Cretaceous-Palaeogene extinction does not affect mammalian disparity.

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Abstract

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Introduction

Throughout history, life on Earth has suffered a series of mass extinction events resulting in drastic declines in global biodiversity (e.g. Raup, 1979; Benton and Twitchett, 2003; Renne et al., 2013; Brusatte et al., 2015). However, the long-term effects of mass extinctions are more varied (Erwin, 1998), and include species richness increases in some clades (Friedman, 2010) or declines in others (Benton, 1985), changes in morphological diversity (Ciampaglio et al., 2001; Ciampaglio, 2004; Korn et al., 2013) and shifts in ecological dominance (e.g. Brusatte et al., 2008b; Toljagic and Butler, 2013; Benson and Druckenmiller, 2014). These shifts are characterized by the decline of one clade that is replaced by a different unrelated clade with a similar ecological role (e.g. Brachiopoda and Bivalvia at the end Permian extinction; Sepkoski 1981; Clapham et al. 2006 but see Payne et al. 2014). Shifts in ecological dominance are of particular interest because they are a fairly common pattern observed in the fossil record (e.g. Foraminifera; D'Hondt et al. 1996; Coxall et al. 2006; Ichtyosauria; Thorne et al. 2011; Plesiosauria; Benson and Druckenmiller 2014) and are often linked to major macroevolutionary processes such as adaptive (Losos, 2010) or competitive radiations (Brusatte et al., 2008b).

One classical example of a shift in ecological dominance is at the Cretaceous-Palaeogene (K-Pg) mass extinction 66 million years ago (Renne et al., 2013), where the non-avian dinosaurs went extinct, potentially leading to the "rise of the age of the mammals" (Archibald, 2011; Lovegrove et al., 2014). This is based on the idea

3

that placental mammals were able to diversify after the extinction of many terrestrial vertebrates at the K-Pg boundary (including the dominant non-avian dinosaur group; Luo 2007; Archibald 2011; O'Leary et al. 2013; Brusatte et al. 2015). Some authors suggest this reflects placental mammals filling the "empty" niches left after the K-Pg event (Archibald, 2011), others suggest it reflects a release from predation and/or competition (Lovegrove et al., 2014). However, evidence for the diversification of placental mammals after the K-Pg event is mixed. Thorough analysis of the fossil record (e.g. Goswami et al., 2011; O'Leary et al., 2013) supports the idea that placental mammals diversified after the K-Pg event as there are no undebated placental mammal fossils before the K-Pg event and many afterwards (Archibald, 2011; Goswami et al., 2011; Slater, 2013; O'Leary et al., 2013; Wilson, 2013; Brusatte et al., 2015). Conversely, evidence from molecular data suggests that the diversification of placental mammals started prior to the K-Pg extinction event without being drastically affected by it (e.g. Douady and Douzery 2003; Bininda-Emonds et al. 2007; Meredith et al. 2011; Stadler 2011 or Beck and Lee 2014 using morphological data as well). Therefore, whether the diversification of placental mammals began before the K-Pg event, or in response to the extinctions at the K-Pg event, is a matter of great debate (dos Reis et al., 2012; O'Leary et al., 2013; Springer et al., 2013; OLeary et al., 2013; dos Reis et al., 2014).

There are two main reasons why there is still debate about the timing of the diversification of placental mammals. In this paper we focus on solving these issues as follows:

1. **Palaeontological and neontological data show different patterns**. As mentioned above, conclusions about when placental mammals diversified tend to be split depending on what kind of data are used: palaeontological data generally suggest that placental mammals diversified post K-Pg (e.g. O'Leary et al., 2013), whereas neontological data suggest that K-Pg event had little to no effect on mammalian diversification (Bininda-Emonds et al., 2007; Meredith et al., 2011; Stadler, 2011). Fortunately a recently successfully implemented method allows to use cladistic data for both living and fossil taxa along with molecular data for living taxa (the Total Evidence method; Eernisse and Kluge, 1993; Ronquist et al., 2012). This method can also be combined with the tip-dating method (Ronquist et al., 2012; Wood et al., 2013) to get more accurate estimates of diversification times for both fossil and living species (but see Arcila et al., 2015). Recently, two study have been published using the Total Evidence and tip-dating methods to study (1) variation in mammalian body mass (Slater, 2013) and (2) diversification rates (Beck and Lee, 2014) around the K-Pg boundary. Slater (2013) found good support for a shift in mammalian body mass evolution pattern before and after the K-Pg boundary suggesting a clear effect of the K-Pg boundary on mammalian body mass diversification. Whereas, Beck and Lee (2014) found mixed result on diversification rates supporting both a diversification of placental mammals before ("ancient dates" hypothesis) or after ("accelerated rates" hypothesis) the K-Pg boundary.

2. **Diversity can be defined in different ways.** Diversity is a difficult concept to define. In many studies it is measured as phylogenetic diversity or species richness (Stadler, 2011; Meredith et al., 2011; O'Leary et al., 2013), but often the more interesting aspect of diversity is related to the ecological niches the species occupy (Wesley-Hunt, 2005; Brusatte et al., 2008b; Toljagic and Butler, 2013), particularly if we want to make hypotheses about macroevolutionary processes (Pearman et al., 2008; Olson and Arroyo-Santos, 2009; Losos, 2010; Glor, 2010). Sometimes phylogenetic diversity is used as a proxy for other kinds of diversity, however, species richness can be decoupled from morphological diversity (Slater et al., 2010; Ruta et al., 2013; Hopkins, 2013), so phylogenetic diversity may not be the best proxy for ecological diversity. For example in Slater (2013), the diversity of mammalian body mass is studied instead as the sheer number of species. In this particular case, body mass diversity rather than species diversity can be a better proxy for describing mammalian diversity. One can also use morphological diversity, also known as disparity (e.g. Wills et al., 1994; Erwin, 2007; Hughes et al., 2013), as a way to quantify changes in mammalian diversity that should relate to the ecology of the species. However some methods form measuring disparity are outdated and make inappropriate assumptions. Many studies quantifying changes in morphological diversity were proposed > 20 years ago (Foote, 1994; Wills et al., 1994) and are sometimes used without modifications (e.g., Brusatte et al., 2008a,b; Cisneros and Ruta, 2010; Thorne et al., 2011; Prentice

6

88   et al., 2011; Brusatte et al., 2012; Toljagic and Butler, 2013; Ruta et al., 2013; Benton

89   et al., 2014; Benson and Druckenmiller, 2014), even when the statistical

90   assumptions of the methods are violated (see Methods). Additionally, previous

91   methods are based on an underlying assumption that changes in disparity occur

92   by punctuated evolution (e.g. Wesley-Hunt, 2005) which is not always the case

93   (Hunt et al., 2015). Finally, most studies of disparity through time use unequal

94   time units based on biostratigraphy (Brusatte et al., 2008b, 2012; Toljagic and

95   Butler, 2013). This can be tautological as biostratigraphy is already based on

96   changes in fossil assemblages and morphology through time.

