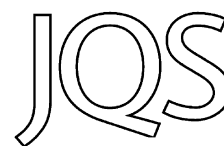


Younger Dryas – early Holocene transition in the south-eastern Iberian Peninsula: insights from land snail shell middens



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ABSTRACT: The land snail *Sphincterochila candidissima* from archeological records in Villena (SE Spain) was studied isotopically to estimate the Younger Dryas (YD)–early Holocene transition in the western Mediterranean. Live-collected individuals exhibited body ($-21.8 \pm 1.6\text{‰}$) and shell ($-5.8 \pm 1.4\text{‰}$) $\delta^{13}\text{C}$ values typical of a C_3 plant diet, probably combined with carbonate ingestion. Calculations of a carbon flux balance-mixing model suggest that living specimens experienced similar metabolic rates, with comparable ratio of input and output fluxes of bicarbonate from the snail hemolymph. All fossil shells showed comparable $\delta^{13}\text{C}$ values among each other, but values were $\sim 2\text{‰}$ higher than living specimens. This may be explained by higher water stress at the YD–Holocene transition or by the Suess effect. Shell $\delta^{18}\text{O}$ values averaged $+1.3 \pm 0.8\text{‰}$ for living individuals, $-0.5 \pm 0.8\text{‰}$ for Holocene (8.4–10.2 cal ka BP) specimens and $+0.4 \pm 0.6\text{‰}$ for YD (12.0–12.4 cal ka BP) snails. An oxygen flux balance-mixing model suggests that YD shells precipitated during relative humidity (RH) values of $\sim 79\text{--}82\%$, after which RH increased gradually reaching maximum values of $\sim 87\text{--}88\%$ at $\sim 8.4\text{--}8.6$ cal ka BP and, from there, RH eventually declined to present values of $\sim 82\%$. Comparisons with other snail data suggest that the xerophilous *Sphincterochila* records different environmental signatures from other contemporaneous taxa.

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KEYWORDS: land snails; shell middens; stable isotopes; western Mediterranean; Younger Dryas.

Introduction

Some prehistoric human groups used to collect and consume edible (i.e. medium to large size: $>10\text{--}15$ mm in length) land snails as a complementary food resource. After consumption, snail shells were frequently discarded in so-called shell middens (sites containing shells and other remains consumed or used by humans accumulated over time). In other cases, shells were discarded to combustion areas. Prehistoric accumulations of shells reflect past socio-economic activities and human-induced ecological and landscape modifications (Burney *et al.*, 2001). Moreover, the isotopic composition of aragonitic land snail shells recovered from archeological sites offers insights into past environmental conditions during ancient human occupation. The carbon isotopic composition ($\delta^{13}\text{C}$) of the shell is principally affected by the $\delta^{13}\text{C}$ values of the oxidized vegetation consumed and assimilated by the snail (Stott, 2002; Metref *et al.*, 2003). The oxygen isotopic composition ($\delta^{18}\text{O}$) of the shell is mainly influenced by four environmental variables: liquid water $\delta^{18}\text{O}$ values, water vapor $\delta^{18}\text{O}$ values, air temperature and relative humidity (Yapp, 1979; Balakrishnan and Yapp, 2004; Balakrishnan *et al.*, 2005a, 2005b). Hence, the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of archeological shells have been increasingly used as paleovegetation and paleoatmospheric proxies, respectively (Balakrishnan *et al.*, 2005b; Colonese *et al.*, 2007, 2010a, 2010b, 2011, 2013a, 2013b; Yanes *et al.*, 2011, 2012, 2013). However, the relationship between the isotopic composition of the shell and the environment can be complicated by other less well-understood factors. For example, the $\delta^{13}\text{C}$ values of the shell may in part be affected by the $\delta^{13}\text{C}$ values of

limestone on which snails live (Goodfriend and Hood, 1983; Goodfriend, 1987; Goodfriend *et al.*, 1999), and further complications may arise if contemporaneous snails experience differing metabolic rates (Balakrishnan and Yapp, 2004). The $\delta^{18}\text{O}$ values of the shell are influenced by multiple atmospheric factors operating jointly (Balakrishnan and Yapp, 2004). The $\delta^{18}\text{O}$ values of the snail body fluid (and, in turn, the shell) are several per mil richer in ^{18}O with respect to environmental water. Balakrishnan and Yapp (2004) explained mathematically this process by a steady-state flux balance model in which water from the snail body fluid is lost through evaporation only. The aforementioned complexities can be minimized by the study of local modern analogs of the same taxa. Thus, establishing local modern snail isotopic baselines are essential to better interpret the environmental significance of the stable isotopes extracted from ancient shells.

While the isotopic compositions of aquatic shells recovered from shell middens have been used intensively over decades to deduce past climatic conditions and the season of shellfish collection (see a recent review and publications by Andrus, 2011; Andrus and Thompson, 2012; Surge and Barrett, 2012; and numerous references therein), land snail shells have been relatively much less well studied. However, the recent growing body of isotopic studies on land snail shells preserved in archeological sites suggests that they are promising paleoenvironmental archives that complement other marine and continental proxies (Balakrishnan *et al.*, 2005b; Colonese *et al.*, 2007, 2010a, 2010b, 2011, 2013a, 2013b; Yanes *et al.*, 2011, 2012, 2013). Land snail shell middens are quite abundant in the Mediterranean region, both in southern Europe and in northern Africa (Lubell, 2004a, 2004b). In the Iberian Peninsula, the southernmost part of Europe, human-

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induced land snail shelly accumulations are common (Gutiérrez-Zugasti, 2011; Fernández-López-de-Pablo *et al.*, 2011a, 2011b; Lloveras *et al.*, 2011). Quaternary shell middens are abundant in several sites of the upper Vinalopó Valley in Villena, Alicante (Fig. 1), in the south-east of Spain (Fernández-López-de-Pablo *et al.*, 2011a, 2011b). These shells provide an excellent opportunity to explore Lateglacial–Holocene environmental shifts in the westernmost part of the Mediterranean using an alternative continental proxy not commonly exploited in the region. In the present study, live-collected specimens were analysed isotopically to establish the first modern isotopic baseline for the xerophilous snail *Sphincterochila candidissima* (Draparnaud, 1801). Secondly, the carbon and oxygen stable isotope compositions of ancient land snail shells and the sediment matrix where shells were preserved were analysed to elucidate the latest Pleistocene–early Holocene transition in south-eastern Spain. New radiocarbon analyses are also reported to better constrain the chronological context of these archaeological sites.

Materials and methods

Climate and vegetation

The Villena basin, Alicante (Fig. 1), exhibits a Mediterranean-type climate, with warm, dry summers and cool, wet winters (Fig. 2), but with continental influence. Local climatic data are available in Torre-García and Alías-Pérez (1996) and the meteorological station for Alicante for the recording period 1971–2000 (Agencia Estatal de Meteorología: www.aemet.es). Average air temperature ranges from 22.8 °C in July–August to 6.4 °C in January (Fig. 2A). The mean annual temperature is 14 °C. Temperature during spring and fall (March–May and September–November) is also 14 °C. Precipitation ranges from a minimum of 5.5 mm in July to a maximum of 55.8 mm in October (Fig. 2A). Total annual

precipitation is 373 mm. During spring and fall only, precipitation is 232 mm, which reveals the current semi-arid nature of the study area. Average relative humidity (RH) is quite stable throughout the year in Alicante, ranging from 62% in April to 69% in October (Fig. 2B). Mean annual RH is 66%. This average value remains the same if only rainy months are considered. Maximum RH values were not available. Air moisture content is probably strongly influenced by the short distance to the Mediterranean Sea. The weighted annual mean oxygen isotopic composition of current precipitation in Alicante, SE Spain, is -7.0‰ vs. SMOW (Araguás-Araguás and Díaz-Teijeiro, 2005). If only fall and spring rain $\delta^{18}\text{O}$ values are considered, the average $\delta^{18}\text{O}$ value of rainfall in Alicante remains equivalent to the annual value.

The study area is characterized by an open-vegetation cover adapted to dry conditions dominated by vascular plants that follow a C_3 photosynthetic pathway. Native C_4 and CAM plants are not present in the sampling locality. The vegetation cover is dominated by pine tree forests of the species *Pinus halapensis* and *P. pinea*, and by shrubs and herbs of species such as *Rosmarinus officinalis* and *Ulex parviflorus* (Torre-García and Alías-Pérez, 1996).

