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# ECOLOGICAL FIDELITY OF PLEISTOCENE–HOLOCENE LAND SNAIL SHELL ASSEMBLAGES PRESERVED IN CARBONATE-RICH PALEOSOLS

YURENA YANES,[1,2]* JULIO AGUIRRE,[3] MARÍA R. ALONSO,[4] MIGUEL IBÁÑEZ,[4] and ANTONIO DELGADO[1]

*[1]Instituto Andaluz de Ciencias de la Tierra (IACT), Universidad de Granada-Consejo Superior de Investigaciones Científicas (UGR-CSIC), Camino del Jueves s/n, 18100 Armilla, Granada, Spain; [2]Huffington Department of Earth Sciences, Southern Methodist University (SMU), Dallas, Texas 75275-0395, USA; [3]Departamento de Estratigrafía y Paleontología, Facultad de Ciencias, Campus de Fuentenueva s/n, Universidad de Granada, 18071 Granada, Spain; [4]Departamento de Biología Animal, Facultad de Biología, Universidad de La Laguna, Avenida Astrofísico Francesco Sánchez s/n, 38206, La Laguna, Tenerife, Canary Islands, Spain*
*e-mail: yurenayanes@ugr.es*

## ABSTRACT

**Studies that assess the ecological fidelity—preservation of the original community—of terrestrial shell accumulations are uncommon but essential to infer accurate changes in past ecosystems. When live-dead comparisons are unavailable, the taxonomic agreement between differing taphofacies may be used to evaluate the fidelity of ancient shelly assemblages. This approach was used to approximate the fidelity of Quaternary land snails preserved in carbonate-rich paleosols from the northeastern islets of the Canary Archipelago. Such macroscopic alteration as fragmentation, corrosion, carbonate coating, and color loss affected shells, however, microscopic analyses concluded substantial diagenetic alterations unlikely. The shell abundance negatively correlated with fragmentation, suggesting that a higher proportion of shells may be a consequence of higher shell input rate and lower shell destruction rate rather than lower sedimentation rate, as predicted by taphonomic models. Strongly and weakly altered taphofacies significantly differed in species abundances. Substantial taphonomic bias was improbable, however, because both taphofacies contained taxa with comparable durability. Temporal fluctuations in taphonomy and ecology suggest variable environmental conditions operated through time. The overall decline in shell abundance from the last glacial to interglacial paleosols may be explained by a decline in humidity and reduced island surface area resulting in lowered snail proliferation, and in turn, a decreased net shell input rate. This study emphasizes that the original community is preserved within the studied terrestrial shell accumulations regardless of the degree of taphonomic alteration. Measures of past taxonomic richness and diversity, therefore, may be used as a reliable measure of the original snail community.**

## INTRODUCTION

Shell assemblages are potentially valuable sources of ancient ecological information capable of capturing the biological signature of a once-living community—taxonomic richness and diversity, competition, predator-prey interactions. Such taphonomy and ecological fidelity studies as preservation of the original community (e.g., Kidwell, 2008), however, are necessary to ensure reliable paleoenvironmental and paleoecological inferences. Taphonomic studies that assessed the ecological fidelity and environmental gradients of recent and fossil marine shell assemblages are common in the literature (e.g., Best and Kidwell, 2000a, 2000b; Zuschin et al., 2000, 2003; Kidwell, 2001, 2007, 2008; Tomašových, 2006; Tomašových et al., 2006a, 2006b; Best, 2008; Brett et al., 2007; Powell et al., 2008; Tomašových and Kidwell, 2009a, 2009b; and references therein). Quantitative taphonomic studies that evaluate the ecological fidelity and quality of terrestrial shell assemblages, however, are sorely underrepresented (but see Pickford, 1995; Cadée, 1999; Rundell and Cowie, 2003; Pearce, 2008; Yanes et al., 2008), despite the great abundance of land mollusks preserved globally in a variety of continental deposits, including caves, paleosols, eolian sediments, archaeological sites, etc. (see review in Goodfriend, 1999).

Fossilized terrestrial shells can remain in the sediment for hundreds to thousands or even millions of years (e.g., Behrensmeyer et al., 2000), even with a number of physicochemical and biological processes operating at different spatiotemporal scales. Despite the resilience of an individual shell, multiple postmortem disturbances— sorting, out-of-habitat-transport, reworking—can distort the original ecological signal of the community (e.g., Kidwell and Flessa, 1996). Quantitative and statistical analyses of relevant taphonomic and ecological features in fossil shell assemblages provide insights into shell accumulation processes and potential postmortem biases (e.g., Tomašových, 2006; Tomašových et al., 2006a, 2006b). Ideally live-dead fidelity studies between comparable shell assemblages evaluate ecological fidelity since the original biotic signal is known (e.g., Kidwell, 2001, 2007, 2008). The ecological fidelity of fossil shelly assemblages that lack live assemblages, however, can be evaluated through the quantitative taxonomic comparisons (i.e., proportional species abundances) between differing taphofacies (Tomašových, 2006).

A quantitative taphonomic study was performed on late Pleistocene–Holocene land snail shells preserved in carbonate-rich paleosols from the semiarid islets of the northeastern (NE) Canary Archipelago. The NE region of the Canary Archipelago (29°N) is an ideal case study to determine ecological fidelity by taxonomic comparisons between taphofacies because the area contains numerous and diverse late Quaternary land snail shells (Yanes, 2003, 2005; Huntley et al., 2008; Yanes et al., 2008). This study estimates the degree to which terrestrial shell assemblages that lack modern analogues preserve ecological information by: (1) evaluating the preservation quality of shell material and likelihood of substantial diagenetic alteration within different taphofacies; (2) identifying which taphonomic processes dominated shell burial conditions, and (3) estimating the ecological fidelity of fossil paleosols through a comparison of the proportional abundances of species. The results from this study offer relevant insights regarding the degree to which late Quaternary paleosols from carbonate-rich semiarid settings retain original biological information and identify the environmental, ecological and taphonomic process that structure these patterns.

## GEOGRAPHICAL SETTING, CHRONOLOGY AND TIME-AVERAGING

The Canary Islands (27°–29°N) are a low-latitude volcanic archipelago located 100 km west of the Moroccan coast on the eastern side of the central Atlantic Ocean. The studied shells were collected in three islets north of Lanzarote Island: La Graciosa, Montaña Clara and

* Corresponding author.

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Alegranza (Fig. 1). These islets exhibit large areas where late Pleistocene-Holocene ancient dunes and paleosols developed (Figs. 2A–E), which contain abundant land snail shells (e.g., Yanes, 2003, 2005; Huntley et al., 2008; Yanes et al., 2008).

Paleosols from these islets range in age from ~44 to ~5 kyr BP (Table 1) based on chronology and aminostratigraphy established by Ortiz et al. (2006) through direct amino acid racemization dating (AAR) of land snail shells calibrated against radiocarbon age dating. Time averaging—the difference between the time of death of the oldest and the youngest individual in the assemblage (Kidwell and Flessa, 1996)—was quantitatively evaluated by Yanes et al. (2007) through the AAR dating technique using 5 to 10 shells per individual paleosol combined with such computer-intensive statistical approaches as Monte Carlo simulation. The results of Yanes et al. (2007) indicated that at least 11 out of a total of 44 paleosols in the study area exhibited clearly multimillennial age mixing of noncontemporaneous shells. The average scale of time averaging per paleosol was ~2,920 years, ranging from as much as ~7,200 years to as little as ~510 years (Yanes et al., 2007). These results are in line with previous time averaging studies of shell-rich accumulations (e.g., Kowalewski and Bambach, 2003) and land vertebrate remains preserved in paleosols (e.g., Behrensmeyer et al., 2000).

The magnitude of time averaging did not correlate with age—older paleosols did not exhibit significantly larger time averaging (Yanes et al., 2007). The apparently constant magnitude of temporal mixing in the Canary Island paleosols through time suggests that the dynamics of shell accumulation were similar across paleosols and were probably associated with the time span of soil formation rather than substantial reworking of shells from older to younger horizons (Yanes et al., 2007).

## MATERIAL AND METHODS

### Sampling Procedure

Seventeen paleosols from four bioclastic eolian sections were sampled, including the Morros Negros (GMN, Figs. 2A, C–D) and Caleta del Sebo (GCS, Fig. 2E) sections from La Graciosa islet, the Caleta de Guzmán section (MCG, Fig. 2B) from Montaña Clara islet, and the Montaña Lobos paleosol from Alegranza islet (AML, Fig. 1, Table 1). The stratigraphy of the studied successions has been described by Ortiz et al. (2006). First, 20 to 25 kg of sediment were collected from each paleosol horizon, resulting in a total of 17 samples from 17 paleosols. Samples were dry sieved through a 1-mm-mesh diameter. The resulting specimens were identified to species level when possible based on their size and shell morphology. Comparisons of processed and unprocessed samples indicate that the field-sampling protocol did not promote artificial shell breakage. Furthermore, because similar sampling procedures were applied in each stratigraphic horizon, the potential bias inherent to the dry-sieving process should have affected all sediment samples equally, resulting in reasonably comparable shell assemblages.

### XRD and SEM Analyses

The severity of microscopic and chemical alteration of the Quaternary deposits was determined by mineralogical analysis and microscopic imaging. The mineralogical composition of nineteen randomly selected shells from eight paleosols (AML-1, GMN-1, GMN-2, GMN-3, GMN-4, GMN-6, GMN-7 and MCG-4) was studied by X-ray diffraction (XRD) analysis using a PANalytical X'Pert (PANalytical B.V., Almelo, the Netherlands) for polycrystalline samples at the Instituto Universitario de Bio-orgánica Antonio González (IUBIO-AG), La Laguna University. The degree of alteration of the shell microstructure was assessed by comparing Scanning Electronic Microscope (SEM) micrographs from four shells from the dominant species *Theba geminata,* two modern shells from Fuerteventura Island and two fossil shells recovered from two paleosols (AML-1 and MCG-4). Fossil specimens were studied in the Centro Andaluz de Medio Ambiente (CEAMA, University of Granada), while modern individuals were studied in the Huffington Department of Earth Sciences (Southern Methodist University).

