University of Cincinnati

Date: 7/13/2016

I, Elizabeth Bullard, hereby submit this original work as part of the requirements for the degree of Master of Science in Geology.

It is entitled:

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

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

A thesis submitted to the graduate school of the University of Cincinnati in partial fulfillment of
the requirements for the degree of

Master of Science

In the Department of Geology
of the College of Arts and Sciences

by

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B.S., Muskingum University, 2012

July 2016

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Abstract

Fossil assemblage faunal compositions may vary through space and time in response to climatic and/or taphonomic factors, but these relationships can be difficult to diagnose and disentangle. Here, we investigate how to disentangle climatic and taphonomic signals of a land-snail-rich volcanic scoria sequence to assess if it was influenced by taphonomic bias, climate change, or both, using a multifaceted approach, combining taphonomic, ecological, body-size, and stable-isotope data. Fossil assemblages were sampled from two beds (Units A and B) in a Pleistocene 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 distributions. The upper unit, B (6 species), showed higher snail diversity and shell concentration and lower taphonomic alteration than the lower unit, A (3 species). Furthermore, larger bodied species (length>10mm) dominated Unit A and were better preserved than smaller species (length<10mm), whereas smaller individuals were more abundant (and better preserved) at Unit B. These differences were likely impacted by physical differences in the matrices surrounding the fossils. Unit A is comprised of larger scoria while Unit B contains small-to-medium-sized scoria and fines upward into a paleosol. Grain size of the scoria matrix therefore seems to affect species preservation, with larger clasts exposing snails to more severe postmortem agents and thus favoring the interstitial preservation of larger-size taxa. 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. Shell oxygen isotope values reveal that the climate shifted from colder/wetter during MIS 8 to warmer/drier at present, which may explain variations in species composition and diversity through time. These data suggest that both taphonomic and climatic factors have

induced these snail patterns in deep time, but quantifying which of these two mechanisms has more significantly influenced the observed results remains uncertain.

Acknowledgements

This work has been funded by grants from the Geological Society of America, Sigma Xi Grants-in-Aid of Research, and the University of Cincinnati.

I would like to thank my advisors, Yurena Yanes and Arnie Miller for their constant support and encouragement both academically and otherwise. Special thanks goes to Alex Wall for assistance during fieldwork and for generously providing some field pictures and the geographic location map included in figures 1 and 2 of this document. Additional thanks go to my committee member, Josh Miller, for his assistance on statistical analysis and data interpretation, and for providing many useful comments. Thanks also go to Miguel Ibáñez and María Rosario Alonso for help with taxonomic identification of land snails, Michal Kowalewski for his assistance with implementation and understanding of statistical analyses for taphonomic data, and Viorel Atudorei (Univ. of New Mexico) is thanked for stable isotope analyses. Finally, I would like to thank my fellow graduate students: Kelsey Feser, Andrew Zaffos, Wesley Parker, Allison Young, Yeon Jee Suh, Jani Sparks, and Liz Haussner for their constant input and discussion as well as unending support and encouragement during this project.

Table of Contents

Acknowledgements.....	iii
List of Figures.....	vi
List of Tables.....	vii
1.1 Abstract.....	1
1.2 Introduction.....	2
1.3 Methods.....	4
1.3.1 Geographical and environmental setting.....	4
1.3.2 Study site and sampling protocol.....	5
1.3.3 Taphonomy and ecology of fossil and modern land snail shells.....	8
1.3.4 Body size measurements.....	10
1.3.5 Statistical analyses.....	10
1.3.6 Stable oxygen isotope analysis.....	12
1.4 Results.....	13
1.4.1 Fossil species composition and abundance.....	13
1.4.2 Taxonomic comparison between fossil and modern snail assemblages.....	15
1.4.3 Body size.....	21
1.4.4 Oxygen stable isotopes.....	25
1.5 Discussion.....	26
1.5.1 Effects of taphonomic processes on species composition, abundance, and preservation.....	26
1.5.2 Preservation differences between adults and juveniles.....	28
1.5.3 Body size differences.....	29

Table of Contents Continued

1.5.4 Climate change.....	29
1.5.5 Evidence for preservation of an ecological signal.....	31
1.5.6 Taxonomic comparison between fossil and modern assemblages.....	32
1.6 Conclusions.....	34
References.....	36
Supplementary Materials.....	41

