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PALAEONTOLOGY MEETS METACOMMUNITY ECOLOGY: THE MAASTRICHTIAN DINOSAUR FOSSIL RECORD OF NORTH AMERICA AS A CASE STUDY

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22 **ABSTRACT**

23 Documenting the patterns and potential associated processes of ancient biotas has always been a
24 central challenge in palaeontology. Over the last decades, intense debate has focused on the
25 organisation of dinosaur–dominated communities, yet no general consensus has been reached on how
26 these communities were organised in a spatial context. Here, we used analytical routines typically
27 applied in metacommunity ecology to provide novel insights into dinosaurian distributions across the
28 latest Cretaceous of North America. To do this, we combined fossil occurrences with functional,
29 phylogenetic and palaeoenvironmental modelling, and adopted the perspective that more reasonable
30 conclusions on palaeoecological reconstructions can be gained from studies that consider the
31 organisation of biotas along ecological gradients at multiple spatial scales. Our results showed that
32 dinosaurs were restricted in range to different parts of the Hell Creek Formation, prompting the
33 recognition of discrete and compartmentalised faunal areas during the Maastrichtian at fine–grained
34 scales, whereas taxa with the broadest ranges included those with narrower distributions when
35 combining data from various geological formations across the Western Interior of North America.
36 Although groups of dinosaurs had coincident range boundaries, their communities responded to
37 multiple ecologically–important gradients when compensating for differences in sampling effort.
38 Metacommunity structures of both ornithischians and theropods were correlated with climatic barriers
39 and potential trophic relationships between herbivores and carnivores, thereby suggesting that
40 dinosaurian faunas were shaped by physiological constraints, limited food resources abundance, and a
41 combination of bottom–up and top–down forces across multiple spatial grains and extents.

42

43 **Key words:** Cretaceous, Dinosauria, metacommunity structure, Ornithischia, palaeoecology,
44 Theropoda.

45

46 U S I N G fossils preserved in sedimentary rocks to elucidate the macroevolutionary patterns and
47 associated processes of life on Earth has been the chief goal for palaeontologists. Over the past 20
48 years, a growing number of scholars have become interested in unravelling the structure of dinosaur
49 communities (see Benson 2018 for a recent review), both as a tool to understand the nature of ancient
50 Mesozoic ecosystems, and as a worthwhile endeavour in itself. Dinosaurs were a remarkably
51 successful, diverse, geographically widespread and temporally long-lived component of Mesozoic
52 terrestrial ecosystems, that appeared in the Middle–early Late Triassic (*c.* 245–230 Ma), and gradually
53 diversified into an extraordinary array of species until the terminal Cretaceous (*c.* 66 Ma), when all
54 non–avian dinosaurs became extinct (Serenó 1999; Weishampel *et al.* 2004; Brusatte *et al.* 2015).
55 Questions on the evolution, ecology and biogeography of dinosaurs have been long-standing areas of
56 controversial debate, with significant recent progress (Dunhill *et al.* 2016; MacLaren *et al.* 2017;
57 Mallon 2019; Chiarenza *et al.* 2019, 2020). However, because of their variable and sometimes
58 enigmatic biology, research on dinosaurian diversity and distributions requires more studies borrowing
59 approaches from other fields.

60 Most previous studies on dinosaur distributions have focused on relating continental
61 configurations and tectonic histories to evolutionary patterns, vicariance, dispersal and extinction (e.g.
62 Sereno 1999; Upchurch *et al.* 2002; Mannion *et al.* 2012), which have helped to identify directions of
63 migration, areas of endemism, and even test the validity of different palaeogeographical
64 reconstructions (e.g. Gates *et al.* 2010; Sampson *et al.* 2010; Dunhill *et al.* 2016). Attention has also
65 been paid to integrating the ways in which environmental preferences may have determined dinosaur
66 faunal distributions (e.g. Butler & Barrett 2008; Noto & Grossman 2010; Chiarenza *et al.* 2019). A
67 major challenge in studying dinosaur-dominated assemblages is a biased fossil record. Only North
68 America boasts a comprehensive record of correlative, intensively sampled and stratigraphically
69 stacked fossiliferous rock beds covering the final 15 myr of the Cretaceous, having produced hundreds
70 of associated skeletons from Alaska to Mexico (Weishampel *et al.* 2004; Brusatte *et al.* 2015). From

71 the late 1960s, the productive Campanian and Maastrichtian (*c.* 72–66 Ma) deposits of the Western
72 Interior Basin (WIB) of North America led to considerable debate regarding the degree of provinciality
73 in dinosaur communities across the ancient landscape of Laramidia, as well as discussions on the
74 putatively high diversity and restricted geographical range of dinosaur lineages when compared to
75 present–day large mammals (Lehman 1987; Gates *et al.* 2010; Sampson *et al.* 2010; Vavrek & Larsson
76 2010; Lucas *et al.* 2016; Dean *et al.* 2020). Currently, the Upper Cretaceous Hell Creek Formation, a
77 fossil–rich package of terrestrial sedimentary rocks associated with the retreat of the epicontinental
78 Western Interior Seaway (WIS), provides the only well–constrained evidence for community–
79 environment relationships in the broader context of palaeogeography, floral zonation, palaeoclimate
80 and sea–level changes (Brusatte *et al.* 2015; Fowler 2020). This suggests some degree of spatial niche
81 partitioning among different dinosaur clades (Lyson & Longrich 2011). Unfortunately, some of the
82 potential outcomes in previous analyses remain without ecological interpretation (Benson 2018),
83 making the translation between observed patterns and existing theory uncertain. Furthermore, while
84 many attempts have been focused on relating dinosaurian distribution to climatic and physical
85 mechanisms (Vavrek & Larson 2010; Lyson & Longrich 2011; Chiarenza *et al.* 2019), testing the
86 imprints of functional and phylogenetic features on the spatial variation of Mesozoic terrestrial faunas
87 has been limited (Fraser *et al.* 2020). Here, we take the next step on the controversial nature of the
88 organisation of dinosaur–dominated communities, and apply analytical methods that have been more
89 typically used in the context of metacommunity ecology and biogeography to provide novel insights
90 into dinosaurian distribution across the latest Cretaceous of North America (Leibold & Mikkelsen
91 2002; Heino & Alahuhta 2015).

92 Metacommunity ecology is a dynamic subdiscipline of ecology that has led to expansive
93 growth in our understanding of the structuring forces of local communities in a spatially–explicit
94 context (Leibold *et al.* 2004). More specifically, the metacommunity concept considers both local and
95 regional processes to evaluate the organisation of biotas along ecological gradients spanning multiple

96 spatial scales (Logue *et al.* 2011), a necessary step in ultimately developing a mechanistic
97 understanding of species diversity and distribution (Viana & Chase 2019). The crucial aspect of spatial
98 scale is that the definition of the study region is consistent with the theoretical questions addressed in
99 the analyses and the ecological mechanisms invoked to explain patterns at each spatial extent
100 (Lavergne *et al.* 2010). For example, while continental–scale patterns are usually related to
101 biogeographical constraints and colonization–extinction dynamics, local–scale patterns more likely
102 reflect abiotic responses to the environment and trophic relationships (Thompson *et al.* 2020). One
103 often–used routine for metacommunity analysis is to test the fit of empirical data with multiple
104 metacommunity types using site–by–species incidence matrices (Leibold & Mikkelsen 2002; Presley
105 *et al.* 2010). This approach evaluates characteristics of species distributions along latent ecological
106 gradients that manifest as a multidimensional continuum of possible structures for multiple ordination
107 axes (*sensu* Leibold & Mikkelsen 2002), with idealisations differing in the degree of coherence, range
108 turnover and range boundary clumping (see Table 1 for definitions). Each possible (non–random)
109 structure assumes that species distributions are moulded by a combination of mechanisms that differ
110 among sites and constitute an ecological gradient, thereby allowing for the generation of hypotheses
111 on how communities are organised in a spatial context (Presley *et al.* 2012).

112 Specifically, this routine of ‘elements of metacommunity structure’ allows us to identify
113 different idealised patterns of species distributions based on their range turnover type (i.e. the number
114 of species replacements, with negative turnover suggesting species loss structures and positive
115 turnover suggesting species replacement structures) and the gradual species loss or replacements
116 (indicating the discrete vs. continuous nature of community boundaries; see fig. 1 for details). For
117 example, species loss structures would appear when species show different ecological tolerances,
118 whereas species replacement structures would emerge when species show similar tolerances but
119 different optima (Gascón *et al.* 2016). Similarly, based on the original conceptions of Clementsian
120 (Clements 1916) and Gleasonian (Gleason 1926) community types, this pattern–based approach

121 permits us to infer whether or not communities change more or less consistently through groups of
122 species that respond in a similar way to ecological gradients, or whether species actually show
123 individualistic responses to these latent gradients (Fig. 1). Although this empirical routine is appealing
124 because of its links to ecological theory and is applicable to different taxa and times (Heino *et al.* 2015;
125 O’Sullivan *et al.* 2019; García–Girón *et al.* 2020a), it has never come to the fore in palaeontological
126 analyses. The fossil record, however, offers a unique deep–time perspective on metacommunity
127 organisation, allowing the resolution of functional, phylogenetic and life history settings that are not
128 evident from only extant taxa but drove macroecological patterns during the Mesozoic (Codron *et al.*
129 2012; Benson *et al.* 2018). These and other considerations represent a compelling argument for
130 bridging the analytical gaps between palaeontology and metacommunity ecology, which should
131 provide further methodological advances and fertile research avenues for both fields.

132 Here, we present a novel application of the analysis of metacommunity structure on the
133 dinosaur record from the Maastrichtian deposits of North America. Following the utilisation of
134 sampling standardisation techniques to mediate for the uneven sampling of the fossil record, we asked
135 whether dinosaur faunas showed similar metacommunity types for both primary and secondary axes
136 of spatial community variation. We also performed analyses for subsets of data based on dinosaur
137 clades (i.e. Ornithischia and Theropoda), each one showing reproductive, ecophysiological and life
138 history similarities (Benson *et al.* 2018). Sauropodomorpha was not examined here because only one
139 genus (*Alamosaurus*) is known from the terminal Cretaceous of North America (Williamson & Weil
140 2008; D’Emic *et al.* 2011). Using this approach, we draw on state–of–the–art functional and
141 phylogenetic information to integrate ecological and evolutionary processes at the metacommunity
142 level. We then compared these data with some of the main ecological gradients (e.g. the palaeoclimate
143 and palaeogeography of the Mesozoic world) that have been proposed to influence dinosaur
144 distributions (e.g. Benson *et al.* 2012; Dunhill *et al.* 2016; Chiarenza *et al.* 2019), in order to determine
145 whether coincident patterns emerged. Further, we examined these patterns at two different spatial

146 scales, including data from the Hell Creek Formation (regional scale) and a combination of Late
147 Cretaceous formations across the WIB of North America (continental scale; Willis & Whittaker 2002),
148 to test whether metacommunity structures and associated ecological gradients were consistent across
149 different spatial grains and extents.

150 Specifically, we hypothesised (**H1**) that dinosaur communities would exhibit distributional
151 patterns along multiple ordination axes and that these patterns on each axis may represent distinct
152 ecologically meaningful responses to the surrounding environment (Presley *et al.* 2009). Second, we
153 predicted (**H2**) that metacommunity structures and their ecological correlates would vary with spatial
154 scale, not least because this aspect of scale determines coherence, range turnover, range boundary
155 clumping and community–environment relationships (Heino & Alahuhta 2015). In this context,
156 lacking evidence of any physical barrier to tetrapod dispersal during the latest Cretaceous of North
157 America (Lucas *et al.* 2016), latitudinally varying factors such as temperature and precipitation would
158 limit dinosaur distribution at the continental scale, as has been suggested for Permo–Triassic Pangean
159 (Whiteside *et al.* 2015) and Cretaceous Laramidian (Gates *et al.* 2010; Sampson *et al.* 2010) and
160 Gondwanan (Benson *et al.* 2012) faunas. On the other hand, compositional variation of dinosaur faunas
161 would be particularly sensitive to fine–grained ecological mechanisms across the Hell Creek
162 landscape, including relationships via trophic habits (see Davies *et al.* 2007 for a similar reasoning on
163 mammals) and habitat preferences associated with fluvial architectural elements (Lyson & Longrich
164 2011). Since dinosaurs were an evolutionary versatile group and achieved substantial phenotypic
165 diversity across multiple lineages (Benson 2018; Benson *et al.* 2018), we further expected (**H3**) that
166 both the functional and phylogenetic features of a community would be good predictors of the
167 underlying distributional patterns. Finally, we predicted (**H4**) that dinosaur clades would also be
168 related to metacommunity organisation, with herbivorous ornithischians being more directly
169 constrained by the prevailing climatic conditions affecting their food plants’ distributions (Engelmann
170 *et al.* 2004; Rees *et al.* 2004; Noto & Grossman 2010).