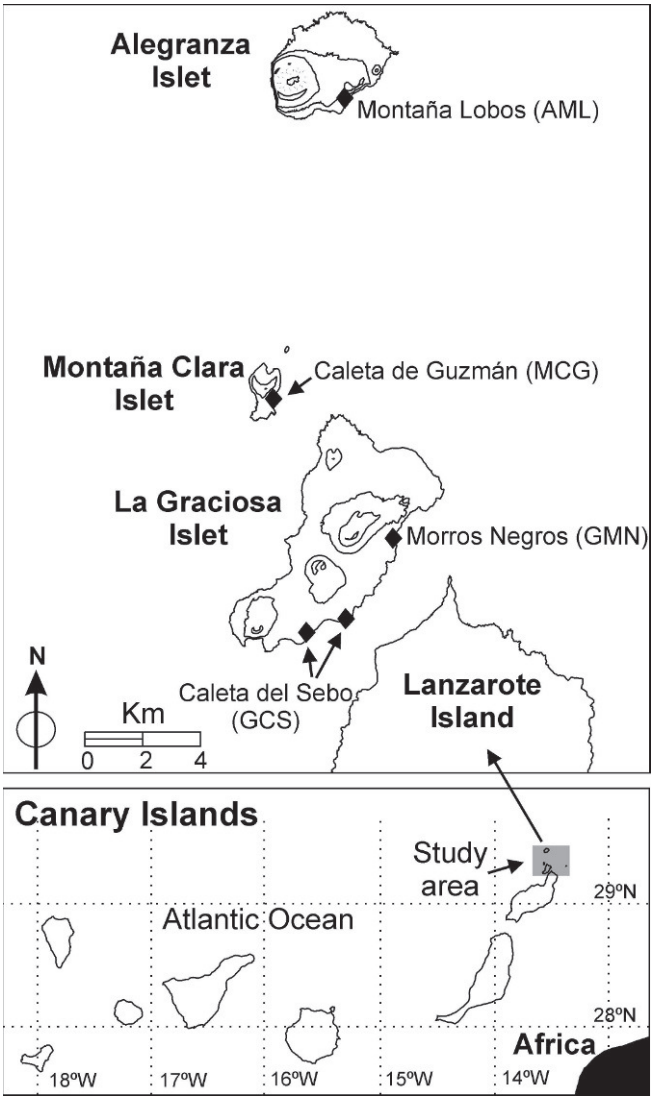


**FIGURE 1**—Geographical location of the islets located to the north of Lanzarote Island, Canary Archipelago. Filled diamonds indicate the location of the studied eolian successions.

### Taphonomic and Paleoecological Study

The following paleoecological measures (1–2) and taphonomic features (3–6) were assessed by absolute counts per paleosol: (1) total number of shell remains (TNR); (2) minimum number of individuals (MNI); (3) fragmentation; (4) corrosion; (5) carbonate coatings; and (6) color preservation (Table 1). TNR was quantified by counting all shell remains with a maximum length >2 mm. MNI was quantified by counting the number of shell remains with an observed embryonic shell or protoconch preserved. Fragmentation was scored as the absolute number of shells in a sampled paleosol that preserved <~90% of the shell (Fürsich and Flessa, 1987). Corrosion, the result of undefined mechanical abrasion and biogeochemical dissolution (Brett and Baird, 1986), was scored when shell remains showed any signs of partial or

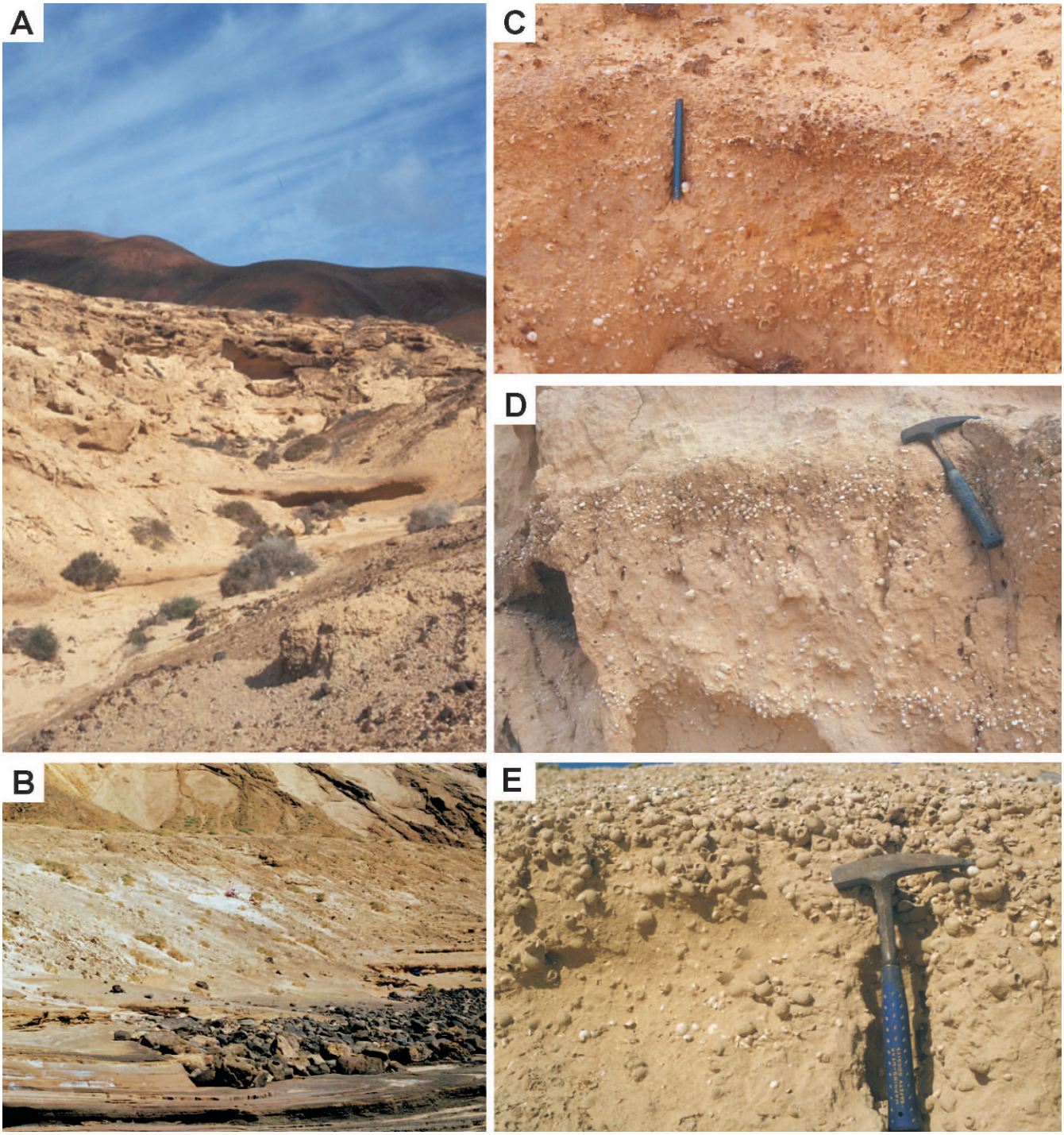


**FIGURE 2**—Eolian successions form the NE islets of the Canary Islands (photographs taken by Y. Yanes, 2002–2003). A) General view of Morros Negros section, La Graciosa Islet. B) General view of Caleta de Guzmán section, Montaña Clara Islet. C) Detailed view of the paleosol GMN-6 (~29.4 kyr BP: Ortiz et al., 2006). D) Detailed view of the paleosol GMN-7 (~16.5 kyr BP: Ortiz et al., 2006). E) Detailed view of the paleosol GCS-3 (~30.3 kyr BP: Ortiz et al., 2006).

total loss of ornamental traits. Carbonate coating was assessed by counting the number of shells with a partial or total calcareous crust. Color preservation was scored when shells showed any original color pattern preserved. Such taphonomic variables as edge roundness, bioerosion, and encrustation were not observed on the shell material.

Additional ecological information collected included: (1) the proportional shell abundance, calculated as the proportion of individuals in the shelly assemblage (=MNI × 100/TNI) and (2) the number of land snail species scored individually per paleosol (see Table 2). The approximate maximum shell length and shell thickness of each snail species was also acquired based on three adult individuals (Table 2). Shells are archived in the Department of Animal Biology, La Laguna University (Canary Islands, Spain), and all sampled material was scored under a binocular microscope.

## Statistical Treatments

Data analyses were performed using *PAST 1.39* software (Hammer et al., 2001) considering statistical significance at $\alpha = 0.05$. Spearman's correlation analyses were used to explore the potential rank-based

**TABLE 1**—Taphonomic and paleoecological results (in absolute numbers) of late Quaternary land snail paleosols from the islets of the NE Canary Archipelago.

| Paleosol ID | Islet | Location | AAR age (kyr BP)* | TNR | MNI | Fragmentation | Corrasion | Carbonate coating | Color preservation |
|---|---|---|---|---|---|---|---|---|---|
| GMN-1A | La Graciosa | Morros Negros | 43.0 ±7.8 | 579 | 390 | 315 | 322 | 144 | 119 |
| GMN-1B | La Graciosa | Morros Negros | 43.0 ±7.8 | 253 | 118 | 170 | 114 | 253 | 11 |
| GMN-2 | La Graciosa | Morros Negros | 43.6 ±6.3 | 822 | 556 | 440 | 628 | 810 | 127 |
| GMN-3 | La Graciosa | Morros Negros | 42.2 ±5.2 | 628 | 484 | 268 | 439 | 586 | 132 |
| GMN-4 | La Graciosa | Morros Negros | 40.2 ±4.8 | 326 | 293 | 102 | 194 | 303 | 54 |
| GMN-5 | La Graciosa | Morros Negros | 43.5 ±4.9 | 68 | 53 | 39 | 43 | 8 | 22 |
| GMN-6 | La Graciosa | Morros Negros | 29.4 ±4.6 | 220 | 157 | 111 | 124 | 212 | 54 |
| GMN-7 | La Graciosa | Morros Negros | 16.5 ±3.9 | 652 | 204 | 513 | 520 | 2 | 44 |
| GCS-1 | La Graciosa | Caleta del Sebo | ~44** | 99 | 62 | 70 | 59 | 99 | 17 |
| GCS-2 | La Graciosa | Caleta del Sebo | ~42** | 575 | 432 | 268 | 229 | 574 | 144 |
| GCS-3 | La Graciosa | Caleta del Sebo | 30.3 ±5.5 | 1,156 | 907 | 475 | 566 | 1063 | 190 |
| GCS-4 | La Graciosa | Caleta del Sebo | 20.6 ±3.4 | 1,482 | 928 | 855 | 1,002 | 922 | 211 |
| MCG-1 | Montaña Clara | Caleta de Guzmán | 40.2 ±7.9 | 254 | 186 | 157 | 51 | 166 | 28 |
| MCG-2 | Montaña Clara | Caleta de Guzmán | ~40** | 69 | 33 | 53 | 25 | 37 | 9 |
| MCG-3 | Montaña Clara | Caleta de Guzmán | 28.5 ±6.4 | 293 | 195 | 149 | 39 | 10 | 79 |
| MCG-4 | Montaña Clara | Caleta de Guzmán | 4.6 ±0.7 | 689 | 451 | 448 | 70 | 0 | 102 |
| AML-1 | Alegranza | Montaña Lobos | 10.1 ±4.0 | 939 | 361 | 820 | 773 | 8 | 95 |

* Amino acid racemization (AAR) ages were adopted from Ortiz et al. (2006);

** Denotes an estimated age based on stratigraphic position. TNR: total number of remains; MNI: minimal number of individuals.

relationship between taphonomic and ecological variables. The Mann-Whitney U test was used to compare the median distribution between two groups of samples. F-test was used to detect potential differences in the variance of two groups of samples. Permutation t-test was used to compare the equality of means between two groups of samples via resampling without replacement by random re-ordering of observations.