List of Figures

1.1 Geographic location and study site.....	5
1.2 Sampling method overview.....	6
1.3 Abundance of species in modern and fossil sites.....	14
1.4 NMDS of fossil assemblages' species and abundance.....	15
1.5 NMDS of fossil and modern assemblages.....	17
1.6 NMDS of preservation for fossil assemblages.....	18
1.7 Results of Wilcoxon tests for differences in taphonomy for fossil assemblages.....	19
1.8 Results of Kruskal-Wallis test for differences in fragmentation in two fossil assemblages.....	19
1.9 Results of ANOSIM and Wilcoxon tests for differences in preservation between adult and juveniles.....	20
1.10 Shell size distributions.....	22
1.11 Shell shape distributions.....	23
1.12 Shell size comparison for fossil and modern.....	24
1.13 Results of oxygen stable isotope analysis for changes in climate from Pleistocene to present.....	25

List of Tables

1.1 Table of taxonomy and abundance for fossil sites, present-day southern sites, and present-day northern sites.....	41
1.2 Table of taphonomic proportions used for analyses.....	42
1.3 Table of taxonomy and abundance for modern sites around Tenerife.....	42

1.1 Abstract

Fossil assemblage faunal compositions may vary through space and time in response to climatic and/or taphonomic factors, but these relationships can be difficult to diagnose and disentangle. Here, we investigate how to disentangle climatic and taphonomic signals of a land-snail-rich volcanic scoria sequence to assess if it was influenced by taphonomic bias, climate change, or both, using a multifaceted approach, combining taphonomic, ecological, body-size, and stable-isotope data. Fossil assemblages were sampled from two beds (Units A and B) in a Pleistocene 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 distributions. The upper unit, B (6 species), showed higher snail diversity and shell concentration and lower taphonomic alteration than the lower unit, A (3 species). Furthermore, larger bodied species (length>10mm) dominated Unit A and were better preserved than smaller species (length<10mm), whereas smaller individuals were more abundant (and better preserved) at Unit B. These differences were likely impacted by physical differences in the matrices surrounding the fossils. Unit A is comprised of larger scoria while Unit B contains small-to-medium-sized scoria and fines upward into a paleosol. Grain size of the scoria matrix therefore seems to affect species preservation, with larger clasts exposing snails to more severe postmortem agents and thus favoring the interstitial preservation of larger-size taxa. 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. Shell oxygen isotope values reveal that the climate shifted from colder/wetter during MIS 8 to warmer/drier at present, which may explain variations in species composition and diversity through time. These data suggest that both taphonomic and climatic factors have

induced these snail patterns in deep time, but quantifying which of these two mechanisms has more significantly influenced the observed results remains uncertain.

1.2 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., Brett 1995; Meldahl et al. 1997; Kowalewski et al. 1998; Behrensmeyer et al. 2000; Kidwell 2001, 2002; Tomasovych 2004, 2006; Behrensmeyer et al. 2005), with far fewer studies focusing on invertebrates from terrestrial systems (Briggs et al. 1990; Carter 1990; Cadee 1999; Yanes et al. 2008, 2011a; Yanes 2012). Terrestrial Quaternary assemblages provide excellent opportunities for quantitative taphonomic investigations (Yanes et al. 2008, 2011a; Yanes 2012) because they are generally well preserved, highly abundant and often exhibit high temporal resolution, useful for assessing biotic responses to environmental and climatic 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 depositional environments (Rousseau 1991; Preece and Day 1994; Pickford 2002; Brooke et al. 2003; Balakrishnan et al. 2005; Yanes et al. 2008, 2011a; Yanes

2012a), are climatically sensitive, and have high preservation potential. 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. 2011b, 2013), and the taphonomic conditions of the shells allow for direct assessment of postmortem processes (Yanes et al. 2008, 2011a; Yanes 2012).

In this context, Tenerife, Canary Islands, is a highly suitable natural laboratory in which to study the potential impacts of climatic factors and taphonomic processes on terrestrial shelly assemblages in deep time because snails are plentiful in both the fossil record and modern ecosystems, and are accessible and well-preserved (Pannell et al. 2011).

Montaña Negra is a Pleistocene cinder cone volcano dated to Marine Isotope Stage (MIS) 8 (Pannell et al. 2011), representing 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 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 meters 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 distinct temperature

and precipitation differences occur 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 coastal scrub and the 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 taphonomic features of land snail shells preserved in a volcanic scoria matrix, (2) evaluate the potential retention of an ecological signature preserved 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.

