

Anthropogenic effect recorded in the live-dead compositional fidelity of land snail assemblages from San Salvador Island, Bahamas

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Received: 25 November 2011 / Accepted: 20 September 2012 / Published online: 7 October 2012
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Abstract Terrestrial malacofaunas that inhabit islands are vulnerable to human activities. Habitat destruction, introduction of exotic species, predators, etc. are distorting the composition and distribution of indigenous snail communities. Specifically, the taxonomic discordance between live and dead assemblages may be the consequence of anthropogenic disturbances rather than natural post-mortem processes. Live-dead fidelity may hence reflect the degree of human alteration in a given locality. This approach was used to study the relative abundance of live and dead land snails from pristine and urbanized localities around San Salvador Island (Bahamas). Thirteen species were encountered from 64 samples containing 5,343 specimens. Taxonomic composition was significantly different between areas of negligible anthropogenic disturbance and those impacted by humans. Although which species of land snails are endemic to San Salvador is unknown, all identified species are native to the Caribbean region and invasive species were not encountered. However, some synanthropic species, found exclusively in urban-developed areas, have not been recovered from the local fossil record, pointing to their relatively recent introduction possibly from nearby islands. Non-metric MDS, Jaccard-Chao index, and Spearman correlation analyses indicated that dead assemblages displayed a good compositional correspondence to live communities at pristine sites, whereas considerable disparity was sometimes observed at human-modified areas. Urbanized areas probably favored the proliferation of synanthropic species whereas dead assemblages may contain anthropophobic taxa that lived there prior to recent human modification. These findings are consistent with previous live-dead fidelity studies of marine molluscan and terrestrial small-mammal assemblages, and suggest that the taxonomic discordance between live and dead assemblages of land snails may be indicative of recent anthropogenic alteration.

Keywords Land snails · Compositional fidelity · Urbanization · Taphonomy · Quaternary · San Salvador Island

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Introduction

Terrestrial island malacofaunas are usually rich (Solem 1984) but they are vulnerable to human activities. Nonmarine (terrestrial and freshwater) mollusks are declining at a rapid rate worldwide (Lydeard et al. 2004), especially in island ecosystems. Various studies have documented the historical degradation of land snail communities caused by human disturbances (e.g., Goodfriend et al. 1994; Cowie and Robinson 2003; Chiba and Roy 2011). Anthropogenic factors such as (1) habitat destruction by agricultural and urban development, (2) introduction of alien predators (rodents, insects, flatworms, carnivorous snails, etc.), and (3) introduction of cosmopolitan non-native species (which compete with native species), can distort the composition and distribution of indigenous anthropophobic (i.e. intolerant to human influence) taxa (e.g., Cowie 2001, 2002; Chiba et al. 2009; Chiba 2010; and references therein).

Several approaches with variable temporal scales are commonly used to evaluate the degree of human impact on land snail richness and composition, including (1) field-surveys performed systematically over short periods of time (years and/or decades); (2) comparisons of modern field-surveys with earlier collections and/or published records (decades and/or centuries); and (3) direct evidence from the fossil record (geological timescale). An alternative approach, not yet rigorously tested for terrestrial malacofaunas, is the extent of taxonomic agreement between dead assemblages and live communities. The taxonomic composition (number of species and their relative abundance) of dead assemblages may differ from that of the live community as a consequence of natural postmortem processes, such as differential transport or preservation of species or age-classes and variations in the magnitude of age-mixing of non-contemporaneous specimens (e.g., Kidwell 2001, 2002). This approach has been used extensively by paleontologists to estimate the ecological fidelity (the degree to which the ecological information from the once living community is reflected in the fossil assemblage) of the fossil record (e.g., Kidwell 2001, 2002; Yanes 2012). Alternatively, recent anthropogenic disturbances, which can cause species extinctions and replacements by the newly introduced synanthropic taxa (species that benefit from human-derived environments), may result in considerable live-dead taxonomic mismatches (Kidwell 2007; Terry 2010). Kidwell (2007) showed that compositional mismatches between live-dead marine mollusks were generally larger in human modified (eutrophic) areas while they matched well in pristine locales. Rundell and Cowie (2003) and Yanes (2012) observed that there was a general high taxonomic agreement between live and dead land snail assemblages inhabiting natural landscapes from various low-latitude islands. However, live-dead taxonomic fidelity studies of land snail assemblages that inhabit human-disturbed areas are rare.

In the present study, the ecological fidelity of live and dead terrestrial malacofaunas inhabiting San Salvador Island (Bahamas) were investigated. San Salvador Island is a carbonate-rich, low altitude (less than 38 m a.s.l.), small ($\sim 163 \text{ km}^2$), subtropical island ($24^{\circ}06'N$) on the eastern edge of the Grand Bahama Bank (Fig. 1). The island has been occupied by humans since A.D. 700, and pre-historic impacts on island environments are perceptible (e.g., Blick 2007). San Salvador Island supports abundant land snail assemblages that inhabit both relatively pristine and currently urbanized locales. While ecological studies on Bahamian *Cerion* species (Gastropoda: Cerionidae) have been undertaken (e.g., Woodruff and Gould 1980; Gould and Woodruff 1990; Quensen and Woodruff 1997; and references therein), the remaining land snail species have received little attention (but see Dall 1905; Maly and Doolittle 1977). Accordingly, the snail species living today on San Salvador Island are largely unknown. The goals of the present study

were (1) to field-survey current terrestrial malacofaunas from rural and urban areas of San Salvador, which will improve existing knowledge of snail richness in the island (what species do actually live on the island and how are they distributed?); and (2) to evaluate the degree of taxonomic agreement between dead assemblages and live snail communities from both relatively pristine and human-impacted locales (do live-dead taxonomic discordances reflect the anthropogenic impact on terrestrial ecosystems?).

Methods

Geographical setting

Multiple samples of both live and dead land snail assemblages were gathered around San Salvador Island from 17 localities during the summer of 2010 (Fig. 1). Snails are relatively abundant all around the island so samples were collected from as many sites as possible to achieve a dataset that covered coastal northern, southern, eastern, western sites of the island, as well as inland areas (Fig. 1). Localities were classified qualitatively in two extreme categories: (1) pristine and (2) human-impacted. In this study, pristine sites are considered those localities with abundant native vegetation and no evidence of current urbanization or landscape modification, whereas human-impacted sites include localities with on-going urban development with noticeable human-induced habitat alteration. This classification does not consider historical anthropogenic impact on San Salvador. Samples collected at sites classified as pristine include (filled circles in Fig. 1): North Point (NP, $n = 4$), Singer Bay (SB, $n = 2$), Rocky Point (RP, $n = 4$), Fernandez Bay (FB, $n = 2$), French Bay (FR, $n = 2$), The Gulf (TG, $n = 2$), Watling's Quarry (WQ, $n = 2$), Pigeon