Cluster analysis of the four taphonomic features, based on the Manhattan distance and group-average linkage method, identified separate taphofacies (groups of paleosols with similar taphonomic signature) within the study area. Taxonomic mismatches among taphofacies, age intervals, islets and paleosols with different time-averaging scales were evaluated through a low-dimensional space ordination of proportional species abundances by using non-metric

**TABLE 2**—Fossil land snail species abundances (in absolute numbers) from the Quaternary paleosols of the NE islets of the Canary Archipelago. Approximate shell maximum length and shell thickness of the last whorl spire is shown for each species.

| Paleosol ID | ~Age (kyr BP)* | SP 1 | SP 2 | SP 3 | SP 4 | SP 5 | SP 6 | SP 7 | SP 8 | SP 9 | SP 10 | SP 11 | SP 12 | SP 13 | SP 14 | SP 15 | SP 16 | SP 17 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MCG-4 | 4.6 | 404 | 55 | 34 | 0 | 0 | 0 | 0 | 0 | 86 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| AML-1 | 10.1 | 781 | 0 | 0 | 0 | 0 | 128 | 0 | 0 | 28 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| GMN-7 | 16.5 | 239 | 11 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 63 | 0 |
| GCS-4 | 20.6 | 149 | 105 | 0 | 0 | 2 | 0 | 31 | 0 | 38 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| MCG-3 | 28.5 | 685 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| GMN-6 | 29.4 | 883 | 360 | 0 | 15 | 2 | 0 | 0 | 0 | 217 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| GCS-3 | 30.3 | 339 | 135 | 0 | 0 | 7 | 0 | 33 | 0 | 106 | 1 | 3 | 0 | 0 | 2 | 0 | 0 | 0 |
| MCG-2 | 40** | 237 | 7 | 0 | 3 | 0 | 0 | 0 | 0 | 45 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| GMN-4 | 40.2 | 49 | 47 | 0 | 1 | 0 | 0 | 1 | 0 | 9 | 0 | 1 | 0 | 2 | 1 | 1 | 0 | 0 |
| MCG-1 | 40.2 | 41 | 14 | 0 | 2 | 0 | 0 | 9 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| GCS-2 | 42** | 419 | 91 | 0 | 0 | 10 | 0 | 67 | 0 | 129 | 12 | 8 | 9 | 0 | 8 | 6 | 1 | 0 |
| GMN-3 | 42.0 | 53 | 6 | 0 | 11 | 0 | 0 | 0 | 0 | 26 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| GMN-1A | 42.2 | 56 | 5 | 0 | 0 | 1 | 0 | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| GMN-1B | 43.0 | 133 | 16 | 0 | 9 | 8 | 0 | 13 | 0 | 34 | 1 | 0 | 4 | 1 | 0 | 1 | 0 | 0 |
| GMN-5 | 43.0 | 666 | 74 | 0 | 96 | 14 | 0 | 127 | 3 | 157 | 2 | 11 | 10 | 1 | 0 | 0 | 0 | 0 |
| GMN-2 | 43.5 | 588 | 27 | 0 | 5 | 4 | 0 | 0 | 0 | 28 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| GCS-1 | 44** | 158 | 67 | 1 | 0 | 0 | 0 | 3 | 0 | 23 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 |
| Maximum length (mm)*** | | 14.6–20.2 | 9.7–14.3 | 12.6–17.7 | 22–35 | 20.0–32 | 12.7–16.5 | 13–18 | 21.8–27 | 6.5–6.8 | 7.2–8.8 | 4.3–4.5 | 9.7–11.3 | 5.1–5.4 | 8–8.5 | 5–8 | 9.8–10.2 | 3.5–5.5 |
| Shell thickness (mm)*** | | 0.16–0.18 | 0.13–0.16 | 0.1–0.13 | 0.2–0.24 | 0.15–0.22 | 0.13–0.19 | 0.24–0.26 | 0.13–0.16 | 0.08–0.11 | 0.05–0.07 | 0.02–0.3 | 0.02–0.3 | 0.02–0.3 | 0.02–0.3 | 0.02–0.3 | 0.01–0.02 | 0.03–0.05 |

* Ages taken from Ortiz et al. (2006).

** Denotes an estimated age.

*** Shell measurements are based on three adult individuals. Land snail species are as follows: SP1: *Theba geminata*, SP2: *T. arinagae*; SP3: *T. impugnata*, SP4: *Rumina decollata*, SP5: *Hemicycla sarcostoma*, SP6: *H. flavistoma*, SP7: *Pomatias lanzarotensis*, SP8: *Canariella plutonia*, SP9: *Monilearia monilifera*, SP10: *Caracollina lenticula*, SP11: *Cryptella alegranzae*, SP12: *C. canariensis*, SP13: *C. famarae*, SP14: *C. parvula*, SP15: *Cryptella* sp., SP16: *Ferussacia fritschi*, SP17: *Granopupa granum*. From SP1 to SP8 = shells with likely high preservation potential (average shell length of 19.5 ± 6.2 mm). From SP9 to SP17 = shells with expected low durability (average shell length of 7.1 ± 2.2 mm).

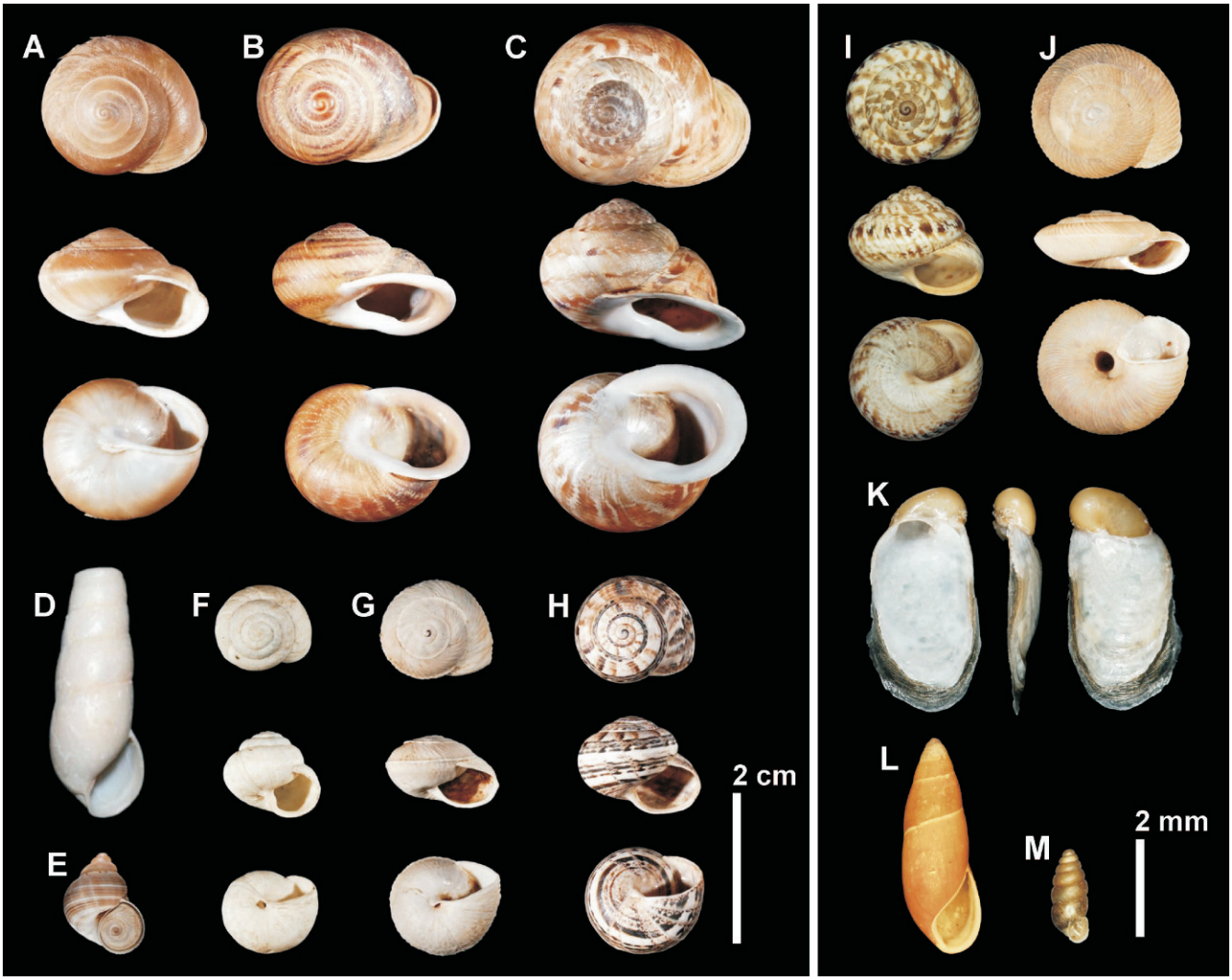


**FIGURE 3**—Land snail species recovered from the fossil record of the NE islets of the Canary Archipelago (Photographs taken by M. Ibáñez, 2002–2004). A) *Canariella plutonia*, B) *Hemicycla flavistoma*, C) *H. sarcostoma*, D) *Rumina decollata*, E) *Pomatias lanzarotensis*, F) *Theba arinagae*, G) *T. impugnata*, H) *T. geminata*, I) *Monilearia monilifera*, J) *Caracollina lenticula*, K) *Crypetlla auriculata* (internal shell of a slug), L) *Ferussacia fristchi*, M) *Granopupa granum*. Species from A to H represent durable taxa (generally larger and thicker shells) whereas from I to M represent fragile taxa (usually smaller and thinner shells) (e.g., Behrensmeyer et al., 2005).

