Palaeogeography, Palaeoclimatology, Palaeoecology 471 (2017) 196–208

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Compositional variability of Pleistocene land snail assemblages preserved in a cinder cone volcano from Tenerife, Canary Islands

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ARTICLE INFO

Article history:
Received 14 July 2016
Received in revised form 2 February 2017
Accepted 2 February 2017
Available online 04 February 2017

Keywords:
Land snails
Taphonomy
Paleoecology
Paleoclimate
Quaternary
Canary Islands

ABSTRACT

A Pleistocene land snail rich scoria sequence was studied to determine if it was influenced by taphonomic bias, climate change, or both, using a multifaceted approach that combines taphonomic, ecological, body size, and stable isotope data. Shell assemblages were sampled from two layers (Units A and B) in a cinder cone volcano of southern Tenerife (Canary Islands), dated to the glacial interval MIS 8 (~299–302 ka). The two units differed in taphonomy, species composition, and abundance, with the upper Unit B showing higher diversity, abundance, and lower alteration than the lower Unit A. Larger bodied species dominated Unit A and were better preserved than smaller species. These mismatches likely resulted from physical differences in the sediment matrix surrounding fossils, with larger scoria grains of Unit A enhancing destruction rates and thus favoring preservation of larger (more durable) taxa than smaller scoria grains of Unit B. Comparisons with modern assemblages from the coastal scrub, the plant biome in which the Pleistocene site currently resides, indicates that no modern analogue exists for these fossil assemblages within this biome. Shell oxygen isotope values reveal that the local climate was colder/wetter during MIS 8 than at present, which also may explain variations in species composition through time. These data suggest that both taphonomic and climatic factors appear to have induced temporal variations in taxonomic composition, but it is difficult to determine which of these has more significantly influenced the observed results.

1. Introduction

Diversity, species composition, individual abundance, and body size data extracted from fossil assemblages may vary through both space and time in response to climatic and/or taphonomic drivers, but these relationships are sometimes difficult to identify and distinguish from one another. In the last few decades there has been intense focus on quantitative taphonomic studies to gain insight into the formation of fossil assemblages and determine the extent to which they preserve an ecological signal. These studies have primarily focused on marine invertebrate assemblages (e.g., Behrensmeyer et al., 2000; Behrensmeyer et al., 2005; Brett, 1995; Kidwell, 2001, 2002; Kowalewski et al., 1998; Tomašových, 2004, 2006), with far fewer studies focusing on invertebrates from terrestrial systems (Briggs et al., 1990; Carter, 1990; Yanes et al., 2008, 2011b; Yanes, 2012). Terrestrial Quaternary assemblages provide excellent opportunities for quantitative taphonomic investigations (Yanes et al., 2008, 2011b; Yanes, 2012) because, in comparison to many other terrestrial animals with no hard skeletons, they are generally well preserved, highly abundant, and often exhibit high temporal resolution, useful for assessing biotic responses to environmental, climatic, and taphonomic changes.

Within Quaternary terrestrial systems, land snails are particularly appropriate for quantitative taphonomic studies focusing on the formation of fossil assemblages and the preservation of an ecological signal because their durable, aragonitic shells are numerous, they can be found in a myriad of Quaternary depositional environments including archaeological sites (Balakrishnan et al., 2005; Yanes et al., 2011a), aeolian deposits (Brooke et al., 2003; Yanes et al., 2008), volcanic ash (Pickford, 2002), tufa (Preece and Day, 1994), loess deposits (Pigati et al., 2013; Rousseau, 1991), paleosols (Yanes et al., 2011b; Yanes, 2012), lake cores (Bonadonna and Leone, 1995), and colluvial, alluvial, and fluvial deposits (personal field observations, 2014–2016). Because most Quaternary land snail species are extant, direct comparison with modern assemblages to compare faunal compositional changes are facilitated (Yanes, 2012). Furthermore, the stable isotope compositions of the shells themselves can be used to reconstruct local paleoclimate and environment information (Balakrishnan et al., 2005; Yanes et al., 2011c, 2013), and the taphonomic conditions of the shells allow for direct assessment of postmortem processes (Yanes et al., 2008, 2011b; Yanes, 2012).

In this context, Tenerife, Canary Islands, is a highly suitable natural laboratory in which to study the potential impacts of climatic factors

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http://dx.doi.org/10.1016/j.palaeo.2017.02.001
0031-0182/

and taphonomic processes on terrestrial shelly assemblages through time because snails are plentiful, easily accessible, and well preserved (Pannell et al., 2011). Montaña Negra is a Pleistocene cinder cone volcano dated to Marine Isotope Stage (MIS) 8 by Pannell et al. (2011), which represents a glacial interval in the northern Hemisphere. The site is rich in fossil land snail species that are all extant in the archipelago and has good age control (302 ± 7–299.9 ± 11.4 ka) allowing for millennial-scale paleoclimate/paleoecological reconstruction. The time frame of the assemblage allows a glimpse into an ecosystem during a glacial time period prior to human presence in the Canary Islands while also providing a potential contrast to today's interglacial. As additional interest, the shelly accumulations at Montaña Negra are preserved in a volcanic scoria sequence, a very unusual setting for fossil preservation that has been only minimally investigated previously.

Montaña Negra resides in the coastal scrub plant biome, a biome located between sea level and up to ~450 m above sea level (m a.s.l.). In the present day, this biome has an overall semi-arid climate dominated by many succulent plants and grasses, though temperature and precipitation differs between the north and south of the island. Direct comparison with modern land snail assemblages in the coastal scrub biome, particularly at present day sites adjacent to Montaña Negra, allows for temporal comparisons between fossil and modern assemblages, which can then be used to infer faunal compositional changes in response to possible changes in climate. The different climatic conditions between the northern and southern coastal scrub also allow for the investigation of the possible movement of species to maintain their preferred climate.

The goals of this study were to (1) explore the main taphonomic features of land snail shells preserved in a volcanic scoria matrix, (2) evaluate the potential retention of an ecological signature within fossiliferous volcanic layers, (3) reconstruct paleoclimatic conditions through time, and (4) compare the glacial land snail assemblages to today's interglacial assemblages in Tenerife to assess the potential response of land snails to changes in climate.

2. Methods

2.1. Geographical and environmental setting

Tenerife (27°60′ to 28°35′N; 16°05′ to 16°55′W) is the largest island of the Canary Archipelago, ~300 km from the Moroccan coast (Fig. 1A). The island as a whole is considered semi-arid, and experiences a Mediterranean-like climate due to its position in the subtropical high-pressure belt at the poleward limits of the Hadley Cell. However, the interplay of Tenerife's geomorphology with the influence of the cool northeast trade winds creates a climate different than expected, given its latitude and proximity to Northwest Africa (Marzol, 2001). The north of the island is more humid than the south owing to the influence of the trade winds, associated with the Azores anticyclone (Marzol, 2001), which creates a "sea of clouds" (Antequera, 1996). Climate data from Tenerife North Airport collected between 1981 and 2010 indicate a mean average temperature of ~16.8 °C, mean average rainfall of ~520 mm, and an average relative humidity of ~73%; while climate data from Tenerife South Airport collected over the same interval convey a warmer, more arid climate, with a temperature of ~21.4 °C, rainfall of ~132 mm, and relative humidity of ~66% (*Agencia Estatal de Meteorología*: http://www.aemet.es). The coastal scrub plant biome on the island (Fig. 1C), between sea level and up to ~450 m a.s.l., is a semi-arid environment dominated by plants well adapted to dryness with many native succulent plants and grasses (Fernández-Palacios and Whittaker, 2008).

2.2. Study site and sampling protocol

Montaña Negra is a Pleistocene cinder cone volcano in the south of Tenerife (Figs. 1B, 2). It is part of a chain of volcanoes trending north-northeast in the Bandas del Sur region (Brown et al., 2003). The lowest exposure is a layer of basaltic black scoria (Unit A) rich in fossilized land snails in the top 60 cm. This deposit has large black scoria clasts at the base and fines upwards into medium-sized, gray scoria lapilli (Pannell et al., 2011). It is overlain by the Lower Aldea Blanca, a phonolitic pumice fall dated to 302 ± 7 ka by Pannell et al. (2011) via the $^{40}Ar/^{39}Ar$ age-dating method. This unit, in turn, is overlain by another scoria deposit, Unit B, which fines upward into an unconsolidated paleosol also rich in land snail fossils. Unit B is topped by the Upper Aldea Blanca (Brown et al., 2003) dated at 299.9 ± 11.4 ka (Pannell et al., 2011). Age dating of the Lower and Upper Aldea Blanca put Unit B right at the beginning of MIS 8 (glacial interval), and Unit A possibly at the very end of MIS 9 (interglacial interval) or beginning of MIS 8.