1.3 Methods

1.3.1 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, approximately 300km from the Moroccan coast (Fig. 1 A). 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 (Fernandopulle 1976). 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 (Font 1956; 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 (Font

1956; Marzol 2001), which creates a “sea of clouds” (Font 1956; Dorta 1996). Climate data from Tenerife North Airport collected between 1981-2010 indicate a mean average temperature of $\sim 16.8^{\circ}\text{C}$, mean average rainfall of $\sim 520\text{mm}$, and an average relative humidity of $\sim 73\%$; while climate data from Tenerife South Airport collected over the same interval convey a warmer, more arid climate, with a mean average temperature of $\sim 21.4^{\circ}\text{C}$, mean average rainfall of $\sim 132\text{mm}$, and an average relative humidity of $\sim 66\%$ (Agencia Estatal de Meteorología: <http://www.aemet.es>). The coastal scrub plant biome on the island (Fig. 1 C), present at the elevation between sea level and up to $\sim 450\text{ m a.s.l.}$, reflects semi-arid conditions, dominated by plants well adapted to aridity with many native succulent plants and grasses (Fernández-Palacios and Whitaker 2008).

Figure 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.

1.3.2 Study site and sampling protocol

Montaña Negra site

Montaña Negra is a Pleistocene cinder cone volcano in the south of Tenerife (Fig. 1 B, Fig. 2). It is part of a chain of volcanoes trending north-northeast in the Bandas del Sur region (Clarke et al 2009; Brown et al. 2003). The lowest exposure is a layer of basaltic black scoria (Scoria Unit A) rich in fossilized land snails in the top 60cm. 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 $^{40}\text{Ar}/^{39}\text{Ar}$ age-dating method. This unit, in turn, is overlain by another scoria deposit, Scoria Unit B, which fines upward into an unconsolidated paleosol also rich in land snail fossils. Finally, this second 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 Scoria Unit B right at the beginning of MIS 8 (glacial interval), and Scoria Unit A possibly at the very end of MIS 9 (interglacial cycle) or beginning of MIS 8.

Figure 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.

Fossil snail collection protocol

Scoria 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 workers hand-picked *in situ* specimens of terrestrial snails for one hour at each station. 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.

Modern snail collection protocol

Modern snail samples 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. 1 A, C). Sites were chosen based on GIS maps detailing coastal scrub areas. Once a site was selected using GIS, preliminary searching was conducted to establish whether any snails were present in the area. Dead land snails were sampled in 30 x 30m plots established at each site and explored by four workers for one hour collecting all encountered specimens (Triantis et al. 2005; Cameron et al. 2013). A single worker sampled individual quadrats rather than working side-by-side in teams of two as in the sampling of fossils assemblages because land snails were not as frequently encountered in the modern settings as in the fossil assemblages. Only dead (i.e., subfossil) snails 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.

1.3.3 *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). 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 was scored as a presence/absence for seven different taphonomic variables: (1) adult or juvenile, (2) fragmentation, (3) shell corrosion, (4) presence of sediment crust, (5) color loss, (6) presence of dendrites, and (7) edge roundness. The first six variables were used for analysis, but edge roundness was removed because any shell that was fragmented had a rough edge.

Variables 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 more than 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. 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.

The six variables were tallied for each species within each station and averaged against the MNI for that species to generate a proportion (Yanes et al. 2008). In the end, however, only the three species (*C. lenticula*, *C. aff. giustii*, and *H. consobrina*) present in both units were used in the taphonomic analysis presented below, because these permitted the most direct comparisons of the preservational tendencies of the two intervals.

Modern snail assemblages from Tenerife consisted of 12 samples. 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 material field collected for this work was deposited in the same collection.

1.3.4 *Body size measurement*

Lengths and widths of shells 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 < 1.5mm), 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.

1.3.5 *Statistical analyses*

To assess within- and between-unit variations in sample compositions, Non-Metric Multidimensional Scaling (NMDS) was used to ordinate the samples in Units A and B, as well as the samples collected from the modern coastal scrub, 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 and Larson 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; Legendre and Legendre 1998; Marchant 1999). Micro-snails and semi-slugs were also removed as they were only irregularly encountered in both fossil and modern assemblages, and have fragile shells which tended to break when collected.

