

SHELL TAPHONOMY AND FIDELITY OF LIVING, DEAD, HOLOCENE, AND PLEISTOCENE LAND SNAIL ASSEMBLAGES

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ABSTRACT

Variations in the taxonomic composition of ancient land snail assemblages can potentially reflect changes in past ecosystems. The use of fossil associations as a paleoenvironmental-paleoecological proxy assumes that the original biological signature is retained, but postmortem processes can distort it. In this study, the fidelity of land snail assemblages was tested by comparing taphonomic and ecological variables recorded by live and dead, middle Holocene and Upper Pleistocene land snail shelly assemblages from San Salvador Island (Bahamas). Shells of living organisms were practically unaltered whereas dead and fossil shells were primarily affected by fragmentation, ornament loss, color loss, and carbonate coating. Taphonomic features fluctuated across space and time likely due to variable environmental conditions and/or time of exposure prior to shell burial. Live assemblages showed good taxonomic agreement with dead assemblages, although the later exhibited a higher number of taxa and individuals than the former. Assemblages that were moderately (dead and Holocene) and strongly (Pleistocene) taphonomically altered did not differ in species abundances, suggesting that the original biological signal was preserved. In contrast, unaltered (live and some dead) assemblages differed taxonomically from moderately and strongly damaged assemblages, likely as a consequence of different scales of time-averaging rather than variable shell-specific destruction rates. Taxonomic richness and simple dominance of time-averaged land snail assemblages were similar at various interglacial time periods (~125 ka, ~5–6 ka, and today). Such apparently equivalent snail richness may suggest that the climatic-environmental and/or ecological conditions at those times were comparable to the present.

INTRODUCTION

Studies that assess whether or not fossil assemblages preserve the original biological signature are relevant for paleontologists and evolutionary biologists because fossils are often used to extract ancient taxonomic data. Such information may be used to infer paleoecological and paleoenvironmental conditions or alternatively, to estimate local biodiversity levels, which in turn can provide data on regional and global trends in biodiversity, including on macroevolutionary timescales (e.g., Powell and Kowalewski, 2002; Bush and Bambach, 2004). In terrestrial settings, land snails are the most useful fossil invertebrates because they are generally abundant and frequently preserved in sedimentary rocks thanks to the relatively high preservation potential of their hard skeleton (e.g., Goodfriend, 1992, 1999). Land snails interact with the environment and other organisms, and fluctuations in their species composition, relative abundance distribution, and diversity often reflect variations in the local physical and/or biological conditions (see review by Solem, 1984). Thus, variations in the number of land snail species and their abundances may be used as a paleoenvironmental and/or paleoecological proxy (e.g., Cook et al., 1993; Pickford, 1995, 2002, 2004; Martinez and Rojas, 2004; Wu et al., 2007). While numerous studies have attempted to understand how modern land snail diversity and richness respond along climatic and ecological gradients (e.g., Chiba, 2002, 2007; Rundell, 2010), little is known about the ecological fidelity (similarity

in composition of dead or fossil shell assemblages to the original community) of ancient land snail shell assemblages (e.g., Carter, 1990; Rundell and Cowie, 2003; Schilthuizen et al., 2003; Yanes et al., 2008, 2011; Cameron et al., 2010), even though estimating the fidelity of the fossil record is essential to report accurate taxonomic richness and biodiversity of the past (e.g., Kidwell and Flessa, 1996; Behrensmeier et al., 2000).

Paleontologists have commonly attempted to estimate the fidelity of dead shelly assemblages from shallow marine soft substrate by comparing their taxonomic composition with living populations (e.g., Kidwell, 2001, 2007, 2008; Olszewski and Kidwell, 2007). Such live-dead taxonomic comparison is ideal because the species composition of the living (precursor) community can be known. Thus, if dead assemblages display good taxonomic agreement with the living communities, postmortem processes probably did not substantially distort the biological signal. Those surficial dead shell assemblages may differ in species composition from the local fossil (buried) assemblages even when live-dead taxonomic agreement is high, however, owing to variable times of exposure to biostratigraphic and/or diagenetic processes, in addition to variations in the scale of age mixing (e.g., Staff and Powell, 1988; Kowalewski, 1996). Shell burial processes and potential taphonomic biases may be estimated through the quantitative study of relevant taphonomic and ecological features of fossil shelly assemblages. Taxonomic comparisons among taphofacies (i.e., samples with differing taphonomic features; Brett and Braid, 1986) that have undergone variable degrees of taphonomic alteration may help to identify biases across fossil shell assemblages (e.g., Tomašových, 2006; Tomašových et al., 2006a, 2006b). Therefore, a three-way comparison of the taphonomic condition and ecological fidelity of land snail living, dead, and fossil assemblages is important to test the potential use of snail paleodiversity to accurately reconstruct changes in ancient ecosystems. These kinds of studies are rather uncommon on terrestrial shelly assemblages compared to marine mollusks, despite the relatively high abundance of land snails in the terrestrial fossil record (e.g., Carter, 1990; Cadée, 1999; Rundell and Cowie, 2003; Pearce, 2008; Yanes et al., 2008, 2011).

In the present study, a total of 2834 shell remains were studied from 61 samples of living, dead, middle Holocene, and Upper Pleistocene land snail shell assemblages collected around San Salvador Island. The quality and fidelity of the land snail shell assemblages was evaluated via quantitative taphonomic and ecological variables, which were treated using uni- and multivariate statistics. The following questions are addressed: (1) What taphonomic features primarily affected land snail shells from San Salvador Island by locality, species, and age level? (2) Do dead shell assemblages display taxonomic composition comparable to local living populations? (3) Is there good taxonomic agreement (fidelity) between samples with variable degrees of taphonomic alteration and different scales of time-averaging? and (4) Can we use land snail paleodiversity fluctuations to accurately infer changes in past ecosystems in the Caribbean?

METHODS

Study Area and Sampling

San Salvador Island (Bahamas) is a carbonate-rich, low altitude (<38 m above sea level) tropical island (24°06'N) located on the eastern