2.3. Fossil snail collection protocol

Units A and B were sampled laterally every 1.5 m along both exposures. With this spacing, the nature of the exposure permitted ten sampling stations in Scoria Unit A and twelve samples in Scoria Unit B (Fig. 2). Two teams of two workers hand-picked in situ specimens and fragments of terrestrial snails (Fig. 1 Supplemental material) for 1 h at each station. The same pairs of researchers consistently worked in tandem, hand-picking snail shells along and throughout the outcrop, to minimize sampling bias associated with switching teams. Samples were stored in labeled zip-lock bags and brought back to the laboratory for subsequent analyses. Individual fossil snail specimens were easily dislodged from the surrounding matrix, and in situ and preliminary laboratory analyses assessing taphonomic damage suggested that the sampling method did not cause artificial breakage or damage to the specimens.

2.4. Modern snail collection protocol

Modern snails were collected from a total of twelve sites around the island in the coastal scrub biome, including sites adjacent to the fossil locality at Montaña Negra (Fig. 1A, C). Sites were chosen based on GIS maps detailing coastal scrub areas and determined to be northern or southern sites based on climatic conditions. Dead land snails were sampled in 30 × 30 m plots established at each site and explored by four workers for 1 h collecting all encountered specimens following established procedures (Cameron et al., 2013; Triantis et al., 2005). Four workers sampled individual quadrats rather than working side-by-side in teams of two as done for the fossil assemblages because snails were not as frequently encountered in the modern settings as in the fossil assemblages. Only dead or subfossil shells were used in the study as they represent a time-averaged assemblage containing multiple generations of snails, thereby mitigating short-term fluctuations, and were far more abundant than live individuals (Rundell and Cowie, 2003; Yanes, 2012). Snail shells were found on the soil surface, beneath scoria and other objects resting on the ground, and attached to foliage. All shell material was deposited in the Malacology laboratory of the Department of Geology at the University of Cincinnati.

2.5. Taphonomy and ecology of fossil and modern land snail shells

We used the "minimum number of individuals" (MNI) to determine species abundances, which counts only specimens that preserved the protoconch (Yanes et al., 2008). Ontogenetic state (adult, juvenile) was only possible for snail shells with a preserved aperture (Yanes et al., 2008). Specimens that were less than half the average size of each species, with a less globular shape, and an umbilicate shell were classified as juveniles (Yanes et al., 2008). The proportions of adults and juveniles within the assemblage were calculated by taking the tallied number of each within each station and dividing them by the total number of adults plus juveniles for that station.

For taphonomic analyses, specimens were analyzed under a binocular microscope and measured with electronic calipers. Each specimen

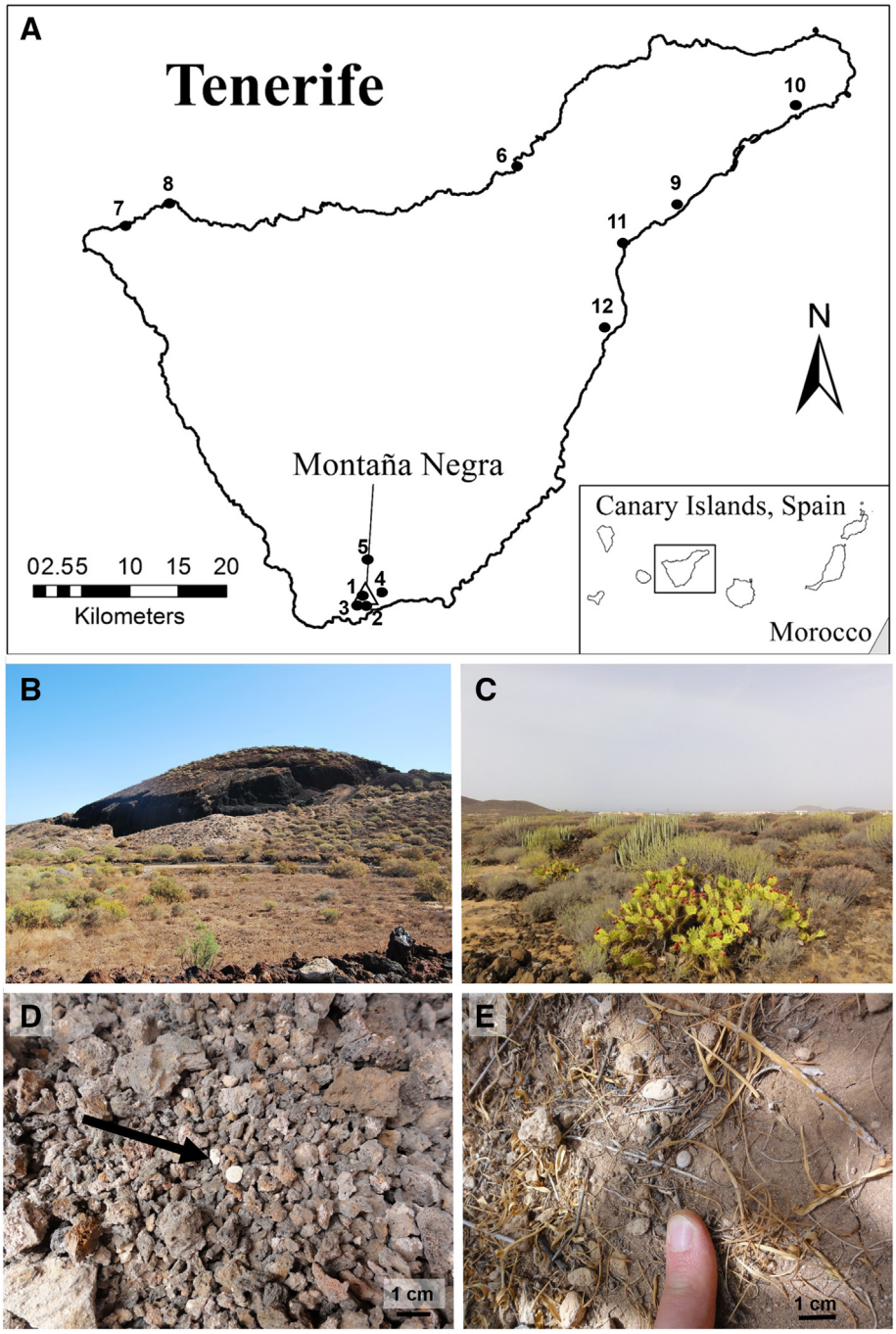

Fig. 1. A. Geographical location of Tenerife Island, Montaña Negra (open triangle), and modern sampling sites (black dots). B. General view of Montaña Negra. C. Coastal scrub biome adjacent to Montaña Negra, Tenerife. D. Fossil *Caracollina lenticula* embedded in scoria. E. Modern *Monilearia phalerata* from a death assemblage near Montaña Negra.

was classified as an adult or juvenile, and was then scored as having the presence or absence of six different taphonomic variables: (1) fragmentation, (2) shell corrosion, (3) presence of sediment crust, (4) color loss, (5) presence of dendrites, and (6) edge roundness. The first five variables were used in subsequent analyses, but edge roundness, which looks at the degree of erosion of a fragmented edge, often used in marine settings as an indication of continued exposure and re-burial of shells, was excluded because all fragmented shells had a rough edge. This observation suggests that fossil shells have not been transported out of habitat or continuously exposed and re-buried. Shells were also analyzed for presence of predation traces or shell repair scars, but no evidence of bioerosion or predation pressure was found in these samples.

Taphonomic properties were collected on individual shells, but then combined for station-level analyses. Fragmentation indicates whether a shell is complete (>95% of shell preserved) or fragmented (<95% of shell preserved) and is calculated by dividing the total number of fragmented shells within each station by the MNI for that station. Corrosion of the shell refers to the damage of shell integrity and loss of ornamentation. It is quantified by dividing the proportion of shells with >5% ornamentation loss by the MNI. The presence of a sediment crust coating the outside of the snail shell was observed for some specimens. The proportion of encrusted shells is calculated by dividing those with any degree of sediment crust covering the shell by the MNI. Color loss is calculated as the proportion of shells that lack original color divided by the MNI.