For numerical analyses, species abundances for each station within each unit were first square-root transformed to lower the weight of particularly abundant species and, therefore, increase the weight of species with moderate or 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, as noted earlier, and Manhattan distance was used to construct the NMDS (Yanes et al. 2008, 2011a). Manhattan distance was chosen 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 assemblages. To compare differences in fragmentation between small and large shells within the same species, the median was used as the middle point, with all shells smaller than that classified as small for the purpose of these comparisons, and shells larger than the middle point classified as large shells. A Wilcoxon test was used to determine if significant differences occurred between the two groups. To compare differences in fragmentation between species within an assemblage, a Kruskal-Wallis test was run.

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: 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 Unit 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. To make this determination, the length and width of each species within each assemblage 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. 2015).

1.3.6 *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 (<5mm), and we

sought to reconstruct the average climatic conditions rather than seasonal trends. Shells were cleaned through an iterative process of sonicating in deionized water and scrubbing with a toothbrush to remove all other matter. 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 Spotl and Vennemann (2003). Samples were loaded in 12ml borosilicate exetainers, which were flushed with He and reacted for 12 hours with H₃PO₄ at 50° C. The resulting CO₂ 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:

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

where $X = ^{18}\text{O}$ for $R = ^{18}\text{O}/^{16}\text{O}$. 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 $\delta^{18}\text{O}$ value is -2.2‰.

1.4 Results

1.4.1 *Fossil species composition and abundance*

A total of 11 species represented by 3,331 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 3,142 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 still contained three species and 189 specimens, but Unit B dropped down to six species and 2,756 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.

Figure 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*.

Figure 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 *Xerotracha orbignii*, *G.d* is *Gibbulinella dealbata*, *C.l* is *Caracollina lenticula*, and *M.p* is *Monilearia phalerata*.

1.4.2 Taxonomic comparison between fossil and modern snail assemblages

A total of 12 samples represented by 23 species and 3,729 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 we therefore documented a

compositional 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 sampled 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*. As before, there is some compositional overlap with Units A and B, i.e., four of the species in the southern sites are also present in Unit B and two in Unit A. As with the modern sites at Montaña Negra, while some of the snail species are present in both modern and fossil sites, their relative abundances are rather different (see Fig. 5).

The northern modern sites (6-12) contained 1,845 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, but the relative abundances of these species is also notably different from the fossil samples and from modern sites on the southern side of the island, 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 further distinguished from one another primarily along axis 2 in NMDS, but with no clear geographic signal (e.g., east versus west).

Figure 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.

1.4.3 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. 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).

Figure 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.

Figure 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.

Figure 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*.

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.

Figure 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.

1.4.4 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, therefore, Unit A is dominated by larger (>10mm), globose species, while Unit B contains several smaller (<5mm), 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.

Figure 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.

Figure 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.

Figure 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.

1.4.5 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. $\delta^{18}\text{O} = -2.3 \pm 0.7\text{‰}$; $n=10$), and they gradually become more positive towards Unit B (Avg. $\delta^{18}\text{O} = -1.5 \pm 0.9\text{‰}$; $n=10$), reaching the highest values in modern shell samples from Montaña Negra (Avg. $\delta^{18}\text{O} = -0.8 \pm 0.9\text{‰}$; $n=5$). Thus, an increase of $\sim 3\text{‰}$ in $\delta^{18}\text{O}$ is documented in the snail shells from $\sim 302\text{ka}$ to the present. A published modern calibration study on Tenerife showed that more negative oxygen isotope values of land snail shells 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.

Figure 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.

1.5 Discussion

1.5.1 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 myriad factors, but, unlike marine and fluvial systems, environmental energy by wind or water is unlikely to be one of them.

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. The most significant taphonomic factors driving the separation between beds are higher shell fragmentation and the presence of a sediment crust on many shells in Unit A (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 40cm 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, 2,756 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 (Briggs et al. 1990; Brett 1995). 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 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 the system observed at Montaña Negra, environmental energy is not likely to be a destructive factor because of the lack of aqueous media in this terrestrial setting, but variations in clast size could still explain the observed patterns. Fine sediments forming the Pleistocene paleosols in the semiarid easternmost Canary Islands often lead to an 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, 2011a). Based on our findings and field observations conducted during the summer of 2015, we propose that scoria clasts, which are larger and more angular, provide an uneven surface, which leave snail shells more exposed to biostratigraphic 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 impact to some extent observed differences between Units A and B in species composition and diversity.

