

An examination of the impact of Olson's Extinction on tetrapods from Texas

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It has been suggested that a transition between a pelycosaurian-grade synapsid dominated fauna of the Cisuralian (early Permian) and the therapsid dominated fauna of the Guadalupian (middle Permian), was accompanied by, and possibly driven by, a mass extinction dubbed Olson's Extinction. However, this interpretation of the record has recently been criticised as being a result of inappropriate time-binning strategies: calculating species richness within international stages or substages combines extinctions occurring throughout the late Kungurian stage into a single event. To address this criticism, I examine the best record available for the time of the extinction, the tetrapod-bearing formations of Texas, at a finer stratigraphic scale than those previously employed. Species richness is calculated using four different time-binning schemes: the traditional Land Vertebrate Faunachrons (LVFs); a re-definition of the LVFs using constrained cluster analysis; individual formations treated as time bins; and a stochastic approach assigning specimens to half-million-year bins. Diversity is calculated at the genus and species level, both with and without subsampling, and extinction rates are also inferred. Under all time-binning schemes, both at the genus and species level, a substantial drop in diversity occurs during the Redtankian LVF. Extinction rates are raised above background rates throughout this time, but the biggest peak occurs in the Choza Formation (uppermost Redtankian), coinciding with the disappearance from the fossil record of several of amphibian clades. This study, carried out at a finer stratigraphic scale than previous examinations, indicates that Olson's Extinction is not an artefact of the method used to bin data by time in previous analyses.

1 **An Examination of the Impact of Olson's Extinction on Tetrapods from Texas**

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24 Abstract

25 It has been suggested that a transition between a pelycosaurian-grade synapsid dominated fauna
26 of the Cisuralian (early Permian) and the therapsid dominated fauna of the Guadalupian (middle
27 Permian), was accompanied by, and possibly driven by, a mass extinction dubbed Olson's
28 Extinction. However, this interpretation of the record has recently been criticised as being a
29 result of inappropriate time-binning strategies: calculating species richness within international
30 stages or substages combines extinctions occurring throughout the late Kungurian stage into a
31 single event. To address this criticism, I examine the best record available for the time of the
32 extinction, the tetrapod-bearing formations of Texas, at a finer stratigraphic scale than those
33 previously employed. Species richness is calculated using four different time-binning schemes:
34 the traditional Land Vertebrate Faunachrons (LVFs); a re-definition of the LVFs using
35 constrained cluster analysis; individual formations treated as time bins; and a stochastic approach
36 assigning specimens to half-million-year bins. Diversity is calculated at the genus and species
37 level, both with and without subsampling, and extinction rates are also inferred. Under all time-
38 binning schemes, both at the genus and species level, a substantial drop in diversity occurs
39 during the Redtankian LVF. Extinction rates are raised above background rates throughout this
40 time, but the biggest peak occurs in the Choza Formation (uppermost Redtankian), coinciding
41 with the disappearance from the fossil record of several of amphibian clades. This study, carried
42 out at a finer stratigraphic scale than previous examinations, indicates that Olson's Extinction is
43 not an artefact of the method used to bin data by time in previous analyses.

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48 **Introduction**

49 A faunal turnover of tetrapods has long been recognised between the Cisuralian and
50 Guadalupian (early and middle Permian, respectively). The former is characterised by a diverse
51 array of amphibians, pelycosaurian-grade synapsids (particularly carnivorous sphenacodontids
52 and herbivorous edaphosaurids), and captorhinids, whereas the latter is dominated by therapsid
53 synapsids, with increased diversity of parareptiles and amphibian diversity substantially reduced
54 (Olson 1962, 1966; Kemp 2005; Sahney & Benton 2008; Ruta et al. 2011; Benton 2012; Benson
55 et al. 2013; Brocklehurst et al. 2013; 2017). These faunal changes were accompanied by
56 ecological shifts, including a transition towards more complex ecosystems with abundant large
57 tetrapods as primary consumers (Olson 1966). However, the nature and progress of the transition
58 is still strongly debated.

59 The possibility of a mass extinction accompanying this transition was first suggested by
60 Olson (1982), who noted a drop in the number of families across Cisuralian/Guadalupian
61 boundary. This drop was principally concentrated among amphibian families (amniote diversity
62 was shown to increase slightly). Sahney & Benton (2008) provided a more detailed examination
63 of diversity through the Permian, still at the family level but with temporal resolution at the stage
64 level. Decreases in both species richness, diversification rate and ecological diversity were
65 apparent through the Kungurian and Roadian (the last stage of the Cisuralian and the first of the
66 Guadalupian respectively). Sahney & Benton (2008) dubbed this mass extinction event “Olson’s
67 Extinction” and hypothesised that it might have been a causal factor in the faunal turnover
68 occurring at this time.

69 The hypothesis of Sahney & Benton has been criticised as being based on family-level
70 data that was not corrected for sampling heterogeneity (Benson & Upchurch 2013, Brocklehurst
71 et al. 2013). Nevertheless, subsequent studies both of tetrapods as a whole (Benton 2012, Benton
72 et al. 2013, Benson & Upchurch 2013, Brocklehurst et al. 2017) and subgroups within Tetrapoda
73 (Ruta & Benton 2008, Ruta et al. 2011, Brocklehurst et al. 2013, 2015), carried out at species
74 and genus levels and employing a variety of sampling correction methods, have identified
75 diversity decreases across the Kungurian/Roadian boundary.

76 Despite this, the theory of Olson's Extinction has been criticised in other ways. Benson &
77 Upchurch (2013) suggested that the mass extinction was an artefact of the geographically patchy
78 fossil record. The record from the Cisuralian is known almost entirely from palaeoequatorial
79 localities, particularly from North America and Europe, whereas that of the Guadalupian is
80 dominated by palaeotemperate localities from Russia and South Africa (Lucas 2004, Kemp
81 2006). Not only does this make it difficult to ascertain over what timescale the extinction took
82 place and to what extent the transition was a global event, but the apparent diversity drop might
83 simply represent a latitudinal diversity gradient (Benson & Upchurch 2013). In most modern
84 clades, diversity is higher in equatorial regions than temperate regions (Willig et al. 2003,
85 Hildebrand 2004), and so it was argued that the shift in sampling locality from more diverse to
86 less diverse latitudes might be the cause of the apparent decrease in species richness (Benson &
87 Upchurch 2013). Brocklehurst et al. (2017), however, argued against this point of view. It has
88 been noted that the latitudinal diversity gradient was not a constant feature through geological
89 time (Archibald et al. 2010, Rose et al. 2011, Yasuhara et al. 2012, Mannion et al. 2012, 2014),
90 and it was demonstrated that, in the few Permian time bins where tetrapod data was available

91 from both palaeoequatorial and palaeotemperate latitudes, the temperate latitudes exhibited
92 higher species richness after correcting for sampling (Brocklehurst et al. 2017).

93 Further criticism of Olson's Extinction was put forward by Lucas (2017a). Lucas argued
94 that the inference of a mass extinction across the Kungurian/Roadian at this time was an artefact
95 of two confounding factors. First, the majority of the studies cited used geological stage or
96 substages as their time bins, thus conflating extinctions occurring throughout the Kungurian into
97 a single event.