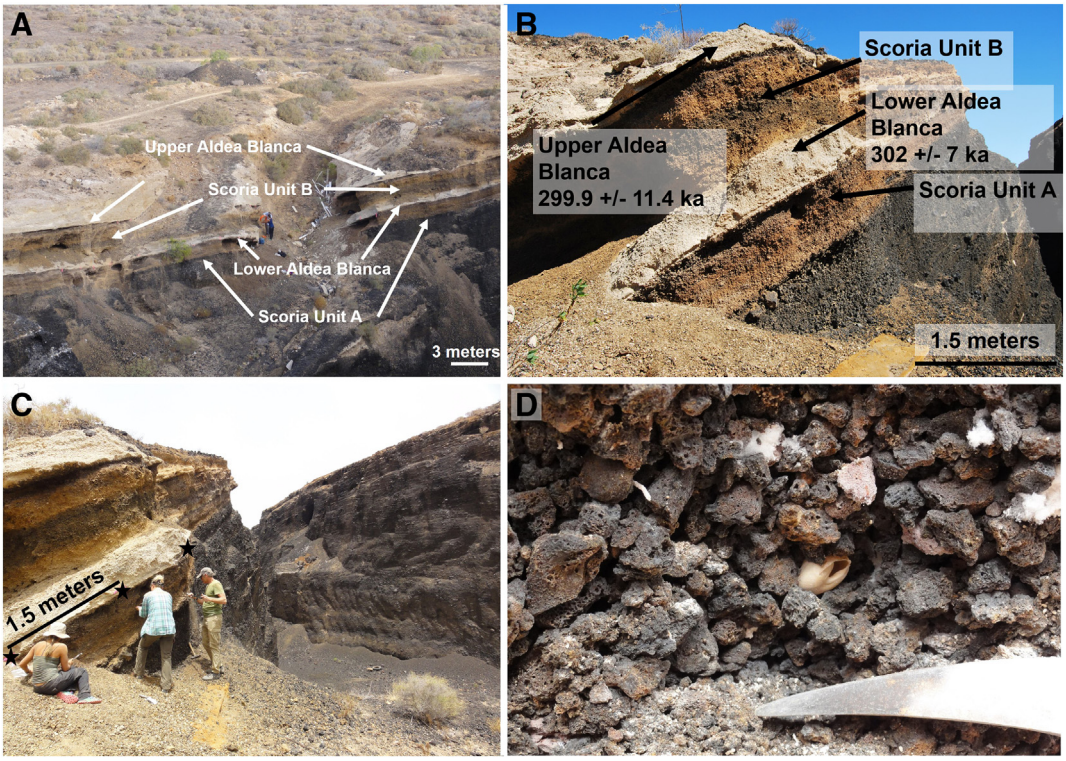

Fig. 2. A. Overhead view of Montaña Negra showing the two sampled outcrops. Both Units A and B and Lower and Upper Aldea Blanca are indicated with white arrows. B. Close up view of Montaña Negra with Units A and B and the Upper and Lower Aldea Blanca Pumice Fall indicated with black arrows. C. Outline of employed sampling method. Black stars indicate station limits. D. Detailed view of the fossil land snail *Hemicycla consobrina* embedded in scoria clasts within Scoria Unit A.

Presence of dendrites quantifies the proportion of shells that show features derived by physical processes, such as dendrites, also divided by the MNI. To determine proportions of adults or juveniles with each of the taphonomic characters, the tallied number of adults or juveniles for that character were added up and divided by the total number of adults or juveniles within that station.

These five variables and the ontogenetic stage were tallied for each species within each station and averaged against the MNI to generate a proportion (Yanes et al., 2008). Only the three species (*C. lenticula*, *C. aff. giustii*, and *H. consobrina*) present in both units were used in the taphonomic analysis because they permitted the most direct comparisons of the preservational tendencies of the two intervals.

Twelve samples were gathered from modern snail assemblages around Tenerife. All modern specimens were identified to species level when possible under a binocular microscope. Snail species identifications were conducted using the most recent published literature and through comparisons with specimens catalogued in the mollusk collection deposited in the Malacology laboratory of the UC Department of Geology. The shelly material for this work was deposited in the same collection.

2.6. Body size measurement

Shell maximum length and width were measured using electronic calipers following standard procedures for globose snail shells (Kerney and Cameron, 1979). Shells that were too small to be accurately measured by this means (length < 1.5 mm), too fragile, or too fragmented were not considered for body size analysis. Only adult shells that had a measurement for both length and width were used in statistical analyses.

2.7. Statistical analyses

To assess within- and between-unit variations in sample compositions, Non Metric Multidimensional Scaling (NMDS) was used to ordinate fossil and modern snail samples in terms of both species abundances and taphonomic variables. NMDS was chosen as it does not involve assumptions about the structure of the data or the form of the response (Cao et al., 2001). Following procedures advocated in many previous studies, fossil species found only at one station and present day species found only at one modern site were not included in these analyses (Clarke and Green, 1988; Marchant, 1999). Micro-snails and semi-slugs were also removed as they were comparatively rare and irregularly encountered, and have fragile shells that tended to break when collected.

For numerical analyses, species abundances were first square root transformed to lower the weight of particularly abundant species and increase the weight of species with moderate to lower abundances (Marchant, 1999). The data were then transformed using a double Wisconsin transformation through which species abundances are each first normalized by their maximum values in all samples and then normalized by total abundances for their respective sites (Oksanen, 1983). Bray-Curtis dissimilarity was used as the distance metric for the species-abundance NMDS to avoid crediting joint absences in dissimilarity calculations (Bray and Curtis, 1957; Clarke and Green, 1988). To compare assemblages based on taphonomic variables, the untransformed proportions of the taphonomic variables only for adult *H. consobrina*, *C. aff. giustii*, and *C. lenticula* were used. Manhattan distance was used to construct the NMDS (Yanes et al., 2008, 2011b) because the taphonomic variables are based on ranks, and many other distance metrics are not appropriate for rank data. To determine what factors were significant in driving the separation of the taphonomic NMDS, Wilcoxon tests were run for five of the taphonomic variables (fragmentation,

corrosion, sediment crust, presence of dendrites, and color loss). Further analyses of taphonomic data included the comparison of fragmentation between small and large shells within individual species in the two assemblages and fragmentation between species within the two units. To compare differences in fragmentation between small and large shells within the same species, the median was used as the middle point. All shells smaller than the median were classified as small for the purpose of these comparisons, and shells larger than the middle point were classified as large shells. A Wilcoxon test was used to determine if significant differences occurred between the two groups. Kruskal-Wallis was used to compare differences in fragmentation between species within an assemblage.

An analysis of similarities (ANOSIM) was used to compare differences in the preservation of adult and juvenile shells. The ANOSIM evaluated whether differences between the two groups were greater than expected by chance. Five different taphonomic variables were used in this analysis including shell fragmentation, presence of sediment crust, color loss, corrosion, and presence of dendrites. As ANOSIM results do not indicate which factors are contributing to the significant differences observed between the two assemblages, Wilcoxon tests were also run afterwards.

Lengths and widths of fossil adult shells for the same three species found in both Units A and B (*H. consobrina*, *C. aff. giustii*, *C. lenticula*) as well as modern *C. lenticula* from present day Montaña Negra were analyzed to assess potential differences in body size. Species were analyzed individually by comparing the means of each assemblage to see if there were significant differences in size between the two units and the modern. The length and width of each species was first log transformed and then bootstrapped 10,000 times using the lowest sample size for that species as the bootstrapped sample size. The observed difference in the means between the two assemblages was then compared to the distribution of the bootstrapped differences in means to determine if the observed difference was greater than expected from random chance. A p-value was calculated as the proportion of bootstrapped values that were equal to or more extreme than the observed difference in means.

All statistical analyses were run in the R statistical package (version 3.1.2, R Development Core Team, 2014) and using the Vegan Package (Oksanen et al., 2016).

2.8. Stable oxygen isotope analysis

Ten shells per fossil horizon of the cosmopolitan species *Caracollina lenticula*, and five shells of *C. lenticula* from each of the 12 modern localities were selected for whole shell oxygen isotopic analysis. Analyses of the entire shell were preferred over intrashell analyses because *C. lenticula* is a short-lived (annual) species with a small body size (<5 mm), and we sought to reconstruct the average climatic conditions rather than seasonal trends. Shells were cleaned in deionized water and scrubbed with a toothbrush to remove all organic and detrital contaminants. Entire shells were ground manually using an agate mortar and pestle. Pulverized shells were analyzed at the Center for Stable Isotopes at the University of New Mexico using the method described by Spötl and Vennemann (2003). Samples were loaded in 12 ml borosilicate exetainers, which were flushed with He and reacted for 12 h with H_3PO_4 at 50 °C. The resulting CO_2 was measured in a Gasbench device coupled to the continuous flow Isotope Ratio Mass Spectrometer (CF-IRMS) Thermo Fisher Scientific Delta V Plus. All oxygen isotopic results are reported in δ notation relative to the international standard VPDB. δ values are defined as:

$$\delta^{18}O = \left[\left({}^{18}O/{}^{16}O_{sample}/{}^{18}O/{}^{16}O_{standard}\right)-1\right] \times 1000‰$$

Reproducibility was better than 0.1‰ based on repeated measurements of the laboratory standard Carrara Marble, which was calibrated against the international standard NBS-19, for which the $\delta^{18}O$ value is −2.2‰.

3. Results

3.1. Fossil species composition and abundance

Eleven species represented by 3331 specimens were collected at Montaña Negra (Fig. 3, Table 1 in Supplementary materials). Unit A contained 189 individuals represented by three species, the large and globose *H. consobrina* (49%), the medium sized and flat *C. aff. giustii* (29%), and the small and flat *C. lenticula* (22%). Scoria Unit B contained 3142 specimens represented by the same three species found in Unit A as well as eight others (n = 11). The assemblage was dominated by *C. lenticula* (78%) with the flat, micro-snail *V. contracta* (9.6%) as the second most abundant species. When rare species, micro-snails, and semi-slugs were removed from the assemblage, Unit A's numbers were unchanged because it did not contain any micro-snails, semi-slugs, or rare species; by contrast, after excluding these taxa, Unit B was reduced to an aggregate of 6 species and 2756 specimens. Even with micro-snails removed, the two scoria units differed significantly in terms of overall abundance and species composition, resulting in a clear separation along the first axis of a NMDS (Fig. 4). Shell shapes in Unit B varied from globose (*H. consobrina*, *M. phalerata*, *X. orbignii*), to flat (*C. lenticula*, *C. aff. giustii*), to long and trochospiral (*G. dealbata*), resulting in a very different shell size and shape distribution from Unit A.