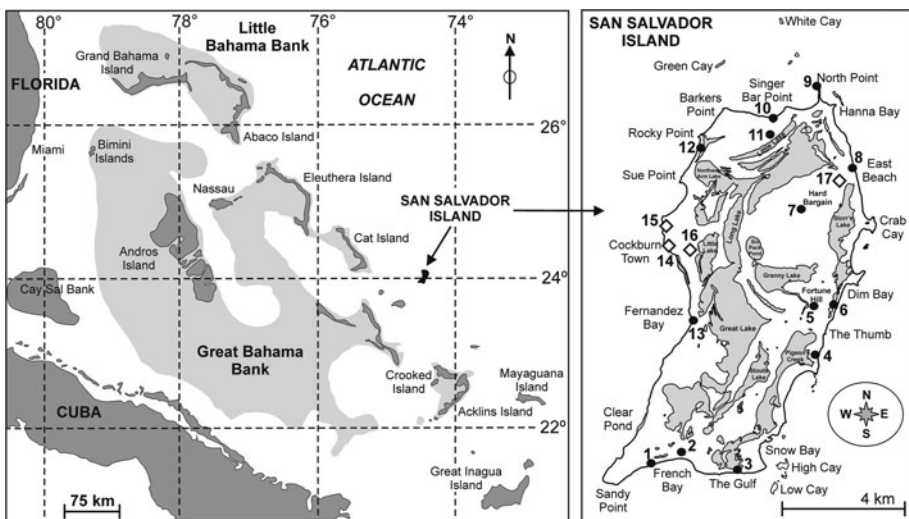


Fig. 1 San Salvador Island and sampling localities. *Filled circles* (1 to 13) are localities with negligible human disturbance; *open diamonds* (14 to 17) are sites with substantial landscape modification by urban development. 1 French Bay (FR), 2 Watling's Quarry (WQ), 3 The Gulf (TG), 4 Pigeon Creek (PC), 5 Fortune Hill (FH), 6 Dim Bay (DB), 7 Hard Bargain (HB), 8 East Beach (EB), 9 North Point (NP), 10 Singer Bay (SB), 11 Death March (DM), 12 Rocky Point (RP), 13 Fernandez Bay (FB), 14 Cockburn Town (CT), 15 The Airport (TA), 16 Little lake (LL), 17 Lighthouse (LH)

Creek (PC, $n = 4$), Dim Bay (DB, $n = 4$), Hard Bargain (HB, $n = 4$), East Beach (EB, $n = 2$), Death March (DM, $n = 4$), and Fortune Hill (FH, $n = 4$). The localities considered as human-impacted include (open diamonds in Fig. 1): the Airport (TA, $n = 6$), Cockburn Town (CT, $n = 4$), The Lighthouse (LH, $n = 8$) and Little Lake ($n = 6$). A total of 64 samples (33 dead and 31 live assemblages) from 17 localities were studied, of which 24 samples come from human-impacted sites and 40 from pristine locales. These localities represent three main habitat-types: (1) coastal sandy locales with open vegetation of palms and shrubs (NP, RP, SB, LL, TG, FR, EB and WQ); (2) coastal rocky localities with open vegetation of shrubs (FB, DB, PC, CT, TA and LH); and (3) inland rocky sites with dense vegetation (HB, FH and DM).

Sampling protocol and studied material

Living specimens were searched for on plants, under rocks and among leaf litter, flipping rocks over and shaking plants following Coppolino (2010). Empty shells (completely exposed) were picked up directly from the soil surface at the same sites where live snails were studied. Sample size ranged from 40 to 307 individuals. In total, 5,343 specimens were collected. For both live and dead samples, all specimens found in $\sim 10 \text{ m}^2$ were counted. Samples from the same locality were $\sim 20 \text{ m}$ apart from each other.

Most live specimens were identified taxonomically in the field. Live specimens with doubtful taxonomic classification were taken to the laboratory of the Gerace Research Center (San Salvador Island) for a more detailed evaluation under the binocular microscope. These live-collected individuals were then returned to the field to protect the local malacofauna. Empty shells on the soil surface were taken to the laboratory and studied under a binocular microscope. The same sampling effort and strategy was applied at each (both pristine and impacted) locality. Small and minute species were also searched for using the same effort and approach at each site. Minute specimens were searched for about one hour, principally under rocks and among leaf litter, where they were always found alive. Because the same researcher sampled each locality, potential sampling biases should have affected all samples equally. Therefore, samples from this study should be reasonably comparable. Specimens were identified at genus or species level when possible based on shell features alone. The total number of individuals was counted for each species and sample. For dead individuals only those with the embryonic shell intact were considered to avoid scoring the same specimen multiple times. The dead shell material exhibited relatively low taphonomic damage (Yanes 2012) and therefore the protoconch was preserved in most specimens. Dead shell assemblages are housed in the Department of Geology of the University of Cincinnati. Several voucher shells of each species are deposited in the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania (catalog numbers CM123483 to CM123495). In this study, the terms synanthropic and anthropophobic species are employed. Synanthropic refers to species that are present in urbanized sites whereas anthropophobic refers to species absent from urban sites (e.g., Horsak et al. 2009).

Statistical analysis

Statistical analyses were performed using R 2.15.0 (R Development Core Team 2012) and PAST 1.39 software (Hammer et al. 2001). Statistical significance is considered at $\alpha = 0.05$. Non-multidimensional scaling ordination (NMDS) was used to explore the spatial ordination of samples using the Bray–Curtis similarity index of the proportional species abundance. Proportional species abundance was square-root transformed to

diminish the effect of dominant taxa. Analysis of similarities (ANOSIM) was employed to test for statistical differences among groups of samples. The Mann–Whitney-U test was used to test whether groups of samples differed in median values.

Live and dead species abundances from each sample were compared using the Jaccard–Chao (J–C) taxonomic similarity index with fossil package in R (Vavrek 2011). This index compensates for differences in sample sizes by incorporating the effect of unseen species pairs (Chao et al. 2005). The J–C index varies from 0 (no shared species) to 1 (all species shared). In addition, Spearman (rank-based) correlation was used to explore similarities in the rank-order species relative abundances. This correlation coefficient varies from -1 (species are ranked in opposite orders in the two samples) to 1 (species order is the same in both samples). Spearman analyses were performed first considering all cases within a sample, and second, omitting those cases in which a species was absent in both the live and dead assemblages (i.e., double-zero cases). Only live–dead samples with a minimum of 1 shared species and more than 2 species in total were considered. Accordingly, 27 live–dead pairs of samples (11 from impacted sites and 16 from pristine sites) were used in the analyses. Both indexes were used jointly and cross-plotted following Kidwell (2007) to explore the potential discordance in the taxonomic composition and species rank-order abundance between dead assemblages and live communities. Outputs from both similarity indexes were then subjected to a bootstrap approach by resampling the mean of simulated data (10,000 iterations) and subsequently tested statistically using the Student's *t* test to evaluate potential differences in mean values by impact grade.