97   Here, we propose an updated approach to test whether mammals diversified

98   before or after K-Pg, using morphological disparity, measured as cladistic disparity (see

99   Methods), as our proxy for diversity. We measured the disparity of living and fossil

100   mammals taken from two previously published studies (Slater, 2013; Beck and Lee,

101   2014). Using a novel time-slicing approach we produce fine-grain estimates of disparity

102   through time under two different models of morphological character evolution (either

103   gradual or punctuated). Finally, to test whether mammals display significant changes

104   in disparity after the K-Pg boundary, we tested whether there is significant changes in

105   disparity through time. When an effect of time was detected, we ran post-hoc tests to

106   measure if there is any significant difference between the disparity at the end of the

107   Cretaceous and the disparity throughout the Cenozoic. We found no significant

108   changes in mammalian disparity between the end of the Cretaceous and any time

7

during the Cenozoic. These results suggest that the extinction of non-avian dinosaurs

any many other terrestrial vertebrate clades at the end of the Cretaceous did not affect

mammalian evolution.

Methods

Cladistic data and phylogenies

We used the cladistic morphological matrices and the Total Evidence tip-dated trees

(Ronquist et al., 2012) from Slater (2013, 103 taxa with 446 morphological characters)

and Beck and Lee (2014, 102 taxa with 421 morphological characters). We chose these

two data sets because they have a similar number of taxa and morphological characters.

Slater (2013) ranges from 310 million years ago (Mya; Late Carboniferous) to the

present and focuses on the clade Mammaliaformes at the family-level. Beck and Lee

(2014) ranges from 170 Mya (Middle Jurassic) to the present and focuses on Eutherians

at the genus-level. We used the first and last occurrences reported in Slater (2013) and

Beck and Lee (2014) as the temporal range of each taxon in our analysis. Both

phylogenies are illustrated in the supplementary material (see Figure S1 and S2 @@@).

Estimating ancestral character states

For both datasets we used the re-rooting method (Yang et al., 1996; Garland and Ives,

2000) to get Maximum Likelihood estimates of the ancestral states for each character at

every node in the tree, using the `rerootingMethod` function from the `R` package

`phytools` (version 0.4-45; Revell, 2012; R Core Team, 2015). Where there was missing

character data for a taxon we followed the method of Lloyd (2015) and treated missing

data as any possible observed state for each character. For example, if a character had

two observed states (0 and 1) across all taxa, we attributed the multi-state "0&1" value

to the taxon with missing data, representing an equal probability of being either 0 or 1.

This allows the ancestral node of a taxon with missing data to be estimated with no

assumptions other than that the taxon has one of the observed character states. To

prevent poor ancestral state reconstructions from biasing our results, especially when a

lot of error is associated with the reconstruction, we only included ancestral state

reconstructions with a scaled Likelihood $\geq$ 0.95. Ancestral state reconstructions with

scaled Likelihoods below this threshold were replaced by missing data ("?").

Building the cladisto-space

To explore variations in mammalian disparity through time (defined here as the

variation in morphologies through time), we use a cladisto-space approach (e.g. Foote,

1994, 1996; Wesley-Hunt, 2005; Brusatte et al., 2008b; Friedman, 2010; Toljagic and

Butler, 2013; Hughes et al., 2013). This approach is similar to constructing a

morphospace based on continuous morphological data (e.g. Friedman, 2010), except a

cladisto-space is an approximation of the morphospace based on cladistic data (i.e. the

discrete morphological characters used to build a phylogenetic tree). Mathematically, a

cladisto-space is an n dimensional object that summarizes the cladistic distances

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between the taxa present in a cladistic matrix (see details below). Hetherington et al.

(2015) have empirically shown inter-taxon distances are not different in a morphospace

or a cladisto-space. However, we prefer referring to this object as a cladisto-space to

make it clear that this space is estimated using cladistic data and not morphometric

data and because both objects have slightly different properties. In fact, because of its

inherent combinatory properties, a cladisto-space is a finite theoretical object limited by

the product of the number of character states (c.f. the morphospace that is an infinite

theoretical object). Thus a cladisto-space will be overloaded if the number of taxa is

higher than the product of the number of character states, although this is rarely an

issue with empirical data (our cladisto-spaces have maximal capacities of 1.9×10^{181}

taxa; Slater, 2013, and 4.5×10^{159} taxa; Beck and Lee, 2014).

To estimate the cladisto-spaces for each of our datasets we first constructed

pairwise distance matrices of length k, where k is the total number of taxa in the

dataset. For each dataset separately, we calculated the $k \times k$ distances using the Gower

distance (Gower, 1971), i.e. the Euclidean distance between two taxa divided by the

number of shared characters. This allows us to correct for distances between two taxa

that share many characters and could be closer to each other than to taxa with fewer

characters in common (i.e. because some pairs of taxa share more characters in

common than others, they are more likely to be similar). For cladistic matrices, using

this corrected distance is preferable to the raw Euclidean distance because of its ability

to deal with discrete or/and ordinated characters as well as with missing data

169 (Anderson and Friedman, 2012). However, the Gower distance cannot calculate

170 distances when taxa have no overlapping data. Therefore, we used the

171 `TrimMorphDistMatrix` function from the `Claddis` R package (Lloyd, 2015) to remove

172 pairs of taxa with no cladistic characters in common. This led us to remove 11 taxa

173 from Slater (2013) but none from Beck and Lee (2014).

174   After calculating our distance matrices we transformed them using classical

175 multidimensional scaling (MDS; Torgerson, 1965; Gower, 1966; Cailliez, 1983). This

176 method (also referred to as PCO; e.g. Brusatte et al. 2015; or PCoA; e.g. Paradis et al.

177 2004) is an eigen decomposition of the distance matrix. Because we used Gower

178 distances instead of raw Euclidean distances, negative eigenvalues can be calculated. To

179 avoid this problem, we first transformed the distance matrices by applying the Cailliez

180 correction (Cailliez, 1983) which adds a constant c^* to the values in a distance matrix

181 (apart from the diagonal) so that all the Gower distances become Euclidean

182 ($d_{Gower} + c^* = d_{Euclidean}$; Cailliez 1983). We were then able to extract n eigenvectors for

183 each matrix (representing the n dimensions of the cladisto-space) where n is equal to

184 $k - 2$, i.e. the number of taxa in the matrix (k) minus the two last eigenvector which are

185 always null after applying the Cailliez correction. Contrary to previous studies (e.g

186 Brusatte et al., 2008a; Cisneros and Ruta, 2010; Prentice et al., 2011; Anderson and

187 Friedman, 2012; Hughes et al., 2013; Benton et al., 2014), we use all n dimensions of our

188 cladisto-spaces and not a sub-sample representing the majority of the variance in the

189 distance matrix (e.g. selecting only m dimensions that represent up to 90% of the

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variance in the distance matrix; Brusatte et al. 2008b; Toljagic and Butler 2013).