171 MATERIAL AND METHODS

172 *Dinosaur occurrence test dataset*

173 Dinosaur occurrences for the Maastrichtian of North America were retrieved from the
174 Palaeobiology Database <PaleoDB.org> on May 2020, using the taxon name ‘*Dinosauria*’ and a time
175 span of 72.1 – 66.0 Ma. Critically, although studies on modern community associations are limited to
176 relatively brief periods of sampling time, fossil assemblages are windows on the faunas of ancient
177 worlds occurring within particular chronostratigraphic units (Benson *et al.* 2018). Although this coarse
178 temporal resolution will undoubtedly confound the data (which is addressed in detail below), it would
179 be problematic to subdivide the time bins further, not least because only a handful of fossil assemblages
180 are sufficiently informative to provide confident community–level estimates so far (Vavrek & Larsson
181 2010). Additionally, due to an insufficient amount of comparative data within high–resolution time
182 bins (Dean *et al.* 2020) and the inherent errors in radiometric dating (Gates *et al.* 2010), the creation
183 of a more tightly constrained correlative window is presently impractical. Here, we only retained
184 occurrences belonging to Ornithischia and Theropoda since these two clades were the most diverse
185 and abundant non–avian dinosaur groups in the latest Cretaceous of North America (Brusatte *et al.*
186 2015). Generic–level identifications were used in our study, and all avian taxa were excluded when
187 delineating community types to keep our data more comparable to previous works (e.g. Vavrek &
188 Larsson 2010; Dean *et al.* 2020). While birds are phylogenetically part of the dinosaurian clade, the
189 different habits and habitats of latest Cretaceous Avialae (either diving or volant taxa) separate these
190 faunas enough from ground–dwelling dinosaurs to justify their functional distinction in the context of
191 the communities modelled here. Although the value of generic taxonomic ranks in community analyses
192 has been debated, palaeontologists have used generic–level clades to investigate distributional patterns
193 and variation in community composition of fossil taxa (e.g. Vavrek & Larsson 2010; Chiarenza *et al.*
194 2019; Dean *et al.* 2020). Indeed, generic–level identifications are preferred over species taxonomic
195 ranks in dinosaur palaeobiology studies as most dinosaur genera (*c.* 87%) are easily diagnosed and

196 monospecific (Weishampel *et al.* 2004; Mannion *et al.* 2012). Moreover, genus–level and species–
197 level diversity patterns generally appear to track each other for Mesozoic tetrapods (Barrett *et al.*
198 2009), and genera are more taxonomically stable than species for many groups (Robeck *et al.* 2000).
199 Here, however, taxa with unclear genus identification were discarded (i.e. we did not incorporate
200 ‘cryptic’ diversity represented by taxonomically undiagnostic fossil remains that potentially represent
201 distinct taxa, nor we did infer ghost lineages based on phylogenetic diversity estimates; Barrett *et al.*
202 2009; Mannion *et al.* 2011), and so were collections lacking formational assignment. If questionable
203 ages appeared (e.g. ages notably deviating from ages of other collections from the same formation),
204 they were either revised or excluded. These data are an up–to–date record of North American dinosaur
205 faunas and therefore incorporate new Late Cretaceous fossils discovered over the past few years.
206 Overall, our pruned dataset comprised 43 dinosaur genera, and consisted of 11 formations across the
207 WIB of North America and 17 well–sampled locations across the Hell Creek landscape.

208 *Explanatory data*

209 *Palaeoclimatic general circulation model.* In this study, we used palaeoclimatic model outputs (here,
210 near–surface [1.5 m] mean annual temperature (*TempMean*), near surface [1.5 m] annual temperature
211 standard deviation (*TempSDann*), annual average precipitation (*PrecMean*) and annual precipitation
212 standard deviation (*PrecSDann*)) from the fully coupled atmosphere–ocean GCM HadCM3L v. 4.5
213 Atmospheric–Ocean General Circulation Model (Valdes *et al.* 2017). More specifically, we followed
214 the nomenclature of Valdes *et al.* (2017) and applied the HadCM3BL–M2.1aE version of the model.
215 The conditions of the model simulations for the Maastrichtian consist of an atmospheric CO₂
216 concentration of 1120 ppmv, which is within the range of uncertainty provided by the recent proxy
217 pCO₂ reconstructions of Foster *et al.* (2017). The model simulations were run for a total of 1422 years,
218 and the climate variables used in our analyses were an annual average of the last 30 years of these
219 simulations. HadCM3L has contributed to the Coupled Mode Intercomparison Project experiments
220 demonstrating skill when it comes to reproducing present–day climates (Collins *et al.* 2001; Valdes *et*

221 *al.* 2017) and has also been used for an array of different palaeoclimate evaluations during the Eocene
222 (Lunt *et al.* 2012), the Oligocene (Li *et al.* 2018) and the Miocene (Bradshaw *et al.* 2012). Detailed
223 information on this palaeoclimatic model, including large-scale circulation (and associated energy and
224 momentum fluxes) and temporal fluctuations, as well as the impacts of fine-scale orographic features
225 on climate signals, are available elsewhere (e.g. Lunt *et al.* 2016; Chiarenza *et al.* 2019).

226 *Palaeogeographical digital elevation models (DEMs).* The Maastrichtian palaeogeography for this
227 study is that of Scotese & Wright (2018), which has been compiled as a palaeo-digital elevation model
228 to facilitate grid-based analyses. In brief, these maps were created from publicly available stratigraphic
229 literature, supplemented by fieldwork, including lithology, palaeoenvironmental information and
230 broad-scale facies identification. For large-scale analyses, these palaeogeographies were upscaled to
231 the palaeoclimatic model resolution (3.75° x 2.5°). This means that topographic and bathymetric
232 information was broadly conserved, as it was resolved at a lower resolution (see Chiarenza *et al.* 2019
233 for a similar approach).

234 *Functional and phylogenetic features.* Each dinosaur taxon was classified into several functional
235 guilds based on body mass (very small, small, medium, large and very large), locomotor mode (bipeds,
236 facultative bipeds –capable of both quadrupedal and bipedal motion– and quadrupeds) and trophic
237 habits (carnivores, omnivores and herbivores, and for the latter, low and high browsers).

238 Body mass is perhaps the single most important and meaningful functional trait for animals, as
239 it ultimately affects many aspects of their biology including metabolic rates, mechanical constraints,
240 ecological performance and lifestyle strategies related to feeding, locomotion and reproduction
241 (Loeuille & Loreau 2006; Iossa *et al.* 2008). Here, we used body mass estimates (*very small* ≤ 10 kg;
242 10 kg < *small* ≤ 100 kg; 100 kg < *medium* ≤ 1000 kg; 1000 kg < *large* ≤ 10000 kg; *very large* >
243 10000 kg; Noto & Grossman 2010) based on adult representatives from the comprehensive dataset of
244 Benson *et al.* (2014), which provides a wide list of dinosaur taxa using the scaling relationship of limb
245 bone robustness (stylopodial circumference; Campione & Evans 2012). To obtain a more

246 comprehensive understanding of body mass distributions in our data, we further applied an inflection
247 point criterion based on the Barry & Hartigan (1993) product partition model with Markov chain
248 Monte Carlo (MCMC). More specifically, this algorithm used the posterior probability of changes
249 over 10000 MCMC iterations, excluding the first 1000 as burn in, to distinguish among different body
250 mass categories in the latest Cretaceous dinosaurs of North America. Interestingly, this Bayesian
251 analysis roughly identified most of the original body mass categories used in our study, with each
252 category broadly representing an order of magnitude (García–Girón *et al.* 2020b, appendix S1, fig.
253 S1).

254 Trophic habits refer to the food processing strategies and diet of an animal, and it generally
255 includes three primary categories, i.e. carnivores, herbivores and omnivores. Further sub–divisions
256 depend on the biological knowledge of the morphology (e.g. teeth morphology and skull) and
257 behaviour of the study organismal group. Here, we assigned herbivores to categories of browse height
258 rather than plant type due to the virtually unknown nature of plant preferences in dinosaurs. More
259 specifically, we roughly assigned a simple maximum browsing limit (*low* ≤ 2 m; *high* > 2 m) based
260 on characters such as limb length and neck posture using Noto & Grossman (2010) and Mallon *et al.*
261 (2013).

262 We further divided locomotor mode into two major categories: quadrupeds and bipeds. For
263 those taxa with intermediate axial and limb morphologies in proportions between those of bipeds and
264 obligate quadrupeds (e.g. Hadrosauridae), we included an additional locomotor division, i.e.
265 facultative bipeds (see Noto & Grossman, 2010 for a similar approach). For the following analyses,
266 we applied the mixed–variables coefficient of distance (i.e. a generalisation of Gower’s distance;
267 Pavoine *et al.* 2009) to extract a functional distance matrix, which described the functional differences
268 between all taxon pairs based on body mass, trophic habits and locomotor mode (e.g. Heino & Tolonen
269 2017). Thereafter, the pairwise output values for the functional distance matrix were synthesised into
270 separate axes using principal coordinate analysis (PCO) and following Duarte *et al.* (2012).

271 The phylogenetic composition of each site was addressed using the phylogenetic fuzzy–
272 weighting method (PCPS) with the Sørensen dissimilarity family as implemented in Debastiani &
273 Duarte (2014). We used the updated version of the composite dinosaur phylogeny of Benson *et al.*
274 (2018) and a birth–death sampling model (as assumed by the *ca13* method; Bapst 2013) to estimate
275 node ages (extinction and speciation rate = 0.935; sampling rate = 0.018; Lloyd *et al.* 2016). The scores
276 of each single community along PCO1, PCO2, PCPS1, and PCPS2 components were then used to
277 indicate the combined functional and phylogenetic features of each community (García–Girón *et al.*
278 2020b, appendix S2, figs. S2 and S3).

279 *Relationships mediated through trophic habits.* To represent relationships between pairs of organismal
280 groups delineated based on their trophic habits, we calculated the interaction matrix scores derived
281 from reciprocal averaging (RA; see below) for herbivores (*HbvRAs*), carnivores (*CrnvRAs*) and
282 omnivores (*OmnvRAs*). In other words, ordination axes (*HbvRA1*, *HbvRA2*, *CrnvRA1*, *CrnvRA2*,
283 *OmnvRA1* and *OmnvRA2*) from RA provided the basis for mapping the imprints of potential trophic
284 relationships between herbivores, omnivores and carnivores on the assembly of Late Cretaceous
285 dinosaur communities at different spatial scales across the WIB of North America.

286 *Dominant rock types and fluvial architectural elements at the regional scale.* The Hell Creek
287 Formation contains a variety of sediments including crevasse–splay sandstones, unconsolidated sands,
288 mudstones, rooted siltstones and carbonaceous shales, which represent medium–sized meandering and
289 laterally accreting fluvial channel systems and associated floodplains (Johnson 2002; Murphy *et al.*
290 2002; Fowler 2020). Here, we used lithological data from Lyson and Longrich (2011) to distinguish
291 between floodplain and channel lithofacies and examined patterns of association between dinosaur
292 faunas and fluvial architectural elements in the Hell Creek landscape.

293 *Metacommunity analyses using site–by–taxon incidence matrices*

294 We examined the elements of dinosaur metacommunity structure based on the original
295 framework proposed by Leibold & Mikkelsen (2002) and the ‘range perspective’ adopted by Presley

296 *et al.* (2010). Metacommunity types (Table 1) were assessed by analysing aspects of **(1)** coherence,
297 **(2)** range turnover and **(3)** range boundary clumping. Before calculating these metrics, site–by–taxon
298 incidence matrices were ordinated via RA. This procedure allowed us to maximise the degree to which
299 sites (i.e. dinosaur–bearing collections for the regional approach and geological formations for the
300 large–scale approach) with the most similar community composition were adjacent in the matrix. RA
301 defines a latent ecological gradient and, therefore, communities can be ordered along such gradient
302 that incorporates multiple ecological mechanisms presumably of importance for the distribution of
303 dinosaurs (Presley & Willig 2010). Importantly, because axes extracted via RA are orthogonal, and
304 because secondary axes have the potential to represent biologically meaningful information beyond
305 that obtained on the first axis (Presley *et al.* 2009), analyses were conducted separately for primary
306 (axis 1) and secondary (axis 2) axes of ordination. In addition, we adapted the step–by–step Lloyd’s
307 (2012) modelling approach to assess the influence of sampling effort on the interaction matrix scores.
308 To do this, we investigated the relationships between the ordinated empirical incidence matrix and
309 sampling proxy values based on linear regressions, accompanied by Akaike’s Information Criterion
310 (AIC_c) to fit the ‘best’ linear vs quadratic model. This equation was applied to calculate predicted
311 rankings and scores for each sampling effort value and the residual ‘unexplained’ signals were
312 subsequently used as a sampling–corrected estimate of the interaction matrix scores (representing
313 fluctuations in the latent ecological gradient that cannot be explained in terms of sampling biases; see
314 Lloyd (2012) for a similar approach). Here, we used the number of discrete tetrapod–bearing
315 collections as a proxy for both geological and human sampling effort (Mannion *et al.* 2011) to mitigate
316 the issue of redundancies (Benton *et al.* 2011). Importantly, this corrective agent summarises aspects
317 of geographical and stratigraphic dispersion, rock volume and research effort (Crampton *et al.* 2003),
318 and correlates with the amount of fossiliferous rock outcrop and other measures of sedimentary rock
319 record quality in terrestrial datasets (Butler *et al.* 2011; Brocklehurst *et al.* 2013).