Land snail species

Although many land snails are hygrophilous or favored under wetter conditions because they are highly sensitive to dehydration, some species are xerophilous, i.e. taxa well adapted to arid conditions through behavioral, physiological or morphological mechanisms (Moreno-Rueda, 2007). This is the case of *Sphincterochila candidissima*, which is abundant in arid environments of the western Mediterranean (Martínez-Ortí, 1999; Martínez-Ortí and Robles, 2003). The species exhibits a white and thick shell, which allows it to reduce water loss during estivation (Moreno-Rueda, 2008). Moreno-Rueda and Collantes-Martin (2007) observed that *S.*

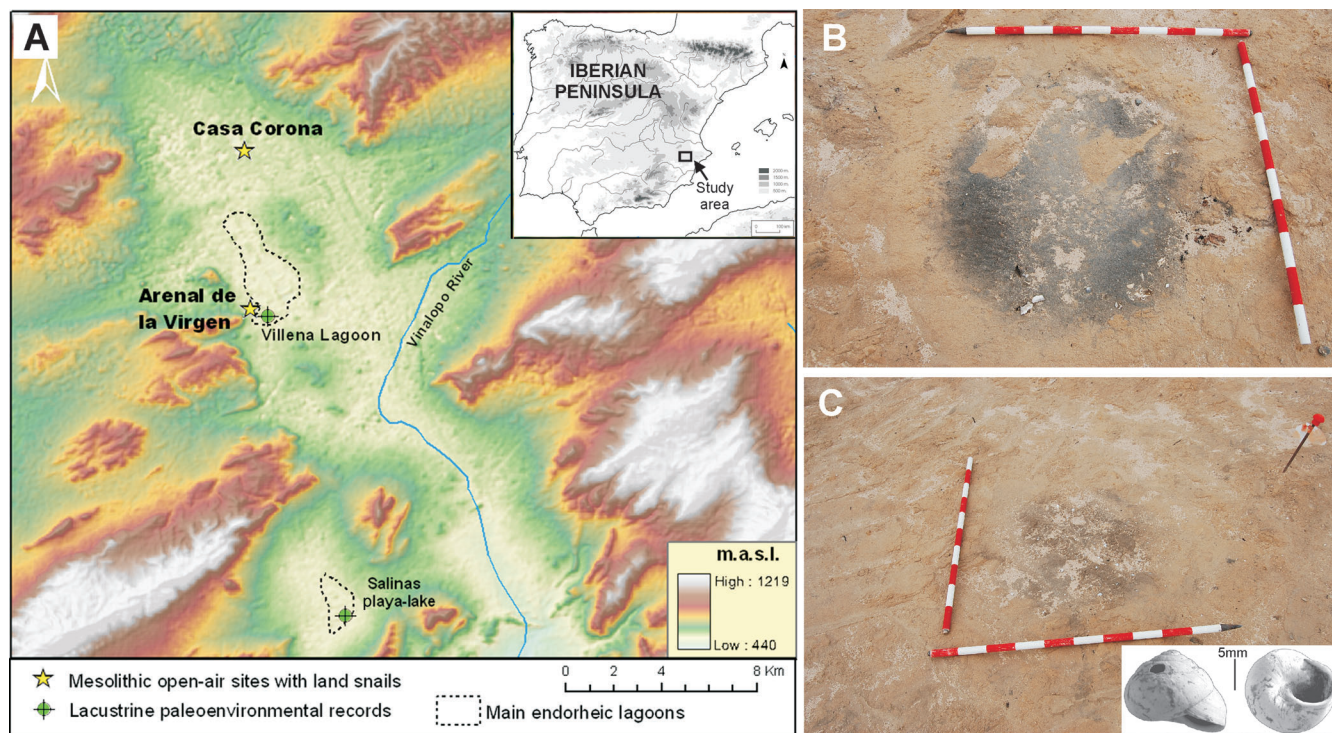


Figure 1. Geographical location and photographs of the studied archaeological sites (adapted after Fernández-López-de-Pablo *et al.*, 2011a, 2011b). (A) Map of the two studied localities (Arenal de la Virgen and Casa Corona). (B) Photograph of the UE142 site, dated at 12.0–12.4 cal ka BP. (C) Photograph of the UE166 site, dated at 9.5–9.6 cal ka BP, and a detailed view of the targeted land snail species (*Sphincterochila candidissima*). This figure is available in colour online at wileyonlinelibrary.com.

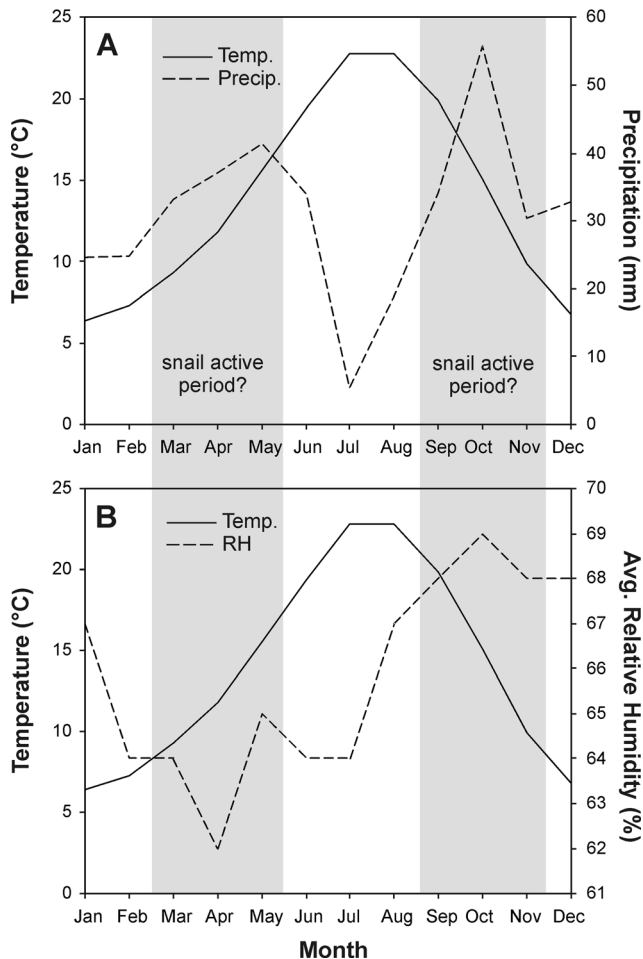


Figure 2. Current atmospheric conditions in the Valle de Vinalopó, Alicante, SE Spain. Temperature and precipitation data were adapted from (Torre-García and Alías-Pérez, 1996), whereas mean relative humidity data were taken from the Spanish Agencia Estatal de Meteorología (www.aemet.es). Gray bands depict possible current snail active periods associated with higher rainfall totals and milder conditions. It is assumed that snail growth is reduced during the summer and the winter months, as suggested by field observations by Moreno-Rueda and Collantes-Martin (2007).

candidissima from Granada (SE Spain) was primarily active during fall and spring. The species hibernates underground to avoid low temperatures and estivates above ground (on plants) to elude soil heat. During periods of inactivity, specimens develop epiphragms that seal the aperture of the shells to minimize desiccation (Martínez-Ortí, 1999). We therefore assumed that calcification of measured specimens took place principally between March and May and between September and November (see gray bands in Fig. 2). *S. candidissima* exhibits a maximum lifespan of ~6 years with two reproductive cycles during spring and fall. It is herbivorous and feeds upon decayed and living plant matter. Considering the significant thickness (~1.2–1.6 mm, $n=5$) and large size (~14–22 mm in length and ~18–25 mm in width; $n=5$) of their shells (Fig. 1C), which should help to prevent dehydration, it is likely that this species ingests carbonates from surrounding sediments and rocks as a source of calcium to build their shells and encourage shell growth.

Archeological context and sampling protocol

Four archeological structures from two archeological, open-air, sites were sampled in the Villena basin (SE Spain), about 80 km inland from the Mediterranean coast (Fig. 1A–C). This

includes two hearths and the filling sediment of a burial pit grave from the Casa Corona site (UE166, UE142 and UE128), and a hearth from the Arenal de la Virgen site (ARVIR-IV), about 6 km south from Casa Corona (Fig. 1A). The study area is located at 500 m above sea level (a.s.l.) on the upper course of the Vinalopó river (Fig. 1A). Shells were preserved together with lithic artifacts and bone remains. Archeological evidence suggests all these deposits are early Mesolithic in age, apart from the UE142 site, which yielded an Epipaleolithic radiocarbon age (Table 1). Land snails are associated with either habitation structures (Fig. 1B,C) or the filling sediments of a burial structure (UE128). Thousands of shells were found on each site and are presently deposited in the Institut Català de Paleoeologia Humana i Evolució Social (IPHES).

Thirty-two entire shells (eight from each archeological structure) were selected for stable isotope analyses. In addition, aliquots of the bulk sediment matrix in which shells were preserved were collected to evaluate the isotopic signature of surrounding carbonates. To establish the first isotopic baseline for *S. candidissima*, nine live specimens from the Arenal de la Virgen region were also collected for subsequent isotopic analyses of the shell and body tissue. The carbon isotope composition of the body tissue was measured as a second proxy for plant diet in addition to the shell. Although surrounding plants were not available for isotopic analyses, the body tissue is a reliable vegetation proxy because it is influenced by the carbon isotopes derived from assimilated plants only (DeNiro and Epstein, 1978) with no contribution from ingested limestone. Bootstrap simulations show that the isotopic measurement of five shells per locality is sufficient to estimate the central tendency and available isotopic variability of both isotopes ($\delta^{18}\text{O}$ and $\delta^{13}\text{C}$). Hence, the measured number of shells per archeological structure ($n=8$) and the modern sample ($n=9$) should offer meaningful average values, regardless of isotopic variance.

