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1 Running head: Ecological fidelity of fossil arthropods
2 Ecological fidelity and spatiotemporal resolution of arthropod death assemblages from rodent
3 middens in the central Atacama Desert (northern Chile)

4
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25

26 ABSTRACT

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

44

45 **Keywords:** arthropods; death assemblages; historical baseline; Holocene; taphonomy; time
46 averaging

47

48 INTRODUCTION

49 Death assemblages, defined by Kidwell and Tomasovych (2013) as taxonomically identifiable
50 individuals from the past generations of extant or recently extinct species at a site, contain unique
51 spatial and temporal information about past communities beyond the scope of modern ecological
52 studies. This information can then be used to reconstruct past climate conditions (Powell et al.,
53 2017), and to explain and predict long-term responses of communities to environmental changes
54 (Elias, 2014; Elias and Matthews, 2014; Terry, 2010a; Terry and Rowe, 2015; Tinner et al., 2013;
55 Yeakel et al., 2014). Yet, the quality of such data is subject to two main sources of biases. First,
56 taphonomic processes occur after an organism's death and affect its incorporation into the fossil
57 record (e.g., burial, compaction, decomposition). Second, time averaging can pool organisms that
58 potentially lived at different times into the same death assemblage (Allison and Bottjer, 2010;
59 Roy et al., 1996). Evaluating the role of these factors, and hence the degree to which fossil
60 records accurately reflect living communities, is essential for obtaining robust ecological
61 information from death assemblages.

62 The live-dead approach is used routinely in paleontological studies to test the fidelity of
63 ancient data to detect and reconstruct the structure of living communities (Kidwell and Bosence,
64 1991). To date, the vast majority of live-dead studies have focused on mollusks from soft
65 sediments (Kidwell, 2001; Kidwell and Bosence, 1991; Kidwell and Tomasovych, 2013;
66 Olszewski and Kidwell, 2007) and both large body-sized vertebrates (Behrensmeyer et al., 1979;
67 Tappen, 1995; Western and Behrensmeyer, 2009) and small mammals in arid terrestrial
68 environments (Terry, 2010a, b; Terry and Rowe, 2015). Despite their importance in the Earth's
69 faunal biomass and total biodiversity as well as their role in many ecosystem processes,
70 arthropods seldom have been the target of live-dead studies. **Among those few studies, most were**
71 **conducted in Northern Europe, and compared modern deposits of arthropod remains to subfossil**
72 **or fossil data for examining past living conditions or anthropogenic impacts on landscapes**

73 (Smith, 1998; Kenward, 2006; Smith et al., 2010, 2014; Forbes et al., 2016). The main use of
74 fossil arthropods in paleoecological reconstructions has been, instead, to infer past climatic
75 conditions from the presence of indicator species (mostly Coleoptera and Diptera) in peatland,
76 wetland, and floodplain deposits worldwide (<https://www.bugscep.com/downloads/qbib.pdf>; see
77 also Ashworth and Nelson, 2014; Coope, 2010; Elias, 2015; Kuzmina, 2015 for recent examples).
78 The lack of modern calibration has limited our understanding of how taphonomic and other
79 biases may affect past arthropod assemblages.

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

95 Fossil middens are amalgamated deposits of plant (macrofossils and pollen), arthropod,
96 and vertebrate remains, including copious fecal pellets of the midden agent, all cemented into a

97 hard mass by crystallized urine (“amberat”). Most of the midden materials, except for some of the
98 pollen from anemophilous species, are presumed to originate from living organisms within the
99 animal’s foraging range. In arid lands, and when protected from the elements in a cave or rock
100 shelter, middens can commonly be thousands of years old. The excellent preservation of plant
101 and animal remains allows for a broad suite of morphological, geochemical, and even genetic
102 analyses (see Kuch et al., 2002; Murray et al., 2012). Fossil rodent middens have provided
103 unparalleled taxonomic and spatial resolution in reconstructing past vegetation change in the
104 Americas during the late Quaternary (Betancourt et al., 2000; Betancourt et al., 1990; de Porras et
105 al., 2015; Latorre et al., 2002; Mujica et al., 2015).

106 Despite their many advantages, middens also have some limitations. The depositional
107 episode that created a particular midden can be brief (months) or prolonged (decades to
108 centuries), and usually indeterminable from stratigraphy or ¹⁴C dating. Even the thickest of
109 deposits (meters deep) tend to be stratigraphically discontinuous. To create a local midden series
110 requires collating and radiocarbon dating a number of individual and separate middens (from
111 different locations in the same rock shelter or different rock shelters in the same area) and their
112 assemblages, which often results in long temporal gaps (Betancourt et al., 2000; Betancourt et al.,
113 1990). Also, there have been few attempts to test and calibrate the reliability of plant macrofossil
114 and pollen assemblages in rodent middens to reflect local plant communities (de Porras et al.,
115 2015; Lesser and Jackson, 2011; Lyford et al., 2004; Nowak et al., 2000).

116 Midden research in the Americas has focused primarily on the rich plant macrofossil and
117 pollen assemblages, and less so on animal remains, including the arthropod assemblages that are
118 the focus of this study. Arthropod remains are common and well preserved enough in packrat
119 (*Neotoma*) middens from western North America to attract the attention of entomologists
120 (Ashworth and Markgraf, 1989; Elias, 1987; Elias, 1990; Elias and Vandevender, 1990; Hall et

121 al., 1989; Hall et al., 1988; Hall et al., 1990; Van Devender and Hall, 1993; Van Devender and
122 Hall, 1994). Elias (1990) surmised that most of the sclerotized exoskeletal remains in packrat
123 middens were not consumed by packrats, but instead derive from facultative arthropods
124 (particularly ground beetles and darkling beetles) that spend the winter in temperature-buffered
125 packrat dens, are packrat parasites, or were drug in on plant material or by other animals. A
126 taphonomic study of arthropods in these middens showed that herbivores are under-represented,
127 whereas scavengers are over-represented (Elias, 1990). Similar arthropod studies have, however,
128 lagged for South American middens.

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

145

146 MATERIALS & METHODS

147 *Study area and rodent middens*

148 This study was located in the southern part of the Salar de Atacama (Chile), ~10 km south of
149 Tilomonte (Latitude: -23.84°; Longitude: -68.18°; altitude: ~2,600 m), near the lower, dry limits
150 of vascular plants in the central Atacama Desert and at the well-studied site of Vegas de
151 Tilocalar/Lomas de Tilocalar, where 46 middens were previously collected, dated, and analyzed
152 spanning the last ~40,000 cal yr BP (Betancourt et al., 2000; de Porrás et al., 2015; Latorre et al.,
153 2002). Midden ages reported here were calibrated using the SHCal13 calibration curve (see Table
154 A). In this area, modern and fossil middens are produced by two main families of rock-dwelling
155 rodents, chinchilla rats (*Abrocoma*, mostly *A. cinerea*: Abrocomidae) and leaf-eared mice
156 (*Phyllotis* spp.: Cricetidae). The agent of deposition (i.e., rodent species) for each of the fossil
157 middens was identified by the size and shape of the fecal pellets in the middens (Díaz et al.,
158 2012). The occurrence of any vegetation, today and in the past, in this hyperarid desert is
159 controlled by the amount and seasonality of precipitation, which vary sharply with latitude and
160 elevation (Latorre et al., 2002). The Tilomonte study site is dominated by sparse (<5% cover)
161 shrubs and succulent annuals and perennial halophytes (e.g., *Cistanthe salsoloides*:
162 Portulacaceae; *Atriplex imbricata*: Amaranthaceae; and *Tessaria absinthioides*: Asteraceae).