multidimensional scaling (NMDS) based on Bray-Curtis similarity. NMDS is a useful method to compare taphofacies because it does not make assumptions about the data type or the interrelationship of samples (e.g., Tomašových, 2006). The proportion of species abundances were square-root transformed prior to analysis to minimize the effect of dominant species. NMDS results were tested for statistical differences using Analysis of Similarities (ANOSIM), a non-parametric test based on distances between pair of samples computed, in this case, from the Bray-Curtis rank distances. The test statistic (R) ranges from −1 to 1 (an R value of 0 indicates no difference between groups), and a randomization approach was used to compute the level of significance of this statistic (e.g., Tomašových, 2006). When statistical differences were obtained, a Similarity Percentage analysis (SIMPER) was used to find out which species were primarily responsible for the observed taxonomic mismatches between groups of samples: e.g., strongly vs. weakly altered taphofacies; interglacial vs. glacial paleosols; La Graciosa vs. Montaña Clara islet; and time-averaged vs. non-time-averaged paleosols. SIMPER analysis calculates the average Bray-Curtis dissimilarity between pairs of inter-group samples. The average dissimilarity between groups can be expressed in terms of the average contribution from each species because the Bray-Curtis dissimilarity measure incorporates the contribution of each species (Clarke, 1993).

## RESULTS

### Land Snail Species

Seventeen land snail taxa were identified (Table 2, Fig. 3), yet two congeneric helicid species, *Theba geminata* (Mousson, 1857) and *T. arinagae* Gittenberger and Ripken, 1987 accounted for more than 80% of the total number of remains (see also Huntley et al., 2008). Fifteen other species showed sporadic occurrence and were considerably less abundant or even rare (see Table 2, Fig. 3): *Pomatias lanzarotensis* (Wollaston, 1878), *Granopupa granum* (Draparnaud, 1801), *Ferusacia fritschi* (Mousson, 1872), *Rumina decollata* (Linnaeus, 1758), *Caracolina lenticula* (Michaud, 1831), *Monilearia monilifera* (Webb and Berthelot, 1833), *Canariella plutonia* (Lowe, 1861), *Theba impugnata* (Mousson, 1857), *Hemicycla sarcostoma* (Webb and Berthelot, 1833), *H. flavistoma* Ibáñez and Alonso, 1991, and five *Cryptella* species (slugs with internal calcitic shells; Fig. 3K).

Taphonomic analysis was performed on the total shell remains to avoid separate analysis by species because medium-size (~15 mm

**TABLE 3**—Semiquantitative estimation by XRD of the mineralogical composition of fossil land snail shells from the NE islets of the Canary Archipelago.

| Shell ID | Islet | Locality | AAR age (kyr BP)* | Species | Aragonite (S.Q. %) | Calcite (S.Q. %) |
|---|---|---|---|---|---|---|
| AML-1-1 | Alegranza | Montaña Lobos | 10.1 ± 4.0 | *Theba geminata* | 100 | 0 |
| AML-1-2 | Alegranza | Montaña Lobos | 10.1 ± 4.0 | *Hemicycla flavistoma* | 100 | 0 |
| GMN-1-1 | La Graciosa | Morros Negros | 43.0 ± 7.8 | *Theba geminata* | 100 | 0 |
| GMN-1-2 | La Graciosa | Morros Negros | 43.0 ± 7.8 | *Theba arinagae* | 100 | 0 |
| GMN-1-3 | La Graciosa | Morros Negros | 43.0 ± 7.8 | *Hemicycla sarcostoma* | 100 | 0 |
| GMN-1-4 | La Graciosa | Morros Negros | 43.0 ± 7.8 | *Theba arinagae* | 100 | 0 |
| GMN-1-5 | La Graciosa | Morros Negros | 43.0 ± 7.8 | *Theba geminata* | 100 | 0 |
| GMN-2-1 | La Graciosa | Morros Negros | 43.6 ± 6.3 | *Pomatias lanzarotensis* | 100 | 0 |
| GMN-2-2 | La Graciosa | Morros Negros | 43.6 ± 6.3 | *Theba arinagae* | 100 | 0 |
| GMN-2-3 | La Graciosa | Morros Negros | 43.6 ± 6.3 | *Theba geminata* | 100 | 0 |
| GMN-2-4 | La Graciosa | Morros Negros | 43.6 ± 6.3 | *Hemicycla sarcostoma* | 100 | 0 |
| GMN-3-1 | La Graciosa | Morros Negros | 42.2 ± 5.2 | *Pomatias lanzarotensis* | 100 | 0 |
| GMN-3-2 | La Graciosa | Morros Negros | 42.2 ± 5.2 | *Theba arinagae* | 100 | 0 |
| GMN-3-3 | La Graciosa | Morros Negros | 42.2 ± 5.2 | *Theba geminata* | 100 | 0 |
| GMN-3-4 | La Graciosa | Morros Negros | 42.2 ± 5.2 | *Hemicycla sarcostoma* | 100 | 0 |
| GMN-4-1 | La Graciosa | Morros Negros | 42.2 ± 5.2 | *Theba geminata* | 100 | 0 |
| GMN-4-2 | La Graciosa | Morros Negros | 40.2 ± 4.8 | *Theba arinagae* | 98 | 2 |
| GMN-6-1 | La Graciosa | Morros Negros | 40.2 ± 4.8 | *Theba geminata* | 100 | 0 |
| GMN-6-2 | La Graciosa | Morros Negros | 29.4 ± 4.6 | *Theba geminata* | 100 | 0 |
| GMN-6-3 | La Graciosa | Morros Negros | 29.4 ± 4.6 | *Rumina decollata* | 77 | 23 |
| GMN-6-4 | La Graciosa | Morros Negros | 29.4 ± 4.6 | *Hemicycla sarcostoma* | 96 | 4 |
| GMN-6-5 | La Graciosa | Morros Negros | 29.4 ± 4.6 | *Theba arinagae* | 100 | 0 |
| GMN-6-6 | La Graciosa | Morros Negros | 29.4 ± 4.6 | *Pomatias lanzarotensis* | 100 | 0 |
| GMN-6-7 | La Graciosa | Morros Negros | 29.4 ± 4.6 | *Hemicycla sarcostoma* | 100 | 0 |
| GMN-6-8 | La Graciosa | Morros Negros | 29.4 ± 4.6 | *Theba geminata* | 98 | 2 |
| GMN-6-9 | La Graciosa | Morros Negros | 29.4 ± 4.6 | *Rumina decollata* | 93 | 7 |
| GMN-7-1 | La Graciosa | Morros Negros | 16.5 ± 3.9 | *Monilearia monilifera* | 100 | 0 |
| GMN-7-2 | La Graciosa | Morros Negros | 16.5 ± 3.9 | *Theba geminata* | 100 | 0 |
| GMN-7-3 | La Graciosa | Morros Negros | 16.5 ± 3.9 | *Theba arinagae* | 100 | 0 |
| GMN-7-4 | La Graciosa | Morros Negros | 16.5 ± 3.9 | *Rumina decollata* | 97 | 3 |
| MCG-4-1 | Montaña Clara | Caleta de Guzmán | 4.6 ± 0.7 | *Theba geminata* | 100 | 0 |
| MCG-4-2 | Montaña Clara | Caleta de Guzmán | 4.6 ± 0.7 | *Theba geminata* | 100 | 0 |
| MCG-4-3 | Montaña Clara | Caleta de Guzmán | 4.6 ± 0.7 | *Theba geminata* | 100 | 0 |
| MCG-4-4 | Montaña Clara | Caleta de Guzmán | 4.6 ± 0.7 | *Rumina decollata* | 100 | 0 |
| MCG-4-5 | Montaña Clara | Caleta de Guzmán | 4.6 ± 0.7 | *Rumina decollata* | 100 | 0 |
| MCG-4-6 | Montaña Clara | Caleta de Guzmán | 4.6 ± 0.7 | *Theba geminata* | 100 | 0 |
| MCG-4-7 | Montaña Clara | Caleta de Guzmán | 4.6 ± 0.7 | *Theba arinagae* | 100 | 0 |
| MCG-4-8 | Montaña Clara | Caleta de Guzmán | 4.6 ± 0.7 | *Pomatias lanzarotensis* | 73 | 26 |
| MCG-4-9 | Montaña Clara | Caleta de Guzmán | 4.6 ± 0.7 | *Theba gemianta* | 72 | 28 |

diameter and ~11 mm height, on average) globose-spherical shells of *Theba* genus (Table 2, Figs. 3F–H) dominated the fossil assemblages. Preliminary laboratory tests suggested that separate taphonomic studies by species were unnecessary for this shell material (Yanes et al., 2008).

The number of land snail species currently extant in the three islets, based on live specimens collected over the last 15 years by members of the Malacology Group of La Laguna University, is substantially lower (n = 8) than the number of recovered fossil land snail species (n = 17) (Yanes, 2005). Extant species in the islets include *Theba geminata*, *T. impugnata*, *Hemicycla sarcostoma*, *H. flavisotma*, *Pomatias lanzarotensis*, *Caracollina lenticula*, *Cryptella alegranzae* Hutterer and Groh, 1991 and *C. famarae* Hutterer and Groh, 1991 (Yanes, 2003, 2005), yet all taxa in this study are present in neighboring Canary islands, except the extinct *C. parvula* (Hutterer, 1990). The current land snail populations are, thus, likely depauperate in species compared to the local Pleistocene–Holocene assemblages. A quantitative survey of extant land snail populations remains to be established in the study area, however, because data on species abundances of modern populations have never been published.

## XRD and SEM Analyses

Semiquantitative estimates of the mineralogical composition of 39 fossil shells via X-ray diffraction indicate that only eight out of 39 shells exhibited minor calcite replacement (10%–20%) of the original aragonite (Table 3), emphasizing that the great majority of shells did not undergo substantial diagenetic alteration.