320 The first metric that we evaluated was *coherence*, i.e. the degree to which dinosaur distributions
321 were arranged along a common latent ecological gradient. This metric is based on calculating the
322 number of embedded absences (i.e. each gap in the range of a taxon; Leibold & Mikkelsen 2002) in
323 the interaction matrix and then comparing the observed value to a null distribution of embedded
324 absences from 1000 simulated matrices. A small number of embedded absences (i.e. embedded
325 absences are significantly lower than expected by chance) leads to positive coherence, while a large
326 number of embedded absences (i.e. embedded absences are significantly larger than expected by
327 chance) means negative coherence. Significantly positive coherence thus suggests that dinosaur
328 distributions are responding similarly to a common ecological gradient represented by the ordinated
329 site-by-taxon presence-absence matrix. Non-significant coherence means that taxa are distributed at
330 random with respect to the axis of ordination, suggesting that taxa are not responding to a common
331 ecological gradient (Leibold & Mikkelsen 2002). In most cases, however, coherence is positive and
332 the use of *range turnover* (i.e. how often species ranges replace each other), which was measured here
333 as the number of empirical replacements for each possible pair of taxa and for each possible pair of
334 sites in the interaction matrix (Presley & Willig 2010), helps determining whether or not there are
335 nested subsets of taxa along the latent ecological gradient. In our study, the number of replacements
336 was compared to a null distribution that randomly shifted the entire ranges of each taxon (Leibold &
337 Mikkelsen 2002). Significantly negative turnover (i.e. the observed replacements are lower than
338 expected by chance) is consistent with nested subsets (i.e. hyperdispersed species loss, random species
339 loss and clumped species loss), whereas significantly high range turnover (i.e. the number of observed
340 replacements is higher than expected by the null model) indicates evenly spaced, Gleasonian or
341 Clementsian metacommunity types (Henriques-Silva *et al.* 2013). These three types of gradients were
342 separated based on evaluation of *range boundary clumping* (i.e. how often multiple taxa have their
343 range limits in the same study sites; Leibold & Mikkelsen 2002; Presley *et al.* 2010), which was
344 analysed using Morisita's index of dispersion and a subsequent χ^2 test that compared the observed and

345 expected distributions of range boundary locations. Index values that are not different from 1 indicated
 346 randomly distributed range boundaries (i.e. Gleasonian and random species loss structures), while
 347 values significantly larger and less than 1 suggested clumped range boundaries (i.e. Clementsian and
 348 clumped species loss structures) and hyperdispersed range boundaries (i.e. evenly spaced gradients
 349 and hyperdispersed species loss structures), respectively. Presley *et al.* (2010) further proposed that
 350 the combination of cases of significant positive coherence and non–significant range turnover can be
 351 interpreted as quasi–structures, i.e. quasi–evenly spaced, quasi–Gleasonian, quasi–Clementsian,
 352 quasi–hyperdispersed species loss, quasi–random species loss and quasi–clumped species loss
 353 gradients (Fig. 2; see Presley *et al.* 2010 for theoretical details).

354 The significance of the index values for coherence and range turnover was tested using the
 355 fixed–proportional null model (Gotelli 2000), where community richness was maintained (i.e. rows
 356 are fixed), but the ranges (i.e. columns) of each taxon were filled based on their marginal probabilities.
 357 Because community richness varies along latent ecological gradients (Presley *et al.* 2009), this null
 358 model incorporates an appropriate amount of empirical realism. In addition, this null model has
 359 desirable type I and type II error rates. By contrast, we also used a strict and conservative fixed–fixed
 360 null model to assess whether the null model used affected our main results. In the fixed–fixed null
 361 model, community richness was maintained (i.e. rows are fixed) and occurrences were the same as
 362 frequencies of occupancy (i.e. columns are fixed). We used 1000 simulations to provide random
 363 matrices for testing coherence and range turnover. Similarly, we calculated a Z–score or standardized
 364 effect size (SES) for the indices of coherence and range turnover for each individual metacommunity:

$$365 \quad SES = \frac{obs - rnd.mean}{rnd.sd}$$

366 where *obs* is the observed index value, *rnd.mean* the mean index value of the null distribution,
 367 and *rnd.sd* the standard deviation of simulated index values (see Gotelli & McCabe 2002).

368 Z–scores allow comparisons among datasets and can subsequently be used in comparative
 369 analyses (see Heino *et al.* 2015). Basically, Z–scores between –1.96 and 1.96 are non–significant at α

370 = 0.05 and, thus, Z-scores of coherence and range turnover can also be used to infer metacommunity
371 structures. We also applied the traditional approach to delineate metacommunity types based on
372 statistical significance from the randomisation tests of coherence and range turnover.

373 *Linear regression models*

374 We ran ordinary least squares (OLS) regressions to analyse community–environment
375 relationships at different spatial scales across the WIB of North America. Statistical dependence
376 among the explanatory variables was assessed using bivariate correlations, and variables with high
377 correlation coefficients ($|\rho| > 0.7$); here, *OmnvRAs*) were excluded from the final models (Dormann *et al.*
378 *et al.* 2013). We applied forward selection with adjusted R^2 values (adj. R^2) to choose statistically
379 significant explanatory variables to the models. Importantly, adj. R^2 values give unbiased estimates of
380 the explained variation by considering different number of explanatory variables (Borcard *et al.* 2018).
381 The forward selection used two different stopping criteria (significant level α and global adj. R^2) to
382 obtain parsimonious regression models (Blanchet *et al.* 2008). Previously, we performed logarithmic
383 transformation of explanatory variables to get normally distributed residuals for the OLS regressions.
384 The effect size of model coefficients was measured using Fisher’s Z to allow comparison among
385 analyses (Cooper *et al.* 2009).

386 To get additional information on the order of importance of different ecological mechanisms
387 on the spatial variation of dinosaur communities, we ran commonality analysis (CA) and decomposed
388 linear regression effects into unique and common variance of predictors (Nathans *et al.* 2012). The
389 unique effects suggest how much variance is solely explained by a single explanatory variable, whereas
390 common effects indicate how much variance is shared by a predictor set. A higher value of common
391 effects compared to unique effects suggests substantial collinearity among explanatory variables.
392 Hence, CA can explicitly identify the magnitude and location of multicollinearity and suppression in
393 OLS regression models (Ray–Mukherjee *et al.* 2014). Perhaps more importantly, compared to other
394 statistical approaches, CA is virtually independent of variable order than can disturb, for example,

395 stepwise multiple regression results (Nathans *et al.* 2012). Besides unique and common effects, we
396 produced structure coefficients (SC; the bivariate correlations between an explanatory variable and the
397 predicted dependent variable's score resulting from the regression model; *sensu* Nathans *et al.* 2012),
398 not least because SC values are independent of collinearity among predictors and have the additional
399 property of ranking independent variables based on their contributions to the regression effect (Kraha
400 *et al.* 2012).

401 Spatial autocorrelation occurring in statistical models may violate the assumption about the
402 independence of residuals, thereby inflating the value of test statistic and increasing the chance of type
403 I errors (Davis 2002). Hence, to evaluate for spatial autocorrelation in the final regressions, we
404 calculated Moran's *I* coefficients based on palaeogeographical coordinates and OLS model residuals
405 using the Bonferroni correction (Cabin & Mitchell 2000).

406 All statistical analyses were performed in R v. 3.6.0. (R Development Core Team 2019). The
407 list of R packages and computational routines that have been used throughout this work are provided
408 in García–Girón *et al.* (2020b, appendix S3, table S1).

409 RESULTS

410 The *Z*-scores for coherence and range turnover from the fixed–proportional (Table 2) or fixed–
411 fixed (García–Girón *et al.* 2020b, appendix S4, table S2) null models were somewhat similar.
412 Accordingly, we only focused on the results based on the fixed–proportional method (i.e. observed
413 community richness was maintained and each taxon range was filled based on their marginal
414 probabilities) because most studies have used it in the context of metacommunity analyses (e.g. Heino
415 *et al.* 2015; Gascón *et al.* 2016; García–Girón *et al.* 2020a). There was a relatively wide variation in
416 the *Z*-scores of coherence, the *Z*-scores of range turnover, and the index of range boundary clumping
417 among dinosaur clades and spatial scales (Table 2). However, results were generally similar regardless
418 of whether communities were ordinated on the primary or secondary axes. Indeed, our analysis showed
419 consistent distributional patterns, resulting in three observed metacommunity types (Table 2, fig. 3).

420 More specifically, fine–grained analyses suggest that dinosaurs showed **(1)** positive coherence (i.e. the
421 number of embedded absences was lower than expected by chance), **(2)** positive range turnover (i.e.
422 the number of replacements was higher than expected by chance) and **(3)** significantly higher range
423 boundary clumping than 1 (based on Morisita’s index of dispersion). The patterns most consistent with
424 these results are Clementsian and quasi–Clementsian (Table 2). In other words, dinosaur
425 metacommunities from the North American Hell Creek Formation were responding similarly to latent
426 ecological gradients, here represented by the primary and secondary axes from RA; and community
427 composition changed consistently in similar places of the underlying ecological gradient. For analyses
428 based on 11 Late Cretaceous formations across the WIB of North America, dinosaur communities
429 exhibited **(1)** positive coherence, **(2)** variable range turnover (i.e. from negative to positive range
430 turnover for analyses based on all dinosaur taxa and for analyses restricted to ornithischians,
431 respectively) and **(3)** coincident range boundaries. Interestingly, when ordinated according to the
432 primary and secondary RA axes, theropod communities fitted best with quasi–clumped species loss
433 (i.e. taxa ranges formed quasi–nested groups, which replaced each other along the latent ecological
434 gradient) and quasi–Clementsian structures (see above), respectively. Note that the same inference can
435 be drawn based on the *p*–values derived from randomisation tests (Table 2, fig. 3).

436 The complex distributional patterns of dinosaur faunas were predicted with relative accuracy
437 by the regression models after forward selection with Monte Carlo permutations ($\text{adj. } R^2_{\text{Cum}} = 0.22\text{--}$
438 0.91 ; García–Girón *et al.* 2020b, appendix S5, table S3). However, as revealed by OLS regressions
439 (García–Girón *et al.* 2020b, appendix S6, table S4) and CA (García–Girón *et al.* 2020b, appendix S7,
440 tables S5 and S6), the most important ecological correlates for variation in community composition
441 varied among dinosaur clades and spatial scales (Fig. 4). Considering the Hell Creek study area,
442 dinosaur community composition (axis 1) was most strongly related to functional features underlying
443 variation in trophic habits (*PCOI*; García–Girón *et al.* 2020b, appendix S2, fig. S2). The most
444 important predictors for ornithischians (axis 1) were the interaction matrix scores from the carnivores,

445 whereas no discernible delineation occurred along the secondary axis. Variation in theropod
446 community composition was mostly strongly related to topography (axes 1 and 2), the interaction
447 matrix scores from the herbivores (axes 1 and 2) and the functional component describing trophic
448 habits (axis 1; *PCOI*; García–Girón *et al.* 2020b, appendix S2, fig. S2). When all latest Cretaceous
449 North American geological formations were examined together, the most influential variables related
450 to the pooled dinosaurian dataset were the standard deviation in annual precipitation (*PrecSDann*; axis
451 1) and the phylogenetic component dictating variation from basal (non–maniraptoran) coelurosaurs to
452 ornithischians (axis 2; García–Girón *et al.* 2020b, appendix S2, fig. S3). Variation in theropod
453 communities was consistent with temperature gradients (*TempSDann*; axis 2) and correlated with
454 scores from the phylogenetic structure underlying variation among maniraptoran subclades (axis 1;
455 García–Girón *et al.* 2020b, appendix S2, fig. S3). Finally, similar to patterns for analyses based on all
456 taxa, the primary and secondary RA axes for ornithischian dinosaurs ordered sites along gradients of
457 precipitation (Fig. 4). CA validated the associations between variation in dinosaur community
458 composition and ecological mechanisms at different spatial scales, although a substantive amount (*c.*
459 50 %) of the regression effect of explanatory variables was partially generated by their common
460 variances, i.e. common effects made a noteworthy contribution to regression equations (García–Girón
461 *et al.* 2020b, appendix S7, tables S5 and S6). Perhaps more importantly, however, SC values
462 reemphasised the pivotal importance of the significant explanatory variables previously identified by
463 OLS models for the spatial variation of dinosaur communities in the WIB of North America (García–
464 Girón *et al.* 2020b, appendix S6, table S4).

465 We found no statistically significant ($p > 0.05$) spatial autocorrelation in the model residuals
466 (García–Girón *et al.* 2020b, appendix S8, table S7). Consequently, our final OLS regressions were
467 likely to rather reliably illustrate some of the most important ecological mechanisms to which dinosaur
468 communities responded during the latest Cretaceous of North America.

469

470 **DISCUSSION**

471 In order to characterise metacommunity organisation of Late Cretaceous animals, it is
472 necessary to study a long-lived, structurally diverse, abundant and widespread clade, as well as an
473 extensive fossil record that is adequate for the implementation of sampling standardisation techniques
474 (Mannion *et al.* 2012). Here, we focused on dinosaurs, a cosmopolitan and ecologically diverse
475 component of Mesozoic terrestrial ecosystems for 160 myr (Weishampel *et al.* 2004), for investigating
476 compositional variation and associated ecological mechanisms in the Maastrichtian of North America.
477 Perhaps more importantly, we present a novel usage of analysis of metacommunity structure (Leibold
478 & Mikkelsen 2002; Leibold *et al.* 2004; Presley *et al.* 2010), a framework that has traditionally been
479 applied in ecology, to empirically complement more conventional ‘mechanistic’ approaches in
480 palaeontology (e.g. Lehman 1987; Sereno 1999; Upchurch *et al.* 2002). This analytical framework
481 enabled us to better understand patterns in dinosaur communities and the factors underlying these
482 patterns from large to finer spatial scales, whether driven by abiotic or biotic agents.

483 We found that the degree of consistency of dinosaurian distributions with a specific idealised
484 pattern, as well as the identification of ecological mechanisms moulding those patterns, was contingent
485 on the spatial scale used for analysis, but not on the ordination axis. This finding refuted our first (**H1**)
486 and supported our second (**H2**) hypotheses. However, all dinosaur communities studied were coherent
487 (i.e. responded consistently to latent ecological gradients), showed clumped boundaries and exhibited
488 multiple ecologically-important gradients when compensating for differences in sample size. Not
489 unexpectedly (**H3** and **H4**), the examined dinosaur clades (here, Ornithischia and Theropoda) showed
490 different structures along main ecological gradients, reflecting the varying ecological roles each clade
491 played in different terminal Cretaceous environments, with functional and phylogenetic features partly
492 determining the underlying distributional patterns. Similarly, we found that relationships between
493 herbivores and carnivores were responsible for the most significant changes in faunal variation within
494 the Hell Creek landscape, whereas dinosaurs’ first order geographical ranges at the continental scale

495 tended to be more a function of changes in precipitation and temperature, thereby suggesting a
496 latitudinal climatic gradient as an interface. These scenarios are not mutually exclusive, and it is thus
497 highly likely that a combination of mechanisms at various spatial scales shaped dinosaur communities
498 in the latest Cretaceous of North America (see fig. 5 for a synthesis).

