RH: Cretaceous-Palaeogene extinction does not affect mammalian disparity.

Mammalian morphological diversity does not increase in response to the extinction of the (non-avian) dinosaurs.

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1 **Abstract**

2

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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). The long-term effects of mass extinctions, however, are more varied (Erwin, 1998), and include species richness increases in some clades (Friedman, 2010) and 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; Liow et al. 2015 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 (Brusatte et al., 2008b) radiations.

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 many terrestrial vertebrates (including the dominant non-avian dinosaur group; Archibald 2011; Renne et al. 2013; Brusatte et al. 2015) went extinct, allowing placental

3

mammals to dominate the fauna (Archibald, 2011; Lovegrove et al., 2014). Some authors suggest this reflects placental mammals filling the "empty" niches left after the K-Pg extinction 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 being driven by the K-Pg extinction 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 extinction event as there are no undebated placental mammal fossils before it 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). Therefore, whether the diversification of placental mammals began before the K-Pg extinction event, or in response to the extinctions at K-Pg, 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. Firstly, palaeontological and neontological data show different patterns; palaeontological data generally suggest that placental mammals diversified after K-Pg (e.g. O'Leary et al., 2013), whereas neontological data suggest that K-Pg extinction event had little to no effect on mammalian diversification

4

(Bininda-Emonds et al., 2007; Meredith et al., 2011; Stadler, 2011). We can solve this issue by using both palaeontological and neontological data in our analyses. The Total Evidence method allows us to use cladistic data for both living and fossil taxa, along with molecular data for living taxa, to build phylogenies (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). Here we use two recent Total Evidence tip-dated phylogenies of mammals (Slater, 2013; Beck and Lee, 2014) to investigate palaeontological and neontological taxa simultaneously.

A second issue is that diversity can be defined in many different ways. In many studies it is measured as taxonomic 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; Benton, 2015). Sometimes taxonomic 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 it may not be the best proxy for ecological diversity. We can instead 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 morphology that

should relate to the ecology of the species. However some methods for measuring

disparity are outdated and make inappropriate assumptions. Many methods for

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 et al., 2011; Brusatte

et al., 2012; Toljagic and Butler, 2013; Ruta et al., 2013; Benton et al., 2014; Benson and

Druckenmiller, 2014), even when the statistical assumptions of the methods are violated

(see Methods). Additionally, previous methods are based on an underlying assumption

that changes in disparity occur by punctuated evolution (e.g. Wesley-Hunt, 2005) which

is not always the case (Hunt et al., 2015). Finally, most studies of disparity through time

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

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

changes in fossil assemblages and morphology through time. To deal with these issues,

we propose an updated approach to test whether mammals diversified before or after

K-Pg, using morphological disparity, measured as cladistic disparity (see Methods), as

our proxy for diversity.

Here we measure the disparity of living and fossil mammals before or after

K-Pg, using data taken from two previously published studies (Slater, 2013; Beck and

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

disparity through time under two different models of morphological character

evolution (either gradual or punctuated). Finally, we tested whether mammals display

significant changes in disparity between the end of the Cretaceous and throughout the Cenozoic. To our knowledge, this study is the first to approach the debate of the effect of the K-Pg event on mammalian evolution using Total Evidence phylogenies and calculating disparity through time in a continuous way (but see Halliday and Goswami, 2013, for a similar question). This new approach allowed us to find no significant changes in mammalian disparity between the end of the Cretaceous and any time during the Cenozoic. These results suggest that the extinction of non-avian dinosaurs and other terrestrial vertebrate clades at the end of the Cretaceous did not affect mammalian morphological 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 datasets because they have a similar number of taxa and morphological characters. Slater (2013) ranges from 310 million years ago (Ma; Late Carboniferous) to the present and focuses on the clade Mammaliaformes at the family-level. Beck and Lee (2014) ranges from 170 Ma (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

7

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

are illustrated in the supplementary material (see Fig S1 and S2 @@@). Both trees

contain few taxa compared to the overall living and fossil mammalian taxonomic

diversity (Wilson and Reeder, 2005; Archibald, 2011). This is mainly due to the fact that

Total Evidence trees need a lot of data (Guillerme and Cooper, In review) and

especially morphological data for living taxa (Guillerme and Cooper, 2015). Therefore,

most Total Evidence studies to date contain usually one or two orders of magnitude

less taxa than more common phylogenies based solely on molecular data (e.g.

thousands of taxa in Bininda-Emonds et al. 2007; Meredith et al. 2011; Jetz et al. 2012 *vs.*

hundreds in Ronquist et al. 2012; Slater 2013; Wood et al. 2013; Beck and Lee 2014).