Results

Land snail species

Thirteen land snail species from 11 families were identified (Table 1; Fig. 2). No slugs were found. Five species of *Cerion* have been recorded from San Salvador (<http://invertebrates.si.edu/cerion/index.cfm>). However, *Cerion* species are hard to identify to species level based on shell features alone because they display large shell morphology variability that may overlap among species. Consequently, *Cerion* species were considered as “*Cerion* spp.” to avoid taxonomic misidentification. Eight of the species have been found preserved in the local Quaternary (from ~ 5 to ~ 125 kyr BP) sedimentary rocks (Yanes 2012) whereas five have not (Fig. 3a). None of the encountered species are endemic to San Salvador but all are native to the Caribbean region. No invasive species (taxa with the potential to harm native ecosystems) were found.

Considered collectively (both live and dead), nine species were collected at pristine localities (Table 2). The dominant taxa were *Cerion* species, which formed ~ 59 % of the total shell material (calculated as the number of *Cerion* individuals with respect to the total number of individuals of all species), followed by *Hemitrochus* (~ 29 %), and *Plagioptycha* (~ 5 %). In contrast, 12 taxa were found at urban localities (Table 2), which were dominated by the genera *Polygyra* (~ 26 %), *Gastrocopta* (~ 22 %), and *Bulimulus* (~ 15 %). Overall, urbanized areas exhibited higher snail richness and evenness than pristine sites. Taxonomic composition of pristine locales matched relatively well with that of the late Pleistocene and middle to late Holocene sedimentary rocks (Fig. 3a, b). In contrast, impacted areas exhibited appreciably different taxonomic composition and species relative abundance than that observed in both pristine and fossil samples (Fig. 3c).

Table 1 Modern land snail species found on San Salvador Island (Bahamas)

Class Gastropoda	Ecological habit (personal field observations, 2010)
Order Stylommatophora	
Family Annulariidae	
<i>Colonella watlingensis</i> ^a	Ground and rock dwelling
<i>Opisthosiphon coloni</i>	Ground and rock dwelling
Family Cerionidae	
<i>Cerion</i> spp. ^a	Tree dwelling at coastal sites Tree and ground dwelling at inland sites
Family Helminthoglyptidae	
<i>Hemistrochus varians</i> ^a	Tree dwelling
Family Oleacinidae	
<i>Oleacina solidula</i> ^a	Ground dwelling
Family Orthalicidae	
<i>Bulimulus sepulchralis</i> ^b	Ground dwelling
Family Polygyridae	
<i>Polygyra plana</i> ^{a, b}	Ground and rock dwelling
Family Pupillidae	
<i>Gastrocopta pellucida</i> ^b	Ground and rock dwelling
<i>Pupoides modicus</i> ^{a, b}	Ground and rock dwelling
Family Subulinidae	
<i>Subulina octona</i> ^b	Ground and rock dwelling
Family Succineidae	
<i>Succinea barbadensis</i> ^b	Ground and rock dwelling
Family Xanthonychidae	
<i>Plagioptycha duclosiana salvatoris</i> ^a	Tree dwelling

^a Denotes species known to be preserved in the local Quaternary rocks

^b Denotes taxa found exclusively at urban-developed areas

Dead assemblages from both pristine and impacted sites combined were consistently richer in snail species (~26 % richer, on average) and showed higher abundance (~34 % more specimens, on average) than live land snail assemblages (Table 2; Fig. 4). The taxonomic composition of land snails differed significantly between human impacted and pristine settings, as revealed by the NMDS ordination (Fig. 5) and the subsequent ANOSIM analysis ($P < 0.001$) (Fig. 5).

Live-dead taxonomic comparisons

Jaccard-Chao indexes and Spearman (rank-based) coefficients were calculated for live-dead pairwise sample from 11 impacted localities and 16 pristine sites (Table 3). Live and dead assemblages from areas with negligible anthropogenic alteration exhibited an average Jaccard-Chao index of 0.81 (± 0.17), an average Spearman's rho coefficient of 0.66 (± 0.22) if all cases within a sample were considered (Fig. 6a), and a value of 0.64 (± 0.34) if cases when a species was absent in both the live and the dead were omitted (Fig. 6b). On the other hand, samples from human impacted areas exhibited average values

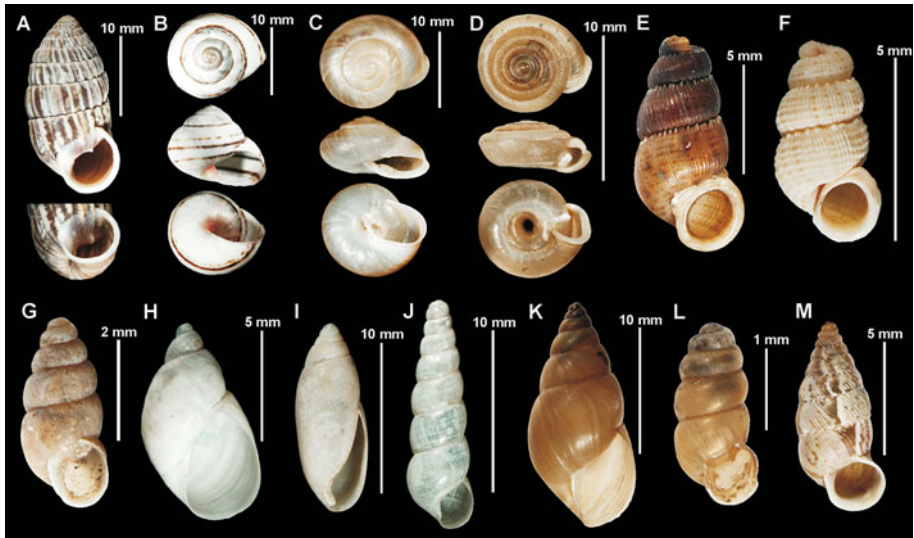


Fig. 2 The land snail species found on San Salvador Island (Bahamas). **a** *Cerion* spp., **b** *Hemitrochus varians*, **c** *Plagioptycha duclosiana salvatoris*, **d** *Polygyra plana*, **e** *Opisthosiphon coloni*, **f** *Colonella watlingensis*, **g** *Pupoides modicus*, **h** *Succinea barbadensis*, **i** *Oleacina solidula*, **j** *Subulina octona*, **k** *Bulimulus sepulcralis*, **l** *Gastrocopta pellucida*, **m** *Microceramus providentia*

of $0.51 (\pm 0.34)$, $0.40 (\pm 0.22)$ and $-0.14 (\pm 0.58)$, respectively (Fig. 6a, b). The scale of live-dead taxonomic agreement was significantly different (Student's *t*, $P < 0.001$) between pristine and impacted locales for both bootstrapped-similarity indexes (Fig. 6c, d). That is, samples from urbanized areas often exhibited appreciably larger taxonomic discordance between live and dead, whereas samples from rural sites showed significantly higher live-dead taxonomic agreement (Table 3; Fig. 6a–d).