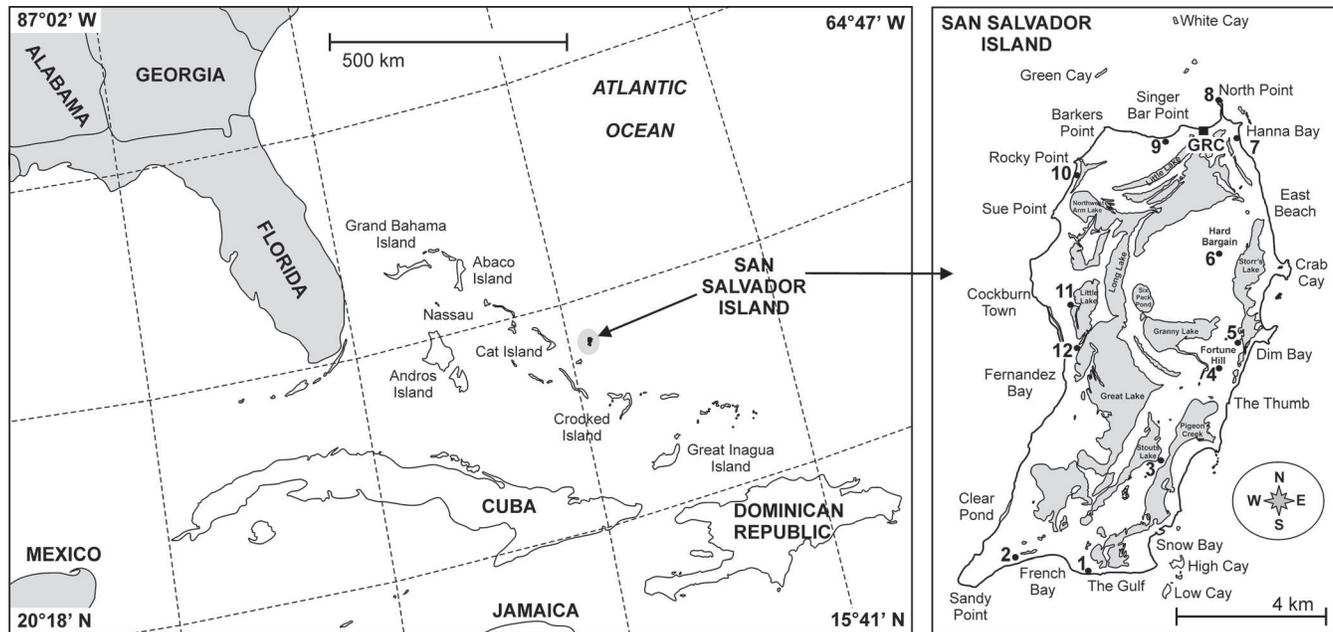


FIGURE 1—Geographical setting of San Salvador Island (Bahamas) and the sampled localities. (1) The Gulf (TG); (2) Watling's Quarry (WQ); (3) Pigeon Creek Quarry (PC); (4) Fortune Hill (FH); (5) Dim Bay (DB); (6) Hard Bargain (HardB); (7) Hanna Bay (HB); (8) North Point (NP); (9) Singer Bar Point (SB); (10) Rocky Point (RP); (11) Little Lake (LL); (12) Fernandez Bay (FB). GRC = Gerace Research Centre.

edge of the Grand Bahama Bank (Fig. 1). The island contains numerous land snail shells that have been generally well preserved in the local Quaternary rocks (e.g., Carew and Mylroie, 1995, 1997; Hearty and Schellenberg, 2008), thus representing an ideal material to investigate changes in ancient terrestrial ecosystems of the West Indies.

A total of 2834 land snail shell remains from 61 samples were collected at ten modern localities and four fossil sites (Fig. 1). Forty-nine samples of modern land snails (21 living and 28 dead shelly samples from the soil surface) were collected from ten locales, which included from north to south: Rocky Point (RP; Fig. 2A–B), Singer Bar Point (SB), North Point (NP), Hard Bargain (HardB), Little Lake (LL), Fernandez Bay (FB; Fig. 2C), Dim Bay (DB), Fortune Hill (FH), Pigeon Creek Quarry (PC), and The Gulf (TG). Samples collected at HardB, FB, FH, DB, and PC were from sites with rocky substrate and dense vegetation of various woody and shrubby species. At the remaining localities samples were from coastal sites usually with a dune (soft) substrate and open vegetation, primarily formed by palm trees and shrubs. Buried recent shells were not found at the sampled localities and therefore all the dead shell material studied came from the soil surface.

Six shelly samples were gathered from two middle Holocene paleosols, North Point (NP; Fig. 2D–E) and Hanna Bay (HB; Fig. 2F). Finally, another six shell samples were collected at two Upper Pleistocene deposits, The Gulf (TG; Fig. 2G) and Watling's Quarry (WQ; Fig. 2H). All fossil assemblages included in this study were recovered from coastal Quaternary carbonate-rich eolian deposits characterized by soft (unlithified) substrate and open vegetation (Fig. 2D–H). Holocene sites were located at the Hanna Bay and North Point Members of the Rice Bay Formation whereas Pleistocene samples were collected from the Cockburn Town and French Bay Members of the Grotto Beach Formation (see Carew and Mylroie, 1995, 1997 for stratigraphic details).

Similar sampling effort was applied to each collected sample. Living (e.g., Fig. 2A) and dead shells on the soil surface (e.g., Fig. 2B–C) were collected by picking up shells directly by hand in randomly placed ~ 10 m² quadrats for 2–3 hours; quadrats at the same locality were placed ~ 50 m apart. Living specimens were collected from the ground, rocks, bushes, and trees, and by flipping over rocks and leaves, as well as among leaf litter (e.g., Coppolino, 2010); all living specimens found

in the ~ 10 m² quadrat were considered. Dead shells were merely found entirely exposed on the soil surface and all dead shell remains (complete and broken) were collected in each quadrat. Although I excavated ~ 30 – 50 cm into the sediment, no shell samples were found. Live-collected land snails were returned to the field after laboratory study to protect the native malacofauna.

Pleistocene and Holocene shell samples were gathered *in situ* by dry sieving sediments through a 1mm mesh; a total of ~ 20 kg of sediments were sieved per sample. This sampling protocol was possible because samples were collected from Quaternary sediments which were mostly unlithified. Comparisons between dry-sieved and non-sieved samples indicated that this sampling approach did not artificially break or abrade shell remains (Yanes et al., 2008, 2011, this study).

Taphonomic Conditions

Shell material was studied under a dissecting microscope in the Gerace Research Centre (GRC) of San Salvador Island, Bahamas (Fig. 1) and specimens deposited in the Instituto Andaluz de Ciencias de la Tierra (CSIC, Granada, Spain). Six taphonomic and paleoecological variables were scored in each sample in terms of presence-absence (see Supplementary Data¹):

1. Total number of shell remains (TNR = shell specimens > 2 mm in maximum dimension). Shelly fragments < 2 mm were disregarded because the complete taxonomic range was captured on skeletons > 2 mm, as well as to simplify the study (Yanes et al., 2008, 2011);
2. Minimum number of individuals (MNI = number of shells with embryonic shell preserved);
3. Fragmentation (number of shells that preserved $< \sim 80\%$ of the shell);
4. Ornamentation loss (shells with partial or total loss of ornamental traits as a consequence of physical abrasion, chemical dissolution, or biological damage, such as lichen-like pitting; Walker et al., 1997);
5. Color loss (number of shells with total loss of the original color patterns)