A visual SEM comparative analysis of the *Theba geminata* shell microstructure from modern live-collected shells and two fossil shells, AML-1 (~10.5 kyr) and MCG-4 (~4.6 kyr), indicates no evidence of recrystallization or secondary overgrowth (Fig. 4). The observed cross-hatched microstructure seen under SEM (Fig. 4) indicates preservation of the original aragonite microstructure.

## Shell Taphonomy

A total of 9,104 shell remains, corresponding to a minimum of 5,810 individuals, were studied. Shells were clearly affected by fragmentation, corrosion, carbonate coating, and color loss (Table 1). The range of shells and shell fragments varied widely among paleosols. The proportion of shell fragments relative to unfragmented shells per paleosol ranged from 31% to 87%. Evidence for shell corrosion varied widely among paleosols, with the number of sampled shell material affected by corrosion ranging from 10% to 82% within a given paleosol. Within the 17 sampled paleosols, anywhere from 4% to 32% of shells retained their color. The most variable taphonomic feature was the extent of carbonate coating, which varied from a total absence to nearly 100% of shell remains containing some kind of carbonate crust (Table 1).

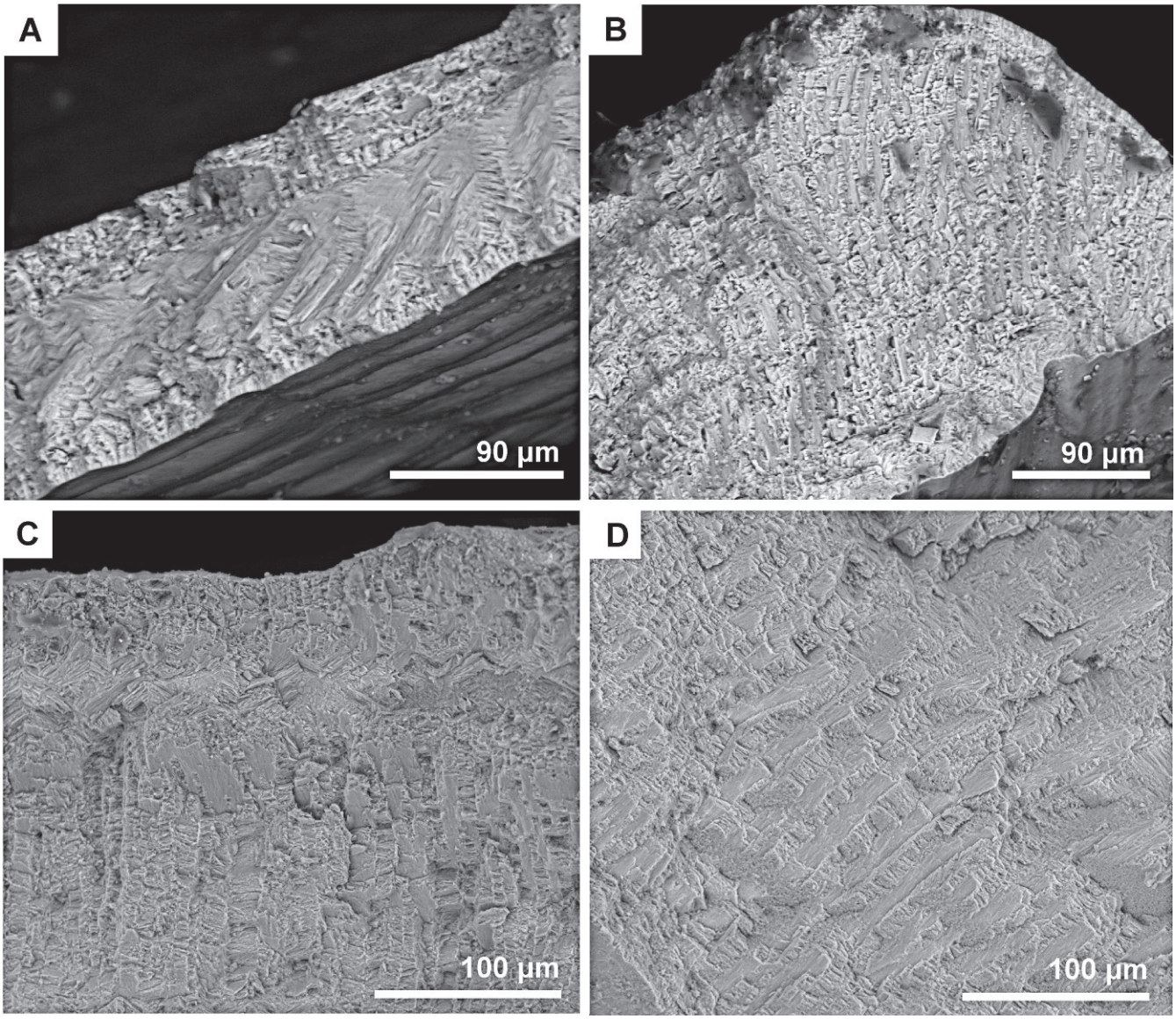


**FIGURE 4**—SEM micrographs of the internal shell microstructure of the dominant *Theba geminata*. A–B) Detail of the shell microstructure of modern individuals. C) Shell microstructure of a fossil shell recovered from the paleosol AML-1 (~10.1 kyr). D) Shell microstructure of a fossil shell collected from the paleosol MCG-4 (~4.9 kyr).

Of the seventeen multiple sequential pairwise comparisons between taphonomic and ecological variables (Table 4), only four were found to be significant. The proportional shell abundance negatively correlates with the proportion of shell fragments, but positively correlates with the proportion of shells with original color preserved (Table 4). The proportion of fragmentation negatively correlates with the proportion of shells with color preserved (Table 4). The positive correlation between the proportion of shells with carbonate crusts and paleosol age (Table 4) indicates that older paleosols exhibit a substantially higher proportion of shells with carbonate coating than do younger paleosols with shell accumulations. The remaining pairwise comparisons did not show significant relationships after applying the Bonferroni correction ($\alpha = 0.05/15 = 0.003$; Table 4).

Ecological and taphonomic variables fluctuated through time (Fig. 5). Proportional shell abundance is substantially higher in paleosols dated as last glacial (~17–43 ka) than dated to be interglacial (~5–10 ka) (Figs. 5A–B). Generally, fragmentation (Figs. 5C–D) is higher in shells from Holocene paleosols, whereas corrosion (Figs. 5E–F), carbonate coating (Figs. 5G–H) and original color preservation (Figs. 5I–J) are considerably higher in shells from late Pleistocene paleosols.

Cluster analysis of taphonomic features ordered the paleosols into two main groups: (1) weakly and (2) strongly altered taphofacies (Fig. 6). The weakly altered taphofacies are characterized by shell assemblages with generally lower fragmentation, higher carbonate coating and higher color preservation, whereas strongly altered taphofacies include shell material with substantially higher proportion of fragmentation, lower presence of carbonate crusts and lower color preservation (Table 1).

## Fidelity of Land Snail Assemblages

Shell abundance did not correlate with the scale of time averaging (Spearman rho, $r_s = -0.12$; $p = 0.723$; $n = 11$). In addition, highly time-averaged paleosols did not exhibit a significantly higher abundance of shells than shell assemblages where time averaging was not confirmed (Mann-Whitney U test, $p = 0.30$). Non-metric multidimensional scaling (NMDS) based on the square-root of the proportion of species abundances and using the Bray-Curtis index distances identified significant differences in species abundance between the following comparisons: (1) weakly and strongly altered taphofacies (Fig. 7A), (2)

**TABLE 4**—Spearman rank correlations between the proportional shell abundance, taphonomic features, and age of land snail assemblages. Bonferroni correction for multiple pairwise comparisons lowered the α value to 0.003 (α = 0.05/15 = 0.003).

| Pair-wise relationship (n = 17) | Spearman *r* | *p*-value |
|---|---|---|
| % shell abundance vs. % fragmentation | −0.870 | <0.001* |
| % shell abundance vs. % corrasion | −0.145 | 0.376 |
| % shell abundance vs. % carbonate coating | 0.286 | 0.266 |
| % shell abundance vs. % color preservation | 0.645 | 0.005** |
| % fragmentation vs. % corrasion | 0.135 | 0.606 |
| % fragmentation vs. % carbonate coating | −0.357 | 0.160 |
| % fragmentation vs. % color preservation | −0.652 | 0.005** |
| % shell corrasion vs. % carbonate coating | 0.030 | 0.907 |
| % shell corrasion vs. % color preservation | −0.127 | 0.626 |
| % carbonate coating vs. % color preservation | 0.137 | 0.599 |
| Age vs. % shell abundance | 0.350 | 0.169 |
| Age vs. % fragmentation | −0.212 | 0.413 |
| Age vs. % corrasion | 0.044 | 0.865 |
| Age vs. % carbonate coating | 0.673 | 0.003* |
| Age vs. % color preservation | 0.325 | 0.203 |

* Denotes when significant correlation is observed after Bonferroni correction.

** Denotes when marginally significant correlation is observed after Bonferroni correction.

glacial and interglacial deposits (Fig. 7B), (3) among the islets (Fig. 7C), and (4) time-averaged versus non-time-averaged paleosols (Fig. 7D). Weakly and strongly altered paleosols significantly differ in species abundances (ANOSIM, R = 0.40; p = 0.01) (Fig. 7A). SIMPER analysis indicate that the weakly altered group contains a higher abundance of *Theba arinagae*, *Hemicycla sarcostoma*, *Pomatias lanzarotensis*, *Monilearia monilifera*, *Rumina decollata* and *Caracollina lenticula* relative to the other paleosols whereas the strongly taphonomically altered paleosols contain a higher abundance of *Theba geminata* and *Hemicycla flavistoma* (Fig. 8A) as compared to the weakly altered group. Species abundances in Holocene paleosols were significantly different than in Pleistocene paleosols (ANOSIM, R = 0.68; p = 0.007) (Fig. 7B). SIMPER analysis indicates a higher abundance of *Theba arinagae*, *Monilearia monilifera*, *Pomatias lanzarotensis,* and *Rumina decollata* in Pleistocene horizons relative to Holocene horizons and a higher abundance of *Theba geminata* and *Hemicycla flavistoma* in the Holocene paleosols relative to Pleistocene paleosols (Fig. 8B). Paleosols from La Graciosa islet contained significantly different species assemblages than those from Montaña Clara islet (ANOSIM, R = 0.29; p = 0.029) (Fig. 7C). SIMPER results indicate that this difference is primarily explained by the abundance of *Theba arinagae*, *Hemicycla sarcostoma*, *Monilearia monilifera*, *Pomatias lanzarotensis*, and *Rumina decollata* in La Graciosa islet and the abundance of *Theba geminata* in Montaña Clara islet (Fig. 8C). Although the species abundances of the Alegranza islet paleosol differ from La Graciosa and Montaña Clara islets paleosols (Fig. 7C), statistical differences were not obtained (ANOSIM, R = 0.86; p = 0.077). The lack of significance could be due to having only one assemblage observed in Alegranza islet. Multimillennial, time-averaged paleosols were statistically different than non-time-averaged assemblages regarding proportional species abundances (ANOSIM, R = 0.54; p = 0.01; Fig. 7D). SIMPER analysis indicates that such difference is the consequence of the higher proportion of *Theba arinagae*, *Pomatias lanzarotensis*, *Monilearia monilifera*, *Ferussacia fristchi,* and *Cryptella* sp. in the non-time-averaged paleosols and the abundance of *Theba geminata*, *Hemicycla sarcostoma,* and *Rumina decollata* in the age-averaged assemblages (Fig. 8D).

