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Oxygen and carbon stable isotopes of modern land snail shells as environmental indicators from a low-latitude oceanic island

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Abstract

Land snails provide a unique opportunity to study terrestrial paleoenvironments because their shells, which are generally highly abundant and well-preserved in the fossil record, contain a temporal record of environmental change in the form of isotope codes. To evaluate the utility of this approach for a low-latitude oceanic setting, 207 modern shells of 18 species of land snail were analyzed for their oxygen and carbon isotope composition along a north and south facing altitudinal gradient (10–2160 m a.s.l.) in Tenerife Island (\sim 28°N) of the Canary Archipelago.

Shells collected at each locality showed a relatively large range in isotope composition which was greater along the south facing transect (drier and hotter), suggesting that the variance in shell isotope values may be related to water-stress. Although pooled isotope values did not generally show strong relationships with environmental variables (i.e., altitude, temperature and precipitation), mean isotope values were strongly associated with some climatic factors when grouped by site. The mean $\delta^{18}O$ value of the shell ($\delta^{18}O_{shell}$) by site displayed a negative correlation with elevation, which is consistent with the positive relationship observed between temperature and the δ^{18} O value of rain ($\delta^{18}O_{rain}$). Calculated δ^{18} O values of the snail body water $(\delta^{18}O_{body})$ derived from observed temperatures and $\delta^{18}O_{shell}$ values (using the equation of Grossman and Ku [Grossman E. L. and Ku T. L. (1986) Oxygen and carbon isotope fractionation in biogenic aragonite. Chem. Geol. (Isotope Geosci. Sec.) 59, 59–74)) displayed a trend with respect to altitude that was similar to measured and hypothetical δ^{18} O values for local rain water. The calculated $\delta^{18}O_{body}$ values from the shell declined 0.17% (VSMOW) per 100 m, which is consistent with the "altitude effect" observed for tropical rains in Western Africa, and it correlated negatively with rainfall amount. Accordingly, lower $\delta^{18}O_{shell}$ values indicate lower temperatures, lower $\delta^{18}O_{rain}$ values and possibly, higher rainfall totals. A positive correlation between the mean δ^{13} C values of shells (δ^{13} C_{shell}) and plants by site suggests that shells potentially record information about the surrounding vegetation. The $\delta^{13}C_{\text{shell}}$ values varied between -15.7 and -0.6% (VPDB), indicating that snails consumed C_3 and C_4/CAM plants, where more negative $\delta^{13}C_{shell}$ values probably reflects the preferential consumption of C_3 plants which are favored under wetter conditions. Individuals with more positive $\delta^{13}C_{shell}$ values consumed a larger percentage of C_4 plants (other potential factors such as carbonate ingestion or atmospheric CO_2 contribution were unlikely) that were more common at lower elevations of the hotter and drier south facing transect. The relatively wide range of shell isotope values within a single site requires the analysis of numerous shells for meaningful paleoclimatic studies. Although small differences were observed in isotope composition among snail species collected at a single sampling site, they were not significant,

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suggesting that isotope signatures extracted from multi-taxa snail data sets may be used to infer environmental conditions over a broad range of habitats.

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1. INTRODUCTION

Land snails are one of the most widely used organisms to estimate climatic characteristics of both modern and ancient terrestrial ecosystems (e.g., Yapp, 1979; Magaritz and Heller, 1980, 1983; Goodfriend and Magaritz, 1987; Goodfriend et al., 1989; Goodfriend, 1992, 1999; Goodfriend and Ellis, 2002; Balakrishnan and Yapp, 2004; Balakrishnan et al., 2005a,b; Colonese et al., 2007).

The δ^{18} O value of the shell (δ^{18} O_{shell}) represents the combined effects of relative humidity, ambient water vapor, water ingested by the snail and the temperature at which the shell precipitated (Balakrishnan and Yapp, 2004), which may vary differentially depending on the study locality and species. Consequently, many studies performed on modern land snail shells have documented a relationship between the δ^{18} O value of rain water (δ^{18} O_{rain}) and the snail shell (e.g., Yapp, 1979; Lécolle, 1985; Zanchetta et al., 2005; Yanes et al., 2008), in addition to other important factors such as relative humidity (Balakrishnan and Yapp, 2004). However, this relationship has not been proven in arid areas (Goodfriend et al., 1989; Colonese et al., 2007).

The relationship between the δ^{13} C value of the shell ($\delta^{13}C_{shell}$) and the plants ($\delta^{13}C_{plants}$) that a snail assimilates is well established in both natural (e.g., Goodfriend and Ellis, 2002; Baldini et al., 2007; Yanes et al., 2008) and laboratory settings (Stott, 2002; Metref et al., 2003). Thus, the carbon isotope composition of the shell should record the integrated δ^{13} C value of plants assimilated by the organisms, which in part is a reflection of the humidity or aridity of an environment (e.g., Goodfriend and Magaritz, 1987; Goodfriend, 1992, 1999; Goodfriend and Ellis, 2000, 2002).

Landscapes that contain altitudinal gradients are sensitive environments for testing ecological and evolutionary responses of biota to climate change over short spatial scales because many environmental variables such as temperature and atmospheric pressure change over relatively short distances (Körner, 2007). Tenerife Island of the Canary Archipelago is a unique site to study the effect of climate on land snails along an altitudinal gradient for several reasons: (1) Tenerife is the third highest oceanic island in the world after two Hawaiian Islands, reaching up to 3718 m at the volcanic peak of El Teide in the center of the island (Rivas-Martínez et al., 1993); (2) the island is strongly influenced by the trade winds; and (3) the island contains a great variety of volcanic soil types. All these factors combine to produce a diverse assemblage of microclimates that range from dry coastal (xerophytic) ecosystems to high mountain landscapes that exist within close proximity of one another. Finally, there are abundant indigenous populations of land snail species present in almost all the microclimates of Tenerife Island. Consequently, a study of the stable isotope composition of land snails is a useful baseline to better understand isotope profiles extracted from fossil shells in future paleoclimatic studies of low latitude environments.

In the present study, the oxygen and carbon isotope composition of multiple species of modern land snails were determined from individual shells collected along an altitudinal gradient from Tenerife Island, Canary Archipelago (from 10 to 2160 m a.s.l.) to determine the relationships between isotope signatures and various environmental parameters, that may be useful indicators of climate dynamics for low-latitude oceanic settings.

2. GEOGRAPHICAL AND ENVIRONMENTAL CONTEXT

Tenerife is a low latitude (\sim 28°N) volcanic island located in the center of the Canary Archipelago, which is situated about 110 km off of the Moroccan coast, NW Africa (Fig. 1). The island is the largest (2034 km²) of the archipelago, reaching the highest altitude in the Atlantic Ocean basin (3718 m a.s.l.).

Tenerife has a Mediterranean climate characterized by hot and dry summers, and wet and warm winters. Nevertheless, multiple micro-climates and ecosystems are recognized due to the altitudinal temperature gradient, the influence of the humid trade winds and the Canarian cool ocean current, and the variety of volcanic soil types on the island (Del-Arco et al., 2006; Fernández-Palacios and Whittaker, 2008). As a consequence, plant communities are spatially distinct on the island and are highly correlated with altitude, wind-exposure, temperature and precipitation (Fernández-Palacios, 1992). Five main bioclimatic belts (terrestrial zonal habitats) are defined with altitude (e.g., Bramwell and Bramwell, 1974; Fernández-Palacios, 1992; Del-Arco et al., 2006; Fernández-Palacios and Whittaker, 2008) (Fig. 2): (1) arid (sub-desert) coastal scrub up to 600 m with African ecosystem affinities, which is dominated by succulent endemic Euphorbia shrubs (including C₄ and CAM plant types); (2) semiarid thermophilous woodlands from 300 to 1100 m, which is a Mediterranean-like ecosystem; (3) humid "laurel" (evergreen) forest in a cloud belt (on windward slopes) from 600 to 1200 m, which is a relict sub-tropical ecosystem with abundant paleo-endemic tree species; (4) humid to dry temperate pine forest from 1100 to 2200 m, dominated by the endemic Pinus canariensis; and (5) dry subalpine scrub over 2000 m, dominated by endemic cushion-like legumes. A "stone desert" exists above 3000 m, which is almost devoid of vegetation and has alpine-like ecosystem affinities (Fernández-Palacios and Whittaker, 2008).



Fig. 1. Geographical location of Tenerife Island and the sample localities (n = 11). North facing sampling sites (n = 5): (1) Benijo (20 m a.s.l.), (2) Taganana (120 m a.s.l.), (3) El Bailadero (540 m a.s.l.), (4) Montaña Cascajo (1500 m a.s.l.), (5) Izaña (2160 m). South facing sampling sites (n = 6): (6) Caletillas (10 m a.s.l.), (7) Güímar (280 m a.s.l.), (8) Camino Real (430 m a.s.l.), (9) San Juan (700 m a.s.l.), (10) Low Vilaflor (980 m a.s.l.), (11) High Vilaflor (1630 m a.s.l.). Gray bands represent 400 m elevation contours.



Fig. 2. Main climatic and vegetation belts with altitude on Tenerife Island, Canary Archipelago.

3. MATERIAL AND METHODS

3.1. Environmental data collection and rain water sampling strategy

Environmental variables, including mean annual temperature (MAT) and precipitation (MAP), were obtained from 11 meteorological stations of the National Meteorological Institute (Spain; Del-Arco et al., 2006); they were selected based on their location (north or south facing slopes) and altitude on the island (Table 1). In addition, 19 water samples were collected during rain events between 2007 and 2008 at Güímar (280 m a.s.l.; Table 1 and Fig. 1).

3.2. Plant collection and identification

A total of 116 samples of foliar plants belonging to 52 species were collected during 2007 and 2008. Plants were collected in nine of the snail-sampling locations (Fig. 1 and Table 1). Plant collection strategy was based on the presence of land snails. A representative sample was collected in the immediate vicinity of snail shells (within a radius of 10 m). Plants were identified to the species level at La Laguna University, Canary Islands, and they were oven-dried at 50 °C and stored for subsequent carbon isotope analysis.

3.3. Land snail sampling strategy and species identification

A total of 207 adult land snail shells were collected during the summers of 2007 and 2008 along a north and south facing altitudinal gradient from Tenerife Island (see Table 1). Five sites were sampled along the north facing slope (from 20 to 2160 m a.s.l.) and six sites were sampled along the south facing slope (from 10 to 1630 m a.s.l.) (Table 1 and Fig. 1).

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Table 1 Geographical setting of the sample localities (n = 11) and summary of the analyzed samples.

