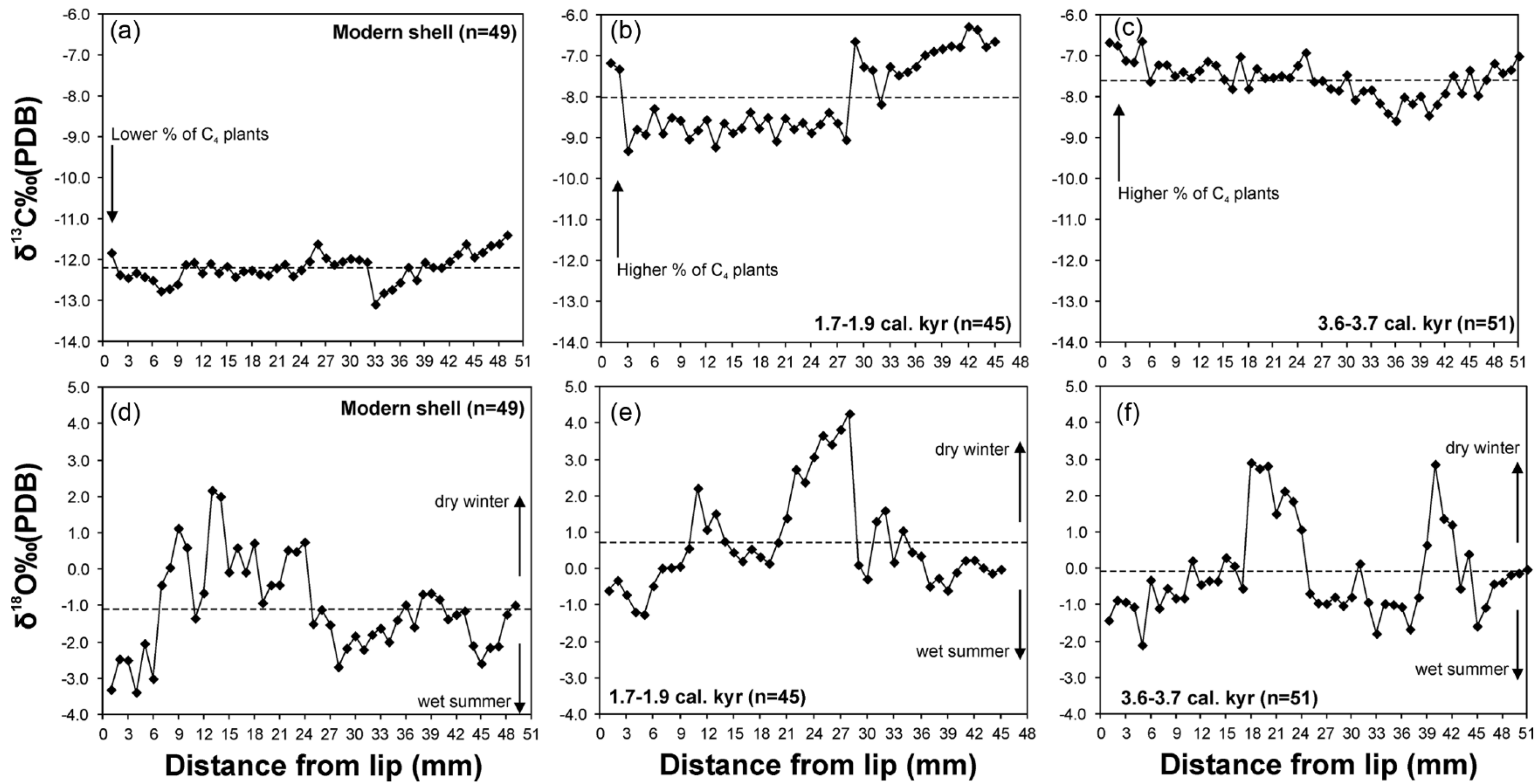

Figure 6. Intra-shell isotopic profiles of three *Plagiodontes* specimens. (a)–(c) Carbon stable isotope values along ontogeny. (d)–(f) Oxygen stable isotope values along ontogeny.
PDB: Pee Dee Belemnite.
Dashed lines depict average values.

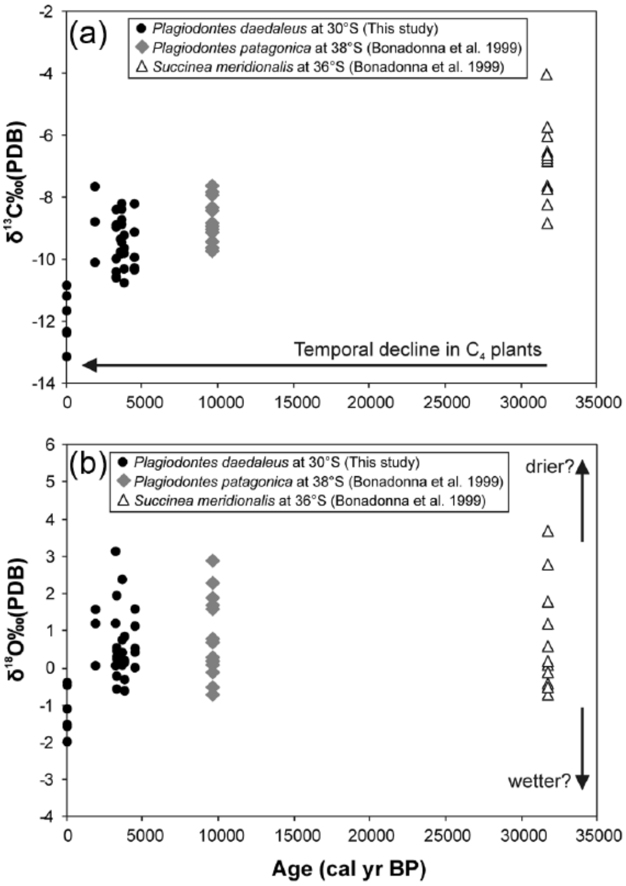

Figure 7. Temporal variations in the stable isotope composition of terrestrial gastropod shells from Argentina since the last glacial to the present: (a) carbon stable isotope values; (b) oxygen stable isotope values.
PDB: Pee Dee Belemnite.
Source: Last glacial and early Holocene data were adapted from Bonadonna et al. (1999) whereas late Holocene data are from the present study.

higher rain $\delta^{18}O$ values) than today. The inferred drier conditions during the late Holocene may have, in turn, favored the expansion of C_4 plants in the study area. Published Late Glacial and early Holocene terrestrial gastropod data from farther south in Argentina (36°S–38°S) display equivalent isotopic values than late Holocene shells from Ongamira (30°S), suggesting that gastropods also recorded somewhat drier conditions and higher abundance in C_4 plants at those times in other regions of Argentina. High-resolution isotopic profiles of terrestrial gastropod shells point to reduced seasonal variation in the $\delta^{13}C$ values of assimilated plants ($\Delta^{13}C$ = 2–3‰), whereas seasonal variation of rain $\delta^{18}O$ values was quite marked ($\Delta^{18}O$ = 5.0–5.5‰). The magnitude of seasonality was comparable between fossil and modern individuals. Conclusively, terrestrial gastropods from South America are valuable paleoenvironmental archives and the combination of entire-shell and intra-shell isotopic analyses offer more informed environmental information.

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