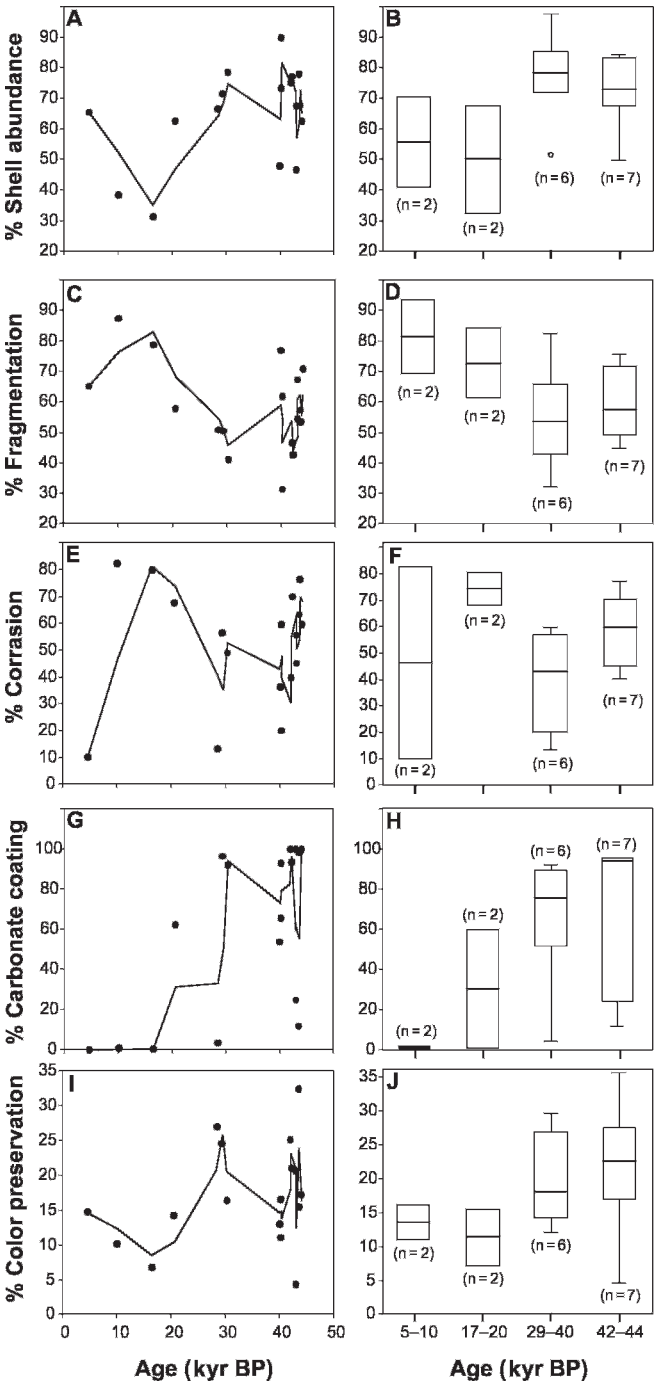


**FIGURE 5**—Shell taphonomy variations through time. Plots from column left represent the taphonomic results per paleosol (filled circles) and solid lines represent 2-point moving average of the data. Plots from the right column represent the taphonomic results averaged per four main age intervals. Boxes represent the 25%–75% quartiles. Horizontal line inside the box is the median value. Whiskers show the minimum and maximum values. A–B) Proportional shell abundance. C–D) Proportion of shell fragments. E–F) Proportion of shell with signs of corrosion. G–H) Proportion of shells with carbonate crusts. I–J) Proportion of shells that preserved original color patterns. Ages were adopted from Ortiz et al. (2006).

## DISCUSSION

### Ecological Fidelity

Taxonomic agreement studies between differing taphofacies can evaluate whether fossil shell assemblages have undergone substantial taphonomic bias (e.g., Tomašových, 2006; Tomašových et al., 2006a, 2006b). Paleosols that vary in degree of preservation often differ in species composition and proportional abundances as a consequence of changes in taphonomic destruction rates (e.g., Tomašových, 2006). Several sources of bias can distort the original biological signal of shell assemblages, including selective preservation (or destruction) of species

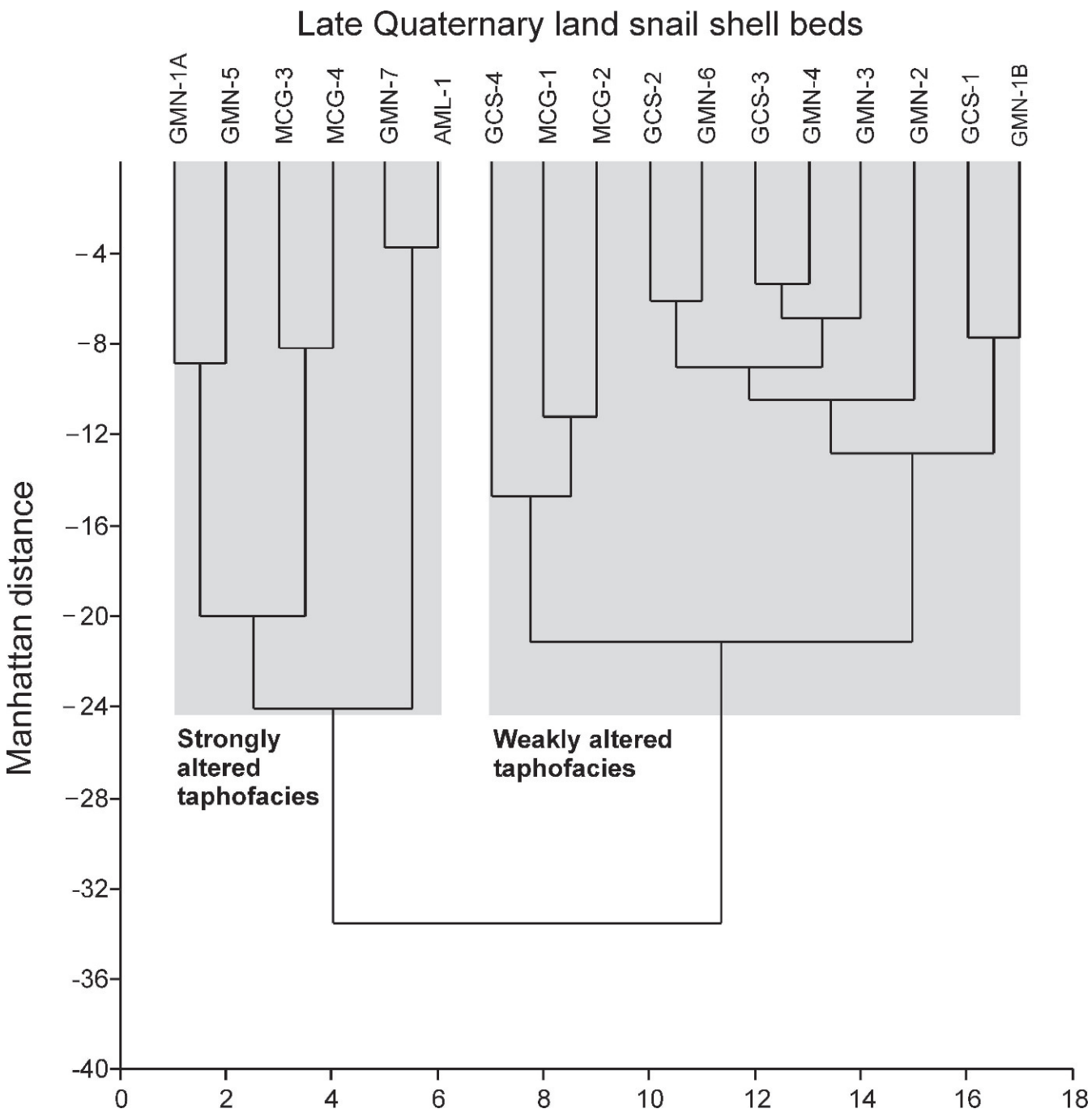


**FIGURE 6**—Low-dimensional spatial ordination of paleosols as determined through cluster analysis based on the Manhattan distance and group linkages using four taphonomic variables: proportional fragmentation, corrosion, color preservation, and carbonate coating.

and out-of-habitat shell transport. Similarly, different scales of time averaging across paleosols may potentially affect species abundances mismatches (e.g., Behrensmeyer et al., 2000; Tomašových and Kidwell, 2009b, 2010). Weakly and strongly altered land snail shell assemblages significantly differed regarding taxonomic composition (Fig. 7A). This taxonomic disagreement could be the result of out-of-habitat transport and or selective preservation or destruction of species. The studied islets exhibit a significantly reduced number of habitats as a consequence of their small area (from 1.1 to 27.2 $km^2$), their low altitude (lower than 300 meters above sea level: m.a.s.l.), the short distances among them (Fig. 1), and the analogous climatic conditions and vegetation. Accordingly, all fossil snail species identified in the study are associated with a similar semiarid coastal carbonate-rich habitat type, such that out-of-habitat transport is improbable.

