

Palaeontology

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

by JORGE GARCÍA–GIRÓN^{1*}, JANI HEINO², JANNE ALAHUHTA³,
ALFIO ALESSANDRO CHIARENZA⁴ *and* STEPHEN L. BRUSATTE⁵

¹Ecology Unit, University of León, Campus de Vegazana S/N, 24071, León, Spain

²Finnish Environment Institute, Freshwater Centre, P.O. Box 413, FI–90014 Oulu, Finland

³Geography Research Unit, University of Oulu, P.O. Box 3000, FI–90014 Oulu, Finland

⁴Department of Earth Sciences, University College London, WC1E 6BT, London, UK

⁵School of GeoSciences, University of Edinburgh, Grant Institute, James Hutton Road, Edinburgh EH9 3FE, UK

JORGE GARCÍA–GIRÓN: jogarg@unileon.es **ORCID ID:** 0000–0003–0512–3088

JANI HEINO: jani.heino@environment.fi **ORCID ID:** 0000–0003–1235–6613

JANNE ALAHUHTA: Janne.Alahuhta@oulu.fi **ORCID ID:** 0000–0001–5514–9361

ALFIO ALESSANDRO CHIARENZA: a.chiarenza15@gmail.com **ORCID ID:** 0000–0001–5525–6730

STEPHEN L. BRUSATTE: Stephen.Brusatte@ed.ac.uk **ORCID ID:** 0000–0001–7525–7319

**Corresponding author:* jogarg@unileon.es – *Telephone number:* +34987293404 – *Fax number:* +34987293404

ABSTRACT

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

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

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

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

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

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

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

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

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

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

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

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

MATERIAL AND METHODS

Dinosaur occurrence test dataset

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

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

Explanatory data

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

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

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

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

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

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

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

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

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

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

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

Metacommunity analyses using site–by–taxon incidence matrices

We examined the elements of dinosaur metacommunity structure based on the original 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).

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

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

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

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

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

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

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

Linear regression models

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

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

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

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

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

RESULTS

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

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

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

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

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

DISCUSSION

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Caveats

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

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

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

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

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

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

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

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

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

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

CONCLUSIONS

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

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

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

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

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

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

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

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

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

This study suggests several additional, potentially fertile lines of inquiry. For example, additional work is needed when it comes to disentangling the effects of other internal (e.g. dinosaur physiology in terms of their nutritional requirements, feeding adaptations, dispersal ability and habitat preferences; Upchurch *et al.* 2002; Barrett & Rayfield 2006; MacLaren *et al.* 2017) and external (e.g. geographical changes caused by variation in sea level and tectonic activity, pedotypes and palynomorphs; Vavrek & Larsson 2010; Gates *et al.* 2012) mechanisms that might have influenced dinosaur metacommunity structures and their associated ecological correlates. In this regard, the applicability of our findings both within and beyond the Late Cretaceous of North America is subject to testing with additional fossil datasets. To this end, further studies need to be conducted at global and regional scales to capture a full picture of how communities and their ecological mechanisms might interact. Similarly, we anticipate that future fossil discoveries will eventually enable the use of reliable abundance data, which might prove to be more informative than simple binary (i.e. presence–absence) data (see Mallon *et al.* 2012). Overall, if metacommunity structure analysis is used for a wide–range of Mesozoic faunas and geographical areas, general associations may emerge among particular distributional patterns and specific taxa, ecological settings and biogeographical contexts. Once these baseline comparisons have been explored, we should collectively advance the goal of 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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Author contributions. JGG conceived the original ideas of this study, with contributions from JH and JA. JGG carried out all analyses and led the writing of the manuscript. JH, JA, AAC and SLB contributed to writing by commenting on the manuscript and/or the source datasets. All authors contributed critically to the final draft and gave final approval for publication.

DATA ARCHIVING STATEMENT

Occurrence data, palaeoenvironmental reconstructions, functional features and additional supporting files for this study (including results and summary statistics) are available in the Dryad Digital Repository:
https://datadryad.org/stash/share/mJ2_qGFy0ikvbX9T3xVmvGJvyenM523ZHWTVsH0ySUQ

SUPPORTING INFORMATION

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

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

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

Appendix S3. R packages and statistical routines.

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

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

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

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

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

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FIGURE CAPTIONS

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

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

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

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

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

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

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

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

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