499 We observed three metacommunity types following the classification proposed by Presley *et*
500 *al.* (2010). Clementsian and quasi–Clementsian metacommunity types (in which the ranges of taxa
501 form associations, which replace each other along ecologically–important gradients) prevailed in fine–
502 grained analyses, whereas quasi–clumped species loss structures (in which the ranges of taxa form
503 quasi–nested groups with discrete community boundaries) were more frequent when the studied
504 geological formations were examined together. Paradoxically, Clementsian and quasi–nested
505 structures represent almost opposite ends with regard to species replacements (Leibold & Mikkelsen
506 2002; Presley & Willig 2010); hence, it was not surprising that rates of range turnover differed across
507 spatial scales (Table 2). In this regard, our results suggest relatively low range turnover levels in the
508 terminal Cretaceous of North America and add further evidence for a lack of discrete faunal
509 bioprovinces and dinosaur endemism within the WIB during the Maastrichtian (but see Lehman 1987;
510 Gates *et al.* 2010, 2012; Sampson *et al.* 2010; Loewen *et al.* 2013). Indeed, this model of fully isolated
511 regional faunas along the WIB has recently been questioned based on uneven sampling and updated
512 age constraints of dinosaur–bearing formations (Lucas *et al.* 2016; Fowler 2017; Fowler & Freedman–
513 Fowler 2020), revealing facies biases and diachroneity of most Late Cretaceous units in North America
514 (Dean *et al.* 2020). Although our analyses do not support the case for complete provinciality, some
515 dinosaurs were restricted in their ranges. In this vein, the consistent clumped boundaries of dinosaur
516 communities indicate multiple ecotones that are ecologically important to particular dinosaurian taxa
517 and are consistent with distributions that are defined by taxon–specific physiological constraints
518 (Presley *et al.* 2010). Similarly, we found that dinosaurs were restricted in range to different parts of

519 the Hell Creek Formation, prompting the recognition of discrete and compartmentalised faunal areas
520 during the Cretaceous at fine-grained scales (Butler & Barrett 2008; Mallon *et al.* 2012).

521 Others also found multiple metacommunity structures while examining different present-day
522 organismal groups and various spatial scales (e.g. Heino & Alahuhta 2015; Heino *et al.* 2015). In our
523 study at fine-grained resolution, dinosaurs fitted best Clementsian and quasi-Clementsian
524 metacommunity types, suggesting some generalities among disparate clades (Presley *et al.* 2010),
525 which nevertheless had different relationships to underlying ecological mechanisms. Specifically,
526 Clements (1916) original conception of patterns of range distributions requires presence of discrete
527 community boundaries as species associations respond in a similar way to structuring mechanisms.
528 Consequently, the quasi-structures we observed here were probably the result of an artefact because
529 niche breadth extended beyond the range in which range turnover is significant (Presley *et al.* 2010),
530 thereby affecting the identification of distributional boundaries. Hence, these results suggest that, as
531 individualistic as the taxon-specific responses might be, there must be some physiological or
532 evolutionary trade-offs associated with biologically-important thresholds, which translated into
533 similar dinosaurian taxa occurring and disappearing at the same zones within the Hell Creek
534 Formation. Alternatively, spatial niche partitioning and shared environmental preferences might have
535 led to the occurrence of tightly associated sets of species, as has been recently discussed for
536 hadrosaurids, nodosaurid ankylosaurs and marginocephalians (Butler & Barrett 2008; Lyson and
537 Longrich 2011; Mallon *et al.* 2012). Unlike Lyson & Longrich (2011), evidence for evolving habitat
538 preferences among dinosaur lineages was not mediated by depositional settings. We propose that this
539 discrepancy probably reflects methodological differences among studies (e.g. Lyson & Longrich 2011;
540 Mallon *et al.* 2012).

541 On the other hand, the quasi-nested (i.e. quasi-clumped species loss) structure of dinosaur
542 metacommunities at the continental scale suggests that taxa with narrower distributions were contained
543 within the ranges of taxa with largest distributions (Patterson & Atmar 1986), with community richness

544 varying along few major ecological gradients (Heino 2011). In this regard, we suggest that ecological
545 mechanisms that impose important physiological stress and limited resource abundance (see below)
546 would have probably limited dinosaur community richness, not least because fewer taxa were adapted
547 to such conditions (e.g. Noto & Grossman 2010). Nevertheless, based on the present descriptive
548 analysis, any comprehensive answer to the question of ecological gradients underlying different
549 metacommunity scenarios would be premature. Interestingly, however, our results indicate that spatial
550 scale is key in determining dinosaur metacommunity organisation, thereby empirically illustrating the
551 importance of clearly defining spatial grain and extent when addressing ecological questions in
552 palaeontology.

553 Finding the ecological correlates of dinosaur communities has proven to be a major challenge
554 for palaeontologists for over 30 years (Lehman 1987, 2001; Sampson *et al.* 2010; Gates *et al.* 2010,
555 2012; Loewen *et al.* 2013; Lucas *et al.* 2016; Chiarenza *et al.* 2019, 2020). Although we cannot identify
556 a single most parsimonious mechanism for dinosaur communities during the Maastrichtian of North
557 America, several discrete, recurring patterns are worthy of mention. Ecological gradients underlying
558 variation along the first two ordination axes differed among dinosaur clades and spatial scales (Fig. 5).
559 Although such context–dependent community–environment relationships have often been observed in
560 present–day animals (Willig & Presley 2016; Murray–Stoker & Murray–Stoker 2020), it was
561 particularly evident that dinosaur faunas responded to different constraining or limiting ecological
562 gradients. One of the most important structuring mechanisms related to compositional variation in the
563 Hell Creek landscape was the first metacommunity trait component (i.e. PCO1), which portrayed
564 variation from assemblages dominated by large carnivores to assemblages mainly comprised of small
565 omnivore dinosaurs (García–Girón *et al.* 2020b, appendix S2, fig. S2). This expands some preliminary
566 attempts to integrate functional and distributional data for Late Cretaceous dinosaurs (e.g. Mallon &
567 Anderson 2013; MacLaren *et al.* 2017), and further underscores the importance of body size and
568 different feeding niches for community organisation and spatial segregation in dinosaurian faunas.

569 Similarly, regardless of dinosaur clade, the primary and secondary axes were correlated significantly
570 with the interaction matrix scores of herbivores and carnivores, indicating that dinosaur communities
571 were probably shaped by bottom–up and top–down forces. This is not a trivial finding since indications
572 of trophic relationships are rare in the fossil record and they usually rely upon serendipitous discoveries
573 (Barrett & Rayfield 2006), including coelurosaur enterolites and cololites (Varricchio 2001), coprolites
574 (Chin *et al.* 2003) and puncture–like bite traces on the bones of megaherbivores (Hone *et al.* 2010).
575 Interestingly, our results broadly complement the conclusions of Davies *et al.* (2007) and Gates *et al.*
576 (2010), who found strong spatial variation among mammalian carnivores and between neosuchian
577 crocodyliforms and their prey, respectively. However, these findings should not be interpreted as
578 indication of direct causality (i.e. proven trophic relationships among dinosaurian groups) but that
579 relationships via trophic habits might have a major effect on variation in dinosaur community
580 composition, which highlights the conservative approach that should guide the interpretation of these
581 signals (Dormann *et al.* 2018; García–Girón *et al.* 2020c).

582 Climate is often the *deus ex machina* of palaeontological studies dealing with fossil
583 distributions, including dinosaurs (reviewed in Lucas *et al.* 2016; Fraser *et al.* 2020). This is best
584 documented for the Maastrichtian, during which several climatic areas —from a southern evaporite
585 area to a high–latitude, temperate and humid belt— have been identified in North America (Upchurch
586 *et al.* 1999; Hay & Floegel 2012). Our study suggests that climatic barriers at large spatial scales
587 (mostly the standard deviation in annual precipitation) limited the distributions of certain dinosaurian
588 taxa, probably as a result of physiological constraints and through the restriction of dietary habit
589 (Barrett 2014), although this suggestion remains to be empirically tested. For example, some
590 ornithischian herbivores could have been restricted to a particular group of plants requiring a limited
591 climatic regime (Engelmann *et al.* 2004; Noto & Grossman 2010; Mallon *et al.* 2012). The carnivorous
592 theropods, however, feeding at a higher trophic level, would have been less directly constrained by
593 annual variations in precipitation (see fig. 5; Engelmann *et al.* 2004). This reasoning is further

594 supported by the structuring role of the second phylogenetic component (PCPS2) underlying
595 geographical variation from ornithischians to basal coelurosaurs (García–Girón *et al.* 2020b, appendix
596 S2, fig. S3). This is an interesting finding because high megaherbivore diversity on Laramidia has been
597 hypothesised to result from non–limited resources (Ostrom 1964; Sampson 2009). However, following
598 Farlow (1987) and Mallon (2019), we speculate that this was not the case for the Maastrichtian
599 dinosaurs of the WIB (at continental scale), re–emphasising the importance of climate in driving
600 dinosaur community composition. Alternatively, these compositional gradients may be caused by
601 certain sets of taxa responding to climatic constraints in a similar manner (Chiarenza *et al.* 2019) or
602 that there were groups of dinosaurs that colonised the study area using the same migration routes (e.g.
603 Farke *et al.* 2014; Fiorillo *et al.* 2018).

604 Whatever the case, climatic barriers have been documented for a number of Cretaceous faunas,
605 including turtles, ornithomimid ornithischians, spinosaurid theropods, dyrosaurid and notosuchian
606 crocodyliforms, and mammals (Brinkman 2003; Novas *et al.* 2005; Mendeiros *et al.* 2007; Benson *et*
607 *al.* 2012). Perhaps more importantly, if the North American Late Cretaceous climate strongly
608 influenced dinosaur distributional patterns, this could introduce a misleading bias into those
609 palaeontological studies that attribute compositional variation solely to Laramide orogenies, allopatric
610 speciation and the eventual expansions and retractions of the WIS (Gates *et al.* 2012; Loewen *et al.*
611 2013). Similar to Benson *et al.* (2012), we are not suggesting that these mechanisms did not influence
612 Maastrichtian dinosaur distributions across the WIB, but that they only provide a partial explanation,
613 in which the role of climate might be underemphasised. However, whether or not climate showed clear
614 breakpoints across large spatial scales during the Maastrichtian world is still open to debate (Amiot *et*
615 *al.* 2004; Mannion *et al.* 2012; Upchurch *et al.* 2015), and a combination of internal, random or
616 contingent mechanisms might have partly driven the distributional patterns observed here. Although
617 our results do not provide a fully clear picture of the relationships between dinosaur metacommunity
618 structures and associated ecological gradients, they at least suggest that baseline comparisons among

619 different regions and organismal groups are worth additional studies for future palaeontological
620 research. Finally, the strong spatial responsiveness of dinosaurian communities to climatic barriers and
621 potential trophic relationships at different spatial grains and extents likely corroborates the
622 observations that global climatic drivers (Chiarenza *et al.* 2020) and a lower collapse threshold of the
623 North American trophic network in the Maastrichtian (Mitchell *et al.* 2012) were determinant agents
624 explaining their sudden end–Cretaceous extinction.

625 *Caveats*

626 Despite these encouraging findings, there are several potential caveats that must be carefully
627 highlighted due to common limitations of both palaeobiological reconstructions and our modelling
628 approach.

629 1. It seems unlikely that our limited dataset can accurately document the generalised global
630 patterns of dinosaur communities. For example, the almost complete absence of sauropod dinosaurs
631 in the latest Cretaceous of North America, compared with their relatively high diversity elsewhere, is
632 a strong evidence that these faunas are not representative of a global reality (Mannion *et al.* 2011;
633 Brusatte *et al.* 2015). While only *Alamosaurus* is currently recognised from the Maastrichtian of North
634 America (Williamson & Weil 2008; D’Emic *et al.* 2011), additional fragmentary material could
635 potentially reveal additional taxa in the future (e.g. see Fronimos and Lehman 2014). Given our current
636 knowledge, this distributional pattern suggests that one must be cautious when attempting to
637 extrapolate results from the limited geographical area that we studied here.

638 2. Despite the North American sedimentary record of Late Cretaceous dinosaur assemblages
639 being the most extensive worldwide, it is still imperfect. As elsewhere, raw data have been biased by
640 preservation and sampling artefacts, including chronologically averaged correlations, spatially biased
641 terrestrial sampling, incomplete preservation of delicate bones and small-bodied animals, erosion of
642 tetrapod-bearing sedimentary rocks, and low preservation potential of some biotopes (Horner *et al.*
643 2011; Barrett *et al.* 2009; Brown *et al.* 2013). For example, it is an unavoidable reality that vertebrate

644 fossil assemblages in terrestrial environments are biased against small-bodied animals (Clauset &
645 Erwin 2008; Brown *et al.* 2013). This different preservation potential of different sized taxa might
646 influence our understanding of dinosaurian distributions through Mesozoic history (Sereno 1999).
647 Therefore, taphonomic size biases must be further assessed before patterns of dinosaur
648 metacommunity structure can be considered accurate or used to compare and interpret the nature of
649 Late Cretaceous ecosystems. Similarly, studies on modern metacommunity patterns are limited to
650 relatively brief periods of sampling time. By contrast, the Maastrichtian stage represents *c.* 6 myr and
651 time averaging effects are undoubtedly confounding the data (*sensu* Vavrek & Larsson 2010). Hence,
652 the suggestion that all dinosaur communities maintained cohesive units seems unlikely, especially
653 when studies on shorter time scales during the Pleistocene have shown that mammal species reorganise
654 their communities in time scales of less than 2 myr (Potts & Deino 1995; McGill *et al.* 2005). At its
655 finest resolution, however, even the Hell Creek Formation is not well-enough dated or sampled to
656 examine community-level trends on a 1000–10000-year timescale (Pearson *et al.* 2002). In this
657 regard, although the dinosaur communities we studied here are not necessarily time-equivalent, they
658 represent a reasonable average of ecological conditions and are close enough to warrant empirical
659 comparison.