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Geographi	cal location		Geophysical	l context				Land	snail shel	ls		Plant t	issues		Rain w	aters	
Locality	Latitude (N)	Longitude (W)	Habitat	Slope	Altitude (m a.s.l.)	MAT (°C)	MAP (mm)	# shells	# snail species	$\begin{array}{c} \delta^{18}O_{shell} \ \%_{o} \\ (VPDB) \end{array}$	$\begin{array}{c} \delta^{13}C_{shell} \ \%_{oo} \\ (VPDB) \end{array}$	# plants	# plant species	$\begin{array}{c} \delta^{13}C_{plant} \ \% \\ (VPDB) \end{array}$	# waters	$\begin{array}{c} \delta^{18}O_{rain} \ \% \\ (VSMOW) \end{array}$	
Benijo	28°34′33″	16°11′06″	Semiarid shrub	Ν	20	20.8	263.4	11	3	0.8 ± 0.5	-11.0 ± 1.6						
Taganana	28°34′05″	16°12′34″	Semiarid shrub	Ν	120	19.6	348.5	18	6	0.9 ± 0.6	-10.8 ± 1.8	2	2	-27.7 ± 3.5			
El Bailadero	28°32′47″	16°12′51″	Evergreen forest	Ν	540	15.9	682.7	18	2	0.3 ± 0.4	-11.2 ± 0.7	12	8	-29.9 ± 0.7			
Montaña Cascaio	28°29'30"	16°25′35″	Humid pine forest	Ν	1500	12.6	914.2	10	4	0.5 ± 0.5	-7.9 ± 1.2	5	2	-25.8 ± 1.1			
Izaña	28°18'10"	16°30′50″	Dry subalpine scrub	N	2160	9.6	460.4	13	1	-0.1 ± 0.8	-6.9 ± 0.8	21	11	-25.3 ± 1.5			
Caletillas Güímar	28°22'26″ 28°18'33″	16°21′53″ 16°23′30″	Arid scrub Semiarid shrub	S S	10 280	21.3 20.5	114.1 315.6	37 11	6 2	$\begin{array}{c} 1.2 \pm 1.1 \\ 1.1 \pm 1.5 \end{array}$	$\begin{array}{c} -7.8 \pm 2.1 \\ -11.8 \pm 1.4 \end{array}$	19	15	-25.2 ± 3.3	19	-1.9 ± 0.9	
Camino Real	28°17'33"	16°23′31″	Semiarid shrub	S	430	17.3	298.4	13	3	0.7 ± 0.7	-7.5 ± 3.1	12	12	-28.5 ± 1.3			
San Juan	28°19'39"	16°24′57″	Semiarid woodlands	S	700	16.8	246.3	51	7	0.8 ± 0.7	-9.1 ± 1.8	25	18	-24.3 ± 5.3			
Low Vilaflor	28°07'30"	16°37′31″	Semiarid pine forest	S	980	16.1	552.3	16	4	0.5 ± 0.7	-8.3 ± 2.1	7	4	-30.9 ± 0.9			
High Vilaflor	28°10′01″	16°37′43″	Arid pine forest	S	1630	14.6	418.8	9	3	-0.5 ± 1.3	-8.5 ± 2.9	13	5	-26.8 ± 2.0			

MAT, mean annual temperature; MAP, mean annual precipitation.

Although the collection of a single species in all sampling sites was preferred, this was not possible due to the wide range of microclimates that occurred along both altitudinal transects. Consequently, the collection represented all species present at each locality.

Taxonomic identifications were performed in the Malacology Laboratory at La Laguna University (Canary Islands). All land snail shells were identified to the species level using a binocular microscope. Only recently dead individuals were collected to protect the native terrestrial malacofauna of the island, therefore, taxonomic identifications were based exclusively on shell morphology.

3.4. Stable isotope analysis

All samples, including meteoric waters, plant tissues and snail shells, were prepared and analyzed in the stable isotope laboratory of the Savannah River Ecology Laboratory, University of Georgia. Samples were analyzed using a Finnigan Delta^{plus} XL continuous flow isotope ratio mass spectrometer (CF-IRMS). All stable isotope results are reported in δ notation relative to the international standard Vienna-Standard Mean Ocean Water (VSMOW) for waters or Vienna-Pee Dee Belemnite (VPDB) for plants and shells. The δ values are defined as:

 δ^{13} C or δ^{18} O = [(R_{sample}/R_{standard}) - 1] × 1000 (in ‰) where $R = {}^{13}$ C/ 12 C or 18 O/ 16 O.

3.4.1. Rain water sample preparation and laboratory analysis Twelve ml exetainersTM containing a small aliquot (<0.2 ml) of 104% H₃PO₄ acid were flushed with 0.3% CO₂ in He to replace air in the headspace. One half ml of water was then injected through a septum into the vial and left to equilibrate at 25 °C for 48 h. The headspace was then analyzed using a Gas Bench II peripheral device connected to the CF-IRMS. Precision was $\pm 0.1\%$ (1 σ standard deviation) based on multiple measurements of the international GISP and V-SMOW water standards, and in-house water standards (n = 9).

3.4.2. Plant sample preparation and laboratory analysis

Dry plant foliar tissues were ground with a mechanical blender before analysis. About 5 mg of ground plant tissue was weighed into a pre-cleaned tin capsule that was crimped and then combusted using a Carlo Erba Elemental Analyzer (NC 2500). The CO₂ produced after combustion was analyzed using the CF-IRMS. Multiple in-house standards were analyzed as a check on the analytical precision of the analysis, which was better than $\pm 0.1\%$ (1 σ standard deviation, n = 20).

3.4.3. Shell sample preparation and laboratory analysis

Each entire shell was pulverized by hand with an agate mortar and pestal. Powdered shell carbonate was rinsed with deionized water and then ultrasonically cleaned. Fine-grained organic matter (shell organic matrix and periostracum) were removed by placing the powdered sample in a bath of 3% sodium hypochlorite for 48 h. Subsequently, the powder was rinsed three times with deionized water and dried in an oven at 40 °C.

A small aliquot of powder (~150 µg) from each shell was placed in a 6 ml exetainerTM vial that was subsequently flushed with helium to replace the headspace. The carbonate was then converted to CO₂ gas by adding 0.5 ml of 104% H₃PO₄ at 25 °C. The resulting CO₂ was analyzed isotopically after 24 h using the GasBench II and the CF-IRMS. Carbon and oxygen isotope values were calibrated against the international standard NBS-19 and in-house standards. The precision of the analyses was better than $\pm 0.1\%$ (1 σ standard deviation) for both carbon and oxygen isotopes based on the repeated measurement of NBS-19 and in-house standards (n = 22).

3.5. Statistical analyses

All statistical analyses were performed using PAST 1.39 software (Hammer et al., 2001) considering statistical significance at α =0.05. Data were evaluated prior to statistical test selection. Generally, data were not normally distributed (Shapiro–Wilk test, p < 0.05) and did not show equality of variances (F test, p < 0.05). Consequently, non-parametric tests were chosen for statistical data analysis. Spearman's rank correlation analyses were used to explore the potential linear relationship between two variables (e.g., $\delta^{18}O_{shell}$ or $\delta^{13}C_{shell}$ vs. altitude, temperature, precipitation or $\delta^{13}C_{plant}$). Regression equations were also computed to estimate the slope and intercept of linear relationships between the variables. The Mann-Whitney U test was used to assess whether two sample populations have distributions with the same median value (e.g., shell isotope composition by site comparing habitats of similar altitudes from the north and south facing transects). Finally, the Kruskal-Wallis test was used to evaluate if multiple univariate samples were taken from populations with equal medians (e.g., stable isotope composition among land snail species within the same sampling site).

4. RESULTS

4.1. Environmental gradients: mean annual temperature and precipitation

The mean annual temperature (MAT) varied from 21.3 °C at 10 m a.s.l. (Caletillas) to 9.6 °C at 2160 m a.s.l. (Izaña), declining 0.5 °C per 100 m (Table 1 and Fig. 3a). Mean annual precipitation (MAP) increased from 114 mm at 10 m a.s.l. to 914 mm at 1500 m a.s.l. (Montaña Cascajo). Above this elevation, precipitation averaged \sim 420 mm (Table 1 and Fig. 3b). In general, temperature was slightly lower and precipitation was higher for sampling sites from the north facing slope (see filled circles in Fig. 3a–b).

4.2. Oxygen isotope composition of rain water

The oxygen isotope composition of rain water ($\delta^{18}O_{rain}$) collected at Güímar (280 m a.s.l.) ranged from -3.6% to -0.5% (VSMOW; Table 2), with a mean annual value of



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Fig. 3. Environmental parameters at Tenerife Island with altitude. Environmental data (n = 11) were collected from the National Meteorological Institute (Spain; Del-Arco et al., 2006). (a) Mean annual temperature (°C) along elevation. (b) Mean annual precipitation (mm) along elevation. (c) Oxygen isotope composition of rain water collected in Güímar (280 m) in 2007–2008 (filled circles represent mean and whiskers represent 1 σ standard deviation) compared to the precipitation (gray bars). Numbers between brackets indicate the number of water samples collected. Note that the δ^{18} O values become more negative when precipitation amount is higher (i.e., amount effect). MMT: mean monthly temperature.

 $-1.9 \pm 0.9\%$ (n = 19). This range of δ^{18} O_{rain} values is consistent with previous values obtained for the eastern Canary Islands (-2.6% to -0.7%; Yanes et al., 2008).

The $\delta^{18}O_{rain}$ values varied by 3.1‰, with more negative values occurring during the winter when precipitation amounts were higher and more positive values occurred during the summer months when rainfall amounts were lower (Table 2 and Fig. 3c).

4.3. Carbon stable isotope composition of plants

The $\delta^{13}C_{\text{plant}}$ values (n = 116) ranged from -32.2% to -11.6% (VPDB; Table 3). Based on the frequency distribu-

tion of the carbon isotope values (Fig. 4a), the majority of the plant species (n = 109) were classified as C₃ plant types, with $\delta^{13}C_{\text{plant}}$ values ranging from $-32.3\%_{o}$ to $-23.1\%_{o}$ (VPDB) and averaging $-27.1\%_{o} \pm 2.3$ (Table 3 and Fig. 4a). Six plant samples were classified as CAM plants (all corresponding to succulent life forms of the Cactaceae, Crassulaceae and Aizonaceae families) with $\delta^{13}C_{\text{plant}}$ values ranging from $-22.2\%_{o}$ to $-11.6\%_{o}$ (VPDB) (Table 3 and Fig. 4a), and only one plant sample (grass of Graminae family) was classified as a C₄ plant type ($-13.5\%_{o}$) (Table 3 and Fig. 4a). This classification is also consistent with the published literature on some of the genera and species of plants included in this study (e.g., Morales et al., 1982; Méndez et al., 1991; Mies et al., 1996; Méndez, 2001; Bi et al., 2005; Mort et al., 2007; Yanes et al., 2008).

Plants that follow C_4 and CAM photosynthetic pathway are common in the driest areas of Tenerife (Méndez et al., 1991; Méndez, 2001), especially in the sub-desertic coastal scrub zone (between 0 and 600 m a.s.l.). All CAM and C_4 plant species were found below 700 m along the south facing slope, which is consistent with the finding that these ecophysiological pathways are more common in low altitude/coastal (hotter and drier) settings. Although some C_4 and CAM plants were also present in dry areas along the north facing slope, no specimens were collected from there.

The mean carbon isotope composition of plants by site did not show a clear trend with altitude (Fig. 4b), which is in contrast to previous studies that have observed a positive relationship between C₃ plant δ^{13} C values and elevation associated with greater carboxylation efficiency at high altitudes (e.g., Körner et al., 1988, 1991). Plants from the south facing slope showed higher δ^{13} C_{plant} values than plants collected along the north facing transect at comparable elevations (see Fig. 4b), most likely due to greater water-stress conditions (e.g., Farquhar et al., 1989). The mean δ^{13} C_{plant} values by site correlated negatively

The mean $\delta^{13}C_{\text{plant}}$ values by site correlated negatively with mean annual precipitation ($r_s = -0.70$, p = 0.04; n = 9; Fig. 4c), in agreement with previous studies from tropical Northeast Africa (Liu et al., 2007). No relationship was observed between mean $\delta^{13}C_{\text{plant}}$ values and temperature.