The variable shell size and thickness among land snail taxa may present variable preservation potential within a shell assemblage (e.g., Behrensmeyer et al., 2005). Accordingly, snail species could be classified as species with high preservation potential (i.e., larger and thicker shells) or species with low preservation potential (i.e., smaller and thinner shells). Land snail species studied here can be classified into two statistically distinctive groups based on their shell size (Mann-Whitney U test, $p = 0.0006$): (1) larger and thicker shells, with an average shell length of 19.5 ± 6.2 mm and an average shell thickness of 0.17 ± 0.04 mm (species from A to H in Fig. 3), and (2) smaller and thinner

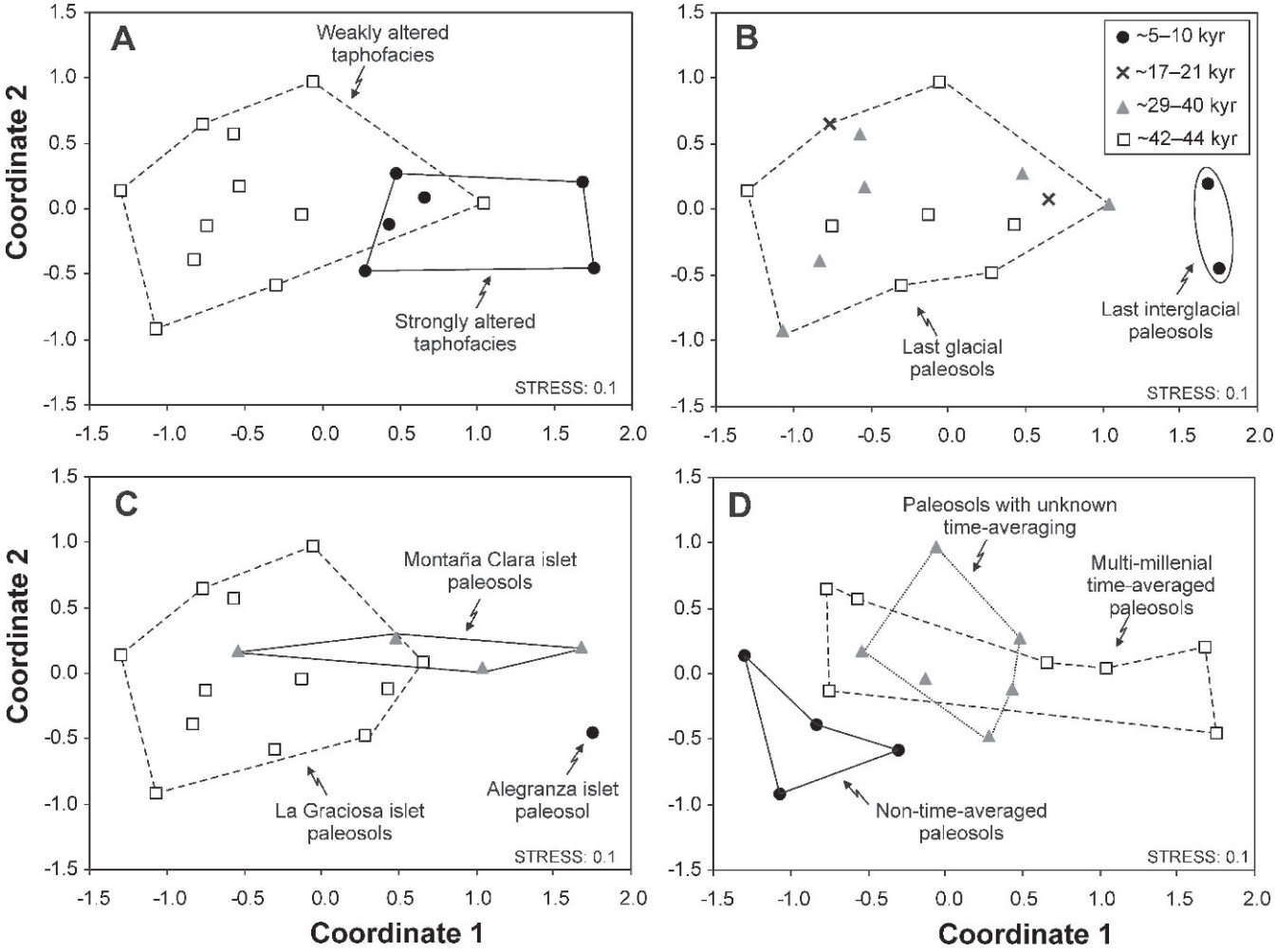


**FIGURE 7**—Non-metric multidimensional scaling (NMDS) ordination of Pleistocene-Holocene paleosols (n = 17) based on Bray-Curtis similarity using the square-root transformed proportional abundance of land snail species. A) Weakly and strongly taphonomically-altered paleosols. B) Last glacial (~44–17 kyr) and last interglacial (~10–5 kyr) paleosols. C) Among islets. D) Non-time-averaged and multi-millennial time-averaged paleosols.

shells, with an average shell length of 7.1 ± 2.2 mm and an average shell thickness of 0.04 ± 0.02 mm (species from I to L in Fig. 3). Accordingly, species with high preservation potential should embrace all larger taxa, which are predicted to have high durability in the taphonomic active zone (TAZ). In contrast, species with expected low preservation potential (i.e., fragile shells) would include taxa with relatively small and thin skeletons (e.g., Behrensmeyer et al., 2005). SIMPER analysis (Fig. 8A) shows that the species accountable for the taxonomic mismatches between taphofacies do not differ in durability, so postmortem bias cannot be demonstrated with the presented data. The original community, therefore, appears to have been preserved in both weakly and highly altered taphofacies.

The differences in taxonomic composition regarding paleosol age (Fig. 7B) and islets (Fig. 7C) emphasize that other factors beyond mechanical taphonomic bias—differential shell-specific destruction rates—likely affected species abundances. Land snail species abundances significantly differed between multimillennial time-averaged paleosols and paleosols where time averaging was not demonstrated (Fig. 7D), but no differences on species preservation rates were observed between the two groups of samples (Fig. 8D). Recent evaluations (Tomašových and Kidwell, 2009b, 2010) on the effects of time-averaging on live-dead marine shell assemblages indicate that high and low age-mixed assemblages tend to differ with respect to species abundances due to different temporal mixing of generations and within habitat mixing across temporal scales. Generally, highly time-averaged beds display lower taxonomic variation in space and time (lower dispersion in the multivariate space of the NMDS) than low-averaged assemblages as a consequence of the loss of temporal resolution due to time averaging (e.g., Tomašových and Kidwell, 2009b, 2010). On the contrary, the NMDS results indicate that non-time-averaged paleosols exhibit a lower dispersion of species abundances than do strongly age-averaged assemblages (Fig. 7D). Both groups of samples exhibited Bray-Curtis index values with significantly different variances (F test, $p = 0.143$) and the mean value of such dispersion was marginally statistically significant (Permutation t-test, $p = 0.062$; N = 10,000 iterations). These results suggest that the effects of time-averaging on species abundances of terrestrial snails may be minor. Moreover, time-averaged paleosols did not exhibit a significantly higher proportion of shells as compared to non-time-averaged paleosols, which supports the hypothesis that time-averaging effects may be negligible and, therefore, taxonomic variations across paleosols arise primarily from ecological mechanisms. Caution in interpretation is warranted, however, due to the uneven sample sizes between groups and the small number of paleosols with minimal time-averaging (n = 4) relative to those with multi-millennial time-averaging (n = 7). Thus, additional research is recommended to further test this hypothesis for terrestrial shelly accumulations.