98 Second, Lucas (2017a) argued that incorrect ages were applied to numerous geological
99 formations, in particular the San Angelo and Chickasha formations of Texas and Oklahoma,
100 respectively. The ages of these formations have long been a point of contention. Early estimates
101 placed them in the latest Leonardian (late Kungurian) (Lucas & Heckert 2001, Lucas 2004), but
102 discovery of a specimen, from Chickasha, of the parareptile *Macroleter*, previously only known
103 from the Middle Permian of Russia, caused Reisz & Laurin (2001) to argue for an equivalency
104 between this formation and the Kazanian-aged (earliest Guadalupian) faunas of Russia. Lucas
105 (2002) rejected their arguments based on the ammonite fauna of the Blaine Formation, a marine
106 formation immediately overlying the San Angelo, which he claimed supported a Leonardian age.
107 Reisz & Laurin (2002) criticised the interpretation of Lucas, suggesting that a key taxon in the
108 arguments had a much longer range than suggested and highlighting previous studies of the
109 Blaine formation interpreting it as Guadalupian in age. Lozovsky (2003) also used ammonite
110 biostratigraphy to support a Roadian age for the Chickasha and San Angelo formations, and
111 these ages have been adopted in most subsequent studies (e.g. Sahney & Benton 2008, Benton
112 2012, Brocklehurst et al. 2013, 2017). However, Lucas (2017a) still supports a latest Kungurian
113 age for these two formations. He therefore suggested that an extinction across the

114 Kungurian/Roadian boundary cannot be assessed in a global framework, as there is no
115 stratigraphic overlap between the North American and Russian formations.

116 It is not the purpose of this paper to argue against these two criticisms of Lucas (2017a).

117 Indeed, I am fully prepared to agree that time-binning strategies employing the geological stages
118 or substages, while often necessary for global analyses where the correlations between the
119 regional biostratigraphic schemes are inexact, have the potential to produce spurious results.

120 Such binning strategies produce time-averaged diversity estimates for a time bin that can differ
121 from the true standing diversity at any one time in the bin (Raup 1972, Lucas 1994, Foote 1994,

122 Miller & Foote 1996, Alroy 2010a, Gibert & Escarguel 2017). Instead it is my intention to

123 approach the question of Olson's extinction from a different angle, one that addresses the issues

124 of binning strategy while bypassing the disagreements surrounding the ages of the San Angelo

125 and Chickasha formations. In fact, the framework of this analysis is one suggested by Lucas

126 himself (Lucas 2017a): when the fossil record is geographically patchy with uncertain global

127 correlations, it is better to study mass extinctions using the "best sections" method, focussing one

128 or a few well sampled, stratigraphically dense fossiliferous sections to examine the progress of

129 the extinction. While only providing a local perspective on the event under study, this method

130 does allow more detailed analysis than is provided in global studies with coarse temporal

131 resolution.

132 The "best section" of tetrapods in the Cisuralian is doubtless that of Texas, which

133 represents a reasonably continuous sequence from the late Carboniferous until the end of the

134 Cisuralian (Romer 1928, 1935, Hook 1989, Lucas 2006, 2017a). A detailed examination of the

135 Cisuralian tetrapod record from Texas, covering the stratigraphic sequence from the Pueblo

136 Formation until the San Angelo Formation, allows much higher resolution than previous studies.

137 Moreover, it renders the debate regarding the age of the San Angelo formation moot. The issue is
138 no longer whether there is a Kungurian/Roadian boundary event, but instead whether an
139 extinction event is identified between the Redtankian and Littlecrotonian land vertebrate
140 faunachrons (biostratigraphic time bins based on the tetrapod fossil record, the former correlating
141 in Texas with the Clear Fork Group, the latter with the San Angelo Formation). The presence of
142 an extinction event between these two faunachrons is assessed at both genus and species levels,
143 with four different time-binning systems and results shown both with and without sampling
144 correction.

145

146 **Materials and Methods**

147 *Data*

148 Data on the number of specimens of tetrapod species in each time bin was assembled
149 from a variety of sources. The primary literature and the paleobiology database, downloaded
150 from the fossilworks website (<http://fossilworks.org>) on October 2017, were the principal
151 sources, but were supplemented by observation of specimens in museum collections and also by
152 data sent from some museums (Museum of Comparative Zoology, Harvard; Field Museum of
153 Natural History, Chicago; American Museum of Natural History, New York; Yale Peabody
154 Museum, New Haven; University of California Museum of Palaeontology, Berkeley; Sam Noble
155 Oklahoma Museum of Natural History, Norman). Specimens of uncertain provenance were not
156 included. The data was examined at both species and genus level. While it has often been the
157 preference to examine data at the species-level (Sepkoski [1984] argued that as the species are
158 the real “units” of evolution, it is at that level that evolution should be studied), Lucas (2017a)
159 suggested that the genus is preferable for early Permian tetrapods to avoid the influence of large

160 numbers of singletons (single-specimen taxa), which under poor sampling produce a great deal
161 of “noise” in the evolutionary signal (Alroy 1998, Foote 2000). The data does not include a large
162 number of species represented by only a single specimen (18 out of 102), but more than half (65)
163 the taxa represent single-occurrences (present in only one formation). The final datasets are
164 provided in Data S1 and S2.

165

166 *Time bins*

167 Four methods were used to define time bins, each successively dividing the early Permian
168 into smaller portions of time. The first set of bins used are the land vertebrate faunachrons
169 (LVFs): the biostratigraphic bins based on the first and last appearances of key tetrapod genera
170 (Lucas 1998). As these are biostratigraphic bins, their boundaries should correspond to major
171 periods of turnover among tetrapods, and so the diversity estimates within each faunachron
172 should provide a better approximation of the standing diversity at any point in time than using
173 the international stages. In fact, since the boundaries of the Cisuralian LVFs are primarily based
174 on the section under study, they are more likely to coincide with events relevant to the taxa under
175 study.

176 The second binning scheme used represents a redefinition of the land vertebrate
177 faunochrons using a clustering approach. CONISS is a constrained clustering analysis, which
178 groups stratigraphic sections into hierarchical clusters based on the taxonomic distances between,
179 while maintaining the order of the stratigraphic sequence (Grimm 1987). The taxonomic
180 distances between the formations were calculated using Alroy (2015a)’s modification of the
181 Forbes metric, applying the RAC correction suggested by Brocklehurst et al. (2018a) to account
182 for differences in the evenness of the relative abundance distributions, which under incomplete

183 sampling can bias the distances observed. The functions to carry out the RAC method are
184 available on Dryad (Brocklehurst et al 2018b) on Dryad. The CONISS analysis was carried out
185 in R version 3.3.2 (R core team 2016), using functions from the package rioja (Juggins 2009).
186 The boundaries of the original LVFs were then shifted to ensure that formations which were
187 clustered together were grouped in the same bin.

188 The third binning scheme simply treats each formation as a time bin. The
189 lithostratigraphy was devised by Plummer & Moore (1921) and dated based on the marine strata
190 which intercalate with the terrestrial strata. This provides a finer resolution than the land
191 vertebrate faunachrons (11 bins rather than 5) and later refinements of the lithostratigraphy (e.g.
192 Hentz 1988).

193 The fourth and final binning scheme uses a stochastic approach, in an attempt to address
194 the time averaging that occurs when coarse time bins covering several million years are
195 employed. The ages of the top and bottom of each formation were used as maximum and
196 minimum bounds on the ages of each specimen known from within that formation. The period of
197 time under study was split into half-million-year time bins, and each specimen was assigned at
198 random to one of the bins between its maximum and minimum age brackets. 100 such datasets
199 were generated, and the analyses of diversity and extinction rate were applied to all 100. Such
200 stochastic methods have been shown to provide more accurate estimates of standing diversity
201 than binning approaches, even when the origination and extinction are biased towards coinciding
202 with the boundaries of bins (Gibert & Escarguel 2017).