4.4. Land snail species

The 207 shells collected in this study belong to 18 species and 10 genera grouped in eight families (Table 4 and Fig. 5 and Appendix). Fourteen species are endemic to the Canary Islands and the other four species are cosmopolitan with a widespread geographical distribution (Table 4). The number of individuals collected per sampling site is summarized in Table 1 (see also Appendix). The altitudinal range at which all snail species were found as well as their associated habitat and biology is summarized in Table 4. The majority of snail species included in this study (n = 15) are exclusively herbivorous (as reveled by personal field observations and unpublished radula studies), except Rumina decollata and the Plutonia species (Table 4), which are primarily herbivorous although may show an opportunistic omnivorous diet through the ingestion of other snail eggs and bodies and other invertebrates (Hyman, 1967; Ibáñez et al., 1987; Valido et al., 1999). Species longevity may vary from

Dxygen isotope composition of rain waters from Güímar (280 m a.s.l.), Tenerife Island, Canary Archipelago.											
Sample ID	$\delta^{18}O_{rain}$ ‰ (VSMOW)	MMP (mm)	MMT (°C)	Month of collection	Year of collection						
RW_001	-2.6	291.7	17.7	December	2007						
RW_002	-2.2	291.7	17.7	December	2007						
RW_210	-3.0	227.4	16.6	January	2008						
RW_200	-3.6	147.0	17.7	March	2008						
RW_201	-0.7	147.0	17.7	March	2008						
RW_203	-2.3	147.0	17.7	March	2008						
RW_204	-2.2	147.0	17.7	March	2008						
RW_206	-3.0	147.0	17.7	March	2008						
RW_207	-1.4	147.0	17.7	March	2008						
RW_208	-2.3	147.0	17.7	March	2008						
RW_209	-0.9	147.0	17.7	March	2008						
RW_211	-2.9	147.0	17.7	March	2008						
RW 032	-0.7	13.0	20.6	June	2007						
RW_033	-0.5	13.0	20.6	June	2007						
RW 034	-1.5	13.0	20.6	June	2007						
RW_035	-1.2	13.0	20.6	June	2007						
RW 036	-1.4	13.0	20.6	June	2007						
RW 037	-1.5	13.0	20.6	June	2007						
RW_038	-1.4	13.0	20.6	June	2007						

MMP, mean monthly precipitation; MMT, mean monthly temperature.

annual to multiannual, although the great majority of land snails display a lifespan from 1 to 2 years (Heller, 1990). Hence, they presumably record monthly/yearly environmental information while they are active during their lifespan, as previously documented through stable isotope sclerochronology of single land snail shells from other low-latitude islands (Baldini et al., 2007) and North Africa (Leng et al., 1998).

4.5. Stable isotope composition of shells

Table 2

Considered collectively (n = 207), the $\delta^{18}O_{shell}$ values of the pooled individuals ranged from $-2.9\%_{oo}$ to $3.9\%_{o}$ (VPDB; Appendix). A weak ($R^2 = 0.15$) decline of $\delta^{18}O_{shell}$ values was observed ($r_s = -0.32$, p < 0.01 for n = 207) when raw data were plotted against elevation (Fig. 6a). The magnitude of the decline ($0.06\%_{o}/100$ m) is consistent with the value of $0.03-0.05\%_{o}/100$ m reported by Balakrishnan et al. (2005a, Fig. 9) for the Southern Great Plains of North America. The significance of the relationship ($R^2 = 0.70$) increased ($r_s = -0.86$, p < 0.01; n = 11) when mean $\delta^{18}O_{shell}$ values were plotted with altitude (Fig. 6b), while the regression equations remained similar, with both trends showing a decline in $\delta^{18}O_{shell}$ values of $0.06\%_{oo}$ per 100 m (Fig. 6a–b).

The $\delta^{13}C_{\text{shell}}$ values of the pooled individuals (n = 207) varied between $-13.8\%_{o}$ and $-0.6\%_{o}$ (VPDB) (Appendix). No correlation was observed with altitude for pooled data (Fig. 6g) or for mean values by site (Fig. 6h).

Data were also evaluated separately by transect. Pooled $(R^2 = 0.22; r_s = -0.48, p < 0.01; n = 70)$ and mean $(R^2 = 0.76; r_s = -0.80, p = 0.10; n = 5) \delta^{18}O_{\text{shell}}$ values from the north facing transect declined with elevation $0.04\%_{00}$ per 100 m. However, the strength and significance of this relationship needs to be further explored, probably by increasing the number of sampling sites along elevation.

Additionally, pooled $\delta^{13}C_{shell}$ values significantly increased with elevation 0.2‰ per 100 m ($R^2 = 0.71$; $r_s = 0.84$, p < 0.01; n = 70). For the south facing transect, pooled ($R^2 = 0.15$; $r_s = -0.29$, p < 0.01; n = 137) and mean ($R^2 = 0.92$; $r_s = -0.94$, p < 0.01; n = 6) $\delta^{18}O_{shell}$ values declined with altitude 0.09–0.1‰ every 100 m, suggesting that this trend maybe magnified across drier/hotter habitats. In contrast, the $\delta^{13}C_{shell}$ values did not show any relationship with altitude.

4.5.1. Isotopic variability within habitats and between the north and south facing slopes

Land snails displayed a wide range of $\delta^{18}O_{shell}$ values not only across habitats but within sampling sites (Fig. 6a-b). In general, land snails from the south facing slope (drier and hotter) showed greater variability (Table 5 and see also Fig. 6a–b), with a range in $\delta^{18}O_{\text{shell}}$ values $(\Delta^{18}O_{shell})$ that varied from 2.3% in the semiarid shrub at 430 m to 4.7% in the arid coastal scrub at 10 m (Table 5). In contrast, the $\Delta^{18}O_{shell}$ values from northern slope sites ranged from 1.4% in the humid evergreen forest at 540 m to 2.9% in the semiarid shrub at 120 m (Table 5). No significant relationship was observed between $\Delta^{18}O_{shell}$ values and precipitation or temperature. The observed oxygen isotope range by site (from 1.4% to 4.7%) is similar to values reported in previous studies of modern land snail shells from low-latitude oceanic islands (2.7%): Baldini et al., 2007; 2.8‰: Yanes et al., 2008). Finally, the $\delta^{18}O_{shell}$ values of the north and south facing transect did not display significant differences at comparable elevations (Table 6 and see also Fig. 6a-b).

Snails exhibited a large range of $\delta^{13}C_{shell}$ values within sampling sites as well; especially among habitats of the south facing transect (Fig. 6g–h). The range in $\delta^{13}C_{shell}$ values ($\Delta^{13}C_{shell}$) from the southern slope sites varied from 4.6% for the semiarid shrub at 280 m to as much as Table 3

Family	Plant species	Photosyntheticpathway	п	$\delta^{13}C_{plant}\%$	o (VPDB)	Life form	Altitude (m a.s.l.)
Adiantaceae	Asplenium onopteris	C ₃	1	-30.7		Herbaceous fern	540
Aizoaceae	Mesembryanthemum nodiflorum	CAM	1	-22.1		Succulent herb	10
Apiaceae	Torilis avensis	C ₃	1	-28.5		Perennial herb	700
Asteraceae	Conyza bonariensis	C ₃	1	-28.3		Shrub	700
Boraginaceae	Echium wildpretii	C ₃	1	-26.6		Annual herb	2160
Cactaceae	Opuntia dilenni	CAM	1	-11.6		Succulent shrub	430
Caprifoliaceae	Viburnum rigidum	C ₃	1	-31.7		Small tree	540
Caryophyllaceae	Polycarpaea cf. amistata	C ₃	2	-27.8	± 1.4	Perennial herb	10
Chenopodiaceae	Rumex lunaria	C ₃	1	-27.3		Shrub	430
Cistaceae	Cistus monpeliensis	C ₃	6	-28.0	± 1.1	Shrub	430-980
	Cistus symphytifolius	C ₃	2	-27.1	± 0.1	Shrub	700
Compositae	Allagopapus dichotomus	C ₃	2	-26.8	±1.9	Shrub	10 - 700
	Argyranthemum frutescens	C ₃	2	-26.4	± 0.1	Shrub	430-700
	Argyranthemum teneriffae	C ₃	1	-27.4		Shrub	2160
	Artemisia canariensis	C ₃	2	-28.7	± 1.8	Aromatic shrub	430-700
	Artemisia thuscula	C ₃	2	-29.1	± 0.7	Aromatic shrub	120-700
	Carlina xeranthemoides	C ₃	1	-24.5		Shrub	2160
	Launaea arborescens	C ₃	1	-26.2		Spiny shrub	10
	Pericallis lanata	C ₃	1	-32.2		Perennial herb	700
	Schizogyne sericea	C ₃	2	-27.3	± 2.7	Shrub	10
Convolvulaceae	Phyllis molla	C ₃	1	-31.3		Small glabrous sub-shrub	540
	Plocama pendula	C ₃	2	-24.6	± 0.6	Shrub with pendulous branches	10
Crassulaceae	Aeonium arboreum	CAM	1	-22.2		Succulent shrub	700
	Aeonium holochrysum	CAM	3	-17.1	± 2.3	Succulent shrub	430-700
	Aichryson laxum	C ₃	1	-30.5		Annual herb	540
Cruciferae	Descurainia bourgeana	C ₃	2	-25.7	± 0.8	Shrub	1630
	Erycimus scoparius	C ₃	1	-24.4		Small shrub	2160
Dennstaedtiaceae	Pteridium aquilinum	C ₃	1	-30.6		Herb fern	540
Dipsacaceae	Pterocephalus lasiospermus	C_3	4	-25.8	± 1.7	Shrub with hairy stems	1630-2160
Ericaceae	Erica arborea	C ₃	4	-29.7	±1.5	Small tree	700
	Erica platycodon	C ₃	2	-30.0	± 0.8	Evergreen shrub	540
Euphorbiaceae	Euphorbia balsamifera	C ₃	1	-25.0		Shrub with milky latex	10
	Euphorbia lamarckii	C ₃	2	-24.0	± 0.8	Shrub with milky latex	10-430
Fabaceae	Aspalthium bituminosum	C ₃	3	-26.4	± 1.0	Perennial herb	120-700
Geraniaceae	Chamaecytisus proliferus	C ₃	2	-26.9	± 1.0	Herb	1630-2160
Graminae	Undet.	C_4	1	-13.5		Grass	10
Labiatae	Lavandula multifida ssp.canariensis	C ₃	1	-26.6		Shrub	10
	Micromeria hyssopifolia	C ₃	5	-29.0	± 0.4	Dwarf shrub	430-980

Lauraceae	Laurus novocanariensis	C3	4	-31.1	± 1.2	Tree	540
Leguminosae	Adenocarpus viscosus	C3	5	-24.9	± 0.8	Shrub	1630
	Spartositisus supranubius	C3	0	-24.3	± 0.3	Aromatic erect caduceus shrub	2160
Oleaceae	Jasminum odoratissimum	C3	0	-26.8	± 0.2	Shrub	700
Pinaceae	Pinus canariensis	C3	21	-26.0	± 1.5	Evergreen tree with needle-like leaves	700 - 2160
Poaceae	Piptathemum miliaceum	C3	1	-25.9		Herb	10
Rosaceae	Rubus ulmifolius	C3	б	-27.9	± 3.4	Woody shrub	430 - 700
Rubiaceae	Periploca laevigata	C3	б	-25.1	± 0.9	Shrub	10 - 430
Scrophulariaceae	Campylanthus salsoloides	C3	1	-24.6		Succulent-leaves shrub	430
	Scrophularia glabrata	C3	1	-24.1		Small shrub	2160
Sinopteridaceae	Cosentinia vellea	C3	1	-32.0		Herbaceous fern	700
Solanaceae	Nicotiana glauca	C3	1	-25.7		Shrub	10
Umbelliferae	Astydamia latifolia	C3	1	-28.3		Succulent-leaves perennial herb	10
Zygophyllaceae	Zygophyllum fontanesii	C ₃	1	-25.9		Small succulent shrub	10
n, number of analyze	d plant individuals.						



