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Ecological fidelity and spatiotemporal resolution of arthropod death assemblages from rodent middens in the central Atacama Desert (northern Chile)

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ABSTRACT

Evaluating the magnitude and direction of biases affecting the ecological information captured by death assemblages is an important prerequisite for understanding past, present, and future community-environment relationships. Here, we establish the ecological fidelity and spatiotemporal resolution of an overlooked source of fossil remains: the soil arthropod assemblages found in rodent middens (that span from the present to >44,420 cal yr BP) collected in the central Atacama Desert of northern Chile. We evaluated the "live-dead agreement" across four sources of soil arthropod data; two contemporary surveys of live communities (i.e., live), and two sources of death assemblages (i.e., dead). Although live-dead agreements and diversity indices are highly variable among samples (live and dead assemblages), our results consistently demonstrate that an average fossil midden (i) better captures the structure and composition of living communities than species richness *per se*; (ii) offers a spatially-resolved picture of those communities at local scales; and (iii) is only weakly affected by time-averaging. The fine spatiotemporal resolution of fossil midden records in the Atacama, and most likely other areas of the world where rodent middens occur offers ecological information on the structure and composition of fossil arthropod assemblages potentially over many thousands of years. This information is reliable enough to establish historical baselines before past and ongoing anthropogenic impacts.

1. Introduction

Death assemblages, defined by Kidwell and Tomasovych (2013) as taxonomically identifiable individuals from the past generations of extant or recently extinct species at a site, contain unique spatial and temporal information about past communities beyond the scope of modern ecological studies. This information can then be used to reconstruct past climate conditions (Powell et al., 2017), and to explain and predict long-term responses of communities to environmental changes (Elias, 2014; Elias and Matthews, 2014; Terry, 2010a; Terry and Rowe, 2015; Tinner et al., 2013; Yeakel et al., 2014). Yet, the quality of such data is subject to two main sources of biases. First, taphonomic processes occur after an organism's death and affect its incorporation into the fossil record (e.g., burial, compaction, decomposition). Second, time averaging can pool organisms that potentially lived at different times into the same death assemblage (Allison and Bottjer, 2010; Roy et al., 1996). Evaluating the role of these factors, and hence the degree to which fossil records accurately reflect living communities is essential for obtaining robust ecological information from death assemblages.

The live-dead approach is used routinely in paleontological

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studies to test the fidelity of ancient data to detect and reconstruct the structure of living communities (Kidwell and Bosence, 1991). To date, the vast majority of live-dead studies have focused on mollusks from soft sediments (Kidwell, 2001; Kidwell and Bosence, 1991; Kidwell and Tomasovych, 2013; Olszewski and Kidwell, 2007) and both large body-sized vertebrates (Behrensmeyer et al., 1979; Tappen, 1995; Western and Behrensmeyer, 2009) and small mammals in arid terrestrial environments (Terry, 2010a, b; Terry and Rowe, 2015). Despite their importance in the Earth's faunal biomass and total biodiversity as well as their role in many ecosystem processes, arthropods seldom have been the target of live-dead studies. Among those few studies, most were conducted in Northern Europe, and compared modern deposits of arthropod remains to subfossil or fossil data for examining past living conditions or anthropogenic impacts on landscapes (Smith, 1998; Kenward, 2006; Smith et al., 2010, 2014; Forbes et al., 2016). The main use of fossil arthropods in paleoecological reconstructions has been, instead, to infer past climatic conditions from the presence of indicator species (mostly Coleoptera and Diptera) in peatland, wetland, and floodplain deposits worldwide (https://www.bugscep.com/downloads/qbib.pdf; see also Ashworth and Nelson, 2014; Coope, 2010; Elias, 2015; Kuzmina, 2015 for recent examples). The lack of modern calibration has limited our understanding of how taphonomic and other biases may affect past arthropod assemblages.

An understudied source of fossil arthropod remains are late Quaternary middens made by rodents (several families) and possible other animals (e.g. hyraxes: *Procavia*) and preserved in rock crevices, shelters, and caves throughout arid and semi-arid regions of the world (Pearson and Betancourt, 2002). The first midden studies were pioneered in the western North America beginning in the late 1980's, where more than two-thousand middens made by packrats (also called woodrats; *Neotoma*: Cricetidae) have been radiocarbon dated and analyzed (e.g., Betancourt et al., 1990). Analogous middens made by other small mammals have been studied from three other continents (e.g., Betancourt and Saavedra, 2002; Chase et al., 2012; McCorriston et al., 2002; Pearson and Betancourt, 2002). In South America, where our particular study is focused, middens are made by rodents in four different families: *Abrocoma* (Abrocomidae), *Phyllotis* (Cricetidae), *Lagidium* (Chinchillidae), and possibly *Octodontomys* and *Octomys* (Octodontidae; Betancourt and Saavedra, 2002; Holmgren et al., 2001; Latorre et al., 2002). These South American rodents are considered dietary generalists and feed almost exclusively on surrounding vegetation and infrequently on ground-dwelling invertebrates (<0.1% of diet; Cortés et al., 2002; Elias, 1990; López-Cortés et al., 2007; Sobrero et al., 2010).

Fossil middens are amalgamated deposits of plant (macrofossils and pollen), arthropod, and vertebrate remains, including copious fecal pellets of the midden agent, all cemented into a hard mass by crystallized urine ("amberat"). Most of the midden materials, except for some of the pollen from anemophilous species, are presumed to originate from living organisms within the animal's foraging range. In arid lands, and when protected from the elements in a cave or rock shelter, middens can commonly be thousands of years old. The excellent preservation of plant and animal remains allows for a broad suite of morphological, geochemical, and even genetic analyses (see Kuch et al., 2002; Murray et al., 2012). Fossil rodent middens have provided unparalleled taxonomic and spatial resolution in reconstructing past vegetation change in the Americas during the late Quaternary (Betancourt et al., 1990, 2000; de Porras et al., 2015; Latorre et al., 2002; Mujica et al., 2015).

Despite their many advantages, middens also have some limitations. The depositional episode that created a particular midden can be brief (months) or prolonged (decades to centuries), and usually indeterminable from stratigraphy or ^{14}C dating. Even the thickest of deposits (meters deep) tend to be stratigraphically discontinuous. To create a local midden series requires collating and radiocarbon dating a number of individual and separate middens (from different locations in the same rock shelter or different rock shelters in the same area) and their assemblages, which often results in long temporal gaps (Betancourt et al., 1990, 2000). Also, there have been few attempts to test and calibrate the reliability of plant macrofossil and pollen assemblages in rodent middens to reflect local plant communities (de Porras et al., 2015; Lesser and Jackson, 2011; Lyford et al., 2004; Nowak et al., 2000).

