



Pleistocene–Holocene environmental change in the Canary Archipelago as inferred from the stable isotope composition of land snail shells

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ABSTRACT

The isotopic composition of land snail shells was analyzed to investigate environmental changes in the eastern Canary Islands (28–29°N) over the last ~50 ka. Shell $\delta^{13}\text{C}$ values range from -8.9% to 3.8% . At various times during the glacial interval (~15 to ~50 ka), moving average shell $\delta^{13}\text{C}$ values were 3% higher than today, suggesting a larger proportion of C_4 plants at those periods. Shell $\delta^{18}\text{O}$ values range from -1.9% to 4.5% , with moving average $\delta^{18}\text{O}$ values exhibiting a noisy but long-term increase from 0.1% at ~50 ka to $1.6\text{--}1.8\%$ during the LGM (~15–22 ka). Subsequently, the moving average $\delta^{18}\text{O}$ values range from 0.0% at ~12 ka to 0.9% at present. Calculations using a published snail flux balance model for $\delta^{18}\text{O}$, constrained by regional temperatures and ocean $\delta^{18}\text{O}$ values, suggest that relative humidity at the times of snail activity fluctuated but exhibited a long-term decline over the last ~50 ka, eventually resulting in the current semiarid conditions of the eastern Canary Islands (consistent with the aridification process in the nearby Sahara). Thus, low-latitude oceanic island land snail shells may be isotopic archives of glacial to interglacial and tropical/subtropical environmental change.

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Introduction

The Canary Archipelago (27–29°N), ~100 km off the Moroccan Coast, is an excellent area to study subtropical climatic variations since it is affected by recurrent interactions between atmospheric (i.e., trade winds, Saharan winds, etc.) and oceanic (i.e., Canarian cool current, seasonal coastal upwelling, etc.) circulation systems, which are in turn, linked to the seasonal migration of the intertropical convergence zone (ITCZ) and monsoon wind shifts in West Africa (e.g., Moreno et al., 2001). The eastern Canary Islands contain eolian deposits with alternating sequences of dunes and paleosols (e.g., Petit-Maire et al., 1986; Rognon and Coudé-Gaussen, 1988, 1996a,b; Damnati et al., 1996; Ortiz et al., 2006), which contain abundant late Quaternary land snail shells (Yanes et al., 2007, 2008a; Huntley et al., 2008) that represent a rare, relatively continuous, terrestrial fossil record in the islands.

Land snails offer the prospect of a carbon and oxygen isotope record of environmental changes. Shell $\delta^{13}\text{C}$ values are commonly

used to document variations in the proportions of C_3/C_4 plants in paleovegetation (e.g., Goodfriend and Ellis, 2000, 2002; Stott, 2002; Metref et al., 2003; Balakrishnan et al., 2005a,b; Baldini et al., 2007; Colones et al., 2007, 2010; ZongXiu et al., 2007; Yanes et al., 2008b, 2009).

Shell $\delta^{18}\text{O}$ is often empirically related to the local rainwater $\delta^{18}\text{O}$ values (e.g., Lécolle, 1985; Goodfriend, 1991; Zanchetta et al., 2005), but snail body fluid (and corresponding shell) is enriched in ^{18}O with respect to unmodified rainwater (Yapp, 1979). According to Balakrishnan and Yapp (2004), this is explained by a flux balance model in which shell is deposited at oxygen isotope equilibrium with body fluid that experiences ^{18}O enrichment as a consequence of evaporation while snails are forming shell. The factors that most affect the oxygen isotopic composition of the shell are: (1) rain $\delta^{18}\text{O}$, (2) relative humidity (RH), (3) atmospheric water vapor $\delta^{18}\text{O}$, and (4) temperature (Balakrishnan and Yapp, 2004).

Here, we report the first isotope study of fossil land snail shells and bulk sediment carbonates from the late Quaternary eolian successions of the eastern Canary Islands. These data represent a source of information on lower latitude environmental changes recorded at the soil–air interface in the westernmost part of the Saharan Climatic Zone. Interpretations are derived from application of the aforementioned model to the land snail data. Environmental changes deduced

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for the Canary Islands are discussed in the context of published results from mid and high-latitude climatic proxies.

Background

Sample setting and eolian successions

The study area includes the easternmost islands of the Canary Archipelago: Fuerteventura, Lanzarote, La Graciosa, Montaña Clara and Alegranza (Fig. 1; Table S1). These islands consist primarily of Miocene to Holocene subaerial volcanic rocks (e.g., Coello et al., 1992)

and contain abundant late Quaternary eolian deposits with numerous fossil land snail shells of multiple native species suitable for paleoecological and paleoenvironmental studies (e.g., Huntley et al., 2008; Yanes et al., 2008a).

The eolian successions are comprised of bioclastic dunes which were transported inland during glacial times, when sea level was lower (e.g., Rognon and Coudé-Gausson, 1988, 1996a,b). These eolian dunes are capped by ~20- to 60-cm-thick paleosols (Fig. S1) which have a carbonate-dominated matrix, and they are not well-developed (entisol and/or luvis calcisol paleosols: Williamson et al., 2004; Alonso-Zarza et al., 2008). Eolianites contain a mixture of marine and

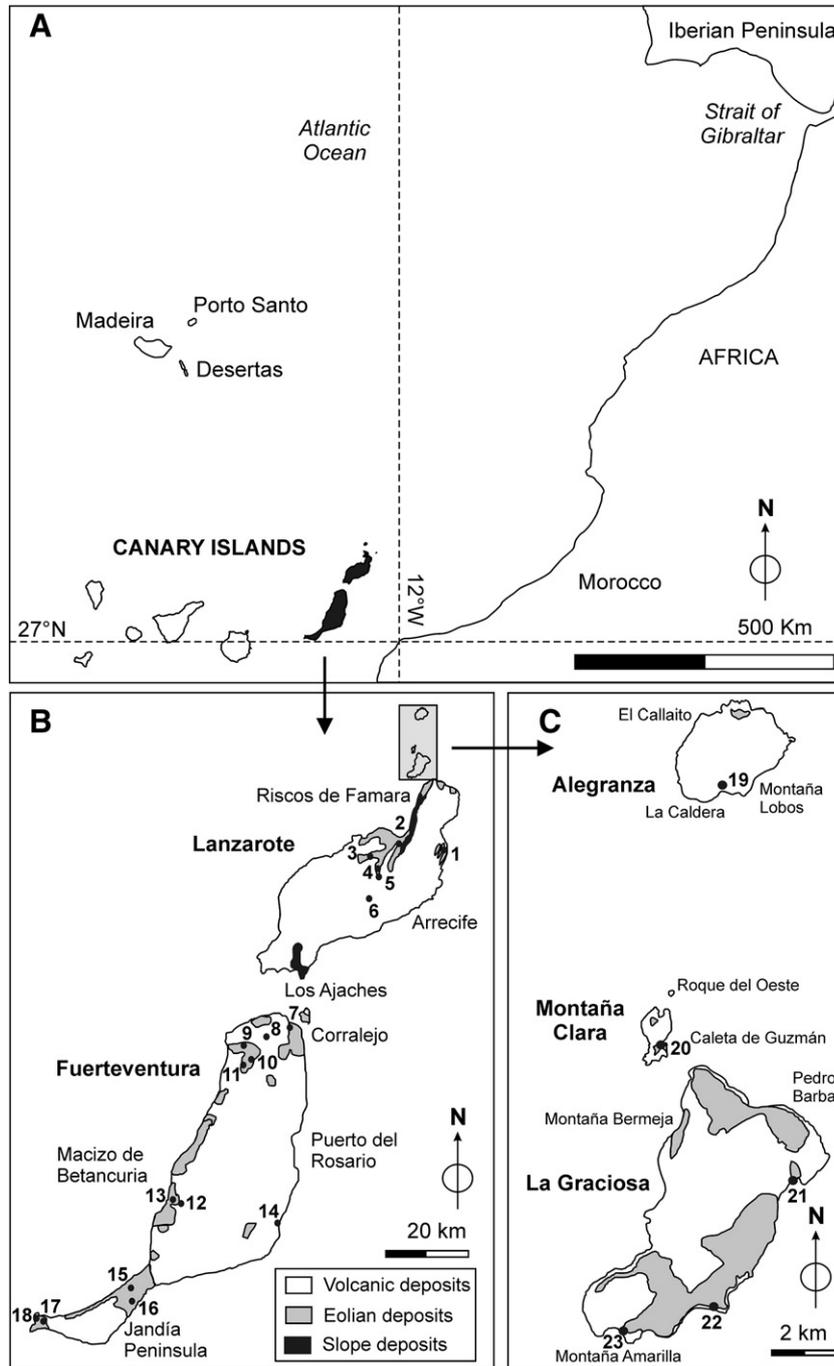


Figure 1. A. Geographical location of the eastern Canary Islands and location of the sampled eolian sections. B. Lanzarote Island: (1) Mala (LMA), (2) Las Casitas (LLC), (3) Muñique (LMN), (4) Tao (LTA), (5) Loma de San Andrés (LLA), (6) Montaña Guatisea (LMG). Fuerteventura Island: (7) Corralejo (FCO), (8) El Quemado (FQE), (9) Montaña Costilla (FMC), (10) Barranco de la Cal (FBC), (11) Barranco de los Encantados (FBE), (12) Barranco del Tabaibejo (FBT), (13) Jable de Vigocho (FJV), (14) Pozo Negro (FPN), (15) Atalaya Grande (FAG), (16) Barranco del Pecenescal (FBP), (17) Montaña Azufra (FMA), (18) Degollada de Agua Cabras (FAC). C. Alegranza islet: (19) Montaña Lobos; Montaña Clara islet (20) Caleta de Guzmán; La Graciosa islet: (21) Morros Negros, (22) Caleta del Sebo, (23) La Cocina.

continental carbonates (calcite, magnesium calcite, and aragonite) with total proportions of 50–90% by weight (Damnati et al., 1996). In addition, there are minor amounts of clay minerals such as authigenic smectite and African-derived illite–kaolinite (Damnati et al., 1996). Quartz grains from the Sahara and basaltic clasts (augite, olivine, chlorite, titanomagnetite, palygorskite; Williamson et al., 2004) from erosion and weathering of local rocks are also common. A large proportion (>65% by weight) of the dust (~20–40 µm) originates from the Sahara (Rognon and Coudé-Gaussen, 1988, 1996a,b; Damnati et al., 1996; Williamson et al., 2004).