Note that our cladisto-spaces represent an ordination of all possible mammalian morphologies coded in each study through time. It is unlikely that all morphologies will co-occur at each time point, therefore, the disparity of the whole cladisto-space is expected to be $\geq$ the disparity at any specific point in time.

Calculating disparity

Disparity can be estimated in many different ways (e.g. Wills et al., 1994; Ciampaglio, 2004; Thorne et al., 2011; Hopkins, 2013; Huang et al., 2015), however most studies estimate disparity using four metrics: the sum and products of ranges and variances, each of which gives a slightly different estimate of how the data fits within the cladisto-space (Foote, 1994; Wills et al., 1994; Brusatte et al., 2008a,b; Cisneros and Ruta, 2010; Thorne et al., 2011; Prentice et al., 2011; Brusatte et al., 2012; Toljagic and Butler, 2013; Ruta et al., 2013; Benton et al., 2014; Benson and Druckenmiller, 2014). The sum and products of ranges and variances are based on the ranges and variances of the eigenvectors calculated from a distance matrix. However, these metrics do not take into account the covariance among eigenvectors. This is only statistically valid if the eigenvectors are independent. In multidimensional scaling, all n eigenvectors are calculated from the same distance matrix and are therefore not independent, thus covariances among eigenvectors should be included when estimating disparity. Furthermore, range metrics are also strongly affected by the uneven sampling of the fossil record (Butler et al., 2012) Additionally, because we include all n dimensions in

12

the analysis (see above), the products of ranges and variances will tend towards zero since the scores of the last dimension are usually really close to zero themselves. These features make using the sum and products of ranges and variances unfeasible in our study. Instead, we use a different metric that comes with no statistical assumptions for measuring the dispersion of the data in the cladisto-space: the median distance from centroid (similar but not equivalent to Wills et al. 1994; Korn et al. 2013; Huang et al. 2015) calculated as:

$$Disparity = Md\sqrt{\sum_{i=1}^{k}(\mathbf{v}_{n_i} - Centroid_n)^2} \tag{1}$$

where:

$$Centroid_n = \frac{\sum_{i=1}^{k}(\mathbf{v}_{n_i})}{k} \tag{2}$$

k is the size of the distance matrix (i.e. the total number of taxa), $\mathbf{v}_n$ is any of the n eigenvectors (i.e. any of the n dimension of the cladisto-space), $Centroid_n$ is the centroid euclidean distance of the nth eigenvector (equation 2) and Md is the median value of the distance from centroid (equation 1). Note that we also calculated the sum and products of ranges and variances in the supplementary material (@@@).

Estimating disparity through time

Changes in disparity through time are generally investigated by calculating the disparity of taxa that occupy the cladisto-space during specific time intervals (e.g Cisneros and Ruta, 2010; Prentice et al., 2011; Hughes et al., 2013; Hopkins, 2013;

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Benton et al., 2014; Benson and Druckenmiller, 2014). These time intervals are usually

defined based on biostratigraphy (e.g. Cisneros and Ruta, 2010; Prentice et al., 2011;

Hughes et al., 2013; Benton et al., 2014) but can also be arbitrarily chosen time periods

of equal duration (Butler et al., 2012; Hopkins, 2013; Benson and Druckenmiller, 2014).

However, this approach suffers from two main biases. First, if biostratigraphy is used to

determine the time intervals, disparity may be distorted towards higher differences

between time intervals because biostratigraphical periods are geologically defined

based on differences in the morphology of fossils found in the different strata. Second,

this approach assumes that all characters evolve following a punctuated equilibrium

model, because disparity is only estimated once for each interval resulting in all

changes in disparity occurring between intervals, rather than also allowing for gradual

changes within intervals (Hunt et al., 2015).

To address these issues, we use a "time-slicing" approach that considers subsets

of taxa in the cladisto-space at specific equidistant points in time, as opposed to

considering subsets of taxa between two points in time. This results in even-sampling

of the cladisto-space across time and permits us to define the underlying model of

character evolution (such as punctuated or gradual). In practice, time-slicing considers

the disparity of any element present in the phylogeny (branches, nodes and tips) at any

point in time. When the phylogenetic elements are nodes or tips, the eigenvector scores

for the nodes (estimated using ancestral state reconstruction as described above) or tips

are directly used for estimating disparity. When the phylogenetic elements are branches

14

249 we chose the eigenvector score for the branch using one of two evolutionary models:

250 1. **Punctuated evolution.** This model selects the eigenvector score from either the
251   ancestral node or the descendant node/tip of the branch regardless of the position
252   of the slice along the branch. Similarly to the time interval approach, this reflects
253   a model of punctuated evolution where changes in disparity occur either at the
254   start or at the end of a branch over a relatively short time period and clades
255   undergo a long stasis period during their evolution (Gould and Eldredge, 1977;
256   Hunt, 2007). We applied this model in three ways:

257   (i) selecting the eigenvector score of the ancestral node of the branch

258   (ii) selecting the eigenvector score of the descendant node/tip of the branch

259   (iii) randomly selecting either the eigenvector score of the ancestral node or the
260   descendant node/tip of the branch

261   Method (i) assumes that changes always occurs early on the branch (accelerated
262   transition, ACCTRAN) and (ii) assumes that changes always occur later (delayed
263   transition, DELTRAN). We prefer not to make either assumption so we report the
264   results from (iii), although the ACCTRAN and DELTRAN results are available in
265   the Supplementary Information @@@.

266 2. **Gradual evolution.** This model also selects the eigenvector score from either the
267   ancestral node or the descendant node/tip of the branch, but the choice depends
268   on the distance between the sampling time point and the end of the branch. If the

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269   sampling time point falls in the first half of the branch length the eigenvector

270   score is taken from the ancestral node, conversely, if the sampling time point falls

271   in the second half of the branch length the eigenvector score is taken from the

272   descendant node/tip. This reflects a model of gradual evolution where changes in

273   disparity are gradual and cumulative along the branch. Under this model, the

274   gradual changes could be either directional or random, however, directional

275   evolution have been empiricaly shown to be rare (only 5% of the time Hunt, 2007).