660 3. A contemporary challenge that requires more research attention is the assignment of functional
661 features to different dinosaurian taxa, a theme that continues to arouse passionate debate (Noto &
662 Grossman 2010; MacLaren *et al.* 2017; Mallon 2019). Fortunately, altering one or more features for
663 various taxa has little or no impact on our functional distance matrices (Pavoine *et al.* 2009), though
664 more than these might alter some of the results.

665 4. Mechanisms other than the surrounding environment might also affect compositional variation
666 among localities (Thompson *et al.* 2020). For example, dispersal constraints are very important for
667 metacommunity organisation at different spatial scales (Heino 2011). However, metacommunity
668 structure analysis based on site-by-taxon incidence matrices cannot explicitly detect the effects of

669 dispersal, even if they exist (Presley *et al.* 2010). This is because this type of approach indirectly
670 assumes that there is a latent ecological gradient driving variation in community composition (Presley
671 & Willig 2010). Indeed, the only way dispersal could potentially be identified by metacommunity
672 structure analysis would be if dispersal constraints were correlated with the latent ecological gradient
673 identified in the interaction matrix (Meynard *et al.* 2013).

674 5. As we did not measure all possible ecological correlates of metacommunity structure, it is
675 possible that some variables not measured affected Maastrichtian dinosaur communities within the
676 WIB. However, as we incorporated a set of ecological gradients that are known to be important
677 structuring variables in dinosaur-dominated ecosystems (Gates *et al.* 2010, 2012; Loewen *et al.* 2013;
678 Lucas *et al.* 2016; Chiarenza *et al.* 2019), this should not be a critical issue in our study.

679 6. Finally, including both avian lineages and interspecific interactions between dinosaurs and
680 other organismal groups inhabiting Late Cretaceous ecosystems might also alter the patterns we
681 observed here. Note, however, that allowing certain fixed boundaries when delineating community
682 types is not a concession to our limitations at identifying the multiple faunal elements of North
683 American Maastrichtian ecosystems, but rather a more operative characterisation of the potential
684 ecological drivers underlying dinosaurian distributions (Steen *et al.* 2017).

685 Importantly, these potential caveats do not dismiss the validity and significance of our results
686 but highlight the risk of too lenient interpretation of empirical data. Indeed, the patterns detected in
687 this study remain intriguing, and the addition of more organismal groups, study areas and ecological
688 settings would complement our results. This is a fruitful avenue that requires more research in the
689 future to enable deeper insights into metacommunity organisation of Mesozoic faunas.

690 **CONCLUSIONS**

691 A great deal of effort has been spent characterising diversity patterns through the Mesozoic
692 (e.g. Barrett *et al.* 2009; Mannion *et al.* 2012; Close *et al.* 2017); however, these estimates usually tell
693 us little about the ecological mechanisms (whether abiotic or biotic) responsible for producing these

694 patterns, nor how species were distributed in geographical space. Thus far, the simultaneous evaluation
695 of the elements of metacommunity structure (i.e. coherence, range turnover and range boundary
696 clumping) has never been used in analysis of fossil assemblages, although it offers a multitude of
697 opportunities to find patterns of compositional variation and community–environment relationships in
698 palaeobiological systems. When applied to dinosaur communities from the latest Cretaceous of North
699 America, we found that:

700 1. The degree of consistency of dinosaurian distributions with a specific idealised pattern, as well
701 as the identification of ecological mechanisms moulding those patterns, was somewhat contingent on
702 the spatial scale used for analysis, i.e. Clementsian and quasi–Clementsian metacommunity types
703 prevailed in the Hell Creek landscape, whereas quasi–nested subsets were more frequent when
704 multiple study geological formations within the WIB were examined together.

705 2. Dinosaurs were restricted in range to different parts of the Hell Creek Formation, prompting
706 the recognition of discrete and compartmentalised faunal areas during the Maastrichtian at fine–
707 grained scales.

708 3. The quasi–nested structure at the continental scale emphasises that species–poor dinosaur
709 faunas comprised subsets of those in progressively richer communities (i.e. taxa with the broadest
710 ranges included those taxa with progressively smaller ranges; Patterson & Atmar 1986). Importantly,
711 this previous finding indicates low range turnover across the latest Cretaceous of North America and
712 adds further evidence for a lack of provinciality and dinosaur endemism within the WIB.

713 4. All study dinosaur communities had clumped boundaries and indicated multiple ecologically–
714 important gradients when compensating for differences in sampling effort.

715 5. Regardless of dinosaur clade (here, ornithischians and theropods), compositional variation was
716 correlated with climatic barriers at the largest spatial scale, indicating that palaeoclimate is of primary
717 importance in determining the occurrence of dinosaurs, probably as a result of physiological
718 constraints and through the restriction of dietary habits.

719 6. Relationships mediated through trophic habits had a major role on variation in dinosaur
720 community composition in the Hell Creek landscape, thereby suggesting that dinosaurian faunas were
721 probably shaped by bottom–up and top–down forces at fine–grained scales.

722 It is worth stressing that this study does not attempt to explain how different metacommunity
723 structures arise among different dinosaur lineages and spatial scales; instead, it showed that they
724 arose, and explored the ecological implications that followed. Indeed, whatever the final conclusions
725 about dinosaur palaeoecology, the analytical tools applied in this study hopefully suggest a new way
726 of approaching the structure and associated ecological settings of ancient communities.

727 This study suggests several additional, potentially fertile lines of inquiry. For example,
728 additional work is needed when it comes to disentangling the effects of other internal (e.g. dinosaur
729 physiology in terms of their nutritional requirements, feeding adaptations, dispersal ability and habitat
730 preferences; Upchurch *et al.* 2002; Barrett & Rayfield 2006; MacLaren *et al.* 2017) and external (e.g.
731 geographical changes caused by variation in sea level and tectonic activity, pedotypes and
732 palynomorphs; Vavrek & Larsson 2010; Gates *et al.* 2012) mechanisms that might have influenced
733 dinosaur metacommunity structures and their associated ecological correlates. In this regard, the
734 applicability of our findings both within and beyond the Late Cretaceous of North America is subject
735 to testing with additional fossil datasets. To this end, further studies need to be conducted at global
736 and regional scales to capture a full picture of how communities and their ecological mechanisms
737 might interact. Similarly, we anticipate that future fossil discoveries will eventually enable the use of
738 reliable abundance data, which might prove to be more informative than simple binary (i.e. presence–
739 absence) data (see Mallon *et al.* 2012). Overall, if metacommunity structure analysis is used for a
740 wide–range of Mesozoic faunas and geographical areas, general associations may emerge among
741 particular distributional patterns and specific taxa, ecological settings and biogeographical contexts.
742 Once these baseline comparisons have been explored, we should collectively advance the goal of
743 understanding the circumstances under which ancient communities existed, interacted and evolved

744 within limits that are not so broad as to be meaningless. All of these ideas suggest that some excellent
745 opportunities for theoretical and methodological advances could occur on the interface between
746 palaeontology and metacommunity ecology.

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786

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788 JA. JGG carried out all analyses and led the writing of the manuscript. JH, JA, AAC and SLB
789 contributed to writing by commenting on the manuscript and/or the source datasets. All authors
790 contributed critically to the final draft and gave final approval for publication.

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793 DATA ARCHIVING STATEMENT

794 Occurrence data, palaeoenvironmental reconstructions, functional features and additional supporting
795 files for this study (including results and summary statistics) are available in the Dryad Digital
796 Repository:

797 https://datadryad.org/stash/share/mJ2_qGFy0ikvbX9T3xVmvgJvyenM523ZHWTVsH0ySUQ

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800 SUPPORTING INFORMATION

801 Additional supporting files can be found in the Dryad Digital Repository (García–Girón *et al.* 2020b):

802 Appendix S1. Body mass distributions based on product partition models with Markov
803 sampling computations

804 Appendix S2. Functional and phylogenetic features for each spatial scale and study clade.

805 Appendix S3. R packages and statistical routines.

806 Appendix S4. Elements of metacommunity structure for the conservative fixed–fixed null
807 model.

808 Appendix S5. Results for the forward selection of explanatory variables.

809 Appendix S6. Results for ordinary least squares (OLS) regression models.

810 Appendix S7. Results for commonality analysis (CA) for each spatial scale and study clade.

811 Appendix S8. Measuring the spatial autocorrelation of OLS model residuals.

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816 **REFERENCES**

- 817 AMIOT, R., LÉCUYER, C., BUFFETAUT, E., FLUTEAU, F., LEGENDRE, S. and MARTINEAU, F. 2004.
818 Latitudinal temperature gradient during the Cretaceous Upper Campanian–Middle Maastrichtian: $\delta^{18}\text{O}$ record
819 of continental vertebrates. *Earth and Planetary Science Letters*, **226**, 255–272.
- 820 BAPST, D. W. 2013. A stochastic rate–calibrated method for time–scaling phylogenies of fossil taxa. *Methods*
821 *in Ecology and Evolution*, **4**, 724–733.
- 822 BARRETT, P. M. 2014. Paleobiology of Herbivorous Dinosaurs. *Annual Review of Earth and Planetary*
823 *Sciences*, **42**, 207–230.
- 824 BARRETT, P. M. and RAYFIELD, E. J. 2006. Ecological and evolutionary implications of dinosaur feeding
825 behaviour. *Trends in Ecology and Evolution*, **21**, 217–224.
- 826 BARRETT, P. M., MCGOWAN, A. J. and PAGE, V. 2009. Dinosaur diversity and the rock record. *Proceeding*
827 *of the Royal Society B: Biological Sciences*, **276**, 2667–2674.
- 828 BARRY, D. and HARTIGAN, J. A. 1993. A Bayesian analysis for change point problems. *Journal of the*
829 *American Statistical Association*, **88**, 309–319.
- 830 BENSON, R. B. G. 2018. Dinosaur Macroevolution and Macroecology. *Annual Review of Ecology, Evolution,*
831 *and Systematics*, **49**, 379–408.
- 832 BENSON, R. B. G., RICH, T. H., VICKERS–RICH, P. and HALL, M. 2012. Theropod fauna from southern
833 Australia indicates high polar diversity and climate–driven dinosaur provinciality. *PLoS One*, **5**, e37122.
- 834 BENSON, R. B. G., CAMPIONE, N. E., CARRANO, M. T., MANNION, P. D., SULLIVAN, C.,
835 UPCHURCH, P. and EVANS, D. C. 2014. Rates of dinosaur body mass evolution indicate 170 million years
836 of sustained ecological innovation on the avian stem lineage. *PLoS Biology*, **12**, e1001896.
- 837 UPCHURCH, P., HUNT, G., CARRANO, M. T. and CAMPIONE, N. 2018. Cope’s rule and the adaptive
838 landscape of dinosaur body size evolution. *Palaeontology*, **61**, 12–48.
- 839 BENTON, M. J., DUNHILL, A. M., LLOYD, G. T. and MARX, F. G. 2011. Assessing the quality of the fossil
840 record: insights from vertebrates. 63–94. In MCGOWAN, A. J. and SMITH, A. B. (eds). *Comparing the*
841 *Geological and Fossil Records: Implications for Biodiversity Studies*. Geological Society, **358**, 310 pp.

- 842 BLANCHET, F. G., LEGENDRE, P. and BORCARD, D. 2008. Forward selection of explanatory variables.
843 *Ecology*, **89**, 2623–2632.
- 844 BORCARD, D., GILLET, F. and LEGENDRE, P. 2018. 2nd edn. *Numerical Ecology* with R. Springer
845 International Publishing, Luxemburg, 201 pp.
- 846 BRADSHAW, C. D., LUNT, D. J., FLECKER, R., SALZMANN, U., POUND, M. J., HAYWOOD, A. M. and
847 ERONEN, J. T. 2012. The relative roles of CO₂ and palaeogeography in determining late Miocene climate:
848 results from a terrestrial model–data comparison. *Climate of the Past*, **8**, 1257–1285.
- 849 BRINKMAN, D. B. 2003. A review of nonmarine turtles from the Late Cretaceous of Alberta. *Canadian*
850 *Journal of Earth Sciences*, **40**, 557–571.
- 851 BROCKLEHURST, N., KAMMERER, C. F. and FRÖBISCH, J. 2013. The early evolution of synapsids, and
852 the influence of sampling on their fossil record. *Paleobiology*, **39**, 470–490.
- 853 BROWN, C. M., EVANS, D. C., CAMPIONE, N. E., O'BRIEN, L. J. and EBERTH, D. A. 2013. Evidence for
854 taphonomic size bias in the Dinosaur Park Formation (Campanian, Alberta), a model Mesozoic terrestrial
855 alluvial–paralic system. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **372**, 108–122.
- 856 BRUSATTE, S. L., BUTLER, R. J., BARRETT, P. M., CARRANO, M. T., EVANS, D. C., LLOYD, G. T.,
857 MANNION, P. D., NORELL, M. A., PEPPE, D. J., UPCHURCH, P. and WILLIAMSON, T. E. 2015. The
858 extinction of the dinosaurs. *Biological Reviews*, **90**, 628–642.
- 859 BUTLER, R. J. and BARRETT, P. M. 2008. Palaeoenvironmental controls on the distribution of Cretaceous
860 herbivorous dinosaurs. *Naturwissenschaften*, **95**, 1027–1032.
- 861 BUTLER, R. J., BENSON, B. J., CARRANO, W. T., MANNION, P. D. and UPCHURCH, P. 2011. Sea level,
862 dinosaur diversity and sampling: investigating the 'common cause' hypothesis in the terrestrial realm.
863 *Proceeding of the Royal Society B: Biological Sciences*, **278**, 1165–1170.
- 864 CABIN, R. J. and MITCHELL, R. J. 2000. To Bonferroni or not to Bonferroni: When and how are the questions.
865 *Bulletin of the Ecological Society of America*, **81**, 246–248.
- 866 CAMPIONE, N. E. and EVANS, D. C. 2012. A universal scaling relationship between body mass and proximal
867 limb bone dimensions in quadrupedal terrestrial tetrapods. *BMC Biology*, **10**, 60.