1.5.2 Preservation differences between adults and juveniles

Adult and juvenile shells of all six macro-species were present in Unit B, although adults were significantly more abundant. This was most likely driven by the difference in shell durability (Kowalewski 1998; Tomasovych 2004) and possibly by natural taphonomic bias against smaller skeletal hard parts (Behrensmeyer et al. 2000; Miller et al. 2014). While this bias can clearly be observed within the fossil assemblage (see Table 2 in Supplementary Materials), all adult macro-snails within the assemblage had juvenile counterparts preserved. Juvenile shells did not show significant taphonomic alteration (Fig. 9), i.e., they were generally pristine, as observed in many other previously published studies (Tomasovych 2004; Yanes 2008). It is, however, interesting that while adults have an overall higher taphonomic alteration, only one taphonomic feature, sediment crust, is primarily driving this difference. It is possible that this pattern may be associated with residence time in the taphonomically active zone. Once they entered the death assemblage, juveniles were more prone to dissolution and destruction than adults because their shells are more fragile, which can greatly influence not only their abundance within a fossil assemblage, but also their residence time (Kowalewski 1998; Tomasovych 2004). Instead of accruing taphonomic alteration, juveniles might simply disappear from the assemblage altogether (Kowalewski 1998; Tomasovych 2004), which may contribute to the observed preservation of juveniles in this study – they either get preserved as they are, implying a rapid “trip” through the taphonomically active zone, or they don’t survive at all.

1.5.3 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).

1.5.4 Climate change

The oxygen stable isotope values of land snail shells reflects a significant climate change from ~302ka ($\delta^{18}\text{O} = \sim -2.2$) to the present ($\delta^{18}\text{O} = \sim -0.8$) in southern Tenerife (Fig. 13), pointing to significantly cooler/wetter conditions during the Pleistocene than today. These results are consistent with findings by Yanes et al. (2011, 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 – 301ka (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 indicate 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 indicates a significant cooling trend at the end of MIS 9 and into MIS 8 (Desprat et al. 2009), which matches well with the lowest $\delta^{18}\text{O}$ values of snail shells from Scoria Unit A.

While high-resolution paleoclimate data for this area are lacking during the beginning of MIS 8, studies from Europe and Asia indicate a cold, dry period with limited vegetation and steppe-like conditions (Sancetta & Silvestri 1984; Karkanis et al. 2008; Alexandrowicz et al. 2014; Gozhik et al. 2014; Sprafke et al. 2014). Climate reconstructions from the southwestern United States show a similar signal with the beginning of MIS 8 being cool and dry, but this pattern switched to cool and wet as time transpired (Railsback et al. 2015). 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 distinct climate regimes that we observed represented by a trend from colder and wetter in the oldest assemblage, Unit A, to a warmer and drier scenario dominating today (Fig.

13) could have impacted snail communities, both directly through altering the species assemblages and indirectly by enhancing different biostratigraphic and diagenetic processes. Changes in the amount of precipitation, temperature, and the ambient plant assemblage can have a great impact on snail communities (Aubry et al. 2005; Cameron et al. 2010; Baur and Baur 2013). The significant change from MIS 8 (glacial) to today (interglacial) may have caused snails either to become extirpated or move to different parts of the island or to different altitudes to maintain their preferred climatic and environmental condition (Baur and Baur 2013).

It is also possible that the cooler/wetter conditions during the interval represented by Unit A enhanced shell dissolution, leading to higher rates of destruction and ultimately the disappearance of smaller shells (Fig. 8, 11).

1.5.5 Evidence for preservation of an ecological signal

While taphonomic factors likely contributed to compositional differences between Units A and B, these differences may at least partly reflect an ecological signal.

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 relatively enhanced preservation of both adults and juveniles and multiple shell size-classes and shapes (Fig. 7, 11) suggests that taphonomic destruction was minor for this assemblage (Tomasovych 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 natural taphonomic bias often under-represents small 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.

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 (Fig. 3, 11) and is more taphonomically altered (Fig. 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 Unit A and B (Fig. 13) may have had profound effects on species compositions and density (Aubry et al. 2005; Cameron et al. 2010; Baur and Baur 2013). Although taphonomic bias was noticeable for the snail assemblage in Unit A, we cannot rule out the possibility that climate change also impacted the taxonomic composition and shell abundances of this Pleistocene bed.