276   We therefore considered that changes from a character state A to B where just

277   dependant on the branch length.

278   We applied our time-slicing approach to the two cladisto-spaces calculated from Slater

279   (2013) and Beck and Lee (2014), time-slicing the phylogeny every five million years

280   from 170 Mya to the present resulting in 35 sub-samples of the cladisto-space. For each

281   sub-sample, we estimated its disparity assuming punctuated (ACCTRAN, DELTRAN

282   and random) and gradual evolution as described above. To reduce the influence of

283   outliers on our disparity estimates, we bootstrapped each disparity measurement by

284   randomly re-sampling with replacement a new sub-sample of taxa from the observed

285   taxa in the sub-sample 1000 times. We then calculated the median disparity value for

286   each sub-sample along with the 50% and the 95% confidence intervals.

287   We also reported the number of phylogenetic elements (branches, nodes and

288   tips) in each sub-sample representing the observed taxonomic diversity. Disparity may

289   be higher in sub-samples with more phylogenetic elements simply because there are

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290 more taxa represented. To test whether our analyses were biased in this way, we

291 rarefied our sub-samples during the bootstrap procedure by randomly re-sampling a

292 fix number of taxa across each sub-sample. In Slater (2013), the minimum number of

293 taxa in each sub-sample from 170 to present was 8. In Beck and Lee (2014), the

294 minimum number of taxa however was 3, however, from 150 Mya until the present, the

295 minimum number of taxa is 8. To make both data sets comparable, we used 8 as a

296 minimum number of taxa for the rarefied bootstrap measurements in Beck and Lee

297 (2014) ignoring therefore the sub-sample between 170 and 150 Mya. We report both

298 results of the bootstrapped measurements and the rarefied bootstrap measurements.

299   To compare our results to previous studies we also repeated our analyses using

300 the time interval approache based on biostratigraphy (e.g. Cisneros and Ruta, 2010;

301 Prentice et al., 2011; Hughes et al., 2013; Benton et al., 2014) using each geological stage

302 from the Middle Jurassic to the present. We report the results of these analyses in the

303 Supplementary Materials (@@@).

304   Finally, to assess if the K-Pg boundary had a significant effect on mammals

305 disparity, we performed Anderson (2001)'s Permutational Analysis of Variance (also

306 referred to as PERMANOVA or NPANOVA; e.g. Brusatte et al., 2008a; Ruta et al., 2013)

307 to test whether there was a significant effect of time on our calculated disparity. We

308 calculated the euclidean distance of the ordinated data with 1000 permutations on both

309 data sets and on both evolutionary scenario using the `adonis` function from the `R`

310 package `vegan` (Oksanen et al., 2015). When a significant effect of time on disparity was

17

measured, we ran a series of *post-hoc* t-test between the time sub-samples (Anderson and Friedman, 2012; Zelditch et al., 2012; Smith et al., 2014) to test whether there was a significant effect between of the K-Pg boundary. We measured the difference between the last sub-sample of the Cretaceous (65 Mya) to all the slices of the Cenozoic to test whether there was either:

1. no effect of the K-Pg event: no significant difference between the last Cretaceous sub-sample and any of the Cenozoic sub-samples.

2. a direct effect of the K-Pg event: significant difference between the last Cretaceous sub-sample and the first Cenozoic sub-sample.

3. a lag effect of the K-Pg event: a significant difference between the last Cretaceous sub-sample and some sub-samples during the Cenozoic.

Because these *post-hoc* t-tests involve multiple p-values (13 comparisons), we corrected each p-value by multiplying them by the number of comparisons (Holm-Bonferonni correction; Holm, 1979).

Results

Both data sets do display a change in taxonomic diversity after and before the K-Pg boundary (Figure 1): respectively a decrease in Eutherians (data from Beck and Lee, 2014) and an increase in Mammaliaformes (data from Slater, 2013). However, these variations in taxonomic diversity are not linked with changes in disparity (Figure 2). In

18

330 both data sets, we measured similar changes in morphological disparity in the last 170

331 Million years for both the full data sets and the rarefied data sets (Figure 1 and 2) We

332 measured a significant effect of time on disparity in Eutherians under both gradual and

333 punctuated evolution model and in Mammaliaformes only under the gradual evolution

334 model only (table 1). For the Eutherians data set, we detected at least one significant

335 difference between the disparity in the last sub-sample of the Cretaceous and any

336 sub-sample of the Cenozoic suggesting an effect of the K-Pg boundary on disparity

337 (table 2). However, once corrected for taxonomic diversity, we did not detect any

338 significant difference, either under gradual or punctuated evolution model (table 3). For

339 the Mammaliaformes data set under gradual evolution model, there was no significant

340 difference between the disparity in the last sub-sample of the Cretaceous and any