Fig. 4. Carbon isotopic composition of plants from Tenerife

Island. (a) Frequency distribution of the $\bar{\delta}^{13}C$ values of plants (n = 116). (b) Mean carbon isotope composition of plants by site along altitude (n = 9). (c) Relationship between δ^{13} C values of plants and mean annual precipitation by site. Numbers between brackets show the number of individuals analyzed per sampling site. Circles represent the mean value and whiskers represent 1σ standard deviation of the data per sampling site. Solid lines and associated equations represent the regression of the data.

11.3% in the semiarid woodlands at 700 m (Table 5). On the contrary, snails from the north facing habitats displayed $\Delta^{13}C_{shell}$ values that ranged from 1.9% in the humid evergreen forest at 540 m to 4.0% within the semiarid shrub at 20 m (Table 5 and see also Fig. 6g-h). This range by site (from 1.9% to 11.3%) is also in agreement with previous studies at low-latitude oceanic settings (8.6%: Baldini et al., 2007; 11.1‰: Yanes et al., 2008). In addition, a signifTable 4

Taxonomic composition and biology of the land sna	ils c	ollected in this s	tudy.		
		Altitude (m a.s.l.)	Habitat	Dietary habits (personal observations)	Minimum longevity (Heller, 1990)
<i>Class Gastropoda</i> Superorder Heterobranchia Order Pulmonata Suborder Stylommatophora					
Family Cochlicellidae Monilearia phalerata (Webb and Berthelot, 1833)	a	20–980	Arid coastal scrub to arid pine forest	Herbivorous	Annual to biannual
Family Enidae Napaeus bechi (Alonso and Ibáñez, 1993) Napaeus propinquus (Shuttleworth, 1852) Napaeus variatus (Webb and Berthelot, 1833)	a a a	1500–1630 980 10–120	Humid and semiarid pine forest Semiarid pine forest Arid coastal scrub to semiarid shrub	Herbivorous Herbivorous Herbivorous	Annual to biannual Annual to biannual Annual to biannual
Family Ferussaciidae Ferussacia folliculus (Gmelin, 1791)		120–980	Semiarid shrub to semiarid pine forest	Herbivorous	Annual to biannual
Family Helicidae Cornu aspersum (Müller, 1774) Hemicycla bethencourtiana (Shuttleworth, 1852)	a	280 10–700	Semiarid shrub Arid coastal scrub to semiarid	Herbivorous Herbivorous	Annual to biannual Annual to biannual
Hemicycla bidentalis (Lamarck, 1822)	a	120–540	Semiarid shrub to humid evergreen	Herbivorous	Annual to biannual
Hemicycla aff. consobrina retrodens (Mousson, 1872)	a	700	Semiarid woodlands	Herbivorous	Annual to biannual
Hemicycla plicaria (Lamarck, 1816)	a	10	Arid coastal scrub	Herbivorous	Annual to biannual
Family Hygromiidae Canariella hispidula (Lamarck, 1822) Canariella planaria (Lamarck, 1822) Xerotrichia nubivaga (Mabille, 1882)	a a a	10–1500 20–120 1500–2160	Arid coastal scrub to humid pine forest Semiarid shrub Humid pine forest to dry subalpine	Herbivorous Herbivorous herbivorous	Annual to biannual Annual to biannual Annual to biannual
Xerotrichia orbignyi (d'Orbigny, 1836)	a	10-120	scrub Arid coastal scrub to semiarid shrub	Herbivorous	Annual to biannual
Family Subulinidae Rumina decollata (Linnaeus, 1758)		280	Semiarid shrub	Herbivorous/omnivorous	Annual to biannual
Family Trissexodontidae Caracollina lenticula (Michaud, 1831)		10–980	Arid coastal scrub to semiarid pine forest	Herbivorous	Annual to biannual
Family Vitrinidae Plutonia blauneri (Shuttleworth, 1852) Plutonia lamarkii (Férussac, 1821)	a a	700–1630 540	Semiarid woodlands to arid pine forest Humid evergreen forest	Herbivorous/omnivorous Herbivorous/omnivorous	Annual to biannual Annual to biannual

^a Endemic to the Canary Islands.



Fig. 5. Photograph representing all land snail genera (n = 10) collected in this study. (a) *Rumina decollata*. (b) *Cornu aspersum*. (c) *Hemicycla bidentalis*. (d) *Napaeus variatus*. (e) *Ferussacia folliculus*. (f) *Caracollina lenticula*. (g) *Xerotrichia orbignyi*. (h) *Monilearia phalerata*. (i) *Canariella planaria*. (j) *Plutonia blauneri*.

icant negative relationship was observed between $\Delta^{13}C_{shell}$ values and mean annual precipitation ($r_s = -0.66$, p = 0.03; n = 11), suggesting that a larger range of carbon isotope values is expected at drier sites, most likely due to the presence of C₄ plants and water-stressed C₃ plants (e.g., Farquhar et al., 1989). Accordingly, the $\delta^{13}C_{shell}$ values of the north and south facing transect displayed significant differences at comparable altitudes (Table 6). For instance, the shells from Benijo (20 m) and El Bailadero (540 m) in the north transect showed more negative carbon isotope values than shells collected at comparable elevations in the south facing slope (Caletillas at 10 m and Camino Real at 430 m, respectively; Table 6 and see also Fig. 6g–h).

4.5.2. Relationship between shell isotope composition and environment

The pooled $\delta^{18}O_{\text{shell}}$ values were weakly correlated $(R^2 = 0.14)$ to mean annual temperature $(r_s = 0.37, p < 0.01; n = 207;$ Fig. 6c), but when mean values were compared to mean annual temperature by site, the relationship was stronger $(R^2 = 0.60)$ and significant $(r_s = 0.89, p < 0.01; n = 11;$ Fig. 6d). Both trends (pooled data and mean values) exhibited an increase of 0.1% per 1 °C (Fig. 6c–d). No clear relationships were observed between pooled (Fig. 6e) and mean (Fig. 6f) $\delta^{18}O_{\text{shell}}$ values with mean annual precipitation. Moreover, pooled and mean $\delta^{13}C_{\text{shell}}$ values of both transects combined did not show conclusive relationships with temperature or precipitation.

Data from the north facing transect alone may have a positive relationship with mean annual temperature for pooled ($R^2 = 0.24$; $r_s = 0.48$, p < 0.01; n = 70) and mean ($R^2 = 0.83$; $r_s = 0.80$, p = 0.10; n = 5) $\delta^{18}O_{shell}$ values, increasing $0.08\%/_{00}/1$ °C. However, further data collection would be recommended to corroborate the strength and significance of this potential relationship. Similarly, pooled ($R^2 = 0.11$; $r_s = 0.29$, p < 0.01; n = 137) and mean ($R^2 = 0.74$; $r_s = 0.94$, p < 0.01; n = 6) $\delta^{18}O_{shell}$ values from the south facing slope increased with temperature

0.2%/1 °C. Although pooled data showed a weak relationship, mean values by site displayed a tighter correlation. No meaningful relationships were observed between $\delta^{18}O_{shell}$ values and mean annual precipitation for any transect separately.

Only pooled ($R^2 = 0.60$; $r_s = -0.65$, p < 0.01; n = 70) $\delta^{13}C_{\text{shell}}$ values from the north facing slope declined significantly with mean annual temperature 0.4%/1 °C. No relationships were observed with precipitation. In contrast, the $\delta^{13}C_{\text{shell}}$ values from the south facing slope did not correlate with temperature or precipitation.

4.5.3. Isotope differences among land snail species

The $\delta^{18}O_{shell}$ values of all species from a single sampling locality were compared (Table 7 and Fig. 7) and, generally, no significant differences were observed among species within the same locality. Only two out of the ten comparisons (Caletillas and Güímar) displayed significant differences in oxygen isotope composition among species (Table 7). Specifically, *C. hispidula* (0.8‰), and *H. bethencourtiana* (0.6‰) showed significantly lower $\delta^{18}O_{shell}$ values than *C. lenticula* (1.5‰) *H. bidentalis* (1.9‰) and *F. folliculus* (1.9‰) from the Caletillas locality at 10 m (Fig. 7e). Additionally, *C. aspersum* (2.3‰) was significantly higher in $\delta^{18}O_{shell}$ value than *R. decollata* (-0.6‰) collected in Güímar at 280 m (Fig. 7f).

The $\delta^{13}C_{\text{shell}}$ values of different species of land snails were also compared (Table 7 and Fig. 8), and only the species of two sampling sites (Benijo and Low Vilaflor) showed significant differences in their $\delta^{13}C_{shell}$ values (Table 7). In particular, C. planaria (-12.6‰) had lower $\delta^{13}C_{shell}$ values than C. lenticula (-9.9%) and M. phalerata (-9.2%) at Benijo (20 m a.s.l.; Fig. 8a). In addition, *N. propinquus* (-4.3_{%o}) had lower $\delta^{13}C_{\text{shell}}$ values than *C. lenticula* (-8.7%), F. folliculus (-10.0%) and M. phalerata (-9.4%), at Low Vilaflor (980 m; Fig. 8i). The remaining species collected from a single location did not show significant differences in their $\delta^{13}C_{shell}$ values (Table 7 and Fig. 8a-j). Interestingly, the opportunistic omnivorous species (R. decollata and Plutonia) did not show differences compared to other herbivorous taxa by site (Table 7), suggesting those individuals followed an herbivorous diet or alternatively, they consumed invertebrates having carbon isotopic composition that were similar to the surrounding vegetation.

5. DISCUSSION

5.1. Relationship between $\delta^{18}O_{shell}$, temperature and precipitation

The range of $\delta^{18}O_{shell}$ values of all pooled individuals $(\Delta^{18}O_{shell} = 6.8\%)$ reflects the large environmental variability of Tenerife island across landscapes.

Isotopic variability within sites (Table 5 and Fig. 6a–b) may reflect the monthly/yearly climatic variations that are expressed at the habitat level, not demonstrated here but previously documented by others (Leng et al., 1998; Baldini et al., 2007) assuming that most of the snails have a minimum lifespan of 1–2 years (Heller, 1990). Observed $\delta^{18}O_{rain}$

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Fig. 6. Stable isotope composition of modern land snail shells against environmental variables. Pooled (a) and mean (b) $\delta^{18}O_{shell}$ values against elevation. Pooled (c) and mean (d) $\delta^{18}O_{shell}$ values against mean annual temperature. Pooled (e) and mean (f) $\delta^{18}O_{shell}$ values against mean annual precipitation. Pooled (g) and mean (h) $\delta^{13}C_{shell}$ values against elevation. The $\delta^{13}C_{shell}$ values vs. temperature and precipitation are not shown because no significant correlations were observed. See text for evaluation of the data separately by transect. Solid lines and associated equations represent the regression of the data. Error bars represent the 1σ standard deviation of the data by sampling site. Numbers between brackets represent the number of shells analyzed.

values at Güímar (280 m) showed a seasonal isotopic variability of 3.1% (Table 2). Accordingly, $\delta^{18}O_{shell}$ values from the same locality showed an isotopic variability of 4% (Table 5), reinforcing the hypothesis that seasonal isotopic variability of the local rain water may be preserved in land snail shells and may partially explain the observed range of values by site.