Midden research in the Americas has focused primarily on the rich plant macrofossil and pollen assemblages, and less so on animal remains, including the arthropod assemblages that are the focus of this study. Arthropod remains are common and well preserved enough in packrat (*Neotoma*) middens from western North America to attract the attention of entomologists (Ashworth and Markgraf, 1989; Elias, 1987, 1990; Elias and Vandevender, 1990; Hall et al., 1988, 1989, 1990; Van Devender and Hall, 1993, 1994). Elias (1990) surmised that most of the sclerotized exoskeletal remains in packrat middens were not consumed by packrats, but instead derive from facultative arthropods (particularly ground beetles and darkling beetles) that spend the winter in temperature-buffered packrat dens, are packrat parasites, or were dragged in on plant material or by other animals. A taphonomic study of arthropods in these middens showed that herbivores are under-represented, whereas scavengers are over-represented (Elias, 1990). Similar arthropod studies have, however, lagged for South American middens.

In the present study, we aimed to establish the ecological fidelity and spatiotemporal resolution of arthropod death assemblages found in rodent middens from the central Atacama Desert (22–24° S latitude) in northern Chile. To this end, we used the live-dead approach to compare four sources of soil arthropod data: two contemporary surveys of live communities ("local live data" and "regional live data"), and two sources of death assemblages ("modern dead data" and "fossil data" in modern and fossil middens, respectively). Specifically, we ask: (1) do arthropod assemblages found in rodent middens reflect living arthropod communities (live-dead agreement)? (2) What is the spatial resolution of those death assemblages? And (3) what is the magnitude and direction of the effect of time and time-averaging on community structure and composition? We hypothesized that: (1) the death assemblages may be biased towards highly sclerotized and ground-dwelling arthropods such as Coleoptera (Elias, 1990); (2) the live communities found in the close vicinity of fossil middens may represent a subset of the regional species pool (Elias, 1990), and thus be more similar to death assemblages than the regional fauna; and (3) because fossil middens represent temporal "snapshots" of past floristic assemblages (i.e., limited effect of time averaging; de Porras et al., 2015), the effect of time averaging on the structure and composition of arthropod assemblages also may be limited.

2. Materials & methods

2.1. Study area and rodent middens

This study was located in the southern part of the Salar de Atacama (Chile), ~10 km south of Tilomonte (Latitude: 23.84°; Longitude: 68.18°; altitude: ~2600 m), near the lower, dry limits of vascular plants in the central Atacama Desert and at the well-studied site of Vegas de Tilocalar/Lomas de Tilocalar, where 46 middens were previously collected, dated, and analyzed spanning

the last ~40,000 cal yr BP (Betancourt et al., 2000; de Porras et al., 2015; Latorre et al., 2002). Midden ages reported here were calibrated using the SHCal13 calibration curve (see Table A). In this area, modern and fossil middens are produced by two main families of rock-dwelling rodents, chinchilla rats (*Abrocoma,* mostly *A. cinerea*: Abrocomidae) and leaf-eared mice (*Phyllotis* spp.: Cricetidae). The agent of deposition (i.e., rodent species) for each of the fossil middens was identified by the size and shape of the fecal pellets in the middens (Diaz et al., 2012). The occurrence of any vegetation, today and in the past, in this hyperarid desert is controlled by the amount and seasonality of precipitation, which vary sharply with latitude and elevation (Latorre et al., 2002). The Tilomonte study site is dominated by sparse (<5% cover) shrubs and succulent annuals and perennial halophytes (e.g., *Cistanthe salsoloides*: Portulacaceae; *Atriplex imbricata*: Amaranthaceae; and *Tessaria absinthioides*: Asteraceae).

2.2. Live arthropod communities found in vicinity of rodent middens: “local live data"

Several sampling methods exist to provide an accurate assessment of the local ground-dwelling arthropod community, yet their capture efficiency depends upon the species characteristics (e.g., surface activity, population density), the trap-related features (e.g., size, shape, bait/preservative type, and material of constructions), as well as the sampled environments (e.g., Zou et al., 2012). Among all sampling methods, pitfall traps are used extensively for sampling ground-dwelling communities (Pekár, 2002; Phillips and Cobb, 2005), especially in hyperarid environments (Cheli and Corley, 2010). Sticky traps were, however, the only realistic alternative in our study sites, as the rocky shelters of rodents preclude the proper burial of pitfall traps. Sticky traps consist of a piece of cardboard with a sticky surface that can catch both crawling and flying species (Atakan and Canhilal, 2004). Within the close proximity of rock shelters (both within and <15 m outside the caves), we set ten squared plots each containing 16 sticky traps (Nb. total = 160). Within a given plot, the sticky traps (catching surface: 20 cm × 15 cm) were located from two to seven meters away from each other depending on the configuration of the rock shelters. All plots were ~60 m apart. Finally, each sticky trap was checked every day in the morning over five consecutive days. Arthropods were kept in 70% alcohol and later identified in the laboratory using a dissecting microscope.

2.3. Live communities present in the region: “regional live data"

To evaluate the specificity of arthropod communities living in rodent middens (compared to both local data and death assemblages), we sampled live arthropod communities in distant sites (“regional live data”). These distant sites thus provide information on the composition of the regional fauna. To this end, we set 15 squared plots at ca. 0.5–3 km away from our closest fossil or modern midden sites. Each plot contained 16 traps (sticky and/or pitfall traps), which were spaced from each other by seven meters. All plots were separated by ~60 m. Pitfall traps consisted of plastic cups (radius: 7.5 cm x height: 10.5 cm) set with antifreeze (ethylene glycol) or no preservative was added (Cheli and Corley, 2010). Each trap was checked every day in the morning over four consecutive days. Arthropods were kept in 70% alcohol and later identified under a dissecting microscope.

Pitfall traps and sticky traps are two passive sampling methods that can catch both crawling and, to a lesser extent, flying arthropods (Zou et al., 2012). Yet, the proportion of each trap type—pitfalls with (N = 100) or without (N = 100) preservatives and sticky traps (N = 200)—may influence the probability of catching a given species. We therefore estimated the trap-type standardized catch of each species for all habitats combined (local and regional data; see Terry, 2010b for more details). Our results indicate high consistency between estimated and observed abundances of each taxon except for the abundant Entomobryomorpha (Collembola), which was mainly caught in pitfalls set with ethylene glycol (taxa code = 1; Table B; Fig. 1).

2.4. Modern death assemblages: “modern dead data"

Replicated samples of time-averaged surficial death assemblages were collected close to fossil and modern middens ($N_{tot} = 60$). Modern middens were identified by the lack of amberat (crystallized urine) and occasional presence of green leaves and twigs. Each sample consisted in cylindrical volumes (radius: 22 cm x height: 2 cm) of soil debris, including recent rodent fecal pellets, plant material, dead arthropod remains, and rocks of various sizes. The exact magnitude of time averaging represented by these “modern” samples is unknown but most likely to be within the last few decades.

