



# Taphonomy and compositional fidelity of Quaternary fossil assemblages of terrestrial gastropods from carbonate-rich environments of the Canary Islands

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Quaternary aeolian deposits of the Canary Islands contain well-preserved terrestrial gastropods, providing a suitable setting for assessing the taphonomy and compositional fidelity of their fossil record over ~13 kyr. Nine beds (12, 513 shells) have been analysed in terms of multivariate taphonomic and palaeoecological variables, taxonomic composition, and the stratigraphic and palaeontological context. Shells are affected by carbonate coatings, colour loss and fragmentation. Shell preservation is size-specific: juveniles are less fragmented and show colour preservation more commonly than adults. In palaeosols, the adult shell density correlates negatively with the proportion of fragmented adults, negatively with the proportion of juveniles, and positively with the proportion of adults with coatings. High bioturbation intensity in palaeosols is associated with low shell fragmentation and high proportion of shells with coatings. These relationships imply that high adult density in palaeosols was driven by an increase in shell production rate (related to a decrease in predation rates on adults and a decrease in juvenile mortality) and a decrease in shell destruction rate (related to an increase in durability enhanced by carbonate precipitation). In dunes, the relationships between taphonomic alteration, shell density and bioturbation are insignificant. However, dune assemblages are characterized by a lower frequency of shells with coatings and higher rates of colour loss, indicating lower shell durability in dunes than in palaeosols. Additionally, non-random differences in the coating proportion among palaeosols imply substantial temporal variation in the rate of carbonate crust formation, reflecting long-term changes in bioturbation intensity that covaries positively with shell preservation. Dunes and palaeosols do not differ in species abundances despite differences in the degree of shell alteration, suggesting that both weakly and strongly altered assemblages offer data with a high compositional fidelity. Carbonate-rich terrestrial deposits originating in arid conditions can enhance the preservation of gastropods and result in fossil assemblages that are suitable for palaeoecological and palaeoenvironmental studies of terrestrial ecosystems. □ *Aeolian deposits, Canary Islands, land snail shell assemblages, Quantitative Taphonomy, Quaternary.*

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In recent years, taphonomic studies of shell-rich accumulations have become increasingly quantitative, as researchers recognized that such strategy (1) offers insights into the processes that led to the formation of fossil assemblages, (2) helps to estimate the extent of time-averaging (age mixing of fossils) within assemblages, and (3) provides clues regarding the accuracy (fidelity) with which the original biological

signals are preserved by those assemblages (e.g. Allison & Briggs 1991; Flessa & Kowalewski 1994; Kowalewski *et al.* 1994, 1998; Brett 1995, 1998; Meldahl *et al.* 1997; Martin 1999; Behrensmeier *et al.* 2000, 2005; Kidwell 2001, 2002; Yesares & Aguirre 2004). However, these quantitative strategies have been applied primarily to marine shell beds. In contrast, only several in-depth quantitative taphonomic

studies have been devoted to freshwater (Hanley & Flores 1987; Cohen 1989; Cummins 1994; Brown *et al.* 2005) and terrestrial (Briggs *et al.* 1990; Carter 1990; Cadée 1999; Rundell & Cowie 2004; Castillo *et al.* 2006) shell concentrations, and their taphonomy is thus poorly known.

Land snail shells are one of the most common terrestrial remains preserved in a great variety of deposit types such as caves (e.g. Ložek 1964), loess (e.g. Rousseau 1990), tufa (e.g. Preece & Day 1994), archaeological deposits (e.g. Balakrishnan *et al.* 2005), aeolian deposits (e.g. Brooke *et al.* 2003a, b; Castillo *et al.* 2006), and palaeosols (e.g. Ložek 1964; Retallack 1998, 2001; Pickford 2002; Ortiz *et al.* 2006). They are used widely in interpreting palaeoclimate and palaeoenvironments (e.g. Goodfriend 1999), inferring ecological and evolutionary processes (e.g. Goodfriend & Gould 1996; Chiba 1998, 2004), and constraining Quaternary geochronology (e.g. Goodfriend *et al.* 1996; Brooke *et al.* 2003a, b; Ortiz *et al.* 2006). Given their wide applicability in geosciences and considering that their preservation potential is assumed to be generally low (Cadée 1999), evaluating how and under what conditions land snail shells can be preserved is of particular importance. The taphonomic investigation of terrestrial gastropod shell accumulations is the primary goal of this project, which targets Quaternary successions of the Canary Islands.

In the eastern islands of the Canary Archipelago, thick sequences of Late Quaternary aeolian deposits consisting of alternations of marine dunes and palaeosols are preserved among volcanic rocks. These deposits contain abundant vertebrates (Michaux *et al.* 1991; Boye *et al.* 1992) and invertebrates, including terrestrial gastropods (Yanes *et al.* 2004), brood cells of solitary bees (e.g. Alonso-Zarza & Silva 2002), and nests of coleopterans (Genise & Edwards 2003). Terrestrial gastropods of the Canary Islands have been the target of numerous taxonomic, zoogeographic (e.g. Alonso *et al.* 2006; Castillo *et al.* 2006; Ibáñez *et al.* 2006), and geochronological studies (Hillaire-Marcel *et al.* 1995; Ortiz *et al.* 2006).

The study area is an attractive target for taphonomic studies of terrestrial shell deposits for several reasons. First, the literature on taphonomic processes affecting shell accumulations formed in dune and palaeosol settings is very limited. Second, Ložek (1964) explicitly suggested that carbonate-rich deposits are favourable for preservation of land snails. The dunes and palaeosols of the Canary Islands, composed of marine bioclastic carbonates, provide an opportunity to test this hypothesis directly. Finally, recent quantitative analyses of shells dated by amino-acid racemisation have established the levels of time-averaging affecting the sites targeted in this study (Yanes *et al.* 2007),

providing a useful starting point for an in-depth taphonomic study.

Specifically, this study aims to (1) quantify the taphonomic characteristics of fossil assemblages with dispersed and loosely-packed snail shells, (2) assess size-specific differences in preservation by comparing juvenile and adult shells, (3) evaluate environmental effects on shell preservation by contrasting their preservation in dune versus palaeosol settings, and (4) analyse temporal variations in taphonomic preservation of shells over an interval of ~13 kyr of the Early Quaternary. In addition to those four goals, this study also provides a testing ground for evaluating the compositional fidelity (i.e. the quantitative faithfulness of the representation of species composition to the original biological signal) of fossil gastropod assemblages from terrestrial settings, and for assessing whether such assemblages provide useful information about the ecology of gastropod-dominated communities. The compositional fidelity of a fossil assemblage cannot be tested confidently by direct comparison to local living communities without many assumptions. However, we indirectly evaluate fidelity by analysing differences in composition among samples differing in the degree of taphonomic alteration (Tomašových 2006).

## Methods

### *Geographical location and sampling strategy*

Lanzarote Island, the easternmost island of the Canary Archipelago (Fig. 1), is a volcanic, oceanic island located ~160 km off the coast of Morocco (29°N and 22°W). Pliocene to Holocene volcanics (Fig. 1A) are commonly found here (Coello *et al.* 1992; Carracedo & Rodríguez-Badiola 1993). The northern part of the island includes extensive aeolian deposits consisting primarily of bioclastic sands of marine origin. This study focuses on Mala Section (LMA), located in the Mala village in the north-eastern part of Lanzarote Island (Fig. 1A). The section consists of Quaternary aeolian deposits dated between  $39.8 \pm 4.6$  kyr BP at the base and  $27.4 \pm 4.4$  kyr BP (Ortiz *et al.* 2006) at the top (Fig. 1B–2). The Mala section is formed by couplets of alternating dune and palaeosol beds with well-preserved and abundant shells of land snails and insect cells (Fig. 1B–2). Seven of the palaeosol beds and two of the dune beds were sampled and dry-sieved using 1-mm mesh size. Six to nine replicate samples, spaced laterally at a distance of ~0.5 m, were taken from each of the nine targeted beds (Table 1). Each replicate sample consists of about 5 kg of sediment before sieving.

Table 1. Taphonomic features of the land snail assemblages from the Mala section (Lanzarote, Canary Archipelago).

Sample ID	Age (kyr BP)	Type of sediment	Total number of species	TNR		MNI		FR		CC		CP		B
				Adults	Juveniles	Nests								
LMA-1A-1	38.6 ± 6.9	Dune	2	72	10	23	8	61	2	72	10	18	8	56
LMA-1A-2	38.6 ± 6.9	Dune	2	112	19	46	19	78	1	112	19	20	10	76
LMA-1A-3	38.6 ± 6.9	Dune	2	60	13	20	12	49	1	26	4	20	7	70
LMA-1A-4	38.6 ± 6.9	Dune	3	121	12	45	12	80	0	69	3	31	9	60
LMA-1A-5	38.6 ± 6.9	Dune	2	108	17	28	13	88	4	68	12	40	10	49
LMA-1A-6	38.6 ± 6.9	Dune	1	49	5	20	5	31	0	32	2	20	2	58
LMA-1A-7	38.6 ± 6.9	Dune	3	92	11	31	11	68	0	82	7	12	5	62
LMA-1A-8	38.6 ± 6.9	Dune	4	89	20	33	17	65	4	56	7	39	11	40
LMA-1A-9	38.6 ± 6.9	Dune	2	61	10	22	9	43	1	46	6	24	8	48
LMA-1B-1	38.6 ± 6.9	Palaeosol	3	210	145	73	140	168	31	210	145	51	29	50
LMA-1B-2	38.6 ± 6.9	Palaeosol	4	171	134	76	128	120	14	171	134	28	31	62
LMA-1B-3	38.6 ± 6.9	Palaeosol	4	263	116	114	112	188	8	263	116	68	42	43
LMA-1B-4	38.6 ± 6.9	Palaeosol	5	218	122	102	120	146	7	218	122	31	22	55
LMA-1B-5	38.6 ± 6.9	Palaeosol	3	178	98	58	96	131	9	178	98	48	37	26
LMA-1B-6	38.6 ± 6.9	Palaeosol	3	192	119	65	115	149	11	192	119	49	31	17
LMA-2B-1	39.8 ± 4.6	Palaeosol	3	143	60	42	54	121	11	143	60	40	19	24
LMA-2B-2	39.8 ± 4.6	Palaeosol	3	152	106	44	96	132	21	142	86	58	31	28
LMA-2B-3	39.8 ± 4.6	Palaeosol	3	96	56	23	50	84	18	70	30	32	17	16
LMA-2B-4	39.8 ± 4.6	Palaeosol	7	173	97	59	88	138	19	141	88	50	23	20
LMA-2B-5	39.8 ± 4.6	Palaeosol	6	182	72	61	67	150	10	144	59	39	28	19
LMA-2B-6	39.8 ± 4.6	Palaeosol	7	154	94	67	90	126	16	130	77	41	33	18
LMA-3B-1	34.9 ± 5.3	Palaeosol	4	134	16	16	12	126	7	9	0	44	11	14
LMA-3B-2	34.9 ± 5.3	Palaeosol	4	69	6	13	5	60	1	8	1	25	3	16
LMA-3B-3	34.9 ± 5.3	Palaeosol	4	241	30	16	21	238	11	38	0	58	26	12
LMA-3B-4	34.9 ± 5.3	Palaeosol	4	258	42	31	29	254	21	52	0	106	30	11
LMA-3B-5	34.9 ± 5.3	Palaeosol	3	102	11	15	6	101	5	13	0	43	7	17
LMA-3B-6	34.9 ± 5.3	Palaeosol	5	347	35	48	28	337	8	29	0	148	27	13