Discussion

San Salvador may be considered a relatively pristine island. Only ~900 permanent residents live on the island and the urbanization is concentrated in just a few localities. Moreover, pre-historic occupation seems to have been at a level similar to the current population (e.g., Blick 2007). However, the island is small (21 km length and 8 km width) and therefore, even minor anthropogenic modifications may alter terrestrial ecosystems. Various synanthropic land snail species (e.g., *Gastrocopta*, *Subulina*, *Microceramus*, *Bulimulus*), not known in the local fossil record (Dall 1905; Yanes 2012), were present and sometimes abundant in human-impacted areas. This suggests that, perhaps, synanthropic species were introduced recently from nearby islands like Cat Island (Fig. 1), the sixth largest Bahamian island and closest to San Salvador. Alternatively, synanthropic species may be present in pristine (and fossil) sites but were overlooked (or not preserved). If so, synanthropic species (already present on the island but with minimal representation) could have proliferated at urban sites, which offer new enhanced environmental and/or substrate conditions for them. Synanthropic species here (Fig. 2j–m) exhibit thin and small shells that are likely to decay more readily than those of other species with highly durable (thick and large) hard shells, like *Cerion*. However, other anthropophobic snails with comparable

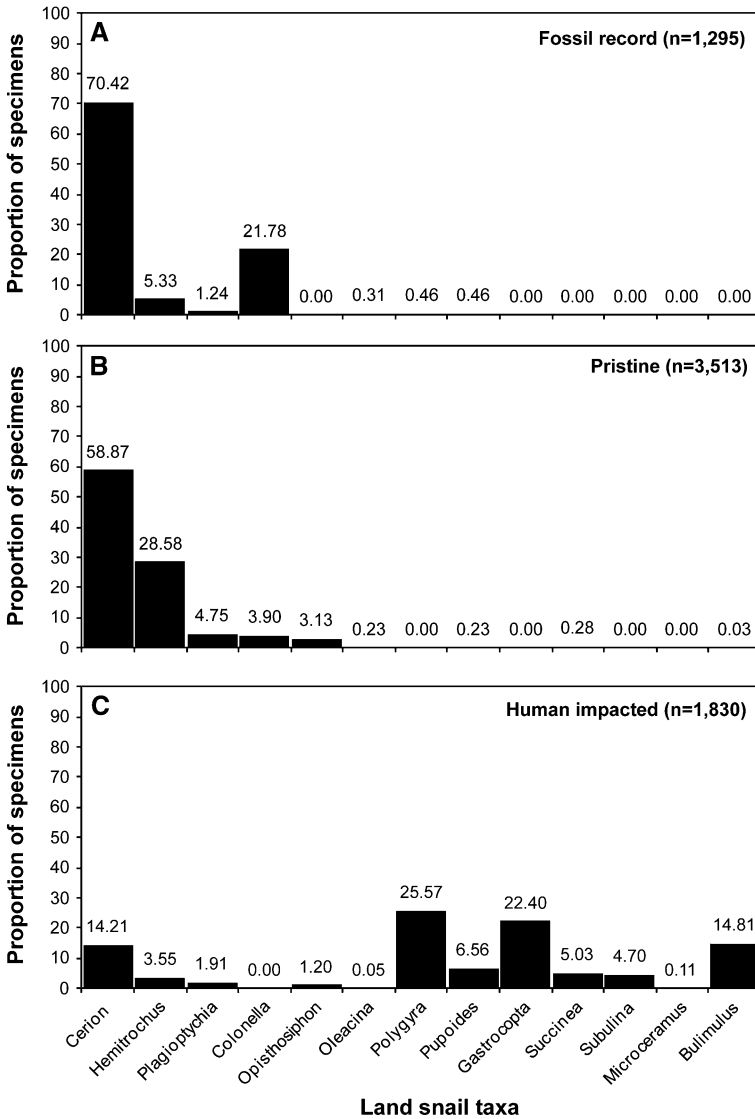


Fig. 3 Proportional species abundance of fossil and modern (both live and dead combined) land snails from San Salvador. **a** Samples from late Pleistocene (~125 kyr) and middle Holocene (~5 kyr) sedimentary rocks (data from Yanes 2012). **b** Samples from sites with current negligible human influence. **c** Samples from localities with substantial urban development

shell size and/or thickness (Fig. 2b–i) were preserved in fossil sites as well (Fig. 3). Thus, differences in shell durability among species probably did not affect the observed patterns severely (see also Yanes et al. 2011).

Despite the apparently minor current human influence on San Salvador, the taxonomic composition and distribution of land snails has been modified in the urbanized as opposed to pristine parts of the island. In most pristine localities, synanthropic land snail taxa were not found or exhibited negligible abundance (Fig. 3). This suggests that pristine sites are

Table 2 Abundance of live and dead land snails from San Salvador (Bahamas)

Sample ID	Locality ^b	Habitat type	Impact grade	Age	<i>Cerion</i> spp.	<i>H. varians</i>	<i>P. ductosiana</i>	<i>C. watlingensis</i>	<i>O. colomi</i>
DB-dead-1 ^a	DB	IR	P	D	180	20	5	0	12
DB-dead-2 ^a	DB	IR	P	D	252	37	3	0	15
DB-live-1 ^a	DB	IR	P	L	60	0	0	0	0
DB-live-2 ^a	DB	IR	P	L	60	0	0	0	0
DM-dead-1	DM	IR	P	D	56	24	11	18	8
DM-dead-2	DM	IR	P	D	64	38	8	15	13
DM-live-1	DM	IR	P	L	3	38	0	0	0
DM-live-2	DM	IR	P	L	5	35	0	0	0
EB-dead-1	EB	CS	P	D	0	58	6	0	0
EB-live-1	EB	CS	P	L	0	43	0	0	0
FB-dead-1 ^a	FB	CS	P	D	1	35	33	2	3
FB-dead-2 ^a	FB	CS	P	D	1	57	37	1	4
FH-dead-1 ^a	FH	IR	P	D	78	35	5	29	0
FH-dead-2 ^a	FH	IR	P	D	81	0	2	4	0
FH-live-1 ^a	FH	IR	P	L	66	7	1	0	0
FH-live-2 ^a	FH	IR	P	L	48	2	0	0	0
FR-dead-1	FR	CS	P	D	24	42	0	0	0
FR-live-1	FR	CS	P	L	8	33	0	0	0
HB-dead-1 ^a	HB	IR	P	D	33	6	8	19	4
HB-dead-2 ^a	HB	IR	P	D	54	3	13	49	8
HB-live-1 ^a	HB	IR	P	L	44	1	0	0	0
HB-live-2 ^a	HB	IR	P	L	60	0	0	0	0
NP-dead-1 ^a	NP	CS	P	D	68	0	0	0	1
NP-dead-2 ^a	NP	CS	P	D	69	0	0	0	0
NP-live-1 ^a	NP	CS	P	L	53	0	0	0	0