A total of 59 shell beds from 24 eolian deposits were sampled from the five eastern islands (Fig. 1, Fig. S1, Table S1). The shells were dated by amino acid racemization (AAR) calibrated against radiocarbon (Ortiz et al., 2006). The sections display variable thickness and numbers of horizons (see Fig. S1). The stratigraphic succession (Fig. S1) exhibited a good correspondence with the AAR and radiocarbon ages (Ortiz et al., 2006). Stable isotope analyses were performed on 329 fossil entire-shells, on 109 intra-shell samples from two modern and five fossil specimens (Appendices S1 and S2, respectively), and on 40 bulk sediment samples (Appendix S3).

Environmental setting

The eastern Canary Islands are situated in a warm and dry climatic zone, with a sub-desertic climate. Their low altitude and the orientation parallel to the prevailing winds contribute to the dryness of the climate (Dorta, 2005). The average annual precipitation is >210 mm/yr, with long intervals of dryness (Reyes-Betancort et al., 2001). Rain water in the study area (Madeira and Canary Islands) has an annual, weighted average $\delta^{18}\text{O}$ value of ~−3.5‰ (IAEA: <http://www.iaea.org/>). The average RH is ~70% (Dorta, 2005). Monthly average temperatures range between 16°C and 24°C, and the annual

average is ~20°C. Average temperature of the rainy months (from October to April) is ~19°C (Reyes-Betancort et al., 2001; Dorta, 2005).

The vegetation of the study area contains over 800 species (e.g., Reyes-Betancort et al., 2001; Scholz, 2005) characterized by herbaceous-shrub xerophytes, halophytes and psamophytes. Around 67 plant taxa have been classified as C₄ plants in the Canary Archipelago (Méndez et al., 1991; Rodríguez-Delgado et al., 1991; Méndez, 2001; Yanes et al., 2008b), and C₃, C₄ and CAM plants are present in the islands nowadays.

AAR age

Subaerial Quaternary deposits are commonly geographically scattered (e.g., Fig. 1) and can pose correlation problems. Temporal relationships among Quaternary land snails in such deposits can be addressed with AAR dating calibrated against radiocarbon (Cook et al., 1993; Goodfriend et al., 1996; Hearty, 1997, 2003; Brooke et al., 2003a,b; Hearty et al., 2004; Hearty and Kaufman, 2009). Ortiz et al. (2006) showed that the eastern Canary Islands exhibited a generally good correspondence among AAR, radiocarbon ages and field-stratigraphy. The AAR ages of snail shells ranged from 4.6 (±0.7) ka to 55.7 (±5.5) ka (Table 4 in Ortiz et al., 2006). Uncertainty in AAR (Table 1) is represented by the standard deviation of the ages of multiple shells from the same horizon (Ortiz et al., 2006). Although the AAR method commonly has a large age uncertainty, the AAR data of Ortiz et al. (2006) are the most complete chronology presently available for this material. Such aminochronology is consistent with previous local studies (e.g., Petit-Maire et al., 1986; Rognon and Coudé-Gaussen, 1988, 1996a,b; Hillaire-Marcel et al., 1995; Damnati et al., 1996). Yanes et al. (2007) suggested that the multimillennial-age mixing of various shell beds, as expected for shell-rich assemblages (see review in Kowalewski and Bambach, 2003), was a consequence of the progressive accumulation of successive

Table 1
Mean carbon and oxygen stable isotope composition of modern and fossil entire land snail shells from the eastern Canary Islands.

Nominal AAR age (ka) ^a	n	$\delta^{13}\text{C}\text{‰}$ (PDB)	$\delta^{18}\text{O}\text{‰}$ (PDB)	Nominal AAR age (ka) ^a	n	$\delta^{13}\text{C}\text{‰}$ (PDB)	$\delta^{18}\text{O}\text{‰}$ (PDB)
Modern ^b	17	−5.2 ± 2.7	0.9 ± 0.7	31.1 ± 3.2	4	−5.7 ± 1.1	1.6 ± 0.3
4.6 ± 0.7	11	−3.9 ± 1.8	1.2 ± 0.7	31.2 ± 5.6	5	−3.7 ± 3.1	0.2 ± 0.3
5.4 ± 1.1	10	−2.7 ± 2.8	0.5 ± 0.9	31.5 ± 5.7	10	−3.5 ± 1.6	0.5 ± 0.5
6.3 ± 2.4	4	−6.6 ± 1.1	0.0 ± 0.4	33.5 ± 3.2	4	−3.6 ± 4.6	0.9 ± 1.3
9.2 ± 3.5	5	−6.1 ± 1.6	0.2 ± 0.5	33.7 ± 6.1	5	−5.4 ± 1.1	0.8 ± 1.1
10.1 ± 3.5	12	−1.1 ± 3.2	0.7 ± 0.4	34.9 ± 5.3	6	−4.0 ± 1.0	1.6 ± 0.5
11.8 ± 3.5	2	−5.3 ± 2.4	−0.8 ± 1.5	37.5 ± 4.2	5	−4.3 ± 0.8	0.5 ± 0.7
12.3 ± 2.8	13	−5.8 ± 1.6	0.4 ± 0.6	38.0 ± 4.0	6	−4.8 ± 1.6	−0.4 ± 0.2
15.2 ± 3.4	15	−2.6 ± 3.9	2.0 ± 1.3	38.6 ± 6.9	2	−3.2 ± 2.1	1.3 ± 0.8
15.6 ± 2.9	5	−3.6 ± 1.4	1.6 ± 0.5	38.9 ± 9.1	5	−6.2 ± 1.0	0.4 ± 0.8
16.5 ± 3.9	4	−3.6 ± 0.9	1.7 ± 0.8	39.8 ± 4.6	2	−1.5 ± 0.1	2.3 ± 0.4
19.6 ± 4.6	5	−2.9 ± 1.0	1.5 ± 0.5	40.2 ± 7.9	8	−3.0 ± 3.1	0.5 ± 0.8
20.6 ± 3.4	5	−3.6 ± 2.1	1.8 ± 0.6	42.2 ± 5.2	4	−2.2 ± 2.8	1.4 ± 0.9
21.5 ± 3.8	5	−2.0 ± 1.5	1.6 ± 0.4	42.5 ± 6.2	4	−5.2 ± 0.8	0.1 ± 0.6
21.6 ± 4.4	13	−2.5 ± 3.3	1.6 ± 0.6	42.9 ± 4.0	5	−2.0 ± 1.8	0.1 ± 0.3
23.4 ± 4.5	5	−2.1 ± 1.5	0.6 ± 0.4	43.0 ± 7.8	5	−2.1 ± 1.0	1.4 ± 0.6
23.5 ± 4.5	5	−2.6 ± 2.0	1.7 ± 0.4	43.3 ± 6.1	5	−5.0 ± 0.6	0.0 ± 0.5
24.1 ± 4.5	5	−2.0 ± 1.4	0.5 ± 0.5	43.5 ± 4.9	5	−3.5 ± 2.5	0.0 ± 0.3
24.8 ± 4.6	6	−2.6 ± 3.5	0.7 ± 0.6	43.6 ± 6.3	7	−3.7 ± 1.9	1.4 ± 0.9
25.5 ± 5.5	5	−4.1 ± 1.4	0.6 ± 0.3	43.8 ± 7.3	10	−3.8 ± 2.2	−0.1 ± 0.4
27.4 ± 4.4	3	−4.2 ± 0.4	2.1 ± 1.3	44.7 ± 6.5	4	−2.9 ± 2.2	1.3 ± 0.4
28.1 ± 5.1	5	−1.5 ± 1.6	1.1 ± 0.4	46.6 ± 6.5	1	−6.5	0.1
28.2 ± 5.1	3	−3.3 ± 1.4	1.1 ± 0.7	47.2 ± 4.6	2	−5.6 ± 1.3	0.0 ± 0.2
28.5 ± 6.4	1	−1.8	1.9	47.8 ± 5.7	2	−4.7 ± 0.1	0.5 ± 0.5
29.4 ± 4.6	10	−4.1 ± 2.6	0.2 ± 0.9	48.1 ± 5.6	1	−0.3	0.9
29.7 ± 5.0	4	−3.6 ± 1.6	0.9 ± 0.7	49.2 ± 8.5	5	−1.0 ± 2.3	0.7 ± 0.2
29.9 ± 5.4	5	−2.9 ± 2.9	−0.1 ± 1.4	50.1 ± 13.0	5	−3.6 ± 1.1	0.3 ± 0.4
30.2 ± 6.7	8	−3.7 ± 1.2	0.5 ± 0.5	50.5 ± 9.3	5	−5.6 ± 1.1	−0.3 ± 0.8
30.3 ± 5.3	10	−4.1 ± 1.5	1.0 ± 0.8	55.7 ± 5.5	12	−5.2 ± 2.1	0.3 ± 1.0
30.6 ± 4.2	1	−2.1	2.0				

n: Number of entire-shells analyzed of equivalent age; ^aage data taken from Ortiz et al. (2006); ^bmodern isotopic data taken from Yanes et al. (2008b); ± indicates standard deviation of the observed range of the measured values.