203 For all four binning schemes, the absolute ages were derived from Lucas (2017a, b),
204 using his correlations of the formations to the international stages. Thus, the Littlecrotonian LVF
205 and the San Angelo formation are deemed to be latest Kungurian rather than Roadian. For most

206 of the binning schemes, this does not make a difference; when analysing only the Texas “best
207 section”, the question of whether an extinction event is identified between the Redtankian and
208 Littlecrotonian is more relevant than the precise timing of the boundary. Where the absolute ages
209 do make a difference is in calculating extinction rates using the stochastic binning scheme. By
210 compressing the Redtankian and Littlecrotonian into a smaller period of time, the density of the
211 specimens sampled is increased. This will lower extinction rates estimated under the gap-fillers
212 method (see below): counts of two-timers will increase and counts of part-timers and gap-fillers
213 will decrease (terminology from Alroy 2014). The use of a Kungurian age for the Littlecrotonian
214 is therefore more conservative, biasing against the inference of a mass extinction.

215

216 *Diversity and Rate Estimates*

217 For each time bin in each binning scheme, diversity (species richness) estimates were
218 calculated using two methods. The first is a taxic diversity estimate, a simple count of the
219 number of species observed in each time bin without sampling correction. The second employs
220 shareholder quorum subsampling (SQS; Alroy 2010), which standardises the coverage (the
221 proportion of the rank abundance distribution sampled) in each time bin, and has been shown by
222 both simulation studies and empirical data to be a robust method of correcting for preservation
223 and sampling heterogeneity (Alroy 2010; Chao and Jost 2012; Close et al. 2018). Coverage is
224 measured using Good’s U (the proportion of singletons relative to the total sample size).
225 Diversity was estimates at four levels of coverage: 0.6-0.9 at intervals of 0.1 (a quorum of 0.6
226 allowed diversity to be calculated in all time bins in all binning schemes). SQS diversity
227 estimates were calculated in R using version 3.3 of the function available on the website of John
228 Alroy (<http://bio.mq.edu.au/~jalroy/SQS.html>). The stochastic binning method allows the

229 implementation of the more precise and accurate methods of calculating extinction rates using
230 the gap fillers method (Alroy 2014). Since this method is based on estimating sampling from the
231 patterns of occurrences in a moving “window” covering four time bins, it is impractical to apply
232 it to the short time series produced by the three other binning strategies. The gap-fillers method
233 was implemented, applying the “two for one” correction (Alroy 2015b) to increase precision,
234 using custom functions written in R. As suggested by Alroy (2014), sampling heterogeneity was
235 accounted for by classical rarefaction (standardising the sample size by number of occurrences)
236 rather than by standardising coverage. 10000 subsampling iterations were carried out, each
237 drawing five occurrences per time bin. Origination rates were calculated using the same
238 equations; the methods used to calculate sampling apply equally well in reverse (Alroy 2014).
239 This was carried out using custom code, provided in Data S3.

240

241 **Results**

242 *Redefined Land Vertebrate Faunachrons*

243 When clustering the formations using CONISS, a number of changes are made to the
244 boundaries of the LVFs (Fig. 1). The Littlecrotonian and Redtankian remain as they were defined
245 previously. The lower boundary of the Mitchellcreekian is shifted downwards to include the
246 Belle Plains Formation, found to cluster more closely with the Clyde than the Admiral
247 Formation. The Admiral Formation itself clusters with the Putnam Formation, and so the
248 Seymourian LVF is redefined to include these two. Thus, the Coyotean LVF contains only the
249 Pueblo and Moran formations.

250 It is worth clarifying here that this analysis is not intended to cast doubt on the LVFs as
251 originally defined; rather they represent a biostratigraphic scheme more specific to the Texas

252 section. The changes to the Coyotean LVF are most likely due to this being primarily defined by
253 taxa from the well sampled early Cisuralian localities in New Mexico (Lucas 1998, 2017b),
254 which are not included in this study.

255

256 *Diversity estimates*

257 Raw, uncorrected species and genus-level diversity estimates indicate a substantial fall in
258 diversity between the Redtankian and Littlecrotonian, based on all four time-binning schemes
259 (Fig. 2). The finer resolution time bins (formation-level and half-million-year time bins) indicate
260 that the Arroyo Formation represents the peak richness, and number of genera and species
261 declined throughout the Redtankian.

262 When the data are binned by the Land Vertebrate Faunachrons (whether original or
263 redefined), subsampling by SQS supports the Littlecrotonian as the time of lowest diversity
264 (Figs. 3-4). The status of the Redtankian as a diversity peak is less clear; when the original LVFs
265 are used, the Mitchellcreekian is found to contain a similar richness to the Redtankian (Fig. 3).
266 However, the redefined LVFs indicate a substantial increase between these two bins (Fig. 4).

267 The higher-resolution-binning schemes both indicate the drop in subsampled diversity
268 occurs throughout the Redtankian (Figs. 5-6). The Arroyo formation produced the highest
269 species and genus richness of this faunachron, and the diversity decreases in the Vale Formation
270 and reaches a trough in the Choza formation. When subsampling is applied, species and genus
271 richness is found to increase slightly between the Choza and San Angelo formations.

272

273 *Extinction and Origination rates*

274 Three peaks in extinction rate are identified at the both at the genus and species level: at
275 the top of the Belle Plains, Arroyo and Choza formations (the latter being the largest) (Fig. 7).
276 During the time covered by the Vale Formation, extinction rates fall, but remain above
277 background levels. The principal difference between the species and genus curves is the relative
278 height of the Belle Plains extinction peak; at the species level it is higher than the Arroyo peak.

279 Peaks in origination rates at the species level are observed at the bottom of the Arroyo
280 and the San Angelo formations (Fig. 8). The former of these peaks is not observed at the genus
281 level, although the latter is still prominent.

282

283 **Discussion**

284 Having argued against an extinction of tetrapods across the Kungurian/Roadian boundary
285 (due to the inappropriate time-binning strategies used in other diversity studies and the
286 disagreement over the age of the San Angelo and Chickasha formations), Lucas (2017a) briefly
287 examined the possibility of a mass extinction between the Redtankian and Littlecrotonian LVFs
288 in the “best section” of Texas. Although he noted a peak in extinction rates during the
289 Redtankian and a decrease in genus richness during the Littlecrotonian, he was dubious over the
290 reality of a mass extinction. First, he suggested that families previously suggested to be major
291 components of the extinction, Edaphosauridae and Ophiacodontidae (Brocklehurst et al. 2013),
292 had already disappeared prior to the end of the Redtankian. Lucas also examined diversity
293 changes through the Redtankian using the specimen lists compiled by Olson (1958, 1989) for the
294 Arroyo, Vale and Choza formations, demonstrating that diversity was decreasing throughout the
295 Redtankian, rather than there being a single decline at the end of the LVF.

296 All diversity estimates presented here support a decrease in species and genus richness
297 between the Redtankian and Littlecrotonian. The diversity estimates at finer stratigraphic scales
298 support the observations of Lucas (2017a): the decline occurs throughout the Redtankian from a
299 peak in the Arroyo formation to a trough in the Choza formation, followed by a slight, but not
300 substantial, recovery in the San Angelo formation. The same inferences may be made from
301 origination and extinction rates. While origination rates peak at the bottom of the Arroyo
302 formation (explaining the peak in species richness at this time), extinction rates are noticeably
303 higher in the Arroyo formation than the background rates experienced for most of the early
304 Permian. Only once prior to this are extinction rates reliably inferred to reach similar levels: at
305 the top of the Belle Plains Formation. The extinction rates experienced in the Choza Formation
306 are considerably higher than any other time in the early Permian, and origination rates do not rise
307 until later, at the bottom of the San Angelo formation (coinciding with the post-extinction
308 recovery).