The chronological context was determined by accelerator mass spectrometry radiocarbon dating of two charcoal samples recovered from ARVIR-IV (Fernández-López-de-Pablo *et al.*, 2011a, 2011b) and UE166, and two land snail shells from UE142 and UE128 (Table 1). Samples were analysed in the Beta Analytic Radiocarbon Dating Laboratory using standard procedures. Due to the potential ingestion of limestone by *Sphincterochila* throughout its lifespan, the shell aperture was selected for radiocarbon dating because it is likely to have been less affected by carbonate ingestion (Goodfriend *et al.*, 1999). To test this hypothesis, the shell aperture of a live-collected land snail from the region was also radiocarbon dated (Table 2). Radiocarbon results were calibrated using the CALIB 6.1 program and the IntCal09 curve (Stuiver and Reimer, 1993). Radiocarbon analyses conducted in the shell margin were used to estimate the age of the shells and not to quantify if and how limestone affected the carbon isotopic composition of the shell.

Shell preservation

Before stable isotope analysis, three shells from ARVIR-IV were selected to evaluate their preservation status via X-ray diffraction. Analyses were made using a Bruker-AXS D8-Discover diffractometer equipped with parallel incident beam (Göbel mirror), vertical θ - θ goniometer, XYZ motorized stage and with a GADDS (General Area Diffraction System) in the IPHES. The X-ray diffraction results demonstrated that shells contained only aragonitic crystals and therefore recrystallization or secondary overgrowths are considered insignificant. The shell material studied here is thus suitable for geochemical analyses and paleoenvironmental reconstruction.

Table 1. Radiocarbon results of archeological sites from Villena, Alicante, SE Spain.

Sample ID	Locality	Laboratory no.	Sample type	Species	$\delta^{13}\text{C}$ (‰ PDB)	^{14}C age (a BP)	Corrected age (a BP) [†]	2 σ calibrated age (cal a BP)
ARVIR-IV	Arenal Virgen	Beta-243772*	Charcoal	<i>Quercus</i> sp.	−25.8	7750 ± 40		8590–8430
UE166	Casa Corona	Beta-323497	Charcoal	<i>Quercus</i> sp.	−24.2	8520 ± 50		9550–9450
UE128	Casa Corona	Beta-330865	Land snail shell lip	<i>Sphincterochila candidissima</i>	−6.1	9110 ± 40	8900 ± 40	10 190–9900
UE142	Casa Corona	Beta-330866	Land snail shell lip	<i>Sphincterochila candidissima</i>	−5.5	10 520 ± 40	10 310 ± 40	12 380–11 980

*Data adapted from Fernández-López-de-Pablo *et al.* (2011a, 2011b).

[†] ^{14}C ages from the shell lip were corrected by the expected age anomaly of 210 a associated with dead carbon ingestion during the oldest ontogenetic stage (Table 2 and text).

Stable isotope analysis

Samples were prepared and analysed in the Stable Isotope Laboratory of the Department of Earth and Environmental Sciences, University of Kentucky. The snail body was separated manually from the shell, rinsed with deionized water, oven-dried at 40 °C overnight and homogenized using an electric blender. About 1.5 mg of each organic sample was weighed in a tin capsule, crimped and combusted in a Costech Elemental Analyzer (ESC 4010). The CO_2 and N_2 produced after combustion were analysed using a Finnigan Delta^{PLUS} XP isotope ratio mass spectrometer. Analytical uncertainty was ± 0.1‰ based on the recurrent measurements of in-house standards dispersed periodically throughout each run sequence ($n = 10$).

Adult shells were cleaned mechanically in distilled water with ultrasonication, and subsequently oven-dried at 40 °C overnight. Entire shells were finely ground by hand using an agate mortar and pestle. Whole-shell analyses of numerous individuals per age interval were preferred over intra-shell analyses of a few specimens because the goal of this study was to estimate the average (dominant) environmental conditions rather than seasonal variations. The analysis of a reasonably high number of whole shells should portray a representative average environmental signature despite potential differences in seasonal behaviors among individuals. About 150 µg of carbonate was placed in a 6-mL ExetainerTM vial that was subsequently flushed with helium. The carbonate was converted to CO_2 gas by adding 0.1 mL of 100% H_3PO_4 at 25 °C. The CO_2 was analysed after 24 h using the GasBench II connected to the isotope ratio mass spectrometer. Stable isotope results are reported in δ notation relative to the international standard Pee Dee Belemnite (PDB). The δ values are defined as:

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

where $R = ^{13}\text{C}/^{12}\text{C}$ or $^{18}\text{O}/^{16}\text{O}$. Analytical uncertainty was ± 0.1‰ based on the periodic measurements of in-house and international standards throughout each sequence ($n = 18$).

Results

Radiocarbon results

The shell aperture of a live-collected *Sphincterochila* specimen from Arenal de la Virgen exhibited a ^{14}C age of 102 ± 0.30 (percentage modern carbon, pMC), which indicates that fossil specimens probably exhibit an age anomaly of about 210 a in the shell lip (Table 2). This result points to a minimal limestone ingestion by *Sphincterochila* at the oldest ontogenetic stage. Such age anomaly estimates were used to correct the ages obtained from archeological shells. Radiocarbon analyses of the shell aperture of two fossil *Sphincterochila* shells indicate an age of 12.0–12.4 cal ka BP for the UE142 site, coinciding with the Younger Dryas (YD) period of the northern hemisphere (e.g. Rasmussen *et al.*, 2011), and an age of 9.9–10.2 cal ka BP for the UE128 site (Table 1). Two samples of charcoal of oak (*Quercus* sp.) from two hearths of Casa Corona (UE166) and Arenal de la Virgen (ARVIR-IV) exhibited an age of 9.5–9.6 and 8.4–8.6 cal ka BP, respectively (Table 1). It is assumed that these four radiocarbon ages (Table 1) represent the chronological context of all shells and sediments analysed isotopically in this work.

Stable isotopes of land snail tissues

Bulk body tissue samples of live-collected *Sphincterochila* shells from Villena, Alicante (SE Spain), ranged in $\delta^{13}\text{C}$ values from −23.9 to −19.6‰ (Table 3; Fig. 3A), and averaged $-21.8 \pm 1.6\text{‰}$ ($n = 9$). Shell $\delta^{13}\text{C}$ values of living specimens ranged from −7.2 to −3.2‰ (Table 3; Fig. 3A), averaging $-5.8 \pm 1.4\text{‰}$ ($n = 9$). The $\delta^{13}\text{C}$ values of snail body and shell correlated positively ($r = 0.80$, $P = 0.0089$, $n = 9$; Fig. 3A).

The $\delta^{13}\text{C}$ values of all fossil shells ranged from −5.0 to −1.6‰ (Table 4; Fig. 4A), averaging $-3.5 \pm 1.0\text{‰}$ ($n = 32$). Shells recovered from each archeological site (UE142, UE128, UE166 and ARVIR-IV) showed respective average $\delta^{13}\text{C}$ values of $-3.1 \pm 1.2\text{‰}$ ($n = 8$), $-2.7 \pm 1.0\text{‰}$ ($n = 8$), $-4.2 \pm 0.4\text{‰}$ ($n = 8$) and $-3.7 \pm 0.9\text{‰}$ ($n = 8$). Overall, YD–early Holocene (~8.4–12.5 cal ka BP) shells were, on

Table 2. Radiocarbon analysis of a live-collected *Sphincterochila candidissima* shell from the Arenal de la Virgen locality, Villena, Alicante.

Sample ID	Locality	Collection year	Laboratory no.	Sample type	Species	$\delta^{13}\text{C}$ (‰, PDB)	Shell ^{14}C (pMC)	Contemporary ^{14}C (pMC)	Age anomaly (years)
AVIR-0	Arenal Virgen	2011	Beta-347475	Land snail shell lip	<i>Sphincterochila candidissima</i>	−5.1	102.4 ± 0.30	105	210

pMC, % modern carbon. Contemporary ^{14}C value for comparison was taken from extrapolation of data in Levin and Heshaimer (2000).

Table 3. Carbon and oxygen stable isotope values of live-collected *Sphincterochila candidissima* specimens from Casa Corona, Villena, Alicante, SE Spain.