3.2. Taxonomic comparison between fossil and modern snail assemblages

A total of 12 samples represented by 23 species and 3729 individuals were collected in the present day coastal scrub biome around Tenerife (Table 3 in Supplementary material).

The sites at Montaña Negra (sites 1, 2, and 3) contained 532 specimens and five species, including two micro-snail species, along with three macro-snails, *H. consobrina*, *M. phalerata*, and *C. lenticula*, all of which were also found in fossil Unit B at Montaña Negra. Two of these three species were recovered in Unit A as well. While there was a taxonomic overlap between the present day coastal scrub biome at Montaña Negra and the Pleistocene record at the same locality, the makeup of the assemblages is very different. Unit A is dominated by *H. consobrina*, but the abundance of this species is rather low in the modern. In Unit B, *C. lenticula* dominates the assemblage with *M. phalerata* exhibiting a very low abundance. This pattern switches in the modern, and *M. phalerata* becomes the dominant species in two of the assemblages and *C. lenticula* was not recovered at one of the modern sites. The compositional differences between the modern and fossil sites are reflected by their positions in NMDS space (Fig. 5).

Other modern samples from the coastal scrub biome gathered at southern sites further from Montaña Negra (sites 4 and 5) contained, in aggregate, 833 individuals and nine species, including two micro-snails and seven macro-snails: *C. lenticula*, *F. folliculus*, *H. consobrina*, *M. phalerata*, *X. orbignii*, *N. variatus*, and *P. laevigatus*. Although there is some compositional overlap with Units A and B, their relative abundances are rather different (see Fig. 5).

The northern modern sites (6–12) contained 1845 specimens and 21 species (see Table 3 in Supplementary material), though only 12 macro-snails were included in the analyses once rare species were removed: *C. fortunata*, *C. hispidula*, *C. lenticula*, *G. dewinteri*, *H. bidentalis*, *M. persimilis*, *M. phalerata*, *N. variatus*, *N. baeticatus*, *O. lactea*, *P. laevigatus*, *X. orbignii*. These sites contained three species also recovered from Unit B, but only one found in Unit A, and the relative abundances of these species is also notably different from the fossil samples and southern modern sites, as indicated by their positions in ordination space (Fig. 5). Differences between southern and northern modern sites were driven primarily by the greater abundance of *M. phalerata*. The northern sites, in turn, are

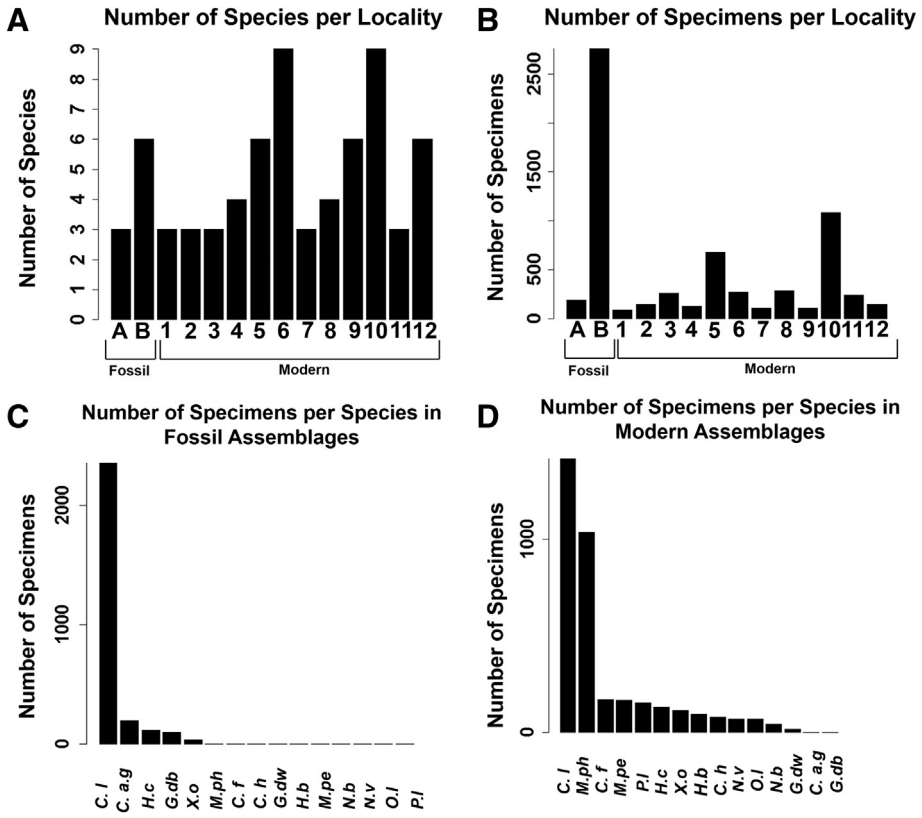

Fig. 3. A. Raw number of macro-snail species per fossil and modern localities. B. Raw number of macro-snail shells per locality. C. Raw number of specimens for each of the fifteen macro-snail species found in both the fossil and modern assemblages. D. Raw number of specimens for each of the fifteen macro-snail species found in both the fossil and modern assemblages. Key: *C.f* is *C. fortunata*, *C.a.g* is *C. aff. giustii*, *C.h* is *C. hispidula*, *C.l* is *C. lenticula*, *G.db* is *G. dealbata*, *H.b* is *H. bidentalis*, *H.c* is *H. consobrina*, *M.pe* is *M. persimilis*, *M.ph* is *M. phalerata*, *N.b is N. baeticatus*, *N.v* is *N. variatus*, *O.l* is *O. lactea*, *P.l* is *P. laevigatus* and *X.o* is *X. orbignii*.

further distinguished from one another primarily along axis 2 in NMDS, but with no clear geographic signal (e.g., east versus west).

3.3. Taphonomy

Differences in preservation between the two units (Table 2 in Supplementary materials) were also compared using NMDS (Fig. 6). Clear separation along the first axis was apparent, and was mostly driven by shell fragmentation ($p = 0.002$), and presence of sediment crust ($p = 0.008$) as determined by a Wilcoxon Test. Corrosion, color loss, and presence of dendrites were not significantly different for the two units (Fig. 7). Comparisons between large and small shells within species in B showed that no size was preferentially more fragmented than the other for any of the species. Wilcoxon tests looking at the comparisons between large and small shells within species in A showed that smaller shells were preferentially more fragmented for two species, *C.*

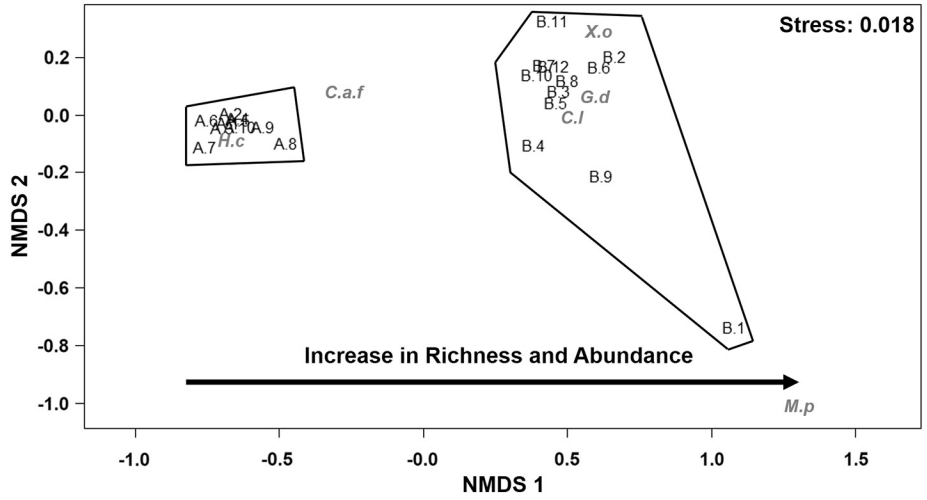

Fig. 4. Non-metric Multidimensional Scaling (NMDS) of Units A and B based on species abundance of six macro-snail species. Key to species: *H.c* is *Hemicycla consobrina*, *C.a.f* is *Canariella aff. giustii*, *X.o* is *Xerotricha orbignii*, *G.d* is *Gibbulinella dealbata*, *C.l* is *Caracollina lenticula*, and *M.p* is *Monilearia phalerata.*

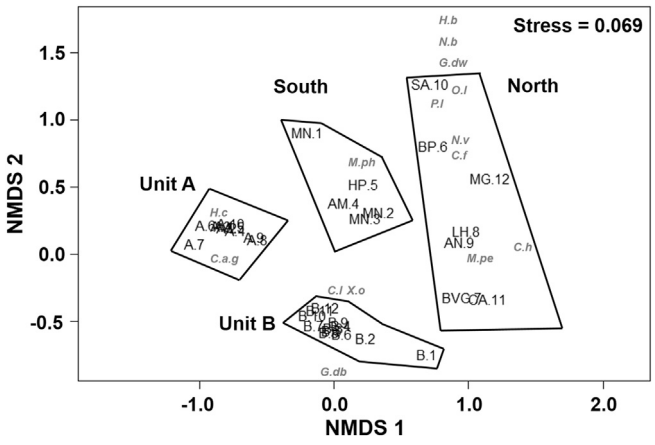

Fig. 5. NMDS showing the ordination of species abundance data for Pleistocene Scoria Units A and B, along with northern and southern modern localities representing the coastal scrub biome.