163

164 *Live arthropod communities found in vicinity of rodent middens: "local live data"*

165 Several sampling methods exist to provide an accurate assessment of the local ground-dwelling
166 arthropod community, yet their capture efficiency depends upon the species characteristics (e.g.,
167 surface activity, population density), the trap-related features (e.g., size, shape, bait/preservative
168 type, and material of constructions), as well as the sampled environments (e.g., Zou et al., 2012).

169 Among all sampling methods, pitfall traps are used extensively for sampling ground-dwelling
170 communities (Pekár, 2002; Phillips and Cobb, 2005), especially in hyperarid environments (Cheli
171 and Corley, 2010). Sticky traps were, however, the only realistic alternative in our study sites, as
172 the rocky shelters of rodents preclude the proper burial of pitfall traps. Sticky traps consist of a
173 piece of cardboard with a sticky surface that can catch both crawling and flying species (Atakan
174 and Canhilal, 2004). Within the close proximity of rock shelters (both within and < 15 m outside
175 the caves), we set ten squared plots each containing 16 sticky traps (Nb. total = 160). Within a
176 given plot, the sticky traps (catching surface: 20 cm x 15 cm) were located from two to seven
177 meters away from each other depending on the configuration of the rock shelters. All plots were
178 ~60 m apart. Finally, each sticky trap was checked every day in the morning over five
179 consecutive days. Arthropods were kept in 70% alcohol and later identified in the laboratory
180 using a dissecting microscope.

181

182 *Live communities present in the region: "regional live data"*

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

193 Pitfall traps and sticky traps are two passive sampling methods that can catch both
194 crawling and, to a lesser extent, flying arthropods (Zou et al., 2012). Yet, the proportion of each
195 trap type—pitfalls with (N=100) or without (N=100) preservatives and sticky traps (N=200)—
196 may influence the probability of catching a given species. We therefore estimated the trap-type
197 standardized catch of each species for all habitats combined (local and regional data; see Terry,
198 2010b for more details). Our results indicate high consistency between estimated and observed
199 abundances of each taxon except for the abundant Entomobryomorpha (Collembola), which was
200 mainly caught in pitfalls set with ethylene glycol (taxa code = 1; Table B; Figure 1).

201

202 *Modern death assemblages: "modern dead data"*

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

210 Arthropod remains were identified to the **lowest** taxonomic level when possible using our
211 reference database of modern arthropods, the collection of the Museo Nacional de Historia
212 Natural in Santiago (Chile), and by reference to specialists. The minimum number of individuals
213 (MNI; a proxy of species abundance) of each species was calculated by counting the maximum
214 number of analogous arthropod remains belonging to a given species (Terry, 2010a). For
215 instance, if we identified one thorax, three head capsules, and nine elytra (four left-sided and five
216 right-sided elytra) that were found apart from each other but belonging to the same species, we

217 reported a MNI of five individuals (four complete pairs of elytra plus one). We did not use the
218 number of leg remains due to the difficulty to identify and attribute those remains to any given
219 specimens.

220

221 *Fossil death assemblages: "fossil data"*

222 In this study, we included a total of 46 **samples of** fossil middens, covering a time span of
223 >40,000 cal yr BP from Vegas de Tilocalar/Lomas de Tilocalar (Table A). **Middens were**
224 **extracted by using a hammer and chisel, cleaned in the field for surface contaminants, and split**
225 **along clear stratigraphic units when recognizable. A "sample" can thus correspond to a small**
226 **fossil midden or a distinct stratigraphic unit from a large fossil midden. Hereafter, those samples**
227 **are referred to "fossil middens".** Latorre et al. (2002) describe the original extraction, location and
228 processing of these middens. Of possible consideration to taphonomy is the potential
229 fragmentation and mechanical damage done to fragile arthropod remains during midden
230 processing. Middens are typically soaked for 2-3 weeks (enough to dissolve the crystallized
231 urine) followed by wet screening of dissolved midden materials with water faucet. They are then
232 dried on cardboard plates at 50-60°C in a rack oven for an average of two to three days. Dried
233 midden samples were then sieved into size classes using USGS Standard Soil Sieves (mainly #10
234 and #18), and hand sorted for three hours each under a microscope for arthropod remains. **This**
235 **standardized methodology was used for the sake of consistency with previous studies on**
236 **paleomiddens (Betancourt et al., 2000; Betancourt and Saavedra, 2002; Latorre et al., 2002;**
237 **Latorre et al., 2003; Diaz et al., 2012; de Porrás et al., 2015), and because the sizes and weights**
238 **of fossil middens can vary across locations.** The identity of fossilized arthropod species and MNI
239 were **then** established using the same procedure as used for "modern dead data" described above
240 **(see Table C for a list of taxa identities).**

241

242 *Live-dead agreements of ecological information*

243 The degree to which ecological information obtained from death assemblages reflect that of
244 modern communities was evaluated using various complementary measures of community
245 structure and composition: species richness, evenness, composition, and abundance (Terry,
246 2010a, b). Species richness was compared using individual-based rarefaction curves
247 (*rareNMtests*-package in R; Chao et al., 2014). Species evenness was evaluated using the
248 Probability of Interspecific Encounter (PIE) as $H/\log(S)$, where H correspond to the Shannon
249 index, and S the number of species. PIE is the probability that two randomly picked individuals
250 belong to two different species and correspond to the steepest slope of a rarefaction curve.
251 Species composition was estimated by calculating the percentages of "live species" from modern
252 communities found in death assemblages and "dead species" found in modern communities
253 (Kidwell and Bosence, 1991). This procedure was extended to include all type of data (local live,
254 regional live, modern dead, and fossil data). Similarity in species composition (presence/absence)
255 among death assemblages and live communities was assessed using the Simpson's turnover index
256 (0 = dissimilar; 1 = similar; *vegan*-package; Koleff et al., 2003). Both Simpson's turnover and
257 Raup-Crick indices can handle variations in sample sizes when evaluating similarities in species
258 richness. The Raup-Crick index was not chosen, however, because it is too sensitive to the
259 composition of the regional species pool, which was unknown for death assemblages (Chase and
260 Myers, 2011). Similarity in species rank abundances among death assemblages and modern
261 communities was evaluated with the Spearman rank correlation test (Terry, 2010a, b). Similarity
262 in species relative abundances among death assemblages and live communities was estimated
263 with the Horn-Morisita index (0 = dissimilar; 1 = similar; *vegan*-package). All of these measures
264 of community structure and composition (rarefied species richness, Simpson's turnover,

265 Spearman Rho, Horn-Morisita) were selected for their robustness to variations in sample sizes
266 among data types.

267

268 *Effect of time and time averaging*

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

281

282 RESULTS

283 *Live-dead agreements of ecological information*

284 The agreement among all four sources of soil arthropod data was highly variable among samples
285 and across the various measures of community structure and composition used in this study.