generations of shells during the sedimentation process (paleosol genesis), which takes from hundreds to thousands of years. Since dunes are somewhat sealed by paleosols, shell reworking from older into younger beds was improbable (Yanes et al., 2007). The AAR dates of Ortiz et al. (2006) were adopted as credible indicators of the comparative ages of shells.

Methods

Sampling strategy, species and shell preservation

Fossil shells ($n=329$) were collected from 30 to 50 cm into the exposed surface to avoid possible contamination or reworked material. Bulk paleosol and dune samples were collected directly from 40 stratigraphic horizons.

Ten species were included in this study. The assemblages were dominated by *Theba geminata* (Mousson, 1857) and *T. arinagae* Gittenberger & Ripken, 1987 (Yanes, 2003; Yanes, 2005; Huntley et al., 2008; Yanes et al., 2008a), which were continuous and abundant throughout space and time. Modern *Theba* specimens display an herbivorous and epifaunal strategy with an annual/bi-annual life cycle (Cowie, 1984). The majority of shells belong to the *Theba* genus ($n=278$). The remaining eight species ($n=51$), which were discontinuous in the record and less abundant, included *Rumina decollata* (Linnaeus, 1758) ($n=15$), *Pomatias lanzarotensis* (Wollaston, 1878) ($n=10$), *Monilearia monilifera* (Webb & Berthelot, 1833) ($n=9$), *M. granostriata* (Mousson, 1857) ($n=2$), *Hemicycla sarcostoma* (Webb & Berthelot, 1833) ($n=9$), *Ferussacia folliculus* (Gmelin, 1791) ($n=1$), *Caracollina lenticula* (Michaud, 1831) ($n=1$), *Candidula ultima* (Mousson, 1872) ($n=1$) and *Canariella plutonia* (Lowe, 1861) ($n=2$).

Prior to stable isotope analysis, XRD results of 94 specimens indicate that shells preserved their aragonite composition (Yanes et al., 2007, 2008a). Thus, substantial diagenetic alterations were unlikely. Scanning Electron Microscope (SEM) micrographs of modern (Fig. S2A–B) and fossil (Fig. S2C–D) shell fragments of *Theba geminata* showed no evidence of recrystallization.

Stable isotope analyses

Entire shells and bulk sediment samples were analyzed in the Huffington Department of Earth Sciences (SMU, USA), the Savannah River Ecology Laboratory (UGA, USA) and the Instituto Andaluz de Ciencias de la Tierra (CSIC, Spain). Samples were analyzed using a Finnigan Delta^{plus} XL continuous flow isotope ratio mass spectrometer and a dual inlet Finnigan MAT 252 isotope ratio mass spectrometer. All carbonate isotopic results are reported in δ notation relative to the international standard PDB. The δ values are defined as:

$$\delta X = \left[\left(R_{\text{sample}} / R_{\text{standard}} \right) - 1 \right] \times 1000 (\text{‰})$$

where $X=^{13}\text{C}$, for $R=^{13}\text{C}/^{12}\text{C}$; or $X=^{18}\text{O}$, for $R=^{18}\text{O}/^{16}\text{O}$. Analytical uncertainty was $\pm 0.1\text{‰}$ for both $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$. For $\delta^{18}\text{O}$ values of water, the standard is SMOW (IAEA: <http://www.iaea.org/>).

Shells were cleaned ultrasonically in deionized water and pulverized with an agate mortar and pestle. Organic matter was removed by placing the sample in a reagent-grade 3% NaOCl solution for 48 h at room temperature ($\sim 22^\circ\text{C}$). Samples were thereafter rinsed with deionized water and dried in an oven at 40°C . The NaOCl method was tested at SMU on a powdered shell of *Cepaea hortensis* (Müller, 1774). Within analytical uncertainty, the treatment with reagent-grade 3% NaOCl ($<0.0002\%$ Ca impurity) had no significant effect on the shell isotopic values. This is consistent with Wierzbowski (2007), who found that 5% NaOCl treatment had no substantial effect on aragonite shell $\delta^{18}\text{O}$ ($\leq \pm 0.1\text{‰}$) or $\delta^{13}\text{C}$ ($\leq \pm 0.2\text{‰}$) values. Conse-

quently, the variations in shell isotopic values of this study are not biased by NaOCl treatment. All shells were treated at room temperature with 3% NaOCl as a precaution to minimize possible organic matter interferences.

Intra-shell aliquots were collected from seven pre-cleaned (as described above) shells using an electronic dremel along ontogeny. Shell carbonate ($\sim 150\ \mu\text{g}$) was placed in a 6 ml exetainer™ vial and flushed with helium. The carbonate was converted to CO_2 gas by adding 0.5 ml of 100% H_3PO_4 at 25°C . The CO_2 was analyzed after 24 h using the GasBench II and the CF-IRMS. Results were calibrated against the international standards NBS-18 and NBS-19 and in-house standards. The precision of the analyses was $\pm 0.1\text{‰}$ (1σ standard deviation) for $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ based on the repeated measurement ($n=30$) of standards. Replicate analyses of shells had a precision of $\pm 0.2\text{‰}$ for both isotopes.

Sediment samples were homogenized by grinding under methanol in a mortar and pestle and treated with 3% H_2O_2 overnight to eliminate organic contaminants. Samples were rinsed with deionized water and dried at room temperature. The carbonate ($\sim 10\text{--}20\ \text{mg}$) was reacted overnight in vacuum with 100% H_3PO_4 at 25°C . The CO_2 was analyzed on a Finnigan MAT 252 mass spectrometer. Analytical uncertainty was $\pm 0.1\text{‰}$ for both isotopes.

Results

Carbon and oxygen isotopic composition of fossil land snail shells

Fossil shell $\delta^{13}\text{C}$ values are plotted against age in Figure 2A and scatter over a range from -8.9‰ to $+3.8\text{‰}$ (Table 1; Appendices S1). Shells of similar age but from different locales showed comparable values (Appendices S1). Average $\delta^{13}\text{C}$ values of age-equivalent shells are shown in Figure 2B along with the uncertainties (error bars) of AAR ages.

The substantial scatter and the large overlap of shell $\delta^{13}\text{C}$ values among beds suggest the simultaneous presence of C_3/C_4 plants on the islands over the last $\sim 50\ \text{ka}$ (Fig. 2A). Although not all time intervals are equally well represented by numbers of analyzed shells, there is general accord of the average isotopic compositions of age-equivalent shells. Thus, this unevenness of temporal distribution of numbers of samples and the effects of possible overlap associated with the uncertainties of AAR ages may be mitigated by the 3-point moving average (Fig. 2C) of the mean values (Fig. 2B). Notwithstanding the rather large uncertainties in the AAR ages, if the emphasis is on overall, longer-term temporal variations, moving averages should have some credibility. This approach suggests that recent snails ingested higher proportions of C_3 plants than the snails at $\sim 20\text{--}24\ \text{ka}$.

Carbon and oxygen isotopic compositions of shells are not correlated. Fossil shell $\delta^{18}\text{O}$ values range from -1.9‰ to $+4.5\text{‰}$ (Fig. 3A; Table 1; Appendix S1). The isotopic scatter among shell beds probably reflects environmental variability at the microhabitat scale in which snails live (e.g., Balakrishnan et al., 2005a,b). Overlaps in $\delta^{18}\text{O}$ values suggest some similarities in the extremum values of microhabitats through time (Fig. 3A), since snails tend to be active under optimum conditions, and thus select for a restricted range of environmental variability. Notwithstanding the scatter (Fig. 3A), average $\delta^{18}\text{O}$ values of age-equivalent shells may be sources of information on larger scale, longer term, climatic variations, because a large standard deviation does not automatically imply inaccuracy of the mean as an indicator of the average conditions in a locale. Moreover, a moving average of the means emphasizes longer-term trends.