Table 2 continued

Sample ID	Locality ^b	Habitat type	Impact grade	Age	<i>Cerion</i> spp.	<i>H. varians</i>	<i>P. duclosiana</i>	<i>C. watlingensis</i>	<i>O. coloni</i>
NP-live-2 ^a	NP	CS	P	L	65	0	0	0	0
PC-dead-1 ^a	PC	CR	P	D	8	102	10	0	8
PC-dead-2 ^a	PC	CR	P	D	16	54	5	0	0
PC-live-1 ^a	PC	CR	P	L	62	34	0	0	0
PC-live-2 ^a	PC	CR	P	L	55	44	0	0	0
RP-dead-1 ^a	RP	CS	P	D	53	8	3	0	0
RP-dead-2 ^a	RP	CS	P	D	62	7	2	0	0
RP-live-1 ^a	RP	CS	P	L	56	1	0	0	0
RP-live-2 ^a	RP	CS	P	L	43	2	0	0	0
Sample ID	<i>O. solidula</i>	<i>P. plana</i>	<i>P. modicus</i>	<i>G. pellucida</i>	<i>S. barbadensis</i>	<i>S. octona</i>	<i>M. providentia</i>	<i>B. septulcralis</i>	Total
DB-dead-1 ^a	1	0	0	0	1	0	0	0	219
DB-dead-2 ^a	0	0	0	0	0	0	0	0	307
DB-live-1 ^a	0	0	0	0	0	0	0	0	60
DB-live-2 ^a	0	0	0	0	0	0	0	0	60
DM-dead-1	1	0	0	0	0	0	0	0	118
DM-dead-2	0	0	0	0	2	0	0	0	140
DM-live-1	0	0	0	0	0	0	0	0	41
DM-live-2	0	0	0	0	0	0	0	0	40
EB-dead-1	0	0	0	0	0	0	0	0	64
EB-live-1	0	0	0	0	0	0	0	0	43
FB-dead-1 ^a	0	0	0	0	0	0	0	0	74
FB-dead-2 ^a	0	0	0	0	1	0	0	0	101
FH-dead-1 ^a	0	0	0	0	0	0	0	0	147

Table 2 continued

Sample ID	<i>O. solidula</i>	<i>P. plana</i>	<i>P. modicus</i>	<i>G. pellucida</i>	<i>S. barbadensis</i>	<i>S. octona</i>	<i>M. providentia</i>	<i>B. sepulcralis</i>	Total
FH-dead-2 ^a	0	0	0	0	0	0	0	0	87
FH-live-1 ^a	0	0	0	0	0	0	0	0	74
FH-live-2 ^a	0	0	0	0	0	0	0	0	50
FR-dead-1	0	0	0	0	0	0	0	0	66
FR-live-1	0	0	0	0	0	0	0	0	41
HB-dead-1 ^a	0	0	0	0	0	0	0	0	70
HB-dead-2 ^a	6	0	0	0	0	0	0	0	133
HB-live-1 ^a	0	0	0	0	0	0	0	0	45
HB-live-2 ^a	0	0	0	0	0	0	0	0	60
NP-dead-1 ^a	0	0	0	0	0	0	0	0	69
NP-dead-2 ^a	0	0	0	0	0	0	0	0	69
NP-live-1 ^a	0	0	0	0	0	0	0	0	53
NP-live-2 ^a	0	0	0	0	0	0	0	0	65
PC-dead-1 ^a	0	0	0	0	0	0	0	0	128
PC-dead-2 ^a	0	0	0	0	0	0	0	0	75
PC-live-1 ^a	0	0	0	0	0	0	0	0	96
PC-live-2 ^a	0	0	0	0	0	0	0	0	99
RP-dead-1 ^a	0	0	0	0	0	0	0	0	64
RP-dead-2 ^a	0	0	0	0	0	0	0	0	71
RP-live-1 ^a	0	0	0	0	0	0	0	0	57
RP-live-2 ^a	0	0	0	0	0	0	0	0	45

Table 2 continued

Sample ID	Locality ^b	Habitat type	Impact grade	Age	<i>Cerion</i> spp.	<i>H. varians</i>	<i>P. duclosiana</i>	<i>C. watlingensis</i>	<i>O. coloni</i>
SB-dead-1 ^a	SB	CS	P	D	95	9	14	0	12
SB-live-1 ^a	SB	CS	P	L	45	0	0	0	0
TG-dead-1 ^a	TG	CS	P	D	130	86	1	0	20
TG-live-1	TG	CS	P	L	3	43	0	0	0
WQ-dead-1	WQ	CS	P	D	5	61	0	0	2
WQ-live-1	WQ	CS	P	L	2	39	0	0	0
CT-dead-1	CT	CR	I	D	0	0	0	0	0
CT-dead-2	CT	CR	I	D	0	0	0	0	0
CT-live-1	CT	CR	I	L	0	0	0	0	0
CT-live-2	CT	CR	I	L	0	0	0	0	0
LH-dead-1	LH	CR	I	D	2	0	0	0	2
LH-dead-2	LH	CR	I	D	0	0	0	0	0
LH-dead-3	LH	CR	I	D	0	0	6	0	5
LH-dead-4	LH	CR	I	D	0	0	4	0	4
LH-live-1	LH	CR	I	L	0	0	0	0	0
LH-live-2	LH	CR	I	L	0	0	0	0	0
LH-live-3	LH	CR	I	L	0	0	0	0	0
LH-live-4	LH	CR	I	L	0	0	0	0	0
LL-dead-1	LL	CS	I	D	118	0	2	0	2
LL-dead-2	LL	CS	I	D	40	9	17	0	1
LL-dead-3	LL	CS	I	D	41	20	6	0	8
LL-live-1	LL	CS	I	L	12	20	0	0	0
LL-live-2	LL	CS	I	L	22	1	0	0	0
LL-live-3	LL	CS	I	L	25	15	0	0	0
TA-dead-1	TA	CR	I	D	0	0	0	0	0

Table 2 continued

Sample ID	Locality ^b	Habitat type	Impact grade	Age	Cerion spp.	<i>H. varians</i>	<i>P. duclosiana</i>	<i>C. watlingensis</i>	<i>O. coloni</i>
TA-dead-2	TA	CR	I	D	0	0	0	0	0
TA-dead-3	TA	CR	I	D	0	0	0	0	0
TA-live-1	TA	CR	I	L	0	0	0	0	0
TA-live-2	TA	CR	I	L	0	0	0	0	0
TA-live-3	TA	CR	I	L	0	0	0	0	0
Sample ID	<i>O. solidula</i>	<i>P. plana</i>	<i>P. modicus</i>	<i>G. pellucida</i>	<i>S. barbadensis</i>	<i>S. octona</i>	<i>M. providentia</i>	<i>B. sepiulteralis</i>	Total
SB-dead-1 ^a	0	0	0	0	5	0	0	0	135
SB-live-1 ^a	0	0	8	0	0	0	0	1	54
TG-dead-1 ^a	0	0	0	0	0	0	0	0	237
TG-live-1	0	0	0	0	0	0	0	0	46
WQ-dead-1	0	0	0	0	1	0	0	0	69
WQ-live-1	0	0	0	0	0	0	0	0	41
CT-dead-1	0	38	1	0	2	0	0	0	41
CT-dead-2	0	44	0	0	57	0	0	11	112
CT-live-1	0	2	4	48	0	0	0	0	54
CT-live-2	0	3	7	41	0	0	0	0	51
LH-dead-1	0	21	0	0	19	9	0	50	103
LH-dead-2	0	17	0	0	2	3	1	38	60
LH-dead-3	0	3	0	0	4	29	1	74	121
LH-dead-4	0	9	0	0	1	24	0	51	93
LH-live-1	0	1	0	58	0	5	0	1	65
LH-live-2	0	1	1	52	0	3	0	1	58
LH-live-3	0	0	0	7	0	6	0	27	40