Arthropod remains were identified to the lowest taxonomic level when possible using our reference database of modern arthropods, the collection of the Museo Nacional de Historia Natural in Santiago (Chile), and by reference to specialists. The minimum number of individuals (MNI; a proxy of species abundance) of each species was calculated by counting the maximum number of analogous arthropod remains belonging to a given species (Terry, 2010a). For instance, if we identified one thorax, three head capsules, and nine elytra (four left-sided and five right-sided elytra) that were found apart from each other but belonging to the same species, we reported a MNI of five individuals (four complete pairs of elytra plus one). We did not use the number of leg remains due to the difficulty to identify and attribute those remains to any given specimens.

2.5. Fossil death assemblages: “fossil data"

In this study, we included a total of 46 samples of fossil middens, covering a time span of >40,000 cal yr BP from Vegas de Tilocalar/Lomas de Tilocalar (Table A). Middens were extracted by using a hammer and chisel, cleaned in the field for surface contaminants, and split along clear stratigraphic units when recognizable. A “sample” can thus correspond to a small fossil midden or a distinct stratigraphic unit from a large fossil midden. Hereafter, those samples are referred to as “fossil middens”. Latorre et al. (2002) describe the original extraction, location, and processing of these middens. Of possible consideration to taphonomy is the potential fragmentation and mechanical damage done to fragile arthropod

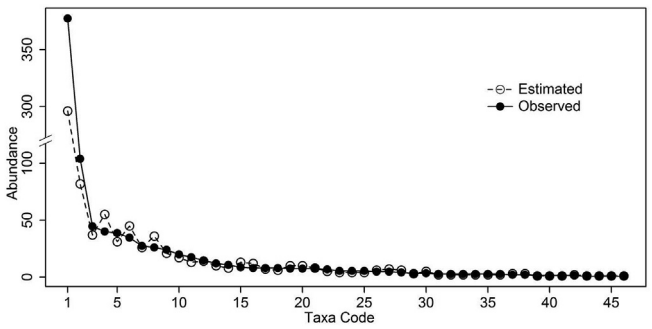

Fig. 1. Trap-type standardized catch of each modern taxon compared with uncorrected abundances. Local and regional data are pooled. Note the axis break on the y-axis. See Table B for the list of codes and associated taxa identities.

remains during midden processing. Middens are typically soaked for 2–3 weeks (enough to dissolve the crystallized urine) followed by wet screening of dissolved midden materials with the water faucet. They are then dried on cardboard plates at 50–60 °C in a rack oven for an average of two to three days. Dried midden samples were then sieved into size classes using USGS Standard Soil Sieves (mainly #10 and #18), and hand sorted for 3 h each under a microscope for arthropod remains. This standardized methodology was used for the sake of consistency with previous studies on fossil middens (Betancourt et al., 2000; Betancourt and Saavedra, 2002; Latorre et al., 2002, 2003; Diaz et al., 2012; de Porras et al., 2015), and because the sizes and weights of fossil middens can vary across locations. The identity of fossilized arthropod species and MNI were then established using the same procedure as used for "modern dead data" described above (see Table C for a list of taxa identities).

2.6. Live-dead agreements of ecological information

The degree to which ecological information obtained from death assemblages reflect that of modern communities was evaluated using various complementary measures of community structure and composition: species richness, evenness, composition, and abundance (Terry, 2010a, b). Species richness was compared using individual-based rarefaction curves (*rareNMtests*-package in R; Chao et al., 2014). Species evenness was evaluated using the Probability of Interspecific Encounter (PIE) as H/log(S), where H corresponds to the Shannon index, and S the number of species. PIE is the probability that two randomly picked individuals belong to two different species and correspond to the steepest slope of a rarefaction curve. Species composition was estimated by calculating the percentages of "live species" from modern communities found in death assemblages and "dead species" found in modern communities (Kidwell and Bosence, 1991). This procedure was extended to include all type of data (local live, regional live, modern dead, and fossil data). Similarity in species composition (presence/absence) among death assemblages and live communities was assessed using the Simpson's turnover index (0 = dissimilar; 1 = similar; *vegan*-package; Koleff et al., 2003). Both Simpson's turnover and Raup-Crick indices can handle variations in sample sizes when evaluating similarities in species richness. The Raup-Crick index was not chosen, however, because it is too sensitive to the composition of the regional species pool, which was unknown for death assemblages (Chase and Myers, 2011). Similarity in species rank abundances among death assemblages and modern communities was evaluated with the Spearman rank correlation test (Terry, 2010a, b). Similarity in species relative abundances among death assemblages and live communities was estimated with the Horn-Morisita index (0 = dissimilar; 1 = similar; *vegan*-package). All of these measures of community structure and composition (rarefied species richness, Simpson's turnover, Spearman Rho, Horn-Morisita) were selected for their robustness to variations in sample sizes among data types.

2.7. Effect of time and time averaging

We used two procedures to estimate the direction and magnitude of time averaging on community structure and composition. First, we successively pooled the fossil middens through time to simulate time averaging and compared the resulting assemblages with local live communities (pooled local live data) and modern death assemblages (pooled modern dead data) using the Simpson's turnover index, Spearman rank correlation, and Horn-Morisita index. To evaluate the effect of single (and pooled) midden ages on those agreements, we regressed these measures of community composition against time and assessed the significance of relationships using simple Spearman rank correlations. We expect a significant effect of midden ages if, for example, a lower agreement is consistently recovered from very old than from more recent fossil middens. Second, we repeated the procedure previously described using species richness, Shannon and Simpson indices on individual and successively pooled fossil middens. All analyses were performed in R version 3.3.0 (R Core Team, 2015).

3. Results

3.1. Live-dead agreements of ecological information

The agreement among all four sources of soil arthropod data was highly variable among samples and across the various measures of community structure and composition used in this study. Rarefied species richness was not statistically different between all four sources of data when samples were pooled by data type (Fig. 2A; Table 1). Individual samples treated separately showed, however, large variability in species richness within each source of data (Fig. 2B). Regional live communities ("regional data") and modern death assemblages ("modern dead data") displayed the lowest and highest evenness, respectively (0.74 ± 0.05, 0.92 ± 0.01; Table 1). In contrast, local live communities ("local live data") and fossil death assemblages ("fossil data") exhibited intermediate values of evenness (0.83 ± 0.02, 0.86 ± 0.02; Table 1).