- 868 CHIARENZA, A. A., MANNION, P. D., LUNT, D. J., FARNSWORTH, A., JONES, L. A., KELLAND, S–J.
869 and ALLISON, P. A. 2019. Ecological niche modelling does not support climatically–driven dinosaur diversity
870 decline before the Cretaceous/Paleogene mass extinction. *Nature Communications*, **10**, 1091.
- 871 CHIARENZA, A. A., FARNSWORTH, A., MANNION, P. D., LUNT, D. J., VALDES, P. J., MORGAN, J. V.
872 and ALLISON, P. A. 2020. Asteroid impact, not volcanism, caused the end–Cretaceous dinosaur extinction.
873 *Proceedings of the National Academy of Sciences of the United States of America*, **117**, 17084–17093.
- 874 CHIN, K., EBERTH, D. A., SCHWEITZER, M. H., RANDO, T. A., SLOBODA, W. J. and HORNER, J. R.
875 2003. Remarkable preservation of undigested muscle tissue within a Late Cretaceous tyrannosaurid coprolite.
876 *Palaios*, **18**, 286–294.
- 877 CLAUSET, A. and ERWIN, D. H. 2008. The evolution of species body size. *Science*, **321**, 399–401.
- 878 CLEMENTS, F. E. 1916. *Plant succession. An analysis of the development of vegetation*. Carnegie Institution,
879 Washington D. C., 588 pp.
- 880 CLOSE, R. A., BENSON, R. B. J., UPCHURCH, P. and BUTLER, R. J. 2017. Controlling for the species–area
881 effect supports constrained long–term Mesozoic terrestrial vertebrate diversification. *Nature Communications*,
882 **8**, 15381.
- 883 CODRON, D., CARBONE, C., MÜLLER, D. W. H. and CLAUSS, M. 2012. Ontogenetic niche shifts in
884 dinosaurs influenced size, diversity and extinction in terrestrial vertebrates. *Biology Letters*, **8**, 620–623.
- 885 COLLINS, M., TETT, S. F. B. and COOPER, C. 2001. The internal climate variability of HadCM3, a version
886 of the Hadley Centre coupled model without flux adjustments. *Climate Dynamics*, **17**, 61–81.
- 887 COOPER, H., HEDGES, L. V. and VALENTINE, J. C. 2009. 2nd edn. *The Handbook of Research Synthesis*.
888 Russel Sage Foundation, New York, 615 pp.
- 889 CRAMPTON, J. S., BEU, A. G., COOPER, R. A., JONES, C. M., MARSHALL, B. and MARWELL, P. A.
890 2003. Estimating the rock volume bias in paleobiodiversity studies. *Science*, **301**, 358–360.
- 891 DAVIES, T. J., MEIRI, S., BARRACLOUGH, T. G. and GITTLEMAN, J. L. 2007. Species co–existence and
892 character divergence across carnivores. *Ecology Letters*, **10**, 146–152.
- 893 DAVIS, J. C. 2002. 3rd edn. *Statistics and Data Analysis in Geology*. John Wiley & Sons, New York, 656 pp.

- 894 DEAN, C. D., CHIARENZA A. A. and MAIDMENT, S. C. R. 2020. Formation binning: a new method for
 895 increased temporal resolution in regional studies, applied to the Late Cretaceous dinosaur fossil record of North
 896 America. *Palaeontology*, published online 11 June 2020. doi: 10.1111/pala.12492
- 897 DEBASTIANI, V. J. and DUARTE, L. D. S. 2014. PCPS – an R–package for exploring phylogenetic
 898 eigenvectors across metacommunities. *Frontiers of Biogeography*, **6**, 144–148.
- 899 D’EMIC, M. D., WILSON, J. A. and WILLIAMSON, T. E. 2011. A sauropod dinosaur pes from the latest
 900 Cretaceous of North America and the validity of *Alamosaurus sanjuanensis* (Sauropoda, Titanosauria). *Journal*
 901 *of Vertebrate Paleontology*, **31**, 1072–1079.
- 902 DORMANN, C. F., ELITH, J., BACHER, S., BUCHMANN, C., CARL, G., CARRÉ, G., GARCÍA–
 903 MARQUÉZ, J. R., GRUBER, B., LAFOURCADE, B., LEITAO, P. J., MÜNKEMÜLLER, T., MCCLEAN,
 904 C., ORBORNE, P. E., REINEKING, B., SCHRÖDER, B., SKIDMORE, A. K., ZURELL, D. and
 905 LAUTENBACH, S. 2013. Collinearity: A review of methods to deal with it and a simulation study evaluating
 906 their performance. *Ecography*, **36**, 27–46.
- 907 DORMANN, C. F., BOBROWSKI, M., DEHLING, D. M., HARRIS, D. J., HARTIG, F., LISCHKE, H.,
 908 MORETTI, M. D., PAGEL, J., PINKERT, S., SCHLEUNING, M., SCHMIDT, S. I., SHEPPARD, C. S.,
 909 STEINBAUER, M. J., ZEUSS, D. and KRAAN, C. 2018. Biotic interactions in species distribution modelling:
 910 10 questions to guide interpretation and avoid false conclusions. *Global Ecology and Biogeography*, **27**, 1004–
 911 1016.
- 912 DUARTE, L. D. S., PRIETO, P. V. and PILLAR, V. D. 2012. Assessing spatial and environmental drivers of
 913 phylogenetic structure in Brazilian *Araucaria* forests. *Ecography*, **35**, 952–960.
- 914 DUNHILL, A. M., BESTWICK, J., NAREY, H. and SCIBERRAS, J. 2016. Dinosaur biogeographical structure
 915 and Mesozoic continental fragmentation: a network–based approach. *Journal of Biogeography*, **43**, 1691–1704.
- 916 ENGELMANN, G. F., CHURE, D. J. and FIORILLO, A. R. 2004. The implications of a dry climate for the
 917 paleoecology of the fauna of the Upper Jurassic Morrison Formation. *Sedimentary Geology*, **167**, 297–308.
- 918 FARKE, A. A., MAXWELL, W. D., CIFELLI, R. L. and WEDEL, M. J. 2014. A Ceratopsian dinosaur from
 919 the lower Cretaceous of Western North America, and the biogeography of Neoceratopsia. *PLoS One*, **9**,
 920 e112055.

- 921 FARLOW, J. O. 1987. Speculations about the diet and digestive physiology of herbivorous dinosaurs.
922 *Paleobiology*, **13**, 60–72.
- 923 FIORILLO, A. R., MCCARTHY, P. J., KOBAYASHI, Y., TOMSICH, C. S., TYKOSKI, R. S., LEE, Y–N.,
924 TANAKA, T. and NOTO, C. R. 2018. An unusual association of hadrosaur and therizinosaur tracks within Late
925 Cretaceous rocks of Denali National Park, Alaska. *Scientific Reports*, **8**, 11706.
- 926 FOSTER, G. L., ROYER, D. L. and LUNT, D. J. 2017. Future climate forcing potentially without precedent in
927 the last 420 million years. *Nature Communications*, **8**, 14845.
- 928 FOWLER, D. W. 2017. Revised geochronology, correlation, and dinosaur stratigraphic ranges of the
929 Santonian–Maastrichtian (Late Cretaceous) formations of the Western Interior of North America. *PLoS One*,
930 **12**, e0188426.
- 931 FOWLER, D. W. 2020. The Hell Creek Formation, Montana: A stratigraphic review and revision based on a
932 sequence stratigraphic approach. *Geosciences*, **10**, 435.
- 933 FOWLER, D. W. and FREEDMAN–FOWLER, E. A. 2020. Transitional evolutionary forms in chasmosaurine
934 ceratopsid dinosaurs: evidence from the Campanian of New Mexico. *PeerJ*, **8**, e9251.
- 935 FRASER, D., SOUL, L. C., TÓTH, A. B., BALK, M. A., ERONEN, J. T., PINEDA–MUÑOZ, S.,
936 SHUPINSKIM A. B., VILLASEÑOR, A., BARR, W. A., BEHRENSMEYER, A. K., DU, A., FAITH, J. T.,
937 GOTELLI, N. J., GRAVES, G. R., JUKAR, A. M., LOOY, C. V., MILLER, J. H., POTTS, R. and LYONS, S.
938 K. 2020. Investigating biotic interactions in deep time. *Trends in Ecology and Evolution*, published online 13
939 October 2020. doi: 10.1016/j.tree.2020.09.001
- 940 FRONIMOS, J. A. and LEHMAN, T. M. 2014. New specimens of a titanosaur sauropod from the Maastrichtian
941 of Big Bend National Park, Texas. *Journal of Vertebrate Paleontology*, **34**, 883–899.
- 942 GARCÍA–GIRÓN, J., HEINO, J., BAASTRUP–SPOHR, L., CLAYTON, J., DE WINTON, M., FELDMANN,
943 T., FERNÁNDEZ–ALÁEZ, C., ECKE, F., HOYER, M. V., KOLADA, A., KOSTEN, S., LUKÁCS, B. A.,
944 MORMUL, R. P., RHAZI, L., RHAZI, M., SASS, L., XU, J. and ALAHUHTA, J. 2020a. Elements of lake
945 macrophyte metacommunity structure: Global variation and community–environment relationships. *Limnology*
946 *and Oceanography*, published online 30 July 2020. doi: 10.1002/lno.11559

- 947 GARCÍA–GIRÓN, J., HEINO, J., ALAHUHTA, J., CHIARENZA A. A. and BRUSATTE, S. L. 2020b. Data
 948 from: Palaeontology meets metacommunity ecology: the Maastrichtian dinosaur fossil record of North America
 949 as a case study. *Dryad Digital Repository*.
 950 https://datadryad.org/stash/share/mJ2_qGFy0ikvbX9T3xVmvGJvyyenM523ZHWTvSH0ySUQ
- 951 GARCÍA–GIRÓN, J., HEINO, J., GARCÍA–CRIADO, F., FERNÁNDEZ–ALÁEZ, C. and ALAHUHTA, J.
 952 2020c. Biotic interactions hold the key to understanding metacommunity organisation. *Ecography*, **43**, 1180–
 953 1190.
- 954 GARCÍA–GIRÓN, J., HEINO, J., ALAHUHTA, J., CHIARENZA, A. A. and BRUSATTE, S. L. 2020c. Data
 955 from: Palaeontology meets metacommunity ecology: the Maastrichtian dinosaur fossil record of North America
 956 as a case study. FigShare Digital Repository. doi: 10.6084/m9.figshare.12896177
- 957 GASCÓN, S., ARRANZ, I., CAÑEDO–ARGÜELLES, M., NEBRA, A., RUHÍ, A., RERADEVALL, M.,
 958 CAIOLA, N., SALA, J., IBÁÑEZ, C., QUINTANA, X. D. and BOIX, D. 2016. Environmental filtering
 959 determines metacommunity structure in wetland microcrustaceans. *Oecologia*, **181**, 193–305.
- 960 GATES, T. A., SAMPSON, S. D., ZANNO, L. E., ROBERTS, E. M., EATON, J. G., NYDAM, R. L.,
 961 HUTCHISON, J. H., SMITH, J. A., LOEWEN, M. A. and GETTY, M. A. 2010. Biogeography of terrestrial
 962 and freshwater vertebrates from the late Cretaceous (Campanian) Western Interior of North America.
 963 *Palaeogeography, Palaeoclimatology, Palaeoecology*, **291**, 371–387.
- 964 GATES, T. A., PRIETO–MARQUEZ, A. and ZANNO, L. E. 2012. Mountain building triggered Late
 965 Cretaceous North American megaherbivore dinosaur radiation. *PLoS One*, **7**, e42135.
- 966 GLEASON, H. A. 1926. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical*
 967 *Club*, **53**, 7–26.
- 968 GOTELLI, N. J. 2000. Null model analysis of species co–occurrence patterns. *Ecology*, **81**, 2606–2621.
- 969 GOTELLI, N. J. and MCCABE, D. J. 2002. Species co–occurrence: A meta–analysis of J. M. Diamond’s
 970 assembly rules model. *Ecology*, **83**, 2091–2096.
- 971 HAY, W. W. and FLOEGEL, S. 2012. New thoughts about the Cretaceous climate and oceans. *Earth–Science*
 972 *Reviews*, **115**, 262–272.
- 973 HEINO, J. 2011. A macroecological perspective of diversity patterns in the freshwater realm. *Freshwater*
 974 *Biology*, **56**, 1703–1722.