Table 2 continued

Sample ID	<i>O. solidula</i>	<i>P. plana</i>	<i>P. modicus</i>	<i>G. pellucida</i>	<i>S. barbadiensis</i>	<i>S. octona</i>	<i>M. providentia</i>	<i>B. sepulchralis</i>	Total
LH-live-4	0	5	0	26	1	5	0	8	45
LL-dead-1	1	1	0	0	0	0	0	0	124
LL-dead-2	0	25	0	0	6	0	0	7	105
LL-dead-3	0	23	0	0	0	0	0	2	100
LL-live-1	0	0	0	33	0	0	0	0	65
LL-live-2	0	8	10	0	0	0	0	0	41
LL-live-3	0	1	0	0	0	0	0	0	41
TA-dead-1	0	70	10	0	0	2	0	1	83
TA-dead-2	0	141	3	0	0	0	0	0	144
TA-dead-3	0	52	0	0	0	0	0	0	52
TA-live-1	0	3	62	36	0	0	0	0	101
TA-live-2	0	0	13	60	0	0	0	0	73
TA-live-3	0	0	9	49	0	0	0	0	58

IR inland rocky substrate, *CS* Coastal soft substrate, *CR* Coastal rocky substrate, *P* pristine, *I* impacted, *D* dead assemblage, *L* Live assemblage

^a Data from Yanes (2012)

^b See text for site names

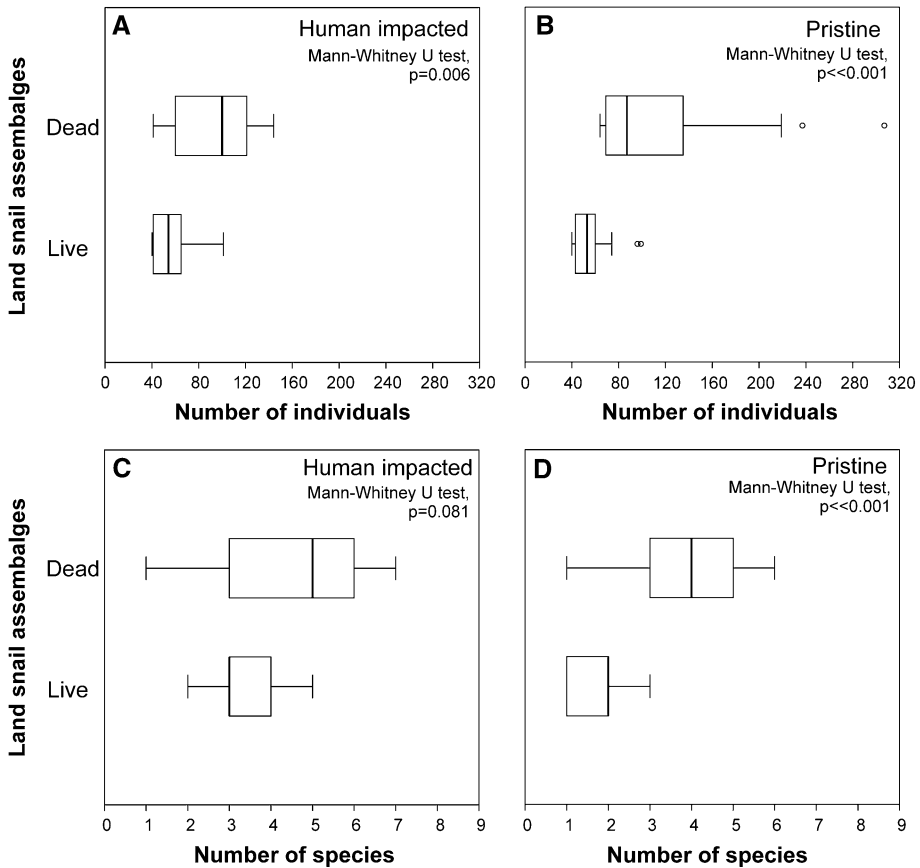


Fig. 4 Box plots of land snail richness and abundance. **a** Abundance at impacted sites. **b** Abundance at pristine locales. **c** Number of species at impacted sites. **d** Number of species at pristine locales. Boxes represent the upper and lower quartiles, solid lines inside the box represent the median value, and whiskers represent the extreme values. Circles represent outliers

not commonly occupied by synanthropic species. Similarly, in most human-modified locales, anthropophobic snails that are abundant in the fossil record (e.g., *Cerion*, *Hemistrochus*, *Plagioptycha*, *Colonella*) were almost never found alive (Table 2). This emphasizes that the anthropogenic conditions possibly precluded the proliferation of species that dominate in unmodified sites. Samples from impacted areas generally exhibited higher snail richness and evenness than pristine and fossil samples (Fig. 3). Urbanized sites have been recognized to be hotspots of biodiversity for several animal and plant groups, many times supporting even more species than rural areas (e.g., Knapp et al. 2008). Human-impacted sites in San Salvador offer new habitats (previously nonexistent) with artificial humidity, food, materials, patchiness, etc. (e.g., Knapp et al. 2008), which should have favored land snail proliferation, particularly beneficial for synanthropic species. Whereas Knapp et al. (2008) observed similar alpha-diversity of land snails from both urban and rural areas of Central Germany, the present study showed higher snail richness in anthropogenic locales. This discrepancy indicates that snail richness in urban-rural gradients is not expected to show a similar pattern everywhere.

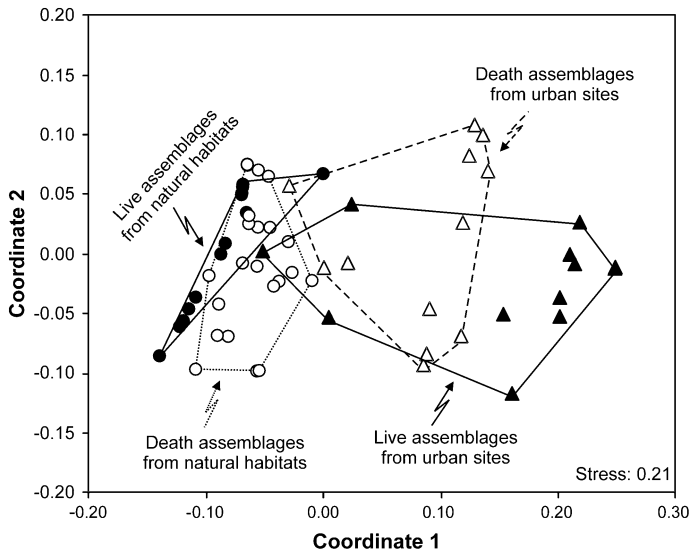


Fig. 5 NMDS ordination of proportional abundance of land snails from human impacted (*triangles*) and pristine (*circles*) localities on San Salvador Island (Bahamas) using the Bray–Curtis similarity index