Overall, the percentages of "live species" and "dead species" found in each data type were low and varied from 17.0% to 40.0% (Table 2). The highest percentages of "live species" were found between local and regional data (38.78%) and between dead and fossil data (40.0%). The lowest values were found between regional and dead data (22.22%) and between regional and fossil data

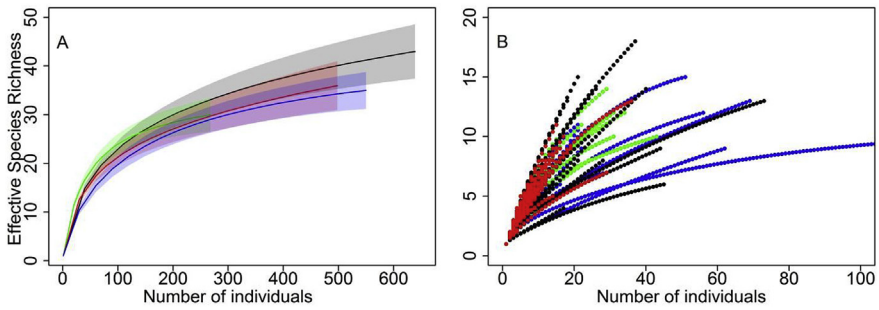

Fig. 2. Rarefaction curves of effective species richness for all data pooled by data type (A), and for all individual samples (B). Local live communities (green); regional live communities (blue); modern death assemblages (red); fossil death assemblages (black). For the sake of visual clarity, 95% CI are not shown for individual samples. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Rarefied richness (S±95%CI; n = 240) and mean Pielou's evenness (PIE±SE) for samples pooled by data type.

	S	PIE
Local	29.43 ± 3.24	0.83 ± 0.02
Regional	28.02 ± 2.57	0.74 ± 0.05
Dead	28.71 ± 3.04	0.92 ± 0.01
Fossil	32.38 ± 3.13	0.86 ± 0.02

Table 2
Percentages of "live species" (above diagonal) and "dead species" (below diagonal) found in each data type.

	Local	Regional	Dead	Fossil
Local	–	38.78	30.23	28.57
Regional	35.19	–	22.22	20.45
Dead	26.53	21.74	–	40.0
Fossil	21.82	17.31	35.82	–

(20.45%). The percentages between local data and death assemblages were intermediate (29–30%). These patterns were quantitatively similar for the percentages of "dead species" found in each data type (Table 2).

The averaged similarity in species presence/absence between samples within a given data type was not significantly different across data types (all pairwise comparisons between live-live = LL, regional-regional = RR, modern dead-modern dead = DD, and fossil-fossil = FF; Simpson's turnover; Appendix A; Fig. 3A). Similar patterns were observed when evaluating rank abundances (Spearman rank test; except significant differences between RR and DD; Appendix B; Fig. 3B) and species composition and abundances (Horn-Morisita; Appendix C; Fig. 3C). On average, 50 ± 0.1% of Spearman rank correlations were significant (see Figure A for the distribution of p-values grouped by data type). Species richness, rank abundances and species composition were significantly different when comparing local live communities and death assemblages (LL-LD and LL-LF comparisons; Appendix A-C; Fig. 3). In addition, the agreements between regional data and death assemblages were significantly different and on average lower than comparisons between local live data and death assemblages (all RR-RD and RR-RF comparisons; Appendix A-C; Fig. 3). Finally, when repeating those analyses with arthropods identified at the family levels, agreements between local live communities and death assemblages become not significantly different regardless of the community measure (Simpson's turnover, Spearman, and Horn-Morisita; Figure B; Appendix D-F). Agreements between regional data and death assemblages remained, however, significantly different with respect to rank abundances and family composition (Spearman, Horn-Morisita; Figure B; Appendix D-F).

All measures of community structure and composition (i.e., evenness, percentages of "live-dead species", Simpson's turnover, Spearman rank, and Horn-Morisita index), but the rarefied species richness, agree that the regional fauna is relatively unique compared to local live, modern dead, and fossil data. For instance, in terms of relative abundances, local live communities and modern dead and fossil assemblages are dominated by Coleoptera, whereas the regional fauna is dominated by Entomobryomorpha (Order; Fig. 4). In addition, Hemiptera were relatively more abundant in the regional communities than in any other data type. Finally, two important differences were observed between live communities and death assemblages. First, Ixodida (ticks) and Siphonaptera (fleas) only were found in death assemblages (both dead and fossil data). Ticks and fleas are likely present in modern live communities but were not caught with our sampling design (i.e., sampling biases). Second, Entomobryomorpha, Acari, Diptera and Zygentoma were found in live communities but were not preserved in death assemblages, probably due to taphonomic processes (Fig. 4).

3.2. Effect of time and time averaging

In subsequent analyses, we excluded the regional data due to their relatively unique community structure and composition compared with local live, modern dead, and fossil data. In addition, to isolate the effect of time averaging on death assemblages, we also restricted our datasets to the orders present in all three data types (i.e., excluding taphonomic processes and sampling biases; Fig. 4). The effect of time averaging on species richness was significant, but only noticeably at millennial scales (all pooled fossil middens) compared with local live and modern dead data (Fig. 5A). The species richness within each fossil midden is variable, and not consistently higher than that in local live communities or in modern death assemblages, suggesting a limited effect of time averaging on death assemblages of single fossil middens (Fig. 5B).

As data from fossil middens are successively pooled though time, the mean local-fossil Simpson's turnover decreases and then increases, whereas the mean Spearman agreement remains relatively constant, and the Horn-Morisita similarity increases (green points; Fig. 6). In addition, most Spearman rank correlations are not significant (Figure C). Pooling successive middens through time does not necessarily improve the local live-fossil agreement in terms of

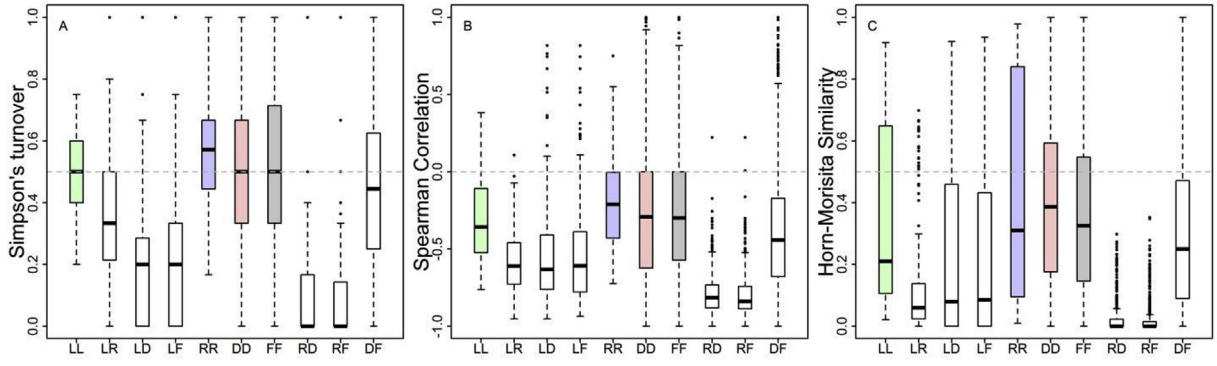

Fig. 3. Live-dead agreement of Simpson's turnover index (A), Spearman rank correlation (B), and Horn-Morisita index (C) for all pairwise comparisons by data type. Analyses were performed at the morphospecies level. L = local live communities (green); R = regional live communities (blue); D = modern death assemblages (red); F = fossil death assemblages (black) (e.g., LL = all pairwise comparisons within local data; LR = all pairwise comparisons between local and regional data). See main text and Appendix A-C for statistical significance of pairwise comparisons. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