341 sub-sample of the Cenozoic in both the raw and the rarefied data (table 4).
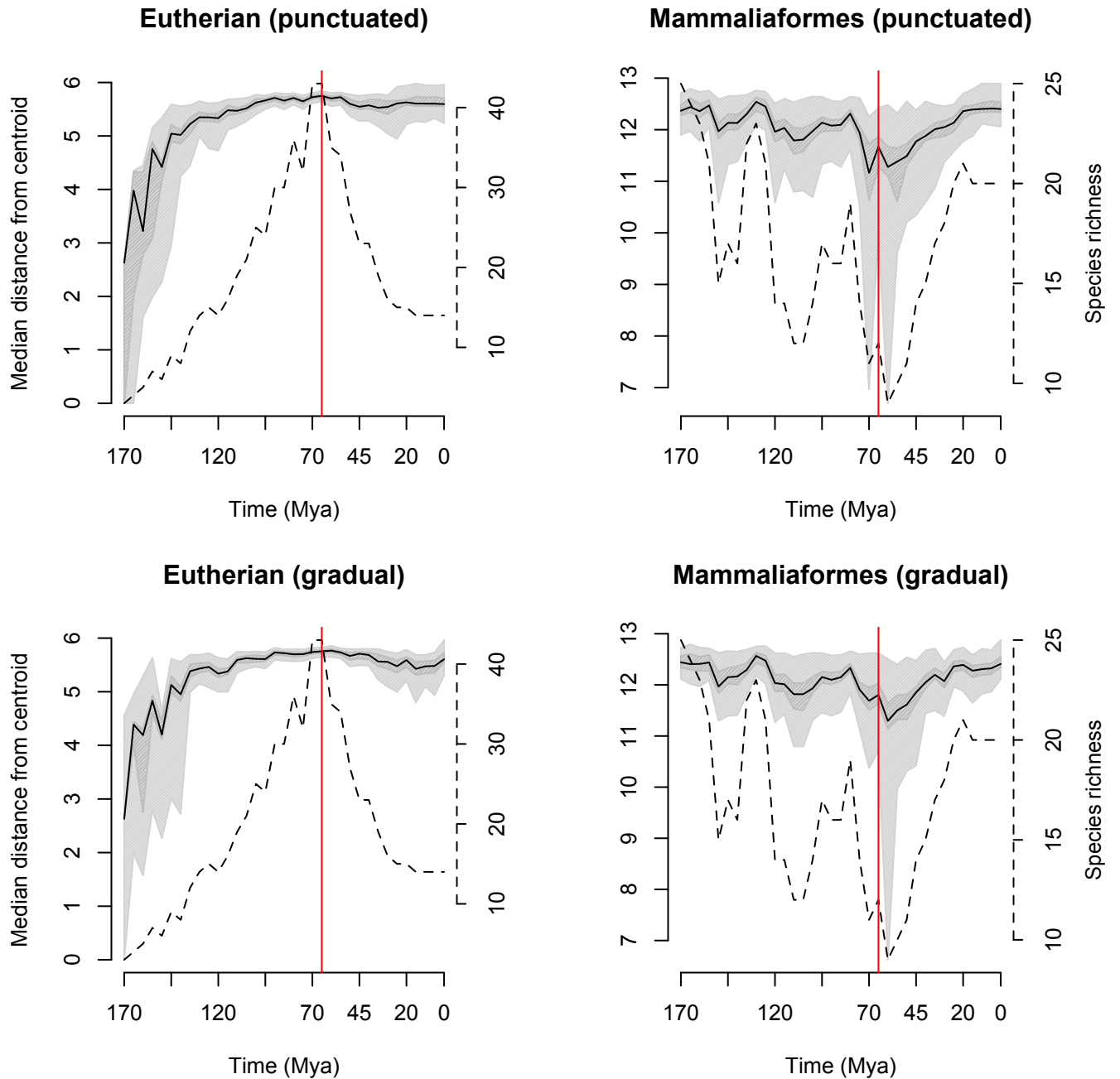
Figure 1: Observed variations of disparity through time among Eutherian and Mammaliaformes under punctuated or gradual evolution model. The x axis represents the time in Million of years ago (Mya). The y axis represents the disparity measured as the median distance from centroid per sub-sample. The solid black lines is the mean disparity from the bootstrapped pseudo-replicates, the confidence intervals (CI) are represent by the grey polygons (50% CI in dark grey and 95% CI in light grey). The dashed line represent the species richness in each sub-sample (values are reported on the right hand
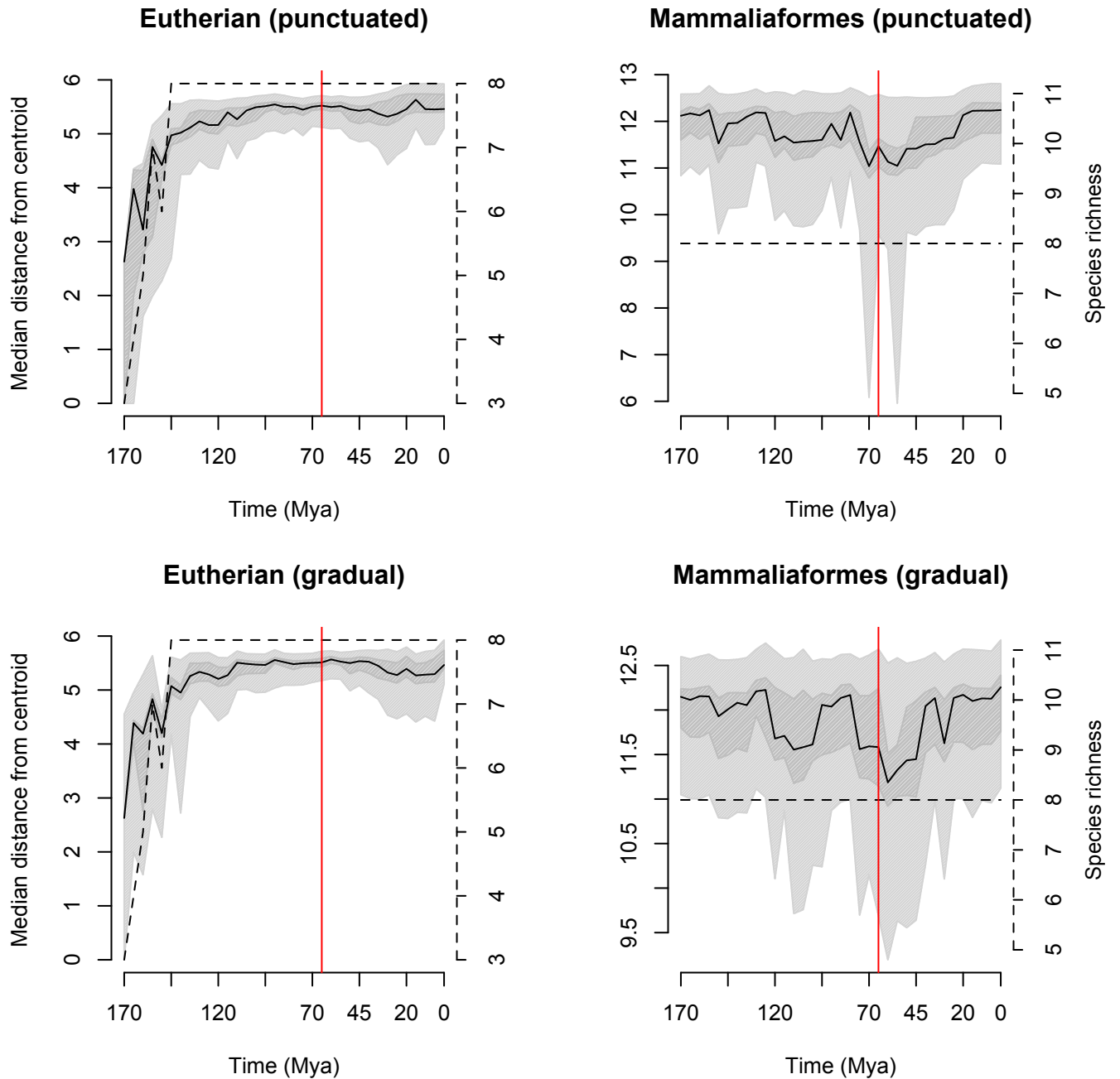
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Figure 2: Rarefied variations of disparity through time among Eutherian and Mammaliaformes under punctuated or gradual evolution model. The x axis represents the time in Million of years ago (Mya). The y axis represents the disparity measured as the median distance from centroid per sub-sample. The solid black lines is the mean disparity from the bootstrapped pseudo-replicates; the confidence intervals (CI) are represent by the grey polygons (50% CI in dark grey and 95% CI in light grey). The dashed line represent the species richness in each sub-sample (values are reported on the right hand side of

Table 1: Permanova results of testing the effect of time on the ordinated distance matrix using euclidean distance with 1000 permutations. Data: Eutherian (data from Beck and Lee, 2014); Mammaliaformes, (data from Slater, 2013). Model: evolutionary model. Significant effects are highlighted in bold: one star (*) signifies a p-value between 0.05 and 0.005; two starts between 0.005 and 0.0005 and three stars < 0.0005.