309 Does this period of elevated extinction rates and declining diversity constitute a mass
310 extinction? Lucas (2017a) argued not, since it was a prolonged decline throughout the
311 Redtankian LVF. Unfortunately, there is no set definition of a “mass extinction”, and while the
312 general consensus does seem to be elevated extinction over a short period of time, there is no
313 indication of how short a time that should be. Discussion of mass extinctions in the scientific
314 literature have included events where extinction rates were substantially higher than background
315 rates over periods of millions of years. For example, discussion of the late Devonian mass
316 extinction (one of the “big five” mass extinctions) has in the past suggested a duration of up to
317 three million years (Racki 2005); the end Triassic extinction (another of the big five) is thought
318 to represent periods of elevated extinction rate bracketing the entire Rhaetian stage (Ward et al.

319 2001, 2004), a duration of almost seven million years based on the most recent timescale of the
320 International Commission on Stratigraphy. Moreover, if one is to follow the stratigraphic ages
321 espoused by Lucas (1998, 2002, 2004, 2006, 2017a,b), the Redtankian would be compressed into
322 a period covering less than four million years. During these four million years, extinction rates
323 remain consistently higher than background levels. The Arroyo Formation records a substantial
324 increase in extinction, and the Choza Formation records extinction rates that have more-than
325 doubled those of the Arroyo, higher than in any other formation. The number of tetrapod species
326 observed in the Choza Formation is less than a quarter of those observed in the Arroyo
327 Formation, and subsampling does not diminish the extent of the diversity loss.

328 It is worth noting at this point that mass extinctions appearing in the fossil record as
329 prolonged declines is an issue that has a long history of discussion in the published literature,
330 going back to the work of Signor & Lipps (1982). The fact that the last appearance of a taxon in
331 the fossil record is not its last true appearance, combined with differential preservation
332 probabilities of different taxa, causes a set of species, which in reality died out nearly
333 simultaneously, to appear to have died out over a longer period of time (Butterfield 1995), a
334 phenomenon dubbed the Signor-Lipps effect. Lucas (2017a) acknowledged the Signor-Lipps
335 effect in his introduction but did not mention it in his discussion of specific extinction events. He
336 also employed no sampling correction when examining diversity and extinction rate, instead
337 arguing that “whatever biases exist may be roughly equivalent in the Permian tetrapod record
338 across times and localities” (Lucas 2017a, p. 35). This is simply not true: there is a wealth of
339 literature detailing analyses of the quality of the fossil record of Paleozoic tetrapods, all
340 suggesting the opposite and emphasising the need for sampling correction (Benson & Upchurch
341 2013; Brocklehurst et al. 2013, 2014, 2017; Verriere et al. 2016).

342 Another argument put forward by Lucas (2017a) to show that Olson's Extinction does
343 not qualify as a genuine mass extinction is that many of the clades previously deemed to have
344 died out at this time actually disappeared before the end of the Redtankian, and the number of
345 actual casualties of the event, at the family level, was very restricted. Brocklehurst et al. (2013)
346 previously noted Edaphosauridae and Ophiacodontidae as "casualties", but Lucas (2017a)
347 countered that the former's last appearance is from the Arroyo formation rather than the end of
348 the Redtankian LVF, and that the latter is not known from beyond the Mitchellcreekian LVF. In
349 the case of the Ophiacodontidae, this is actually not the case, and the family survived into the
350 Redtankian. Lucas (2017a) based his assertion on the last record of *Ophiacodon*, and the
351 abundant record of *Varanosaurus*, represented in the Arroyo Formation by the species *V.*
352 *acutirostris* (Broili 1904, Case 1907, 1910, Romer & Price 1940) and *V. witchitaensis* (NB Pers.
353 Obs), was discounted as representing a taxon of uncertain assignment. However, almost three
354 decades of study, both anatomical and cladistic, support the ophiacodontid affinity of
355 *Varanosaurus* (Sumida 1989, Berman et al. 1995, Benson 2012, Brocklehurst et al. 2016), and I
356 see no reason not to count it as the youngest record of Ophiacodontidae. Regarding
357 Edaphosauridae, only one species of *Edaphosaurus* is known from the Arroyo formation (*E.*
358 *pogonias*), but it still represents one of the most abundant herbivores in this fauna (Data S1).
359 Neural spine material of *Edaphosaurus* is also known from the Hennessey Formation (Daly
360 1973), a Redtankian aged formation in Oklahoma. It is clear, therefore, that both
361 Ophiacodontidae and Edaphosauridae survived into the Redtankian. While they may not have
362 survived beyond the lowest of the Redtankian formations, this does not remove them from the
363 Olson's Extinction casualty list. As already discussed, extinction rates were raised considerably

364 above background levels throughout the Redtankian, and extinctions of the taxa of the Arroyo
365 formation should be included in event.

366 Even if we are to limit our discussion to clades which went extinct at the end of the
367 Choza Formation, there are still multiple clades above the genus level which may be included in
368 the list of casualties of Olson's extinction, mostly amphibians. Probably the most prominent are
369 the Eryopidae, since they represent one of the few cases where we have data on their
370 disappearance from both palaeoequatorial (USA) and palaeotemperate localities (Brocklehurst et
371 al. 2017). Eryopids represent among the most abundant of the large amphibians throughout the
372 Cisuralian, and *Eryops* itself survives until the Choza Formation (Data S1). Crucially, two
373 eryopid species are known from the latest Kungurian of Russia: *Clamorosaurus borealis* and *C.*
374 *nocturnus* from the Inta formation (Gubin 1983). Eryopids are not known beyond the Kungurian
375 in either the palaeoequatorial or palaeotemperate latitudes beyond this time (Brocklehurst et al.
376 2017). The Trimerorhachidae and Lysorophia are two more clades highly abundant throughout
377 the Cisuralian, but which do not survive beyond the Choza formation (Data S1). Both are also
378 known from the Redtankian aged Hennessey formation in Oklahoma, but not from the
379 Littlecrotonian Chickasha formation (Brocklehurst et al. 2017). The Choza Formation represents
380 the greatest peak in extinction rate in the entire Cisuralian in this particular section, both at the
381 genus and species level, with extinction rates more than double the next highest peak. Therefore,
382 even if one discounts the losses occurring earlier in the Redtankian, it is difficult to deny the
383 presence of a severe extinction event at the Redtankian/Littlecrotonian boundary.

384 There has not been much work on the environmental context surrounding this event, but
385 the extended period of extinction has been suggested to coincide with substantial climatic
386 changes recorded in the Texas sequence. The sediments of the Vale formation record a transition

387 from an environment dominated by large perennial streams to one of braided channels, with
388 indications that flow was interrupted by substantial periods of drying (Olson 1958). The Choza
389 formation indicates a trend towards ever increasing aridity, with the uppermost deposits formed
390 almost entirely from anhydrites (Olson 1958). More work needs to be done on this crucial time
391 period, and until further research on environmental changes at this time is carried out these
392 questions cannot be answered with great certainty.

393

394 **Conclusions**

395 No matter what time-binning scheme is employed, no matter whether the data is
396 examined at the species or genus level, and no matter whether the data is corrected for sampling
397 or not, a substantial mass extinction event is observed in tetrapods during the Redtankian Land
398 Vertebrate Fanuachron. Throughout the Redtankian, extinction rates were raised substantially
399 above background levels, rising to a peak in the uppermost Choza Formation. Tetrapod diversity
400 declines throughout this period, and by the end of the Redtankian, species richness is less than a
401 quarter of that observed at the start.

402

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411

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579

580 **Figure Captions**

581 Fig. 1: The time bins used in the diversity analysis

582 Legend: A) The tetrapod bearing formations in Texas; B) the Land Vertebrate Faunachrons
583 (LVFs) redefined by CONISS; C) the original LVFs. The cluster dendrogram indicates
584 the grouping of the formations by CONISS.

585

586 Fig. 2: Taxic Diversity Estimates

587 Legend: Diversity estimates without correcting for sampling, using four different methods of
588 time-binning the data. A) Species level diversity estimate; B) Genus level diversity
589 estimate.