Dead assemblages contained more species and specimens than live communities (Table 2; Fig. 4), which is consistent with the bulk of previous studies that have evaluated the live–dead compositional fidelity in shell-bearing organisms (e.g., Kidwell 2001, 2002, 2007; Rundell and Cowie 2003; Erthal et al. 2010; Yanes 2012). This may be the consequence of both (1) time-averaging and (2) sampling bias. Dead (time-averaged) shell assemblages embrace individuals that are accumulated across seasons and years whereas live assemblages represent a snapshot (e.g., Kidwell 2002). Consequently, higher numbers of specimens and species are commonly observed in dead rather than live assemblages. Additionally, live individuals of some land snail species are more difficult to find because they tend to hide during the hottest parts of the day to prevent desiccation. In particular, small and minute species are likely to be overlooked more easily in live communities than in dead shell accumulations (Rundell and Cowie 2003). Despite all these potential sampling biases, the observed high live–dead taxonomic agreement at pristine sites suggests that the results from this study should have not been biased strongly by the sampling protocol. Field surveys from this study were performed during the summer. Although dead assemblages contain shells accumulated across seasons and years, it would be interesting to repeat field surveys during other seasons, in particular to evaluate potential taxonomic variation in live assemblages (does the degree of live–dead taxonomic agreement vary seasonally?).

Live and dead assemblages from pristine localities showed similar taxonomic compositions based on 16 live–dead pairwise comparisons (Fig. 6a–d). The dominant taxa in live assemblages were also dominant in dead assemblages while rare live taxa were also rare in dead accumulations, in agreement with previous land snail studies (Rundell and Cowie 2003; Yanes 2012), freshwater shell assemblages (Erthal et al. 2010), and marine shells from soft benthic environments (e.g., Kidwell 2001, 2002). Consequently, dead assemblages that have undergone taphonomic processes have nonetheless preserved the taxonomic composition of the live communities. Hence, land snails collected at modern and

Table 3 Results of taxonomic similarity analyses of live and dead land snail assemblages

Live-dead sample ID	Locality (Acronym)	Jaccard–Chao	Spearman’s rho (all cases considered)	Spearman’s rho (double-zero cases omitted)	No of species shared	Total no of species	Impact grade
DM-1	Death March (DM)	0.678	0.674	0.778	2	6	Pristine
DM-2	Death March (DM)	0.729	0.674	0.778	2	6	Pristine
DB-1	Dim bay (DB)	0.822	0.504	0.664	1	6	Pristine
DB-2	Dim bay (DB)	0.821	0.565	0.775	1	4	Pristine
FH-1	Fortune Hill (FH)	0.803	0.853	0.800	3	4	Pristine
FH-2	Fortune Hill (FH)	0.896	0.390	0.316	2	3	Pristine
FR-1	French Bay (FR)	1.000	1.000	1.000	2	2	Pristine
HB-1	Hard Bargain (HB)	0.557	0.598	0.447	2	5	Pristine
HB-2	Hard Bargain (HB)	0.406	0.503	0.655	1	6	Pristine
PC-1	Pigeon Creek (PC)	0.859	0.647	-0.056	2	4	Pristine
PC-2	Pigeon Creek (PC)	0.933	0.839	0.500	2	3	Pristine
RP-1	Rocky Point (RP)	0.953	0.851	1.000	2	3	Pristine
RP-2	Rocky Point (RP)	0.972	0.851	1.000	2	3	Pristine
SB-1	Singer Bay (SB)	0.617	0.127	-0.060	1	7	Pristine
TG-1	The Gulf (TG)	0.911	0.758	0.738	2	4	Pristine
WQ-1	Watling’s Quarry (WQ)	0.957	0.768	0.949	2	4	Pristine
TA-1	Airport (TA)	0.628	0.522	0.154	2	5	Human-impacted
TA-2	Airport (TA)	0.019	0.319	-1.000	1	3	Human-impacted
CT-1	Cockburn Town (CT)	0.111	0.480	-0.800	2	4	Human-impacted
CT-2	Cockburn Town (CT)	0.054	0.065	-0.789	1	5	Human-impacted
LH-1	Lighthouse (LH)	0.771	0.421	-0.094	3	7	Human-impacted
LH-2	Lighthouse (LH)	0.937	0.399	-0.113	3	7	Human-impacted
LH-3	Lighthouse (LH)	0.716	0.389	0.300	2	7	Human-impacted
LH-4	Lighthouse (LH)	0.686	0.533	0.110	3	7	Human-impacted

Table 3 continued

Live-dead sample ID	Locality (Acronym)	Jaccard–Chao	Spearman's rho (all cases considered)	Spearman's rho (double-zero cases omitted)	No of species shared	Total no of species	Impact grade
LL-1	Little Lake (LL)	0.183	-0.017	-0.506	1	7	Human-impacted
LL-2	Little Lake (LL)	0.641	0.484	0.342	3	8	Human-impacted
LL-3	Little Lake (LL)	0.840	0.796	0.880	3	6	Human-impacted

Only samples with at least one species shared between live and dead assemblages and a minimum of two species were used in the analyses