Sample ID	Body tissue		Shell	
	$\delta^{13}\text{C}$ (‰ PDB)	$\delta^{13}\text{C}$ (‰ PDB)	$\delta^{18}\text{O}$ (‰ PDB)	$\Delta^{13}\text{C}_{\text{shell-body}}$
ARVIR-0-snail-1	-19.6	-3.5	1.9	16.1
ARVIR-0-snail-2	-23.9	-6.3	0.3	17.7
ARVIR-0-snail-3	-19.9	-3.2	2.7	16.7
ARVIR-0-snail-4	-20.5	-5.7	1.3	14.7
ARVIR-0-snail-5	-22.4	-5.8	2.2	16.6
ARVIR-0-snail-6	-21.4	-6.4	1.7	15.0
ARVIR-0-snail-7	-22.5	-7.2	0.4	15.2
ARVIR-0-snail-8	-23.7	-6.9	0.4	16.8
ARVIR-0-snail-9	-22.3	-6.7	1.1	15.6

average, $\sim 2.3\text{‰}$ higher in $\delta^{13}\text{C}$ than living specimens (Fig. 4A).

The $\delta^{18}\text{O}$ values of modern snail shells ranged from $+0.3$ to $+2.7\text{‰}$ (Table 3; Fig. 4B), and averaged $+1.3 \pm 0.8\text{‰}$ ($n=9$). In contrast, fossil shells exhibited an average value of $-0.3 \pm 0.9\text{‰}$ ($n=32$), ranging from -2.8‰ to $+1.1\text{‰}$ (Table 4; Fig. 4B). Fossil shells were, on average, $\sim 1.6\text{‰}$ lower in $\delta^{18}\text{O}$ than live individuals (Fig. 4B). Shells recovered from each archeological site (UE142, UE128, UE166 and ARVIR-IV) displayed average $\delta^{18}\text{O}$ values of $+0.4 \pm 0.6\text{‰}$ ($n=8$), $-0.2 \pm 0.6\text{‰}$ ($n=8$), $-0.6 \pm 0.8\text{‰}$ ($n=8$) and $-0.8 \pm 1.0\text{‰}$ ($n=8$), respectively.

Stable isotopes of bulk sediments

Modern carbonates from sediments in the study area showed a $\delta^{13}\text{C}$ value of -4.5‰ (Table 5). Ancient carbonate-rich sediment samples in which shells were preserved showed an average $\delta^{13}\text{C}$ value of $-5.5 \pm 0.4\text{‰}$ ($n=4$), ranging from -6.0‰ in ARVIR-IV to -5.1‰ in UE166 (Table 5). The carbon isotopic signature of modern and ancient bulk sediments was significantly different from that of modern and fossil land snail shells (Fig. 5).

Bulk modern soil sediment showed a $\delta^{18}\text{O}$ value of -4.9‰ (Table 5). Bulk sediment samples from the YD site and various early Holocene sites exhibited an average $\delta^{18}\text{O}$ value of -6.1‰ ($n=4$), ranging from -8.3‰ in UE166 to -5.2‰ in ARVIR-IV (Table 5). The oxygen isotopic composition of bulk sediment samples and measured *Sphincterochila* shells was notably different (Fig. 5).

Discussion

Comparison among modern pulmonate land snail species

Modern *S. candidissima* shells from Villena, Alicante (SE Spain), showed average carbon and oxygen isotope values of -5.8 ± 1.4 and $+1.3 \pm 0.8\text{‰}$, respectively. In contrast, published data of other modern land snail species from various localities in Spain show minimal isotopic differences among each other, but significantly different values from those obtained from living *Sphincterochila* shells here (Fig. 6). The herbivorous *Cernuella virgata* (Da Costa, 1778) from Granada and Jaén, southern Spain ($n=32$), exhibit respective average $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of $-9.3 \pm 1.0\text{‰}$ and $-0.6 \pm 0.9\text{‰}$ (Yanes *et al.*, 2011, 2013). The omnivorous *Rumina decollata* (Linnaeus, 1758) from Granada ($n=4$) shows average values

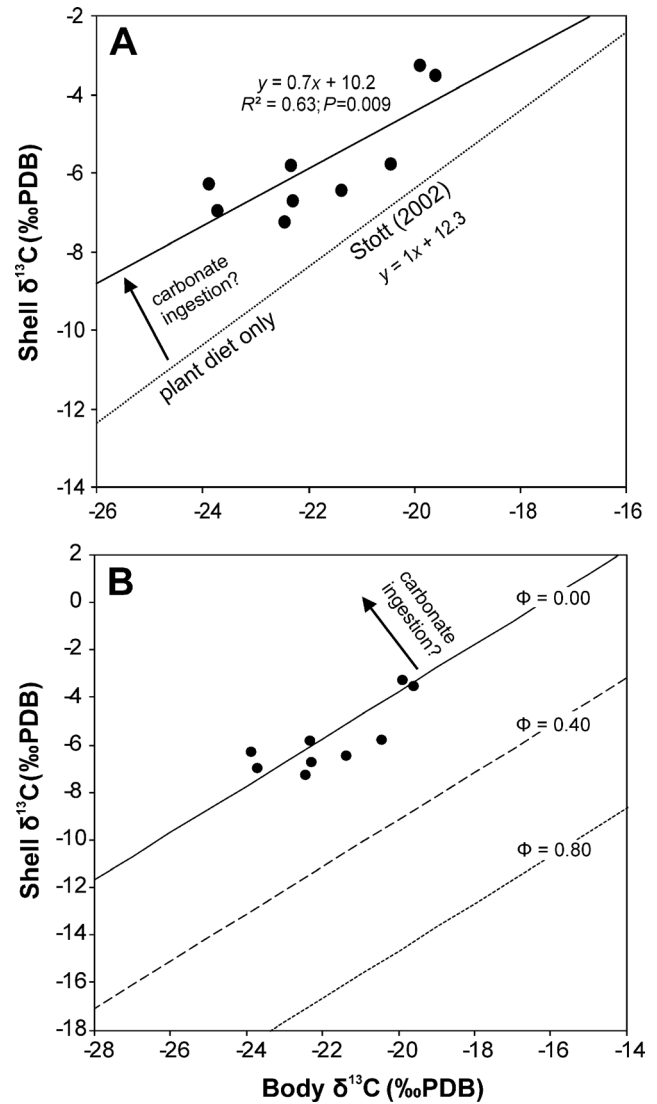


Figure 3. Carbon stable isotope values of live-collected land snails from Villena, Alicante, SE Spain. (A) Discontinuous line depicts the relationship between the $\delta^{13}\text{C}$ values of body and shell from cultured experiments by Stott (2002) with negligible limestone influence into the shell. Continuous line depicts the relationship between the $\delta^{13}\text{C}$ values of body and shell of live-collected *Sphincterochila candidissima* individuals. (B) Calculations of the carbon flux balance mixing model by Balakrishnan and Yapp (2004). Lines represent model calculations assuming a temperature of calcification of $\sim 14^\circ\text{C}$ and variable ratios of input and output fluxes of bicarbonate from the snail body fluid. Solid dots depict measured snails in the present study.

of -9.8 ± 0.5 and $-1.5 \pm 0.3\text{‰}$, respectively (Yanes *et al.*, 2012). The herbivorous *Cepaea nemoralis* (Linnaeus, 1758) from Cantabria, northern Spain ($n=12$), exhibits respective average values of -10.3 ± 1.1 and $-1.1 \pm 0.7\text{‰}$ (Yanes *et al.*, 2012). Thus, *Sphincterochila* shells are, on average, $\sim 4\text{‰}$ higher in $\delta^{13}\text{C}$ values and $\sim 2\text{‰}$ higher in $\delta^{18}\text{O}$ values than other species collected from modern ecosystems in southern and northern Spain (Fig. 6). Interestingly, carbon and oxygen isotope values of *Sphincterochila* correlate positively, whereas they do not correlate for the other species (Fig. 6). This distinctive isotopic signature of modern *Sphincterochila* may be explained by ethological and physiological mechanisms different from those shown by other taxa not as well adapted to dry conditions. As Moreno-Rueda (2007) observed in field surveys, *Sphincterochila* is adapted to arid to semi-arid conditions and may withstand

Table 4. Carbon and oxygen stable isotope values of *Sphincterochila candidissima* shells recovered from various archaeological sites in Villena, Alicante, SE Spain.