590

591 Fig 3: Subsampled diversity estimates (Original Land Vertebrate Faunachrons)

592 Legend: Numbers of species (A) and genera (B) in each land vertebrate faunachron (original
593 definitions), corrected for sampling heterogeneity using shareholder quorum
594 subsampling. Legend indicates quorum level.

595

596 Fig 4: Subsampled diversity estimates (redefined Land Vertebrate Faunachrons)

597 Legend: Numbers of species (A) and genera (B) in each land vertebrate faunachron (definitions
598 based on CONISS), corrected for sampling heterogeneity using shareholder quorum
599 subsampling. Legend indicates quorum level.

600

601 Fig 5: Subsampled diversity estimates (Formations)

602 Legend: Numbers of species (A) and genera (B) in each formation, corrected for sampling
603 heterogeneity using shareholder quorum subsampling. Legend indicates quorum level.

604

605 Fig 6: Subsampled diversity estimates (half-million-year time bins)

606 Legend: Means of the numbers of species (A) and genera (B) found in each half-million-year
607 time bin in each of the 100 stochastic distributions of specimens, corrected for sampling
608 heterogeneity using shareholder quorum subsampling. Legend indicates quorum level.

609

610 Fig 7: Extinction Rates

611 Legend: Median (thick black lines) of the extinction rates calculated for each half-million-year
612 time bin in each of the 100 stochastic distributions of specimens at the genus (A) and
613 species (B) levels. Dashed lines indicate standard error around the median.

614

615 Fig 8: Origination Rates

616 Legend: Median (thick black lines) of the origination rates calculated for each half-million-year
617 time bin in each of the 100 stochastic distributions of specimens at the genus (A) and
618 species (B) levels. Dashed lines indicate standard error around the median.

619

620

621

Figure 1

The time bins used in the diversity analysis

A) The cluster dendrogram indicating the grouping of the formations by CONISS; B) The tetrapod bearing formations in Texas; C) the Land Vertebrate Faunachrons (LVFs) redefined by CONISS; D) the original LVFs.

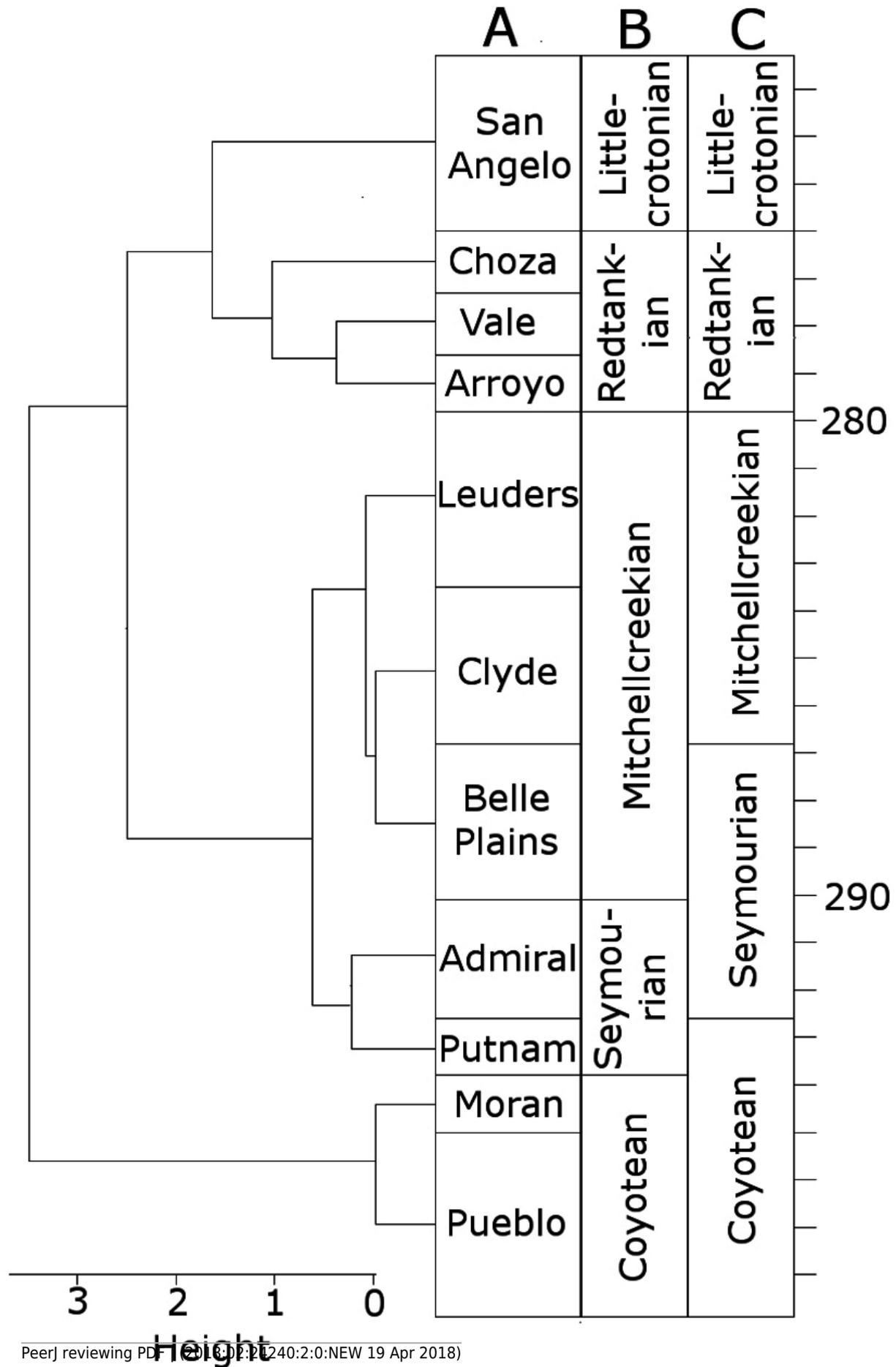


Figure 2

Taxic diversity estimates

Diversity estimates without correcting for sampling, using four different methods of time-binning the data. A) Species level diversity estimate; B) Genus level diversity estimate.