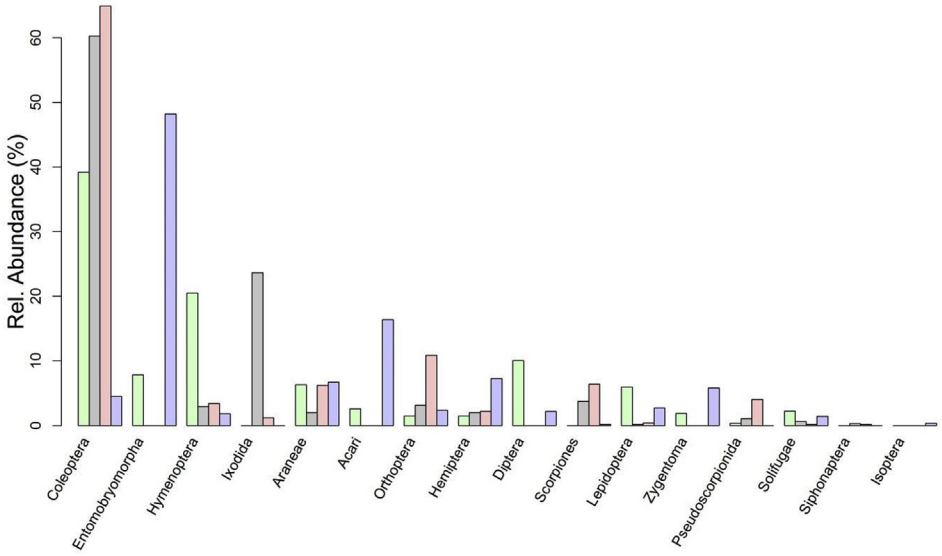

Fig. 4. Comparison of relative order abundances pooled by data type. Local (green); regional (blue); dead (red); fossil (black) data. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

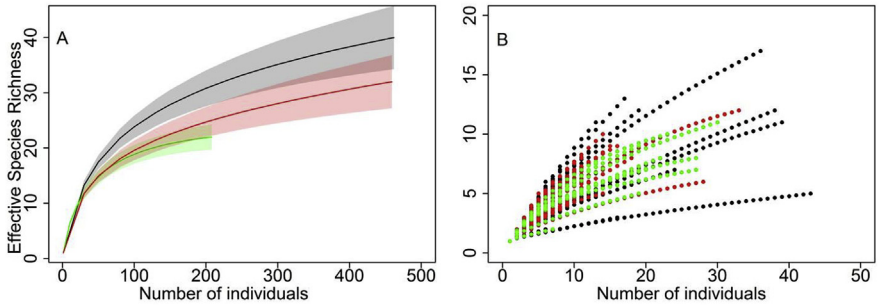

Fig. 5. Rarefaction curves of effective species richness for restricted datasets pooled by data type (A), and for all individual samples (B). These datasets were restricted to the orders present in local live communities (green), modern death assemblages (red), and fossil death assemblages (black; i.e., excluding taphonomic and sampling biases). For the sake of visual clarity, 95% CI are not shown for individual samples. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

species presence/absence or rank abundances (Fig. 6A, and C). The mean local live-fossil agreement in species composition, however, improved from 0.39 (local live-fossil agreement with individual middens) to 0.59, which corresponds to a plateau reached when six successively occurring middens are pooled (Fig. 6E). Similar patterns occur when successively pooled middens are compared to pooled modern dead data (Fig. 6B, D, and F). The modern dead-fossil agreements (Simpson's Turnover, Spearman Rho, Horn-Morisita) were, however, higher than the local live-fossil agreements.

Variations in local live-fossil and modern dead-fossil agreements were not significantly related to midden ages for all measures of community structure and composition. Those relationships become significant when pooling up to six (plateau) successive middens through time (Fig. 7; Table D). Note that those combinations of three and six pooled middens encompass an average temporal window of 1056 ± 276.84 and 2165 ± 397.53 cal yr BP, respectively, when all middens, except the oldest ones (>40,000 cal yr BP; $N = 3$), are included (Table 3). These examples from individual middens up to three and six pooled middens thus represent a range of combinations that increase agreements in species composition and abundances (Horn-Morisita) but also decrease the temporal resolution of resulting assemblages (from centennial to millennial scales; Table 3).

We found similar results when the above analyses were repeated using several indices of diversity within each fossil midden (i.e., Shannon and Simpson indices). On average, single fossil middens harbor 6.48 ± 0.58 species (±SE; from 1 to 18). Species richness increases linearly as successive middens are pooled through time until all middens are pooled together (Fig. 8A). The Shannon's diversity reaches a plateau (~2.47 ± 0.03) after pooling ten successive middens (Fig. 8B) whereas three successive middens are needed for the Simpson index to reach its plateau (~0.78 ± 0.02; Fig. 8C). Finally, none of the diversity indices are significantly affected by the midden ages, and pooling successively occurring middens does not significantly change these patterns (Fig. 9A–C) with one exception; a significant (and positive) relationship appears between species richness and the increasing amount of time from present when six successive middens are pooled (purple points, Fig. 9A; Table D).