Table 1. Continued

Sample ID	Age (kyr BP)	Type of sediment	Total number of species	TNR		MNI		FR		CC		CP		B
				Adults	Juveniles	Nests								
LMA-4B-1	30.6 ± 4.2	Palaeosol	3	133	95	51	73	102	28	2	0	43	55	10
LMA-4B-2	30.6 ± 4.2	Palaeosol	2	154	131	57	108	110	26	1	2	50	79	5
LMA-4B-3	30.6 ± 4.2	Palaeosol	3	108	125	37	89	82	38	3	0	32	70	40
LMA-4B-4	30.6 ± 4.2	Palaeosol	3	166	120	72	90	112	40	7	1	49	59	31
LMA-4B-5	30.6 ± 4.2	Palaeosol	3	175	121	71	81	131	44	1	0	60	57	18
LMA-4B-6	30.6 ± 4.2	Palaeosol	2	183	174	83	109	124	73	3	1	72	102	20
LMA-5A-1	31.1 ± 3.2	Dune	6	111	51	68	48	67	7	76	23	12	28	110
LMA-5A-2	31.1 ± 3.2	Dune	4	110	35	58	33	75	3	56	21	27	24	113
LMA-5A-3	31.1 ± 3.2	Dune	8	91	121	70	53	88	8	62	17	22	36	127
LMA-5A-4	31.1 ± 3.2	Dune	4	100	30	52	30	72	0	35	8	30	16	58
LMA-5A-5	31.1 ± 3.2	Dune	5	95	26	45	24	74	4	35	9	26	15	104
LMA-5A-6	31.1 ± 3.2	Dune	4	123	22	47	22	91	4	64	7	31	16	60
LMA-5B-1	31.1 ± 3.2	Palaeosol	8	224	59	165	48	129	9	64	11	62	26	27
LMA-5B-2	31.1 ± 3.2	Palaeosol	6	144	23	82	19	105	5	81	31	22	11	24
LMA-5B-3	31.1 ± 3.2	Palaeosol	3	97	13	48	12	61	2	52	9	16	4	18
LMA-5B-4	31.1 ± 3.2	Palaeosol	6	206	20	118	18	146	5	71	7	33	8	6
LMA-5B-5	31.1 ± 3.2	Palaeosol	8	188	23	108	19	118	7	29	5	49	11	11
LMA-5B-6	31.1 ± 3.2	Palaeosol	6	233	37	161	33	157	6	190	26	29	2	34
LMA-6B-1	27.7 ± 4.4	Palaeosol	5	169	54	96	48	122	19	35	13	91	41	10
LMA-6B-2	27.7 ± 4.4	Palaeosol	5	202	67	121	56	152	25	19	0	113	30	21
LMA-6B-3	27.7 ± 4.4	Palaeosol	5	116	44	60	28	105	13	13	0	57	18	8
LMA-6B-4	27.7 ± 4.4	Palaeosol	5	112	31	43	23	100	20	7	1	62	14	10
LMA-6B-5	27.7 ± 4.4	Palaeosol	5	165	60	92	51	121	18	17	7	111	17	5
LMA-6B-6	27.7 ± 4.4	Palaeosol	5	125	35	71	31	89	15	11	0	77	12	12
LMA-7B-1	28.2 ± 5.1	Palaeosol	5	389	73	265	63	206	22	381	73	58	20	68
LMA-7B-2	28.2 ± 5.1	Palaeosol	4	276	66	175	59	165	16	276	66	91	28	31
LMA-7B-3	28.2 ± 5.1	Palaeosol	5	302	57	230	46	174	7	302	57	v89	30	58
LMA-7B-4	28.2 ± 5.1	Palaeosol	5	148	31	100	31	86	5	148	31	v69	10	46
LMA-7B-5	28.2 ± 5.1	Palaeosol	6	256	38	168	38	156	0	256	38	100	7	62
LMA-7B-6	28.2 ± 5.1	Palaeosol	7	277	53	184	51	160	8	277	53	103	21	72

TNR, total number of shell remains; MNI, minimum number of individuals; FR, number of fragmented shells; CC, number of shells with carbonate coating; CP, number of shell with colour preservation; B, bioturbation expressed as number of insect nests. Numerical ages by amino acid dating calibrated against radiocarbon reported after Ortiz *et al.* (2006).

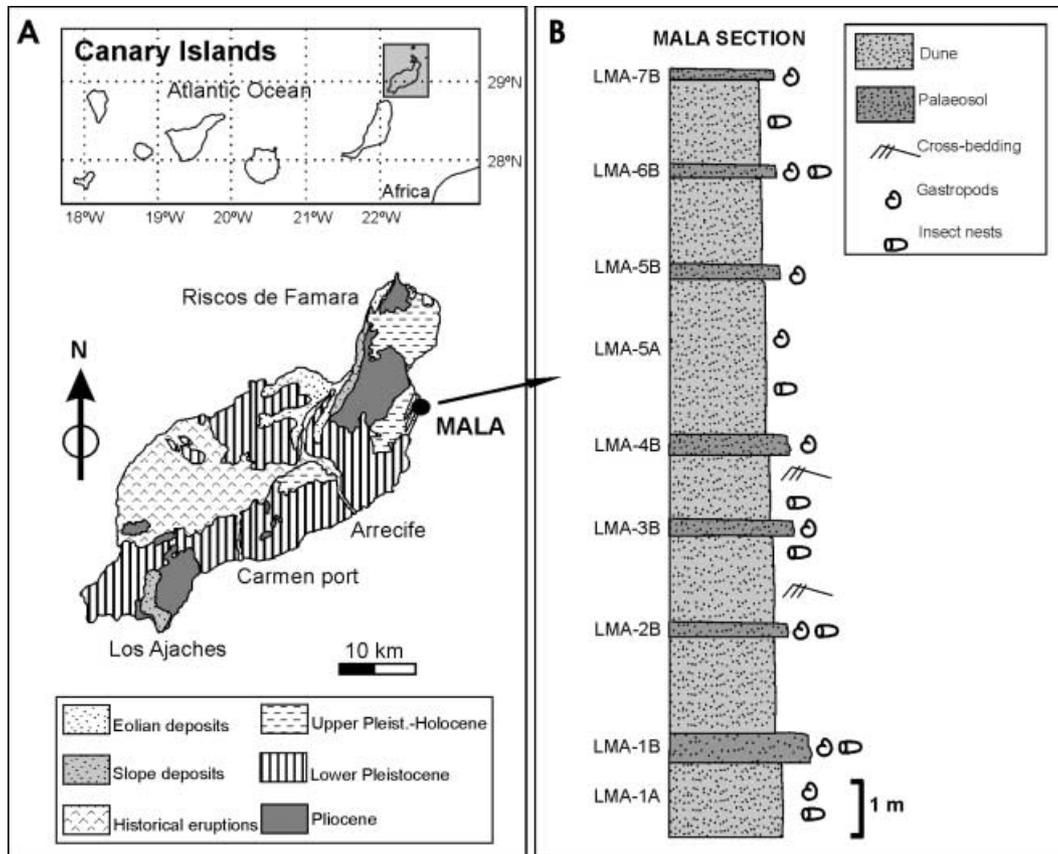


Fig. 1. □A. Geographical location of the Lanzarote Island and the Mala locality. □B. Stratigraphic column of the Mala section (LMA). Labels at the left margin of the stratigraphic column indicate the sampled beds (seven palaeosols and two dunes).

### Laboratory study and data analysis

The sampled material, consisting of a total of 57 samples and 12, 513 specimens (Table 1), was deposited at the Animal Biology Department (University of La Laguna). All specimens were analysed in the laboratory under binocular microscope. A total of eight palaeoecological and taphonomic variables were tallied for each sample, and then averaged across sets of samples collected from the same horizon to estimate a mean score per sampled bed: (1) minimum number of individuals (MIN), (2) fragmentation, (3) pedogenic carbonate coating, (4) roundness of fragments, (5) colour preservation, (6) proportion of juveniles and adults, (7) mineralogical composition of the shell, and (8) intensity of bioturbation by insects (coleopterans and hymenopterans). The first five variables were evaluated separately for adult and juvenile shells of land snails.

All specimens with length below ~6 and width below ~8 mm (i.e. specimens with dimensions twice lower than the average values) were classified as juveniles. Adults display a more globose shape with no umbilicate shell, while juveniles show a slightly depressed

globular shape and commonly possess umbilicate shell (Fig. 3A). In addition, the aperture size relative to the whole shell size is significantly larger in juvenile specimens than in adults (Fig. 3A). Specimens were classified as juveniles only if both size and morphology criteria were fulfilled. Note that specimens were assigned to juveniles and adults only when the aperture was preserved.

Minimum number of individuals considered only specimens that preserve the embryonic shell (= protoconch). Because each sample was standardized in terms of sediment volume, MNI represents a measure of shell density. The proportion of juveniles is measured as the number of juveniles divided by the sum of MNI, and the proportion of adults as the number of adults divided by the sum of MNI. These measures thus sum to unity and summarize whether size-frequency distributions are dominated by juveniles or adults. Fragmentation is measured as the number of fragments divided by the sum of fragments and whole specimens. Complete shells are defined as those that preserve more than 90% of the original entire skeleton, while fragmented shells represent any piece of gastropod shells that have lost more than the 10%

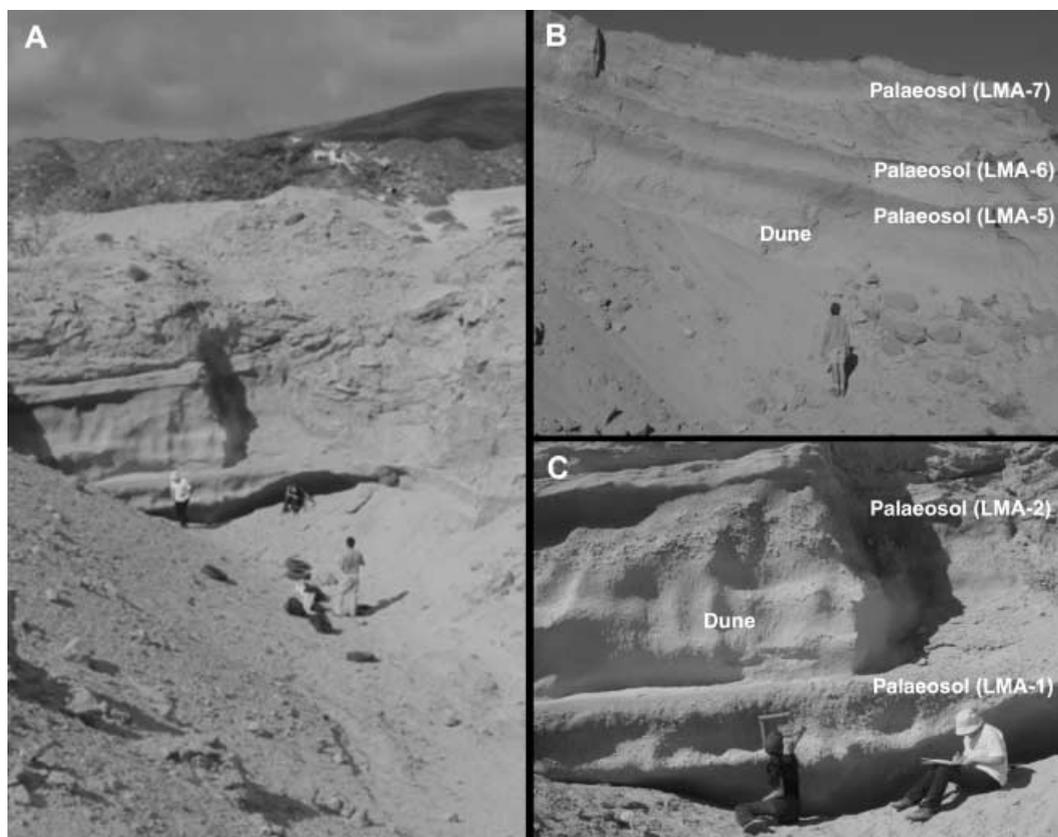


Fig. 2. □A. General view of the Mala section on the Lanzarote Island. The darker beds correspond to palaeosols while the brighter layers represent dunes. □B. A close-up view of the upper part of the Mala section, showing some of the sampled palaeosols. □C. A close-up view of the lower part of the Mala section, showing the oldest sampled stratigraphic beds.