The observed relationship between mean $\delta^{18}O_{shell}$ values (by site) and temperature (Fig. 6d) suggests this variable maybe a controlling factor in the $\delta^{18}O$ value of shells from Tenerife Island. The $\delta^{18}O$ values of aragonite shells grown in isotope equilibrium are, in the simplest case, a function of the temperature and the oxygen isotopic composition of the waters from which they grew (Lécolle, 1985; Grossman and Ku, 1986; Balakrishnan and Yapp, 2004; Zanchetta et al., 2005; Yanes et al., 2008). Grossman and Ku (1986) proposed the paleotemperature equation for the aragonite– water system as follows: T (°C) = 19.7–4.34 ($\delta^{18}O_{aragonite} \delta^{18}O_{water}$). Using this relationship, the oxygen isotope composition of snail body water ($\delta^{18}O_{body}$) can be estimated from the mean annual temperature and mean $\delta^{18}O_{shell}$ value at each site, assuming that shell material was deposited throughout the year (Table 8). Calculated $\delta^{18}O_{body}$ values ranged from -2.4% to 1.6% (VSMOW), with more positive

Table 5		
Oxygen and carbon iso	tope variability of land sna	il shells within habitats.

Geophysical variab	les			$\delta^{18}O_{she}$	11‰ (VF	PDB)		$\delta^{13}C_{shell'oo}$ (VPDB)			
Locality	Habitat	Slope	Altitude (m a.s.l.)	Mean	Min	Max	$\Delta^{18}O$	Mean	Min	Max	$\Delta^{13}C$
Benijo	Semiarid shrub	Ν	20	0.8	-0.1	1.6	1.6	-11.0	-13.0	-9.0	4.0
Taganana	Semiarid shrub	Ν	120	0.9	-0.4	2.5	2.9	-10.8	-13.0	-9.6	3.4
El Bailadero	Humid evergreen forest	Ν	540	0.3	-0.3	1.1	1.4	-11.2	-12.0	-10.1	1.9
Montaña Cascajo	Humid pine forest	Ν	1500	0.5	-0.5	1.3	1.8	-7.9	-10.4	-6.7	3.7
Izaña	Dry subalpine scrub	Ν	2160	-0.1	-1.9	0.7	2.6	-6.9	-9.2	-6.0	3.2
Caletillas	Arid coastal scrub	S	10	1.2	-0.9	3.9	4.7	-7.8	-11.1	-0.6	10.6
Güímar	Semiarid shrub	S	280	1.1	-0.9	3.1	4.0	-11.8	-13.8	-9.2	4.6
Camino Real	Semiarid shrub	S	430	0.7	-0.3	2.0	2.3	-7.5	-11.5	-2.5	9.0
San Juan	Semiarid woodlands	S	700	0.8	-1.3	2.7	4.0	-9.1	-11.9	-0.7	11.3
Low Vilaflor	Semiarid pine forest	S	980	0.5	-1.0	1.9	3.0	-8.3	-10.6	-3.9	6.7
High Vilaflor	Arid pine forest	S	1630	-0.5	-2.9	1.4	4.4	-8.5	-15.7	-6.6	9.1

Min, minimum value; Max, maximum value; Δ^{18} O, range of δ^{18} O_{shell} values; Δ^{13} C, range of δ^{13} C_{shell} values.

Table 6

Comparison of the oxygen and carbon isotope composition of land snail shells between the north (N) and south (S) facing transects collected at similar (comparable) elevations.

Slope	Elevation (m a.s.l.)	Locality	п	$\begin{array}{c} Median \; \delta^{18}O_{shell} \overset{o\!\!\!\!\!o}{_{\!\!\!\!oo}} \\ (VPDB) \end{array}$	Mann–Whitney U test	<i>p</i> -Value	$\begin{array}{c} Median \; \delta^{13}C_{shell} \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ $	Mann–Whitney U test	p-Value
N	20	Benijo	11	1.0	168.5	0.40	-10.6	34.5	< 0.01
S	10	Caletillas	37	1.0			-7.8		
Ν	120	Taganana	18	1.0	90.5	0.72	-11.2	62.5	0.11
S	280	Güímar	11	1.6			-12.0		
Ν	540	El Bailadero	18	0.4	88.5	0.26	-11.2	33.0	< 0.01
S	430	Camino Real	13	0.5			-7.0		
Ν	1500	Montaña Cascajo	10	0.4	22.0	0.07	-7.4	44.0	0.97
S	1630	High Vilaflor	9	-0.4			-7.8		

n, number of shells analyzed.

values expressed at lower altitude and more negative $\delta^{18}O_{body}$ values at higher elevation (Table 8 and Fig. 9a), declining 0.17‰ per 100 m (Fig. 9a), coinciding with an observed "altitude effect" (-0.16%/100 m) for rain water from Tropical Western Africa (Gonfiantini et al., 2001), which supports the contention that $\delta^{18}O_{shell}$ values are faithful environmental recorders of the rain water at low-latitudes.

The calculated $\delta^{18}O_{body}$ value from the shells at 280 m (1.3_{00}) can be compared to the observed $\delta^{18}O_{rain}$ value at Güímar (-1.9%); Tables 1 and 8) to determine if the shells are deposited in isotopic equilibrium with ambient waters at this site. The calculated $\delta^{18}O_{body}$ value was $\sim 3.2\%$ higher than the observed mean $\delta^{18}O_{rain}$ value (Table 8). This finding is consistent with Balakrishnan and Yapp (2004), who concluded that the best model to explain $\delta^{18}O_{shell}$ values is one in which aragonite is deposited in oxygen isotope equilibrium with body fluid that has undergone isotopic enrichment as a consequence of body water loss through evaporation. Further, Balakrishnan and Yapp (2004) observed that calculated $\delta^{18}O_{shell}$ values using a model that included isotopic modification as a consequence steady-state processes (e.g., evaporation) offered the best approximation to the observed $\delta^{18}O_{shell}$ values (see Fig. 5 in Balakrishnan and Yapp, 2004). Semi-hypothetical $\delta^{18}O_{rain}$ values may be determined at each site using the observed $\delta^{18}O_{rain}$ value for Güímar as a reference and applying a value of -0.16% per 100 m determined by Gonfiantini et al. (2001) (see Table 8), which is geographically, climatically and latitudinally comparable to the Canary Islands. The humid evergreen forest at 540 m (El Bailadero) in the north facing transect is characterized by the presence of a humid "cloud sea", high relative humidity and low evaporative losses, which is consistent with a reduced difference (1.6‰) between the calculated $\delta^{18}O_{body}$ value and the semi-hypothetical $\delta^{18}O_{rain}$ values. Similarly, low altitude locations from the south facing slope (i.e., at 10 and 280 m) displayed the largest difference (3.0‰ and 3.2‰, respectively), coinciding with low rainfall totals, low relative humidity and high temperatures at these sites (Table 8).

Finally, the calculated $\delta^{18}O_{body}$ values were negatively correlated with mean annual precipitation ($r_s = -0.75$, p = 0.01; n = 11; Fig. 9b), indicating that relatively low $\delta^{18}O_{rain}$ values may also be influenced by an "amount effect" (Dansgaard, 1964; Rozanski et al., 1993). Because the calculated $\delta^{18}O_{body}$ values are related to the $\delta^{18}O_{rain}$ values, the use of $\delta^{18}O_{shell}$ values appears to be a useful proxy to estimate not only $\delta^{18}O_{rain}$ values, but relative precipitation amounts in a landscape, where lower $\delta^{18}O_{shell}$

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Table 7

Variability of stable isotope values among species by site. Only species with three or more individuals were included for statistical testing. Izaña locality (at 2160 m) was excluded because only one species was collected.

Locality	Species	n	$\begin{array}{l} Median \\ \delta^{18}O_{shell} \ \ \ \ \ \ \ \ \ \ \ \ \ $	Kruskal– Wallis test	<i>p</i> -Value	Median $\delta^{13}C_{\text{shell}_{00}}$ (VPDB)	Kruskal–Wallis test	<i>p</i> -Value
Benijo (20 m, N slope)	C. planaria C. lenticula M. phalerata	5 3 3	1.1 0.2 0.8	2.4	0.31	-12.6 -9.9 -9.2	7.5	0.02
Taganana (120 m, N slope)	C. planaria F. folliculus M. phalerata	6 4 3	1.0 0.7 1.1	0.7	0.75	-11.1 -11.3 -9.9	4.4	0.12
El Bailadero (540 m, N slope)	H. bidentalis P. lamarkii	15 3	0.2 0.7	3.2	0.08	-11.2 -10.7	0.4	0.70
Cañada Guancheros (1500 m, N slope)	C. hispidula P. blauneri	3 6	0.7 0.7	0.6	0.44	-7.5 -8.1	0.6	0.44
Caletillas (10 m, S slope)	C. hispidula C. lenticula H. bethencourtiana H. plicaria X. orbignyi	5 7 15 5 4	0.8 1.5 0.6 1.9 1.9	10.9	0.03	-8.4 -8.2 -7.3 -10.1 -8.4	8.9	0.06
Güímar (280 m, S slope)	C. aspersum R. decollata	6 5	$2.3 \\ -0.6$	6.6	0.01	-12.3 -11.7	0.7	0.41
Camino Real (430 m, S slope)	H. bethencourtiana M. phalerata	5 5	0.7 0.4	0.2	0.68	$-10.9 \\ -6.0$	2.5	0.12
San Juan (700 m, S slope)	C. hispidula C. lenticula F. folliculus H. aff. consobrina retrodens H. bethencourtiana M. phalerata	11 4 3 5 3 16	1.5 0.4 1.0 1.0 0.8 1.5	6.3	0.27	-7.8 -9.3 -8.8 -8.8 -9.2 -7.8	3.2	0.67
Low Vilaflor (980 m, S slope)	C. lenticula F. folliculus M. phalerata N. propinquus	5 3 5 3	$0.7 \\ -0.2 \\ 0.3 \\ 0.5$	2.4	0.50	-8.7 -10.0 -9.4 -4.3	7.9	0.05
High Vilaflor (1630 m, S slope)	X. nubivaga P. blauneri	3 4	$-0.7 \\ 0.2$	0.5	0.48	-7.9 -6.9	2.0	0.16

n, number of individuals analyzed.

values are related to lower $\delta^{18}O_{rain}$ values and possibly to higher precipitation amounts. However, the $\delta^{18}O_{body}$ values from the two highest locations at 1630 and 2160 m fell substantially below the regression line (Fig. 9b). Other factors not explored here, such as relative humidity (Balakrishnan and Yapp, 2004), may also have contributed to the $\delta^{18}O_{shell}$ values. Mean annual relative humidity (RH) values were available for three sampling sites (at 10 m: 0.67; at 540 m: 0.73; and at 2160 m: 0.47). To test quantitatively the potential role of RH, the expected mean δ^{18} O value of snail body water and shell were calculated using the steady-state flux balance model proposed by Balakrishnan and Yapp (2004). The environmental factors (assumed to be representative of the local environment) used for calculations were: (1) temperature, (2) relative humidity (RH) as decimal fraction, and (3) $\delta^{18}O_{rain}$ values at the time of snail activity (see