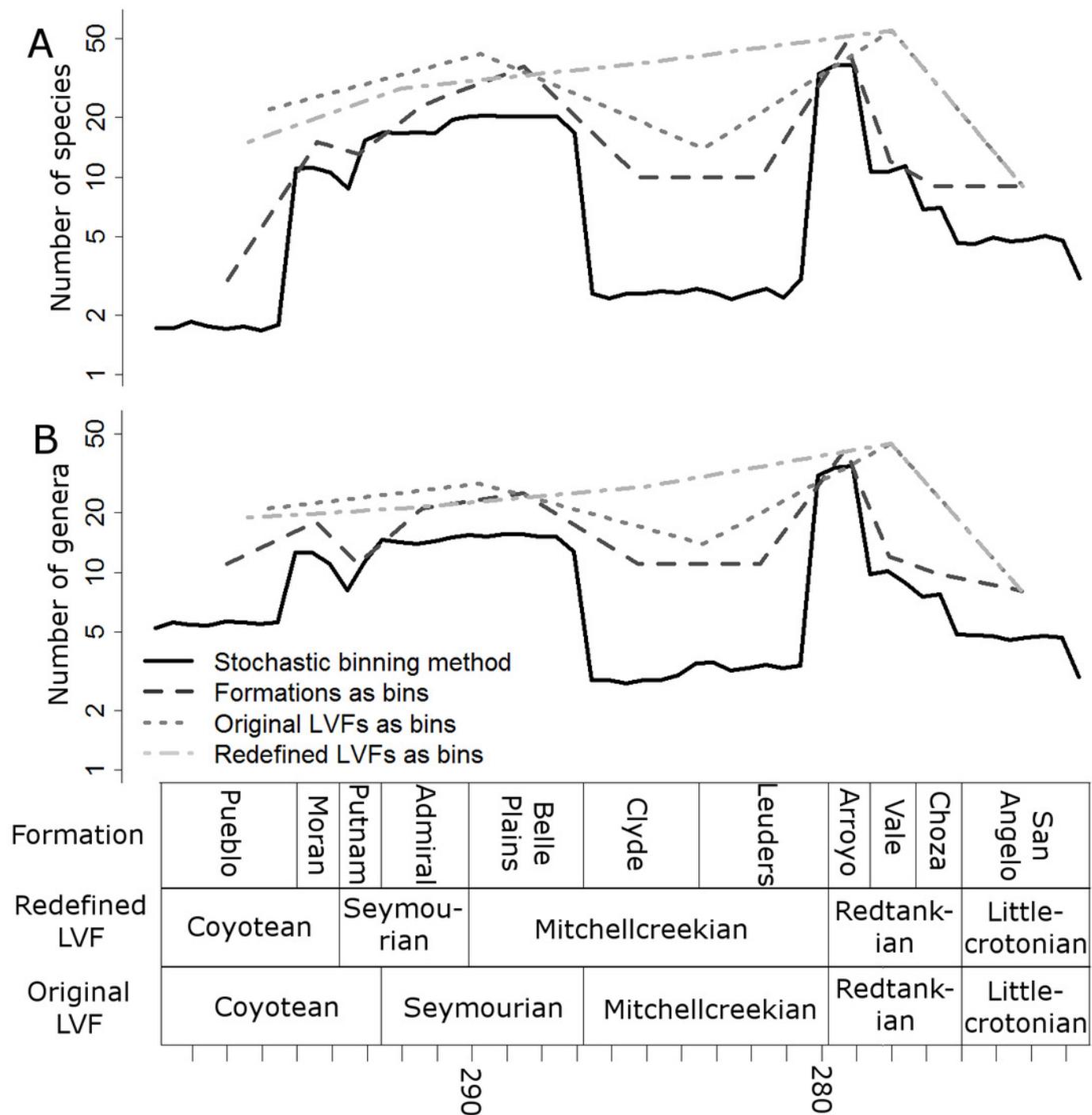


Figure 3

Subsampled diversity estimates (Original Land Vertebrate Faunachrons)

Numbers of species (A) and genera (B) in each land vertebrate faunachron (original definitions), corrected for sampling heterogeneity using shareholder quorum subsampling. Legend indicates quorum level.

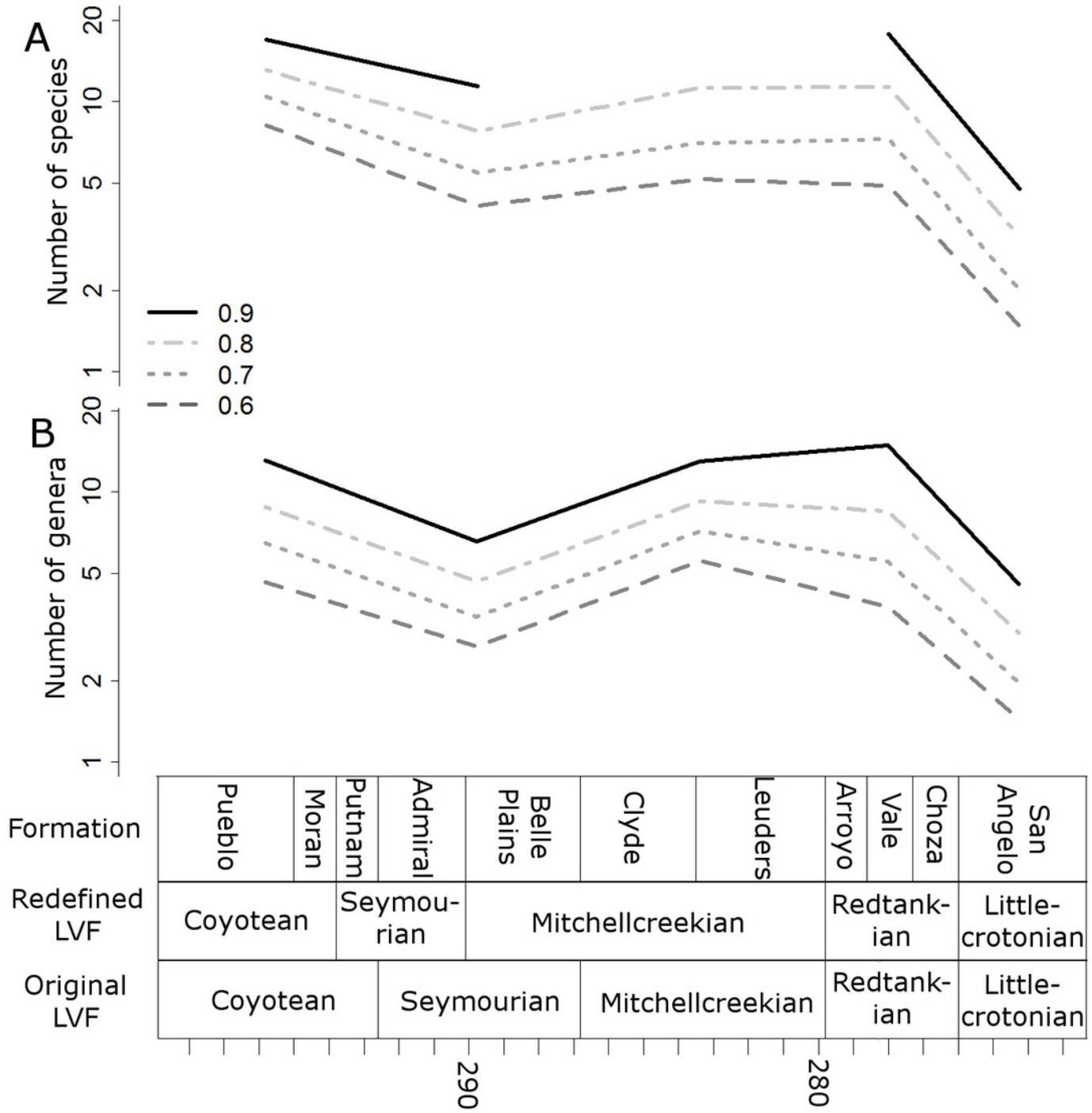


Figure 4

Subsampled diversity estimates (redefined Land Vertebrate Faunachrons)

Numbers of species (A) and genera (B) in each land vertebrate faunachron (definitions based on CONISS), corrected for sampling heterogeneity using shareholder quorum subsampling.

Legend indicates quorum level.