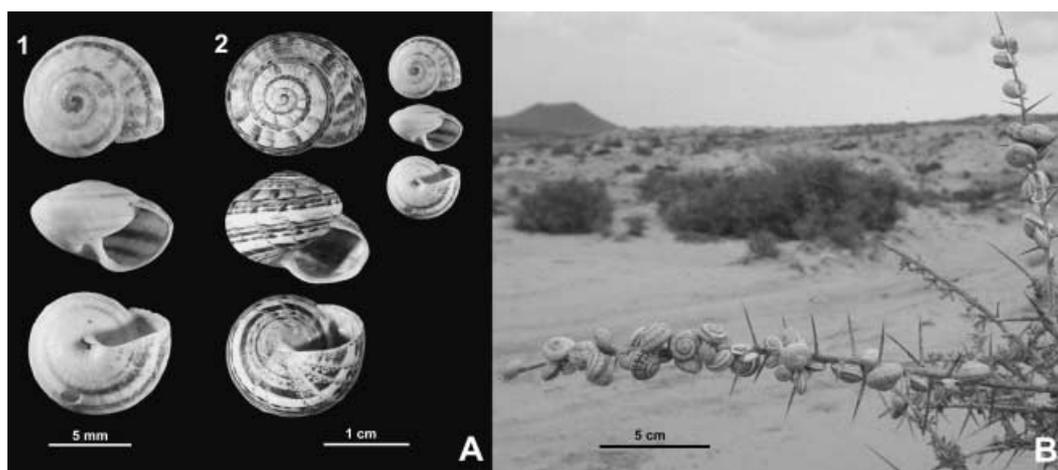


Fig. 3. □A. Photograph of the most common land snail species (*Theba geminata*) in the studied shell assemblages, in juvenile (1) and adult (2) ontogenetic state. Note that adult individuals have globose-spherical shape with no umbilicate shell, while juveniles display a depressed globose shape and in many cases, umbilicate shell. □B. Photograph of numerous live specimens of the land snail *Theba geminata* from the Cantera de Melián locality, Fuerteventura Island-Canary Archipelago, aggregated on a shrub during a resting time.

of the shell. The sampling procedure (dry sieving) did not contribute notably to shell breakage (distinct complete specimens noted in the unprocessed material were invariably recovered afterwards in the sieved material). Moreover, the fragmentation

pattern (i.e. fragment size) does not vary strongly among samples, so even if the bias is notable, it should affect all compared samples and groups of samples in a similar manner, making comparative analyses reasonably robust.

Colour preservation was quantified as the proportion of shells with some original colour preserved. Carbonate coating was quantified as the proportion of shells with a calcareous crust. Roundness refers to the degree of smoothing of the edges of the shell fragments. Further quantitative analyses do not incorporate this variable because no fragmented shells showed any traces of rounding. The intensity of bioturbation is measured as the number of insect nests per sample (= per 5 kg of sieved sediments). In order to identify the mineralogical composition, X-ray diffraction analyses (using PANalytical X'Pert (PANalytical B.V., Almelo, the Netherlands) for polycrystalline samples) were performed for 16 gastropod shells in the Instituto Universitario de Bio-orgánica Antonio González (IUBIO-AG) of the University of La Laguna-Spain.

In order to interpret taphonomic pathways, two distinct sources of variation in taphonomic alteration need to be constrained (Best & Kidwell 2000): (1) intrinsic factors that are related to traits of shell producers, and (2) extrinsic factors that correspond to environmental factors. Gastropod species of the Mala section are generally similar in their intrinsic properties, including their mode of life, shell size, thickness, and ornamentation. They can be divided into three morphological groups: (1) long trochospiral shells, such as *Rumina*, *Ferussacia* and *Pomatias* species; (2) laminar or spatula-like shells, such as the skeleton of *Cryptella* and *Caracollina* species; and (3) globose-spherical shells, such as *Theba*, *Hemicycla*, *Plutonia* and *Monilearia* species. Large-sized shells (~26 mm) are represented by *Hemicycla*, *Rumina* and *Plutonia* species; medium-sized shells (~15 mm) are represented by *Theba* and *Pomatias* species; and small-sized shells (~7 mm) are represented by *Cryptella*, *Monilearia*, *Caracollina* and *Ferussacia* species. The two first morphological groups are rare (3.6 and 1.4%, respectively), while the last one accounts for more than the 95% of individuals, and more than 80% of the fossil assemblages are characterized by medium-sized individuals. Gastropod species living today in the Mala section area display, in general, an epifaunal life habit (personal observations, 2004). The exception is *Pomatias lanzarotensis*, which displays the infaunal mode of life during some parts of the day, but this species represents only ~1.6% of all specimens included in this study. *Theba* is most likely characterized by an annual to biennial cycle life, which was demonstrated in the congeneric species *Theba pisana* (e.g. Cowie 1984). All of the sampled species, when observed today, are mainly active at night and/or during wet weather. At all other times, they tend to aggregate on shrubs and bushes (Fig. 3B), which are their primary food source (personal observations, 2004).

Therefore, although taphonomic variables represent pooled estimates of preservation traits of all species, variation in intrinsic factors is minimized, owing to the strong dominance of globose-spherical and medium-sized shells of the epifaunal genus *Theba* (Fig. 3A–B). However, we control for variation in ontogenetic stage by separate analyses of preservation of juveniles and adults. In order to control for variation in extrinsic factors, we analysed separately preservation patterns in palaeosols and dunes.

Multiple approaches are used to analyse differences in preservation between (1) nine beds (i.e. do individual beds represent unique taphofacies?), (2) juveniles and adults, (3) dunes and palaeosols, and (4) seven time intervals. These included univariate analyses, focused on means of taphonomic variables (with 95% bootstrapped confidence intervals), and multivariate analyses ordinating 57 samples in low-dimensional space, using non-metric multidimensional scaling (NMDS) and the Manhattan distance. Analyses of similarities (ANOSIM) evaluate whether non-random differences in taphonomic preservation can be demonstrated for (1) all beds, (2) juveniles and adults, (3) dunes and palaeosols, and (4) seven time intervals. NMDS and ANOSIM were based on six taphonomic variables, including proportions of juvenile and adult fragments, juveniles and adults with colour preservation, and juveniles and adults with carbonate coatings. Spearman rank correlation coefficient was used to measure the relation between palaeoecological and taphonomic variables on one hand and shell density on the other hand. To evaluate compositional fidelity, all samples were subdivided into two groups differing in the taphonomic alteration. The two groups were discriminated with cluster analysis based on the Manhattan distance and group-averaging linkage method. Proportional abundances of 11 land snail species were available for 54 samples. Finally, NMDS and ANOSIM analyses based on Bray–Curtis similarity and untransformed proportional species abundances were used to evaluate whether there are non-random compositional differences among weakly and highly altered taphofacies (1) in the complete succession of the Mala section, and (2) separately for the lower and upper parts of the Mala section.

## Results

### *Diversity and taxonomic composition*

A total of 11 land snails taxa were identified in the sorted samples (Table 2). Two species, represented by *Theba geminata* and *T. arinagae*, dominate in dunes and palaeosols, and their relative abundances generally

Table 2. Taxonomic composition of the studied land snail assemblages from Mala section, Lanzarote Island-Canary Archipelago.

Class Gastropoda	
Superorder Caenogastropoda	
Order Neotaenioglossa	
Family Pomatiidae	
<i>Pomatias lanzarotensis</i> (Wollaston, 1878)*	
Superorder Heterobranchia	
Order Pulmonata	
Suborder Stylommatophora	
Family Ferussaciidae	
<i>Ferussacia fritschi</i> (Mousson, 1872)*	
Family Helicidae	
<i>Hemicycla sarcostoma</i> (Webb & Berthelot, 1833)‡	
<i>Theba arinagae</i> (Gittenberger & Ripken, 1987)*†	
<i>Theba geminata</i> (Mousson, 1857)*	
<i>Theba impugnata</i> (Mousson, 1857)*	
Family Hygromiidae	
<i>Canariella plutonia</i> (Lowe, 1861)‡	
<i>Caracollina lenticula</i> (Michaud, 1831)	
Family Cochlicellidae	
<i>Monilearia monilifera</i> (Webb & Berthelot, 1833)*	
Family Parmacellidae	
<i>Cryptella</i> sp.‡	
Family Subulinidae	
<i>Rumina decollata</i> (Linnaeus, 1758)	

\*Endemic species to the Canary Islands.

†Extinct species to Lanzarote and Fuerteventura islands.

‡Endemic genus to the Canary Islands.

exceed 70%. *Theba* dominates (93%) in the lower part of the Mala section (beds 1A–5A). In the upper part of the Mala section (beds 5B–7B), in addition to abundant *Theba* (56%), *Monilearia monilifera* is also common (30%). Other species, represented mainly by *Canariella plutonia*, *Pomatias lanzarotensis*, *Theba impugnata* and *Rumina decollata*, are rare (< 1%). The local sample-level species richness ranges between two and eight species (Table 1). The sample-level

richness, rarefied to the minimum number of 58 individuals, varies across samples between two and six species.

### Preservation of gastropod assemblages

X-ray diffraction analyses of 16 gastropods show that gastropod shells generally retain their original aragonitic composition, although partial replacement by calcite occurred in several specimens (Table 3). The proportion of calcitic replacement is mostly below 10%, although one shell of *Theba arinagae* contained 33% of calcite. Shell fragments do not show any signs of rounding, bioerosion or encrustation by other organisms. In addition, evidence for shell repair was not found in the studied shell material; although it is noteworthy here that Cadée (1995) reported high frequency of shell repair (up to 40%) in land snail species from multiple regions of Europe. Seventy-five per cent of adult shells and 65% of juveniles are fragmented, 54% of adult shells and 50% of juveniles are coated by carbonate crusts, and 32% of adult shells and 47% of juveniles show colour preservation.

In both dunes and palaeosol beds, shells are dispersed or loosely packed rather than densely packed, and tend to be randomly oriented and weakly sorted. The two dunes and seven palaeosols show relatively high variations in mean values of MNI, bioturbation, and proportions of fragmentation, coatings, and colour preservation (Fig. 4A). NMDS ordination and ANOSIM, based on taphonomic variables for combined (juvenile + adult) shell data (Fig. 4B), indicate that within-bed variation in taphonomic preservation is invariably lower than between-bed variation in preservation (global  $R = 0.81$ ,  $P < 0.0001$ ). Twenty-one pairwise comparisons between seven palaeosols

Table 3. Semi-quantitative estimation by X-ray diffraction of the mineralogical composition of several land snail shell species of the Mala section, Lanzarote Island, Canary Archipelago. Numerical ages by amino-acid dating calibrated against radiocarbon reported after Ortiz et al. (2006).