Balakrishnan and Yapp, 2004). For the calculations, it was assumed that the snail water was lost via evaporation $(\theta = 0)$ and that the water vapor was in isotopic equilibrium with the rain (see Balakrishnan and Yapp, 2004 for detailed explanation). The calculations yielded significantly higher values than the measured values for both $\delta^{18}O_{body}$ and $\delta^{18}O_{\text{shell}}$. However, snails are only active at values of RH higher than 0.70, mostly at night or immediately after rain events (e.g., Balakrishnan and Yapp, 2004 and references therein). Consequently, the available mean values of RH are not probably representative of the times of snails activity. In fact, the model predicted accurate values when RH was 0.92, 0.96 and 0.94 for the localities at 10, 540 and 2160 m, respectively (holding all other factors constant). These relatively high values of RH are possible at night or immediately after a rain event within the microhabitat



Fig. 7. Comparison of the $\delta^{18}O_{shell}$ values among land snail species collected at a single locality. Only species with three or more analyzed individuals were included in the comparisons. Shells collected from the Izaña locality at 2160 m were excluded because only one species was collected. Boxes represent the 25–75% quartiles. Horizontal line inside the box is the median value. Whiskers show the minimum and maximum values. Kruskal–Wallis test results are only shown where significant differences were obtained (e and f). Numbers between brackets represent the number of shells analyzed.

where snails are active. Therefore, further investigation of additional environmental controlling factors (such as relative humidity) is still needed for future projects in the study area.

5.2. Shell carbon isotope composition and its relationship with the vegetation

It has been demonstrated that the carbon isotope composition of shell carbonate from land snails is primarily composed of respiratory CO₂ derived from the assimilation of plant based food resources (McConnaughey et al., 1997; McConnaughey and Gillikin, 2008), and consequently, $\delta^{13}C_{shell}$ values have been used to estimate the proportion of C₃/C₄ plants in the diet (e.g., Goodfriend and Hood, 1983; Goodfriend, 1992, 1999; Goodfriend and Ellis, 2002; Stott, 2002; Metref et al., 2003; Balakrishnan and Yapp, 2004; Balakrishnan et al., 2005a,b). Even though some studies have shown additional factors may influence $\delta^{13}C_{shell}$ values, such as the ingestion of foreign carbonates (Goodfriend and Hood, 1983; Goodfriend, 1987, 1999; Goodfriend and Ellis, 2002; Yates et al., 2002; Yanes et al., 2008), plant diet seems to be the factor that primarily controls the $\delta^{13}C$ of snail shell carbonate (e.g., McConnaughey et al., 1997; Stott, 2002; Metref et al., 2003; McConnaughey and Gillikin, 2008).

The large range of $\delta^{13}C_{shell}$ values for land snails in Tenerife Island (15.1‰) nearly spans the range of values known for C_3 and C_4 plants, thus higher $\delta^{13}C_{shell}$ values could be attributed to individuals that have incorporated carbon from C_4 plants and lower $\delta^{13}C_{\text{shell}}$ values to those snails that mostly assimilated C3 plants. The frequency distribution of the pooled $\delta^{13}C_{\text{shell}}$ values (Fig. 10a) is consistent with the hypothesis that the great majority of snails (n = 195) ingested primarily C3 plants. All individuals that showed higher $\delta^{13}C_{shell}$ values were collected in the south facing slope below 980 m a.s.l. (see Appendix). This result is consistent with the observed frequency distribution of $\delta^{13}C_{plant}$ values (Fig. 4a), where C₃ plants are dominant at all landscapes and C₄ and CAM plants are present at low altitude settings in the south slope. Furthermore, a broad isotopic variability was observed not only across habitats but within each site (Table 5 and Fig. 6g-h). Shells collected in habitats from the south facing transect had a much wider range of $\delta^{13}C_{shell}$ values (-15.7% to -0.6%) compared to the north transect (-13.0% to -6.0%). This could be due to two factors: (1)

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Fig. 8. Comparison of the $\delta^{13}C_{shell}$ values among land snail species collected at a single locality. Note that only species with three or more analyzed individuals were included in the comparisons. Shells collected from the Izaña locality at 2160 m were excluded because only one species was collected. Boxes represent the 25–75% quartiles. Horizontal line inside the box is the median value. Whiskers show the minimum and maximum values. Kruskal–Wallis test results are only shown where significant differences were obtained (a and i). Numbers between brackets represent the number of shells analyzed.

the presence of C₄ plants in the drier–hotter environments and/or (2) greater water-stressed conditions of the C₃ plants in the south facing transect (e.g., Farquhar et al., 1989). In fact, negative correlation between $\Delta^{13}C_{shell}$ values and precipitation suggests that a larger range of $\delta^{13}C_{shell}$ values is expected at drier sampling sites.

The aridity or humidity of a given landscape can influence the relative distribution of C_3 and C_4 /CAM plants

Table 8 Calculated δ^{18} O values of snail body water and semi-hypothetically observed δ^{18} O_{rain} values by site.

							and a stand	-)	
Altitude (m a.s.l.)	Slope	n	MAT (°C)	MAP (mm)	Mean δ ¹⁸ O _{shell} ‰ (VPDB)	Calculated $\delta^{18}O_{body}$ (VSMOW)	$\begin{array}{l} \text{Semi-hypothetical} \\ \delta^{18}O_{rain} \ \%_{o} \\ (\text{VSMOW}) \end{array}$	$\begin{array}{l} \Delta^{18}O~(\delta^{18}O_{body}-\\ \delta^{18}O_{rain}) \end{array}$	Habitat
10	S	37	21.3	114.1	1.2 ± 1.1	1.6	-1.4	3.0	Arid coastal scrub
20	Ν	11	20.8	263.4	0.8 ± 0.5	1.1	-1.4	2.5	Semiarid shrub
120	Ν	18	19.6	348.5	0.9 ± 0.6	0.9	-1.6	2.5	Semiarid shrub
280	S	11	20.5	315.6	1.1 ± 1.5	1.3	-1.9 ^a	3.2	Semiarid shrub
430	S	13	17.3	298.4	0.7 ± 0.7	0.1	-2.1	2.2	Semiarid shrub
540	Ν	18	15.9	682.7	0.3 ± 0.4	-0.6	-2.2	1.6	Humid evergreen forest
700	S	51	16.8	246.3	0.8 ± 0.7	0.2	-2.5	2.7	Semiarid woodlands
980	S	16	16.1	552.3	0.5 ± 0.7	-0.3	-3.0	2.7	Semiarid pine forest
1500	Ν	10	12.6	914.2	0.5 ± 0.5	-1.4	-3.8	2.4	Humid pine forest
1630	S	9	14.6	418.8	-0.5 ± 1.4	-1.6	-3.9	2.3	Arid pine forest
2160	Ν	13	9.6	460.4	-0.1 ± 0.8	-2.4	-4.9	2.5	Dry subalpine scrub

n, number of analyzed shells; MAT, mean annual temperature; MAP, mean annual precipitation. ^a Measured $\delta^{18}O_{rain}$ value.

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Fig. 9. Bivariate plot showing the relationship between the calculated δ^{18} O values of the snail body water and elevation (a) and mean annual precipitation (b).

which can influence the $\delta^{13}C_{shell}$ values (e.g., Goodfriend and Ellis, 2000, 2002). The C₃ plants are favored under higher rainfall regimes typical of a Mediterranean climate, so they tend to be dominant in landscapes characterized by higher humidity, while C₄ (and CAM) tend to be dominant in drier landscapes, indicative of more severely water-stressed conditions (e.g., Ehleringer and Monson, 1993). Accordingly, more negative $\delta^{13}C_{shell}$ values may indicate a wetter environment dominated by C₃ plants while more positive values suggest drier conditions dominated by C₄ plants (e.g., Goodfriend and Ellis, 2000, 2002; Balakrishnan et al., 2005a,b; Baldini et al., 2007; Yanes et al., 2008).

A significant correlation was observed when comparing the mean δ^{13} C values of shells and plants by site ($r_s = 0.73$, p = 0.02; n = 9), suggesting that mean δ^{13} C_{shell} values may provide information about the surrounding vegetation (Table 1 and Fig. 10b).

The observed difference between the δ^{13} C values of the shell and plants ranged from 16.8 to 22.1% by site (Fig. 10c), which is consistent with previous studies that have shown that $\delta^{13}C_{\text{shell}}$ values are 8–19% more positive than the carbon of the assimilated diet because of isotope exchange between respiratory CO₂ and HCO₃⁻ from which the shell is constructed (McConnaughey and Gillikin, 2008 and references therein). It has been suggested that the offset is greatest when atmospheric CO₂ contributes to shell carbon (e.g., McConnaughey and Gillikin, 2008). However, simple mass balance equations indicate that there is no sig-

nificant effect of atmospheric CO₂ on δ^{13} C_{shell} values at any reasonably expected concentration (Balakrishnan and Yapp, 2004). In this study, a positive significant correlation was observed between the difference in the δ^{13} C values of the shell and plants and mean annual precipitation ($r_s = 0.76$, p = 0.02; n = 9), indicating that larger offsets between shell and diet may be expected under wetter conditions (Fig. 10d).

The shells from this study with higher δ^{13} C values could be explained by a contribution of carbon from C₃ plants and inorganic carbonates rather than carbon from C₄ plants. However, the soils from Tenerife Island are characterized by a low content of carbonates (i.e., volcanic soils) supporting the interpretation of C₄ plants consumption. Furthermore, shells that displayed the highest δ^{13} C values were collected from the dry/hot settings of the south facing transect below 980 m (Figs. 6g–h and 9a), supporting the contention that carbon isotope values are related to the availability of C₄ plants. Further investigation to estimate the magnitude of various controlling factors upon the $\delta^{13}C_{shell}$ is still needed to better understand the $\delta^{13}C$ values of shells from land snails.

5.3. Reliability of multi-taxa land snail isotope profiles

The land snail species from Tenerife Island are expected to display some differences in their physiology, ecology, behavior and diet habits since they belong to significantly different habitats (from arid coastal settings to high mountain landscape). Alternatively, there are important similarities among species; for example, all snail species included in this study are grazers that consume plants most likely in proportion to their availability in the landscape (Hyman, 1967; Yanes et al., 2008). In addition, snail species generally do not estivate nor hibernate due to the suppressed seasonality of low-latitude oceanic islands. Consequently, the daily behavior of land snails (resting during the hottest hours of the day) should not change substantially throughout the year (Yanes et al., 2008). Our results suggest that no significant differences exist between the oxygen and carbon isotope compositions of land snail species from a single sampling site (Table 6 and Figs. 7 and 8). These findings are consistent with previous studies that have shown that the oxygen isotope composition of the shell is non-species dependent (Goodfriend and Ellis, 2002; Zanchetta et al., 2005 and references therein).