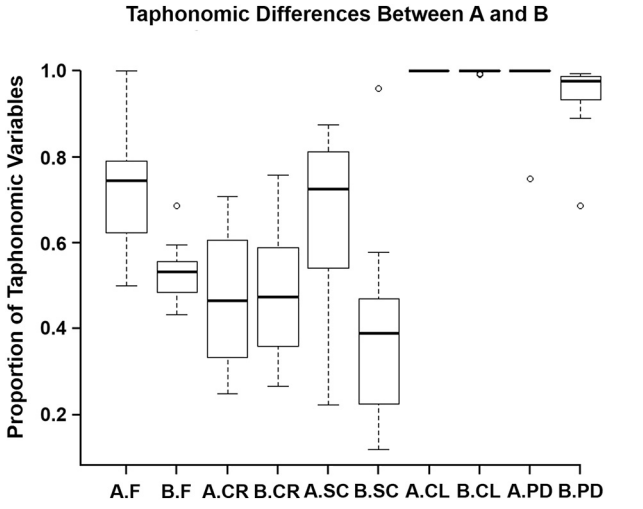

Fig. 7. Differences in shell preservation between Units A (A) and B (B). F is fragmentation, CR is corrosion, SC is sediment crust, CL is color loss, PD is presence of dendrites. Values closer to 1 indicate more alteration of shell while 0 is more pristine.

lenticula ($p = 0.001$) and *H. consobrina* ($p = 0.0001$), but not for *C. aff. giustii* ($p = 0.11$). The proportion of fragmentation of all species within Units A and B were statistically comparable (Fig. 8).

Juveniles were only present in Unit B. Preservation for adults and juveniles in Unit B was also compared using univariate analyses and ANOSIM (Fig. 9) based on the same five taphonomic characteristics. Results from the ANOSIM indicate a difference in the preservation of adults and juveniles ($R = 0.159$, $p < 0.001$) with adults having a higher proportion of occurrence for all five taphonomic variables, though occurrence of a sediment crust returns the only significant difference ($p = 0.007$) when a Wilcoxon test is run between adults and juveniles for all five taphonomic characteristics.

3.4. Body size

Shells of the three species present in Scoria Units A and B (*Caracollina*, *Hemicycla*, and *Canariella*) were similar in terms of length and width (Fig. 10). However, the aggregate distribution of shell shapes and body size of the snail community as a whole was different between the two horizons (Fig. 11). While species shared by the two assemblages had similar distributions on the best fit line, albeit with many more individuals in Unit B, the three additional species in Unit B occupy a different part of morphospace than Unit A (Fig. 11). Overall, Unit A is dominated by larger (>10 mm), globose species, while Unit B contains several smaller (<5 mm), elongate species.

While the shell sizes of *C. lenticula* were statistically indistinguishable between Units A and B, length and width of individuals from both of these Pleistocene units were significantly different than present day specimens from Montaña Negra. Modern shells exhibited a significantly larger length ($p = 0.0037$ for A, $p < 0.001$ for B) and width ($p < 0.001$ for A and $p < 0.001$ for B) when compared to the fossil individuals (Fig. 12) using the bootstrap method and a two-tailed *t*-test.

3.5. Oxygen stable isotopes

Entire shell stable oxygen isotope values of *C. lenticula* from Montaña Negra suggest that local climate has varied from the Pleistocene to the present (Fig. 13). On average, oxygen isotope values are more negative in Unit A (Avg. $\delta^{18}O = -2.3 \pm 0.7‰$; $n = 10$), and they gradually become more positive towards Unit B (Avg. $\delta^{18}O = -1.5 \pm 0.9‰$; $n = 10$), reaching the highest values in modern shell samples from Montaña Negra (Avg. $\delta^{18}O = -0.8 \pm 0.9‰$; $n = 5$). Thus, an increase of ~3‰ in $\delta^{18}O$ values is documented in the snail shells from ~302 ka to the

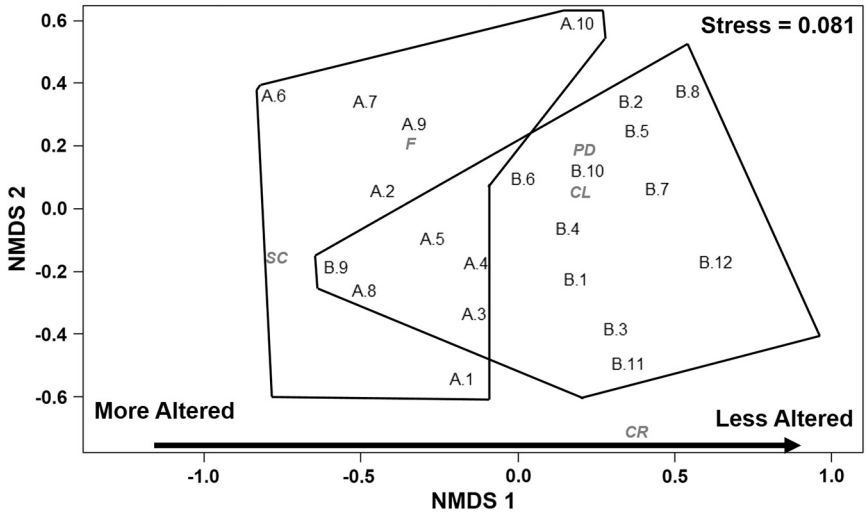

Fig. 6. NMDS of five taphonomic variables examined in land snail shelly assemblages retrieved from Pleistocene Units A and B. F is proportion of fragmented shells, SC is proportion of shells with a sediment crust, PD is proportion of shells with presence of dendrites, CL is proportion of shells with color loss, and CR is proportion of shells that are corroded.

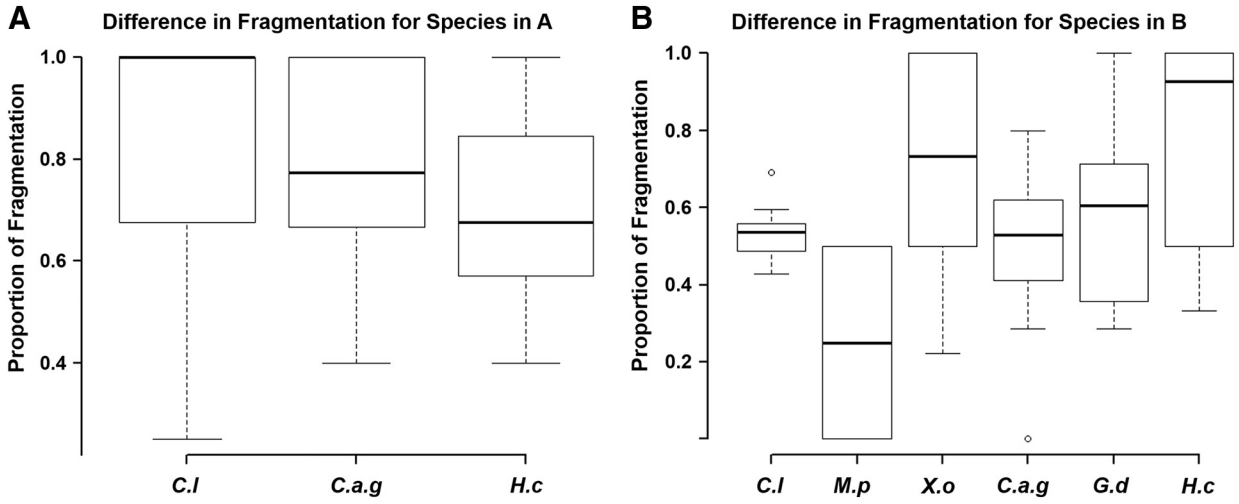

Fig. 8. Difference in fragmentation for land snail species separately by fossil Unit. A. Three species in A. *C.l* is *Caracollina lenticula*, *C.a.g* is *Canariella aff. giustii*, *H.c* is *Hemicycla consobrina*. B. Six species in B. *M.p* is *Monilearia phalerata*, *X.o* is *Xerotrichia orbignii*, *G.d* is *Gibulinella dealbata*.

present. A published modern calibration study on Tenerife showed that more negative shell $\delta^{18}O$ values reflect colder/wetter conditions while higher values indicate warmer/drier conditions (Yanes et al., 2009). Thus, Unit A was characterized by colder/wetter conditions with a transition to somewhat warmer/drier conditions in Unit B. The snails also record a significantly warmer/drier signal today than for either Pleistocene horizon, pointing to a noticeable climate change not only between the two Pleistocene units, but also from the Pleistocene to the present interglacial.