Average $\delta^{18}\text{O}$ values of age-equivalent shells are shown in Figure 3B together with the uncertainty of AAR ages (error bars in Fig. 3B). Generally, age-equivalent shells from different locales had analytically indistinguishable mean $\delta^{18}\text{O}$ values (Appendices S1). Three-point moving averages (Fig. 3C) of the mean values exhibit an overall increase in shell $\delta^{18}\text{O}$ values from $\sim 0.1\text{‰}$ at $\sim 50\ \text{ka}$ to $\sim 1.6\text{‰}$

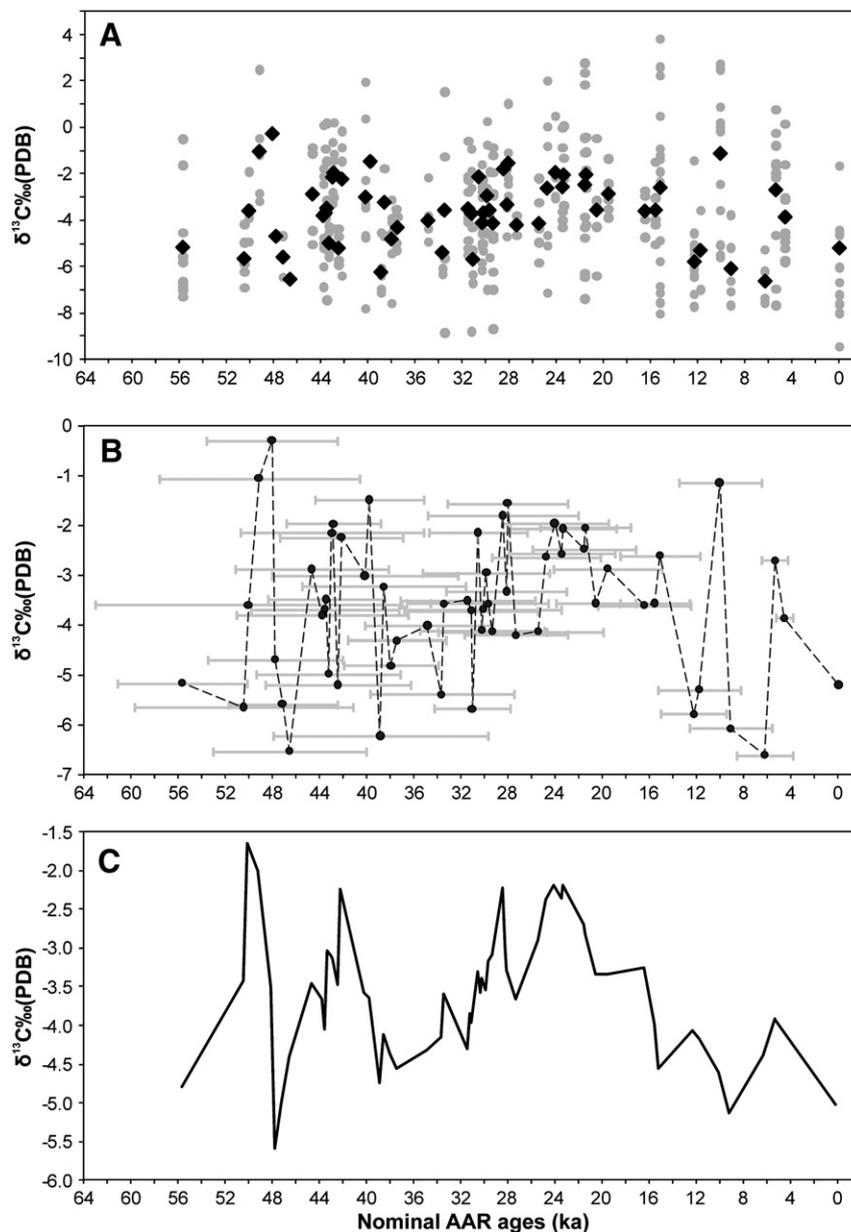


Figure 2. Stable carbon isotopic composition of fossil land snail shells from the Canary Islands through time. (A) Individual entire-shell $\delta^{13}\text{C}$ values (gray circles) and average age-equivalent samples (black diamonds). (B) Mean $\delta^{13}\text{C}$ values of age-equivalent shells (dashed line). Age uncertainty is indicated by gray error bars. (C) 3-point moving average of the mean $\delta^{13}\text{C}$ values through time.

1.8‰ during the LGM (~15–22 ka). The moving averages also indicate that there was an abrupt decline in post-LGM $\delta^{18}\text{O}$ followed by an irregular, but overall increase of shell $\delta^{18}\text{O}$ values to modern values of ~0.9‰ (Fig. 3C). This coincides with the pattern of change found by Colonese et al. (2010) in shell $\delta^{18}\text{O}$ values from the late Pleistocene to Holocene in southern Italy.

Carbon and oxygen isotopic composition of fossil land snail shells among taxa

Shells from all “rare” land snail species (those with low abundance and sporadic in the fossil record) displayed ranges of isotopic values that overlapped with those of the dominant *Theba* species (Appendices S1). The overall isotopic variations through time of the dominant species alone did not differ from those observed when all ten species were considered in combination. These results are consistent with studies of modern land snails from Tenerife Island, for which the stable isotope composition of multiple species did not substantially

differ among taxa (Yanes et al., 2009). Consequently, the isotopic compositions of all species were used to infer the environmental conditions of the last ~50 ka in the eastern Canary Islands.

Intra-shell carbon and oxygen isotopic variability of modern and fossil shells

Intra-shell $\delta^{13}\text{C}$ values of two modern *Theba geminata* individuals exhibited ranges ($\Delta^{13}\text{C}$) of 0.5‰ and 1.7‰, while corresponding $\delta^{18}\text{O}$ values had ranges ($\Delta^{18}\text{O}$) of 0.3‰ and 0.5‰ (Table 2; Fig. S2A–B; Appendix S2). The magnitude of the modern intra-shell isotopic ranges was smaller than in fossil individuals. $\Delta^{13}\text{C}$ values of five fossil shells ranged from 1.2‰ to 3.3‰ and $\Delta^{18}\text{O}$ values from 1.2‰ to 2.8‰ (Table 2; Fig. S2C–G). The patterns of intra-shell isotopic variations differed among specimens through ontogeny (Fig. S2). Many studies have increasingly used the isotopic composition through the ontogeny of the organisms’ hard skeleton in an attempt to reconstruct high resolution (daily, monthly and/or seasonal) climatic conditions

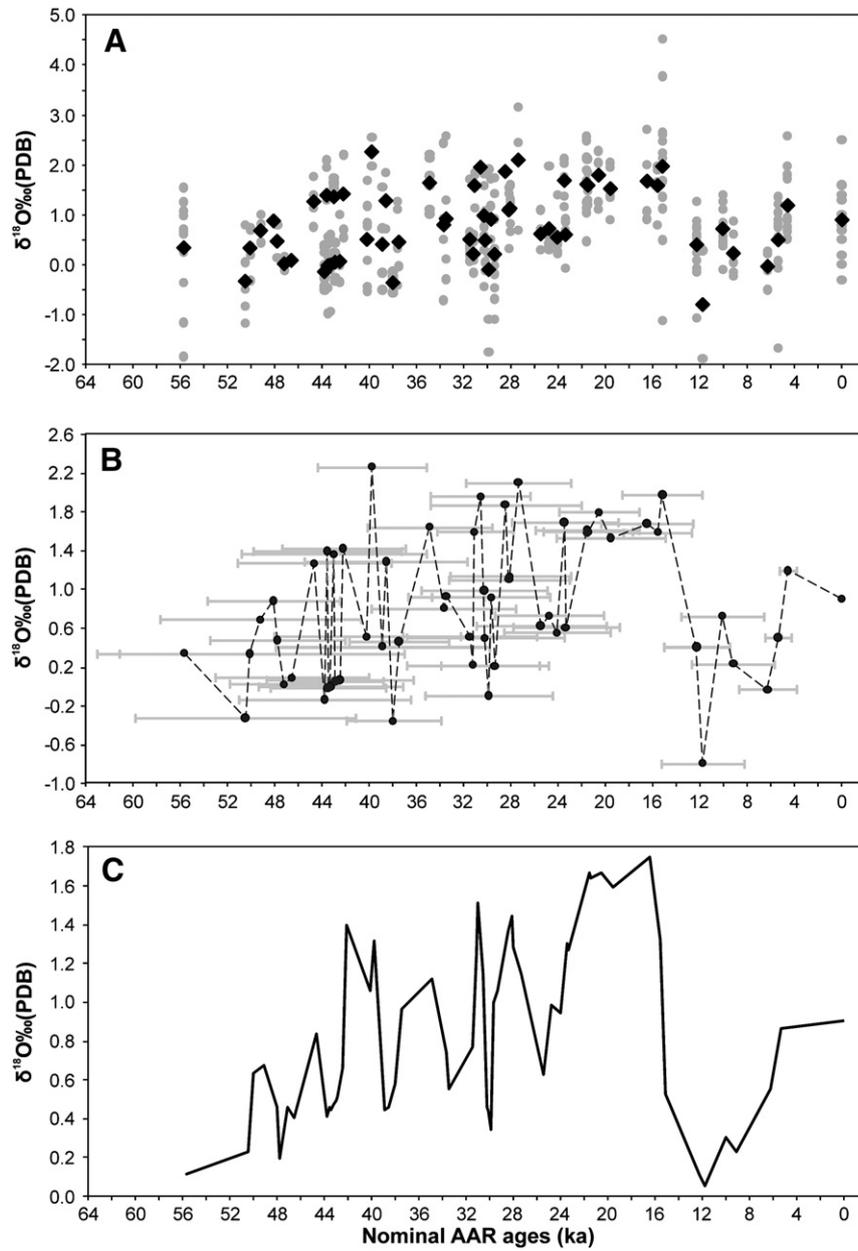


Figure 3. Stable oxygen isotopic composition of fossil land snail shells from the Canary Islands through time. (A) Individual entire-shell $\delta^{18}\text{O}$ values (gray circles) and average $\delta^{18}\text{O}$ values of age-equivalent samples (black diamonds). (B) Mean $\delta^{18}\text{O}$ values of age-equivalent shells (dashed line). Age uncertainty is indicated by gray error bars. (C) 3-point moving average of the mean $\delta^{18}\text{O}$ values through time.