4. Discussion

Altogether, these results demonstrate that individual fossil middens capture a highly resolved spatiotemporal picture of the structure and composition of common arthropod species and, to a lesser extent, rare species compared to raw species counts. The

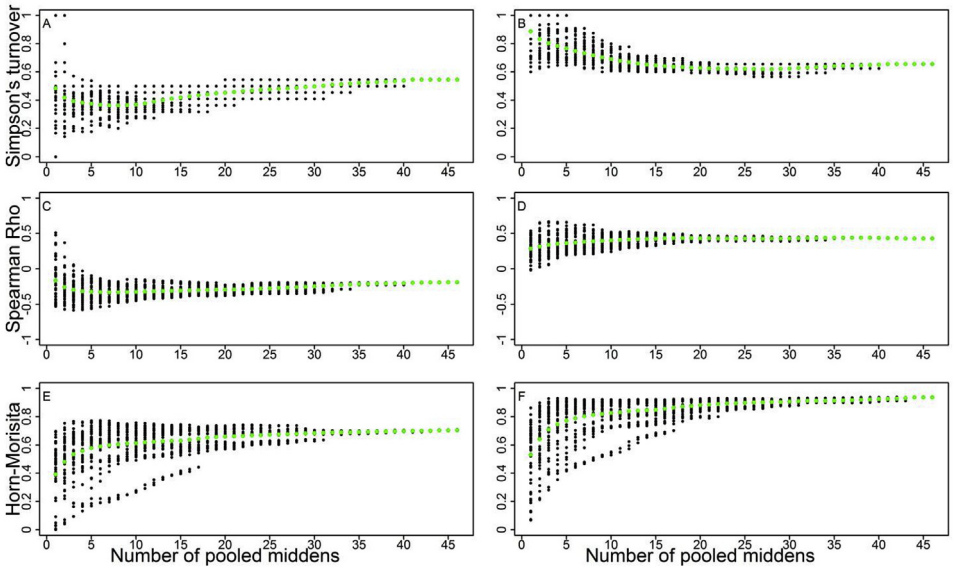

Fig. 6. Live-dead agreement of Simpson's turnover index (A, B), Spearman rho (C, D) and Horn-Morisita index (E, F) as a function of analytical time-averaging. Fossil middens are successively pooled through time to simulate time averaging and compared with local live (A, C, E) and modern dead (B, D, F) data pooled by data type. The x-axis shows all combinations of successively pooled middens, from one (all middens treated separately) to 46 (all middens pooled together). Black dots = raw values; green dots = mean values. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

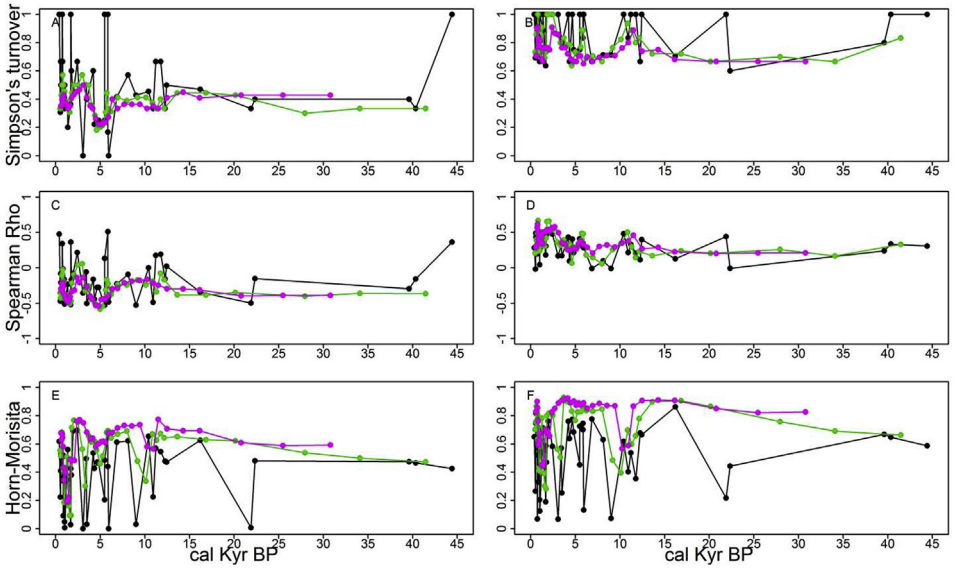

Fig. 7. Live-dead agreement of Simpson's turnover index (A, B), Spearman rho (C, D) and Horn-Morisita index (E, F) as a function of time (cal Kyr BP). Fossil middens are successively pooled through time to simulate time averaging and compared with local live (A, C, E) and modern dead (B, D, F) data pooled by data type. The black line depicts individual fossil middens; then all possible combinations of three, and six sequential fossil middens are displayed in green, and purple, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 3
Mean magnitude of time averaging (time bins in cal yr BP±SE) when pooling successively occurring fossil middens (from two to six); i.e., the average difference between the age of the first and last pooled midden. Nb. pooled middens = number of pooled paleomiddens All: all middens are included; Restricted: only the oldest middens are excluded (>40,000 cal yr BP; N = 3).

Nb. pooled middens	All	Restricted
2	978 ± 406.88	521.9 ± 159.28
3	1905.45 ± 596.78	1055.61 ± 276.84
4	2857.67 ± 847.28	1472.75 ± 343.21
5	3443.1 ± 982.03	1813.85 ± 367.57
6	4042.68 ± 1119.15	2164.74 ± 397.53

agreements between local live, modern dead, and fossil data in species composition and abundances are significantly different but are statistically indistinguishable from one another when evaluated at the family level. Yet, these agreements present substantial variability. The main biasing factors that could influence the ecological fidelity of arthropod death assemblages to modern live communities include taphonomic processes, spatial resolution, midden age, and temporal resolution, sampling biases of modern and fossil surveys, and finally the true signal of past climate conditions, each of which is discussed below. Because the effect of taxonomic resolution on live-dead agreements was evaluated previously, it will not be discussed hereafter (Albano et al., 2016).

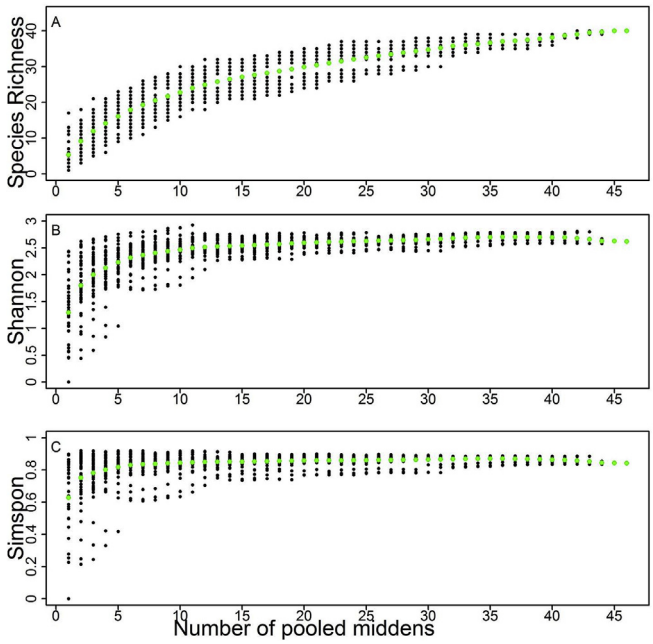

Fig. 8. Species richness (A), Shannon (B) and Simpson (C) diversity indices of fossil middens as a function of analytical time averaging. Fossil middens are successively pooled through time to simulate time averaging. The x-axis shows all combinations of successively pooled middens, from one (all middens treated separately) to 46 (all middens pooled together). Black dots = raw values; green dots = mean values. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