286 Rarefied species richness was not statistically different between all four sources of data when
287 samples were pooled by data type (Figure 2A; Table 1). Individual samples treated separately
288 showed, however, large variability in species richness within each source of data (Figure 2B).

289 Regional live communities ("regional data") and modern death assemblages ("modern dead
290 data") displayed the lowest and highest evenness, respectively (0.74 ± 0.05 , 0.92 ± 0.01 ; Table1). In
291 contrast, local live communities ("local live data") and fossil death assemblages ("fossil data")
292 exhibited intermediate values of evenness (0.83 ± 0.02 , 0.86 ± 0.02 ; Table 1).

293 Overall, the percentages of "live species" and "dead species" found in each data type were
294 low and varied from 17.0% to 40.0% (Table 2). The highest percentages of "live species" were
295 found between local and regional data (38.78%) and between dead and fossil data (40.0%). The
296 lowest values were found between regional and dead data (22.22%) and between regional and
297 fossil data (20.45%). The percentages between local data and death assemblages were
298 intermediate (29-30%). These patterns were quantitatively similar for the percentages of "dead
299 species" found in each data type (Table 2).

300 The averaged similarity in species presence/absence between samples within a given data
301 type was not significantly different across data types (all pairwise comparisons between live-
302 live=LL, regional-regional=RR, modern dead-modern dead=DD, and fossil-fossil=FF; Simpson's
303 turnover; Appendix A; Figure 3A). Similar patterns were observed when evaluating rank
304 abundances (Spearman rank test; except significant differences between RR and DD; Appendix
305 B; Figure 3B) and species composition and abundances (Horn-Morisita; Appendix C; Figure 3C).
306 On average, $50 \pm 0.1\%$ of Spearman rank correlations were significant (see Figure A for the
307 distribution of p-values grouped by data type). Species richness, rank abundances and species
308 composition were significantly different when comparing local live communities and death
309 assemblages (LL-LD and LL-LF comparisons; Appendix A-C; Figure 3). In addition, the
310 agreements between regional data and death assemblages were significantly different and on
311 average lower than comparisons between local live data and death assemblages (all RR-RD and
312 RR-RF comparisons; Appendix A-C; Figure 3). Finally, when repeating those analyses with

313 arthropods identified at the family levels, agreements between local live communities and death
314 assemblages become not significantly different regardless of the community measure (Simpson's
315 turnover, Spearman, and Horn-Morisita; Figure B; Appendix D-F). Agreements between regional
316 data and death assemblages remained, however, significantly different with respect to rank
317 abundances and family composition (Spearman, Horn-Morisita; Figure B; Appendix D-F).

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

331

332 *Effect of time and time averaging*

333 In subsequent analyses, we excluded the regional data due to their relatively unique community
334 structure and composition compared with local live, modern dead, and fossil data. In addition, to
335 isolate the effect of time averaging on death assemblages, we also restricted our datasets to the
336 orders present in all three data types (i.e., excluding taphonomic processes and sampling biases;

337 Figure 4). The effect of time averaging on species richness was significant, but only noticeably at
338 millennial scales (all pooled fossil middens) compared with local live and modern dead data
339 (Figure 5A). The species richness within each fossil midden is variable, and not consistently
340 higher than that in local live communities or in modern death assemblages, suggesting a limited
341 effect of time averaging on death assemblages of single fossil middens (Figure 5B).

342 As data from fossil middens are successively pooled through time, the mean local-fossil
343 Simpson's turnover decreases and then increases, whereas the mean Spearman agreement remains
344 relatively constant, and the Horn-Morisita similarity increases (green points; Figure 6). In
345 addition, most Spearman rank correlations are not significant (Figure C). Pooling successive
346 middens through time does not necessarily improve the local live-fossil agreement in terms of
347 species presence/absence or rank abundances (Figure 6A, and C). The mean local live-fossil
348 agreement in species composition, however, improved from 0.39 (local live-fossil agreement
349 with individual middens) to 0.59, which corresponds to a plateau reached when six successively
350 occurring middens are pooled (Figure 6E). Similar patterns occur when successively pooled
351 middens are compared to pooled modern dead data (Figure 6B, D, and F). The modern dead-
352 fossil agreements (Simpson's Turnover, Spearman Rho, Horn-Morisita) were, however, higher
353 than the local live-fossil agreements.

354 Variations in local live-fossil and modern dead-fossil agreements were not significantly
355 related to midden ages for all measures of community structure and composition. Those
356 relationships become significant when pooling up to six (plateau) successive middens through
357 time (Figure 7; Table D). Note that those combinations of three and six pooled middens
358 encompass an average temporal window of 1056 ± 276.84 and 2165 ± 397.53 cal yr BP,
359 respectively, when all middens, except the oldest ones ($> 40,000$ cal yr BP; $N = 3$), are included
360 (Table 3). These examples from individual middens up to three and six pooled middens thus

361 represent a range of combinations that increase agreements in species composition and
362 abundances (Horn-Morisita) but also decrease the temporal resolution of resulting assemblages
363 (from centennial to millennial scales; Table 3).

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

375

376 DISCUSSION

377 Altogether, these results demonstrate that individual fossil middens capture a highly resolved
378 spatiotemporal picture of the structure and composition of common arthropod species and, to a
379 lesser extent, rare species compared to raw species counts. The agreements between local live,
380 modern dead, and fossil data in species composition and abundances are significantly different,
381 but are statistically indistinguishable from one another when evaluated at the family level. Yet,
382 these agreements present substantial variability. The main biasing factors that could influence the
383 ecological fidelity of arthropod death assemblages to modern live communities include:

384 taphonomic processes, spatial resolution, midden age and temporal resolution, sampling biases of

385 modern and fossil surveys, and finally the true signal of past climate conditions, each of which is
386 discussed below. Because the effect of taxonomic resolution on live-dead assemblages was
387 evaluated previously, it will not be discussed hereafter (Albano et al., 2016).

388

389 *Taphonomic processes*

390 In agreement with our prediction and that of other Quaternary arthropod death assemblage
391 studies, hard-bodied taxa are better preserved than soft-bodied taxa. Amongst the well-preserved
392 arthropods, Coleoptera dominate fossil midden assemblages, a pattern also observed in fossil
393 middens from the Sonoran and Chihuahuan Deserts in North America (Elias, 1990; Hall et al.,
394 1989; Hall et al., 1988; Van Devender and Hall, 1993). The dominance of Coleoptera in both
395 local live communities and death assemblages thus reflect a true feature of communities living in
396 arid environments (past and present), rather than the sole effect of taphonomic processes that
397 enhance the presence of those highly-sclerotized taxa (Pizarro-Araya et al., 2008).

398 In contrast, Entomobryomorpha, Acari, Diptera, and Zygentoma are the taxa most
399 impacted by taphonomic processes; they are completely absent from death assemblages (Figure
400 4). Although those taxa are absent from death assemblages sampled at our study site, they could
401 potentially be recovered as in other paleontological or archaeological studies (Langdon et al.,
402 2010; Braga et al., 2016). In fact, we have found two dipteran larvae (*Brachycera* spp.) from
403 paleomiddens sampled elsewhere in the central Atacama (unpublished data) suggesting that the
404 effect of taphonomic processes on fossil arthropod remains may not be uniform across locations.
405 Yet, those two observations represent a very small fraction of all fossil remains we identified,
406 thus highlighting the strong influence of taphonomic processes acting upon Diptera. Because
407 dipterans could be abundant in living communities (third most abundant taxa in local live
408 communities; Figure 4) and may play a crucial role in nutrient cycling (feeding upon rodent fecal

409 pellets), the low preservation of dipterans in paleomiddens is particularly detrimental to a full
410 understanding of the functioning of past midden assemblages.