Sample ID	Sample type	Locality	Age (2 σ cal a BP)	$\delta^{18}\text{O}$ (‰ PDB)	$\delta^{13}\text{C}$ (‰ PDB)
UE 142-1	Shell	Casa Corona	12 380–11 980	0.6	−1.9
UE 142-2	Shell	Casa Corona	12 380–11 980	0.5	−2.1
UE 142-3	Shell	Casa Corona	12 380–11 980	1.1	−4.0
UE 142-4	Shell	Casa Corona	12 380–11 980	1.1	−3.8
UE 142-5	Shell	Casa Corona	12 380–11 980	0.1	−2.4
UE 142-6	Shell	Casa Corona	12 380–11 980	−0.8	−2.0
UE 142-7	Shell	Casa Corona	12 380–11 980	0.5	−4.9
UE 142-8	Shell	Casa Corona	12 380–11 980	0.4	−4.0
UE 128-1	Shell	Casa Corona	10 190–9900	−0.5	−4.1
UE 128-2	Shell	Casa Corona	10 190–9900	−0.7	−3.1
UE 128-3	Shell	Casa Corona	10 190–9900	−0.1	−3.2
UE 128-4	Shell	Casa Corona	10 190–9900	−0.7	−1.8
UE 128-5	Shell	Casa Corona	10 190–9900	0.6	−1.6
UE 128-6	Shell	Casa Corona	10 190–9900	0.9	−2.2
UE 128-7	Shell	Casa Corona	10 190–9900	−0.6	−3.7
UE 128-8	Shell	Casa Corona	10 190–9900	−0.2	−1.9
UE 166-1	Shell	Casa Corona	9550–9450	−2.0	−4.1
UE 166-2	Shell	Casa Corona	9550–9450	0.1	−3.6
UE 166-3	Shell	Casa Corona	9550–9450	−1.3	−4.1
UE 166-4	Shell	Casa Corona	9550–9450	0.3	−4.5
UE 166-5	Shell	Casa Corona	9550–9450	−0.2	−4.6
UE 166-6	Shell	Casa Corona	9550–9450	0.0	−3.9
UE 166-7	Shell	Casa Corona	9550–9450	−0.9	−4.8
UE 166-8	Shell	Casa Corona	9550–9450	−0.9	−4.2
ARVIR-IV-1	Shell	Arenal Virgen	8590–8430	−1.1	−3.7
ARVIR-IV-2	Shell	Arenal Virgen	8590–8430	−0.8	−4.1
ARVIR-IV-3	Shell	Arenal Virgen	8590–8430	0.0	−3.1
ARVIR-IV-4	Shell	Arenal Virgen	8590–8430	−0.5	−5.0
ARVIR-IV-5	Shell	Arenal Virgen	8590–8430	−0.4	−2.2
ARVIR-IV-6	Shell	Arenal Virgen	8590–8430	−1.8	−4.6
ARVIR-IV-7	Shell	Arenal Virgen	8590–8430	0.5	−2.8
ARVIR-IV-8	Shell	Arenal Virgen	8590–8430	−2.8	−4.2

dry episodes better than other sympatric species. *Sphincterochila* seems to be capable of a retarded rate of water loss through evaporation from the body fluid (Moreno-Rueda, 2007 and references therein). This physiological mechanism may result in snail body fluids (and shells) with significantly higher $\delta^{18}\text{O}$ values than those from other species. As water is lost by evaporation from snail body fluids, the light isotopes would evaporate preferentially, whereas the heavy isotopes would remain in the body fluid, resulting ultimately in ^{18}O -enriched shells. Also, *Sphincterochila* is capable of being active at warmer/drier times and may feed upon plants at times of higher water stress than other contemporaneous snails. Moreover, *Sphincterochila* shells are relatively thick and large, which suggests that this species may require higher carbonate intake to promote shell growth than other species with thinner and smaller shells such as *Cernuella* and *Rumina*. This could also explain the observed higher $\delta^{13}\text{C}$ values of modern *Sphincterochila* shells. While some previous studies have suggested that multiple land snail species often show similar isotopic values (e.g. Yanes *et al.*, 2009), the results here suggest that the carbon and oxygen isotopic signature of *Sphincterochila* shells is not directly comparable with other contemporaneous snail taxa (see also Goodfriend and Magaritz, 1987).

Paleovegetation estimates

The $\delta^{13}\text{C}$ values of the shell and the body tissue correlated significantly, which indicates that both proxies record similar environmental information (Fig. 3A, B). Assuming that snail body is $\sim 1\text{‰}$ higher than plant diet (DeNiro and

Epstein, 1978), living specimens in the study area should have consumed plant matter with an average $\delta^{13}\text{C}$ value of -22.9‰ . This value overlaps with the natural range of $\delta^{13}\text{C}$ values for C_3 plants. However, the relatively high $\delta^{13}\text{C}$ values observed in snail body tissues suggest that consumed C_3 plants were ^{13}C -enriched possibly due to greater water stress (Dawson *et al.*, 2002). This seems reasonable considering that the study site is semi-arid and local plants and animals may experience water deficiency. The regression line computed for the $\delta^{13}\text{C}$ values of *Sphincterochila* shell and body tissue shows a slope of 0.7 (Fig. 3A), which differs from the slope of 1 observed in cultured snails by Stott (2002). This is possibly explained by the effect of limestone ingestion into the shell $\delta^{13}\text{C}$ values. The $\delta^{13}\text{C}$ values of the shell are, on average, 16‰ higher than the body tissue (Table 3). This large $\delta^{13}\text{C}$ offset between shell and body may be explained by limestone ingestion (Yanes *et al.*, 2008).

The carbon snail flux balance-mixing model proposed by Balakrishnan and Yapp (2004) can be used to evaluate potential variations in metabolic rates among contemporaneous specimens and also estimate potential effects from carbonate ingestion. Model calculations were carried out assuming that temperature of calcification was $\sim 14^\circ\text{C}$, on average. Other choices of temperature did not change model outputs drastically (see also Balakrishnan and Yapp, 2004). Most specimens clustered closely to the line for $\Phi = 0.00$, which implies that the ratio of influx and outflux of bicarbonate from the snail body fluid was the same among measured individuals. Thus, live-collected snails experienced comparable metabolic rates. Specimens that plotted directly on the line for $\Phi = 0.00$ or to the left possibly reflect that some

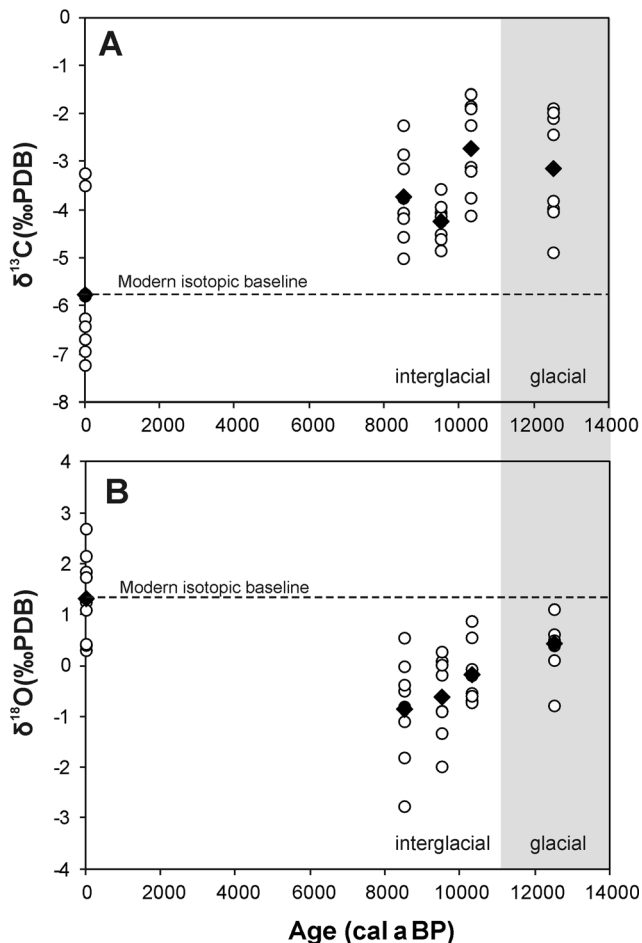


Figure 4. Stable isotope values of YD–Holocene *Sphincterochila candidissima* shells from Villena, Alicante, SE Spain. (A) Carbon stable isotope values of the shell. (B) Oxygen stable isotope values of the shell. Dashed horizontal lines depict the average value of living specimens in the study area. Filled diamonds represent the average value per age interval.

individuals ingested other carbon sources besides C_3 plants, such as limestone (Balakrishnan and Yapp, 2004).

The $\delta^{13}C$ values of modern and fossil sediments, which range from -8.3 to -4.9‰ (Table 4), reflect the influence of continental rather than marine carbon sources into the bulk carbonate-rich sediment matrix analysed. The $\delta^{13}C$ values of fossil snail shells are significantly higher than those from the sediment matrix (Fig. 5). This suggests that fossil shells are reasonably free of sediments and exhibit distinctive isotopic populations. While YD shells showed similar $\delta^{13}C$ values to early Holocene shells, all fossil shells were significantly higher in $\delta^{13}C$ ($-3.5 \pm 1.0\text{‰}$; $n = 32$) than living individuals ($-5.8 \pm 1.4\text{‰}$; $n = 9$) (Fig. 4). This pattern may be explained

by several compelling hypotheses. (1) C_3 plants ingested by snails may have experienced stronger water-stress conditions in the transition from the YD to the early Holocene than today. Drought conditions induce plants to persist for longer with closed stomata to prevent water loss. This physiological mechanism causes ^{13}C -enriched tissues in C_3 plants (Dawson *et al.*, 2002), which in turn will be recorded in the snail shell. (2) Modern shell $\delta^{13}C$ values may be affected by the *Suess* effect, i.e. isotopic depletion of surface carbon reservoirs due to the burning of fossil fuels, and therefore they are anomalously lower in $\delta^{13}C$ values by about 1.6‰ (Marino and McElroy, 1991). If modern snails are corrected for the *Suess* effect, then fossil and modern snails show comparable shell $\delta^{13}C$ values. (3) Specimens during the YD and the early Holocene ingested more limestone or carbonates with higher $\delta^{13}C$ values than at present. (4) Fossil snails consumed some C_4 or CAM plants, whereas today snails consume C_3 plants exclusively. This last hypothesis is not convincing because pollen studies indicate that native C_4 and CAM plants have not been present in the study area throughout the late Quaternary (Carrión *et al.*, 2001, 2010). The snail $\delta^{13}C$ results presented here can be explained more simply by higher water-stress among C_3 plants in the YD–Holocene transition, and/or by the effects of the *Suess* effect upon modern plants and snails. A pending challenge in snail research investigations is to quantify if and how carbonates ingested by the snail affect the $\delta^{13}C$ values of the shell. Also, to the best of our knowledge, the potential relationship between shell size and thickness and the proportion of carbonate ingested has not been assessed.