Table 2

Carbon and oxygen stable isotope composition of modern and fossil snail shells sampled subsequently through ontogeny.

Shell ID	Nominal AAR age (ka) ^a	n	$\delta^{13}\text{C}_{\text{‰}}$ (PDB)				$\Delta^{13}\text{C}$	$\delta^{18}\text{O}_{\text{‰}}$ (PDB)				
			Mean	Min	Max			Mean	Min	Max	$\Delta^{18}\text{O}$	
TGL-1	Modern	9	-7.8	±0.2	-8.0	-7.5	0.5	0.3	±0.2	0.1	0.6	0.5
TGF-1	Modern	8	-6.5	±0.6	-7.1	-5.4	1.7	0.1	±0.1	-0.1	0.2	0.3
FAG-6	5.4 ±1.1	23	-4.9	±0.4	-5.6	-3.6	2.0	-0.1	±0.4	-0.8	0.7	1.5
LTA-2	12.3 ±2.8	22	-5.7	±0.3	-6.1	-4.5	1.6	0.9	±0.3	0.3	1.6	1.3
FBP-1	15.2 ±3.4	7	-2.3	±1.2	-4.6	-1.2	3.3	2.6	±0.4	1.8	3.0	1.2
GLC-5	24.8 ±4.6	15	-5.9	±0.5	-6.9	-5.2	1.7	2.1	±0.7	0.0	2.9	2.8
FAG-1	55.7 ±5.5	25	-3.1	±0.6	-4.7	-2.4	2.3	0.1	±0.5	-1.3	0.8	2.0

n: Number of samples per shell; Min: minimum; Max: maximum; Δ : range of values; ^aage data taken from Ortiz et al. (2006); ± indicates standard deviation of the observed range of the measured values.

through the organisms' life. This approach appears to be feasible for aquatic organisms because the environmental controls (temperature and water isotopic composition) affecting the shell biomineralization process are relatively well understood (Grossman and Ku, 1986). However, the interactions of environmental factors that control land snail shell isotopic values are significantly more complex than those for aquatic taxa. The relatively large values for intra-shell $\Delta^{13}\text{C}$ and $\Delta^{18}\text{O}$ (see also Leng et al., 1998; Goodfriend and Ellis, 2002; Baldini et al., 2007) emphasize the importance of analyzing entire shells that are carefully homogenized rather than portions of the shell (e.g., Balakrishnan et al., 2005a; Kehrwald et al., 2010).

Carbon and oxygen isotopic composition of bulk paleosol and dune carbonates

The $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of bulk paleosol and dune carbonates varied between -5.2‰ and 0.7‰ (Fig. 4A–B) and between -1.0‰ and 1.3‰ , respectively (Fig. 4C–D; Table 3; Appendix S3). Paleosol and dune $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values correlated positively ($r_s = 0.69$; $p < 0.001$; $n = 40$). The isotopic compositions of the sediment carbonates did not correlate with the aragonite/calcite ratio estimated from XRD analysis.

Relatively low sediment $\delta^{13}\text{C}$ (from -1.5‰ to -1‰) and $\delta^{18}\text{O}$ ($\sim 0.5\text{‰}$) values were observed before the LGM ($\sim 25\text{--}50$ ka). More positive values ($\sim 0\text{‰}$ for $\delta^{13}\text{C}$ and $\sim 0.9\text{‰}$ for $\delta^{18}\text{O}$) were common around the LGM ($\sim 15\text{--}22$ ka). Early to mid-Holocene values ($\sim 5\text{--}10$ ka) displayed a slight increase in $\delta^{13}\text{C}$ (to -0.5‰) and no significant change in $\delta^{18}\text{O}$ (0.8‰) (Fig. 4A–D; Table 3; Appendix S3).

Discussion

Paleosol and dune $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$

Paleosols may contain pedogenic and non-pedogenic carbonates, which complicate paleoenvironmental interpretations. The $\delta^{13}\text{C}$ and

Table 3

Carbon and oxygen stable isotope composition of bulk paleosol and dune samples.

Nominal AAR age (ka) ^a	<i>n</i>	$\delta^{13}\text{C}\text{‰}$ (PDB)	$\delta^{18}\text{O}\text{‰}$ (PDB)			
5.4	±1.7	1	-0.2	1.0		
6.3	±2.4	1	-1.0	0.6		
11.8	±4.0	2	-0.7	±1.1	0.6	±0.6
15.2	±3.4	1	-1.4	1.2		
16.5	±3.9	1	0.7	1.2		
20.6	±3.4	1	-0.3	0.4		
23.2	±4.2	1	-0.1	1.3		
24.8	±4.4	1	0.0	0.6		
27.0	±4.5	2	-0.2	±0.6	0.8	±0.7
28.2	±5.1	1	-1.0	1.2		
29.4	±4.6	1	-0.3	1.0		
30.3	±5.5	2	-0.4	±0.7	0.7	±0.5
31.1	±3.2	3	-0.7	±0.5	0.8	±0.2
31.5	±5.7	1	-0.5	0.7		
33.5	±3.2	1	-2.5	0.2		
34.9	±5.3	1	0.2	0.8		
37.6	±4.9	5	-2.0	±2.2	0.3	±0.7
38.9	±6.4	5	-1.3	±0.8	0.7	±0.3
43.0	±7.8	1	-0.6	0.4		
44.7	±6.5	1	0.0	1.1		
47.2	±4.6	3	-2.7	±2.2	0.1	±0.9
47.8	±5.7	3	-0.4	±1.1	0.8	±0.2
55.7	±5.5	1	-1.4	0.3		

n: Number of bulk paleosol and dune samples of equivalent age; ^aage data taken from Ortiz et al. (2006); ± indicates standard deviation of the observed range of the measured values.

$\delta^{18}\text{O}$ values of bulk sediment carbonates likely represent contributions from mixtures of marine-derived and continental-derived bioclasts together with some pedogenic carbonates and Saharan silt (e.g., Damnati et al., 1996). The difficulty of separating these fractions precluded measurement of their respective end member isotopic compositions.