¹ palaios.ku.edu

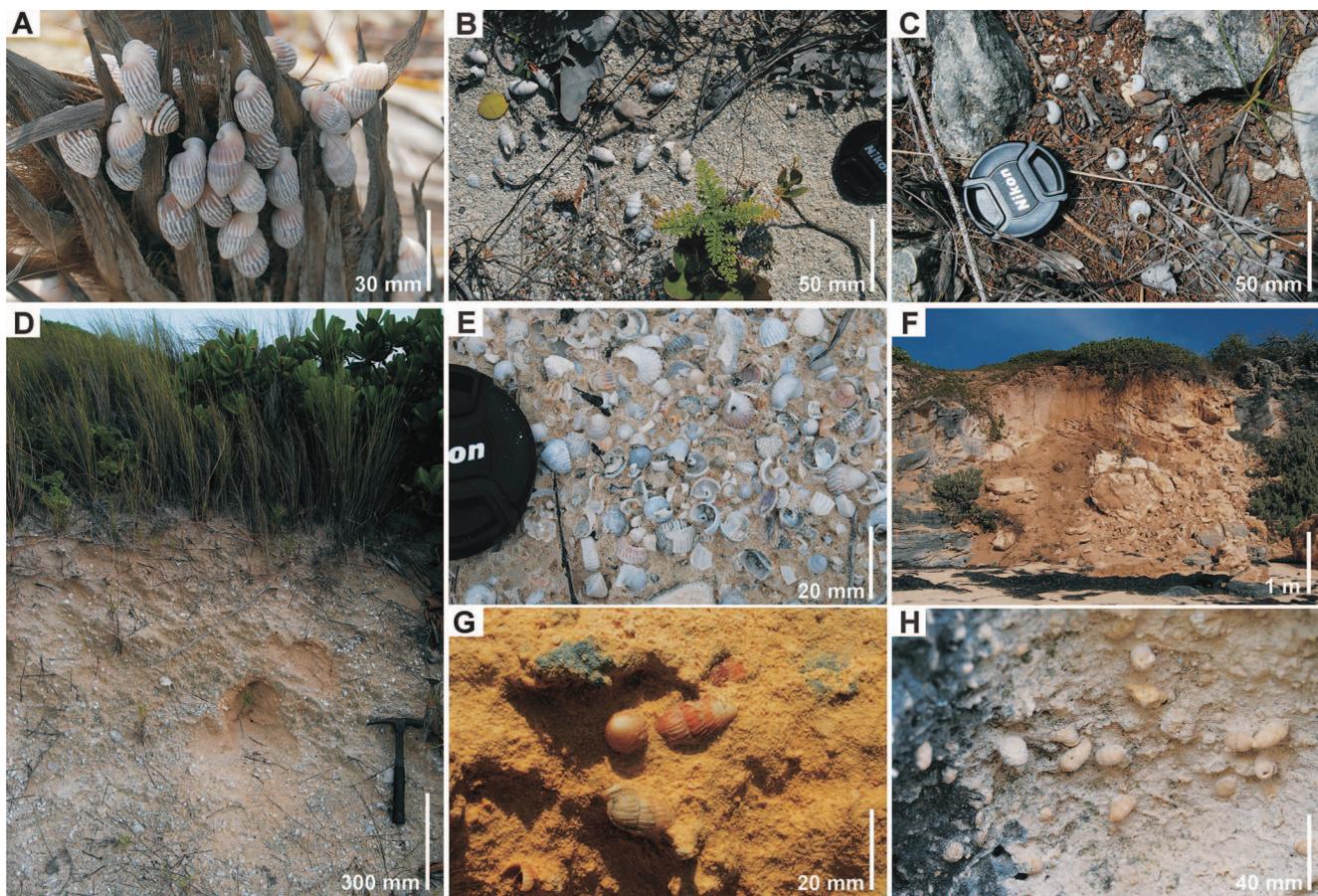


FIGURE 2—Study land snail shell material and sampled sites from San Salvador Island, Bahamas (images by Y. Yanes, 2010). A) Living *Cerion* spp. and *Hemitrochus varians* population from Rocky Point. B) Dead shell assemblage gathered from the sandy substrate of Rocky Point. C) Dead land snail assemblage collected from the rocky substrate of Fernandez Bay. D) General view of the middle Holocene paleosol at North Point. E) Detailed view of middle Holocene shells from North Point. F) General view of the middle Holocene deposit at Hanna Bay. G) Detailed view of Upper Pleistocene shells from The Gulf. H) Detailed view of Upper Pleistocene shells from Watling's Quarry.

6. Carbonate coatings (number of shell remains with the presence of a partial or total carbonate crust).

Taphonomic conditions 2 to 6 were evaluated as percentages with respect to the TNR. Only three of the nine land snail taxa were studied taphonomically, *Cerion* spp., *Hemitrochus varians*, and *Plagioptycha duclosiana salvatoris*. These three species were selected because they were highly abundant and displayed significantly different shell shape, size, and thickness (i.e., differing shell durability).

Time-Averaging

Samples were qualitatively assigned to three different time-averaging classes (i.e., variable scales of age-mixing of non-contemporaneous shells). Living snail populations are considered to display no time-averaging, whereas both dead and fossil shelly assemblages are expected to show time-averaging. A previous study of buried land snails in Quaternary eolian deposits from the Canary Islands suggests that the scale of age mixing is multimillennial for many shelly samples, with an average magnitude of ~2900 years (Yanes et al., 2007). Such a quantitative estimate based on amino acid (AAR) dating of multiple specimens preserved in the same stratigraphic horizon was also linked to the time span of soil formation. Accordingly, fossil (buried) shell assemblages from San Salvador Island, which are also preserved in carbonate-rich Quaternary eolian sites, are assumed to display multimillennial age mixing. The magnitude of time-averaging in dead (surficial) land snail shells has never been quantified by age dating; however, previous studies have attempted to quantify the approximate

half-life of land snail shells on the soil surface. Cadée (1999) performed field experiments on a dune area and observed that unburied snail shells decay as a consequence of both dissolution and bioerosion by other snails. He estimated that shells had a half-life of multiple years, and that the decay rate varied among species with variable shell durability (i.e., thicker and larger shells were more durable). Pearce (2008) calculated from field experiments that the decomposition rate of snail shells on a humid forest floor was ~6.7% per year, with a half-life varying from ~7–12 years. He pointed out that shell half-life is likely to be longer, up to hundreds of years, in carbonate-rich dry (desert) settings, depending also on shell durability. Based on these published experimental studies, surficial (completely exposed) dead shell assemblages from rocky and dune substrates on San Salvador Island could exhibit a decadal to centennial scale of time-averaging. All in all, the following assumptions are considered in the present study: (1) living snails are non averaged, (2) dead (surficial) assemblages exhibit a decadal to centennial time-averaging (= low time-averaging), and (3) fossil (buried) assemblages display a multimillennial time-averaging (= high time-averaging).

Species Abundances

Land snail species abundances (Table 1) were available for 41 shelly samples (out of the 61 taphonomically studied shell assemblages), including all the Pleistocene and Holocene shell samples ($n = 12$), some live ($n = 13$), and some dead ($n = 16$) samples. Snail species were identified under a binocular microscope based on shell size and morphology. The total number of individuals of each identified land snail species was counted per sample (Table 1). The number of

TABLE 1—Land snail species relative abundances of 41 samples from San Salvador Island, Bahamas.