Paleoatmospheric estimates

The $\delta^{18}O$ of land snail shells showed an average value of $+0.4 \pm 0.6\text{‰}$ during 12.0–12.4 cal ka BP. This then declined gradually to the lowest average value of $-0.8 \pm 1.0\text{‰}$ at 8.4–8.6 cal ka BP. Consecutively, shell $\delta^{18}O$ values may have fluctuated but ultimately increased to the modern average value of $+1.3 \pm 0.8\text{‰}$. This fluctuation in shell $\delta^{18}O$ values of over $\sim 2\text{‰}$ suggests that atmospheric conditions during the Lateglacial–Holocene transition in SE Spain were different from today. The snail evaporative steady-state flux balance model of Balakrishnan and Yapp (2004) is combined with published proxy data to quantitatively evaluate the environmental significance of these temporal fluctuations in shell $\delta^{18}O$ values (Fig. 7A). Balakrishnan and Yapp (2004) observed that it is reasonable to assume that liquid water ingested by the snail and water vapor are in isotopic equilibrium. They also showed that it is useful to assume that water loss from snail body fluid occurred exclusively by evaporation. Both assumptions are adopted in the present study for model calculations. This model suggests that the most important environmental controls upon shell $\delta^{18}O$ values are the $\delta^{18}O$ values of the rain and the water vapor,

Table 5. Carbon and oxygen stable isotope values of bulk sediment samples in which fossil shells were immersed. Modern surrounding bulk sediments were also analysed for comparison.

Sample ID	Sample type	Locality	Age (cal a BP)*	$\delta^{13}C$ (‰ PDB)	$\delta^{18}O$ (‰ PDB)
UE142-sed	Sediment	Casa Corona	12 380–11 980	−5.4	−5.5
UE128-sed	Sediment	Casa Corona	10 190–9900	−5.4	−5.6
UE166-sed	Sediment	Casa Corona	9550–9450	−5.1	−8.3
ARVIR-IV-sed	Sediment	Arenal Virgen	8590–8430	−6.0	−5.2
ARVIR-mod-sed	Sediment	Casa Corona	Modern	−4.5	−4.9

*It is assumed that sediments have similar age to shells and charcoal samples used for radiocarbon dating.

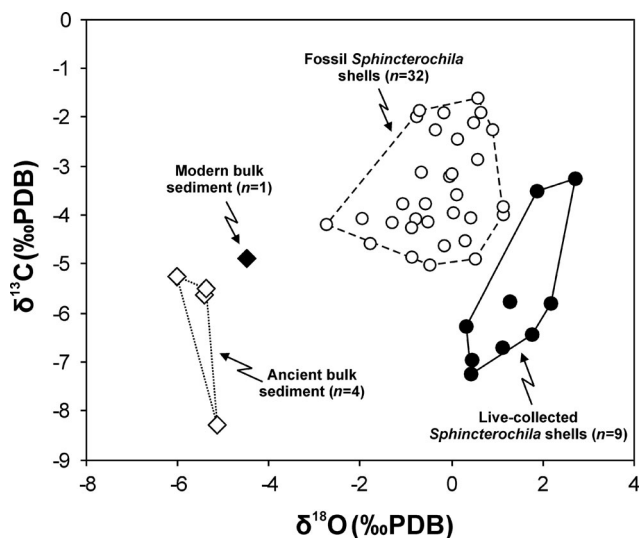


Figure 5. Carbon and oxygen stable isotope values of bulk carbonate sediments ($n=5$) and *Sphincterochila candidissima* shells ($n=41$) from Villena, Alicante, SE Spain.

the ambient temperature and RH as a decimal fraction (see Balakrishnan and Yapp, 2004 for further details).

Live-collected land snails deposit shell material under current environmental conditions, i.e. air temperatures of $\sim 14^{\circ}\text{C}$ and rain $\delta^{18}\text{O}$ values of -7.0‰ (SMOW) (Araguás-Araguás and Diaz-Teijeiro, 2005). Outputs of the model by Balakrishnan and Yapp (2004), constrained with observed environmental data, suggest that living specimens, with a measured average shell $\delta^{18}\text{O}$ value of $+1.3\text{‰}$, can only be explained if calcification occurred at RH values of $\sim 82\%$, on average (Fig. 8A). This predicted RH value by the model is 16% higher than the observed average annual value for the study area. However, considering that snails can only be active at RH values above 70–75%, and that they tend to be active during the wettest times, principally at night, a

predicted value of 82% seems reasonable. Even though the study area is considered semi-arid today ($<380\text{ mm}$ of annual precipitation), RH values can be high due to the close proximity to the Mediterranean Sea, especially at the soil–air interface, at night and during the rainy season, when snails are more active and grow shell material. Consequently, this model seems useful for the target species and the study area and can be used to infer credible paleoclimatic scenarios in the western Mediterranean.

To infer possible paleoclimatic scenarios in the western Mediterranean, calculations of the snail model should first be constrained by independent proxy data. It is broadly accepted that the environmental variable that most affects the $\delta^{18}\text{O}$ values of precipitation is the air temperature at mid-to-high latitudes (Dansgaard, 1964). Spatial studies on present precipitation illustrate that temperature is the main environmental factor controlling seasonal variations in rain $\delta^{18}\text{O}$ values at localities with a Mediterranean-type climate of the northern hemisphere (Bowen, 2008). Recent studies, however, suggest that other atmospheric variables (e.g. vapor condensation height, raindrop re-evaporation and storms trajectories) could also influence the $\delta^{18}\text{O}$ values of the precipitation at middle latitudes, especially at sub-hourly, weekly, seasonal and inter-annual scales (Buenning *et al.*, 2013). However, air temperature is probably the main environmental variable that affects the $\delta^{18}\text{O}$ values of the precipitation at the multi-millennial scale in mid latitudes. This assumption is adopted in the present study.

The $\delta^{18}\text{O}$ values of the precipitation in the Greenland Ice Core (GRIP2) were several per mil lower during the latest glacial than during the Holocene (Fig. 7B) as a response of lower temperatures (Dansgaard *et al.*, 1989, 1993; GRIP Members, 1993; Grootes *et al.*, 1993; Johnsen *et al.*, 1997). Several published marine and continental proxies repeatedly suggest that at mid-to-high latitudes of the northern hemisphere, precipitation was several per mil lower in $\delta^{18}\text{O}$ than at present, linked to lower air temperatures (e.g. Verbruggen *et al.*, 2010; Rasmussen *et al.*, 2011). In contrast, during the early Holocene, $\delta^{18}\text{O}$ values of the precipitation in the northern hemisphere were largely comparable to present values associated with subdued variations of temperature throughout the Holocene. Alkenone proxies of marine deep sea cores in the western Mediterranean (Fig. 7C) reveal that the sea surface temperature was $\sim 6^{\circ}\text{C}$ lower during 12.0–12.4 cal ka BP than today, whereas during the early Holocene temperatures were comparable to present values (Martrat *et al.*, 2004, 2007).

Rain $\delta^{18}\text{O}$ values decrease $\sim 0.58\text{‰}$ every $\sim 1^{\circ}\text{C}$ of temperature decrease (Rozanski *et al.*, 1993). If around 12.0–12.4 cal ka BP air temperatures were $\sim 6^{\circ}\text{C}$ lower than today in the study area, as suggested by alkenone proxies in the western Mediterranean (Cacho *et al.*, 2001; Martrat *et al.*, 2004, 2007; Moreno *et al.*, 2005), then rain $\delta^{18}\text{O}$ values possibly showed an average value of $\sim -10.5\text{‰}$ (SMOW). During the early Holocene (~ 8.4 – 10.2 cal ka BP), rain $\delta^{18}\text{O}$ values were probably similar to present-day values, considering that temperature (as inferred from alkenone proxies) has been comparable as well (Cacho *et al.*, 2001; Martrat *et al.*, 2004, 2007; Moreno *et al.*, 2005).