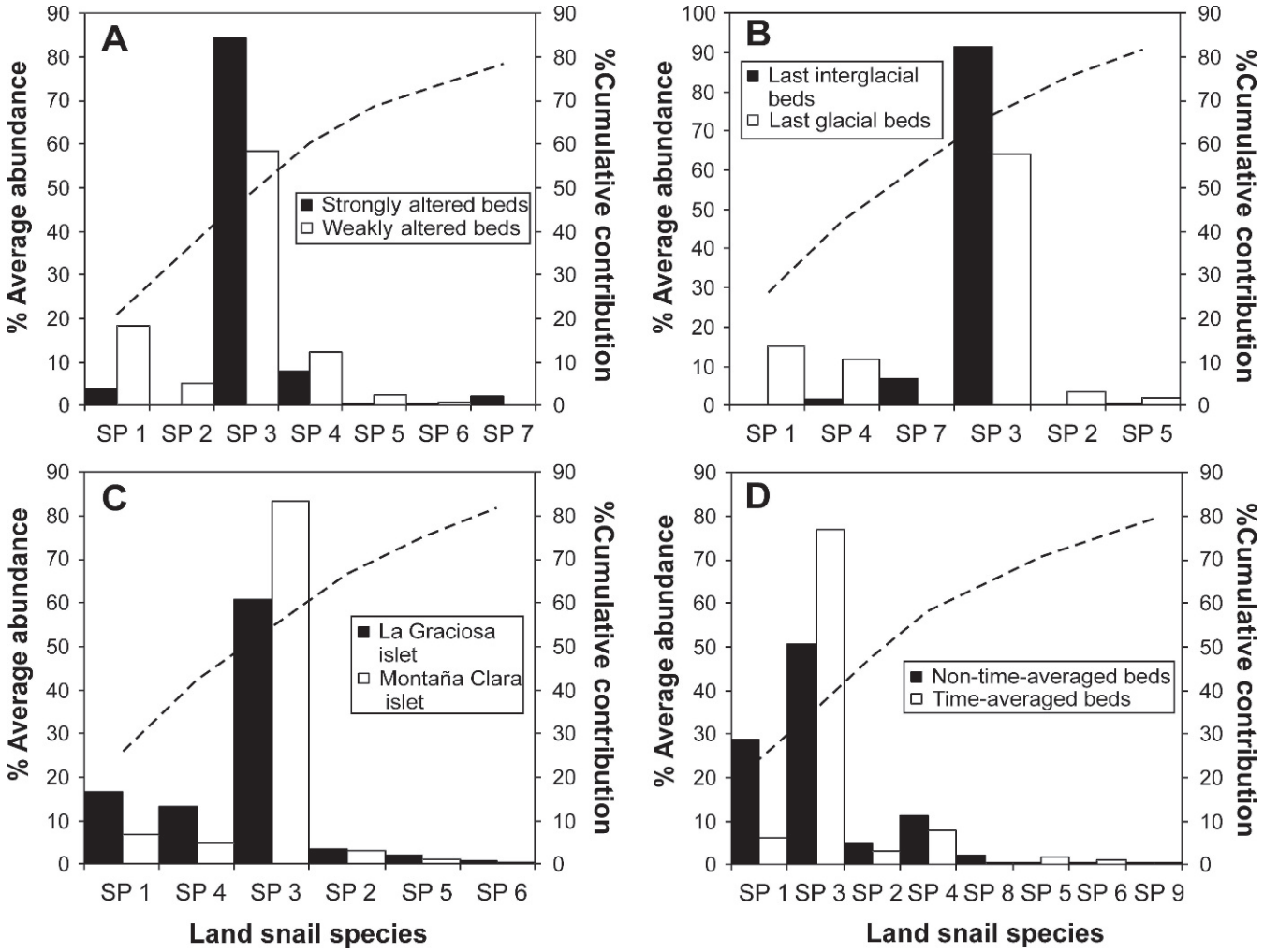


**FIGURE 8**—SIMPER analysis results indicating the average species abundance that most account for the Bray-Curtis dissimilarities between groups. Bars represent the average proportional abundances of species and dashed lines represent the proportional contribution of species that cumulatively explain the mismatches between groups. A) Taxonomic dissimilarity between taphofacies. B) Taxonomic dissimilarity between age intervals. C) Taxonomic dissimilarity between La Graciosa and Montaña Clara islets. D) Taxonomic dissimilarity between non-time-averaged and multimillennial time-averaged paleosols. Snail species are as follows: SP 1 = *Theba arinagae*, SP 2 = *Pomatias lanzarotensis*, SP 3 = *T. geminata*, SP 4 = *Monilearia monilifera*, SP 5 = *Rumina decollata*, SP 6 = *Hemicycla sarcostoma*, SP 7 = *H. flavistoma*, SP 8 = *Ferussacia fritschi*, SP 9 = *Cryptella* sp. Note that SP 4, SP 8, and SP 9 represent taxa with likely low durability shells, whereas the rest of species embody shells classified as highly durable (see text and Fig. 3).

## Temporal Variation in Ecology and Taphonomy

Taphonomic and ecologic characteristics of shell remains varied through the Pleistocene and Holocene in the paleosols analyzed in this study (Fig. 5). Snail assemblages exhibited greater shell abundance in paleosols exposed during the last glacial, whereas shell abundance declined in paleosols from the Last Glacial Maximum (LGM: ~17–20 kyr BP in this study) and Holocene (Figs. 5A–B). Thus, higher shell input rates occurred during the formation of paleosols throughout the last glacial whereas lower shell input rates likely dominated in paleosols formed during the last interglacial (Figs. 5A–B). The decline in shell input rates inferred from the interglacial paleosols is interpreted as an indication of declining biological productivity.

Moisture is one of the most important environmental factors affecting land snail abundance because snails are highly sensitive to desiccation via evaporation of body water under dry conditions (Solem, 1984; Cook, 2001). Indeed, land snail abundance correlates with humidity, and humidity is then an especially crucial ecological driving factor in semiarid habitats (e.g., Heller, 1984; Cook, 2001; Martin and Sommer, 2004; Chiba, 2007). The oxygen isotopic composition of fossil land snail shells from the eastern Canary Archipelago indicates that the Canary Island climate has not remained steady over the last glacial-interglacial cycle (Yanes, 2005; Yanes et al., 2011). Relative humidity has fluctuated but experienced overall a decline over the last ~50,000 years BP, resulting in the current semiarid conditions in the area observed today (Yanes et al., 2011, fig. 5), which is consistent with the aridification process in the nearby northwest Africa (e.g., Gasse et al., 1990, 2008; Gasse, 2000). The general decline in snail shell abundances from the oldest (Pleistocene) to the Holocene paleosols (Figs. 5A–B) could be explained in part by an overall drop in humidity because greater shell abundance often reflects the species' optimum climatic conditions (e.g., Tomašových et al., 2006b). The documented wetter conditions during the last glacial period in the eastern Canary Islands (Yanes et al., 2011), therefore, offered a favorable environmental scenario for ancient land snail populations that presumably enhanced their proliferation (e.g., Heller, 1984; Solem, 1984; Cook, 2001; Martin and Sommer, 2004; Chiba, 2007).

Variations in island area (i.e., habitable space) resulting from sea-level fluctuations during glacial–interglacial cycles can affect snail population size (e.g., Davison and Chiba, 2008). The islets of the NE Canary Archipelago were interconnected due to substantially lower sea level during the last glacial interval (García-Talavera, 1997, 1999).

Thus, a greater abundance of snails is expected on oceanic islands during glacial cycles than interglacial periods (e.g., Davison and Chiba, 2008). This matching pattern of declining island area (and relative humidity) with the decrease of proportional shell abundances through time supports the hypothesis that more abundant shells represent higher net shell input rates (i.e., higher biological productivity). The data indicate that both island area (habitable space) and humidity appear to have played an important role as controlling factors on shell abundance in the study region. Nonetheless, such additional ecological factors as inter- and intraspecific interactions and predation remain to be evaluated in order to discern their influence on the fluctuation of local land snail abundances (e.g., Huntley et al., 2008).

Paleosols from the last glacial period generally exhibit a lower proportion of fragmentation (Figs. 5C–D) and higher percentages of both carbonate coating (Figs. 5G–H) and color preservation (Figs. 5I–J). In contrast there are no definite patterns of corrosion observed through time (Figs. 5E–F). This suggests that shells found in Pleistocene paleosols were destroyed at lower rates than those from Holocene paleosols. Carbonate coatings are preferentially found in paleosols with lower taphonomic alteration, suggesting that carbonate coatings enhanced shell preservation (see also Yanes et al., 2008). Carbonate coating genesis occurs from a complex combination of environmental and temporal factors. Time appears to have been an important controlling factor in carbonate crust formation during paleosol development from the last glacial period of the Canary Islands because shells found in older paleosols exhibit more carbonate coatings than those in younger paleosols (e.g., Retallack, 2001; Pustovoytov, 2003).

### Shell Preservation and Shell Abundance Genesis

Paleontologists need to understand the scale of shell input and sedimentation rates during paleosol genesis because relatively high shell abundance levels in a stratigraphic horizon may be a consequence of either a lack of sediment input or high biological production (Tomašových et al., 2006a). Several hypothetical scenarios have been proposed to explain shell concentration genesis (Kidwell, 1985, 1986) and are summarized by Tomašových et al. (2006b) based on net sedimentation rate and net shell-input rate. The R-sediment model (Kidwell, 1985, 1986), where sedimentation rates vary and shell input rates are constant, predicts a positive correlation between shell abundance and taphonomic alteration as a consequence of longer shell exposure during lower sedimentation. Alternatively, the R-shell model (Kidwell, 1985, 1986), where sedimentation rates are constant while shell input rates vary, predicts a negative correlation between shell abundance and taphonomic alteration as a response of higher net shell input rate and or a decrease of shell destruction rate (Tomašových et al., 2006b). In the present study, the negative correlation between land snail shell abundance and fragmentation at the assemblage level (Table 4) corresponds with a variable shell input rate as suggested by the R-shell model. This indicates that the higher shell abundance for some paleosols may be a consequence of the rise of dead-shell production rates during high productivity times in the Canary Islands—times when the proportion of recently dead organisms increased. This proposed burial scenario for land snail shells is further supported by additional environmental and taphonomic evidence.

Highly time-averaged paleosols may potentially accumulate a larger number of noncontemporaneous shells (=higher shell abundance) than paleosols with minimal time averaging (e.g., Behrensmeyer et al., 2000). The lack of a significant relationship between the scale of time averaging and shell abundances in the Canary Island paleosols indicates that the proportion of shells was not severely affected by the scale of time averaging. In addition, the scale of time averaging did not correlate with paleosol age because the extent of time averaging remained steady across horizons (Yanes et al., 2007). These results denote a net sedimentation rate that was relatively uniform across the studied paleosols (i.e., similar time of soil formation) and support the hypothesis that variations in net shell input rates rather than net sedimentation rates affect shell abundances across paleosols. Variations in shell abundances of land snails from the NE islets of the Canary Islands likely reflect changes in biological productivity of snails and, as such, may be used to infer oscillations in the local environmental and ecological conditions.

Pleistocene–Holocene land snail shells from carbonate-rich paleosols have negligible diagenetic alterations from the original aragonitic composition and microstructure as confirmed by XRD results (Table 3) and SEM micrographs (Fig. 4). This result coincides with previous findings of minimal diagenetic alteration of last glacial terrestrial shell remains from Mala section, Lanzarote Island (Yanes et al., 2008). The significance of these results is twofold. First, the excellent microstructure preservation implies a low probability of Pleistocene–Holocene terrestrial shells being chemically altered and removed from the fossil record through such diagenetic processes as dissolution and recrystallization. The lack of diagenetic removal of shell remains supports the hypothesis that variations in shell abundance can be attributed to biological, rather than chemical, processes. Second, the shell material analyzed in this study is suitable for such future geochemical analyses as stable isotopes and or trace element analyses to infer quantitatively the paleoenvironment of the Canary Islands during the Pleistocene and Holocene.

## CONCLUSIONS

Pleistocene-Holocene (~44–5 kyr BP) land snail shell assemblages from the islets of the NE Canary Archipelago were studied through XRD, SEM micrographs, and relevant quantitative taphonomic and ecological variables. Shell material has not been diagenetically modified and, therefore, is suitable for future geochemical studies to infer paleoenvironmental conditions. Higher shell abundance reflects net shell input rate and lower shell destruction rate rather than lower sedimentation rate. Shell assemblages were grouped into two distinctive taphofacies, which contain significantly different proportional species abundances. Both strongly and weakly altered taphofacies, however, hold shelly taxa with similar durability and, therefore, strongly variable shell-specific destruction rates were unlikely during paleosol formation. Temporal variations among different taphonomic and ecological variables indicate variable environmental conditions during the shell burial process over the last glacial-interglacial cycle. The apparent decline in shell abundance from the Pleistocene to the Holocene may be explained in part by the documented local ultimate decrease in relative humidity and island area, which reduced the biological productivity of the land snails, resulting in lowered net shell input rates. This study demonstrates that land snail shell assemblages potentially preserve the original community and may be used to faithfully infer changes in ancient terrestrial ecosystems.

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