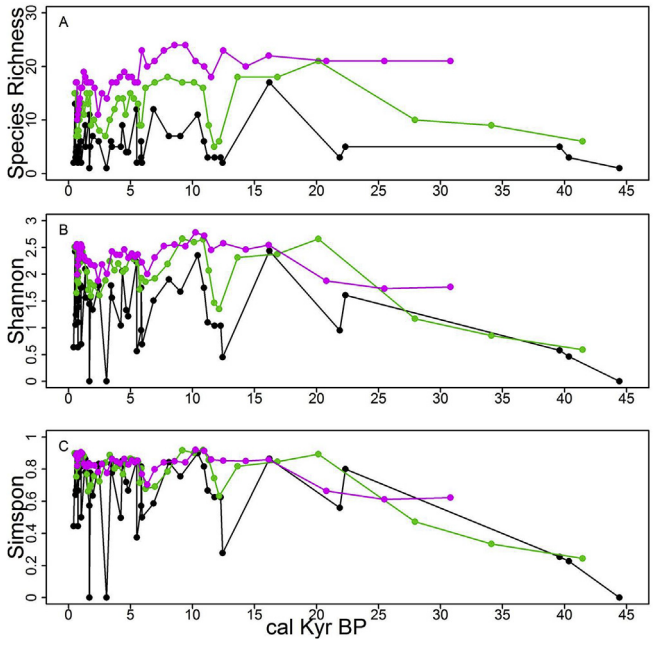

Fig. 9. Species richness (A), Shannon (B) and Simpson (C) diversity indices of fossil middens as a function of time (cal Kyr BP). Fossil middens are successively pooled through time to simulate time averaging. The black line depicts individual fossil middens; then all possible combinations of three, and six sequential fossil middens are displayed in green, and purple, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

4.1. Taphonomic processes

In agreement with our prediction and that of other Quaternary arthropod death assemblage studies, hard-bodied taxa are better preserved than soft-bodied taxa. Amongst the well-preserved arthropods, Coleoptera dominate fossil midden assemblages, a pattern also observed in fossil middens from the Sonoran and Chihuahuan Deserts in North America (Elias, 1990; Hall et al., 1988, 1989; Van Devender and Hall, 1993). The dominance of Coleoptera in both local live communities and death assemblages thus reflect a true feature of communities living in arid environments (past and present), rather than the sole effect of taphonomic processes that enhance the presence of those highly-sclerotized taxa (Pizarro-Araya et al., 2008).

In contrast, Entomobryomorpha, Acari, Diptera, and Zygentoma are the taxa most impacted by taphonomic processes; they are completely absent from death assemblages (Fig. 4). Although those taxa are absent from death assemblages sampled at out study site, they could potentially be recovered as in other paleontological or archaeological studies (Langdon et al., 2010; Braga et al., 2016). In fact, we have found two dipteran larvae (*Brachycera* spp.) from fossil middens sampled elsewhere in the central Atacama (unpublished data) suggesting that the effect of taphonomic processes on fossil arthropod remains may not be uniform across locations. Yet, those two observations represent a very small fraction of all fossil remains we identified, thus highlighting the strong influence of taphonomic processes acting upon Diptera. Because dipterans could be abundant in living communities (third most abundant taxa in local live communities; Fig. 4) and may play a crucial role in nutrient cycling (feeding upon rodent fecal pellets), the low preservation of dipterans in fossil middens is particularly detrimental to a full understanding of the functioning of past midden assemblages.

The absence of Entomobryomorpha, Acari, Diptera, and Zygentoma from death assemblages may partly explain the significant difference in agreements in species richness, rank abundances, and, to a lower extent, species composition between live communities and death assemblages (Fig. 3). At the family level, both modern and fossil death assemblages reflect, however, the composition of local live communities without significant differences (Figure B; Appendix D-F). These results suggest that taphonomic processes related to the consolidation cycles of middens may have a greater negative effect on species richness than species composition (i.e., species identities and abundances). Furthermore, we argue that modern death assemblages can be used reliably as modern analogs for fossil-live comparisons of community structure and composition. This result has important implications for midden studies because modern references of live communities are almost never collected, and they are more difficult to obtain than modern death assemblages.

4.2. Spatial resolution

Another key finding is the relative specificity of the regional fauna compared to local live communities and death assemblages (modern and fossil). This pattern was highlighted by all measures of community structure and composition (PIE's evenness, Simpson's turnover, Spearman rho and Horn-Morisita similarity) but the rarefied richness was not significantly different among all data types. Contrary to our expectations, however, local live communities do not represent a subset of the regional pool but rather a relatively distinct set of species. Likewise, most arthropods found in North American *Neotoma* middens are considered facultative inquiline taxa that spend, at least, part of the year in packrat dens (Elias, 1990). In the absence of arthropod remains from past regional pools, observations from modern communities do not

allow us to ascertain, however, that the specificity of the midden-associated fauna was also true in the past. Yet, our results suggest that rodent-associated death assemblages record a reliable signal for arthropod communities at local scales.

This high spatial resolution of midden-associated arthropod communities (fossil and modern) may contribute to the high variability in live-dead agreements (Fig. 3). In the study area, local live communities, modern dead, and fossil assemblages were collected at elevations ranging from ca. 2400 to 2800 masl. Although the altitudinal effect on midden-associated arthropod communities is unknown, it may induce some variability among samples within and among data types (local live, modern dead, and fossil data). The heterogeneous deposition of middens across the landscape is an intrinsic feature of this system that needs to be considered explicitly when dealing with higher spatial scales than in the present study. When sufficient middens are available, pooling middens within a given spatial bin (2-D surface and/or altitudinal grid) may help reduce inter-midden variations in community structure and composition.

4.3. Midden age and temporal resolution

The exact depositional rate of rodent middens, be they modern death or fossil, is unknown, making it difficult to assess the effect of time averaging on midden-associated arthropod assemblages. Yet, by combining local live communities, modern death assemblages, and fossil arthropod assemblages (local, dead, and fossil data, respectively), we evaluated a time-averaging effect that potentially span from a few decades to millennial time scales. As expected, time averaging was significant only when fossil data were pooled over millennial scales (Fig. 5), confirming our hypothesis that any fossil midden represents only a snapshot of past faunal assemblages (potentially less than a century; Fig. 5; Elias, 1990; Van Devender and Hall, 1993) akin to past floristic ones (de Porras et al., 2015; Latorre et al., 2002). AMS (accelerator mass spectrometry) ^{14}C dating of individual arthropod and plant remains, though costly, may be the only means of accurately quantifying time averaging.