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

423

424 *Spatial resolution*

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

433 remains from past regional pools, observations from modern communities do not allow us to
434 ascertain, however, that the specificity of the midden-associated fauna was also true in the past.
435 Yet, our results suggest that rodent-associated death assemblages record a reliable signal for
436 arthropod communities at local scales.

437 This high spatial resolution of midden-associated arthropod communities (fossil and
438 modern) may contribute to the high variability in live-dead assemblages (Figure 3). In the study
439 area, local live communities, modern dead, and fossil assemblages were collected at elevations
440 ranging from ca. 2,400 to 2,800 masl. Although the altitudinal effect on midden-associated
441 arthropod communities is unknown, it may induce some variability among samples within and
442 among data types (local live, modern dead, and fossil data). The heterogeneous deposition of
443 middens across the landscape is an intrinsic feature of this system that needs to be considered
444 explicitly when dealing with higher spatial scales than in the present study. When sufficient
445 middens are available, pooling middens within a given spatial bin (2-D surface and/or altitudinal
446 grid) may help reduce inter-midden variations in community structure and composition.

447

448 *Midden age and temporal resolution*

449 The exact depositional rate of rodent middens, be they modern death or fossil, is unknown,
450 making it difficult to assess the effect of time averaging on midden-associated arthropod
451 assemblages. Yet, by combining local live communities, modern death assemblages, and fossil
452 arthropod assemblages (local, dead, and fossil data, respectively), we evaluated a time-averaging
453 effect that potentially span from a few decades to millennial time scales. As expected, time
454 averaging was significant only when fossil data were pooled over millennial scales (Figure 5),
455 confirming our hypothesis that any fossil midden represents only a snapshot of past faunal
456 assemblages (potentially less than a century; Figure 5; Elias, 1990; Van Devender and Hall,

457 1993) akin to past floristic ones (de Porrás et al., 2015; Latorre et al., 2002). AMS (accelerator
458 mass spectrometry) ¹⁴C dating of individual arthropod and plant remains, though costly, may be
459 the only means of accurately quantifying time averaging.

460 Midden age did not have a significant influence on local live-fossil and dead-fossil
461 agreements in species richness, rank abundances, and composition (Figure 7; Table D). Likewise,
462 no significant correlation was found between the midden age and any measures of diversity
463 (species richness, and Shannon and Simpson's indices; Figure 9), suggesting that the effects of
464 taphonomic processes are relatively constant over time. In our series of 46 middens ranging from
465 410 to >44,420 cal yr BP, 40 were recovered within the last 15,000 cal yr BP (Table A).
466 Therefore, even though old middens harbor a similar arthropod diversity as in most recent ones,
467 they are recovered to a lesser extent with increasing age.

468 Finally, we did not see major differences in the relationships between midden age and
469 live-dead agreements or diversity indices as middens were successively pooled through time.
470 Rather, pooling up to three successively-occurring middens: (i) improved the live-dead
471 agreements in species composition; (ii) reduced the inter-midden variability in species richness
472 and composition; while (iii) keeping a relatively well-resolved temporal window (1056±276.84
473 cal yr BP; Table 3, Figure 6-8). Care must be taken, however, when pooling fossil middens. First,
474 it is not always possible to pool middens through time as the number of middens in a given series
475 can vary from only five to a couple of hundred (Betancourt et al., 2000; de Porrás et al., 2015;
476 Elias, 1987; Elias and Vandevender, 1990, 1992; Hall et al., 1989; Hall et al., 1988; Hall et al.,
477 1990; Latorre et al., 2002; Latorre et al., 2003; Mujica et al., 2015). Second, abrupt changes in
478 community structure and composition could go undetected when pooling middens over a large
479 temporal window. Although a single fossil midden appropriately reflect the composition of
480 arthropod assemblages (our study, Elias, 1990; Elias and Vandevender, 1990), we argue that

481 pooling middens may reduce the noise from the signal of past climate conditions when sufficient
482 material is available.

483

484 *Sampling biases of modern and fossil surveys*

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

498 Another important sampling consideration is related to fossil midden weights. The
499 indurated midden weight, washed weight (i.e., after dissolving the amberat), the percent weight
500 loss in washing can greatly vary amongst middens, and potentially influence the number of
501 arthropod taxa recovered (Van Devender and Hall, 1994). These variations in midden weights
502 can be attributed to the relative proportion and composition of accumulated debris (e.g., sands,
503 gravels, plant remains, and fecal pellets). To avoid relying on midden weight we standardized our
504 protocol to the amount of time spent while screening washed and then dried materials (~3 hours;

505 Latorre et al., 2002). Our series of 46 middens yielded 639 specimens belonging to 43 taxa. In
506 comparison, several series of 8 to 191 middens from the late Quaternary (<45,000 yr BP) located
507 in the Sonoran and Chihuahuan desert have yielded from 17 to 85 taxa (Elias and Vandevender,
508 1992; Hall et al., 1989; Hall et al., 1988; Hall et al., 1990; Van Devender and Hall, 1993; Van
509 Devender and Hall, 1994). In those studies, however, the midden weight was not published, if
510 recorded, and no standardized protocol was used, precluding meaningful comparisons of species
511 richness amongst studies. The study of arthropod remains from fossil middens is in its infancy,
512 and we advocate for the use of a standardized protocol in future studies.

513

514 *Signal of past climate conditions*

515 Once the taphonomy of how arthropod remains are preserved over space and time are better
516 understood, midden series can reveal the true biological signal of arthropod community response
517 to environmental changes. We show that artefacts can induce some variability among middens,
518 which could be reduced by pooling three successively occurring middens. In this context,
519 temporal variations in live-dead assemblages in species composition showed three abrupt declines
520 around ~10,100 cal yr BP, ~3,300 cal yr BP, and in the last 1,700 cal yr BP (three pooled
521 middens; Figure 7). An explanation for such declines can in part be due to onsets of intense
522 aridity, such as has been attributed to the strong decline in the diversity of the Chihuahuan Desert
523 insect fauna was also observed in the last 2,500 ¹⁴C years, using fossil records from packrat
524 middens (Elias, 1992). In addition, those declines were also highlighted by temporal variations in
525 Shannon diversity, and to a lesser extent Simpson diversity (Figure 9). This suggests that
526 relatively rare species probably were more impacted than abundant ones. With the occurrence of
527 one midden every $\sim 308 \pm 56.6$ cal yr BP, on average, over the last 13,000 cal yr BP (Table A),
528 the midden series evaluated in this study provides a robust paleoenvironmental reconstruction of

529 the arthropod faunas over the entire Holocene and key insights into the community-environment
530 relationship to be made over the same period of time.

531

532 CONCLUSIONS

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

548

549 DATA AVAILABILITY

550 Data supporting this manuscript will be provided in Dryad.

551

552 AUTHORS'S CONTRIBUTION

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

558

559 CONFLICTS OF INTERESTS

560 We have no conflicts of interests.

561

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571

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758

759 SUPPLEMENTARY ONLINE INFORMATION

760 **Table A:** Calibrated and uncalibrated midden ages.