Sample ID	Sediment level type	Age (kyr BP)	Species	Aragonitic (SQ %)	Calcite (SQ %)
LMA-1A-1	Dune	38.6 ± 6.9	<i>Theba arinagae</i>	100	0
LMA-1B-1	Palaeosol	38.6 ± 6.9	<i>Theba geminata</i>	100	0
LMA-2B-1	Palaeosol	39.8 ± 4.6	<i>Theba arinagae</i>	67	33
LMA-2B-2	Palaeosol	39.8 ± 4.6	<i>Theba geminata</i>	100	0
LMA-3B-1	Palaeosol	34.9 ± 5.3	<i>Theba geminata</i>	100	0
LMA-4B-1	Palaeosol	30.6 ± 4.2	<i>Theba geminata</i>	100	0
LMA-5A-1	Dune	31.1 ± 3.2	<i>Theba geminata</i>	94	6
LMA-5B-1	Palaeosol	31.1 ± 3.2	<i>Canariella plutonia</i>	100	0
LMA-5B-2	Palaeosol	31.1 ± 3.2	<i>Pomatias lanzarotensis</i>	96	4
LMA-5B-3	Palaeosol	31.1 ± 3.2	<i>Theba impugnata</i>	96	4
LMA-6B-1	Palaeosol	27.4 ± 4.4	<i>Monilearia monilifera</i>	100	0
LMA-6B-2	Palaeosol	27.4 ± 4.4	<i>Rumina decollata</i>	88	12
LMA-6B-3	Palaeosol	27.4 ± 4.4	<i>Theba arinagae</i>	92	8
LMA-7B-1	Palaeosol	28.2 ± 5.1	<i>Monilearia monilifera</i>	97	3
LMA-7B-2	Palaeosol	28.2 ± 5.1	<i>Rumina decollata</i>	94	6
LMA-7B-3	Palaeosol	28.2 ± 5.1	<i>Theba arinagae</i>	91	9

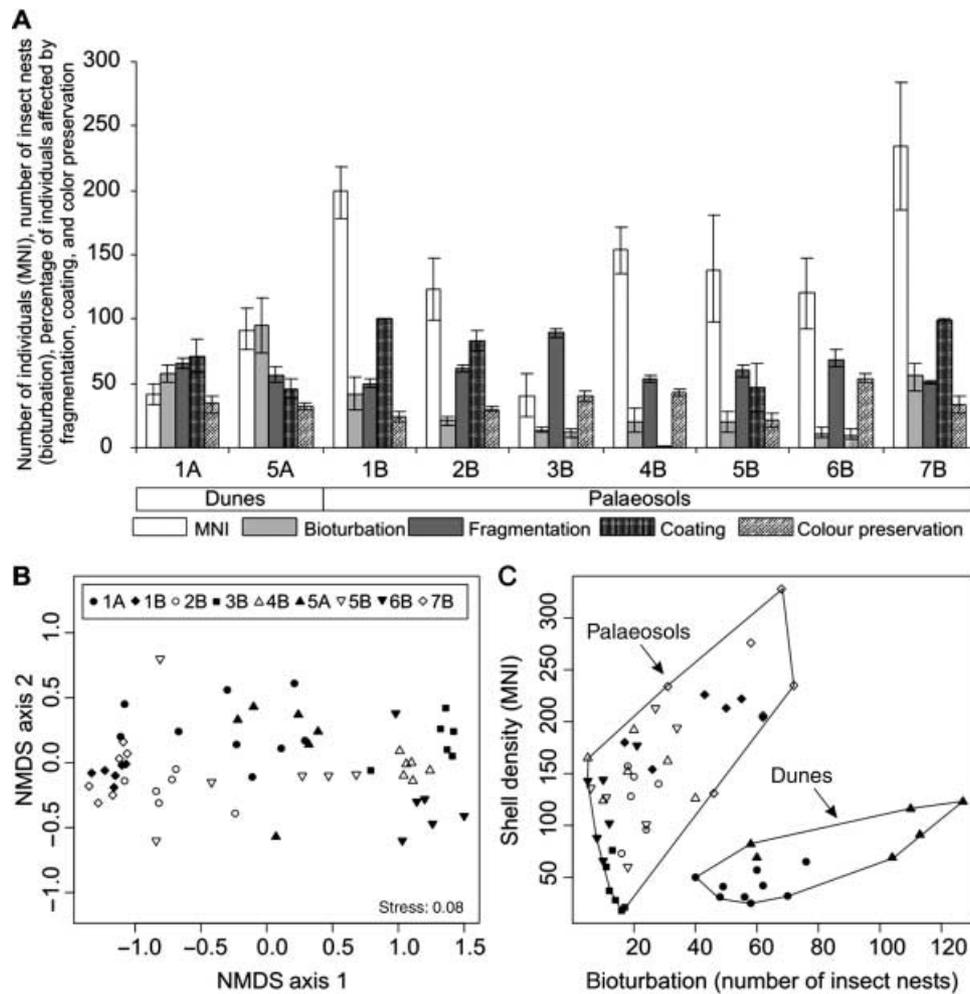


Fig. 4. □A. Mean values of five variables with 95% bootstrapped confidence intervals. □B. Non-metric multidimensional scaling of six shell-specific taphonomic variables based on the Manhattan distance. □C. Relationship between bioturbation intensity and shell density (MNI) in dunes and palaeosols. MNI, minimum number of individuals.

show moderately high to high  $R$  values (0.56–1), and their  $P$ -values do not exceed 0.004 (the alpha value after the Bonferroni correction for 21 comparisons is 0.0024). This analysis suggests that there are non-random differences in gastropod preservation among palaeosol beds that can be considered as representing unique taphofacies. In contrast, the pairwise difference between the two dunes is very low ( $R = 0.02$ ,  $P = 0.33$ ), suggesting that the two dunes represent a comparable taphofacies.

Cluster analysis reveals two groups of taphofacies (Fig. 5). The highly altered taphofacies are characterized by high proportions of carbonate coatings (91% of adults and 93% of juveniles) and low proportions of specimens with colour preservation (25% of adults, 34% of juveniles), whereas the better preserved taphofacies are characterized by low proportions of carbonate coatings (28% of adults and 18% of juveniles) and moderate proportions of specimens with colour

preservation (36% of adults and 56% of juveniles). These groupings are used to evaluate differences in species abundances between taphofacies (i.e. groups of samples differing in the degree of taphonomic alteration) and thus to indirectly assess their compositional fidelity (see below).

#### *Relationship between taphonomic alteration, shell density, and bioturbation*

The proportion of fragments negatively correlates with the proportion of coatings (Spearman  $r = -0.35$ ,  $P = 0.007$ ), and correlates positively with the proportion of specimens with colour preservation (Spearman  $r = 0.29$ ,  $P = 0.029$ ). The proportion of coatings is highly and negatively correlated with the proportion of specimens with colour preservation (Spearman  $r = -0.6$ ,  $P < 0.0001$ ). The relationships between the shell density and the alteration, and between the bioturbation intensity

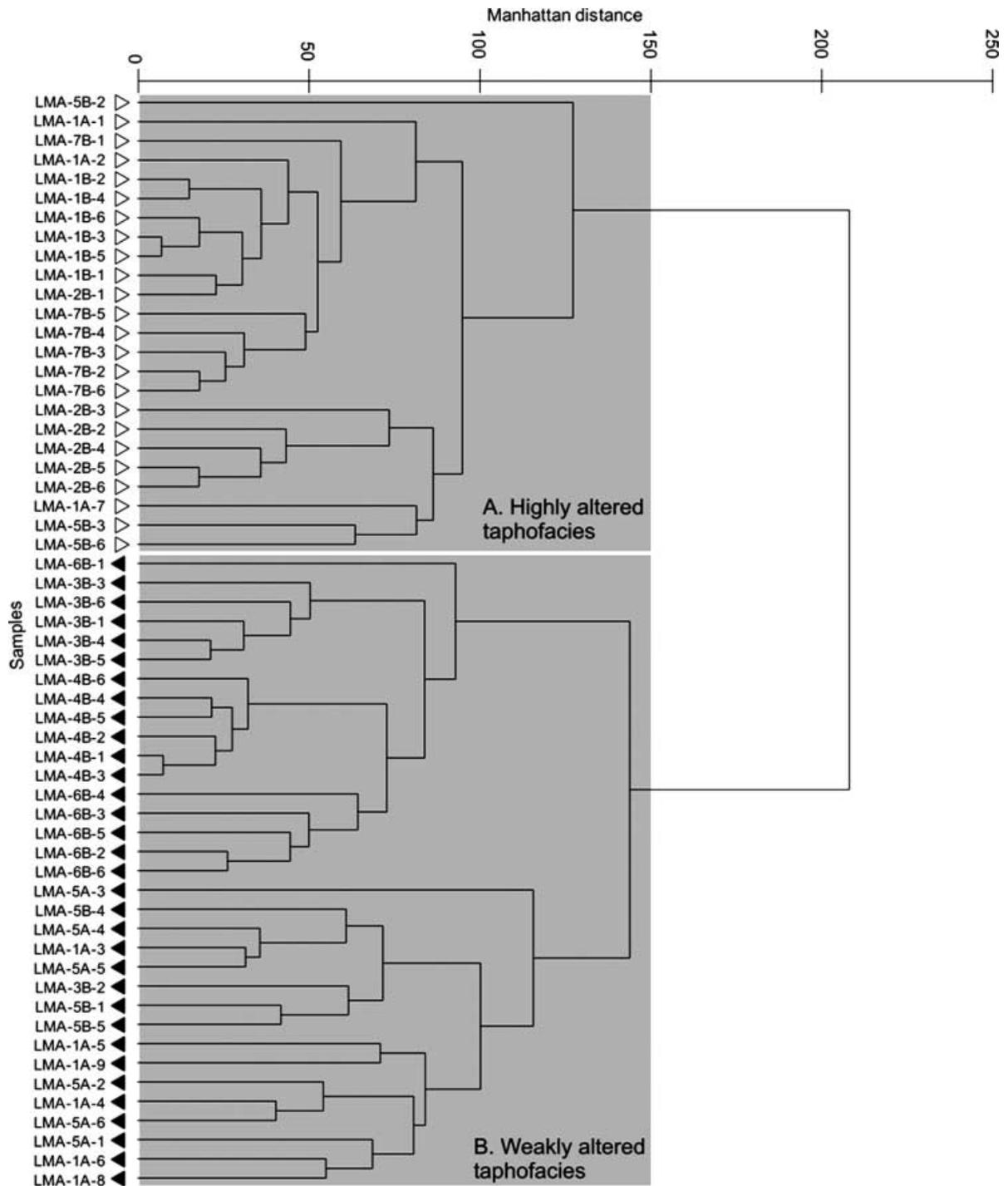


Fig. 5. Cluster analysis of the samples based on Manhattan distance and group average clustering method. Samples group into two major clusters delineating two taphofacies representing different degrees of alteration. Between-sample distances are based on six taphonomic variables, including fragmentation, colour preservation, and carbonate coatings of adults and juveniles.

and the alteration, were evaluated separately for palaeosols and dunes (Table 4). In palaeosols, the proportion of fragmented adults correlates negatively with the density of adult shells (Fig. 6B, Spearman  $r = -0.35$ ,  $P = 0.021$ ), and the proportion of fragmented juveniles correlates with the density of juvenile shells

(Fig. 6A, Spearman  $r = -0.84$ ,  $P < 0.0001$ ). In addition, the proportion of coated juveniles and adults covaries positively with the shell density of juveniles (Spearman  $r = 0.34$ ,  $P = 0.029$ ) and adults (Spearman  $r = 0.41$ ,  $P = 0.0077$ ), respectively. Colour preservation of juveniles negatively correlates with juvenile shell density

Table 4. Spearman rank correlations between shell density and taphonomic alteration of adults and juveniles, and between bioturbation intensity and taphonomic alteration of adults and juveniles.