4. Discussion

4.1. How did snails die and get preserved in volcanic scoria deposits?

The process through which the specimens investigated here became preserved in this volcanic sequence remains unclear. It is possible that snails and other organisms colonized the newly formed substrate shortly after the volcanic event, when clasts settled and cooled. Subsequently, snails may have then died and fallen among the spaces and cavities of the scoria, accumulating over time. When the next volcanic event occurred, the living snail assemblage was then massively killed, but probably not preserved. It is difficult to envision that snail shells could have survived the volcanic event on the ground surface. Instead, only those dead shells already encased below the ground surface were likely to have survived successive volcanic eruptions.

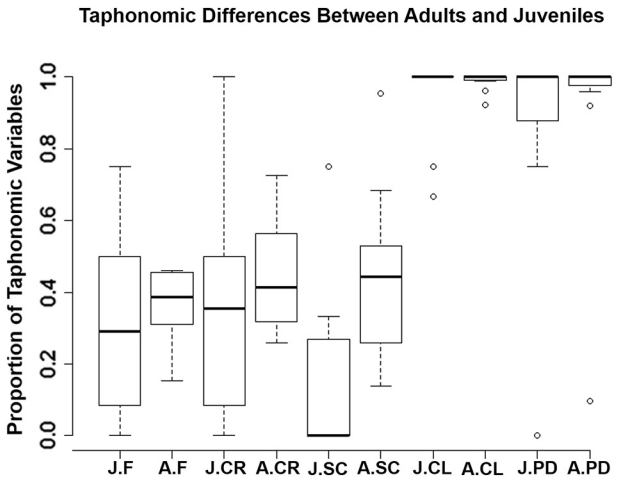

Fig. 9. Boxplots showing the difference in the degree of taphonomic alteration between adult and juvenile shells of the same land snail species. Key: J is juvenile and A is adult, F is proportion of fragmented shells, CR proportion of corroded shells, SC is proportion of shells with a sediment crust, CL is proportion of shells with color loss, PD is proportion of shells with presence of dendrites.

4.2. Effects of taphonomic processes on species composition, abundance, and preservation

The difference in composition, abundance, and preservation between the fossil assemblages of Units A and B (Figs. 4, 6, 11) may result from different environmental factors, but, unlike marine and fluvial systems, environmental energy by wind or water is unlikely to have driven the observed patterns.

4.2.1. Clast size

There is a distinct separation of Units A and B in terms of shell abundance (Figs. 3, 4, 11) and taphonomic condition (Figs. 6, 7), with higher abundance and better preservation of land snails in B than in A. Shells in Unit A show higher fragmentation and more presence of a sediment crust than shells in Unit B (Fig. 7). While Unit A lacks any fine sediment, Unit B has a layer of fine grained matrix at its base and an unconsolidated paleosol at its top (Pannell et al., 2011). The span of this paleosol is 40 cm and contained the highest number of species and individuals within Unit B (see also Pannell et al., 2011). The marked drop in species and abundance from Unit B (6 species, 2756 specimens) to Unit A (3 species, 189 specimens) may be driven, at least in part, by a change from smaller scoria clasts and a fine grained paleosol in B to larger scoria clasts in A. Similar findings showing a reduction in shell abundance from Unit B to A were documented previously by Pannell et al. (2011). This suggests that clast size may play a role in mediating shell abundance, with finer sediment enhancing the preservation of more land snail specimens relative to courser scoria clasts. The higher degree in shell fragmentation observed in Unit A may therefore be associated with coarser scoria clasts. While marine and fluvial studies usually document higher abundance and better preservation in finer grained matrices, this is primarily driven by the energy of the environment, and not by the preservational matrix itself (Brett, 1995; Briggs et al., 1990). However, marine studies conducted in low energy, tropical environments have found that substrate type, i.e., fine sediment or hard substrata, have more of an impact on preservation potential. When

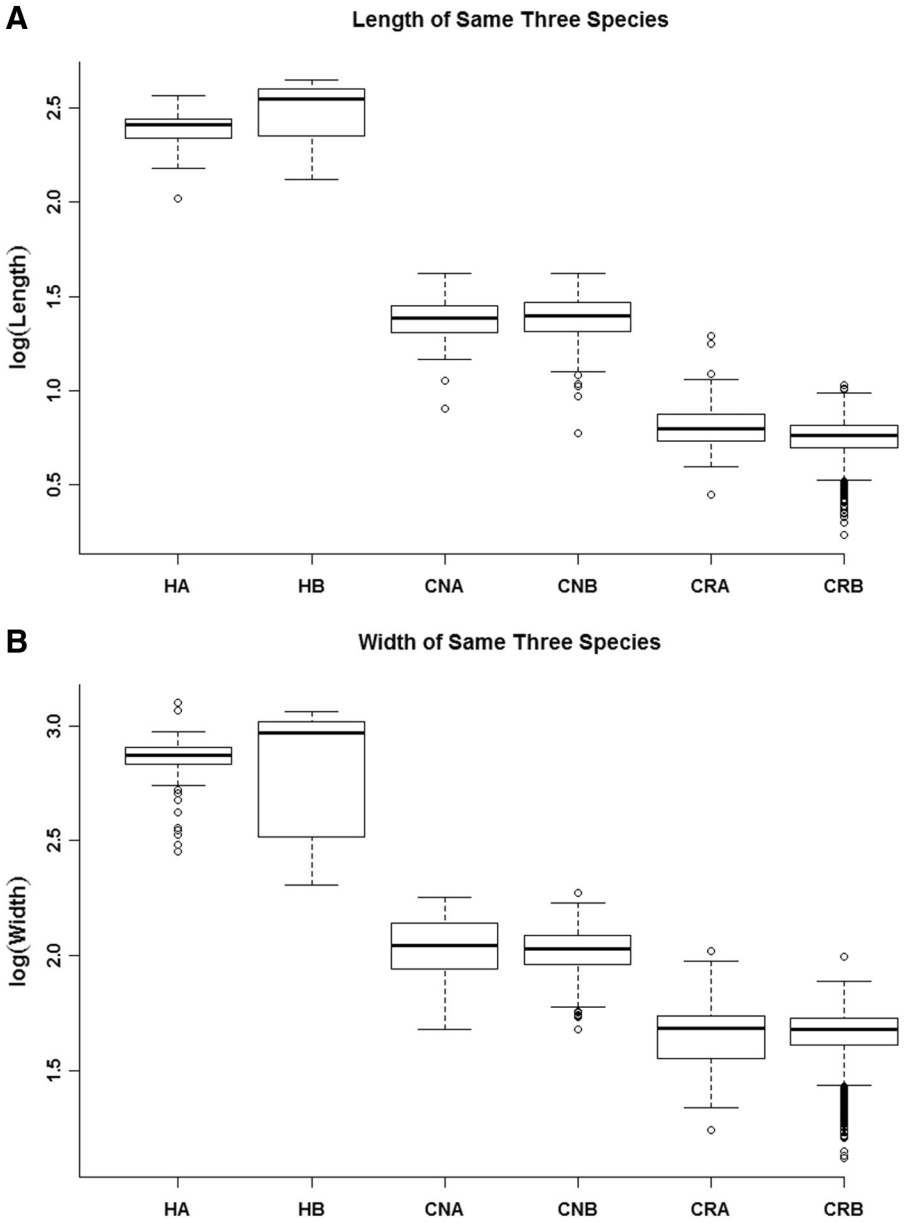

Fig. 10. Boxplots showing log-transformed length (A) and width (B) of three species that were preserved in both units. Key: HA is *Hemicycla consobrina* of Unit A, HB is *Hemicycla consobrina* of Unit B, CNA is *Canariella aff. giustii* of Unit A, CNB *is Canariella aff. giustii* of Unit B, CRA is *Caracollina lenticula* of Unit A, and CRB is *Caracollina lenticula* of Unit B.

environmental energy is low, substrates dominated by fine sediments further enhance shell preservation relative to hard substrate or gravely matrix (Best and Kidwell, 2000). Longer intervals of shells exposure in larger clast matrix result in greater destruction rates (Best and Kidwell, 2000). In Montaña Negra, environmental energy is not likely to be a destructive factor because of the lack of aqueous media, but variations in clast size could still explain the observed patterns. Fine sediments forming the Pleistocene paleosols in the semi-arid easternmost Canary Islands often lead to excellent preservation of land snails because their high calcium carbonate content, along with the high degree of bioturbation by hymenopterids and coleopterids, which enhances evaporation and carbonate precipitation rates, both result in better preservation of shells (Yanes et al., 2008, 2011b). Along with personal field observations during 2015, these findings suggest that scoria clasts, which are larger and more angular, provide an uneven surface, which leave snail shells more exposed to biostratinomic and diagenetic agents. Thus, snail fossils preserved in sediments with coarser clast size are likely to exhibit lower preservation potential (higher taphonomic destructive rates) than fine grained sediments, and this may have resulted in taphonomic differences between Units A and B.