Sample ID	Age level	<i>Plagiogytha</i>										Total
		<i>Cerion</i> spp.	<i>Hemitrochus</i> <i>varians</i>	<i>duclosiana</i> <i>salvatoris</i>	<i>Chondropoma</i> aff. <i>dentatum</i>	<i>Polygyra</i> aff. <i>septemvolva</i>	<i>Succinea</i> sp.	<i>Pupilla</i> sp.	<i>Bulimulus</i> <i>sepulcralis</i>	<i>Oleacina</i> <i>solidula</i>		
DB-live-1	Live	60	0	0	0	0	0	0	0	0	60	
DB-live-2	Live	60	0	0	0	0	0	0	0	0	60	
FH-live-1	Live	66	7	1	0	0	0	0	0	0	74	
FH-live-2	Live	48	2	0	0	0	0	0	0	0	50	
HardB-live-1	Live	44	1	0	0	0	0	0	0	0	45	
HardB-live-2	Live	60	0	0	0	0	0	0	0	0	60	
NP-live-1	Live	53	0	0	0	0	0	0	0	0	53	
NP-live-2	Live	65	0	0	0	0	0	0	0	0	65	
PC-live-1	Live	62	34	0	0	0	0	0	0	0	96	
PC-live-2	Live	55	44	0	0	0	0	0	0	0	99	
RP-live-1	Live	56	1	0	0	0	0	0	0	0	57	
RP-live-2	Live	43	2	0	0	0	0	0	0	0	45	
SB-live-1	Live	45	0	0	0	0	0	8	1	0	54	
DB-dead-1	Dead	180	20	5	12	0	1	0	0	1	219	
DB-dead-2	Dead	252	37	3	15	0	0	0	0	0	307	
FB-dead-1	Dead	1	35	33	5	0	0	0	0	0	74	
FB-dead-2	Dead	1	57	37	5	0	1	0	0	0	101	
FH-dead-1	Dead	78	35	5	29	0	0	0	0	0	147	
FH-dead-2	Dead	81	0	2	4	0	0	0	0	0	87	
HardB-dead-1	Dead	33	6	8	23	0	0	0	0	0	70	
HardB-dead-2	Dead	54	3	13	57	0	0	0	0	6	133	
NP-dead-1	Dead	68	0	0	1	0	0	0	0	0	69	
NP-dead-2	Dead	69	0	0	0	0	0	0	0	0	69	
PC-dead-1	Dead	8	102	10	8	0	0	0	0	0	128	
PC-dead-2	Dead	16	54	5	0	0	0	0	0	0	75	
RP-dead-1	Dead	53	8	3	0	0	0	0	0	0	64	
RP-dead-2	Dead	62	7	2	0	0	0	0	0	0	71	
SB-dead-1	Dead	95	9	14	12	0	5	0	0	0	135	
TG-dead-1	Dead	130	86	1	20	0	0	0	0	0	237	
HB-Holocene-1	Holocene	31	25	1	24	0	0	0	0	0	81	
HB-Holocene-2	Holocene	61	22	0	6	0	0	0	0	0	89	
HB-Holocene-3	Holocene	68	19	0	4	0	0	0	0	4	95	
NP-Holocene-1	Holocene	105	0	1	52	0	0	0	0	0	158	
NP-Holocene-2	Holocene	96	3	0	32	0	0	0	0	0	131	
NP-Holocene-3	Holocene	74	0	1	49	0	0	0	0	0	124	
TG-Pleistocene-1	Pleistocene	109	0	0	18	0	0	0	0	0	127	
TG-Pleistocene-2	Pleistocene	86	0	1	21	1	0	0	0	0	109	
TG-Pleistocene-3	Pleistocene	81	0	0	21	5	0	0	0	0	107	
WQ-Pleistocene-1	Pleistocene	99	0	7	34	0	0	0	0	0	140	
WQ-Pleistocene-2	Pleistocene	52	0	0	5	0	0	0	0	0	57	
WQ-Pleistocene-3	Pleistocene	50	0	5	16	0	0	0	0	0	71	

individuals varied between 45–99 for living snails, 64–307 for dead shells, 84–158 for Holocene assemblages, and 57–140 for Pleistocene assemblages (Table 1). *Cerion* species are complicated to identify at species level based on the hard skeleton alone because of the large shell size and shape variability per species, in addition to frequent interspecies hybridization (e.g., Rose, 1989; Goodfriend and Gould, 1996; Baldini et al., 2007). Although up to five *Cerion* species have been catalogued in San Salvador Island (Harasewych and Villacampa, 2001), including *C. fraternum* Pilsbry, 1902, *C. inconspicuum* Dall, 1905, *C. lacunorum* Dall, 1905, *C. rodrigo* Gould, 1997, and *C. waltlingense* Dall, 1905, I lumped all as *Cerion* spp. in order to avoid misattribution of individuals to species. The rest of the land snail taxa were identified at the generic or specific level when possible.

Land snail species included in the present study display variable ecological habits and shell sizes (Table 2). *Cerion* spp. were found attached to trees and shrubs between 50 and 100 cm above the ground surface as well as on the soil surface below leaves and in the leaf litter. *Hemitrochus varians* and *Plagiogytha duclosiana salvatoris* were often found attached to trees and shrubs above ~50 cm from the soil surface. The remaining taxa were observed mostly on the ground, below leaves, rocks and/or among leaf litter (Table 2). All species tended to rest during the day and became active mostly at night or during rain events; they did not aestivate during the summer season (field observations,

2010). Humidity seems to be an important environmental factor for snails' activity in the Bahamas based on the observed active periods. Sizes were also quite variable across taxa, suggesting variable shell durability (Table 2). While *Cerion* shells are quite durable because they exhibit the largest and thickest shells, the remaining species showed comparatively smaller and thinner (weaker) shells (Table 2).

Statistical Analyses

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 relationship between variables and the live-dead taxonomic agreement based on rank-order abundances. Kruskal-Wallis and Mann-Whitney U tests were used to test whether groups of samples differed significantly in median values. Permutation t-test was used to compare the equality of means between two groups of samples via resampling without replacement by random reordering of observations (Hammer and Harper, 2006).

Taphofacies, defined here as shell assemblages with comparable taphonomic traits (Brett and Baird, 1986) were identified by hierarchical cluster analysis of the taphonomic data (proportion of fragmentation, ornament loss, color loss, carbonate coating) based on

TABLE 2—Intrinsic shell features of land snail species.

Snail species	n	Length (mm)	Width (mm)	Thickness (mm)	Ecological habit (field observations, 2010)
<i>Cerion</i> spp.	5	24.91 ± 1.07	10.63 ± 0.24	0.83 ± 0.12	ground and tree dwelling
<i>Hemirochus varians</i>	5	11.44 ± 0.54	12.06 ± 0.49	0.35 ± 0.09	tree dwelling
<i>Plagioptycha duclosiana salvatoris</i>	3	7.10 ± 0.56	12.80 ± 3.61	0.24 ± 0.03	tree dwelling
<i>Chondropoma</i> aff. <i>dentatum</i>	5	9.91 ± 0.79	4.12 ± 0.59	0.62 ± 0.11	ground and rock dwelling
<i>Polygyra</i> aff. <i>septemvolva</i>	3	2.86 ± 0.15	7.53 ± 0.69	0.44 ± 0.14	ground and rock dwelling
<i>Succinea</i> sp.	4	9.34 ± 1.17	5.03 ± 0.57	0.12 ± 0.04	ground and rock dwelling
<i>Bulimulus sepulchralis</i>	6	15.04 ± 1.32	7.37 ± 0.70	0.10 ± 0.04	ground and rock dwelling
<i>Pupilla</i> sp.	3	3.03 ± 0.25	1.80 ± 0.20	0.01 ± 0.00	rock dwelling
<i>Oleacina solidula</i>	5	12.83 ± 2.05	5.10 ± 0.48	0.48 ± 0.17	ground and rock dwelling

n = number of individuals

the Manhattan distance and group-average linkage method (e.g., Yanes et al., 2008, 2011).

Taxonomic mismatches among taphofacies were evaluated for 41 shelly samples (out of the 61 studied samples) through a low-dimensional space ordination of the proportional species abundance by using non-metric multidimensional scaling (NMDS) based on Bray-Curtis similarity, which does not impose hierarchy of the samples (e.g., Hammer and Harper, 2006). The proportions of species abundances were previously square-root transformed to reduce the effect of the dominant species. Other scales of data transformation yielded comparable results. NMDS results were tested for statistical differences using analysis of similarities (ANOSIM).