Stage	Relationship	Spearman $r$	$P$ -value	Relationship	Spearman $r$	$P$ -value
<i>Paleosols</i> ( $n = 42$ )						
Juveniles	Fragmentation vs. shell density	-0.35	0.021	Fragmentation vs. bioturbation	-0.54	0.0002
Juveniles	Coating vs. shell density	0.34	0.029	Coating vs. bioturbation	0.65	< 0.0001
Juveniles	Colour preservation vs. shell density	-0.39	0.012	Colour preservation vs. bioturbation	-0.47	0.002
Adults	Fragmentation vs. shell density	-0.84	< 0.0001	Fragmentation vs. bioturbation	-0.52	0.0004
Adults	Coating vs. shell density	0.41	0.0077	Coating vs. bioturbation	0.65	< 0.0001
Adults	Colour preservation vs. shell density	-0.19	0.24	Colour preservation vs. bioturbation	-0.36	0.018
<i>Dunes</i> ( $n = 15$ )						
Juveniles	Fragmentation vs. shell density	0.08	0.78	Fragmentation vs. bioturbation	-0.3	0.28
Juveniles	Coating vs. shell density	-0.37	0.17	Coating vs. bioturbation	-0.23	0.41
Juveniles	Colour preservation vs. shell density	-0.23	0.41	Colour preservation vs. bioturbation	-0.39	0.15
Adults	Fragmentation vs. shell density	-0.14	0.62	Fragmentation vs. bioturbation	-0.03	0.91
Adults	Coating vs. shell density	-0.16	0.57	Coating vs. bioturbation	-0.11	0.7
Adults	Colour preservation vs. shell density	-0.62	0.15	Colour preservation vs. bioturbation	-0.72	0.0023

The Bonferroni correction lowers the alpha value to 0.0083 (0.05/6). However, this correction is highly conservative because the multiple tests are not independent.

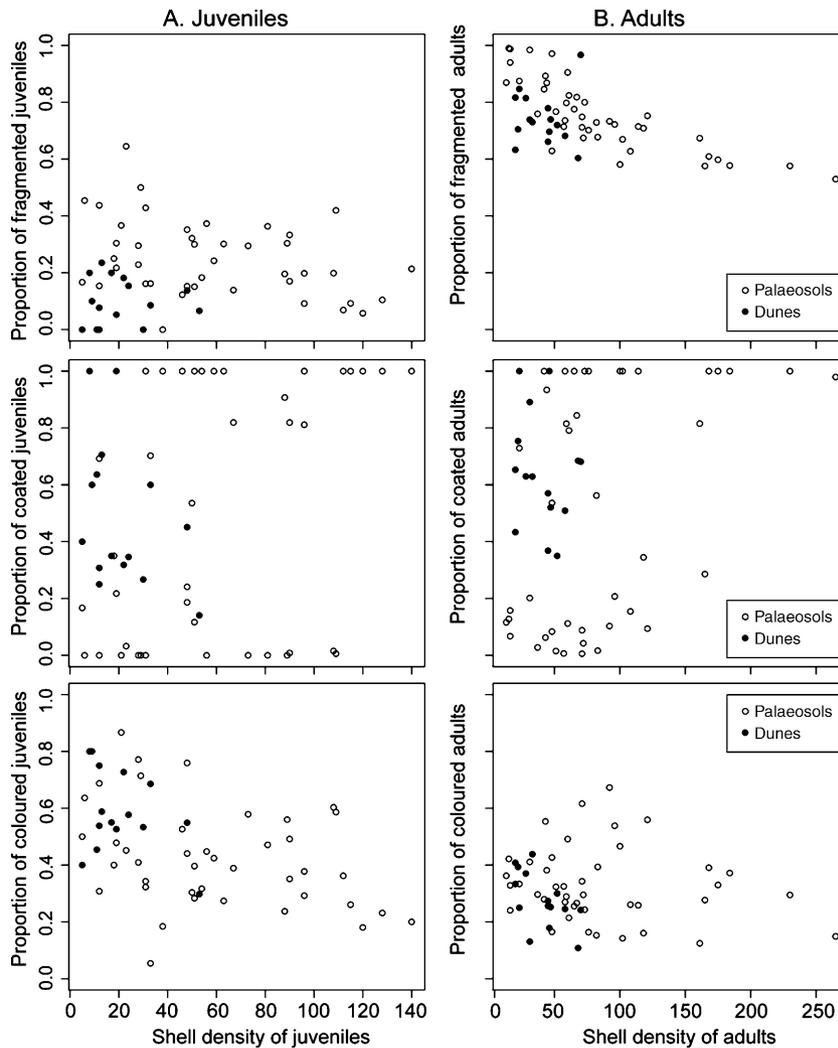


Fig. 6. Bivariate relationships between shell density (minimum number of individuals) and the proportion of the three taphonomic variables (fragmentation, carbonate coating and colour preservation) in juveniles (the left column) and adults (the right column).

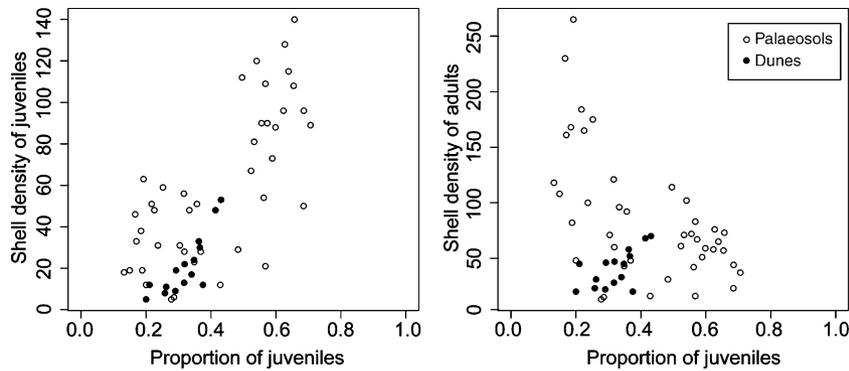


Fig. 7. Bivariate relationships demonstrating non-random correlations between the proportion of juveniles and the shell density of juveniles (the left column) and the shell density of adults (the right column).

(Spearman  $r = -0.39$ ,  $P = 0.012$ ). Whole shells thus tend to be coated and lack colour, and densely-packed palaeosol beds are characterized by the higher proportion of whole adult shells with carbonate coatings. In contrast to palaeosols, the relationships between the shell density and taphonomic alteration are low and insignificant in dunes (Table 4).

The relationships between the bioturbation intensity and taphonomic alteration are also high and significant in palaeosols, in contrast to dunes (Table 4). In palaeosols, the bioturbation intensity covaries positively with the proportion of coated adults (Spearman  $r = 0.65$ ,  $P < 0.0001$ ) and coated juveniles (Spearman  $r = 0.65$ ,  $P < 0.0001$ ). There are also significant negative relationships between the bioturbation intensity and the proportion of coloured juveniles (Spearman  $r = -0.36$ ,  $P = 0.018$ ) and coloured adults (Spearman  $r = -0.47$ ,  $P = 0.002$ ), and significant negative relationships between the bioturbation intensity and the proportion of fragmented adults (Spearman  $r = -0.54$ ,  $P = 0.0002$ ) and fragmented juveniles (Spearman  $r = -0.52$ ,  $P = 0.0004$ ). Whole shells with carbonate coatings and loss of colour are thus more common in palaeosols with high intensity of bioturbation.

#### *Relationship between shell density and size structure of gastropod assemblages*

Non-random relationships between the shell density and the size structure of gastropod assemblages reveal whether biological variations in density of gastropod populations were related to differences in mortality of their size/age classes. The relationship between the proportion of juveniles and juvenile shell density (i.e. MNI of juveniles) is significantly positive (Fig. 7, Spearman  $r = 0.68$ ,  $P < 0.0001$ ), and the relationship between the proportion of juveniles and adult shell density is significantly negative in palaeosols (Spearman  $r = -0.53$ ,  $P = 0.0003$ ). In contrast, both juvenile

(Spearman  $r = 0.83$ ,  $P = 0.0001$ ) and adult shell density (Spearman  $r = 0.6$ ,  $P = 0.018$ ) positively correlate with the proportion of juveniles in dunes (Fig. 7). Therefore, the variations in juvenile and adult shell density were related to changes in the dominance of ontogenetic size stages both in palaeosols and in dunes.

In palaeosols, the proportion of adults in a sample correlates negatively with the proportion of fragmented adults in that sample (Spearman  $r = -0.49$ ,  $P = 0.0012$ ), but does not show any significant correlations with other taphonomic variables or bioturbation. The relationship between the proportion of adults and the proportion of fragmented adults is insignificant in dunes (Spearman  $r = -0.24$ ,  $P = 0.38$ ). The relationship between the proportion of adults and adult fragmentation in palaeosols thus indicates that variations in fragmentation rates were coupled with variations in mortality rates of adult gastropods.

#### *Differences in preservation between juveniles and adults*

Univariate and multivariate analyses show that juveniles and adults differ significantly in the degree of taphonomic alteration. Adults are more commonly fragmented and show colour preservation less commonly than juveniles, both in the palaeosol and in the dune samples (Fig. 8A–B). Seventy-five per cent of adults in the palaeosol samples and 74% of adults in the dune samples are fragmented. In contrast, only 25% of juveniles are fragmented in the palaeosol samples and 10% in the dune samples. Adults with preserved colour patterns are uncommon, both in the palaeosol (33%) and in the dune (28%) samples. In contrast, juveniles with colour preservation are more common, both in the palaeosol (43%) and in the dune (59%) samples. Adults and juveniles do not differ in the proportion of carbonate coating. NMDS (Fig. 8C–D) and analyses of similarities performed separately for

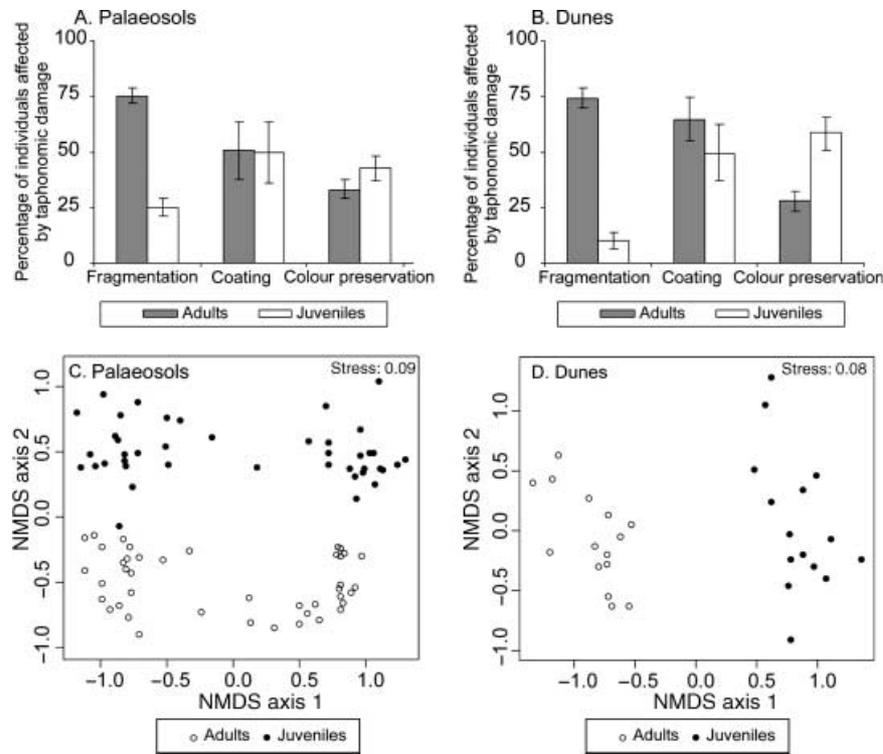


Fig. 8. Differences in preservation between juveniles and adults. □A. Univariate comparisons of palaeosol samples. □B. Univariate comparisons of dunes samples. □C. Non-metric multidimensional scaling (NMDS) for palaeosol samples. □D. NMDS for dune samples.

palaeosols and dunes show a high segregation of adults and juveniles in a two-dimensional space and moderate to very large  $R$  values (ANOSIM,  $R$ [palaeosols] = 0.41,  $P < 0.0001$ ,  $R$ [dunes] = 0.96,  $P < 0.0001$ ).