4.3. Preservation differences between adults and juveniles

Adult and juvenile shells of the six macro-species were both present in Unit B, though adults were more abundant likely due to their higher shell durability (Kowalewski et al., 1998; Tomašových, 2004) and taphonomic bias against smaller skeletal hard parts (Behrensmeyer et al., 2000; Miller et al., 2014). While this bias can be observed (see Table 2 in Supplementary materials), macro-snail species were represented by several juvenile counterparts. Juvenile shells were generally pristine (Fig. 9) as observed in some previously published studies (Tomašových, 2004; Yanes et al., 2008). While adults exhibited higher taphonomic alteration, only one taphonomic feature, sediment crust, is primarily driving this difference. This may be associated with a higher residence time of adult shells in the taphonomically active zone, whereas the fragile shells of juveniles experienced accelerated decay rates

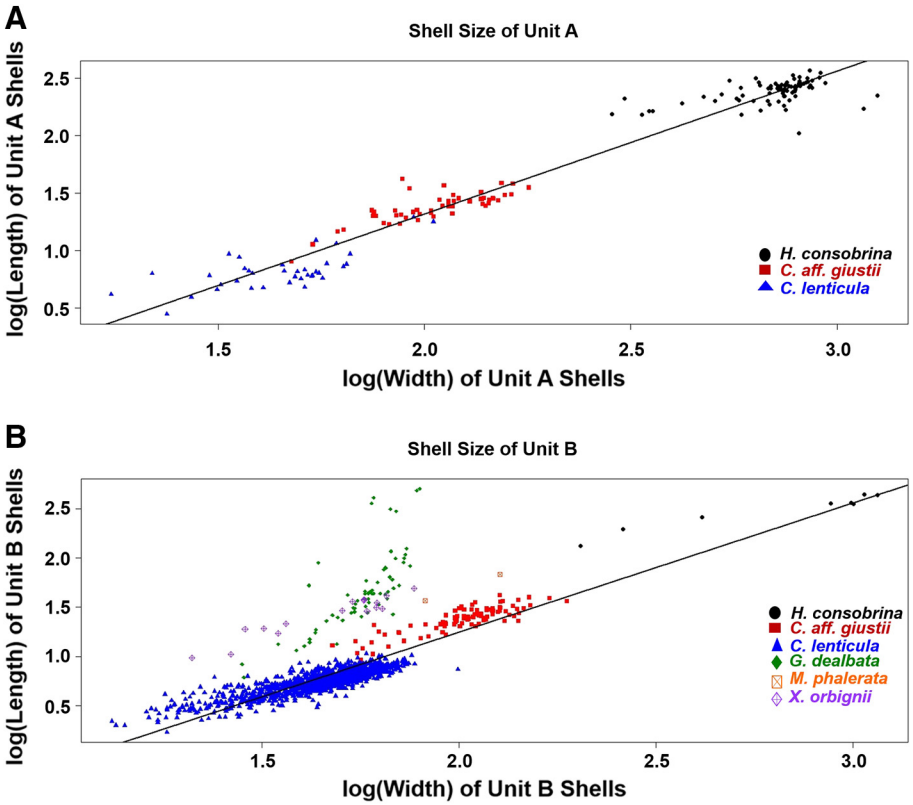

Fig. 11. Graphs showing the log-transformed length and width of adult macro-shells in Pleistocene Units A and B. Solid line depicts the linear model for length against width. A. Three macro-snails from Unit A. B. Six macro-snails from Unit B.

(Kowalewski et al., 1998; Tomašových, 2004). Juveniles either get preserved as they are, implying a rapid "trip" through the taphonomically active zone, or they do not survive at all.

4.4. Body size differences

Adult body sizes of the species present in both Units A and B were statistically indistinguishable (Fig. 10), which suggests that potential differences in climate did not affect snail growth rates or lifespan between ~302 and ~299 ka (Fig. 13). Nevertheless, the snail community preserved in Unit A (with a larger scoria clast matrix) was dominated by larger body size snails whereas the assemblage in Unit B (with a smaller clast matrix) was rich in juveniles and smaller, more elongate species not found in Unit A (Fig. 11).

Interestingly, Pleistocene *C. lenticula* shell size is statistically smaller than modern individuals of the same species at Montaña Negra (Fig. 12). This may be explained by climate change, which has been identified in the oxygen stable isotopes of the snail shells. Pleistocene snails appear to have lived under significantly colder/wetter conditions than present day counterparts. It is possible that an increase in aridity at present day and the need to conserve water plays a role in determining ultimate snail shell size, and thus *C. lenticula* seems to have responded to this shift in climate by increasing the length and width of its shell, which will decrease its surface area to volume ratio and thus increase its water retention (Nevo et al., 1983).

4.5. Climate change

The oxygen stable isotope values of land snail shells reflects a significant climate change from ~302 ka ($\delta^{18}O = \sim -2.2$) in comparison to the present ($\delta^{18}O = \sim -0.8$) in southern Tenerife (Fig. 13), pointing to significantly cooler/wetter conditions during MIS 8 than today. These results are consistent with findings by Yanes et al. (2011b, 2013) for the easternmost Canary Islands (Lanzarote and Fuerteventura), where Pleistocene land snails recorded significantly cooler/wetter conditions than today. The inferred Pleistocene colder/wetter scenario here is in good agreement with other published proxy data in nearby regions. Data collected from deep sea cores within the Canary Basin show a compositional change in planktonic foraminifera with tropical and subtropical forms disappearing around 307–301 ka (Jansen et al., 1986). This suggests that a change in ocean and atmospheric circulation had already begun within the basin, with a possible enhancement of the advection of cool eastern water masses due to an increase in the strength of the trade winds which would have moved the cool northern surface water along northwest Africa (Jansen et al., 1986). This trend is highly characteristic of glacial stages (Jansen et al., 1986), and indicates that the transition from interglacial to glacial was potentially well underway when the fossil assemblage at Scoria Unit A was forming. This is further supported by pollen and oxygen isotope data from benthic foraminifera from the northwestern Iberian margin, which also point to a significant cooling trend at the end of MIS 9 and into MIS 8 (Desprat et al., 2009), matching with the lowest $\delta^{18}O$ values of snail shells from Scoria Unit A. Our stable isotope data from snails preserved at Scoria Unit B suggest conditions were warmer/drier than during Unit A, but cooler/wetter than today.

The climatic transition from wetter in the oldest assemblage, Unit A, to warmer and drier in Unit B and compared to today (Fig. 13) could have impacted snail communities, both directly through altering the species assemblages and indirectly by enhancing different biostratinomic and diagenetic processes. Changes in the amount of precipitation, temperature, and the ambient plant assemblage can have a great impact on snail communities (Baur and Baur, 2013; Cameron et al., 2010). The significant difference in climate between MIS 8 (glacial) and today (interglacial) may have caused snails either to become

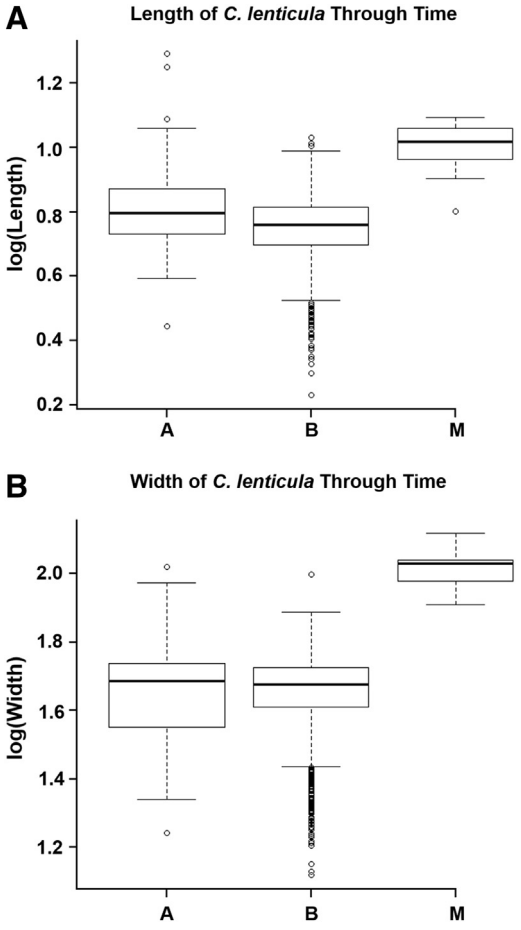

Fig. 12. Boxplots showing log-transformed length (A) and width (B) of all measured adult specimens of *Caracollina lenticula* for Pleistocene Unit A, B, and the present-day, all from Montaña Negra locality. Bootstrapped sample size for two-tailed *t*-test was based on 14 individuals. Key: A is Unit A, B is Unit B, and M is modern assemblages at Montaña Negra.

extirpated or move to different parts of the island or to different altitudes to maintain their preferred environmental conditions (Baur and Baur, 2013).