5.4. Implications for the fossil record

The wide isotopic variability observed in the oxygen and carbon isotope composition of land snail shells within modern ecosystems indicates the complexity in the biomineralization process. This has important implications for the fossil record where time-averaging variations are possible. Fossil shell beds may be represented by the accumulation of numerous generations of snails (= mixing of non-contemporaneous shells accumulated together from hundreds to thousands of years), as previously observed (e.g., Yanes et al., 2007). Hence, numerous fossil shells from a single bed (representative of the shell assemblage) should be analyzed

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Fig. 10. Relationship between $\delta^{13}C$ values of shells and plants. (a) Frequency distribution of $\delta^{13}C$ values of shells from Tenerife Island. (b) Bivariate plot of the mean $\delta^{13}C$ value of snail shells and plants by sampling site. Circles represent the mean value and whiskers represent 1σ standard deviation of the data. (c) Carbon isotope offset between mean $\delta^{13}C$ values of shells and plants ($\Delta^{13}C_{\text{shell-plant}}$) along altitude. (d) Carbon isotope offset between mean $\delta^{13}C$ values of shells and plants ($\Delta^{13}C_{\text{shell-plant}}$) against mean annual precipitation. Solid line and associated equations represent the regression of the data.

in paleoclimatic projects to infer meaningful environmental conditions of ancient terrestrial ecosystems. First, the isotopic range of a shell bed may provide information about the magnitude of environmental variability within the studied age interval (i.e., relatively-stable environment or waterstressed conditions). Second, the mean isotopic value by shell bed may provide useful insights into averaged (dominant) environmental signal across age intervals or sampling sites. Third, stable isotopes extracted from multi-taxa data sets may be useful in estimating past environments when numerous individuals of a single species are not available across space or time.

6. CONCLUSIONS

Oxygen and carbon stable isotopes of land snail shells are useful to infer local environmental conditions within and across sites at low-latitude and oceanic settings. Greater isotopic variability was observed within drier/hotter (water-stressed) habitats from the south facing slope, while northern (wetter/cooler) sampling sites tended to show consistently more constrained isotopic compositions.

Although pooled isotopic data did not generally show strong relationships with the environmental variables (altitude, temperature and precipitation), mean values per site showed more meaningful correlations. Mean $\delta^{18}O_{shell}$ values by site declined with altitude probably in response to a decrease in $\delta^{18}O_{rain}$ values and temperature. Mean $\delta^{13}C_{shell}$ values correlated with the surrounding vegetation, indicating that snail shells record the isotope signal of the consumed plants, where more negative $\delta^{13}C_{shell}$ values are related to a higher proportion of C₃ plants consumed and possibly, wetter conditions. The observed scatter of isotopic values in present-day land snail populations within single habitats necessitates the analysis of numerous fossil shells at a single study site to make meaningful inferences about climate. Finally, $\delta^{18}O_{shell}$ and $\delta^{13}C_{shell}$ values did not significantly differ between species by site, pointing to the utility of multi-taxa data sets for paleoclimatic reconstructions.

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Oxygen and carbon isotopes of modern land snail shells

APPENDIX

Oxygen and carbon isotope composition of land snail shells from Tenerife Island.

SHELL ID	Species	Locality	Elevation (m)	Slope	$\delta^{18}O_{shelloo} (VPDB)$	$\delta^{13}C_{shell 000} (VPDB)$
LS 80-1	Canariella hispidula	Caletillas	10	S	0.6	-8.2
LS_87-1	Canariella hispidula	Caletillas	10	S	1.5	-10.4
LS_87-2	Canariella hispidula	Caletillas	10	S	1.7	-7.8
LS_87-3	Canariella hispidula	Caletillas	10	S	1.3	-7.7
LS_87-4	Canariella hispidula	Caletillas	10	S	1.5	-8.2
LS_30-1	Caracollina lenticula	Caletillas	10	S	0.8	-7.7
LS_30-2	Caracollina lenticula	Caletillas	10	S	1.0	-8.6
LS_30-3	Caracollina lenticula	Caletillas	10	S	0.9	-9.9
LS_9-1	Caracollina lenticula	Caletillas	10	S	-0.2	-8.4
LS_9-2	Caracollina lenticula	Caletillas	10	S	0.8	-9.7
LS_9-3	Caracollina lenticula	Caletillas	10	S	-0.4	-0.6
LS_9-4	Caracollina lenticula	Caletillas	10	S	-0.4	-6.7
LS_12-1	Hemicycla bethencourtiana	Caletillas	10	S	2.6	-10.0
LS_12-2	Hemicycla bethencourtiana	Caletillas	10	S	0.7	-8.0
LS_12-3	Hemicycla bethencourtiana	Caletillas	10	S	2.5	-7.0
LS_12-4	Hemicycla bethencourtiana	Caletillas	10	S	2.8	-7.1
LS_12-5	Hemicycla bethencourtiana	Caletillas	10	S	3.9	-7.3
LS_4-1	Hemicycla bethencourtiana	Caletillas	10	S	0.0	-8.5
LS_4-2	Hemicycla bethencourtiana	Caletillas	10	S	2.5	-6.8
LS_4-3	Hemicycla bethencourtiana	Caletillas	10	S	0.6	-7.7
LS_4-4	Hemicycla bethencourtiana	Caletillas	10	S	-0.1	-8.2
LS_4-5	Hemicycla bethencourtiana	Caletillas	10	S	0.5	-1.7
LS_5-1	Hemicycla bethencourtiana	Caletillas	10	S	1.0	-8.1
LS_5-2	Hemicycla bethencourtiana	Caletillas	10	S	-0.9	-6.8
LS_5-3	Hemicycla bethencourtiana	Caletillas	10	S	0.2	-6.8
LS_5-4	Hemicycla bethencourtiana	Caletillas	10	S	0.3	-6.0
LS_5-5	Hemicycla bethencourtiana	Caletillas	10	S	0.5	-7.6
LS_11-1	Hemicycla plicaria	Caletillas	10	S	1.0	-10.3
LS_11-2	Hemicycla plicaria	Caletillas	10	S	1.9	-10.1
LS_11-3	Hemicycla plicaria	Caletillas	10	S	3.2	-11.1
LS_11-4	Hemicycla plicaria	Caletillas	10	S	1.9	-9.0
LS_11-5	Hemicycia pilcaria	Caletillas	10	5	2.3	-/.1
LS_32-1	Napaeus sp.	Caletillas	10	5	0.8	-4.5
LS_31-1	Xerotrichia orbignyi Yenetrichia erhizuui	Caletillas	10	5	2.9	-/./
LS_31-2	Xerotrichia orbignyi	Caletillas	10	5	1.4	-10.0
LS_31-3	Xerotrichia orbignyi Yenetrichia erhizuui	Caletillas	10	5	2.1	-9.1
LS_31-4	Cananialla planania	Daniio	10	S N	1.0	-/.4
LS_00-1	Canariella planaria	Benijo	20	IN NI	1.1	-12.0
LS_00-2	Canariella planaria	Benijo	20	IN N	0.7	-12.0
LS_00-3	Canaviella planavia	Benijo	20	IN N	1.5	-11.0
LS_00-4	Canariella planaria	Benijo	20	N	1.2	-12.5
LS_00-5	Caracollina lenticula	Benijo	20	N	0.2	_9.9
LS_33-2	Caracollina lenticula	Benijo	20	N	1.0	-9.1
LS_33-3	Caracollina lenticula	Benijo	20	N	0.2	-10.5
LS_34-1	Monilearia phalerata	Benijo	20	N	0.2	-9.0
LS_34-2	Monilearia phalerata	Benijo	20	N	1.6	-10.6
LS_34-4	Monilearia phalerata	Benijo	20	N	-0.1	_9 2
LS_83-2	Canariella planaria	Taganana	120	N	0.9	-11.2
LS_85-1	Canariella planaria	Taganana	120	N	0.9	-94
LS_85-2	Canariella planaria	Taganana	120	N	12	-11.6
LS_85-3	Canariella planaria	Taganana	120	N	1.1	-10.9
LS 85-4	Canariella planaria	Taganana	120	N	1.0	-10.7
LS 85-5	Canariella planaria	Taganana	120	Ν	0.9	-11.7
LS 22-1	Ferussacia folliculus	Taganana	120	Ν	1.4	-11.6
LS 22-2	Ferussacia folliculus	Taganana	120	N	-0.4	-11.2
LS 22-3	Ferussacia folliculus	Taganana	120	Ν	0.0	-11.5
LS 27-1	Ferussacia folliculus	Taganana	120	Ν	1.3	-10.7
LS_7-1	Hemicycla bidentalis	Taganana	120	Ν	0.9	-12.0

(continued on next page)

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Appendix (continued)

SHELL ID	Species	Locality	Elevation (m)	Slope	$\delta^{18}O_{\text{shell}\%}$ (VPDB)	$\delta^{13}C_{\text{shell}}$ (VPDB)
15.7-2	Hemicycla hidentalis	Taganana	120	N	0.0	
LS_20-1	Monilearia phalerata	Taganana	120	N	11	-9.9
LS 28-1	Monilearia phalerata	Taganana	120	N	2.5	-10.0
LS 28-2	Monilearia phalerata	Taganana	120	N	0.8	-9.6
LS 21-1	Napaeus variatus	Taganana	120	Ν	1.5	-13.0
LS 29-1	Xerotrichia orbignyi	Taganana	120	Ν	0.7	-12.1
LS 29-3	Xerotrichia orbignyi	Taganana	120	Ν	1.1	-10.2
LS_8-1	Cornu aspersum	Güímar	280	S	2.4	-11.7
LS_8-2	Cornu aspersum	Güímar	280	S	2.0	-12.6
LS_8-3	Cornu aspersum	Güímar	280	S	2.5	-12.9
LS_8-4	Cornu aspersum	Güímar	280	S	2.3	-13.8
LS_8-5	Cornu aspersum	Güímar	280	S	3.1	-9.6
LS_9-1	Cornu aspersum	Güímar	280	S	0.2	-12.0
LS_86-1	Rumina decollata	Güímar	280	S	-0.6	-11.0
LS_86-2	Rumina decollata	Güímar	280	S	1.6	-9.2
LS_86-3	Rumina decollata	Güímar	280	S	-0.1	-12.1
LS_86-4	Rumina decollata	Güímar	280	S	-0.6	-11.7
LS_86-5	Rumina decollata	Güímar	280	S	-0.9	-13.4
LS_82-1	Canariella hispidula	Camino Real	430	S	0.2	-4.4
LS_15-1	Caracollina lenticula	Camino Real	430	S	0.0	-2.5
LS_15-3	Caracollina lenticula	Camino Real	430	S	0.5	-7.0
LS_6-1	Hemicycla bethencourtiana	Camino Real	430	S	0.6	-10.9
LS_6-2	Hemicycla bethencourtiana	Camino Real	430	S	1.1	-11.5
LS_6-3	Hemicycla bethencourtiana	Camino Real	430	S	1.2	-5.3
LS_6-4	Hemicycla bethencourtiana	Camino Real	430	S	0.7	-11.3
LS_6-5	Hemicycla bethencourtiana	Camino Real	430	S	0.4	-9.9
LS_16-1	Monilearia phalerata	Camino Real	430	S	1.9	-5.5
LS_16-2	Monilearia phalerata	Camino Real	430	5	-0.3	-8.2
LS_10-3	Monilearia phalerata	Camino Real	430	5	0.4	-4./
LS_17-1	Monilearia phalerata	Camino Real	430	5	2.0	-0.0
LS_17-2	Monnearia phalerala Hamiovala bidantalis	El Pailadara	430 540	S N	0.2	-10.8
LS_{14-10}	Hemicycla bidentalis	El Bailadero	540	N	-0.1	-11.2
LS_14-10 LS_14-2	Hemicycla bidentalis	El Bailadero	540	N	0.2	-12.0
LS_14-2 IS_14-3	Hemicycla bidentalis	El Bailadero	540	N	-0.1	-11.9
LS_14-4	Hemicycla bidentalis	El Bailadero	540	N	0.6	-11.7
LS_14-5	Hemicycla bidentalis Hemicycla bidentalis	El Bailadero	540	N	-0.2	-10.7
LS_14-6	Hemicycla bidentalis	El Bailadero	540	N	0.2	-10.4
LS 14-7	Hemicvcla bidentalis	El Bailadero	540	N	0.5	-11.4
LS 14-8	Hemicvcla bidentalis	El Bailadero	540	Ν	-0.3	-10.1
LS 14-9	Hemicycla bidentalis	El Bailadero	540	Ν	0.3	-12.0
LS 3-1	Hemicycla bidentalis	El Bailadero	540	Ν	0.2	-11.0
LS_3-2	Hemicycla bidentalis	El Bailadero	540	Ν	0.5	-11.1
LS_3-3	Hemicycla bidentalis	El Bailadero	540	Ν	0.6	-10.3
LS_3-4	Hemicycla bidentalis	El Bailadero	540	Ν	0.7	-11.9
LS_3-5	Hemicycla bidentalis	El Bailadero	540	Ν	1.1	-11.0
LS_6-1	Plutonia lamarkii	El Bailadero	540	Ν	0.5	-10.5
LS_6-2	Plutonia lamarkii	El Bailadero	540	Ν	0.7	-10.7
LS_6-3	Plutonia lamarkii	El Bailadero	540	Ν	0.9	-11.8
LS_81-1	Canariella hispidula	San Juan	700	S	1.6	-6.5
LS_81-2	Canariella hispidula	San Juan	700	S	1.7	-6.6
LS_81-3	Canariella hispidula	San Juan	700	S	0.0	-10.5
LS_81-4	Canariella hispidula	San Juan	700	S	1.5	-10.4
LS_81-5	Canariella hispidula	San Juan	700	S	2.7	-7.6
LS_120-1	Canariella hispidula	San Juan	700	S	1.7	-11.7
LS_120-2	Canariella hispidula	San Juan	700	S	0.9	-10.6
LS_120-3	Canariella hispidula	San Juan	700	S	0.5	-9.4
LS_121-1	Canariella hispidula	San Juan	700	S	0.7	-7.2
LS_121-2	Canariella hispidula	San Juan	700	S	1.1	-7.8
LS_121-3	Canariella hispidula	San Juan	700	S	1.5	-7.5
LS_14-1	Caracollina lenticula	San Juan	700	S	-0.1	-9.3
LS_14-2	Caracollina lenticula	San Juan	700	S	0.0	-10.2
LS_14-3	Caracollina lenticula	San Juan	700	S	1.4	-9.2