#### *Environmental effects on preservation: dunes versus palaeosols*

MNI tends to be lower in the dune samples (median = 57) than in the palaeosol samples (median = 144) (Mann–Whitney  $U$  test,  $P < 0.0001$ ). In contrast, insect nests are more common in the dune samples (median = 60) than in the palaeosol samples (median = 20) (Mann–Whitney  $U$  test,  $P < 0.0001$ ). Spearman rank correlation between MNI and the number of insect nests (Fig. 4C) is relatively high both in the dune samples ( $r = 0.7$ ,  $P = 0.004$ ) and in the palaeosol samples ( $r = 0.66$ ,  $P < 0.0001$ ).

Analysing differences in shell-specific preservation across all samples, differences between palaeosols and dunes are minimal and insignificant (one-way ANOSIM,  $R = 0.043$ ,  $P = 0.11$ ). However, when samples are partitioned according to their stratigraphic position, differences between palaeosols and dunes become higher and significant (two-way ANOSIM,  $R = 0.38$ ,  $P = 0.003$ ). In addition, because the dune samples represent two time intervals only, separate

comparisons were performed for beds 1 (i.e. LMA-1A vs. 1B) and 5 (i.e. LMA-5A vs. 5B). These two pairwise comparisons show different results. In the first case (Fig. 9A), palaeosols are characterized by higher proportions of coated juveniles and coated adults, and by lower proportions of juveniles and adults with colour preservation. A multivariate test also shows that the dune and palaeosol samples collected from LMA-1 differ significantly from one another (Fig. 9C, ANOSIM,  $R = 0.5$ ,  $P = 0.006$ ). In the second case (Fig. 9B), the differences in proportions of coatings between palaeosols and dunes are weak, but the dune samples are still characterized by a higher proportion of juveniles with colour preservation. The dune and palaeosol samples collected from LMA-5 do not differ from one another when all taphonomic variables are evaluated simultaneously using ANOSIM (Fig. 9D,  $R = 0.16$ ,  $P = 0.08$ ).

#### *Temporal variation in preservation*

Seven age sample groups are included in this study (Table 1). The age of the samples ranges from  $38.6 \pm 6.9$  kyr BP (samples collected near the base of the Mala section) to  $27.7 \pm 4.4$  kyr BP (samples collected near the top of the Mala section). These numerical ages were obtained by Ortiz *et al.* (2006)

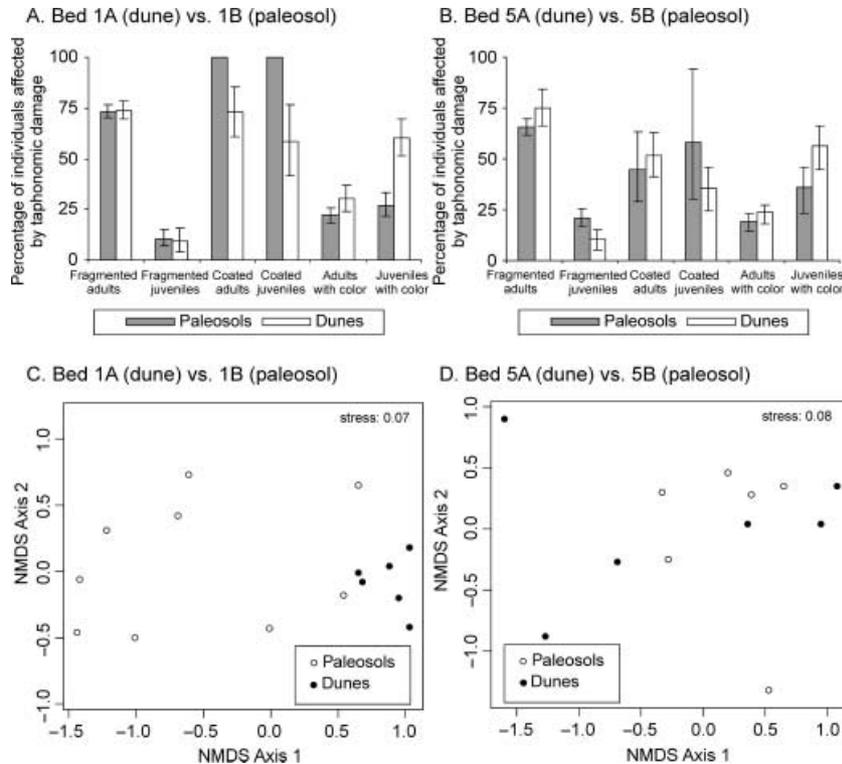


Fig. 9. Differences in shell preservation between samples from dunes and palaeosols collected at the Mala section (Lanzarote, Canary Islands).

through the direct analysis of multiple snail shells (between 2 to 6) by amino acid dating calibrated against radiocarbon. The chronological study of this and other aeolianite deposits from the eastern Canary Islands shows that there is a good correlation between the obtained numerical ages and the stratigraphy of the sampled beds (Ortiz *et al.* 2006). In addition, although some of the analysed samples displayed some level of time-averaging, reworking of shells from older levels in to the younger ones is improbable to have occurred because individual dune levels are sealed by palaeosols (Yanes *et al.* 2007).

Temporal variations in the shell density (MNI) and bioturbation (number of insect nests) show that the peaks in bioturbation partly correspond to the peaks in the shell density in the lower and upper parts of the Mala section, although their rank correlation is insignificant (Spearman  $r = 0.4$ ,  $P = 0.31$  for first differences, Fig. 10A). The temporal relationship between the proportion of fragmented adults and the proportion of juveniles is weak (Spearman  $r = 0.52$ ,  $P = 0.18$  for first differences, Fig. 10B).

To test for differences in preservation of gastropod assemblages through time, ANOSIM and NMDS analyses were performed separately for juveniles and adults (to control for size-specific differences in shell preservation) using the Manhattan distance. Both

analyses show comparable results (Fig. 11A–B). For both ontogenetic age groups, gastropod assemblages vary significantly in preservation across time (Fig. 11A–B, ANOSIM,  $R[\text{juveniles}] = 0.44$ ;  $P < 0.0001$ ,  $R[\text{adults}] = 0.7$ ;  $P < 0.0001$ ; pairwise comparisons are reported in Table 5). The temporal differences in preservation are stronger when analyses are limited to palaeosols (ANOSIM,  $R[\text{juveniles}] = 0.68$ ;  $P < 0.0001$ ,  $R[\text{adults}] = 0.9$ ;  $P < 0.0001$ ), and insignificant when limited to dunes (ANOSIM,  $R[\text{juveniles}] = 0.08$ ;  $P = 0.8$ ,  $R[\text{adults}] = 0.11$ ;  $P = 0.12$ ). The temporal signal is thus related solely to variations in preservation in palaeosols. Samples segregate approximately into two groups that differ from one another in the proportion of coated specimens. The beds 1, 2 and 7 are characterized by high proportions of coatings, whereas the beds 3 through 6 are characterized by low-to-moderate proportions of coatings (Fig. 11C–D). Note that beds 3 through 6 also correspond to the minimum shell density (Fig. 10A), and the lowest proportions of coatings on juveniles and adults correspond to the minimum bioturbation intensity in the bed 4B (Fig. 11C–D).

### Compositional fidelity

The temporal change in community composition and the compositional segregation between assemblages

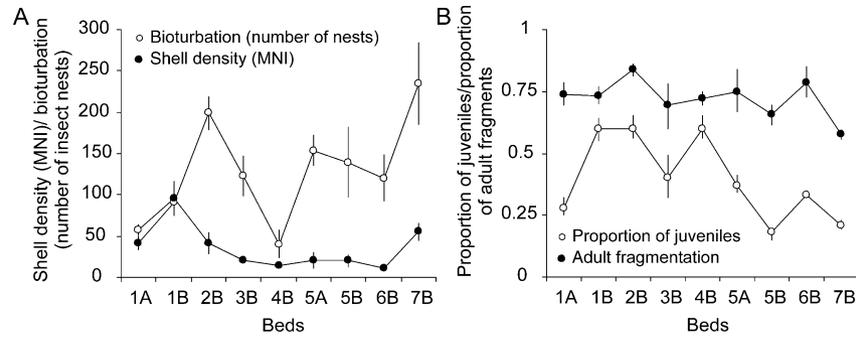


Fig. 10. Variations in bioturbation (number of insect nests), shell density (minimum number of individuals) □A, and proportion of juveniles and proportion of adult fragments □B, through time. The beds with 'A' correspond to dunes, and the beds with 'B' correspond to paleosols.

Table 5. Pairwise analyses of similarities applied to estimate differences in shell-specific preservation of adults and juveniles between pairs of samples of different age.

Pairwise tests	Adults – R statistic	Adults – P-value	Juveniles – R statistic	Juveniles – P-value
1 vs. 2	0.019	0.34	-0.041	0.58
1 vs. 3	0.933	< 0.0001	0.723	0
1 vs. 4	0.925	0.0001	0.691	0
1 vs. 5	0.401	0.0004	0.176	0.019
1 vs. 6	0.952	< 0.0001	0.735	0
1 vs. 7	0.181	0.0691	-0.086	0.77
2 vs. 3	1	0.002	0.998	0.0022
2 vs. 4	1	0.002	1	0.0022
2 vs. 5	0.617	< 0.0001	0.313	0.0084
2 vs. 6	1	0.002	0.967	0.0022
2 vs. 7	0.963	0.002	0.3	0.0065
3 vs. 4	0.967	0.002	0.408	0.0043
3 vs. 5	0.81	0.0001	0.442	0.002
3 vs. 6	0.785	0.002	0.339	0.0238
3 vs. 7	1	0.002	1	0.0021
4 vs. 5	0.644	0.0001	0.358	0.0096
4 vs. 6	0.965	0.002	0.244	0.0065
4 vs. 7	1	0.002	1	0.0022
5 vs. 6	0.866	< 0.0001	0.347	0.0087
5 vs. 7	0.864	< 0.0001	0.529	0.0006
6 vs. 7	1	0.002	1	0.0021

The Bonferroni correction lowers the alpha value to 0.0024 (0.05/21). However, this correction is highly conservative because the multiple tests are not independent.

dominated by *Theba* and assemblages dominated by *Theba* and *Monilearia* do not appear to have been biased notably by taphonomic differences in the quality of preservation. NMDS of 54 samples with 16 gastropod species, based on Bray–Curtis similarity, shows that assemblages from the lower and the upper part of the Mala section are compositionally distinct (Fig. 12A). However, weakly and highly altered taphofacies do not differ in species abundances, underscored by their overlap in NMDS plots (ANOSIM,  $R = 0.03$ ,  $P = 0.15$ , Fig. 12A). Also, when the two time intervals dominated by *Theba* (beds 1A–5A) and *Theba* and *Monilearia* (beds 5B–7B) are analysed separately (Fig. 12B–C), no consistent differences in composition between weakly and highly altered taphofacies can be detected ( $R[\text{beds 1A–5A}] = 0.01$ ,  $P = 0.36$ ,  $R[\text{beds 5B–7B}] = 0.06$ ,  $P = 0.17$ ). With the

exception of one outlying sample of the *Theba* assemblage, compositional variation between samples with high and low alteration does not exceed compositional variation between samples with low alteration in both assemblage types.