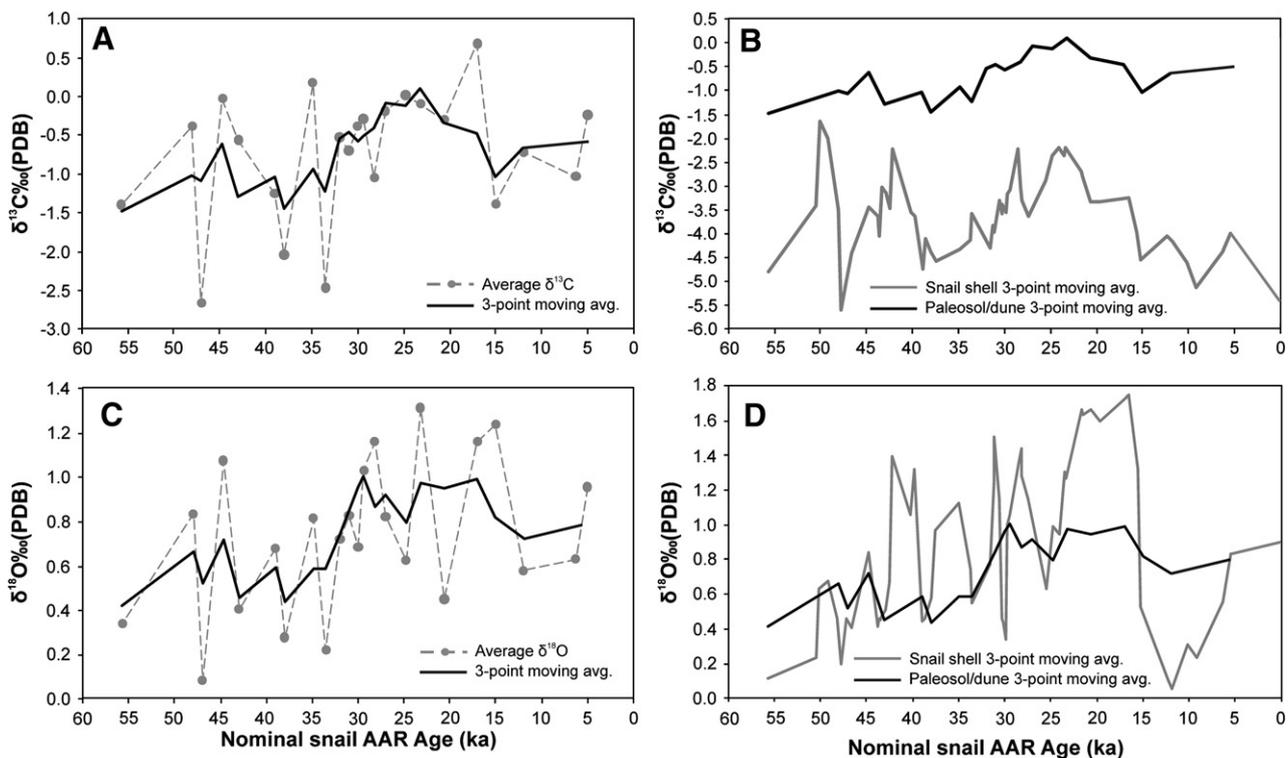


Figure 4. (A) Mean $\delta^{13}\text{C}$ values of age-equivalent bulk paleosol and dune samples (dashed line) and 3-point moving average of average $\delta^{13}\text{C}$ values (continuous line) through time. (B) Comparison of the 3-point moving average $\delta^{13}\text{C}$ values of snail shells (gray line) and bulk paleosol and dune samples (black line) against time. (C) Mean paleosol and dune $\delta^{18}\text{O}$ values (dashed line) and 3-point moving average of $\delta^{18}\text{O}$ values (continuous line) through time. (D) Comparison of the 3-point moving average of $\delta^{18}\text{O}$ values of snail shells (gray line) and bulk paleosol and dune samples (black line) against time.

Although the ages of these carbonate sources remain uncertain, a recent AAR study by [Hearty and Kaufman \(2009\)](#) of fossil land snail *Cerion* shells and bioclastic sediments from the Bahamas indicated that the marine sediments were rapidly transported inland and quickly colonized by snails. Such a quick sedimentation process (thousands to hundreds of years) and the rapid colonization by terrestrial organisms (less than 1000 yr after the newly deposited dunes) suggested no substantial age differences between shells and the sediments in which they were preserved ([Hearty and Kaufman, 2009](#)). Although it has not been established that a corresponding similarity exists in the Canary eolian deposits, it is assumed here as a working hypothesis.

The average $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of bulk sediment samples exhibit smaller amplitude temporal variations ([Fig. 4A](#) and [C](#)) than the shells ([Fig. 4B](#) and [D](#)). Bulk sediment carbonates from which shells were collected provide an important constraint for understanding the range of possible contaminant to which the buried shells have been exposed. The data from the bulk sediments also provide a useful frame of reference, contrasting the small amplitude variations of the bulk sediment with the larger amplitude fluctuations of the shells. This smaller amplitude variation probably reflects the fact that fragments of shells from land snails constitute only a portion of the sediment carbonates and are mixed with varying proportions of marine and pedogenic calcite as well as aragonitic marine mollusk shells. This emphasizes that the multi-component isotopic signal produced by the mixture of carbonates in the sediment is not the principal influence on the isotopic composition of shells recovered from the sediment. Accordingly, the entire-shell data are reasonably free from contaminant carbonate and preserve a distinctly different and interpretable signal.

Environmental controls on shell $\delta^{13}\text{C}$

The $\delta^{13}\text{C}$ values of modern *Theba* shells are primarily a function of the $\delta^{13}\text{C}$ values of the plants and carbonates ingested by the snails ([Yanes et al., 2008b](#)). Simple mass balance equations suggest that ingested carbonate represents between ~20% and 40% of the modern shells ([Yanes et al., 2008b](#)). The ingestion of foreign carbonates, whose proportion may vary among individuals ([Goodfriend and Hood, 1983](#); [Goodfriend, 1987](#); [Goodfriend and Gould, 1996](#); [Yanes et al., 2008b](#)) or even within a single individual along ontogeny ([Goodfriend et al., 1999](#)), adds an additional difficulty to the interpretation of shell $\delta^{13}\text{C}$. However, although the shell $\delta^{13}\text{C}$ values may be shifted by a few per mil due to carbonate ingestion, the temporal pattern of variation in shell $\delta^{13}\text{C}$ provides rough estimates of changes in the mix of plants in the snail diet. The scatter in the $\delta^{13}\text{C}$ values among shells suggests the simultaneous presence of C_3 and C_4 plants over the last ~50 ka in the Canaries. Although some higher shell $\delta^{13}\text{C}$ values may reflect higher $\delta^{13}\text{C}$ values of C_3 plants under water stress during drier times and/or higher contributions of adventitious carbonates, the maximum shell $\delta^{13}\text{C}$ values can be explained most simply if those snails consumed principally C_4 plants.

The maximum (–2.5‰ to –2‰) in the 3-point moving average of the mean shell $\delta^{13}\text{C}$ values at ~24 ka ([Fig. 2C](#)) suggests that snails consumed a higher proportion of C_4 plants at that time. This suggests that environmental conditions were drier (e.g., [Goodfriend and Ellis, 2000, 2002](#)) and/or that atmospheric CO_2 concentrations were lower (e.g., [Koch et al., 2004](#)). Notably, C_4 vegetation was also dominant in Africa during glacial periods (e.g., [Gasse, 2000](#); [Gasse et al., 2008](#)). Consequently, with a caveat about the interpretative complications associated with snail ingestion of carbonate, shell $\delta^{13}\text{C}$ values suggest that C_3 and C_4 plants have been present in the Canary Islands over the last ~50 ka. However, the proportion of C_4 plants appears to have been higher throughout much of the glacial interval (~15 to ~50 ka) than today ([Fig. 2](#)).

Environmental controls on modern shell $\delta^{18}\text{O}$

The evaporative steady-state flux balance model of [Balakrishnan and Yapp \(2004\)](#) was applied to modern snails from the Canary Islands. To predict the shell $\delta^{18}\text{O}$ values, the model develops a quantitative relationship between the amount and isotopic composition of liquid water ingested by the snails, the amount and isotopic composition of liquid water evolved from the snail body fluid, the diffusive evaporative flux of water from the snail body fluid, and the temperature-dependent oxygen isotope fractionation between the snail body fluid and crystallizing aragonite shell. Thus, the model predicts that (1) ambient temperature, (2) the $\delta^{18}\text{O}$ value of ingested water, (3) RH, (4) ambient water vapor $\delta^{18}\text{O}$ values, and (5) the ratio (θ) of the flux of liquid water output from the body fluid (f_o) relative to the flux of liquid water ingested by the snail (f_{in}) during shell formation are important controls on the body fluid/shell $\delta^{18}\text{O}$ values ([Balakrishnan and Yapp, 2004](#)).

[Balakrishnan and Yapp \(2004\)](#) showed that it is useful to assume that water vapor is in isotopic equilibrium with the liquid water ingested by the snail. Also, for $\theta \leq 0.40$, an assumption that snail body fluid is lost only by evaporation (i.e., $\theta = 0$) is a good approximation, and a value of $\theta = 0$ is adopted here ([Balakrishnan and Yapp, 2004](#)).

Two cases were examined to compare model predictions of RH with the modern conditions on the Canary Islands. Case 1: water vapor in isotopic equilibrium with rain ([Fig. 5A](#)) (see [Balakrishnan and Yapp, 2004](#) for further details). Case 2: water vapor with a constant value of –11‰ (marine vapor: [Craig and Gordon, 1965](#)). For both cases, the input parameters were $T = 19^\circ\text{C}$ (average temperature during the rainy season in the islands) and amount-weighted average $\delta^{18}\text{O}$ values of rain of –3.5‰ (SMOW), based on regional IAEA data. Using amount-weighted rain $\delta^{18}\text{O}$ values emphasizes the importance of the wetter intervals when snails form shell material ([Balakrishnan and Yapp, 2004](#)).

For Case 1, measured $\delta^{18}\text{O}$ values (–0.3‰ to 2.5‰: [Yanes et al., 2008b](#)) of modern shells are predicted by the model for RH between 0.86 and 0.94. In contrast, for Case 2, the more negative modern $\delta^{18}\text{O}$ values are not predicted for any physically reasonable RH values (i.e., $\text{RH} \leq 1.00$). Consequently, only the assumptions of Case 1 are used.

The relatively high values of modern RH (from 0.86 to 0.94) predicted by the model (for Case 1) are consistent with modern snail activity primarily at night and/or during or immediately after a rain event—times when snails are active (e.g., [Cook, 2001](#)). Much of the scatter in shell $\delta^{18}\text{O}$ values among individuals may be attributable to variations of ambient environmental parameters among different microenvironments inhabited by those individuals ([Balakrishnan et al., 2005b](#); [Yanes et al., 2009](#)). This emphasizes the need to analyze comparatively large numbers of shells per site to obtain a mean value that is reasonably representative of the average environmental conditions at that locale. The observed average $\delta^{18}\text{O}$ value (0.9‰) of live-collected snails ([Fig. 5A](#)) and the model of [Balakrishnan and Yapp \(2004\)](#) suggest that, on average, for a combination of $T \approx 19^\circ\text{C}$ and rain $\delta^{18}\text{O} \approx -3.5\text{‰}$ (SMOW), the average value of RH was ~0.91 during shell deposition. This RH is consistent with the high humidity that characterizes the times of recent snail activity in the Canary Islands and suggests that meaningful values of RH may be inferred from ancient shells.