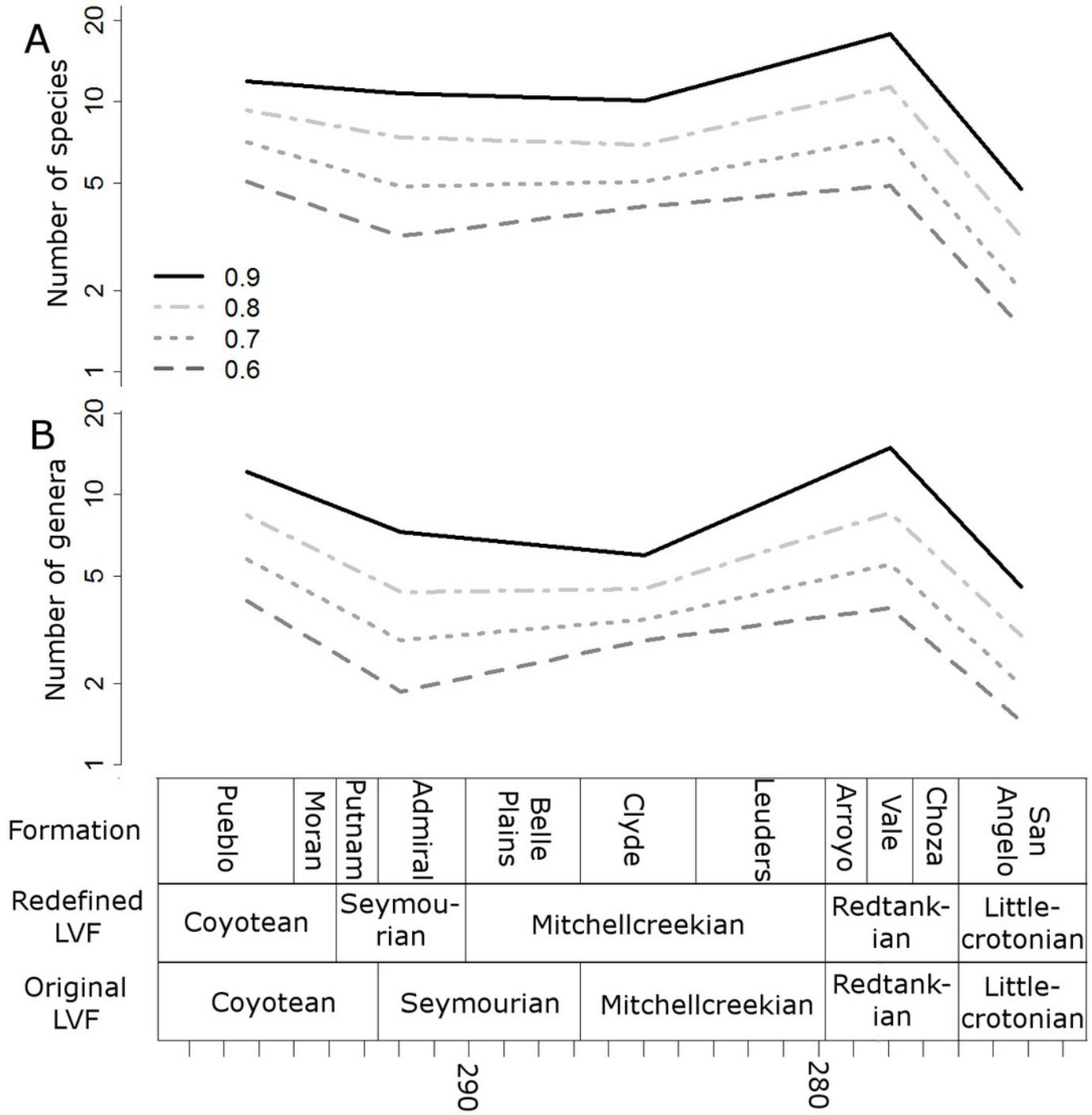


Figure 5

Subsampled diversity estimates (formations)

Numbers of species (A) and genera (B) in each formation, corrected for sampling heterogeneity using shareholder quorum subsampling. Legend indicates quorum level.

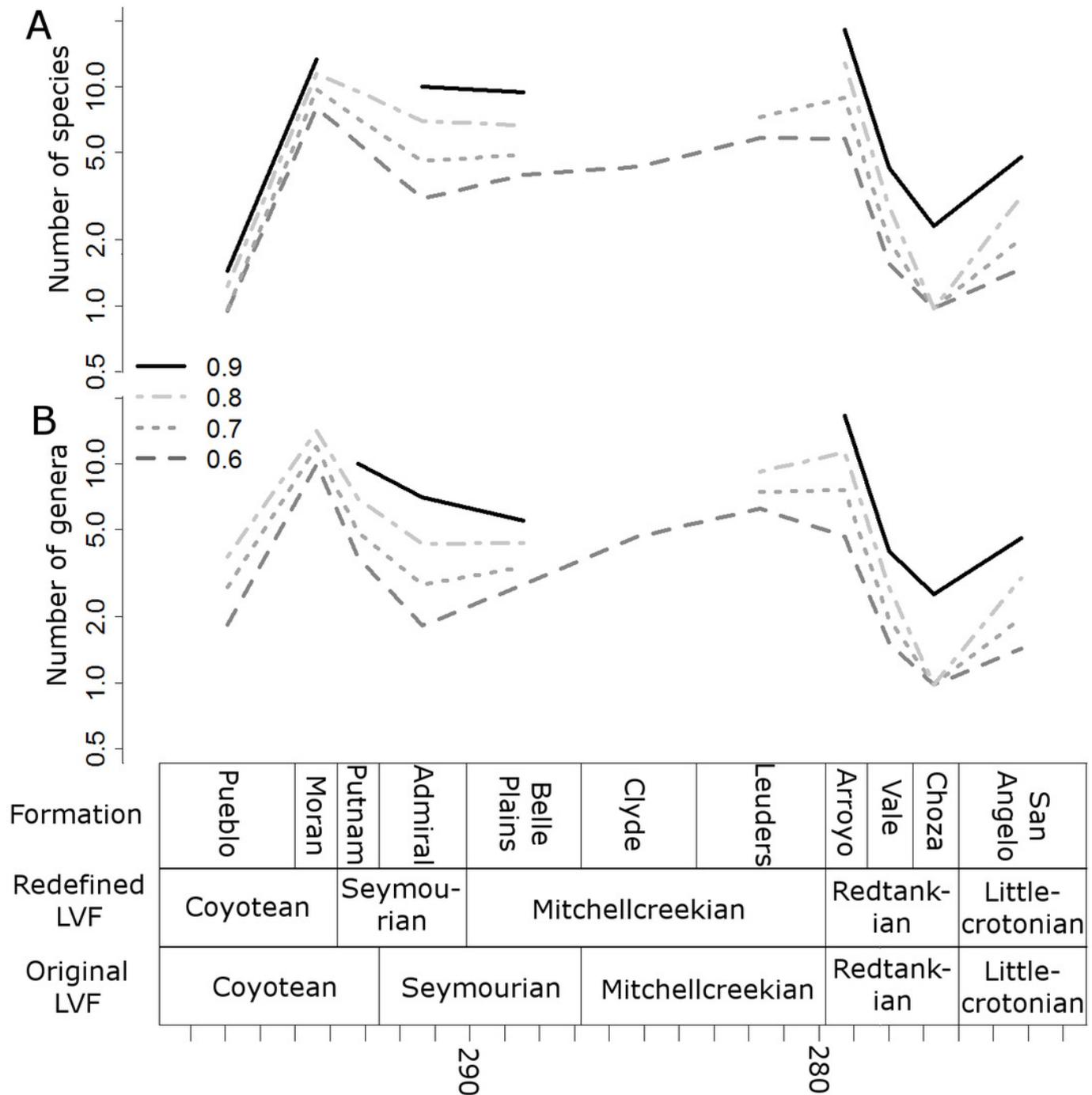


Figure 6

Subsampled diversity estimates (half-million-year time bins)

Means of the numbers of species (A) and genera (B) found in each half-million-year time bin in each of the 100 stochastic distributions of specimens, corrected for sampling heterogeneity using shareholder quorum subsampling. Legend indicates quorum level.