Additionally, the cooler/wetter conditions during the interval represented by Unit A could have enhanced shell dissolution, leading to higher rates of destruction and ultimately the disappearance of smaller/thinner shells (Figs. 8, 11).

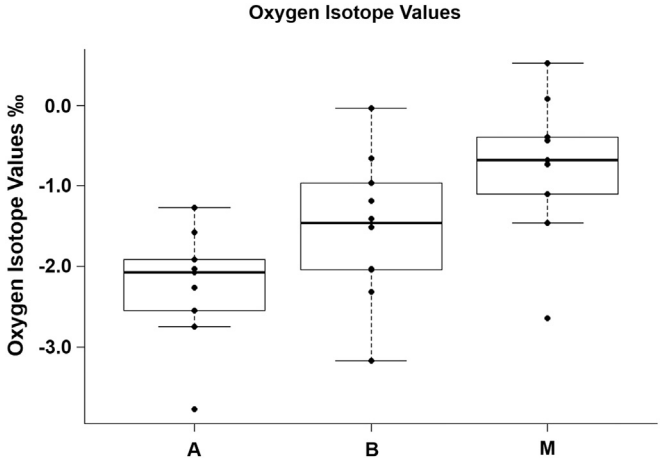

Fig. 13. Stable oxygen isotope values of fossil and modern land snail shells from Montaña Negra. Key: A is Unit A, B is Unit B, and M is the pooled isotope values of modern snail assemblages adjacent to Montaña Negra.

4.6. Evidence for preservation of an ecological signal

While taphonomic factors likely contributed to compositional differences between Units A and B, these differences should also reflect an ecological signal.

4.6.1. Ecological preservation of Unit B

Relative to Unit A, Unit B is a tightly constrained (302 ± 7 ka–299.9 ± 11.4 ka) interval richer in land snail species, with high abundance of shells, the preservation of various ontogenetic stages, both adults and juveniles, and the preservation of various shell size classes and shapes (Figs. 4, 6, 7, 11). The preservation of both adults and juveniles and multiple shell size classes and shapes (Figs. 7, 11) suggests that taphonomic destruction was minor for this assemblage (Tomašových, 2004). This is supported by the observation that the most abundant species was the small size *C. lenticula*, and not the larger *H. consobrina* which would be expected to dominate the assemblage if destructive taphonomic processes were at play, as taphonomic bias often more severely affects smaller/thinner shells (Behrensmeyer et al., 2000). The lack of significant taphonomic overprint suggests that Unit B is probably retaining an ecological signal in at least this respect.

4.6.2. Ecological preservation of Unit A

Unit A has limited temporal constraint, though the assemblage is capped by the Lower Aldea Blanca (dated at 302 ± 7 ka). It has a lower shell abundance and diversity than Unit B (Figs. 3, 11) and is more taphonomically altered (Figs. 6, 7). While the assemblage appears to be taphonomically biased towards larger species and lower diversity (Fig. 11, Table 1 in Supplementary materials), variations in climate may have had an impact as well. The difference in climate between Units A and B (Fig. 13) may have had profound effects on species compositions and density (Baur and Baur, 2013; Cameron et al., 2010).

4.7. Taxonomic comparison between fossil and modern snail assemblages

Units A and B were distinct from all modern assemblages in the coastal scrub around Tenerife (Fig. 5). This may have been expected, as the fossil assemblages at Montaña Negra represent a glacial (cooler) period, while we are now in an interglacial (warmer) period.

Modern sites near Montaña Negra (Fig. 1A, sites 1–3) were similar in species richness to Unit A, as both contained the three macro-snail species *Hemicycla consobrina*, *Monilearia phalerata*, and *Caracollina lenticula*. Unit B contained additional macro-snail species not present in modern sites at Montaña Negra. While the species living at Montaña Negra today are also preserved in the fossil assemblages, both fossil Units had different relative abundances. The modern sites at Montaña Negra are dominated by *M. phalerata*, while *C. lenticula* and *H. consobrina*, the two species that dominate Units B and A respectively, were far less abundant. Also, *C. aff. giustii* was absent from the modern localities altogether, as was *G. dealbata*. This decrease in species is not observed at other southern or northern sites. In the southern sites (4, 5), six macro-snail species are part of the assemblage (Table 3 in Supplementary materials) and four are shared by Unit B, and two by Unit A. The number of species in the northern sites (6–12) is higher than the fossil assemblages, with 14 macro-snail species.

These differences in species composition almost certainly reflect differences in climate. Oxygen isotope data extracted from the snail shells themselves indicate that conditions during MIS 8 were significantly colder/wetter than at present in southern Tenerife. Hence, it is likely that the fossil snail community was associated with cooler/wetter conditions not found today in the coastal scrub, even in the northern (cooler/wetter) part of the island. It is possible that modern snail communities at higher altitudes and in different biomes may exhibit compositions closer to what is preserved in the fossil record. Such a movement of land snails to higher altitudes to maintain their preferred

climate and plant community has been documented in Swiss National Park in the Eastern Alps (Baur and Baur, 2013).

That said, it is possible that no modern analogue can be found on Tenerife in the present day, even at a higher altitude and in a cooler, wetter biome. Given the likelihood that snail species responded individualistically to the changes in climate (Parmesan, 2006), and thus it may not be possible to find a matching community to the fossil record. For example, four of the macro-snails found in Unit B occur in the present day coastal scrub, but two species, *C. aff. giustii* and *G. dealbata* are completely absent from any of the samples. There is also evidence for possible adaptation to the change in temperature and aridity from the Pleistocene to today with the enlarging of the shells of *C. lenticula*, and its presence at Montaña Negra today, though the species is far scarcer in the sites near Montaña Negra and the south than in the fossil record. Regardless, snail communities have experienced a significant change from the Pleistocene to present, and likely responded to changes in local climate.

5. Conclusions

Land snails collected from two Scoria Units (A and B) in a Pleistocene cinder cone in Tenerife (Canary Islands) were investigated, analyzing taxonomy, shell abundance, body size, taphonomy, and isotope geochemistry to examine if and how taphonomic and climatic processes impacted shelly assemblages through time.

Snail assemblages from Unit A (~302 ka) had lower diversity and abundances, were more taphonomically altered, and dominated by larger sized shells than Unit B (~299 ka). Considering that Unit A has a sediment matrix with significantly larger clast size than Unit B, it is likely that differing preservation mechanisms caused differences in ecology, with larger clast sizes associated with higher taphonomic destruction. Unit B preserves a more complete ecological signal, as evidenced by lower taphonomic alteration and more abundant and diverse snail taxa, including adult and juvenile ontogenetic stages.

Oxygen stable isotopic analyses of shells indicate that climate has shifted in southern Tenerife from colder/wetter at ~302 ka, to slightly warmer/drier at ~299 ka, to significantly hot/dry at present. The inferred climate change matches with changes in snail diversity, with modern sites around Montaña Negra decreasing in diversity in response to aridity, and two snails, *C. aff. giustii* and *G. dealbata* not present in the modern coastal scrub biome. Southern localities contain similar diversity to Montaña Negra, but contain two species not found in the fossil assemblage. Northern localities have higher diversity compared to the fossil assemblages with 12 macro-snail species total. This suggests that the Montaña Negra snail assemblages were not only impacted by taphonomic processes but also by climate change.

Comparisons between fossil and modern assemblages indicate limited compositional similarity between glacial age fossil communities and the interglacial community of the present day. This implies that the assemblage at Montaña Negra formed under climatic and environmental conditions not comparable with the coastal scrub of today.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.palaeo.2017.02.001.

Funding

This work has been funded by a 2015 Geological Society of America Graduate Student Research Grant, a 2016 Sigma Xi Grants-in-Aid of Research, and the University of Cincinnati.

Acknowledgements

We thank Alex Wall for assistance during fieldwork, field pictures, and the map included in Figs. 1 and 2; Josh Miller for his assistance on statistical analysis, data interpretation, and comments on the manuscript; Miguel Ibáñez and María Rosario Alonso for help with taxonomic identification; Michal Kowalewski for assistance and implementation and understanding of statistical analyses for taphonomic data; Viorel Atudorei (Univ. of New Mexico) for assistance with stable isotope analyses; and Samantha Tallman for laboratory assistance. Special thanks goes to G. Cadee, Martin Zuschin and the editors of PPP for providing numerous detailed and critical comments that improved the quality and clarity of this study.We thank Alex Wall for assistance during fieldwork, field pictures, and the map included in Figs. 1 and 2; Josh Miller for his assistance on statistical analysis, data interpretation, and comments on the manuscript; Miguel Ibáñez and María Rosario Alonso for help with taxonomic identification; Michal Kowalewski for assistance and implementation and understanding of statistical analyses for taphonomic data; Viorel Atudorei (Univ. of New Mexico) for assistance with stable isotope analyses; and Samantha Tallman for laboratory assistance. Special thanks goes to G. Cadee, Martin Zuschin and the editors of PPP for providing numerous detailed and critical comments that improved the quality and clarity of this study.

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