Paleoclimatic inferences

Fossil shell $\delta^{18}\text{O}$ values exhibit substantial scatter through time ([Fig. 3A](#)), and the magnitude of the scatter is comparable for different ages. However, variations in the mean shell $\delta^{18}\text{O}$ values suggest that climatic conditions were not constant through time. The model of [Balakrishnan and Yapp \(2004\)](#) and independent, proxy-constrained estimates of temperature and rainfall $\delta^{18}\text{O}$ values are used to extract changes in paleohumidity from changes in the fossil shell $\delta^{18}\text{O}$.

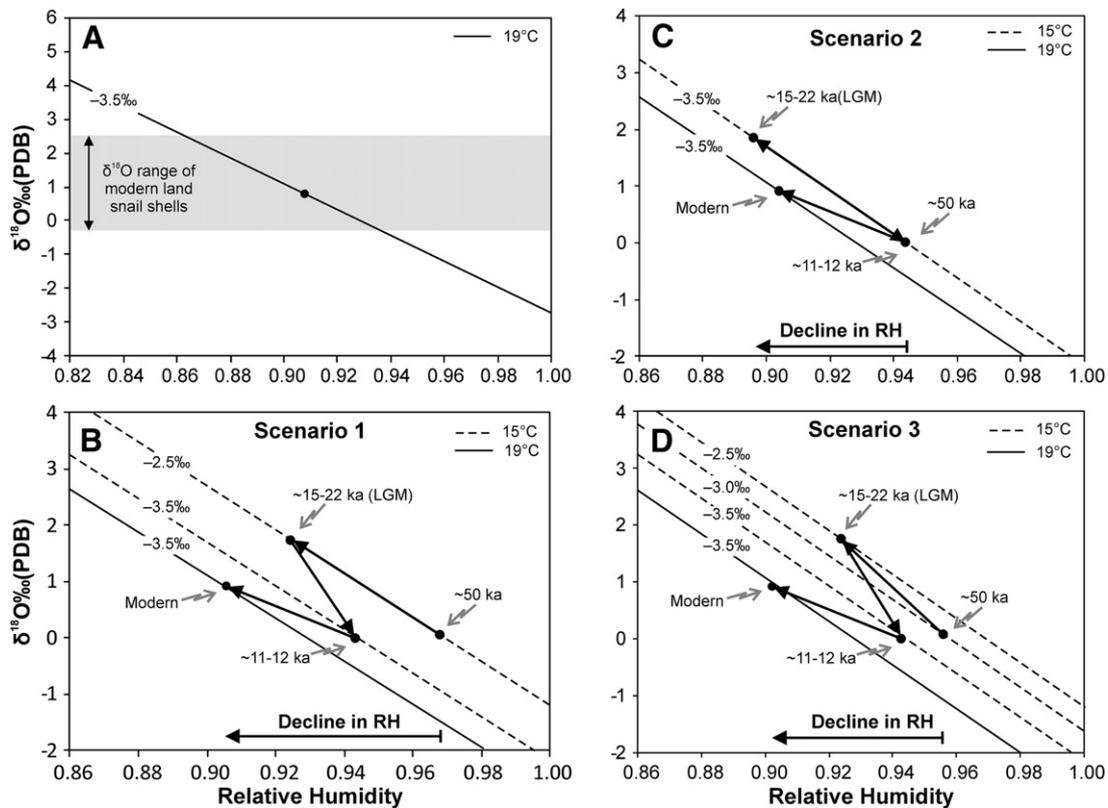


Figure 5. Calculated shell $\delta^{18}\text{O}$ values as a function of relative humidity using the evaporative steady-state flux balance model by Balakrishnan and Yapp (2004). (A) Gray area represents the measured range of shell $\delta^{18}\text{O}$ values of live-collected land snails from the eastern Canary Islands (Yanes et al., 2008b). Filled dot represents the average shell $\delta^{18}\text{O}$ value (0.9‰) for modern shells. (B) Paleoclimatic scenario 1 for the last 50 ka in the Canary Archipelago as inferred from the land snail isotopic record (see text). Calculations were performed using interglacial ($\sim 19^\circ\text{C}$) and glacial ($\sim 15^\circ\text{C}$) temperatures estimated from SST proxies (Zhao et al., 1995; Bard, 2002) and initial interglacial (-3.5‰) and glacial (-2.5‰) rain $\delta^{18}\text{O}$ values estimated from IAEA data and global ocean $\delta^{18}\text{O}$ values, respectively (Zachos et al., 2001; Schrag et al., 2002). (C) Paleoclimatic scenario 2 assuming constant rainwater $\delta^{18}\text{O}$ values. (D) Paleoclimatic scenario 3 using interglacial ($\sim 19^\circ\text{C}$) and glacial ($\sim 15^\circ\text{C}$) temperatures and interglacial (-3.5‰) and glacial (-2.5‰ and -3.0‰) rain $\delta^{18}\text{O}$ values. It is worth noting that the plausible paleoclimatic scenarios require a decline in RH to explain the land snail data (see text).

However, uncertainties in AAR ages favored the use of moving average snail $\delta^{18}\text{O}$ values and interpretations of only longer-term climatic change.

Published ancient sea-surface temperatures (SST) and ocean $\delta^{18}\text{O}$ values were used to estimate paleotemperatures and $\delta^{18}\text{O}$ values of ancient rain for model calculations (Fig. 6). Alkenone ratios in marine sediments (e.g., Zhao et al., 1995; Bard, 2002), indicate that SST in the eastern Atlantic Ocean at 37° and 20°N latitude only vary by 3°C or 4°C between glacial and interglacial intervals (Fig. 6B). These locations bracket the Canary Islands, implying a similar magnitude of glacial–interglacial temperature variation (modern interglacial $T \approx 19^\circ\text{C}$; glacial $T \approx 15^\circ\text{C}$). The SST data (Fig. 6B) suggest that there was no sustained, long-term temperature change in the Canary Islands between ~ 50 and 12 ka.

Globally, $\delta^{18}\text{O}$ values of the oceans were $\sim 1\text{‰}$ higher during the LGM than today (e.g., Zachos et al., 2001; Schrag et al., 2002), because of extensive Northern Hemisphere continental glaciation. Higher oceanic $\delta^{18}\text{O}$ values might be expected to correspond to higher average $\delta^{18}\text{O}$ values of Canary Islands rainfall (i.e., -2.5‰). For the interglacial interval from ~ 12 ka to modern, the data of Zachos et al. (2001) suggest that global ocean $\delta^{18}\text{O}$ values did not vary monotonically (Fig. 6D). We adopt the working hypothesis that longer-term average $\delta^{18}\text{O}$ values of rain in the Canaries did not experience a monotonic shift over this interval and had values around -3.5‰ .

The snail flux balance model (Balakrishnan and Yapp, 2004), combined with the aragonite–water oxygen isotope fractionation equation of Grossman and Ku (1986), was applied to the interpretation of the fossil shell $\delta^{18}\text{O}$ values (Fig. 6A). For Case 1 (see above), three boundary condition scenarios were examined.

Scenario 1. Glacial age temperatures of $\sim 15^\circ\text{C}$ and rain $\delta^{18}\text{O}$ values of $\sim -2.5\text{‰}$ were assumed. For these conditions, shell $\delta^{18}\text{O}$ values of 0.1‰ indicate that ~ 50 ka ago, values of RH were ~ 0.97 (Fig. 5B). For the LGM (~ 15 to 22 ka) with shell $\delta^{18}\text{O}$ values of 1.6‰ to 1.8‰ , RH would have been ~ 0.92 (Fig. 5B). At ~ 12 ka, shell $\delta^{18}\text{O}$ values of $\sim 0\text{‰}$ suggest an RH of ~ 0.95 for rain $\delta^{18}\text{O} \approx -3.5\text{‰}$ (Fig. 5B). Finally, there is the change in the Holocene toward the modern values of 19°C , rain $\delta^{18}\text{O} \approx -3.5\text{‰}$, and $\text{RH} \approx 0.91$ (Fig. 5B). Thus, over the last ~ 50 ka there has been an overall decrease in RH to the modern, semiarid conditions of the eastern Canary Islands.

Scenario 2. Glacial–interglacial temperatures on the Canary Islands were again assumed to change from $\sim 15^\circ\text{C}$ to $\sim 19^\circ\text{C}$. As an extreme case it was assumed that there was no change in the average $\delta^{18}\text{O}$ values (-3.5‰) of rain over the past ~ 50 ka (i.e., glacial–interglacial changes in ocean $\delta^{18}\text{O}$ values did not affect rain $\delta^{18}\text{O}$ values). The model calculations suggest that shells at ~ 50 ka grew at average RH of ~ 0.95 , while at ~ 15 – 22 ka (LGM) RH would have been ~ 0.90 (Fig. 5C). At ~ 12 ka, RH was ~ 0.95 before switching toward the modern value of ~ 0.91 (Fig. 5C).