Calculations of the model of Balakrishnan and Yapp (2004) constrained with the aforementioned paleoenvironmental data from published proxies (Fig. 7) suggest that shells during the YD, with a measured shell $\delta^{18}\text{O}$ value of $+0.4\text{‰}$, possibly deposited carbonate when temperatures were $\sim 8^{\circ}\text{C}$ (i.e. $\sim 6^{\circ}\text{C}$ lower than today, as suggested by the alkenone proxy by Martrat *et al.*, 2004, 2007), average rain $\delta^{18}\text{O}$ values were $\sim -10.5\text{‰}$ (SMOW) (assuming a temperature effect of

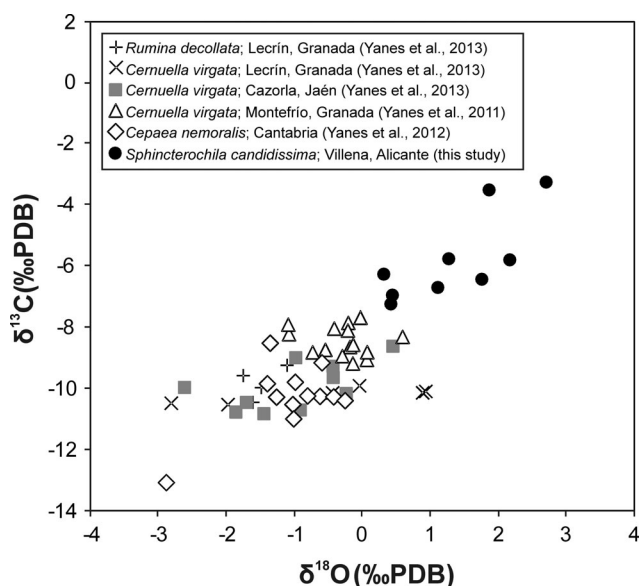


Figure 6. Carbon and oxygen stable isotope values of several modern pulmonate land snail species from the Iberian Peninsula. Filled dots represent data from *Sphincterochila candidissima* shells measured in this study. Remaining symbols depict data from other published snail species collected at various locales in southern (Yanes *et al.*, 2011, 2013) and northern (Yanes *et al.*, 2012) Spain.

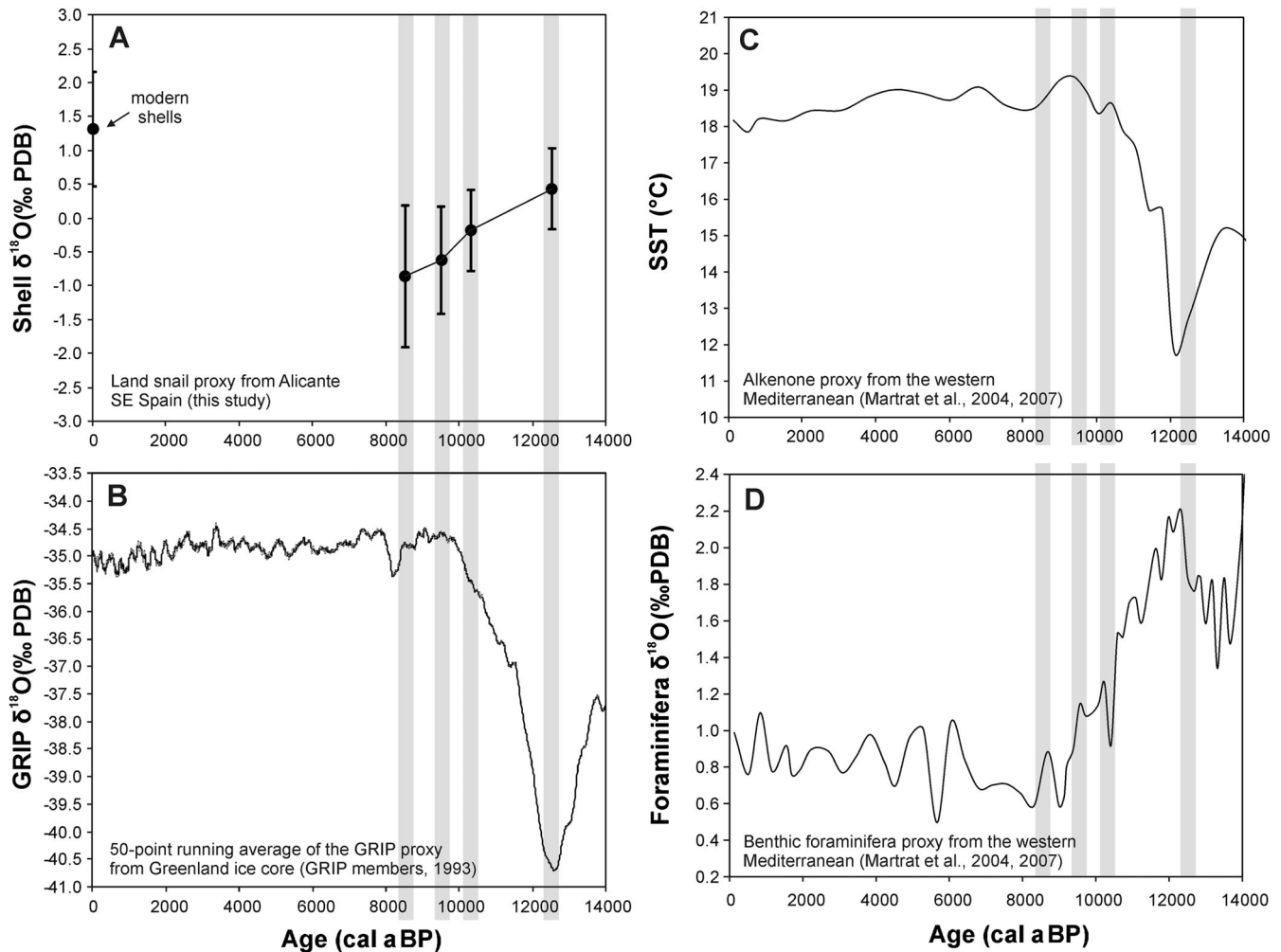


Figure 7. Oxygen stable isotope values of land snail shells from SE Spain compared with independent paleoclimatic proxies. (A) *Sphincterochila candidissima* proxy (this study). (B) Fifty-point running average of the $\delta^{18}\text{O}$ values from Greenland Ice Core (Dansgaard et al., 1989, 1993; GRIP Members, 1993; Grootes et al., 1993; Johnsen et al., 1997). (C) Sea surface temperature (SST) estimates from alkenone data from deep sea cores in the western Mediterranean (Martrat et al., 2004, 2007). (D) $\delta^{18}\text{O}$ values of benthic foraminifera data from deep sea cores in the western Mediterranean (Martrat et al., 2004, 2007). Gray bands depict the age intervals explored in this study.

~0.58‰/1 °C; Rozanski et al., 1993) and RH values of ~0.79 (Fig. 8B). From there, shell $\delta^{18}\text{O}$ values declined gradually to a minimum of -0.8‰ at 8.4–8.6 cal ka BP, as a response to a progressive increase in temperature from ~8 to ~14 °C (Fig. 7C), an increase in rain $\delta^{18}\text{O}$ values from ~-10.5‰ (SMOW) to ~-7.0‰ (SMOW), and an increase in RH from ~0.79 to ~0.87 (Fig. 8B). Finally, shell $\delta^{18}\text{O}$ values may have shifted throughout the Holocene but finally increased to present values of +1.3‰ (Fig. 7A). Modern shells precipitated at temperatures of ~14 °C, rain $\delta^{18}\text{O}$ values of -7.0‰ (SMOW) and RH values of ~0.82, on average (Fig. 8A, B). In general, snail data, in the context of this model, suggest that calcification occurred at drier conditions during the YD, at wetter times during the early Holocene, and ultimately returned to drier conditions at present, but not as dry as during the YD (see arrows in Fig. 8B).

An alternative plausible paleoenvironmental scenario may be inferred if we consider that seawater $\delta^{18}\text{O}$ values may have influenced rain $\delta^{18}\text{O}$ values at the Lateglacial–Holocene transition in the study locality (Fig. 8C). Seawater displayed higher $\delta^{18}\text{O}$ values during the latest glacial (Fig. 7D), as reflected in the benthic foraminifera data from deep sea cores in the western Mediterranean (Martrat et al., 2004, 2007). Seawater was ~1‰ higher in $\delta^{18}\text{O}$ during 12.0–12.4 cal ka BP than today, whereas no significant differences can be deduced between the early Holocene and the present

(Fig. 7D). If higher seawater $\delta^{18}\text{O}$ values during the latest glacial influenced the rain $\delta^{18}\text{O}$ values, then around the YD, rain $\delta^{18}\text{O}$ values could have been ~-9.5‰ (SMOW), on average, whereas early Holocene rain plausibly showed comparable $\delta^{18}\text{O}$ values to today (Fig. 7D). In this alternative paleoenvironmental scenario, the following pattern is inferred (Fig. 8C). On average, YD snails deposited shell material at temperatures of ~8 °C, rain $\delta^{18}\text{O}$ values of ~-9.5‰ (SMOW) and RH values of ~0.82. Thereafter, RH increased to maximum values of ~0.87 at 8.4–8.6 cal ka BP and consecutively declined to present values of ~0.82 (Fig. 8C). This second scenario suggests that conditions in the western Mediterranean were noticeably drier during the YD, became wetter around the early Holocene, and eventually returned to the current drier setting (see arrows in Fig. 8C). In this case, snails suggest that the YD was as dry as today.