Several diversity measures were computed on 41 shell samples to evaluate the variations of the native terrestrial malacofauna through time. The raw number of species was sample-size standardized via rarefaction because the number of taxa is strongly dependent on sample size (Hammer and Harper, 2006). Menhinick's richness index estimates the number of species divided by the square root of the sample size: $M = S/\sqrt{n}$, where S is the raw number of species and n is the number of individuals. This index somewhat adjusts the number of species by the number of individuals encountered in the sample (Hammer and Harper, 2006). The simplest-dominant index (Berger-Parker dominance) was calculated as the number of individuals of the dominant taxon divided by sample size (Hammer and Harper, 2006).

RESULTS

Land snail shells of living specimens did not show signs of taphonomic alteration. Dead, middle Holocene, and Upper Pleistocene shells were, however, affected primarily by fragmentation, ornament loss, and color loss; Pleistocene shells were additionally characterized by carbonate coatings (see Supplementary Data¹). The proportion of shell fragmentation, ornament loss, and color loss correlated with each other ($p < 0.001$) based on Spearman rank-based analysis while the proportion of carbonate coating did not correlate with other taphonomic variables after Bonferroni correction, which lowers the alpha value to 0.00833 (i.e., $0.05/6 = 0.00833$). Evidence of other taphonomic agents such as rounding of fragment edges and encrustation were absent.

The taphonomic features of dead shells varied substantially in space (Fig. 3A). Shells collected on the soil surface at Hard Bargain, Fernandez Bay, and Fortune Hill sites generally exhibited higher taphonomic alteration than other localities (Fig. 3A); however, no significant differences on shell damage were observed between shelly samples from rocky versus soft substrate sites (Mann-Whitney U test, $p > 0.05$). A permutation t-test suggested that ornament loss was marginally significantly higher in rocky compared to soft sites ($p = 0.059$, $N = 10,000$ iterations). The taphonomic variables that most affected dead shells (i.e., fragmentation, ornament loss, color loss) did not differ significantly among snail taxa (Fig. 3B).

Generally, middle Holocene and Upper Pleistocene shell assemblages exhibited higher proportions of fragmentation, ornament loss, and color loss than dead shell assemblages, whereas carbonate coating was present almost exclusively in the Upper Pleistocene shell assemblages (Fig. 3C). As expected, living land snail shells were largely unaltered.

Nine land snail taxa were discriminated from the studied shell material (Table 1), including *Cerion* spp., *Hemirochus varians* (Menke, 1829), *Plagioptycha duclosiana salvatoris* (Pfeiffer, 1867), *Chondropoma* aff. *dentatum* (Say, 1825), *Polygyra* aff. *septemvolva* Say, 1818, *Succinea* sp., *Pupilla* sp., *Bulimulus sepulchralis* Poey, 1851, and *Oleacina solidula* (Pfeiffer, 1840) (Table 1). The majority of land snail species were found at both modern and fossil sites. The relative abundance of different taxa varied across samples (Table 1). *Cerion* spp. was clearly the dominant taxon across samples, representing 72% of the specimens. *Hemirochus varians*, *Chondropoma* aff. *dentatum* and *Plagioptycha duclosiana salvatoris* represented 13.9%, 9.6%, and 3.9% of the combined shell material, respectively. The remaining snail taxa were rare (<1%). The average proportional abundances of the main species are plotted against shell age level (live, dead, middle Holocene, and Upper Pleistocene) in Figure 3D.

Live-dead shell sample comparisons of rank-order abundance showed a positive significant Spearman correlation ($r_s = 0.65$; $p < 0.001$). Nevertheless, dead assemblages contained systematically higher numbers of snail species than living populations even after adjusting for different sample sizes (Table 1). Thus, death assemblages were on average ~32% richer in land snail species than counterpart living assemblages.

Cluster analysis of the shelly samples ($n = 61$) based on the proportion of fragmentation, ornament loss, color loss, and carbonate coating indicate that three main taphofacies can be identified (see Supplementary Data figure¹). Weakly altered taphofacies ($n = 35$) grouped live and some dead shell assemblages. Moderately altered taphofacies ($n = 20$) included some dead shell assemblages and all middle Holocene assemblages. Highly altered taphofacies ($n = 6$) embraced all Upper Pleistocene assemblages.

In terms of species composition, NMDS analysis of 41 shelly samples using the proportional abundance of species indicates that all three taphofacies generally overlapped (Fig. 4A). ANOSIM results revealed that moderately and strongly altered samples did not differ in taxonomic composition ($R = 0.11$; $p = 0.17$). However, weakly altered samples significantly differed in species abundances from moderately ($R = 0.35$; $p = 0.001$) and highly ($R = 0.28$; $p = 0.039$) altered samples. Samples of living assemblages—characterized by zero time-averaging—show little dispersion in the NMDS ordination and little overlap with samples of dead and fossil assemblages, which both show wide dispersion and overlap each other considerably (Fig 5B). ANOSIM confirmed that low and high time-averaged shell samples (dead shells on the soil surface and buried fossil shelly assemblages, respectively) did not significantly differ in species relative abundance ($R = 0.16$; $p = 0.08$); however, non-averaged living assemblages clearly differed in