1.5.6 Taxonomic comparison between fossil and modern snail assemblages

Both Unit 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. 1 A, 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 (6) than what is recorded 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 a very different make-

up than the modern when relative abundances are considered. 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 does not occur at other southern sites, and a completely different pattern exists in comparison to northern sites. In the southern sites (4, 5), six macro-snail species are part of the assemblage (Table 3 in Supplementary Materials). Four of these species are shared by Unit B, and two by Unit A, while two species not seen in the fossil assemblage, *N. variatus* and *P. laevigatus*, are present. The number of species in the northern sites (6-12) is higher than the fossil assemblages at Montaña Negra with 14 macro-snail species included in analyses from the samples of the northern assemblages.

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. Hence, it is likely that the fossil snail community was associated with cooler and/or 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 at Montaña Negra. 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, 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 (Bennett 1997; 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 more scarce 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 it is almost certainly in response to changes in local climate.

1.6 Conclusions

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

Snail assemblages from Unit A (~302ka) had lower diversity and abundances, were more taphonomically altered, and dominated by larger-sized shells than Unit B (~299ka). Considering that Unit A has a notably different sediment matrix than Unit B, with significantly larger clast-size, it is likely that differing preservation mechanisms impacted the observed differences in ecology. Thus, Unit B likely preserves a more complete ecological signal, as evidenced by the better preserved and more abundant and diverse assemblage, including adult and juvenile ontogenetic stages. Our findings indicate that sediments with larger clast sizes may result in higher taphonomic alteration of land snail shells, lower diversity and shell concentrations, and larger snail size classes.

Oxygen stable isotopic analyses of land snail shells indicate that climate has shifted from colder/wetter at ~302ka, to slightly warmer/drier at ~299ka, to significantly hot/dry at present in southern Tenerife. The documented climate change matches well with observed 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 any modern coastal scrub assemblage. Southern localities contain similar diversity to Montaña Negra, but contain two new species not found in the fossil assemblage. Northern localities have an increase in diversity compared to the fossil assemblages with 12 macro-snail species found at these sites. This suggests that the Montaña Negra snail assemblages were not only impacted by taphonomic processes but also by natural climate change.

Comparisons between fossil and modern assemblages suggested only limited compositional similarity between the two glacial-age fossil communities and the interglacial community of the present day. The most notable difference is the marked separation in the NMDS ordination of both fossil assemblages and the modern southern localities, particularly the locality next to Montaña Negra. As low latitude islands tend to experience subdued climatic fluctuations, it is possible that the cooler/wetter north may be more synonymous with what Montaña Negra was like during MIS 8. However, the lack of similarity with these sites implies that the assemblage at Montaña Negra formed under climatic and environmental conditions not compatible with the coastal scrub of today, although a modern analogue might exist at a higher altitude on Tenerife, within a different plant biome.

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Supplementary Material

Table 1. Taxonomy and abundance of fossil Units A and B and southern sites (1-5) and northern sites (6-12) of the present day around Tenerife.