761 **Table B:** List of codes and associated taxa identities from live surveys.

762 **Table C:** List of taxa identities from fossil data.

763 **Appendix A:** Multiple comparison tests of Simpson's turnover indices between data types after

764 Kruskal-Wallis tests. Analyses were performed at the morphospecies level.

765 **Appendix B:** Multiple comparison tests of Spearman rank correlations between data types after

766 Kruskal-Wallis tests. Analyses were performed at the morphospecies level.

767 **Appendix C:** Multiple comparison tests of Horn-Morisita indices between data types after
768 Kruskal-Wallis tests. Analyses were performed at the morphospecies level.

769 **Figure A:** Distribution of p-values after Spearman rank correlations for all pairwise comparisons
770 by data type.

771 **Figure B:** Live-dead agreement of Simpson's turnover index (A), Spearman rank correlation (B),
772 and Horn-Morisita index (C) for all pairwise comparisons by data type. Analyses were performed
773 at the family level.

774 **Appendix D:** Multiple comparison tests of Simpson's turnover indices between data types after
775 Kruskal-Wallis tests. Analyses were performed at the family level.

776 **Appendix E:** Multiple comparison tests of Spearman rank correlations between data types after
777 Kruskal-Wallis tests. Analyses were performed at the family level.

778 **Appendix F:** Multiple comparison tests of Horn-Morisita indices between data types after
779 Kruskal-Wallis tests. Analyses were performed at the family level.

780 **Figure C:** Distribution of p-values after Spearman rank correlations as a function of analytical
781 time-averaging.

782 **Table D:** Statistics of Spearman rank correlations between live-agreements and diversity indices
783 and time in cal yr BP.

784 TABLES

785 Table 1. Rarefied richness ($S \pm 95\% \text{CI}$; $n=240$) and mean Pielou's evenness ($\text{PIE} \pm \text{SE}$) for samples
786 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

787

788

789 Table 2. Percentages of "live species" (above diagonal) and "dead species" (below diagonal)
790 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	-

791

792

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

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

798

799 FIGURES

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

803
804 Figure 2: Rarefaction curves of effective species richness for all data pooled by data type (A), and
805 for all individual samples (B). Local live communities (green); regional live communities (blue);
806 modern death assemblages (red); fossil death assemblages (black). For the sake of visual clarity,
807 95% CI are not shown for individual samples.

808
809 Figure 3: Live-dead agreement of Simpson's turnover index (A), Spearman rank correlation (B),
810 and Horn-Morisita index (C) for all pairwise comparisons by data type. Analyses were performed
811 at the morphospecies level. L=local live communities (green); R=regional live communities
812 (blue); D= modern death assemblages (red); F=fossil death assemblages (black) (e.g., LL=all
813 pairwise comparisons within local data; LR=all pairwise comparisons between local and regional
814 data). See main text and Appendix A-C for statistical significance of pairwise comparisons.

815
816 Figure 4: Comparison of relative order abundances pooled by data type. Local (green); regional
817 (blue); dead (red); fossil (black) data.

818
819 Figure 5: Rarefaction curves of effective species richness for restricted datasets pooled by data
820 type (A), and for all individual samples (B). These datasets were restricted to the orders present
821 in local live communities (green), modern death assemblages (red), and fossil death assemblages

822 (black; i.e., excluding taphonomic and sampling biases). For the sake of visual clarity, 95% CI
823 are not shown for individual samples.

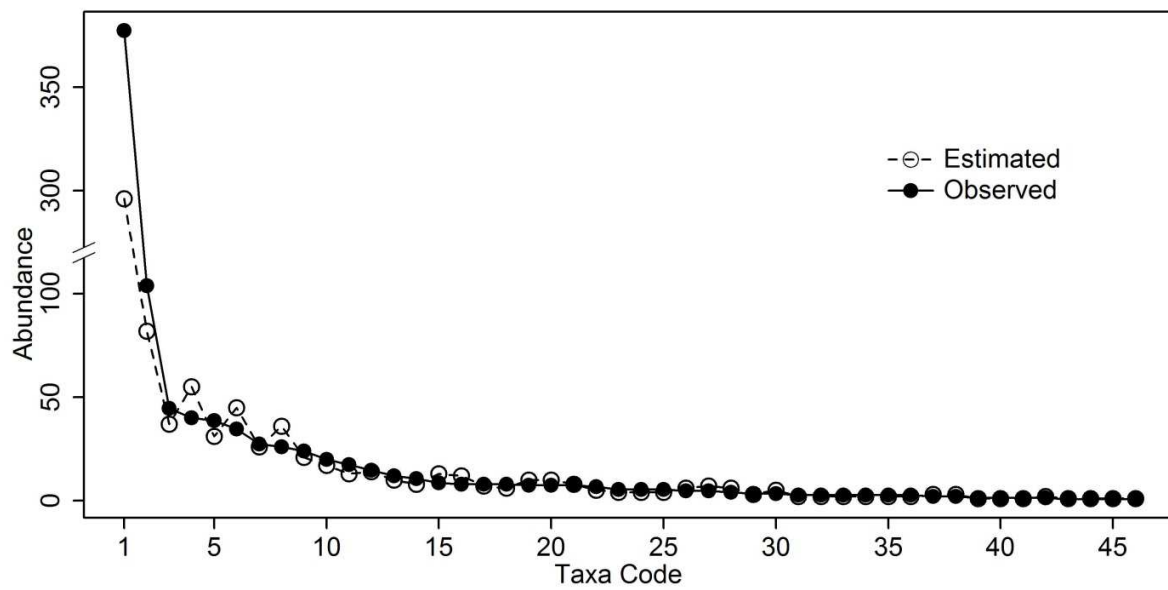
824
825 Figure 6: Live-dead agreement of Simpson's turnover index (A, B), Spearman rho (C, D) and
826 Horn-Morisita index (E, F) as a function of analytical time-averaging. Fossil middens are
827 successively pooled through time to simulate time averaging and compared with local live (A, C,
828 E) and modern dead (B, D, F) data pooled by data type. The x-axis shows all combinations of
829 successively pooled middens, from one (all middens treated separately) to 46 (all middens pooled
830 together). Black dots=raw values; green dots=mean values.

831
832 Figure 7: Live-dead agreement of Simpson's turnover index (A, B), Spearman rho (C, D) and
833 Horn-Morisita index (E, F) as a function of time (cal Kyr BP). Fossil middens are successively
834 pooled through time to simulate time averaging and compared with local live (A, C, E) and
835 modern dead (B, D, F) data pooled by data type. The black line depicts individual fossil middens;
836 then all possible combinations of three, and six sequential fossil middens are displayed in green,
837 and purple, respectively.

838
839 Figure 8: Species richness (A), Shannon (B) and Simpson (C) diversity indices of fossil middens
840 as a function of analytical time averaging. Fossil middens are successively pooled through time to
841 simulate time averaging. The x-axis shows all combinations of successively pooled middens,
842 from one (all middens treated separately) to 46 (all middens pooled together). Black dots=raw
843 values; green dots=mean values.