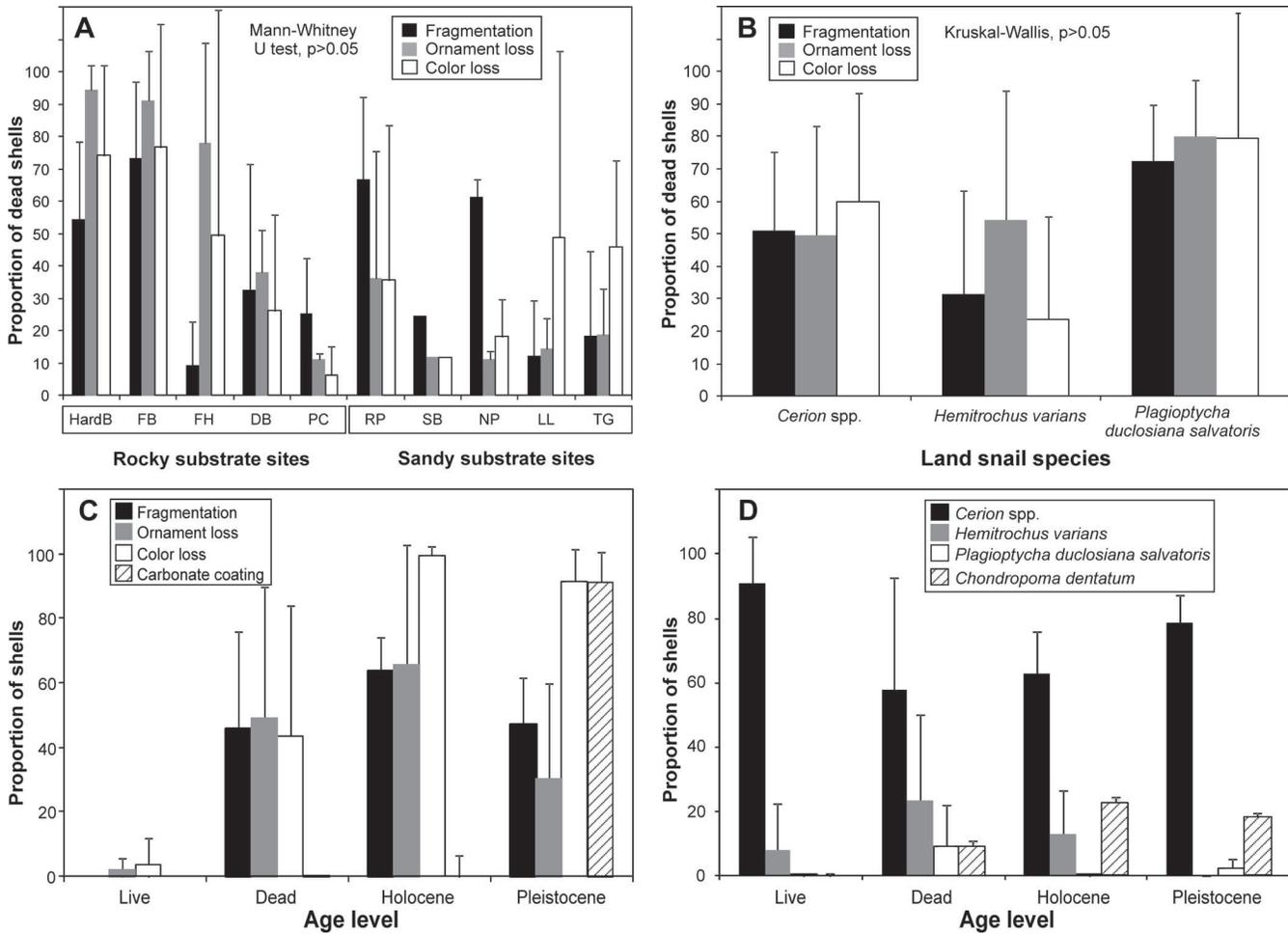


FIGURE 3—Taphonomy and species abundances of land snail shells from San Salvador Island, Bahamas. A) Average taphonomic features of dead shells by locality (rocky sites: HardB = Hard Bargain, FB = Fernandez Bay, FH = Fortune Hill, DB = Dim Bay, PC = Pigeon Creek; sandy sites: RP = Rocky Point, SB = Singer Bar Point, NP = North Point, LL = Little Lake, TG = The Gulf). B) Average taphonomic results of dead shells by main land snail taxon. C) Average taphonomic results per age level: live (n = 21), dead (n = 28), middle Holocene (n = 6) and Upper Pleistocene (n = 6). D) Average proportional abundance of the main land snail species per age level: live (n = 13), dead (n = 16), middle Holocene (n = 6) and Upper Pleistocene (n = 6). Whiskers represent the standard deviation while bars represent the mean value.

taxonomic composition from low time-averaged dead assemblages ($R = 0.28$; $p = 0.001$) and high time-averaged fossil assemblages ($R = 0.70$; $p = 0.001$).

Raw species numbers standardized by rarefaction (Fig. 5A), Menhnick’s richness index (Fig. 5B), and Berger-Parker simple dominance (Fig. 5C) of land snail assemblages from San Salvador Island exhibited matching values at the studied time points (~125 ka, ~5–6 ka, and today). Living snail populations, however, often exhibited considerably lower average values of richness and higher average values of dominance than dead and fossil samples. Living assemblages contained on average 1.7 ± 0.7 species compared to 3.3 ± 1.0 species in death assemblages (Fig. 5A), i.e., dead assemblages were on average ~32% richer in taxa. Mann-Whitney pair-wise comparisons indicate that the median values of those indexes are not significantly different among age groups, except for living snail assemblages (Table 3).

DISCUSSION

Shell Taphonomy in Space and Time

Most dead and all fossil land snail shells were affected by several postmortem processes, while living shells were basically unaltered. Shell breakage was probably the result of a combination of biological factors, especially predation by land crabs, the indigenous hutia rodent

(*Geocapromys ingrahami*), and recently introduced rats (Rose, 1989; Quensen and Woodruff, 1997), as well as physical factors (e.g., wind damage). Because all shell fragments exhibited limited evidence of edge rounding, however, fragmentation by predatory organisms is considered here to have been the dominant factor in shell breakage (see also Yanes et al., 2008). Both ornament and color loss is expected to be a consequence of the action of multiple abiotic (e.g., physical abrasion by sand, dissolution by rain, UV degradation) and biotic (e.g., bioerosion by other snails, microbial maceration, fungal microborring, etc.) agents operating together. Carbonate coating was the consequence of the dissolution of soil carbonates during wetter conditions and the reprecipitation during high evaporation processes (e.g., Retallack, 2001; Pustovoytov, 2003). The fact that carbonate coating was only observed in the oldest shell assemblages suggests that time was an important driving factor in carbonate crust formation.

The degree of taphonomic alteration on dead shells varied across different localities on San Salvador Island (Fig. 3A). This suggests that variable environmental conditions and/or variable exposure time in the taphonomically active zone (TAZ) affected the shell material across locales, if the fauna was held constant. The fact that shells from Hard Bargain, Fernandez Bay, and Fortune Hill localities were substantially more altered, especially in terms of ornament and color loss (Fig. 3A), suggests that shells resided longer in the TAZ at those sites. Moreover, these three sites have a rocky substrate (Fig. 2C), which may have

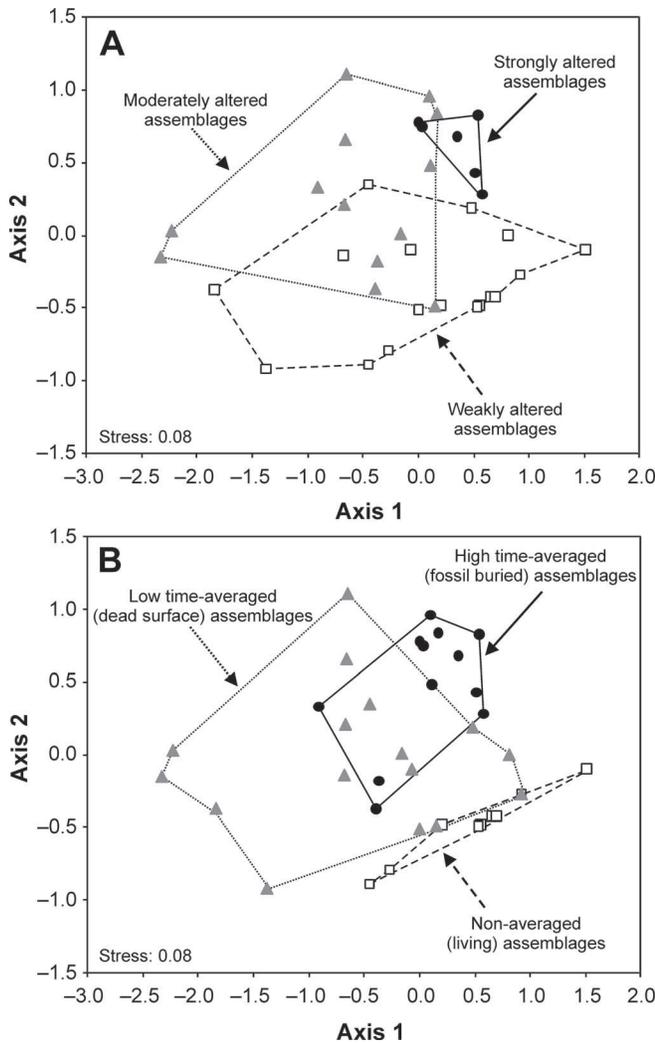


FIGURE 4—Non-metric multidimensional scaling (NMDS) ordination of 41 land snail shell assemblages based on the square-rooted proportional species relative abundances, using Bray-Curtis similarity. A) Shell samples grouped by the magnitude of taphonomic damage. B) Shell samples grouped by the assumed scale of time-averaging (see text).