Data	model	terms	Df	Sum of squares	Mean sum of squares	F Model	R^2	p-value	
Eutherian	gradual	time	34	1825.92	53.703	1.5784	0.0769	**0.0009**	***
		residuals	644	21911.65	34.024		0.9231		
	punctuated	time	34	1597.07	46.973	1.3693	0.0674	**0.0009**	***
		residuals	644	22092.28	34.305		0.9326		
Mammaliaformes	gradual	time	34	6525.61	191.930	1.1660	0.0663	**0.0009**	***
		residuals	558	91852.55	164.610		0.9337		
	punctuated	time	34	5741.25	168.860	1.0167	0.0583	0.2248	
		residuals	558	92672.75	166.080		0.9417		

Discussion

Our results show that there is a significant effect of time on changes in disparity under the assumption of gradual evolution in Mammaliaformes and Eutherians as well as under the assumption of punctuated evolution for Eutherians (table 1). However, regardless the taxonomic level (i.e. family *vs.* genus) and regardless the evolutionary model (i.e. gradual or punctuated evolution), there is no significant difference in disparity between the latests Cretaceous sub-sample and any of the Cenozoic sub-samples (Figure 2). In fact the disparity seems to reach a plateau at the end of the Jurassic (150 Mya) for Eutherians and during the late Triassic (Norian; 220 Mya) for the Mammaliaformes and stays relatively constant after that (see Figure 2 and S4 @@@). These results shows that, within the frame of our data-sets, we did not detect any short term or long term effect of the K-Pg event on mammalian disparity. Therefore, we argue that the extinction of the many terrestrial vertebrates (namely non-avian dinosaurs) at the K-Pg boundary did not directly affected mammals evolution during the Cenozoic, or at least their morphological diversity.

Global pattern of disparity

The observed global patterns of changes in disparity are consistent with previous studies on mammalian disparity and on disparity in metazoans in general. The patterns of disparity seems to plateau at their maximum disparity early in their history (approximatively after 25% and 12% of their history in respectively Mammaliaformes

23

and Eutherians). In fact, this quick increase in disparity early in history is consistent with disparity patterns in metazoans (Hughes et al., 2013). Additionally, as showed previously, disparity display a pattern decoupled from taxonomic diversity (Slater et al., 2010; Ruta et al., 2013; Hopkins, 2013).

Effect of the K-Pg boundary on mammalian disparity

The results for the Mammaliaformes data-set disparity variation are consistent with the most recent studies of Mammalian disparity, showing and early peak of disparity in the Early to Middle Jurassic (Close et al., 2015). However, our results for Eutherians differ from Grossnickle and Polly (2013) that showed a significant decrease in disparity during the late Cretaceous (but see Wilson et al., 2012). These differences can be due to the different input data to calculate disparity (morphometric data in Grossnickle and Polly 2013; and cladistic data in the present study; but see Hetherington et al. 2015), the different method to calculate disparity through time (time bin in Grossnickle and Polly 2013; and time slicing in the present study; see below) or the different focal morphological aspect (dental morphology in Grossnickle and Polly 2013; and overall - including dental - morphology in the present study). Furthermore, we found a fundamental difference with Slater (2013) which shows solid evidences for a change in mode of body mass evolution at the K-Pg boundary using the same data set as in this study. We argue that this difference can be due to the number of traits used in Slater (2013) and the present study. In this study we look at an aggregate of discrete traits (the 446 morphological characters) in opposition of one continuous trait (body mass in

24

Slater, 2013). Both variation in morphology (i.e. from cladistic data) and variation in body mass are two different and aspects of diversity and can likely be decoupled in the same way as taxonomic diversity is decoupled from disparity. However, we believe our results show some robustness because the same absence of signal of an eventual effect the K-Pg boundary as been found in two independent data sets (i.e. Slater, 2013; Beck and Lee, 2014). Furthermore, our results only suggest that disparity is not affected by the K-Pg boundary but they do not allow us to assess the effect of the K-Pg boundary on changes in body mass evolution. Besides, few caveats can be underlined.

Firstly, both our data sets are limited. They do not represent the full known mammalian taxonomic diversity, especially during the Neogene (23–2.58 Mya) where no fossils were represented in both data sets. However, this might not cause a serious under-sampling problem, at least in the Mammaliaformes dataset, since their diversity peaked during the late Cretaceous (Campanian; 72.1–83.6 Mya; Newham et al., 2014). Additionally Raia et al. (2012) have shown that mammalian diversification rates declined throughout the whole Cenozoic. In our study, these findings could suggest that an effect of the K-Pg boundary would be more likely detected during the Palaeogene when mammalian diversification rates where still high. Also, both data sets contains cladistic data for only a few living mammals which can also have a effect of topological accuracy (Guillerme and Cooper, In review, 2015). However, both original phylogenies where built using strong topological constraint to avoid such a caveat (Slater, 2013; Beck and Lee, 2014).

⁴⁰⁴ Secondly, the core of the debate in mammalian evolution is weather *placental*

⁴⁰⁵ mammals originated before or after the K-Pg boundary (dos Reis et al., 2012; O'Leary

⁴⁰⁶ et al., 2013; Springer et al., 2013; OLeary et al., 2013; dos Reis et al., 2014). The infraclass

⁴⁰⁷ Placentalia can be defined as "the least inclusive clade that includes all extant

⁴⁰⁸ placentals" (Beck and Lee, 2014). However, part of the dating debate might be due to

⁴⁰⁹ the lack of clear characters that can be used to define early placental mammals

⁴¹⁰ (Bininda-Emonds et al., 2012; Beck and Lee, 2014). Cartmill (2012) also argues that the

⁴¹¹ use of higher taxa definition in general might be obsolete since "there is only a long,

⁴¹² geologically slow cascade of accumulating small apomorphies". Therefore, in this

⁴¹³ study, we made the deliberate choice to focus on the taxonomic levels (genus *vs.* family)

⁴¹⁴ rather than on the higher clades definitions. We argue that if a significant change in

⁴¹⁵ disparity occurred at the K-Pg boundary in any of such infraclass (Placentalia,

⁴¹⁶ Marsupialia, etc...) it would be detectable even at a higher level (i.e. changes in

⁴¹⁷ Placentalia correspond by definition to changes in Eutheria and Mammaliaformes).