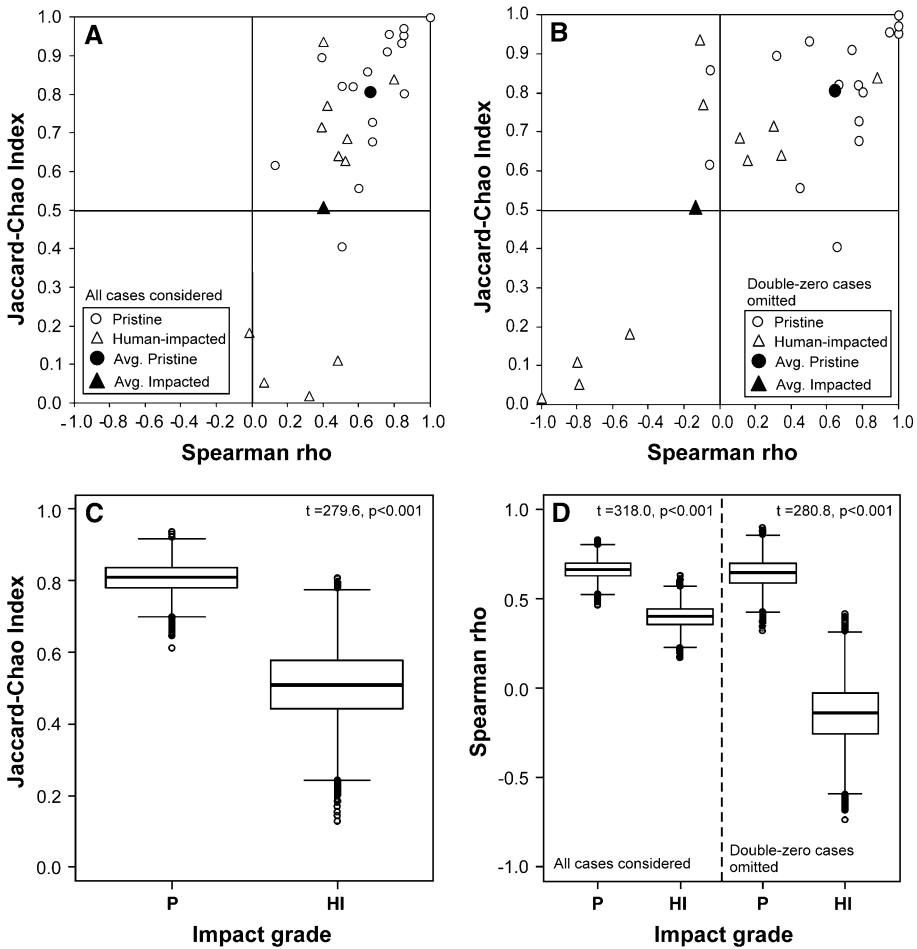


Fig. 6 Cross-plots of live-dead taxonomic similarity of land snail species assemblages from San Salvador (Bahamas). **a** Spearman’s rho calculated considering all cases. **b** Spearman’s rho calculated omitting cases in which a species was absent in both the live and the dead assemblage. **c** Box-plot of the bootstrapped (10,000 iterations) Jaccard–Chao Index of pristine (*P*) and human-impacted (*HI*) samples. **d** Box-plot of the bootstrapped Spearman’s rho coefficient of pristine (*P*) and human-impacted (*HI*) samples. Boxes represent the upper and lower quartiles, solid lines inside the box represent the median value, and whiskers represent 1.5 times the IQ range. Circles represent outliers

past natural environments from carbonate-rich tropical islands are likely to exhibit high ecological fidelity and may be used in additional paleoecological and paleoenvironmental studies (see also Rundell and Cowie 2003; Yanes et al. 2008, 2011; Yanes 2012). In contrast, live-dead assemblages from urban-developed sites displayed, on average, significantly higher taxonomic mismatches based on 11 live-dead pairwise comparisons (Fig. 6c, d). Such live-dead taxonomic disparities may be in part explained by recent human activities. Dead assemblages from impacted locales are likely to be shaped by some anthropophobic species that probably lived there prior to strong landscape modification, whereas various living synanthropic species possibly colonized the area recently, and therefore, their representation in the dead assemblage is still negligible (Kidwell 2007).

While other factors (not explored here) may account for the observed live-dead taxonomic mismatches in anthropogenic sites (e.g., differences in shell preservation in urban as opposed to rural areas), urbanization probably influenced the results to some extent. The new introduction (or recent proliferation) of synanthropic species in human environments possibly favored the degree of taxonomic dissimilarity between live and dead. These results suggest that taxonomic discordances in live-dead land snail assemblages may be used to identify recent anthropogenic effects. Nonetheless, it is expected that the live-dead taxonomic disagreement will gradually turn into agreement as the dead assemblage is replaced with the newly introduced (or expanded) species. Empty shells show a decadal to centennial (or even millennial in carbonate-rich areas) half-life on the soil surface (Cadée 1999; Pearce 2008; Yanes 2012). Thus, the potential anthropogenic effect on the taxonomic dissimilarity between live-dead assemblages may last for decades or centuries. In future snail investigations, it would be interesting to quantify variable scales of impact grades and evaluate the effects of different types of anthropogenic activities besides urbanization. This will allow us to explore how the magnitude of live-dead taxonomic discordance differs across variable scales and types of human activities. It would be also intriguing to explore potential differences in taphonomic processes at urban and rural landscapes. If substrate and microclimate conditions differ notably between them, shell destruction (or preservation) processes may vary as well. Snail live-dead taxonomic mismatches in urban and rural habitats in continental (comparatively less vulnerable) areas rather than tropical islands await future investigation.

This study shows that even small-scale urbanization can alter the land snail taxonomic composition on small islands because (1) the modification of the conditions in the natural habitat may preclude the proliferation of anthropophobic snails, and because (2) the introduction or spread of synanthropic species may replace anthropophobic taxa. Accordingly, land snails from San Salvador are potential indicators of ecosystem health. The fact that synanthropic species displayed negligible abundance at most pristine localities suggests that anthropogenic disturbances have not affected natural ecosystems of the island. Moreover, modern snail diversity from pristine localities is comparable to that observed in the local fossil record (Fig. 3a, b). This emphasizes that snail diversity has been relatively stable through time on natural landscapes of San Salvador (Yanes 2012). However, the results from this research also indicate that urbanization appears to preclude the proliferation of species that dominate in pristine sites, and therefore, species distribution seems to be modified by landscape alteration.

The Bahamas were occupied by the Lucayan Indians, a society with origins in South America that followed maritime and agricultural socio-economic strategies (Blick 2007). Zooarcheological studies have revealed that some native animal groups (i.e., land crabs, marine mollusks and fishes) from San Salvador were overexploited by the aboriginal people, as evidenced by a decline in species richness, decrease in trophic levels and changes in species composition (Blick 2007). About 500–1,000 people occupied San Salvador during prehistoric times (Blick 2007). This estimate is similar to the population that today inhabits the island. The Bahamas Department of Statistics (<http://statistics.bahamas.gov.bs/>) estimated that San Salvador is presently occupied by about 930 people (census during 2010). This estimate is similar to the census of 2000, 1990 and 1980 (Buchan 2000), which suggests that population size is stabilized. Hence, the anthropogenic impact may not be growing on the island. Although no invasive species were encountered and human-population density appears to be steady, it may be prudent to continue to monitor the species composition and distribution of terrestrial malacofaunas of San Salvador as a preventative measure.

Acknowledgments This study was carried out at the Gerace Research Center (GRC), San Salvador Island (Bahamas) which covered the logistics of the project. The Paleontological Society (PS), the Western Interior Paleontological Society (WIPS) and the Spanish grant CGL2011-29898/BTE to Y.Y. funded this study. Special thanks go to T.A. Rothfus (Executive Director of GRC), M. Kowalewski (University of Florida) and T. Dexter (University of Arizona) for their assistance during field work. Rosana Ferrero (Universidad de Córdoba) is thanked for statistical guidance and analyses in R software. Additional thanks go to M. Ibáñez and M.R. Alonso (Universidad de La Laguna) for their assistance with shell photographs, and to T.A. Pearce (Carnegie Museum of Natural History), H.G. Lee (Scientific advisor of Jacksonville shell club), T. Watters (Ohio State University), D.G. Robinson (USDA Animal and Plant Health Inspection Service) for their help with identifications. The critical, detailed and constructive reviews by the associate editor and two anonymous reviewers improved the clarity and quality of this manuscript.

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