enhanced higher taphonomic destruction, whereas many of the remaining dead shelly samples were collected at coastal sandy (soft) sites (Fig. 2B). Environmental conditions were also apparently different at these rocky sites where shells were strongly altered (e.g., higher soil moisture as a consequence of substantially denser vegetation). Thus, higher moisture in heavily vegetated clay-rich soils probably increased shell destruction rates in contrast to dry, sand-rich substrates, where shell burial is likely to be quicker. Even though the Mann-Whitney U test suggested that the median value of shell fragmentation, ornament loss, and color loss of shell samples did not differ significantly between rocky and sand substrates, the permutation t-test suggested significantly higher ornament loss of shells from rocky sites. This finding probably needs to be corroborated by further investigation on a controlled environmental setting where abiotic variables are quantified.

The taphonomic half-life of a hard skeleton is a function of extrinsic and intrinsic factors. If environmental factors remain constant, the durability of the skeleton indicates the taphonomic half-life (e.g., Tomašových, 2004). Land snail shelly taxa can differ in durability as a consequence of variable shell size and thickness (e.g., Carter, 1990; Cadée, 1999; Pearce, 2008; Yanes et al., 2011). *Cerion* spp. specimens display a rather large and thick shell (i.e., highly durable) whereas *H. varians* and *Plagioptycha duclosiana salvatoris* have a comparatively

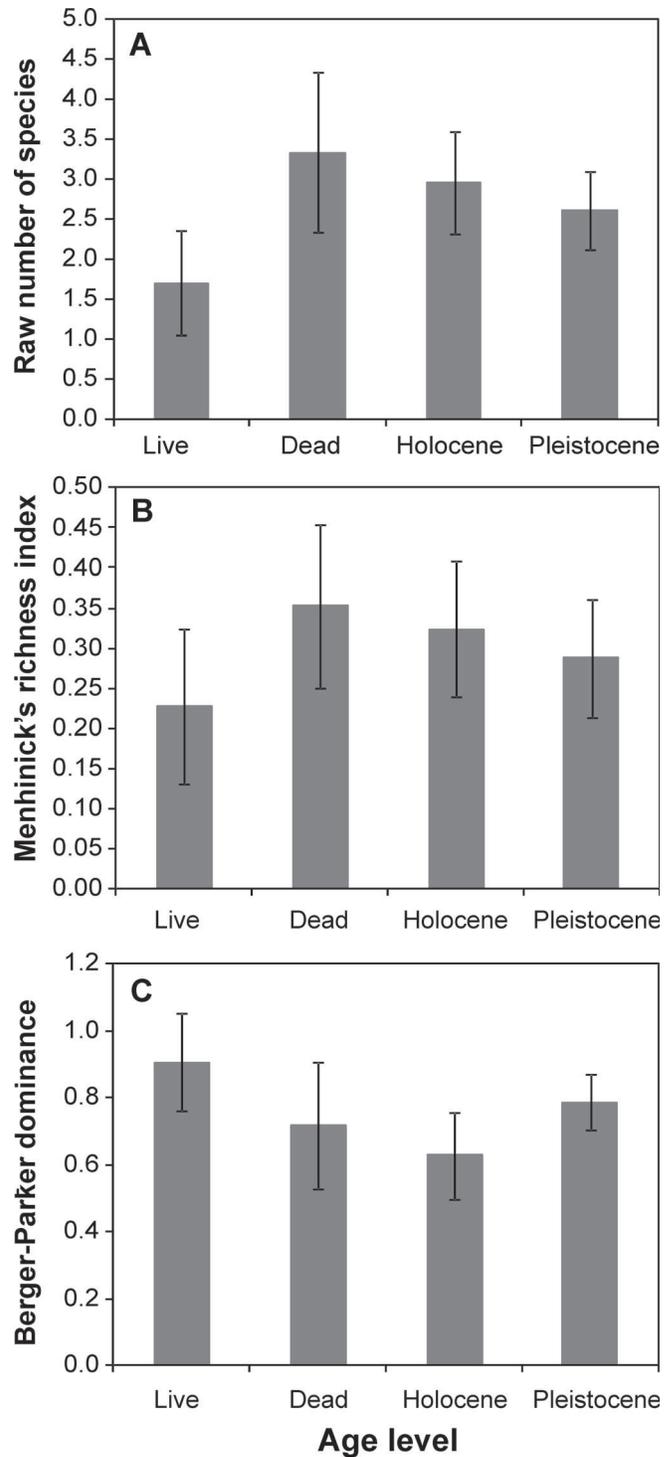


FIGURE 5—Average taxonomic composition of land snails by age level: Live (n = 13), dead (n = 16), middle Holocene (n = 6) and Upper Pleistocene (n = 6). A) Size-standardized raw number of species. B) Menhinick's richness index. C) Berger-Parker simple dominance.

thinner and smaller shell (i.e., likely weaker; Table 2). The average degree of taphonomic alteration of dead shells was comparable among those three taxa, however, regardless of the degree of durability of the hard skeleton (Fig. 3B), suggesting that taphonomic bias (e.g., variable shell-specific destruction rates) were probably minor among samples.

Shell taphonomy varied considerably by geologic age (Fig. 3C). Middle Holocene and Upper Pleistocene assemblages showed higher taphonomic alteration than dead and living shell assemblages (Fig. 3C).

TABLE 3—Mann-Whitney pairwise comparisons of several taxonomic measures by time intervals.

Mann-Whitney pairwise comparisons	Size-standardized species number	Menhinick's richness index	Berger-Parker dominance
Live-dead	0.0002*	0.0061*	0.0044*
Live-Holocene	0.0033*	0.0872	0.0097**
Live-Pleistocene	0.0110	0.2542	0.0393
Dead-Holocene	0.7962	0.4837	0.2851
Dead-Pleistocene	0.2348	0.2101	0.6318
Holocene-Pleistocene	0.7447	0.5752	0.0306

* significant differences after Bonferroni correction

** marginally significant differences after Bonferroni correction

Fossil shells have no doubt experienced longer time exposures to biostratigraphic and diagenetic processes than local living and dead assemblages, thus enhancing taphonomic damage.

Ecological Fidelity of Shell Assemblages

Modern and fossil land snail assemblages from San Salvador Island contain multiple species but are strongly dominated by *Cerion* spp. individuals, an average of 72% of all individuals studied here (Table 1). This emphasizes the fact that *Cerion* species have been highly successful colonizing the island and appear to be better adapted to the various environments of San Salvador Island than other snail taxa (e.g., Rose, 1989). Interestingly, the only locale where other dead land snail species, such as *H. varians*, were dominant over *Cerion* was Fernandez Bay (Table 1), suggesting that the conditions at this locale did not favor *Cerion* proliferation; however, no living snails were found at this location.