Taxa	Unit A	Unit B	South	North
Gastropoda				
Order Pulmonata				
Family Pomatiidae				
<i>Pomatias laevigatus</i> (Webb & Berthelot, 1833)	0	0	17	138
Family Chondrinidae				
<i>Granopupa granum</i> (Draparnaud, 1801)	0	11	37	0
Family Cochlicellidae				
<i>Monilearia persimilis</i> (Shuttleworth, 1852)	0	0	0	165
<i>Monilearia phalerata</i> (Webb & Berthelot, 1833)	0	3	492	543
<i>Monilearia aff. woodwardia</i> (Mousson, 1872)	0	0	0	5
Family Enidae				
<i>Napaeus baeticatus</i> (Webb & Berthelot, 1833)	0	0	0	43
<i>Napaeus variatus</i> (Webb & Berthelot, 1833)	0	0	1	69
Family Ferussaciidae				
<i>Ferussacia folliculus</i> (Gmelin, 1791)	0	0	2	4
Family Helicidae				
<i>Hemicycla bethencourtiana</i> (Shuttleworth, 1852)	0	0	0	77
<i>Hemicycla bidentalis</i> (Lamarck, 1822)	0	0	0	96
<i>Hemicycla consobrina</i> (A. Ferussac, 1821)	92	26	131	0
<i>Hemicycla eurythra</i> (O. Boettger, 1908)	0	0	0	6
<i>Hemicycla plicaria</i> (Lamarck, 1816)	0	0	0	15
<i>Hemicycla sp.</i>	0	0	0	2
<i>Otala lactea</i> (O. F. Muller, 1774)	0	0	0	69
Family Hygromiidae				
<i>Canariella fortunata</i> (Shuttleworth, 1852)	0	0	0	171
<i>Canariella aff. giustii</i> (Ibanez & Alonso, 2006)	55	139	0	0
<i>Canariella hispidula</i> (Lamarck, 1822)	0	0	0	79
<i>Xerotricha orbignii</i> (d'Orbigny, 1836)	0	33	31	85
Family Pristilomatidae				
<i>Vitrea contracta</i> (Westerlund, 1871)	0	302	0	4
Family Pupillidae				
<i>Pupoides coenopictus</i> (Hutton, 1834)	0	4	15	0
Family Streptaxidae				
<i>Gibbulinella dealbata</i> (Webb & Berthelot, 1833)	0	97	0	0
<i>Gibbulinella dewinteri</i> (Bank, Groh & Ripken, 2002)			0	18
Family Trissexodontidae				

<i>Caracollina lenticula</i> (Michaud, 1831)	42	2458	639	774
Family Vertiginidae				
<i>Truncatellina atomus</i> (Shuttleworth, 1852)	0	5	0	0
Family Vitrinidae				
<i>Plutonia mascaensis</i> (Morales, 1987)	0	64	0	0
<i>Plutonia lamarckii</i> (A. Ferussac, 1821)	0	0	0	1
Total	189	3142	1365	2364

Table 2. Table showing taphonomic scores for same three species found in Scoria Units A and B: *H. consobrina*, *C. aff. giustii*, *C. lenticula*. MNI indicates minimum number of individuals, F is proportion of fragmented shells, CR is proportion of shells with corrosion, SC is proportion of shells with a sediment crust, CL is proportion of shells with color loss, PD is proportion of shells with dendrites. A indicates adults, J indicates juveniles, and T are total shells in the assemblage.

Unit-Station	MNI	A	J		F			CR			SC			CL			PD	
A-1	24	18	0	T	A	J	T	A	J	T	A	J	T	A	J	T	A	J
A-2	30	30	0	0.79	0.72	0	0.71	0.72	0	0.54	0.5	0	1	1	0	0.75	0.72	0
A-3	27	27	0	0.67	0.67	0	0.43	0.43	0	0.8	0.8	0	1	1	0	1	1	0
A-4	27	27	0	0.74	0.74	0	0.63	0.63	0	0.52	0.52	0	1	1	0	1	1	0
A-4	9	9	0	0.56	0.56	0	0.56	0.56	0	0.67	0.67	0	1	1	0	1	1	0
A-5	16	16	0	0.5	0.5	0	0.5	0.5	0	0.81	0.81	0	1	1	0	1	1	0
A-6	6	5	0	1	1	0	0.33	0.4	0	0.83	1	0	1	1	0	1	1	0
A-7	8	8	0	0.63	0.63	0	0.25	0.25	0	0.88	0.88	0	1	1	0	1	1	0
A-8	28	26	0	0.75	0.81	0	0.61	0.65	0	0.79	0.81	0	1	1	0	1	1	0
A-9	23	20	0	0.87	0.85	0	0.35	0.3	0	0.57	0.6	0	1	1	0	1	1	0
A-10	18	17	0	0.78	0.76	0	0.28	0.29	0	0.22	0.18	0	1	1	0	1	1	0
Total A	189	176	0	138	127	0	94	88	0	121	114	0	189	176	0	183	171	0
Mean A	18.9	17.6	0	0.73	0.72	0	0.46	0.46	0	0.66	0.68	0	1	1	0	0.98	0.97	0
B-1	100	87	5	0.5	0.46	0.4	0.58	0.54	0.6	0.46	0.53	0	1	1	1	0.99	1	0
B-2	218	213	4	0.47	0.47	0.5	0.27	0.56	0.5	0.32	0.32	0	1	0.98	1	0.99	0.98	1
B-3	194	165	13	0.44	0.4	0.23	0.6	0.59	0.46	0.43	0.5	0	1	0.99	1	0.9	0.92	0.92
B-4	218	175	8	0.54	0.45	0.5	0.44	0.41	0.38	0.48	0.53	0.25	0.99	1	1	0.89	0.97	1
B-5	389	299	4	0.56	0.42	0.75	0.38	0.40	0.25	0.24	0.28	0.25	1	0.99	1	0.98	0.99	0.75
B-6	195	126	7	0.56	0.37	0	0.34	0.27	0	0.58	0.68	0.29	1	1	1	0.69	1	1
B-7	154	95	1	0.55	0.27	0	0.51	0.42	1	0.21	0.23	0	1	1	1	0.99	1	1
B-8	211	123	1	0.53	0.36	0	0.32	0.27	0	0.12	0.14	0	1	1	1	0.97	1	1
B-9	281	157	3	0.69	0.46	0.33	0.54	0.5	0.33	0.96	0.96	0	1	1	1	0.98	1	1
B-10	223	136	2	0.6	0.35	0.5	0.43	0.37	0	0.35	0.4	0	1	0.99	1	0.99	0.99	1
B-11	293	191	4	0.43	0.15	0.25	0.76	0.71	0.5	0.44	0.48	0.75	1	0.93	0.75	0.99	1	1
B-12	147	88	6	0.52	0.25	0.17	0.7	0.73	0.17	0.16	0.17	0.33	0.99	1	0.67	0.98	1	0.83
Total B	2626	1855	58	1406	699	18	1260	824	20	1068	813	10	2621	1834	55	2483	1829	50
Mean B	218.6	154.6	4.8	0.53	0.37	0.3	0.49	0.45	0.35	0.40	0.44	0.16	0.99	0.99	0.95	0.94	0.99	0.88