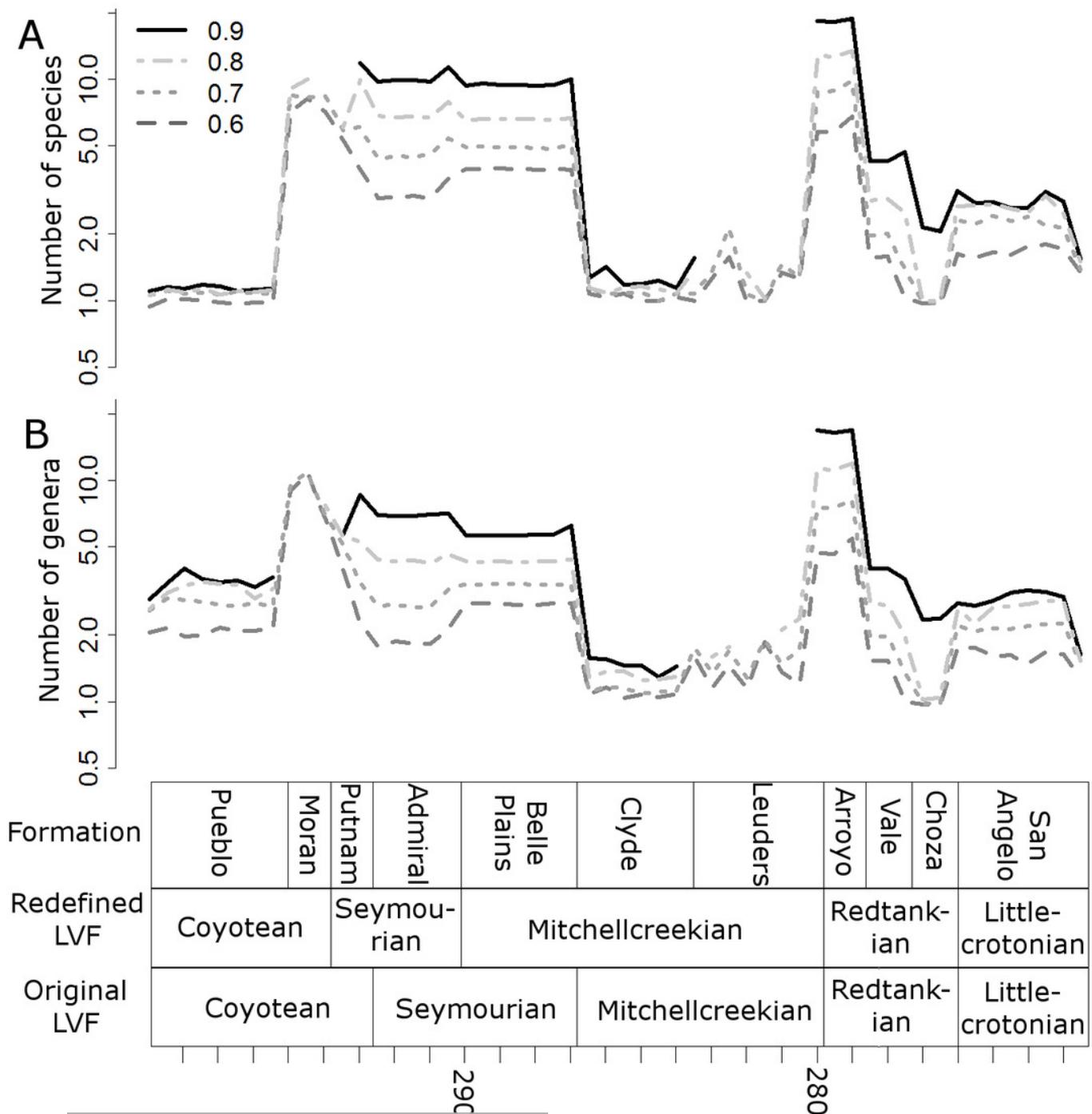


Figure 7

Extinction rates

Median (thick black lines) of the extinction rates calculated for each half-million-year time bin in each of the 100 stochastic distributions of specimens at the genus (A) and species (B) levels. Dashed lines indicate standard error around the median.

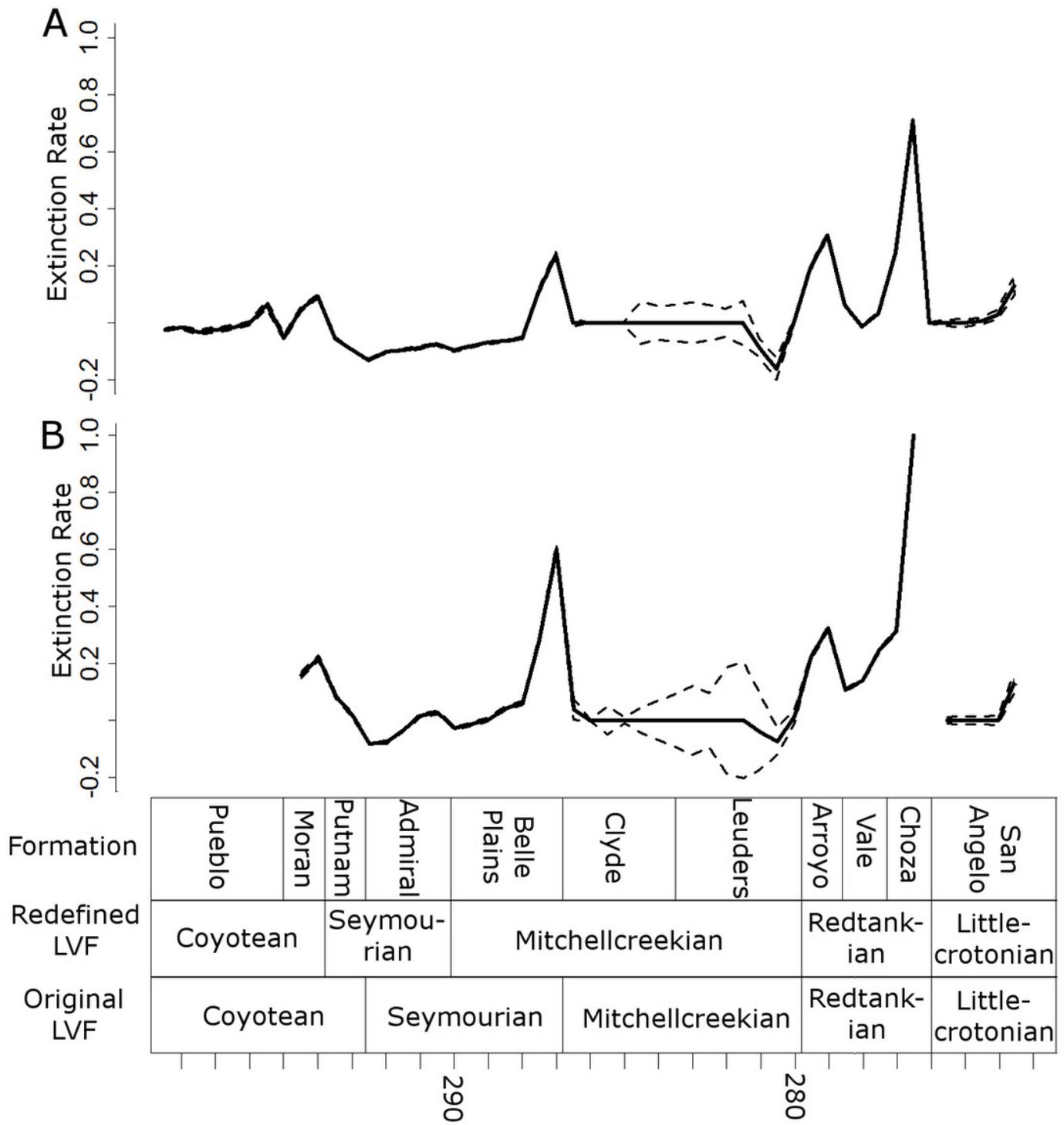


Figure 8

Origination rates

Median (thick black lines) of the origination rates calculated for each half-million-year time bin in each of the 100 stochastic distributions of specimens at the genus (A) and species (B) levels. Dashed lines indicate standard error around the median.