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Oxygen and carbon isotopes of modern land snail shells

Appendix (continued)

SHELL ID	Species	Locality	Elevation (m)	Slope	$\delta^{18}O_{shell}^{0\!\!\prime}_{\!oo}~(VPDB)$	$\delta^{13}C_{shell} \overset{o\!\!\!\!\!o}{_{\!\! oo}} (VPDB)$
LS 14-4	Caracollina lenticula	San Juan	700	S	0.9	-8.7
LS_39-1	Caracollina lenticula	San Juan	700	S	1.0	-9.0
LS_39-2	Caracollina lenticula	San Juan	700	S	-1.3	-10.0
LS_13-1	Ferussacia folliculus	San Juan	700	S	0.3	-10.9
LS_13-3	Ferussacia folliculus	San Juan	700	S	1.3	-10.6
LS_13-4	Ferussacia folliculus	San Juan	700	S	-0.5	-9.6
LS_38-1	Ferussacia folliculus	San Juan	700	S	0.5	-9.3
LS_38-2	Ferussacia folliculus	San Juan	700	S	0.0	-9.6
LS_2-1	Hemicycla aff. retrodens	San Juan	700	S	1.0	-8.8
LS_2-2	Hemicycla aff. retrodens	San Juan	700	S	0.4	-11.1
LS_2-3	Hemicycla aff. retrodens	San Juan	700	2	0.4	-/.3
LS_2-4	Hemicycla aff. retrodens	San Juan	700	5	1.0	-8.1
LS_2-5 LS_13_1	Hemicycla bethencourtiene	San Juan	700	5 5	1.8	-11.9
LS_13-1	Hemicycla bethencourtiana	San Juan	700	5 5	1.0	-8.1
LS_13-3	Hemicycla bethencourtiana	San Juan	700	S	0.7	-10.6
LS_12-1	Hemicycla sp	San Juan	700	Š	1.6	-8.8
LS_12-2	Hemicycla sp.	San Juan	700	S	1.1	-8.5
LS 12-3	Hemicycla sp.	San Juan	700	ŝ	2.1	-9.1
LS 12-4	Monilearia phalerata	San Juan	700	ŝ	1.8	-10.2
LS 12-5	Monilearia phalerata	San Juan	700	ŝ	1.4	-10.8
LS 12-6	Monilearia phalerata	San Juan	700	S	0.6	-8.1
LS 12-7	Monilearia phalerata	San Juan	700	S	1.0	-11.3
LS_119-1	Monilearia phalerata	San Juan	700	S	0.1	-11.5
LS_119-2	Monilearia phalerata	San Juan	700	S	-0.1	-9.7
LS_119-3	Monilearia phalerata	San Juan	700	S	0.5	-10.2
LS_119-4	Monilearia phalerata	San Juan	700	S	1.0	-7.1
LS_119-5	Monilearia phalerata	San Juan	700	S	0.5	-10.4
LS_35-1	Monilearia phalerata	San Juan	700	S	-0.1	-7.5
LS_35-2	Monilearia phalerata	San Juan	700	S	1.5	-0.7
LS_35-3	Monilearia phalerata	San Juan	700	S	0.9	-8.2
LS_35-4	Monilearia phalerata	San Juan	700	S	0.4	-7.8
LS_36-1	Monilearia phalerata	San Juan	700	S	0.5	-9.6
LS_36-2	Monilearia phalerata	San Juan	700	S	1.0	-8.8
LS_36-3	Monilearia phalerata	San Juan	700	S	1.2	-8.4
LS_5-1	Plutonia blauneri	San Juan	700	S	0.2	-8.9
LS_3/-1	Plutonia blauneri	San Juan	/00	2	0.5	-10.3
LS_25-1	Caracollina lenticula	Low Vilation	980	5	1.0	-8./
LS_25-2	Caracollina lenticula	Low Vilation	980	5 5	-0.3	-9.9
LS_25-5 LS_25-4	Caracollina lenticula	Low Vilaflor	980	S	0.7	-8.0 -8.7
LS_25-5	Caracollina lenticula	Low Vilaflor	980	S	1.9	-8.1
LS_24-1	Ferussacia folliculus	Low Vilaflor	980	S	0.7	-8.5
LS 24-2	Ferussacia folliculus	Low Vilaflor	980	ŝ	-0.2	-10.0
LS 24-3	Ferussacia folliculus	Low Vilaflor	980	S	-1.0	-10.6
LS_84-1	Monilearia [°] phalerata	Low Vilaflor	980	S	1.1	-10.5
LS_84-2	Monilearia phalerata	Low Vilaflor	980	S	1.3	-9.4
LS_84-3	Monilearia phalerata	Low Vilaflor	980	S	0.2	-8.3
LS_84-4	Monilearia phalerata	Low Vilaflor	980	S	0.1	-8.2
LS_84-5	Monilearia phalerata	Low Vilaflor	980	S	0.3	-9.8
LS_26-1	Napaeus propinquus	Low Vilaflor	980	S	0.5	-4.7
LS_26-2	Napaeus propinquus	Low Vilaflor	980	S	0.1	-4.3
LS_26-3	Napaeus propinquus	Low Vilaflor	980	S	0.7	-3.9
LS_200-1	Napaeus bechi	Montaña Cascajo	1500	N	0.1	-7.0
LS_201-1	Canariella hispidula	Montaña Cascajo	1500	N	0.5	-7.5
LS_201-2	Canariella hispidula	Montaña Cascajo	1500	N	0.7	-7.3
LS_202-1	Plutonia blauneri	Montana Cascajo	1500	N	1.3	-9.1
LS_202-2	Plutonia blauneri	Montana Cascajo	1500	IN N	1.0	-8.5
LS_202-3	r iuionia blauneri	Montaña Cascajo	1500	IN N	1.0	-10.4
LS_202-4	riulonia diauneri Phitonia blaunori	Montaña Cascajo	1500	IN N	0.2	-1.2
LS_202-3	1 unonia olauneri Plutonia blauneri	Montaña Cascajo	1500	IN N	0.2	-7.0 -6.7
LS_202-0	Nanaeus hechi	High Vilaflor	1630	S	-0.8	-6.8
_~	- aparens seen			~	0.0	

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Appendix (continued)

		2	Elevation (III)	Slope	δ ¹ O _{shell} ‰ (VPDB)	$\delta^{13}C_{\text{shell}_{00}}$ (VPDB)
LS_19-2	Napaeus bechi	High Vilaflor	1630	S	-2.2	-15.7
LS_211-1	Plutonia blauneri	High Vilaflor	1630	S	-2.9	-9.4
LS_211-2	Plutonia blauneri	High Vilaflor	1630	S	1.4	-7.8
LS_211-3	Plutonia blauneri	High Vilaflor	1630	S	-0.7	-7.9
LS_213-1	Xerotrichia nubivaga	High Vilaflor	1630	S	0.2	-8.2
LS_213-2	Xerotrichia nubivaga	High Vilaflor	1630	S	0.4	-7.1
LS_213-3	Xerotrichia nubivaga	High Vilaflor	1630	S	0.2	-6.6
LS_213-4	Xerotrichia nubivaga	High Vilaflor	1630	S	-0.4	-6.7
LS_10-1	Xerotrichia nubivaga	Izaña	2160	Ν	-1.9	-6.7
LS_10-2	Xerotrichia nubivaga	Izaña	2160	Ν	-1.1	-7.5
LS_10-3	Xerotrichia nubivaga	Izaña	2160	Ν	-0.5	-7.0
LS_10-4	Xerotrichia nubivaga	Izaña	2160	Ν	-0.5	-6.5
LS_10-5	Xerotrichia nubivaga	Izaña	2160	Ν	-0.3	-6.9
LS_10-6	Xerotrichia nubivaga	Izaña	2160	Ν	0.0	-6.6
LS_10-7	Xerotrichia nubivaga	Izaña	2160	Ν	0.2	-6.0
LS_10-8	Xerotrichia nubivaga	Izaña	2160	Ν	0.4	-9.2
LS_10-9	Xerotrichia nubivaga	Izaña	2160	Ν	0.5	-6.0
LS_10-10	Xerotrichia nubivaga	Izaña	2160	Ν	0.5	-6.3
LS_10-11	Xerotrichia nubivaga	Izaña	2160	Ν	0.5	-6.8
LS_10-12	Xerotrichia nubivaga	Izaña	2160	Ν	0.6	-7.4
LS_10-13	Xerotrichia nubivaga	Izaña	2160	Ν	0.7	-6.7

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