## Discussion

### *Effects of taphonomic alteration on preservation potential of gastropods*

The overall good preservation of land snail shell assemblages observed in the Mala section likely represents a combined effect of several factors. First, because the original aragonitic composition is retained by the majority of the sampled shells,

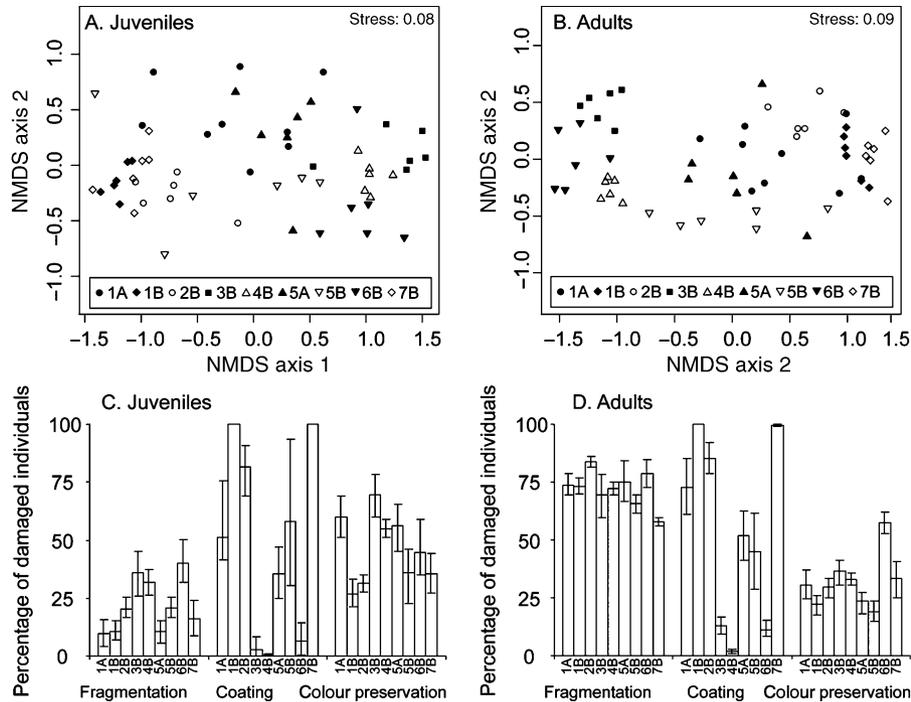


Fig. 11. Temporal variations in preservation of juvenile  $\square$ A, C and adult  $\square$ B, D terrestrial gastropod shells from the Mala section (Lanzarote, Canary Islands). The beds with 'A' correspond to dunes, and the beds with 'B' correspond to palaeosols.

damage from diagenetic processes is unlikely to have been severe. Second, the positive correlation between the shell density and bioturbation (Fig. 4C), the positive correlations between coating and bioturbation intensity (Table 4), and the negative correlations between fragmentation and bioturbation (Table 4) imply the positive relationship between the preservation potential of gastropod shells and the bioturbation intensity in palaeosols. Although bioturbation usually favours sediment oxidation, acidification and free movement of pore waters, it may also enhance precipitation of carbonate crusts owing to enhanced evapotranspiration (Goodfriend *et al.* 1996). Third, the absence of rounding and bioerosion can indicate either (1) a short time of exposure within the upper, mixed zone of the sedimentary column (e.g. owing to high burial rates), and/or (2) a generally low rate of shell destruction. In a recent study, the scale of time-averaging (age mixing) was quantitatively estimated for gastropod shell accumulations in six of the nine beds analysed here (Yanes *et al.* 2007). Two dune beds and one palaeosol bed (LMA-1A, LMA-4B, and LMA-5A) display substantial time-averaging, with specimens from the same bed varying in age by hundreds, or even thousands, of years (Yanes *et al.* 2007). This indicates that the good preservation observed in the studied material is not related to rapid burial of snapshot shell accumulations: gastropod shells have resided in the upper, mixed zone of the sedimentary

column for a notable period of time (Taphonomic Active Zone sensu Davies *et al.* 1989). Consequently, shell destruction rates must have been low in the taphonomic active zone, with shell durability being likely enhanced by the precipitation of carbonate coatings.

Several mutually not exclusive scenarios can explain low shell destruction rates in terrestrial environments of the Canary Islands, especially in palaeosols, where the proportion of coatings is higher than in dunes. First, the presence of carbonate coatings can reflect a buffering effect of a high carbonate content of sediments of the Canary Islands. This is in accord with the predictions of Ložek (1964), implying that time-averaged land snail assemblages in carbonate-rich deposits can have a high preservation potential. However, substantial carbonate dissolution can occur in present-day carbonate-rich environments (Smart *et al.* 1988; Walter & Brunton 1990; Kidwell *et al.* 2005; Best *et al.* 2007; Whitaker & Smart 2007), and carbonate precipitation rates thus can be partly independent of initial carbonate content. Second, high bioturbation rate can enhance evaporation and increase concentrations of capillary waters with respect to calcium carbonate, and thus enhance shell durability via increased rate of carbonate precipitation – the role of bioturbation is supported by positive relationship between the preservation state and the bioturbation intensity in palaeosols. Third, low shell destruction rates can be related to arid and semi-arid conditions

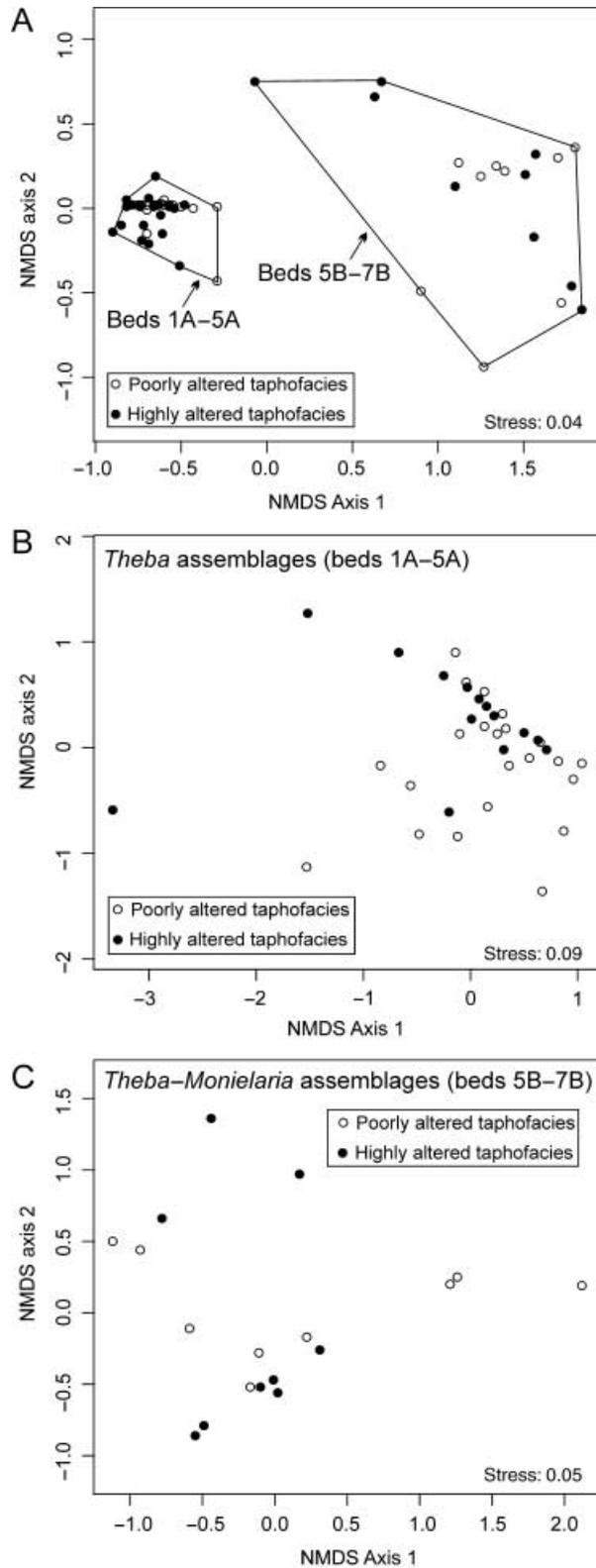


Fig. 12. □A. Differences in composition between weakly and highly altered taphofacies in the Mala section do not obscure temporal trend in species abundances. □B. High compositional overlap between weakly and highly altered taphofacies of the *Theba*-dominated assemblages. With the exception of one outlier sample, compositional variation among samples from highly altered

where groundwater and pedogenic processes generally favour formation of carbonate cements (Retallack 1994; Royer 1999). Fossil preservation in a palaeosol reflects a delicate balance between the chemical conditions during the pedogenesis (evapotranspiration and pH), and the time involved in the soil formation (e.g. Retallack 1998, 2001). Torres (1995) concluded that Quaternary palaeosols in Fuerteventura Island (E Canary Archipelago) were formed in a permanent arid-semiarid environment with a strong evapotranspiration. During wetter conditions, carbonate migrated through the substrate and precipitated due to chemical reactions with the infiltrated rainwater, forming calcium carbonate-rich palaeosols and precipitating carbonate coatings. Therefore, land snail shells in the palaeosols of Lanzarote Island were probably formed in arid-semiarid conditions with strong evapotranspiration similar to those prevailing in the Quaternary palaeosols of the Fuerteventura Island. The preservation of palaeosols requires time intervals of tens to hundreds of thousands of years (e.g. Retallack 1998, 2001). This age estimate is consistent with those provided by Torres (1995) for the amount of time needed for the formation of the Quaternary palaeosols of the Fuerteventura Island, and with estimates of Ortiz *et al.* (2006) and Yanes *et al.* (2007) for the formation time for multiple aeolianite deposits from the study area.

Actualistic observations by Cadée (1999) in a temperate dune area (Island of Texel, Netherlands) indicate that empty shells of terrestrial gastropods can have a very short half-life (~1 year) when exposed to external taphonomic agents, especially to dissolution by freshwater and bioerosion by other snails that need calcium carbonate to form their own shells. The taphonomic half-life of terrestrial land snails in arid and semi-arid settings favourable for carbonate precipitation can thus be substantially longer than taphonomic half-life of land snails in deposits with low carbonate content and/or deposited in more humid conditions (Cadée 1999).