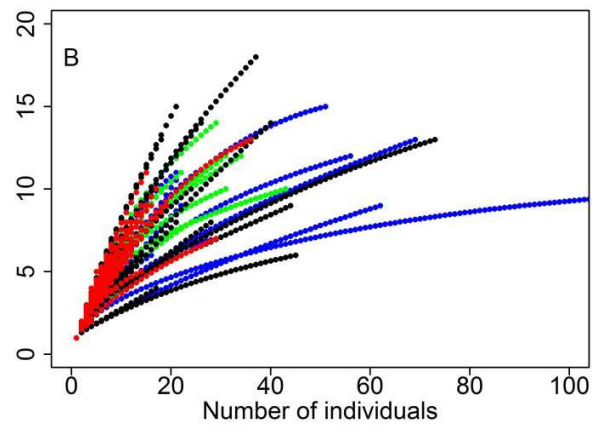
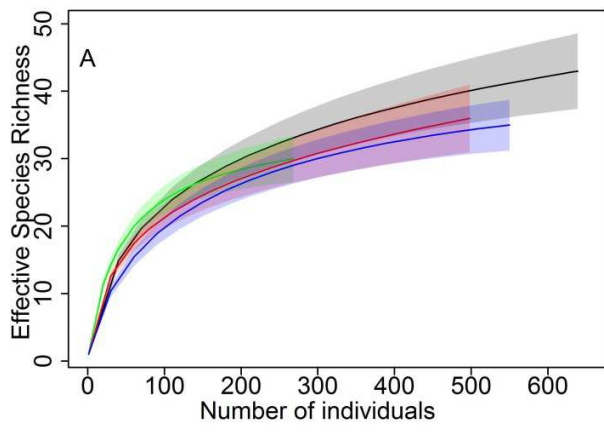
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845 Figure 9: Species richness (A), Shannon (B) and Simpson (C) diversity indices of fossil middens
846 as a function of time (cal Kyr BP). Fossil middens are successively pooled through time to
847 simulate time averaging. The black line depicts individual fossil middens; then all possible
848 combinations of three, and six sequential fossil middens are displayed in green, and purple,
849 respectively.



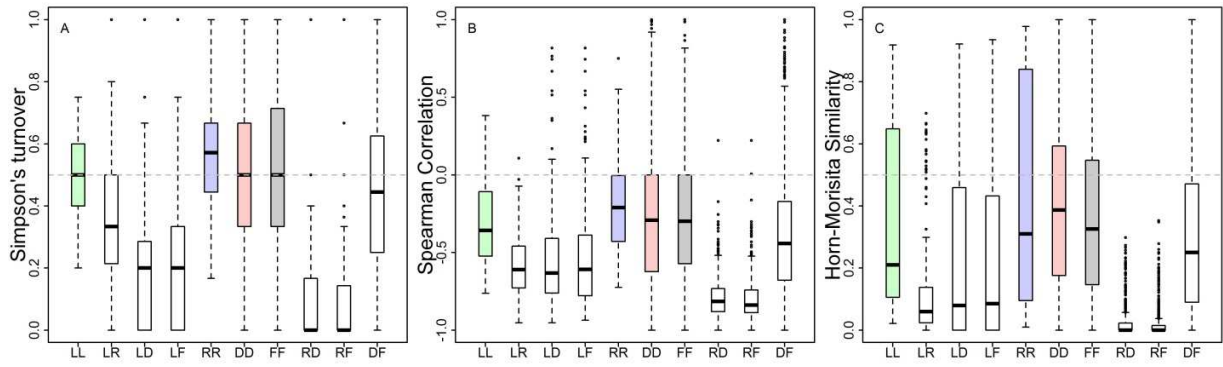
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851 Figure 1



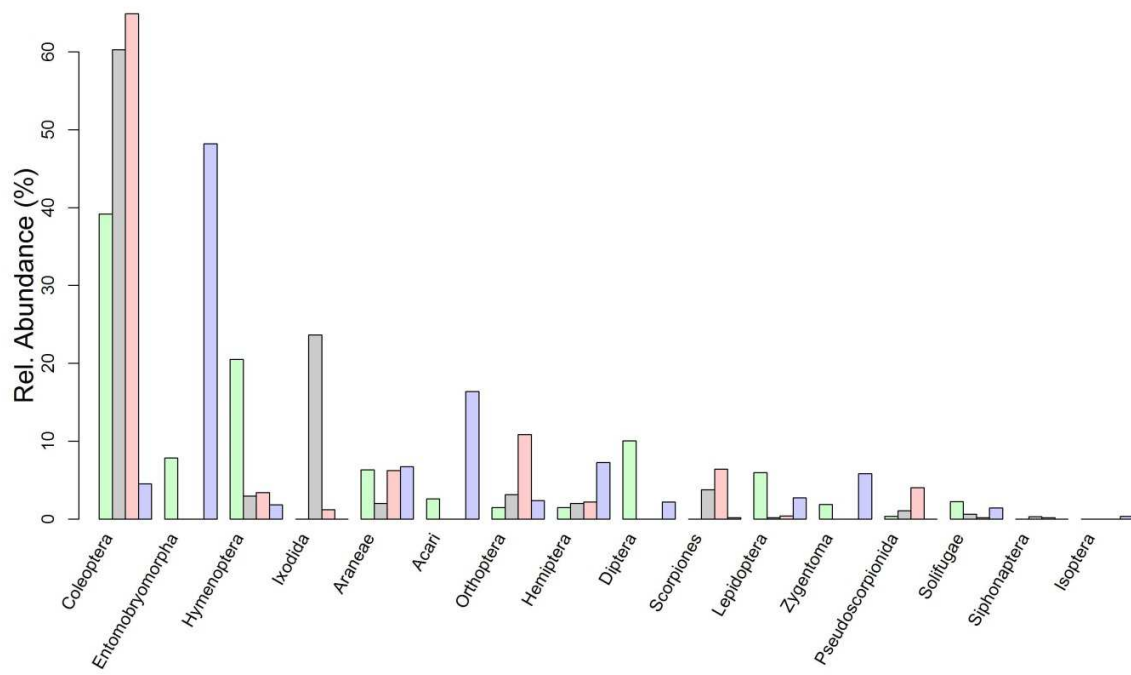
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853 Figure 2



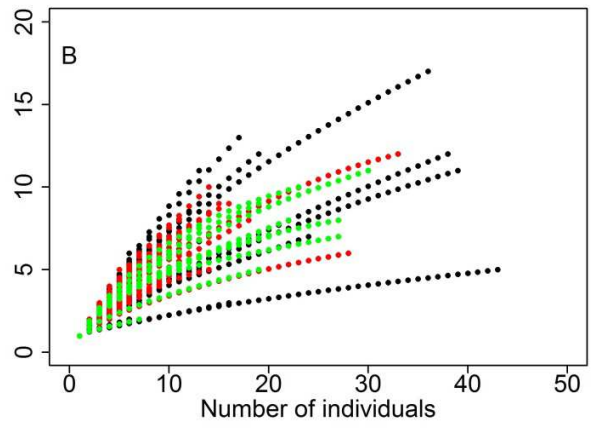
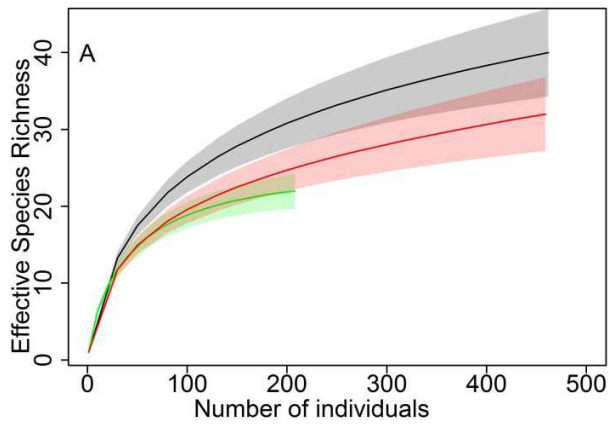
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855 Figure 3