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 ≥ 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 used 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

between the taxa present in a cladistic matrix (see details below). Foth et al. (2012) and

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, i.e. 101 orders of magnitude more taxa than the number of particles in the universe; 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 (Anderson and Friedman, 2012). However, the Gower distance cannot calculate distances when taxa have no overlapping data. Therefore, we used the `TrimMorphDistMatrix` function from the `Claddis` R package (Lloyd, 2015) to remove pairs of taxa with no cladistic characters in common. This led to us removing 11 taxa from Slater (2013) but none from Beck and Lee (2014).

After calculating our distance matrices we transformed them using classical multidimensional scaling (MDS; Torgerson, 1965; Gower, 1966; Cailliez, 1983). This

10

method (also referred to as PCO; e.g. Brusatte et al. 2015; or PCoA; e.g. Paradis et al. 2004) is an eigen decomposition of the distance matrix. Because we used Gower distances instead of raw Euclidean distances, negative eigenvalues can be calculated. To avoid this problem, we first transformed the distance matrices by applying the Cailliez correction (Cailliez, 1983) which adds a constant c^* to the values in a distance matrix (apart from the diagonal) so that all the Gower distances become Euclidean ($d_{Gower} + c^* = d_{Euclidean}$; Cailliez 1983). We were then able to extract n eigenvectors for each matrix (representing the n dimensions of the cladisto-space) where n is equal to $k - 2$, i.e. the number of taxa in the matrix (k) minus the last two eigenvectors that are always null after applying the Cailliez correction. Contrary to previous studies (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), we use all n dimensions of our cladisto-spaces and not a subsample representing the majority of the variance in the distance matrix (e.g. selecting only m dimensions that represent up to 90% of the 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).

Nonetheless, these methods suffer several methodological caveats. First, the range

metrics are affected by the uneven sampling of the fossil record (Butler et al., 2012)

Second, because we include all n dimensions in 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 between taxa and the centroid (similar

but not equivalent to Wills et al. 1994; Korn et al. 2013; Huang et al. 2015) calculated as:

$$Disparity = median\sqrt{\sum (\mathbf{v}_n - Centroid_n)^2} \tag{1}$$

where:

$$Centroid_n = \frac{\sum (\mathbf{v}_n)}{k} \tag{2}$$

and $\mathbf{v}_n$ is any of the n eigenvectors (i.e. any of the n dimension of the cladisto-space),

$Centroid_n$ is the mean value of the nth eigenvector (equation 2) and k is the total number

of taxa. Note that we also calculated the sum and products of ranges and variances and refer to these results 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; 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 used 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

13

of the cladisto-space across time and permits us to define the underlying model of character evolution (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 we chose the eigenvector score for the branch using one of two evolutionary models:

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

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

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

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

   Method (i) assumes that changes always occur early on the branch (accelerated transition, ACCTRAN) and (ii) assumes that changes always occur later (delayed transition, DELTRAN). We prefer not to make either assumption so we report the

14

251 results from (iii), although the ACCTRAN and DELTRAN results are available in

252 the Supplementary Information @@@.

253 2. **Gradual evolution.** This model also selects the eigenvector score from either the

254 ancestral node or the descendant node/tip of the branch, but the choice depends

255 on the distance between the sampling time point and the end of the branch. If the

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

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

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

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

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

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

262 evolution have been empirically shown to be rare (only 5% of the time Hunt,

263 2007). We therefore considered that changes from a character state A to B were

264 only dependent on the branch length.

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

266 (2013) and Beck and Lee (2014), time-slicing the phylogeny every five million years

267 from 170 Ma to the present resulting in 35 subsamples of the cladisto-space. For each

268 subsample, we estimated its disparity assuming punctuated (ACCTRAN, DELTRAN

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

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

271 randomly resampling with replacement a new subsample of taxa from the observed

15

taxa in the subsample 1000 times. We then calculated the median disparity value for

each subsample along with the 50% and the 95% confidence intervals. We also recorded

the number of phylogenetic elements (nodes and tips) in each subsample as a proxy for

representing the taxonomic diversity. To compare our results to previous studies we

also repeated our analyses using the time interval approach based on biostratigraphy

(e.g. Cisneros and Ruta, 2010; Prentice et al., 2011; Hughes et al., 2013; Benton et al.,

2014) using each geological stage from the Middle Jurassic to the present. We report the

results of these analyses in the Supplementary Materials (@@@).