Table 3. Taxonomy and abundance of land snail species recovered from the present-day coastal scrub plant biome around Tenerife Island.

Taxa	1	2	3	4	5	6	7	8	9	10	11	12
<i>Pomatias laevigatus</i>	0	0	0	0	17	4	0	0	0	119	0	15
<i>Granopupa granum</i>	13	8	1	5	10	0	0	0	0	0	0	0
<i>Monilearia persimilis</i>	0	0	0	0	0	21	25	116	3	0	0	0
<i>Monilearia phalerata</i>	80	80	58	28	246	0	0	85	1	449	0	8
<i>Monilearia aff. woodwardia</i>	0	0	0	0	0	0	0	0	0	5	0	0

<i>Napaeus baeticatus</i>	0	0	0	0	0	11	0	0	0	32	0	0
<i>Napaeus variatus</i>	0	0	0	0	1	51	0	0	0	0	0	7
<i>Ferussacia folliculus</i>	0	0	0	0	2	0	0	0	0	4	0	0
<i>Hemicycla bethencourtiana</i>	0	0	0	0	0	0	0	0	0	0	0	77
<i>Hemicycla bidentalis</i>	0	0	0	0	0	3	0	0	0	93	0	0
<i>Hemicycla consobrina</i>	6	4	14	26	81	0	0	0	0	0	0	0
<i>Hemicycla eurythra</i>	0	0	0	0	0	6	0	0	0	0	0	0
<i>Hemicycla plicaria</i>	0	0	0	0	0	0	0	0	0	0	15	0
<i>Hemicycla sp.</i>	0	0	0	0	0	0	0	0	2	0	0	0
<i>Otala lactea</i>	0	0	0	0	0	0	0	0	0	68	0	0
<i>Canariella fortunata</i>	0	0	0	0	0	50	0	0	24	97	0	0
<i>Canariella hispidula</i>	0	0	0	0	0	0	0	0	0	0	45	34
<i>Xerotricha orbignii</i>	0	0	0	8	23	1	27	1	0	7	48	1
<i>Vitrea contracta</i>	0	0	0	0	0	3	0	0	0	1	0	0
<i>Pupoides coenopictus</i>	10	1	0	4	0	0	0	0	0	0	0	0
<i>Gibbulinella dewinteri</i>	0	0	0	0	0	12	0	0	0	6	0	0
<i>Caracollina lenticula</i>	3	65	189	68	314	111	57	83	75	213	152	83
<i>Plutonia lamarckii</i>	0	0	0	0	0	1	0	0	0	0	0	0
Total	112	158	262	139	695	282	109	285	109	1095	260	225