The rank-order abundance of land snail species (Table 1) of live and dead shells at the assemblage level (based on 12 pairwise comparisons) generally showed a high taxonomic agreement (Spearman, $r_s = 0.65$; $p < 0.001$). Thus, species that dominated the living snail assemblage similarly dominated dead shelly assemblages, and species that were rare living were also rare in the dead assemblages (Fig. 3D). This coincides with a previously published study that evaluated live-dead fidelity on land snail assemblages (Rundell and Cowie, 2003), which showed that dead shell assemblages from the tropical islands of the Pacific (Hawaii, American Samoa, and Palau) overall exhibited good taxonomic agreement with living snail counterparts. The findings also agree with the high rank-order agreement found in marine mollusks in pristine soft-sedimentary seafloors (Kidwell, 2001).

Dead assemblages from San Salvador Island showed systematically higher number of species than living populations, in agreement with Pacific land snail assemblages (Rundell and Cowie, 2003) and marine shelly assemblages (e.g., Kidwell, 2002). This excess in land snail richness in dead shelly assemblages over living populations can derive from several causes. First, death assemblages are time-averaged, that is, they represent the progressive accumulation of individuals across seasons and/or years, whereas the sampled living community is represented by a single snapshot (e.g., Kidwell, 2002). Secondly, sampling living land snails is significantly harder than dead assemblages since many species may be small and can be overlooked more easily (Rundell and Cowie, 2003). Lastly, living snails are only active during the wettest times of the day while they tend to remain in a dormant state hidden at cavities or under leaf litter and rocks to avoid desiccation (e.g., Cook, 2001). This behavior increases the challenge of fully sampling all living species present at one locality. Despite the differences in the numbers of individuals and species, live-dead land snail assemblages from San Salvador Island exhibited an overall good taxonomic agreement. A recent study by Tomašových and Kidwell (2011) suggests that the magnitude of biological variability in living assemblages is an important driving factor on the taxonomic composition of dead assemblages. Thus, the taxonomic composition of dead assemblages from stable habitats tends to be more modified in

species composition with respect to the living than those from variable habitats. This is due to the lower biological variability of stable habitats that contributes into the time-averaged dead assemblage (Tomašových and Kidwell, 2011). Interestingly, live and dead land snail assemblages from pristine localities from San Salvador Island display considerably high taxonomic agreement despite the apparent homogeneity of habitats (low biological variability) of the local living snail assemblages. It would be interesting to test if land snails from highly variable habitats in space and time display substantially higher live-dead taxonomic agreement in future snail investigations.

Different rates of shell damage can distort the original community (e.g., Behrensmeier et al., 2000). Thus, it is possible that shell assemblages with variable degrees of taphonomic alteration can potentially differ in taxonomic composition as a consequence of postmortem processes (e.g., Tomašových, 2006; Tomašových et al., 2006a, 2006b). In the present study, strongly (=all Upper Pleistocene samples) and moderately (=some dead and all middle Holocene samples) taphonomically altered shelly samples did not differ statistically in terms of relative species abundance (Fig. 4A). Hence, land snail shell assemblages that have been fossilized in carbonate-rich deposits from tropical islands are likely to exhibit high taxonomic fidelity regardless of the degree of taphonomic alteration (see also Yanes et al., 2008). Weakly altered assemblages (=some dead and all living shelly samples), however, differed significantly in species abundances from moderately and strongly altered taphofacies. Variable shell-specific destruction rates may occur for land snail species with different shell durability, which can lead to variations in taxonomic compositions (e.g., Carter, 1990; Cadée, 1999; Pearce, 2008). The results presented here, however, indicate that no significant differences in taphonomic damage were observed among land snail taxa from San Salvador Island (Fig. 3B). This may require further research because only three of the nine snail taxa were studied taphonomically. The fact that differing taphofacies contained shelly taxa with comparable durability suggests low taphonomic bias (see also Yanes et al., 2011). Nonetheless, the identification of taphonomic bias may be disguised by the overwhelming dominance of the highly durable *Cerion* shells across samples. In fact, the abundance of the dominant taxon displays similar values in dead (modern), Holocene, and Pleistocene assemblages (Fig. 5C). Therefore, further taphonomic research on modern snail assemblages not dominated by *Cerion* shells is recommended.

Non-averaged shell assemblages (=living snails) differed statistically in species abundances from low (dead) and high (fossil) time-averaged shelly assemblages (Fig. 4B). The scale of age mixing of non-contemporaneous shells can affect the degree of taxonomic agreement at the assemblage level, with increasing time-averaging leading to greater richness and lower dominance by a single species (greater evenness; Tomašových and Kidwell, 2009, 2010). The results presented here suggest that high time-averaged (Holocene and Pleistocene) and low time-averaged (dead) shell assemblages did not differ in taxonomic composition (Fig. 4B); however, non-averaged (living) assemblages differed from both dead and fossil time-averaged assemblages in terms of proportional species abundance (Fig. 4B). Hence, the scale of time-averaging appears to have affected the taxonomic composition of land

snail shell assemblages and therefore, the observed taxonomic mismatches between living and dead-fossil samples may be partly or completely a consequence of a variable extent of age mixing (see also Tomašových and Kidwell, 2010). Accordingly, the diversity values from non-averaged snail assemblages may not be comparable to those extracted from time-averaged assemblages. This agrees with the study by Yanes et al. (2011) in which minimally time-averaged and multimillennial-averaged land snail shelly assemblages from Quaternary eolian successions in the Canary Islands differed significantly in terms of species composition.

The taphonomic and ecological results indicate that modern dead and fossil shell assemblages exhibit overall high taxonomic fidelity to each other. Thus, changes in species richness inferred from time-averaged assemblages should reflect past changes in terrestrial ecosystems because such taxonomic variations should primarily arise from ecological mechanisms instead of postmortem biases.

The taxonomic richness (Fig. 5A–B) and simple dominance (Fig. 5C) of land snail shell assemblages did not generally differ among time-averaged dead (modern), middle Holocene (~5–6 ka) and Upper Pleistocene (~125 ka) assemblages (Table 3). This suggests that land snail communities were stable at various interglacial time intervals on San Salvador Island. Fluctuations of abiotic (e.g., humidity, temperature, island area, etc.) and biotic (e.g., competition, predation, etc.) factors are expected to affect the diversity and abundance of terrestrial malacofaunas that inhabit islands (e.g., Chiba, 2007; Huntley et al., 2008; Davison and Chiba, 2008; Yanes et al., 2011). Thus, if land snail communities from San Salvador Island did not substantially change per age interval, it is probable that the dominant climatic/environmental and/or ecological conditions ~125 ka and ~5–6 ka were comparable to those observed today.

CONCLUSIONS

Comparison of living, dead, middle Holocene, and Upper Pleistocene land snail assemblages from San Salvador Island (Bahamas) shows that living and dead assemblages exhibited an overall high taxonomic agreement in rank-order abundance of species. Moderately and strongly taphonomically altered land snail assemblages were comparable in species composition, also pointing to high fidelity. In contrast, weakly altered assemblages exhibited significant taxonomic discordances compared to both moderately and strongly shell-damaged assemblages. Hence, variations in taxonomic composition of land snail assemblages were a consequence of differing time-averaging scales rather than substantial postmortem bias. Thus, direct comparisons of diversity between non-averaged and time-averaged snail assemblages may not be appropriate. Species richness and dominance of time-averaged snail assemblages were similar during three interglacial cycles (~125 ka, ~5–6 ka, and today). This study emphasizes that time-averaged land snail shell assemblages preserved in carbonate-rich tropical islands likely retain the signature of the original community and may be used in paleoecological and paleoenvironmental studies.

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