⁴¹⁸ Also, using Total Evidence tip-dated trees provides more accurate estimates of

⁴¹⁹ diversification times (Ronquist et al. 2012; Wood et al. 2013; Beck and Lee 2014; but see

⁴²⁰ Arcila et al. 2015) and allows the opportunity to look at changes in disparity for both

⁴²¹ living and fossil species.

⁴²² *Methodology improvements for measuring disparity*

⁴²³ Additionally, throughout this paper, we propose several incremental changes to the

⁴²⁴ classic ways to measure disparity. This is how we believe they improve disparity

26

through time analysis:

1. **Using all the axis of the cladisto-space.** Previous studies focusing on disparity have used various ways to select a sub-sample of the the full cladisto-space (i.e. a sub-sample of the ordinated distance matrix) arguing that the m first axis of the cladisto-space usually bear most of the data-set's variance (e.g Brusatte et al., 2008a; Cisneros and Ruta, 2010; Prentice et al., 2011; Anderson and Friedman, 2012; Hughes et al., 2013; Benton et al., 2014). For example in Brusatte et al. (2008b) and Toljagic and Butler (2013), the authors decided to select only the m first dimensions that represent up to 90% of the variance in the distance matrix. The cut-off value is either given arbitrary or by visually detecting a substantial break in the slop of a scree plot of the variance per axis (Wills et al., 1994). We argue that even if the last dimensions of the cladisto-space bears a trivial amount of variance, there is no statistical justification to exclude them. However, by doing so, we included dimensions of the cladisto-space with a near 0 variance and range (variance of 2×10^{-14} and 1.15×10^{-15} and range of 7.31×10^{-7} and 3.33×10^{-7} in respectively Slater 2013 and Beck and Lee 2014) This makes the calculation of certain disparity metrics impossible (see below). An alternative method to avoid these near 0 dimensional axis problem is to simply not ordinated the data and measure disparity just from the k distance matrix (e.g. Benson and Druckenmiller, 2014; Close et al., 2015).

2. **Using the median distance from centroid as a disparity metric.** As stated above

27

(see methods section), we deliberately chose to use the median distance from centroid as a metric from measuring disparity among many other (e.g. Wills et al., 1994; Ciampaglio, 2004; Thorne et al., 2011; Hopkins, 2013; Huang et al., 2015). Using this metric gave use several advantages upon the four classic sum and products of ranges and variance. First, this metric comes with no special statistical assumptions (c.f. sum and products of variance *and* covariance). Secondly, this metric is not affected by the last dimensions of the cladisto-space problem (see above). And thirdly, this metric seems less coupled with taxonomic diversity (especially for the products of ranges and variance and the sum of ranges, see supplementary figures @@@).

3. **Using time slicing method.** Contra to numerous studies focusing on disparity (e.g Cisneros and Ruta, 2010; Prentice et al., 2011; Hughes et al., 2013; Hopkins, 2013; Benton et al., 2014; Benson and Druckenmiller, 2014), we chose not to bin our data in time intervals but rather to look it as a continuous process. We argue that by doing so, we can avoid two caveats of such method:

   (i) firstly, using time intervals based on biostratigraphy is tautologic. In fact, such method is likely to artefactualy emphasize disparity differences between time intervals because the same time intervals are based on notable differences in fossil fauna and flora (see supplementary figures @@@ where differences in disparity through time are much more contrasted in the interval methods than in the slicing methods). But note that not all studies

28

use biostratigraphy and sometimes arbitrarily time bins of equal duration are used which also fix this caveat (Butler et al., 2012; Hopkins, 2013; Benson and Druckenmiller, 2014).

(ii) secondly, in both cases (time bins based on biostratigraphy or arbitrary durations), such method does not allow to specify assumptions on the evolutionary model. In fact, the underlying assumption to such method is that changes in disparity occur between the time intervals in a punctuated evolutionary model fashion. Although directional gradual evolution has been shown to be rare, punctuated (i.e. stasis) and gradual (i.e. random walk) evolution have been shown to be both relatively common (Hunt, 2007; Hunt et al., 2015). Therefore, assuming that evolution is only punctual might be erroneous in some cases and for some traits.

4. **Allowing to choose the evolutionary model.** Finaly, using the time slicing method, allows use to crudely specify the evolutionary model for changes in disparity. Within Eutherians, we showed both support for an effect of time on disparity under both models of evolution. This can reflect the complex combination between the two modes of evolution where morphology (i.e. as inferred from the cladistic data) varies stochastically through time with a mix of random walks (i.e. gradual model) for certain set of characters and stasis (i.e. punctuated model) for others. These results are consistent with previous findings (Hunt, 2007; Hunt et al., 2015). It is also encouraging to see that the distinction

between the two modes of evolution can help understanding the patterns of

changes in disparity at a finer scale. In fact, for Mammaliaformes, there is no

significant effect of time on disparity under the assumption of a punctuated

model of evolution but a clear effect of time when evolution is assumed to be

gradual (see Table 1@@@). When looking at the details of this results, the same

data sets shows also no significant effect of time when using the time bin method

(including nodes) or when assuming that disparity evolves under an ACCTRAN

model (see supplementary permanova results @@@). This suggests that there is an

effect of time on Mammaliaformes with mix between punctuated delay evolution

(DELTRAN) and gradual evolution (random walk). This could be interpreted as

when a particular morphology (i.e. a set of particular states for cladistic

characters) is observed within a clade, this particular morphology will be likely

conserved through time. Other common but more complex models could also be

implemented such as a combined stasis and random walk (Hunt et al., 2015) or

models based on morphological rates rather than just the sheer branch length. For

example, one could use a density of probability for choosing the ordinated data

for either the descendant or the ancestor based on morphological clocks rather

than just branch length.