- 975 HEINO, J. and ALAHUHTA, J. 2015. Elements of regional beetle faunas: faunal variation and compositional
976 breakpoints along climate, land cover and geographical gradients. *Journal of Animal Ecology*, **84**, 427–441.
- 977 HEINO, J. and TOLONEN, K. T. 2017. Ecological drivers of multiple facets of beta diversity in a lentic
978 macroinvertebrate metacommunity. *Limnology and Oceanography*, **62**, 2431–2444.
- 979 HEINO, J., MELO, A. S., SIQUEIRA, T., SOININEN, J., VALANKO, S. and BINI, L. M. 2015.
980 Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects.
981 *Freshwater Biology*, **60**, 845–869.
- 982 HENRIQUES–SILVA, R., LINDO, Z. and PERES–NETO, P. R. 2013. A community of metacommunities:
983 Exploring patterns of species distribution across large geographical scales. *Ecology*, **94**, 627–639.
- 984 HONE, D. W. E., CHOINIÈRE, J., SULLIVAN, C., XU, X., PITTMAN, M. and TAN, Q. 2010. New evidence
985 for a trophic relationship between the dinosaurs *Velociraptor* and *Protoceratops*. *Palaeogeography,*
986 *Palaeoclimatology, Palaeoecology*, **291**, 488–492.
- 987 HORNER, J. R., GOODWIN, M. B. and MYHRVOLD, N. 2011. Dinosaur census reveals abundant
988 *Tyrannosaurus* and rare ontogenetic stages in the Upper Cretaceous Hell Creek Formation (Maastrichtian),
989 Montana, USA. *PLoS One*, **6**, e16574.
- 990 IOSSA, G., SOULSBURY, C. D., BAKER, P. J. and HARRIS, S. 2008. Body mass, territory size, and life–
991 history tactics in a socially monogamous canid, the red fox *Vulpes vulpes*. *Journal of Mammalogy*, **89**, 1481–
992 1490.
- 993 JOHNSON, K. R. 2002. Megaflora of the Hell Creek and lower Fort Union Formation in North Dakota:
994 vegetational response to climate change, the Cretaceous–Tertiary boundary event, and rapid marine
995 transgression. 329–392. In HARTMAN, J. H., JOHNSON, K. R. and NICHOLS, D. J. (eds). *The Hell Creek*
996 *Formation and the Cretaceous–Tertiary boundary in the northern Great Plains: an integrated continental*
997 *record of the end of the Cretaceous*. Geological Society of America, Special Paper, **361**, 520 pp.
- 998 KRAHA, A., TURNER, H., NIMON, K., ZIENTEK, L. R. and HENSON, R. K. 2012. Interpreting multiple
999 regression in the face of multicollinearity. *Frontiers in Psychology*, **3**, 1–10.
- 1000 LAVERGNE, S., MOUQUET, N., THUILLER, W. and RONCE, O. 2010. Biodiversity and climate change:
1001 integrating evolutionary and ecological responses of species and communities. *Annual Review of Ecology,*
1002 *Evolution, and Systematics*, **41**, 321–350.

- 1003 LEHMAN, T. M. 1987. Late Maastrichtian paleoenvironments and dinosaur biogeography in the Western
1004 Interior of North America. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **60**, 189–217.
- 1005 LEHMAN, T. M. 2001. Late Cretaceous dinosaur provinciality. 310–328. In TANKE, D. H. and CARPENTER,
1006 K. (eds). *Mesozoic vertebrate life*. Indiana University Press, Bloomington and Indianapolis, 600 pp.
- 1007 LEIBOLD, M. A. and MIKKELSON, G. M. 2002. Coherence, species range turnover, and boundary clumping:
1008 elements of metacommunity structure. *Oikos*, **97**, 237–250.
- 1009 LEIBOLD, M. A., HOLYOAK, M., MOUQUET, N., AMARASEKARE, P., CHASE, J. M., HOOPEES, M. F.,
1010 HOLT, R. D., SHURIN, J. B., LAW, R., TILMAN, D., LOREAU, M. and GONZALEZ, A. 2004. The
1011 metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*, **7**, 601–613.
- 1012 LEVIN, S. A. 1992. The problem of patterns and scale in ecology. *Ecology*, **73**, 1943–1967.
- 1013 LI, S., XING, Y., VALDES, P. J., HUANG, Y., SU, T., FARNSWORTH, A., LUNT, D. J., TANG, H.,
1014 KENNEDY, A. T. and ZHOU, Z. 2018. Oligocene climate signals and forcings in Eurasia revealed by plant
1015 macrofossil and modelling results. *Gondwana Research*, **61**, 115–127.
- 1016 LLOYD, G. T. 2012. A refined modelling approach to assess the influence of sampling on palaeobiodiversity
1017 curves: new support for declining Cretaceous dinosaur richness. *Biology Letters*, **8**, 123–126.
- 1018 LLOYD, G. T., BAPST, D. W., FRIEDMAN, W. and DAVIS, K. E. 2016. Probabilistic divergence time
1019 estimation without branch lengths: dating the origins of dinosaurs, avian flight and crown birds. *Biology Letters*,
1020 **12**, 20160609.
- 1021 LOEUILLE, N. and LOREAU, M. 2006. Evolution of body size in food webs: does the energetic equivalence
1022 rule hold? *Ecology Letters*, **9**, 171–178.
- 1023 LOEWEN, M. A., IRMIS, R. B., SERTICH, J. W., CURRIE, P. J. and SAMPSON, S. D. 2013. Tyrant dinosaur
1024 evolution tracks the rise and fall of Late cretaceous oceans. *PLoS One*, **8**, 1–14.
- 1025 LOGUE, J. B., MOUQUET, N., PETER, H. and HILLEBRAND, H. 2011. Empirical approaches to
1026 metacommunities: a review and comparison with theory. *Trends in Ecology and Evolution*, **26**, 482–491.
- 1027 LUCAS, S. G., SULLIVAN, R. M., LICHTIG, A. J., DALMAN, S. G. and JASINSKI, S. E. 2016. Late
1028 Cretaceous dinosaur biogeography and endemism in the Western Interior Basin, North America: A critical re-
1029 evaluation. *New Mexico Museum of Natural History and Science Bulletin*, **71**, 195–213.

- 1030 LUNT, D. J., JONES, D., HEINEMANN, M., HUBER, M., LEGRANDE, A., WINGUTH, A., LOPTSON, C.,
1031 MAROTZKE, J., ROBERTS, C. D., TINDALL, J., VALDES, P. and WINGUTH, C. 2012. A model–data
1032 comparison for a multi–model ensemble of early Eocene atmosphere–ocean simulations: EoMIP. *Climate of*
1033 *the Past*, **8**, 1717–1736.
- 1034 LUNT, D. J., FARNSWORTH, A., LOPTSON, C., FOSTER, G. L., MARKWICK, P., O'BRIEN, C. L.,
1035 PANCOST, R. D., ROBINSON, S. A. and WROBEL, N. 2016. Palaeogeographic controls on climate and proxy
1036 interpretation. *Climate of the Past*, **12**, 1181–1198.
- 1037 LYSON, T. R. and LONGRICH, N. R. 2011. Spatial niche partitioning in dinosaurs from the latest cretaceous
1038 (Maastrichtian) of North America. *Proceeding of the Royal Society B: Biological Sciences*, **278**, 1158–1164.
- 1039 MACLAREN, J. A., ANDERSON, P. S. L., BARRETT, P. M. and RAYFIELD, E. J. 2017. Herbivorous
1040 dinosaur jaw disparity and its relationship to extrinsic evolutionary drivers. *Paleobiology*, **43**, 15–33.
- 1041 MALLON, J. C. 2019. Competition structured a Late Cretaceous megaherbivorous dinosaur assemblage.
1042 *Scientific Reports*, **9**, 15447.
- 1043 MALLON, J. C. and ANDERSON, J. S. 2013. Skull ecomorphology of megaherbivorous dinosaurs from the
1044 Dinosaur Park Formation (Upper Campanian) of Alberta, Canada. *PLoS One*, **8**, e67182.
- 1045 MALLON, J. C., EVANS, D. C., RYAN, M. J. and ANDERSON, J. S. 2012. Megaherbivorous dinosaur
1046 turnover in the Dinosaur Park Formation (upper Campanian) of Alberta, Canada. *Palaeogeography,*
1047 *Palaeoclimatology, Palaeoecology*, **350–352**, 124–138.
- 1048 MALLON, J. C., EVANS, D. C., RYAN, M. J. and ANDERSON, J. S. 2013. Feeding height stratification
1049 among the herbivorous dinosaurs from the Dinosaur Park Formation (upper Campanian) of Alberta, Canada.
1050 *BMC Ecology*, **13**, 14.
- 1051 MANNION, P. D., UPCHURCH, P., CARRANO, M. T. and BARRETT, P. M. 2011. Testing the effect of the
1052 rock record on diversity: a multidisciplinary approach to elucidating the generic richness of sauropodomorph
1053 dinosaurs through time. *Biological Reviews*, **86**, 157–181.
- 1054 MANNION, P. D., BENSON, R. B. J., UPCHURCH, P., BUTLER, R. J., CARRANO, M. T. and BARRETT,
1055 P. M. 2012. A temperate palaeodiversity peak in Mesozoic dinosaurs and evidence for Late Cretaceous
1056 geographical partitioning. *Global Ecology and Biogeography*, **21**, 898–908.

- 1057 MCGILL, B. J., HADLY, E. A. and MAURER, B. A. 2005. Community inertia of Quaternary small mammal
1058 assemblages in North America. *Proceedings of the National Academy of Sciences of the United States of*
1059 *America*, **102**, 16701–16706.
- 1060 MENDEIROS, M. A., FREIRE, P. C. and PEREIRA, A. A. 2007. Another African dinosaur recorded in the
1061 paleofauna of the Laje do Coringa site. *Paleontologia: Cenários de Vida*, **1**, 413–423.
- 1062 MEYNARD, C. N., LAVERGNE, S., BOULANGEAT, I., GARRAUD, L., VAN ES, J., MOUQUET, N. and
1063 THUILLER, W. 2013. Disentangling the drivers of metacommunity structure across spatial scales. *Journal of*
1064 *Biogeography*, **40**, 1560–1571.
- 1065 MITCHELL, J. S., ROOPARINE, P. D. and ANGIELCZYK, J. D. 2012. Late Cretaceous restructuring of
1066 terrestrial communities facilitated the end–Cretaceous mass extinction in North America. *Proceedings of the*
1067 *National Academy of Sciences of the United States of America*, **109**, 18857–18861.
- 1068 MURPHY, E. C., HOGANSON, J. W. and JOHNSON, K. R. 2002. Lithostratigraphy of the Hell Creek
1069 Formation in North America. 9–34. In HARTMAN, J. H., JOHNSON, K. R. and NICHOLS, D. J. (eds). *The*
1070 *Hell Creek Formation and the Cretaceous–Tertiary boundary in the northern Great Plains: an integrated*
1071 *continental record of the end of the Cretaceous*. Geological Society of America, Special Paper, **361**, 520 pp.
- 1072 MURRAY–STOKER, D. and MURRAY–STOKER, K. M. 2020. Consistent metacommunity structure despite
1073 inconsistent drivers of assembly at the continental scale. *Journal of Animal Ecology*, **89**, 1678–1689.
- 1074 NATHANS, L., OSWALD, F. L. and NIMON, K. 2012. Interpreting multiple linear regression: a guidebook of
1075 variable importance. *Practical Assessment Research & Evaluation*, **17**, 1–19.
- 1076 NOTO, C. R. and GROSSMAN, A. 2010. Broad–scale patterns of Late Jurassic dinosaur paleoecology. *PLoS*
1077 *One*, **9**, e12553.
- 1078 NOVAS, F. E., DELLA VECCHIA, F. and PAIS, D. 2005. Theropod pedal unguals from the Late Cretaceous
1079 (Cenomanian) of Morocco, Africa. *Revista del Museo Argentino de Ciencias Naturales Bernardino Rivadavia*,
1080 **7**, 167–175.
- 1081 O’SULLIVAN, J. D., KNELL, R. J. and ROSSBERG, A. G. 2019. Metacommunity–scale biodiversity
1082 regulation and the self–organised emergence of macroecological patterns. *Ecology Letters*, **22**, 1428–1438.
- 1083 OSTROM, J. H. 1964. *The Strange World of Dinosaurs*. Putnam Pub Group, New York, 128 pp.

- 1084 PATTERSON, B. D. and ATMAR, W. 1986. Nested subsets and the structure of insular mammal faunas and
1085 archipelagos. *Biological Journal of the Linnaean Society*, **28**, 65–82.
- 1086 PAVOINE, S., VALLET, J., DUFOUR, A–B., GACHET, S. and DANIEL, H. 2009. On the challenge of
1087 treating various types of variables: application for improving the measurement of functional diversity. *Oikos*,
1088 **118**, 391–402.
- 1089 PEARSON, D. A., SCHAEFER, T., JOHNSON, K. R., NICHOLS, D. J. and HUNTER, J. P. 2002. Vertebrate
1090 biostratigraphy of the Hell Creek Formation in southwestern Dakota and northwestern South Dakota.
1091 *Geological Society of America Special Papers*, **361**, 145–167.
- 1092 POTTS, R. and DEINO, A. 1995. Mid–Pleistocene change in large mammal faunas of East Africa. *Quaternary*
1093 *Research*, **43**, 106–113.
- 1094 PRESLEY, S. J. and WILLIG, M. R. 2010. Bat metacommunity structure on Caribbean islands and the role of
1095 endemics. *Global Ecology and Biogeography*, **19**, 185–199.
- 1096 PRESLEY, S. J., HIGGINGS, C. L., LÓPEZ–GONZÁLEZ, C. and STEVENS, R. D. 2009. Elements of
1097 metacommunity structure in Paraguayan bats: multiple gradients require analysis of multiple ordination axes.
1098 *Oecologia*, **160**, 781–793.
- 1099 PRESLEY, S. J., HIGGINGS, C. L. and WILLIG, M. R. 2010. A comprehensive framework for the evaluation
1100 for metacommunity structure. *Oikos*, **119**, 908–917.
- 1101 PRESLEY, S. J., CISNEROS, L. M., PATTERSON, B. D. And WILLIG, M. R. 2012. Vertebrate
1102 metacommunity structure along an extensive elevational gradient in the tropics: a comparison of bats, rodents
1103 and birds. *Global Ecology and Biogeography*, **21**, 968–976.
- 1104 R DEVELOPMENT CORE TEAM. 2019. *R: A language and environment for statistical computing*. R
1105 Foundation for Statistical Computing, Vienna.
- 1106 RAY–MUKHERJEE, J., NIMON, K., MUKHERJEE, S., MORRIS, D. W., SLOTOW, R. and HAMER, M.
1107 2014. Using commonality analysis in multiple regressions: a tool to decompose regression effects in the face of
1108 multicollinearity. *Methods in Ecology and Evolution*, **5**, 320–328.
- 1109 REES, P.C., NOTO, C., PARRISH, J. M. and PARRISH, J. T. 2004. Late Jurassic climates, vegetation, and
1110 dinosaur distributions. *The Journal of Geology*, **112**, 643–654.