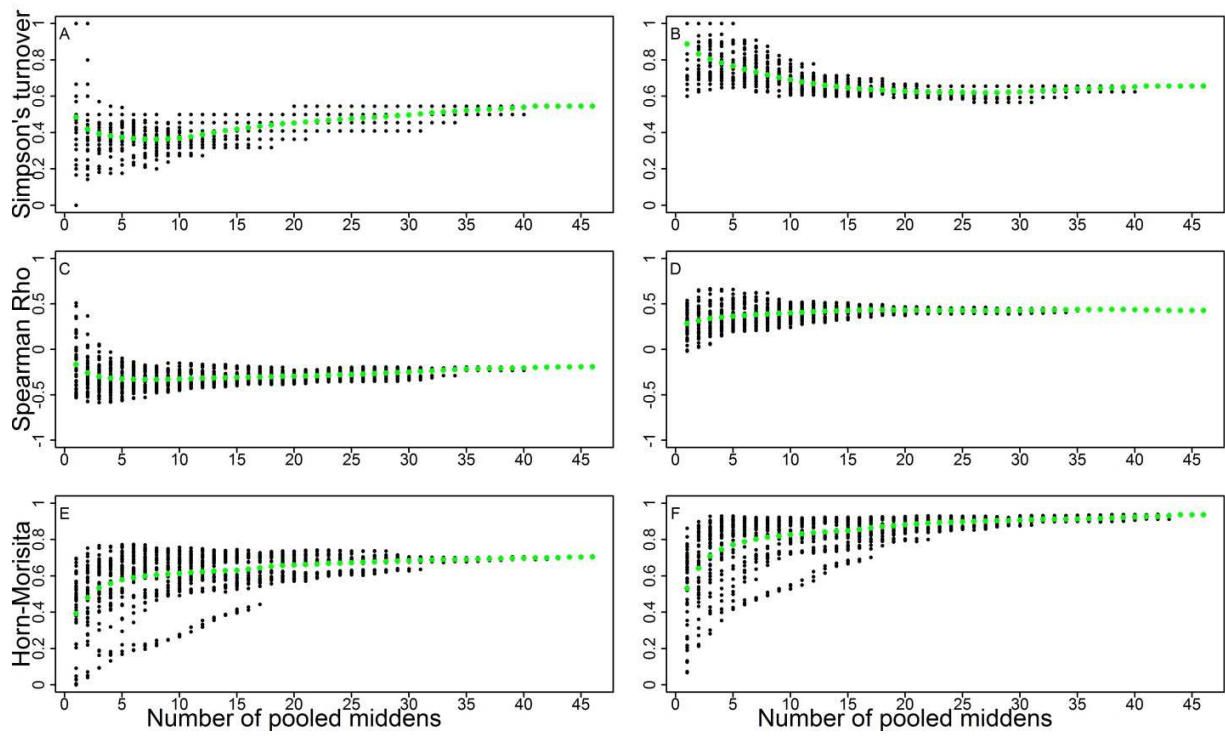
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857 Figure 4



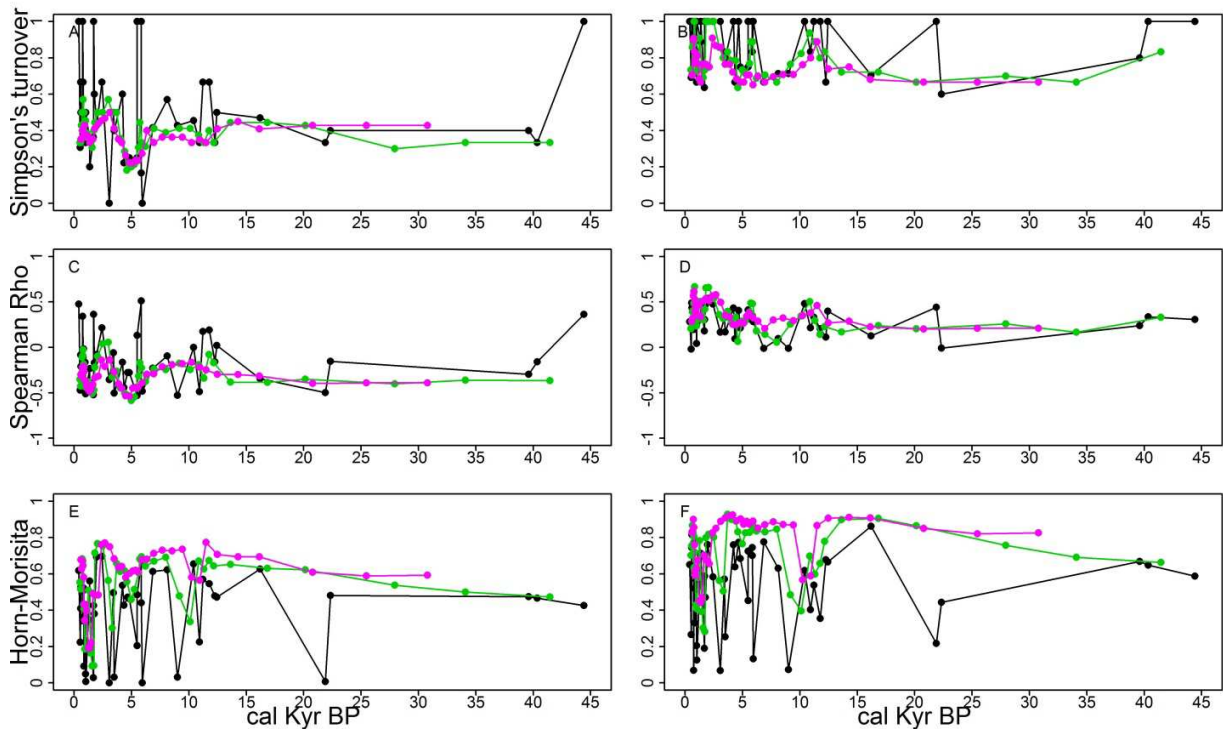
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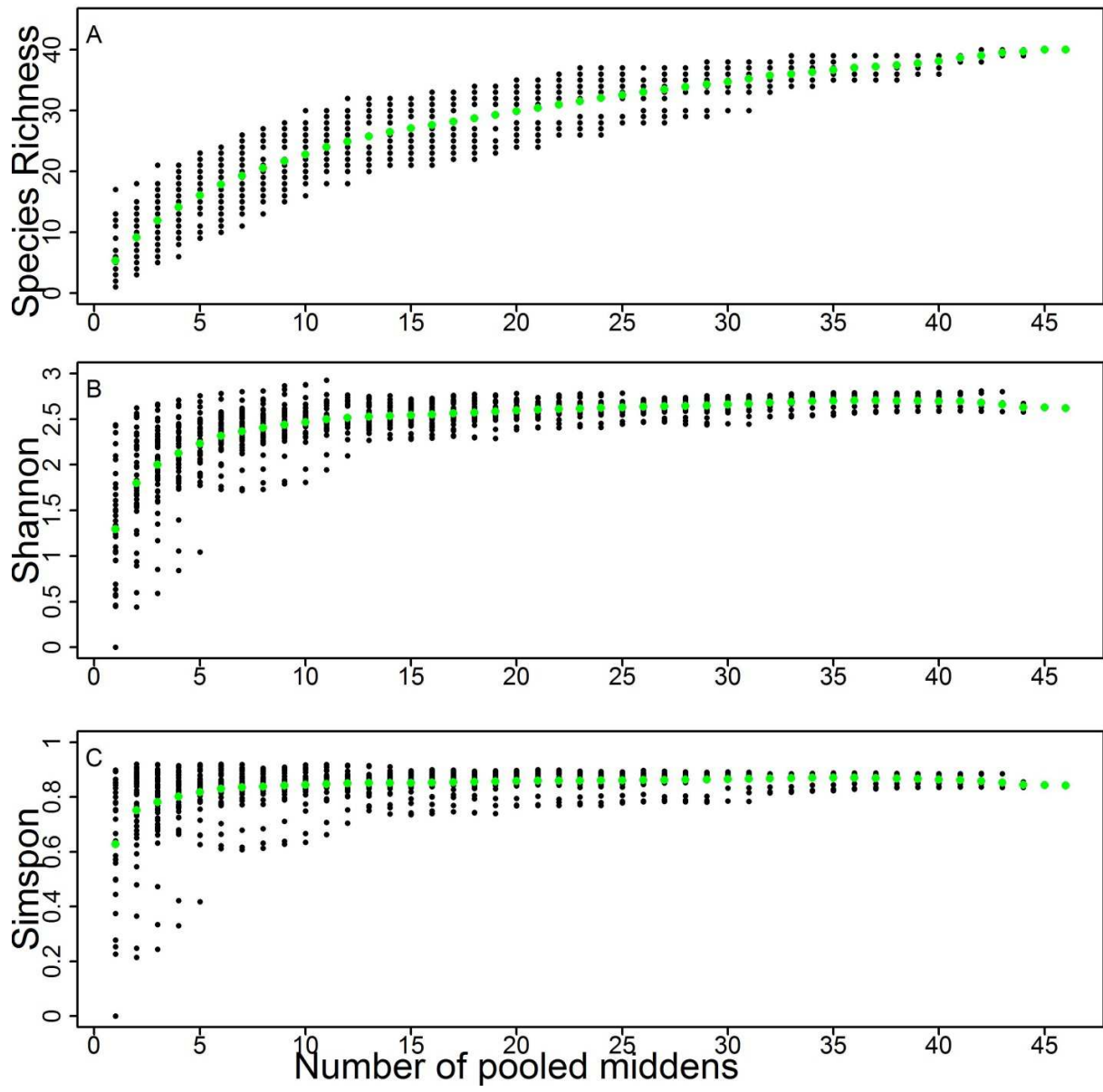
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861 Figure 6