Two major caveats, however, arise from using such a method. First, this method relies

on good estimates of characters states at the nodes of the phylogeny. Estimating

discrete ancestral characters can sometimes be tricky and can lead to low scaled

30

likelihood values supporting any states of a particular character, especially when many data are missing in the observed cladistic matrix. However, in this particular study, we made the methodological choice of selecting only characters with a high scaled likelihood support (> 0.95). Additionally, using trees containing fossil taxa also improves the ability to correctly estimate ancestral characters (David Polly, 2001; Finarelli and Flynn, 2006; Albert et al., 2009; Slater, 2013). Finally, because, this method samples every phylogenetic element (tip, node or edge) through time, disparity calculated close to the root of the tree can exhibit result with large confidence intervals (e.g. when only three phylogenetic elements are sampled see Figure S3 and S@@@). However, it is encouraging to note that measuring disparity from time-slices is decoupled from taxonomic diversity at least after a minimal number of taxa (Slater et al., 2010; Ruta et al., 2013; Hopkins, 2013)

In summary, the majority attempts to solve the debate on whether placental mammals diversified after or before the K-Pg boundary is based on taxonomic diversity and shows unclear evidences on weather the K-Pg extinction event had an effect on mammalian diversification (Meredith et al., 2011; O'Leary et al., 2013; dos Reis et al., 2014; Beck and Lee, 2014). Among the variety of macroevolutionary process proposed to support an effect of the K-Pg boundary on mammalian evolution, some authors proposed the release of ecological niches after the K-Pg boundary (e.g. Archibald, 2011; O'Leary et al., 2013) or a release of competition pressures (e.g. Slater, 2013; Lovegrove et al., 2014). In this study, however, we proposed a different approach looking at

morphological diversity (i.e. disparity) through time using a continuous time sampling

approach that allows use to specify assumption on the mode of evolution (i.e.

punctuated or gradual). We based our analysis on the palaeontological discoveries of

the last decade showing an unprecedented and unexpected taxonomic and

morphological diversity prior to the Cenozoic (Luo, 2007; Close et al., 2015). We found

no evidences for an effect of the K-Pg boundary on changes in mammalian disparity at

both the family and the genus level and under both assumption of gradual or punctual

evolution. We therefore suggest that, contra to popular believe, the extinction of many

terrestrial vertebrates (namely the dominant non-avian dinosaurs) did not significantly

affect the evolution of mammals throughout the Cenozoic.

Data availability and reproducibility

Data will be available on Dryad or Figshare. Code for reproducing the analysis is

available on GitHub (`ithub.com/TGuillerme/SpatioTemporal_Disparity`).

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Table 2: Results of the *post-hoc* t-tests for comparing the disparity at the last sub-sample of the Cretaceous (65 Mya) to all the sub-samples of the Cenozoic for the Eutherians (data from Beck and Lee, 2014). Sub-samples: reference sample (65 Million years ago; Mya) to Cenozoic sample (from 60 Mya to present). Gradual: gradual evolution; punctuated: punctuated evolution. Difference: mean sub-sample difference; Df: degrees of freedom; T: T statistic; p-value: adjusted p-value using Holm-Bonferroni correction. Significant differences are highlighted in bold: one star (*) signifies a p-value between 0.05 and 0.005; two starts between 0.005 and 0.0005 and three stars < 0.0005.

Sub-samples (Mya)	Gradual					Punctuated				
	Difference	Df	T	p.value		Difference	Df	T	p.value	
65:60	0.06	76	1.055	1		0.04	76	0.760	1	
65:55	0.05	75	0.999	1		0.16	75	3.145	**0.0310**	*
65:50	0.15	68	2.412	0.2413		0.08	68	1.403	1	
65:45	0.21	64	3.016	**0.0478**	*	0.18	64	2.685	0.1200	
65:40	0.18	64	2.579	0.1590		0.13	64	2.173	0.4354	
65:35	0.23	60	2.840	0.0800	·	0.21	60	2.962	0.0568	·
65:30	0.27	57	2.927	0.0639	·	0.29	57	3.810	**0.0044**	**
65:25	0.22	56	2.500	0.1999		0.28	56	3.544	**0.0104**	*
65:20	0.16	56	1.922	0.7762		0.25	56	3.117	**0.0374**	*
65:15	0.14	55	1.819	0.9670		0.30	55	3.567	**0.0098**	**
65:10	0.14	55	1.843	0.9203		0.42	55	4.540	**0.0004**	***
65:5	0.14	55	1.790	1		0.30	55	3.377	**0.0176**	*
65:0	0.14	55	1.818	0.9692		0.17	55	2.250	0.3705	

46

Table 3: Results of the *post-hoc* t-tests for comparing the disparity at the last sub-sample of the Cretaceous (65 Mya) to all the sub-samples of the Cenozoic for the rarefied Eutherians (data from Beck and Lee, 2014). Column heads explained same as given in table 2.

Sub-samples	Gradual				Punctuated			
(Mya)	Difference	Df	T	p.value	Difference	Df	T	p.value
65:60	0.04	76	0.218	1	0.01	76	0.064	1
65:55	0.04	75	0.213	1	0.14	75	0.797	1
65:50	0.11	68	0.553	1	0.04	68	0.224	1
65:45	0.15	64	0.716	1	0.13	64	0.600	1
65:40	0.11	64	0.544	1	0.07	64	0.358	1
65:35	0.15	60	0.627	1	0.12	60	0.572	1
65:30	0.15	57	0.636	1	0.17	57	0.772	1
65:25	0.10	56	0.423	1	0.16	56	0.697	1
65:20	0.03	56	0.131	1	0.13	56	0.555	1
65:15	0	55	0.005	1	0.16	55	0.674	1
65:10	-0.01	55	-0.034	1	0.27	55	1.129	1
65:5	0.01	55	0.029	1	0.15	55	0.640	1
65:0	0	55	0.005	1	0.02	55	0.071	1

Table 4: Results of the *post-hoc* t-tests for comparing the disparity at the last sub-sample of the Cretaceous (65 Mya) to all the sub-samples of the Cenozoic for the Mammaliaformes (data from Slater, 2013) under gradual evolution model. Raw data: data without correcting for taxonomic diversity; Rarefied data: rarefied bootstrapped data. Other column heads explained same as given in table 2.

Sub-samples	Raw data				Rarefied data			
(Mya)	Difference	Df	T	p.value	Difference	Df	T	p.value
65:60	0.49	19	0.826	1	0.26	19	0.365	1
65:55	0.45	20	0.734	1	0.31	20	0.428	1
65:50	0.13	21	0.267	1	0.03	21	0.042	1
65:45	-0.05	24	-0.109	1	0.03	24	0.051	1
65:40	-0.22	25	-0.543	1	-0.08	25	-0.118	1
65:35	-0.33	27	-0.858	1	-0.19	27	-0.321	1
65:30	-0.37	28	-0.973	1	-0.21	28	-0.335	1
65:25	-0.48	30	-1.358	1	-0.25	30	-0.394	1
65:20	-0.69	31	-2.030	0.6625	-0.44	31	-0.711	1
65:15	-0.76	30	-2.201	0.4620	-0.53	30	-0.906	1
65:10	-0.86	30	-2.666	0.1593	-0.66	30	-1.241	1
65:5	-0.85	30	-2.668	0.1585	-0.63	30	-1.197	1
65:0	-0.86	30	-2.678	0.1548	-0.62	30	-1.133	1