#### *Relationship between shell input rates and shell density*

In palaeosols, the significant negative relationship between the density of adult and juvenile shells on one hand and the proportion of their fragments on the other (Table 4) implies that the increase in shell density in palaeosols reflects the increase in net shell input rates, rather than the decrease in sedimentation

taphofacies is not higher than that observed among samples from weakly altered taphofacies. □C. High compositional overlap between weakly and highly altered taphofacies of assemblages dominated by *Theba* and *Monilearia*.

rate (Tomašových *et al.* 2006). In dunes, the relationships between the shell density and taphonomic alteration are insignificant and thus inconclusive with respect to the role of shell input rates and sedimentation rates in shell density variations. The increase in shell density with increasing proportion of carbonate coatings is probably not due to increasing residence times because the estimated range of time-averaging in palaeosol beds of the Mala section (Yanes *et al.* 2007) is not related to the proportion of coatings in palaeosols.

In palaeosols, higher shell input rates can be related either to the increase in dead-shell production rates (e.g. high shell density corresponds to times of high productivity, which increases the proportion of recently dead cohorts with good preservation), and/or to the decrease in shell destruction rates (e.g. high shell density corresponds to times when destructive processes such as fragmentation were operating at slower pace). The role of reduced shell destruction rate is implied by the positive relationship between the shell density and the proportions of coatings, which can enhance the durability of land snail shells (Table 4). The positive relationship between the preservation state and the bioturbation intensity indicates that the decrease in shell destruction rates can be related to the increase in bioturbation rates that enhanced the formation of carbonate coatings. However, the negative relationship between the proportion of juveniles and the shell density of adults in palaeosols implies that the increase in adult shell density was related also to the decrease in juvenile mortality. In addition, the negative correlation between the proportion of adults and the degree of adult fragmentation indicates that high rate of fragmentation was related to high mortality of adults.

Most likely, the combined effects of varying shell destruction rates and dead-shell production rates governed variations in the shell density of land snails in palaeosols. Negative relationships between carbonate coatings and fragmentation, and between carbonate coatings and colour preservation, imply a general taphonomic pathway associated with the formation of land snail shell assemblages. Under low rate of precipitation of carbonate coatings, shells become increasingly fragmented and lose original colour patterns in terrestrial environments. With increasing rate of carbonate coating formation, precipitation of crusts may substantially diminish or inhibit effects of destructive processes acting in the taphonomic active zone, both in dunes and in palaeosols. These processes result in time-averaged death assemblages that are composed of well-preserved shells, with shell density largely determined by rates of shell destruction (i.e. rate of carbonate precipitation) and rates of dead-shell

production (i.e. original population sizes and mortality rates) rather than by variation in sediment accumulation/burial rates.

### *Differences between juveniles and adults*

Better preservation of juveniles than adults appears to be a phenomenon independent from the depositional environment, as it is observed both for the palaeosol and for the dune samples. The lower proportion of colour preservation in adults may reflect colour fading during their life (G.C. Cadée personal communication, 2007), and if the juvenile stage is shorter than the adult stage, everything else being equal, the probability of fragmentation (e.g. by predators) will be higher for adults. In this case, the differences in fragmentation and colour preservation might not correspond to size-selective post-mortem processes. Although data about growth rates and duration of juvenile stages of terrestrial gastropods of the Canary Islands are unavailable, the observed differences in the proportion of fragmentation between juveniles and adults (Fig. 8A–B) require a twofold or a threefold increase in the duration of the adult stage relative to the duration of the juvenile stage. Alternatively, the higher degree of fragmentation and greater loss of colour in adults imply that either adult shells are subject to higher destruction rates (assuming that shell alteration is a function of destruction rate) or that destruction rates of juveniles are so high that they do not accrue taphonomic damage. Juveniles can be disintegrated to non-identifiable remains in a very short time because small-sized and thin-shelled individuals are generally more fragile and more prone to destruction than adults (Kowalewski 1996; Tomašových 2004).

High proportions of fragmented adults can be partly related to predation because several birds in the study area consume land snails (mainly *Theba* individuals because of their abundance, accessibility, and larger size) as a regular part of their diet (field observations 2003–2004), although other predators such as rodents and beetles can also prey on land snails (Cadée 1995). For example, the rapacious bird *Neophron percnopterus* (L.), an extant inhabitant of the study area, includes ~3% of snails in its diet (Medina 1999). In addition, pellets (regurgitated compressed by-products of digestion) of the rapacious bird *Corvus corax* (L.) show that other birds also ingest snails in the study area (field observations 2004). Similarly, numerous birds ingest shells of land snails, mainly as an extra calcium carbonate source during the breeding seasons (e.g. Graveland *et al.* 1994; Graveland & Van der Wal 1996; Cadée 1999). In addition, fragmentation due to bird predation can

be underestimated considering that feeding behaviour of some birds (especially regurgitation) may result in fragments that are too small to be captured during dry sieving with 1-mm mesh size sieves. This issue cannot be evaluated fully without further in-depth studies focused on fragmentation patterns resulting from bird predation.

A negative correlation between the proportion of adults and the degree of adult fragmentation implies that fragmentation can be partly related to differences in mortality patterns between juveniles and adults, because a decrease in the proportion of adults relative to juveniles corresponds to samples with high proportions of adult shell fragments (i.e. relative increase in adult mortality is caused by increased predation that leads to higher fragmentation). Although wind-induced transport in aeolian dune sites may lead to abrasion and mechanical breakage of gastropod shells, the complete absence of rounding on shells strengthened by coatings implies that wind abrasion probably did not contribute to high proportion of fragments observed in the Mala section.

### *Environmental and temporal variation in preservation*

Environmental differences associated with contrasting climatic regimes governing alternation of dunes and palaeosols (Herwitz *et al.* 1996; Brooke 2001) also lead to differential preservation of gastropod shells between dunes and palaeosols. The difference in preservation between dunes and palaeosols can be explained by a higher rate of carbonate-coating formation that can obliterate colour preservation in palaeosols, possibly via increased evapotranspiration during more humid conditions when palaeosols were formed and pedogenetic processes were intense, and via higher input of dissolved carbonates coming from bioclastic particles (e.g. Goodfriend *et al.* 1996). Although bioturbation intensity correlates positively with the proportion of coatings in palaeosols, the bioturbation intensity is generally higher in dunes. Therefore, the differences in the proportions of carbonate coatings between palaeosols and dunes were probably not caused by differences in bioturbation intensity. The lower proportion of coatings and higher preservation of colour patterns in dunes in general may imply lower preservation potential of gastropods relative to palaeosols, and thus higher shell destruction rates that can be partly responsible for the low shell density in dunes. Although the high proportions of colour preservation can be a counter-intuitive pattern under high shell destruction rates, the lack of enhanced durability by carbonate coatings may have resulted in disintegration rates that exceeded rates of colour loss.

Differences in taphonomic preservation across time intervals within palaeosols indicate substantial temporal variations in preservation regimes, with the beds 1, 2, and 7 being characterized by a regime with high rates of carbonate crust formation, and the beds 3 through 6 being characterized by reduced rates of crust formation. The increase in the rate of carbonate crust formation may have been driven by temporal increase in bioturbation intensity that positively correlates with the proportion of coatings.

### *Compositional fidelity*

Live-dead fidelity studies of land snail assemblages are rare, although recently Rundell & Cowie (2004) found that rank abundances of living land snails of the Pacific islands were generally preserved in death assemblages. Fossil assemblages differing in the degree of shell preservation are expected to differ in species abundances, given the potential for differential post-mortem sorting, destruction, and between-habitat mixing of species, and composition of highly altered samples can thus substantially differ from composition of weakly altered samples (Tomašových 2006). The ANOSIM and NMDS plots indicate that no consistent differences in composition can be demonstrated between highly altered samples and relatively unaltered samples. Also, highly altered and relatively unaltered sets of samples both show a similar level of variation in taxonomic composition, again suggesting that taphonomic processes did not distort notably the original biological signals. Consistently, temporal differences in community composition that persist across distinct taphofacies also indicate that taphonomic processes did not introduce any substantial compositional bias.

The lack of compositional differences between highly altered and relatively unaltered samples can be probably explained by a generally low destruction rate of land snail shells in carbonate-rich sediments, which not only appear favourable for preservation of morphological details (including shell colour patterns), but also facilitate formation of fossils assemblages with high fidelity records of species abundances and species composition. This is in contrast to deposits where freshwater rapidly dissolves carbonate shells, either owing to initially low carbonate content, lack of bioturbation, and/or higher humidity that can inhibit precipitation of carbonate coatings.

## Conclusions

Taphonomy of Quaternary land snails of the Canary Islands is markedly affected by intrinsic and extrinsic factors. Intrinsic factors are represented by size-specific

differences in fragmentation and colour preservation between juveniles and adults. Extrinsic factors are related to differences in preservation between palaeosols and dunes, most notably to differences in the extent of carbonate coating. In contrast to terrestrial gastropod assemblages found in humid and carbonate-poor environments (Cadée 1999), the studied assemblages show no signs of bioerosion and dissolution.

The randomized sampling design implies that individual beds are characterized by distinct taphonomic signatures (i.e. they effectively represent a series of distinct taphofacies) that follow a set of general patterns. Namely, the proportion of fragments correlates negatively with the proportion of specimens with carbonate coatings and correlates positively with the frequency of colour preservation. Juveniles are characterized by low fragmentation and high proportions of colour preservation, in contrast to adults. The presence of carbonate coating and the high extent of time-averaging indicate that background levels of shell destruction rates were relatively low in carbonate-rich sediments of the Canary Islands, in contrast to generally rapid rates of destruction of land snails observed in environments with high humidity and low carbonate content (Cadée 1999).

In palaeosols, the density of adult land snails is negatively related to the proportion of fragmented adults, negatively related to the proportion of juveniles, and positively related to the proportion of carbonate crusts. Because proportions of adults negatively correlate with proportions of fragmented adults, the increase in fragmentation of adults can be explained as elevated mortality of adults, likely related to periods of intensified predation by birds and other predators. The positive relationship between the proportion of adults and the adult shell density implies that the shell density was also enhanced by lower juvenile mortality. The increase in precipitation rates of carbonate coatings enhanced durability, and thus decreased shell destruction rates. These relationships thus indicate that variations in dead-shell production rates and shell destruction rates governed variations in the shell density of gastropod assemblages.

Preservation differences between palaeosols and dunes can be related to lower shell durability in dunes that can reflect lower meteoric diagenesis and lower evapotranspiration during the formation of dunes. Within palaeosols, temporal variations in taphonomic processes led to substantial changes in rates of carbonate crust formation, probably owing to variations in bioturbation intensity. Despite that, the compositional fidelity of land snail assemblages is probably not substantially biased by taphonomic processes because relatively unaltered and highly altered taphofacies do not differ in terms of abundances of land

snail species, and the temporal trend in community composition persists across different taphofacies. Bioturbated, carbonate-rich sediments deposited in arid and semi-arid conditions can probably increase the taphonomic half-life of land snail shells relative to deposits where carbonate precipitation is inhibited, freshwater rapidly dissolves calcium carbonate and other gastropods harvest calcium carbonate from dead shells (Cadée 1999). Therefore, analyses based on land snail assemblages sampled in carbonate-rich, arid and semi-arid environments, such as those that typify the Canary Islands, can be a particularly suitable target for palaeoecological and biostratigraphic studies.

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