- 1111 ROBECK, H. E., MALEY, C. C. and DONOGHUE, M. J. 2000. Taxonomy and temporal diversity patterns.
 1112 *Paleobiology*, **26**, 171–187.
- 1113 SAMPSON, S. D. 2009. *Dinosaur Odyssey: Fossil Threats in the Web of Life*. University of California Press,
 1114 Berkeley, 352 pp.
- 1115 SAMPSON, S. D., LOEWEN, M. A., FARKE, A. A., ROBERTS, E. M., FORSTER, C. A., SMITH, J. A. and
 1116 TITUS, A. L. 2010. New horned dinosaurs from Utah provide evidence for intracontinental dinosaur endemism.
 1117 *PLoS One*, **5**, 1–12.
- 1118 SCOTESE, C. R. and WRIGHT, N. 2018. *PALEOMAP Paleodigital Elevation Models (PaleoDEMS) for the*
 1119 *Phanerozoic*. Unpublished, <https://www.earthbyte.org/paleodem-resource-scotese-and-wright-2018/>
- 1120 SERENO, P. C. 1999. The evolution of dinosaurs. *Science*, **284**, 2137–2147.
- 1121 STEEN, D. A., BARRETT, K. and GUYER, C. 2017. Conceptualizing communities as natural entities: a
 1122 philosophical argument with basic and applied implications. *Biology & Philosophy*, **32**, 1019–1034.
- 1123 THOMPSON, P. L., GUZMAN, L. M., DE MEESTER, L., HORVÁTH, Z., PTACNIK, R.,
 1124 VANSCHOENWINKEL, B., VIANA, D. S. and CHASE, J. M. 2020. A process-based metacommunity
 1125 framework linking local and regional community ecology. *Ecology Letters*, **23**, 1314–1329.
- 1126 TILMAN, D. 1982. *Resource competition and community structure*. Princeton University Press, New Jersey,
 1127 310 pp.
- 1128 UPCHURCH, G. R., OTTO–BLIESNER, B. L. and SCOTESE, C. R. 1999. Terrestrial vegetation and its effects
 1129 on climate during the latest Cretaceous. *Special Paper of the Geological Society of America*, **332**, 407–426.
- 1130 UPCHURCH, G. R., HUNN, C. A. and NORMAN, D. B. 2002. An analysis of dinosaurian biogeography:
 1131 evidence for the existence of vicariance and dispersal patterns caused by geological events. *Proceeding of the*
 1132 *Royal Society B: Biological Sciences*, **269**, 613–621.
- 1133 UPCHURCH, G. R., KIEHL, J., SHIELDS, C., SCHERER, J. and SCOTESE, C. 2015. Latitudinal temperature
 1134 gradients and high-latitude temperatures during the latest Cretaceous: Congruence of geologic data and climate
 1135 models. *Geology*, **43**, 683–686.
- 1136 VALDES, P. J., ARMSTRONG, E., BADGER, M. P. S., BRADSHAW, C. D., BRAGG, F., CRUCIFIX, M.,
 1137 DAVIES–BARNARD, T., DAY, J. J., FARNSWORTH, A., GORDON, C., HOPCROFT, P. O., KENNEDY,
 1138 A. T., LORD, N. S., LUNT, D. J., MARZOCCHI, A., PARRY, L. M., POPE, V., ROBERTS, W. H. G., STONE,

- 1139 E. J., TOURTE, G. J. L. and WILLIAMS, J. H. T. 2017. The BRIDGE HadCM3 family of climate models:
1140 HadCM3@Bristol v.1.0. *Geoscientific Model Development*, **10**, 3715–3743.
- 1141 VARRICCHIO, D. J. 2001. Gut contents from a Cretaceous tyrannosaurid: implications for theropod digestive
1142 tracts. *Journal of Paleontology*, **75**, 401–406.
- 1143 VAVREK, M. J. and LARSSON, H. C. E. 2010. Low beta diversity of Maastrichtian dinosaurs of North
1144 America. *Proceedings of the National Academy of Science of the United States of America*, **107**, 8265–8268.
- 1145 VIANA, D. S. and CHASE, J. M. 2019. Spatial scale modulates the inference of metacommunity assembly
1146 processes. *Ecology*, **100**, e02576.
- 1147 WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. 2004. 2nd edn. *The dinosauria*. University of
1148 California Press, Berkely, 861 pp.
- 1149 WHITESIDE, J. H., LINDSTRÖM, S., IRMIS, R. B., GLASSPOOL, I. J., SCHALLER, M. F., DUNLAVEY,
1150 M., NESBITT, S. J., SMITH, N. D. and TURNER, A. H. 2015. Extreme ecosystem instability suppressed
1151 tropical dinosaur dominance for 30 million years. *Proceedings of the National Academy of Sciences of the*
1152 *United States of America*, **112**, 7909–7913.
- 1153 WILLIAMSON, T. E. and WEIL, A. 2008. Stratigraphic distribution of sauropods in the Upper Cretaceous of
1154 the San Juan Basin, New Mexico, with comments on North America’s Cretaceous ‘sauropod hiatus’. *Journal*
1155 *of Vertebrate Paleontology*, **28**, 1218–1223.
- 1156 WILLIG, M. R. and PRESLEY, S. J. 2016. Biodiversity and metacommunity structure of animals along
1157 altitudinal gradients in tropical montane forests. *Journal of Tropical Ecology*, **32**, 421–436.
- 1158 WILLIS, J. H. and WHITTAKER, R. J. 2002. Species diversity–scale matters. *Science*, **295**, 1245–1248.
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1166 **FIGURE CAPTIONS**

1167 **FIG. 1.** Conceptual illustration showing the idealised patterns of species distributions (from top to bottom,
 1168 evenly spaced, Clementsian, hyperdispersed species loss, and clumped species loss gradients, see Table 1)
 1169 expected under different metacommunity scenarios. *White circles* refer to different study sites (e.g. different
 1170 geological formations or different discrete dinosaur-bearing collections) and *dinosaur silhouettes* represent the
 1171 genera. *Colour rectangles* indicate differences in environmental conditions (here, defined by two niche axes
 1172 along which species segregate), whereas species tolerance and optima are represented by *black vertical lines*
 1173 and *black points*, respectively. *Ellipses* show the species niche breadth (i.e. the actual functional niche space
 1174 that each species experiences over space and time) with different colours indicating contrasting environmental
 1175 conditions. Here, we only show opposite situations in the type of range turnover (i.e. the number of species
 1176 replacements, with *species turnover* corresponding to the first two examples and *species loss* corresponding to
 1177 examples 3 and 4) and range boundary clumping (i.e. indicating the discrete vs. continuous nature of community
 1178 boundaries, with *hyperdispersed boundaries* corresponding to examples 1 and 3 and *clumped range boundaries*
 1179 corresponding to examples 2 and 4). If community boundaries are clumped (i.e. groups of taxa have coincident
 1180 range boundaries), it means that a single taxon represents the boundary of the ecological gradient for a number
 1181 of sites (sites representing an environmental boundary or ecotone). Silhouettes of representative dinosaurs were
 1182 previously available under Creative Commons licenses (see Acknowledgements).

1183 **FIG. 2.** Schematic representation describing Leibold & Mikkelsen's (2002) elements of metacommunity
 1184 structure (i.e. coherence, range turnover and range boundary clumping). After randomisation tests, the
 1185 combination of coherence (i.e. the degree to which species distributions are moulded by a common latent
 1186 ecological gradient), range turnover (i.e. how often species ranges replace each other) and range boundary
 1187 clumping (i.e. how often multiple species have their range limits in the same study sites) results in seven main
 1188 metacommunity types (random, random species loss, hyperdispersed species loss, clumped species loss, evenly
 1189 spaced, Clementsian and Gleasonian gradients; bold font; see Table 1) and six quasi-structures (quasi-evenly
 1190 spaced, quasi-Clementsian, quasi-Gleasonian, quasi-hyperdispersed species loss, quasi-random species loss
 1191 and quasi-clumped species loss gradients; non-bold font; see Table 1). Presence-absence matrices
 1192 corresponding to the principal metacommunity types are represented as follows: columns indicate different taxa

1193 and rows represent sites (here, different geological formations or different discrete dinosaur-bearing
 1194 collections). Figure modified from Presley *et al.* (2010) and García–Girón *et al.* (2020a). *MI*, Morisita’s Index.

1195 **FIG. 3.** Schematic representation of the idealised metacommunity structures (*Clementsian* and *quasi–*
 1196 *Clementsian*, in which taxa ranges form groups, which replace each other along ecologically–important
 1197 gradients; *quasi–clumped species loss*, in which taxa ranges form quasi–nested groups with discrete community
 1198 boundaries) of **(a)** Hell Creek and **(b)** North American dinosaur faunas (ornithischians and theropods) plotted
 1199 in the space of the *Z*–scores of coherence and range turnover for the primary (dark–coloured silhouettes) and
 1200 secondary (light–coloured silhouettes) axes of ordination extracted via RA. Silhouette size denotes the index of
 1201 range boundary clumping. Dashed lines indicate *Z*–scores between -1.96 and 1.96 . See Table 2 for values of
 1202 the *Z*–scores for coherence, range turnover and the Morisita’s index of dispersion. Silhouettes of representative
 1203 dinosaurs were previously available under Creative Commons licenses (see Acknowledgements).

1204 **FIG. 4.** Relative importance of different ecological mechanisms on the primary (dark–coloured bars) and
 1205 secondary (light–coloured bars) components of dinosaur faunas extracted via RA. We represent the effect sizes
 1206 (obtained through OLS regressions) of each variable in explaining dinosaur distributions (ornithischians and
 1207 theropods) at different spatial scales (i.e. regional, pink bars; and continental, green bars). Effect size was
 1208 measured using Fisher’s *Z*, which allows for comparison among analyses ($*p \leq 0.05$, $**p \leq 0.01$, $***p \leq$
 1209 0.001). *CrnvRA1*, interaction matrix scores from the first ordination axis of carnivorous dinosaur communities;
 1210 *CrnvRA2*, interaction matrix scores from the second ordination axis of carnivorous dinosaur communities;
 1211 *HbvRA1*, interaction matrix scores from the first ordination axis of herbivorous dinosaur communities; *HbvRA2*,
 1212 interaction matrix scores from the second ordination axis of herbivorous dinosaur communities; *PCOI*,
 1213 functional space from the first axis of principal coordinate analysis; *PCPS1*, phylogenetic space from the first
 1214 axis of principal coordinates of phylogenetic structure; *PCPS2*, phylogenetic space from the second axis of
 1215 principal coordinates of phylogenetic structure; *PrecSDann*, annual precipitation standard deviation; and
 1216 *TempSDann*, near surface [1.5 m] annual temperature standard deviation. Silhouettes of representative dinosaurs
 1217 were previously available under Creative Commons licenses (see Acknowledgements).

1218 **FIG. 5.** Schematic illustration of the main results obtained in this study. The colour scales correspond with
 1219 those of Fig. 4. Hell Creek dinosaur communities **(a)** showed positive coherence (i.e. dinosaur distributions
 1220 were moulded by common latent ecological gradients), positive range turnover (i.e. the observed replacements

1221 were lower than expected by chance) and had coincident range boundaries, thereby leading to Clementsian and
1222 quasi–Clementsian gradients (i.e. dinosaur ranges formed discrete and compartmentalised groups, which
1223 replaced each other along the latent ecological gradient). On the other hand, dinosaur communities also fitted
1224 with quasi–Clementsian structures and formed quasi–nested subsets with discrete boundaries when different
1225 geological formations from the WIB of North America were examined together (**b**). The most important
1226 ecological correlates for variation in dinosaur community composition varied among clades and spatial scales,
1227 with relationships between herbivores and carnivores dominating at regional scale, while climatic drivers were
1228 more dominant at continental scales (Fig. 4). *CrnvRAs*, interaction matrix scores from the first two ordination
1229 axes of carnivorous dinosaur communities; *HbvRAs*, interaction matrix scores from the first two ordination axes
1230 of herbivorous dinosaur communities; *PCOI*, functional space from the first axis of principal coordinate
1231 analysis; *PCPS1*, phylogenetic space from the first axis of principal coordinates of phylogenetic structure;
1232 *PCPS2*, phylogenetic space from the second axis of principal coordinates of phylogenetic structure; *PrecSDann*,
1233 annual precipitation standard deviation; and *TempSDann*, near surface [1.5 m] annual temperature standard
1234 deviation. Silhouettes of representative dinosaurs were previously available under Creative Commons licenses
1235 (see Acknowledgements).

1236 **TABLE 1.** A glossary of some of the most relevant concepts dealt with in this paper.

1237 **TABLE 2.** Results of the elements of metacommunity structure analysis for Maastrichtian dinosaurs of the WIB
1238 of North America at different spatial scales.