Testing the effects of the K-Pg extinction on mammalian disparity

We can predict that if the K-Pg event had an effect on mammalian disparity, we would

then expect to see a significant difference between the disparity at the end of the

Cretaceous and at the start of the Paleogene. To test that, we performed t-tests among

the time subsamples before and after the K-Pg boundary (respectively between 70 and

65 Ma Anderson and Friedman, 2012; Zelditch et al., 2012; Smith et al., 2014) for both

datasets (Slater, 2013; Beck and Lee, 2014) and both evolutionary models (gradual and

punctuated). Because the effect of a mass extinction event on a group's evolution might

not be detectable directly after it (i.e. lag effect; CITE), we also tested if there was a

significant difference in disparity between the end of the Cretaceous and any

subsample during the Cenozoic. Because the later tests involved multiple t-tests, we

corrected each p-value by multiplying them by the number of comparisons

(Holm-Bonferonni correction; Holm, 1979).

16

Finally, disparity may be higher in subsamples with more phylogenetic elements simply because there are more taxa represented. Therefore, to test whether our results of the effect of the K-Pg event where driven by taxonomic diversity, we reran the same t-tests (direct effect and lag effect) on both rarefied datasets. In Slater (2013), the minimum number of taxa in each subsample from 170 Ma to present was eight. In Beck and Lee (2014), the minimum number of taxa in each subsample was three, however, from 150 Ma until the present, the minimum number of taxa is eight. To make both datasets comparable, we used eight as a minimum number of taxa for the rarefied bootstrap measurements, therefore in Beck and Lee (2014) we ignored the subsample between 170 and 150 Ma that only has three taxa.

Results

Disparity in Eutheria (data from Beck and Lee, 2014) reaches a plateau at the end of the Jurassic (150 Ma) and in the mean time, the number of tips and nodes (i.e. a proxy for taxonomic richness) increases up to the K-Pg boundary and then decreases throughout the Cenozoic (Fig 1). These changes in disparity do not appear to be fully linked to the number of tips and nodes used to estimate disparity. Changes in disparity among Mammaliaformes (data from Slater, 2013), however, are more idiosyncratic (Fig 1). In fact, disparity reaches a plateau during the Anisian (middle Triassic; 245 Ma) and fluctuates during the rest of the Mesozoic and the Cenozoic (Fig @@@ supplementary). Contra to the patterns observed in Eutheria, disparity changes seems to be more linked

17

Data	Model	Time slices (Ma)	Difference	Df	T	p.value
Beck	Gradual	70:65	Difference	Df	T	p.value

to the number of tips and nodes available for estimating disparity (Fig 1). Note that both evolutionary models (gradual or punctuated) seems to yield to sensibly similar results (Fig 1). When we tested for a direct effect of the K-Pg boundary on both data sets and under both evolutionary models and found ... (Table @) When testing for a lag effect of the K-Pg boundary, we found that ... (Table @)