Both possible paleoatmospheric scenarios proposed here (Fig. 8B, C) point to overall drier conditions during the latest glacial and wetter conditions during the early Holocene. The documented lower RH values here during the YD in the western Mediterranean could be explained by a decrease in net precipitation, as observed in published records from northern Africa and Europe (see recent review by Carlson, 2013). This paleoenvironmental scenario inferred from land snails agrees with published paleoclimatic studies from mid to high latitudes of the northern hemisphere that have used

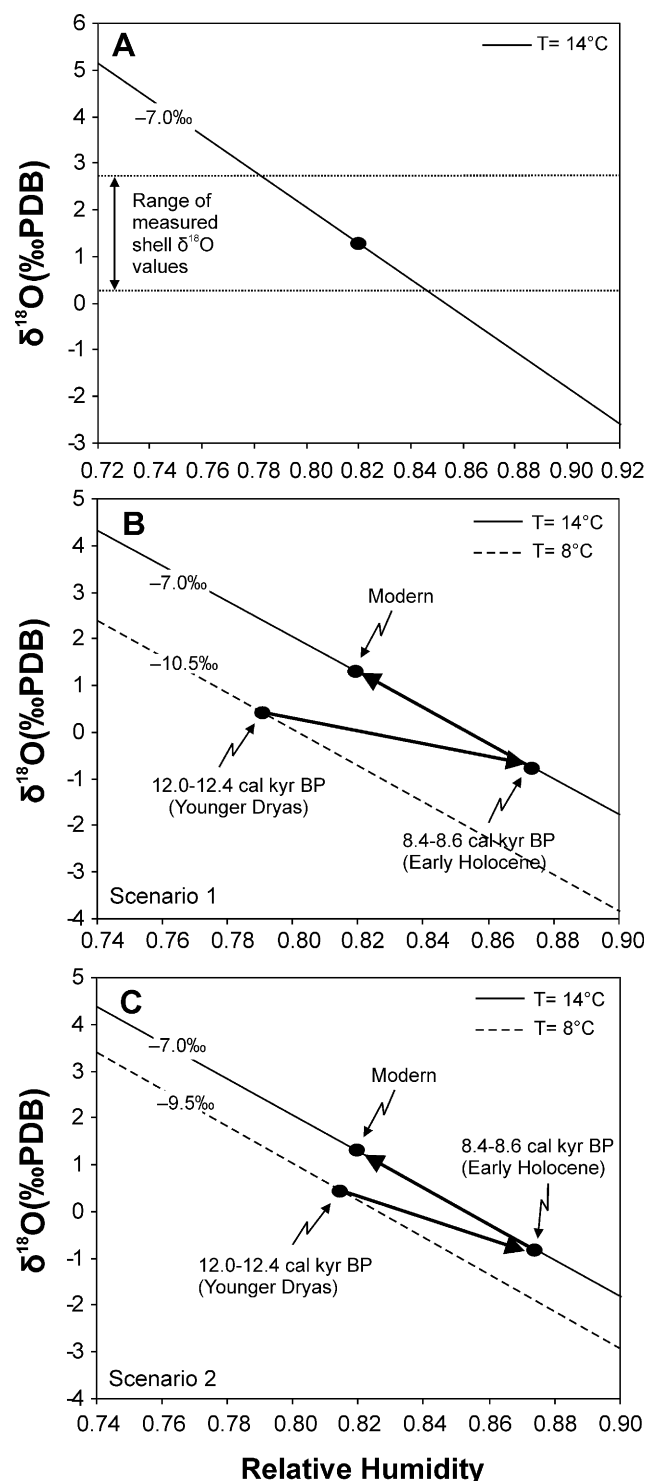


Figure 8. Calculations of the snail evaporative steady-state flux balance mixing model by Balakrishnan and Yapp (2004). (A) Oxygen stable isotope values of live-collected specimens as a function of relative humidity, assuming that calcification occurred at average temperatures of 14°C and rain water values of -7 (SMOW). (B, C) Plausible paleoatmospheric conditions in SE Spain during the YD–early Holocene. Arrows depict hypothetical trajectories of shell $\delta^{18}\text{O}$ values as a function of relative humidity, constrained by published proxy data (see text for explanation).

other continental proxies (e.g. Verbruggen *et al.*, 2010; Ras-mussen *et al.*, 2011). At a more local scale, pollen and ostracod proxies from the nearby Salinas Playa lake (Fig. 1A) reveal much drier hydrological conditions during the YD, whereas a gradual increase in water availability is observed

throughout the early Holocene (Roca and Julià, 1997; Giralt *et al.*, 1999; Giralt and Julià, 2003; Burjachs, 2009).

Measured northern European land snails from the Last Glacial Maximum show higher shell $\delta^{18}\text{O}$ values than at present (Kehrwald *et al.*, 2010). During glacial conditions, lower temperatures favor longer snail hibernation periods and therefore snails are more active during warmer seasons. Thus, Kehrwald *et al.* (2010) proposed that ^{18}O -enriched summer rains might explain the higher shell $\delta^{18}\text{O}$ values observed among glacial shells. In Alicante, SE Spain (38°N), Lateglacial temperatures are estimated to have been $\sim 8^\circ\text{C}$ (Cacho *et al.*, 2001; Martrat *et al.*, 2004, 2007; Moreno *et al.*, 2005). Thus, snails possibly did not have to hibernate as long as northern European snails. Although higher rain $\delta^{18}\text{O}$ values of summer seasons may have affected the snail data here, we propose that variations in RH also played an important role in shell $\delta^{18}\text{O}$ values of snails.

Early Holocene snail records from Granada, southern Spain (Yanes *et al.*, 2011), and eastern pre-Pyrenees, north-east Spain (Colonese *et al.*, 2013a), also suggest prevailing wetter conditions than at present, with Holocene snails from the eastern Iberian Peninsula overall recording comparable regional moisture regimes. *Sphincterochila* shells appear to record convincingly well local and regional environmental conditions in the oxygen isotope composition of the shell. However, considering its distinctive ecological behavior and isotopic signature, *Sphincterochila* shells should not be mixed with other snail species in paleoenvironmental studies. Thus, fossil *Sphincterochila* shells should only be compared with modern shells of the same species.

The results presented here also have important implications for archeologists. Ancient human groups that inhabited the south-eastern Iberian Peninsula throughout the late Quaternary have experienced significantly different moisture regimes. The inferred changing environment from snail shells probably influenced the degree of water availability, and the presence and abundance of different plants and animals. The archaeological record of the Villena basin shows that Epipaleolithic and Mesolithic human communities were resilient to these environmental changes, for example by broadening their diets with the incorporation of alternative food resources such as land snails.

Conclusions

The xerophilous land snail *Sphincterochila candidissima* records valuable local and regional environmental aspects in the isotopic composition of its shell. Due to its affinity for and tolerance to dry conditions, *Sphincterochila* shells exhibit a significantly higher carbon and oxygen isotopic fingerprint than other contemporaneous snail species. This is probably associated with differing ethological and physiological mechanisms: (1) *Sphincterochila* is capable of being active at warmer and/or drier times of the day than other snail taxa from the same habitat; and (2) *Sphincterochila* follows different physiological mechanisms to fight aridity than other contemporaneous snails. While some published studies suggest that multi-taxa snail proxies are reliable because no significant isotopic differences among species are observed, this study shows that *Sphincterochila* is not directly comparable isotopically to other sympatric species. The $\delta^{13}\text{C}$ values of all fossil shells were $\sim 2\text{‰}$ richer in ^{13}C than live-collected shells. This suggests that during the YD–early Holocene, the $\delta^{13}\text{C}$ values of consumed plants were significantly higher than at present because of higher water stress. Alternatively, modern snail shells are anomalously lower in $\delta^{13}\text{C}$ values than fossils due to the Suess effect. The $\delta^{18}\text{O}$ values of

Sphincterochila shells declined gradually from 12.0–12.4 cal ka BP to 8.4–8.6 cal ka BP, and returned to maximum values at present. Snails suggest that calcification during the YD (12.0–12.4 cal ka BP) occurred under drier conditions, whereas during the early Holocene snails grew shell under notably wetter periods. The results agree with other local and regional proxies and stress the usefulness of *Sphincterochila* shells as a paleoenvironmental archive in the Mediterranean region.

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Abbreviations. PDB, Pee Dee Belemnite; RH, relative humidity; YD, Younger Dryas

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