Midden age did not have a significant influence on local live-fossil and dead-fossil agreements in species richness, rank abundances, and composition (Fig. 7; Table D). Likewise, no significant correlation was found between the midden age and any measures of diversity (species richness, and Shannon and Simpson's indices; Fig. 9), suggesting that the effects of taphonomic processes are relatively constant over time. In our series of 46 middens ranging from 410 to >44,420 cal yr BP, 40 were recovered within the last 15,000 cal yr BP (Table A). Therefore, even though old middens harbor a similar arthropod diversity as in most recent ones, they are recovered to a lesser extent with increasing age.

Finally, we did not see major differences in the relationships between midden age and live-dead agreements or diversity indices as middens were successively pooled through time. Rather, pooling up to three successively-occurring middens: (i) improved the live-dead agreements in species composition; (ii) reduced the inter-midden variability in species richness and composition; while (iii) keeping a relatively well-resolved temporal window (1056 ± 276.84 cal yr BP; Table 3, Figs. 6–8). Care must be taken, however, when pooling fossil middens. First, it is not always possible to pool middens through time as the number of middens in a given series can vary from only five to a couple of hundred (Betancourt et al., 2000; de Porras et al., 2015; Elias, 1987; Elias and Vandevender, 1990, 1992; Hall et al., 1988, 1989, 1990; Latorre et al., 2002, 2003; Mujica et al., 2015). Second, abrupt changes in community structure and composition could go undetected when pooling middens over a large temporal window. Although a single fossil midden appropriately reflects the composition of arthropod assemblages (our study, Elias, 1990; Elias and Vandevender, 1990), we argue that pooling middens may reduce the noise from the signal of past climate conditions when sufficient material is available.

4.4. Sampling biases of modern and fossil surveys

Another potential source of variability in live-dead agreements may come from our sampling design of live communities. Indeed, we sampled live communities over a limited period of time (October–December 2016) and only in a single year. Both pitfalls and sticky traps caught crawling and flying insects to a similar extent (Fig. 1), and with high efficiency (Fig. 2). However, fleas and ticks, for instance, were never found in modern communities despite being abundant in death assemblages. Setting traps for a longer period of time (or at different years) may help catch more taxa (e.g., fleas, ticks) in modern communities, thus increasing the similarity in species composition between modern communities and fossil assemblages (i.e., less variable and higher live-dead agreements). However, it would probably not change the fact that Coleoptera dominates both local live communities and death assemblages (modern, dead and fossil) of the Atacama Desert (see Jerez, 2000; Pizarro-Araya et al., 2008 for modern studies of the epigean fauna in the region of Atacama, Chile), or those in North America (Elias, 1990; Hall et al., 1988; Van Devender and Hall, 1993).

Another important sampling consideration is related to fossil midden weights. The indurated midden weight, washed weight (i.e., after dissolving the amberat), the percent weight loss in washing can greatly vary amongst middens, and potentially influence the number of arthropod taxa recovered (Van Devender and Hall, 1994). These variations in midden weights can be attributed to the relative proportion and composition of accumulated debris (e.g., sands, gravels, plant remains, and fecal pellets). To avoid relying on midden weight we standardized our protocol to the amount of time spent while screening washed and then dried materials (~3 h; Latorre et al., 2002). Our series of 46 middens yielded 639 specimens belonging to 43 taxa. In comparison, several series of 8–191 middens from the late Quaternary (<45,000 yr BP) located in the Sonoran and Chihuahuan desert have yielded from 17 to 85 taxa (Elias and Vandevender, 1992; Hall et al., 1988, 1989, 1990; Van Devender and Hall, 1993, 1994). In those studies, however, the midden weight was not published, if recorded, and no standardized protocol was used, precluding meaningful comparisons of species richness amongst studies. The study of arthropod remains from fossil middens is in its infancy, and we advocate for the use of a standardized protocol in future studies.

4.5. Signal of past climate conditions

Once the taphonomy of how arthropod remains are preserved over space and time are better understood, midden series can reveal the true biological signal of arthropod community response to environmental changes. We show that artefacts can induce some variability among middens, which could be reduced by pooling three successively occurring middens. In this context, temporal variations in live-dead agreements in species composition showed three abrupt declines around ~10,100 cal yr BP, ~3300 cal yr BP, and in the last 1700 cal yr BP (three pooled middens; Fig. 7). An explanation for such declines can in part be due to onsets of intense aridity, such as has been attributed to the strong decline in the diversity of the Chihuahuan Desert insect fauna was also observed in the last 2500 ^{14}C years, using fossil records from packrat middens (Elias, 1992). In addition, those declines were also highlighted by temporal variations in Shannon diversity, and to a lesser extent

Simpson diversity (Fig. 9). This suggests that relatively rare species probably were more impacted than abundant ones. With the occurrence of one midden every ~308 ± 56.6 cal yr BP, on average, over the last 13,000 cal yr BP (Table A), the midden series evaluated in this study provides a robust paleoenvironmental reconstruction of the arthropod faunas over the entire Holocene and key insights into the community-environment relationship to be made over the same period of time.

5. Conclusions

To date, this study presents the first explicit assessment of the ecological fidelity and spatiotemporal resolution of arthropod fossil assemblages from South American rodent middens. Three main conclusions can be drawn from our analyses: (1) although live-dead agreements and diversity indices are highly variable among samples, they consistently suggest that an average fossil midden better captures the structure and composition of living communities than species richness *per se*; (2) the spatial resolution of arthropod death assemblages is restricted to the close vicinity of rodent shelters; and (3) the effect of time and time averaging on death assemblages is limited. Altogether, we argue that pooling three successive middens may represent an optimal trade-off between the temporal resolution of death assemblages and inter-midden variations in community structure and composition when trying to detect potential influences of past environmental conditions. We hope this study will stimulate a renewed interest in midden records to disentangle the spatiotemporal variations in complex assemblages (including floristic and faunal assemblages). Regarding the high occurrence of rodent middens in arid environments worldwide, unraveling these paleoecological archives could provide invaluable insights into the natural and human-induced changes in ecosystems.

Data availability

Data supporting this manuscript will be provided upon request.

Authors' contribution

OD & ALG conceived the idea for the study; OD collected modern field data and processed fossil data, performed analyses, and wrote the paper; ALG contributed to the manuscript design and reviewed the manuscript; CL and JLB collected fossil middens, CL provided dating data, laboratory facilities and reviewed the manuscript; JLB contributed ideas and reviewed the manuscript; and GABV helped process fossil samples. OD was a postdoctoral fellow at Rutgers University. All authors gave final approval before publication.

Conflicts of interests

We have no conflicts of interests.

Declarations of interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2019.02.029.

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