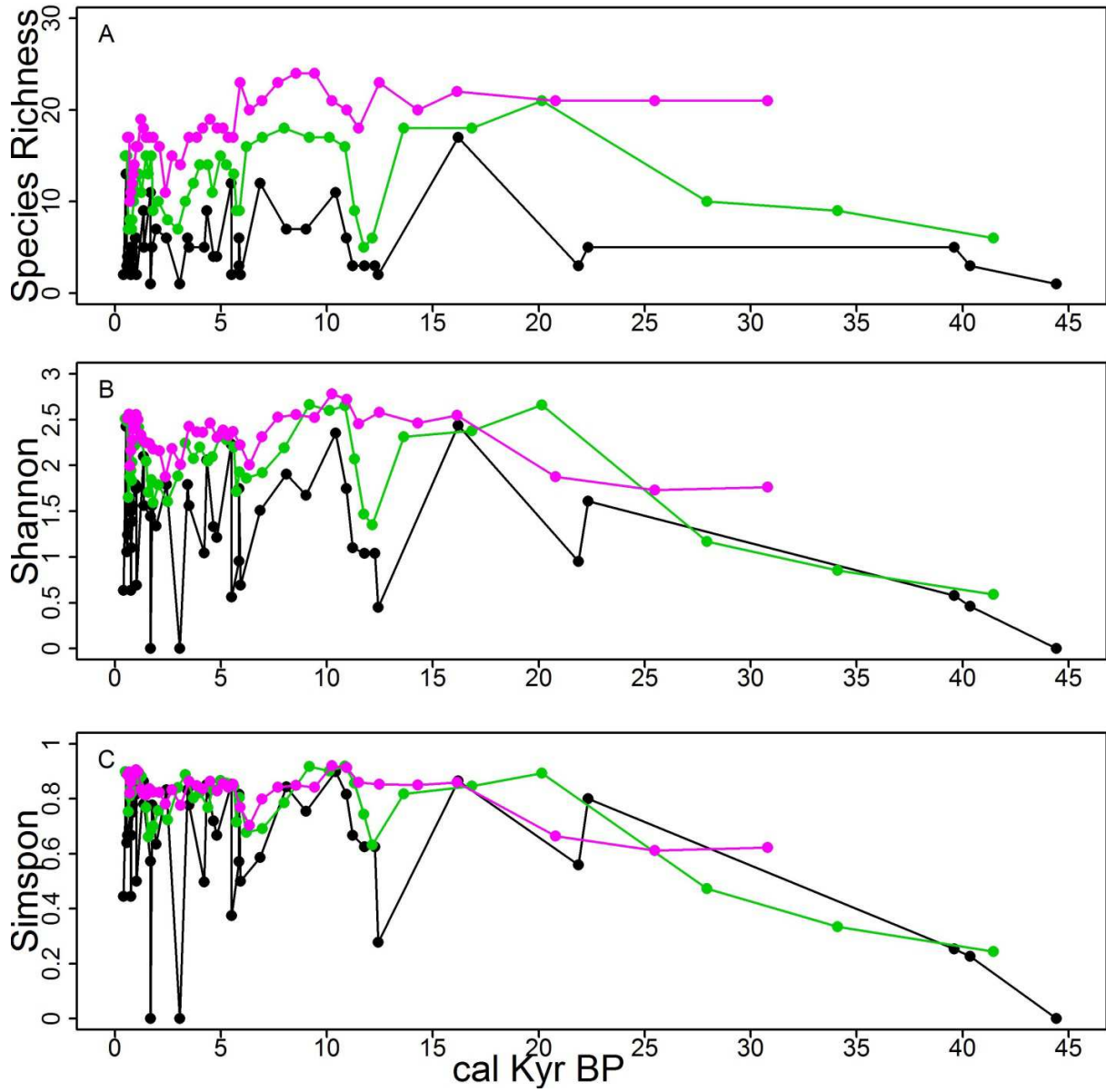
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863 Figure 7



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866 Figure 8



867

868 Figure 9