Scenario 3. Again, the average Canary Islands temperatures are assumed to have changed from $\sim 15^\circ\text{C}$ during the glacial interval to $\sim 19^\circ\text{C}$ during interglacial times. However, closer examination of the benthic foraminifera data (Fig. 6D) suggests that global ocean water $\delta^{18}\text{O}$ values increased by $\sim 0.5\text{‰}$ between ~ 50 ka and ~ 15 – 22 ka (LGM). Assuming that average local rainwater mimicked these ocean changes, long-term average rain $\delta^{18}\text{O}$ values would have been $\sim -3.0\text{‰}$ at ~ 50 ka (Fig. 5D), $\sim -2.5\text{‰}$ at ~ 15 to 22 ka, and $\sim -3.5\text{‰}$ from ~ 12 ka to present. Under these conditions, RH at ~ 50 ka is calculated to have been ~ 0.96 , while during the LGM (~ 15 to 22 ka) RH was

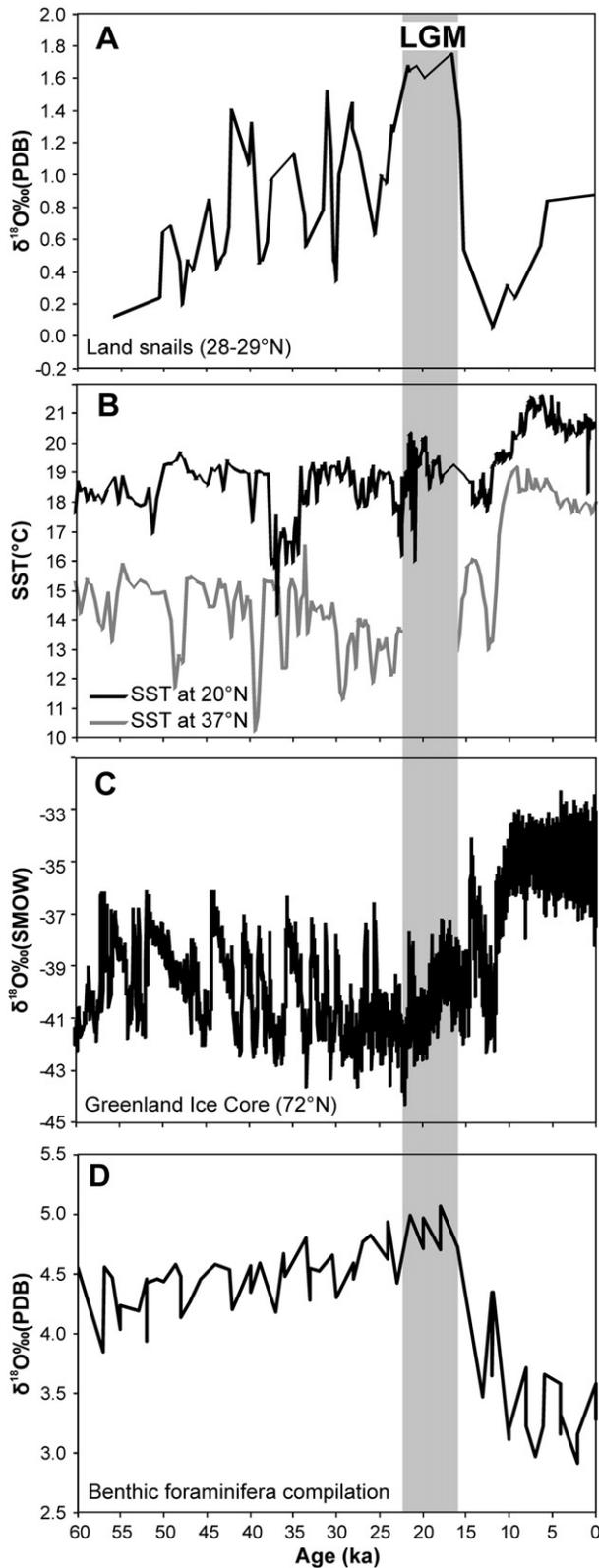


Figure 6. (A) 3-point moving average of mean $\delta^{18}\text{O}$ values of fossil land snail shells from the Canary Islands. (B) Sea surface temperature at Iberian margin (gray line) estimated from alkenone method from deep sea cores SU8118 and MD952042 (Bard, 2002); and at North West Africa from alkenone method from core ODP658C (Zhao et al., 1995). (C) Oxygen isotope composition from Greenland Ice Core (Dansgaard et al., 1989, 1993; GRIP members, 1993; Grootes et al., 1993; Johnsen et al., 1997). (D) Global compilation of benthic foraminifera oxygen isotopic data (Zachos et al., 2001).

~ 0.93 . At ~ 12 ka, RH would have been ~ 0.95 with a subsequent decline to the modern RH of ~ 0.91 (Fig. 5D).

Regardless of which scenario is considered, the model-based interpretations of the shell $\delta^{18}\text{O}$ data for the Canary Islands indicate an overall decrease in RH during the times of snail activity. However, the boundary conditions of Scenario 3 are the best supported by independent proxy data (Fig. 6).

Hadley circulation was weaker and precipitation decreased as a consequence of the southward shift of the Intertropical Convergence Zone (ITCZ) during the LGM (see recent review in Gasse et al., 2008). This may have resulted in the “aridification” of the Sahara zone into the LGM (e.g., Gasse et al., 2008). If so, this might account for the inferred overall decrease in RH in the neighboring Canary Islands during that interval.

Northern Africa experienced a further progressive increase in aridity during the late Holocene (with some brief returns to wetter periods) resulting in the ultimate desiccation of the Sahara (e.g., Gasse et al., 1990; DeMenocal et al., 2000; Swezey, 2001; Jung et al., 2004). The lowest values of RH calculated from the Canary Island land snail data are for the modern samples, which is consistent with the Holocene desiccation of the Sahara. However, the non-uniqueness of our data-constrained, but model-based, climatic interpretation suggests a need for more work to sort out the complexities of climate change in these low latitude islands.

Yanes (2003) and Huntley et al. (2008) observed that *Theba* species from the northeastern islets of the Canary Islands have experienced an overall decline in shell size through time. Multiple environmental and ecological factors control shell size, but humidity appears to be one of the most important. Thus, snail size is often larger under wetter conditions, but smaller at drier times (Goodfriend, 1986). The fact that shells have decreased in size over time in the region supports the proposed progressive decline in RH. Additionally, Yanes (2003, 2005) concluded that shell abundance and snail diversity were higher in glacial paleosols than in Holocene beds from the Canary Archipelago. Among other factors, wetter conditions normally favor snail proliferation and diversification (Cook, 2001). Thus, the proposed decline in RH is also supported by the decrease in shell abundances and diversity.

The relatively high average shell $\delta^{18}\text{O}$ values for the Canarian LGM contrast with the minimum in LGM $\delta^{18}\text{O}$ values from Greenland ice cores (Fig. 6C: Dansgaard et al., 1993). However, the higher LGM shell $\delta^{18}\text{O}$ values are consistent with higher δD or $\delta^{18}\text{O}$ values for LGM proxies (groundwater, tree cellulose, paleosol carbonate and authigenic kaolinite) from ice-free North America (Yapp and Epstein, 1977; Plummer, 1993; Amundson et al., 1996), South America (Mora and Pratt, 2001), and southwestern Africa (e.g., Gasse, 2000; Gasse et al., 2008). Possible explanations include: (1) specificity in the ice-free records such as an increase in the proportion of summer precipitation, which has a higher $\delta^{18}\text{O}$ value (Yapp and Epstein, 1977; Plummer, 1993; Amundson et al., 1996); (2) differing responses to environmental variables other than temperature and meteoric water isotope ratios in the ice-free records such as RH, water vapor $\delta^{18}\text{O}$ values, and ocean $\delta^{18}\text{O}$ values or the amount of precipitation, (e.g., Yapp and Epstein, 1977; Mora and Pratt, 2001); and/or (3) differences in LGM to Holocene climatic transitions between low/mid-latitudes (ice-free) and high latitudes (glaciated). Based on the current work, changes in RH and precipitation $\delta^{18}\text{O}$ values seem to have been the most important influences on Canary Islands land snail shell $\delta^{18}\text{O}$ values.

Conclusion

$\delta^{13}\text{C}$ values of fossil land snail shells from the eastern Canary Archipelago suggest that C_3 and C_4 plants were simultaneously present in the islands over the last ~ 50 ka. However, C_4 plants were likely more abundant at various times during the last glacial cycle, especially around the last glacial maximum (LGM), probably as a response to drier conditions and/or lower atmospheric CO_2 concentrations.

$\delta^{18}\text{O}$ variations of ancient land snail shells from the eastern Canary Islands appear to record oscillations in the relative humidity (RH) over the past ~50 ka, but with an overall decrease to the present. Information on changes in RH was extracted from the isotopic data by application of a published flux balance model constrained by proxy data on regional sea surface temperatures and $\delta^{18}\text{O}$ changes of the global ocean between glacial and interglacial times. The patterns of RH variation were similar among different postulated paleoenvironmental scenarios. The inferred overall changes in RH are generally consistent with published evidence for increasing dryness in nearby northern Africa.

The results from the land snails endorse the use of average $\delta^{18}\text{O}$ values of numerous time-equivalent entire shells to deduce patterns of climate change. Moreover, this successful use of long-term isotopic records of land snails from low-latitude islands in the eastern Atlantic suggests that studies of shells from other low-latitude islands could help to identify patterns of glacial to interglacial variations in the atmosphere over the tropical oceans.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at doi:10.1016/j.yqres.2010.11.004.

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