Next, we tested whether the previous results were linked to changes in the number of available nodes and tips (i.e. as a proxy for taxonomic diversity) by rarefying the data set to a maximum of height nodes or tips per time slices (see Fig supplementary @@@). When testing for a direct effect of the K-Pg boundary, we found ... (Table @) Finally, when testing for a lag effect of the K-Pg boundary, we found that ... (Table @)
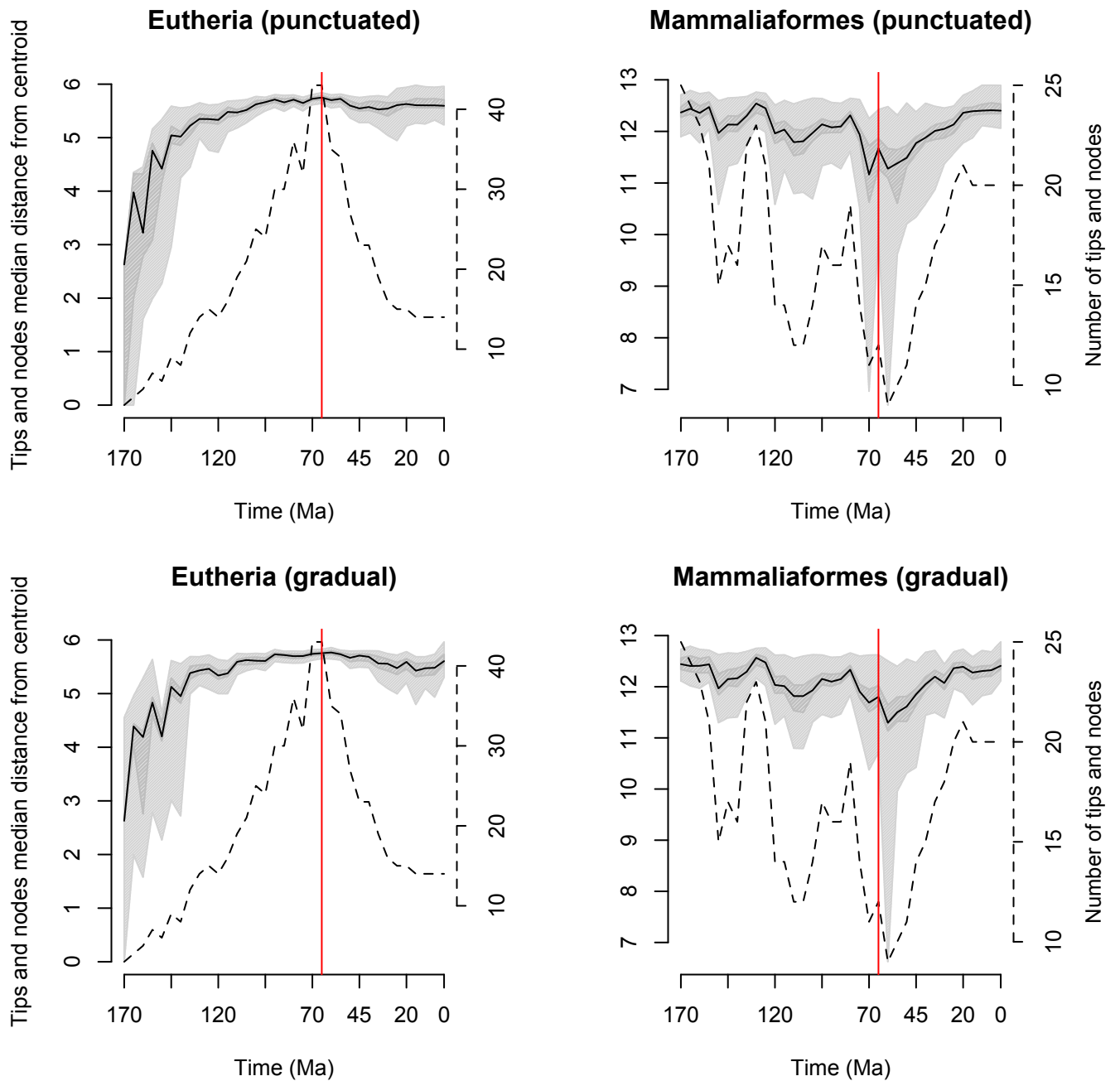
Figure 1: Disparity through time in Eutheria and Mammaliaformes calculated using a model of punctuated or gradual evolution. The x axis represents time in millions of years before the present (Ma). The y axis represents disparity, measured as the median distance from centroid at each time slice. The solid black lines show the mean disparity estimated from 1000 bootstrapped pseudoreplicates; the confidence intervals (CI) are represented by the grey polygons (50% CI in dark grey and 95% CI in light grey). The right hand axis represents species richness, and the dashed line shows the species rich-
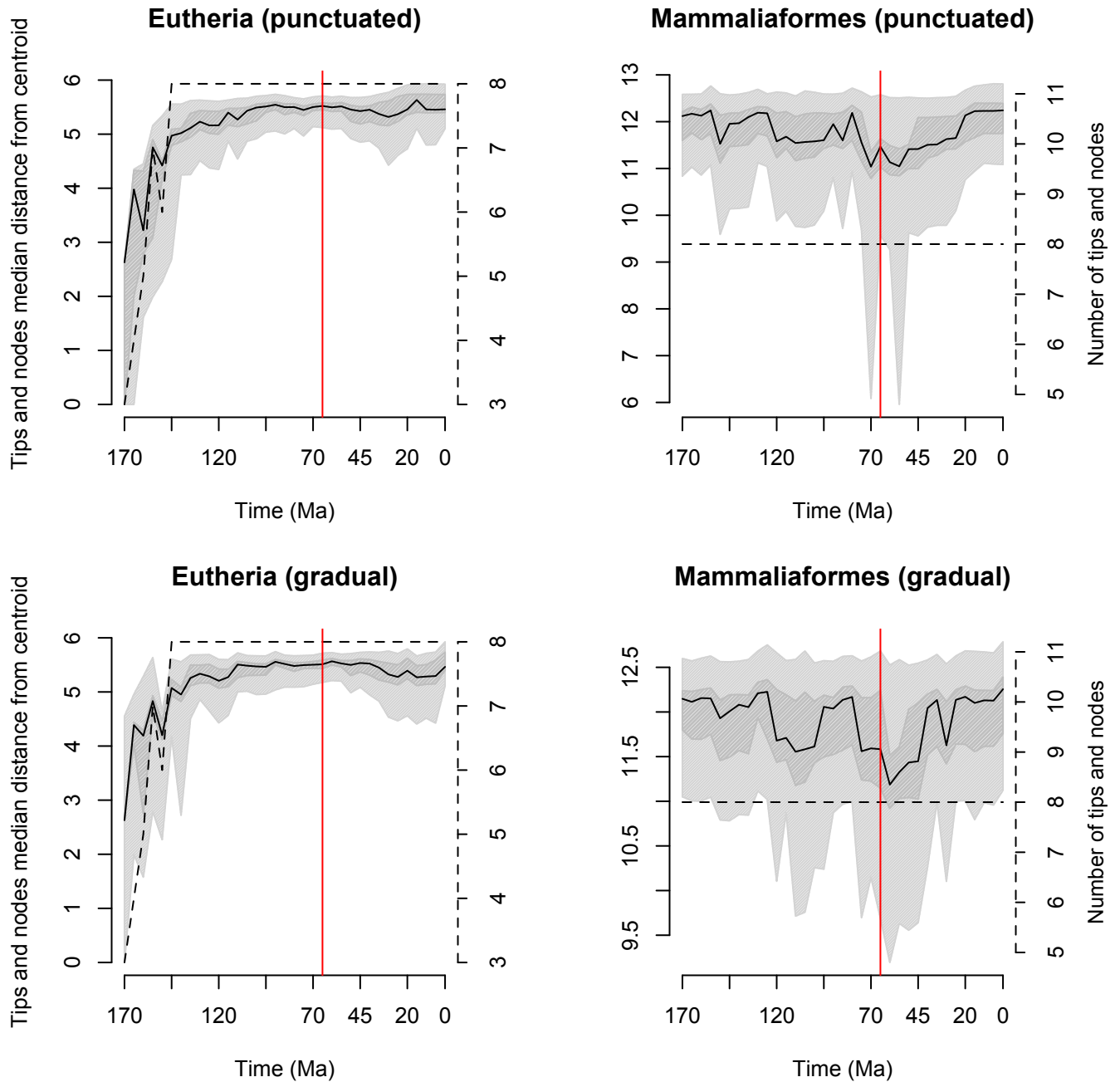
Figure 2: Disparity through time in Eutheria and Mammaliaformes calculated using a model of punctuated or gradual evolution, but controlling for variations in species richness at each time slice using rarefaction. The x axis represents time in millions of years before the present (Ma). The y axis represents disparity, measured as the median distance from centroid at each time slice. The solid black lines show the mean disparity estimated from 1000 bootstrapped pseudoreplicates; the confidence intervals (CI) are represented by the grey polygons (50% CI in dark grey and 95% CI in light grey). The

20

Table 1: PERMANOVA results testing the effect of time on the ordinated distance matrix using Euclidean distance with 1000 permutations. Data: Eutheria (data from Beck and Lee, 2014); Mammaliaformes, (data from Slater, 2013). Significant effects are highlighted in bold. Model = evolutionary model; df = degrees of freedom; *p <0.05; **p <0.01; ***p <0.001

Data	model	terms	df	Sum of squares	Mean sum of squares	F Model	R^2	p-value	
Eutheria	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	5662.25	166.530	1.0005	0.0574	0.4765	
		residuals	558	92877.75	166.450		0.9425		

Discussion

Our analysis shows that disparity changes through time in Eutheria and Mammaliaformes. Initially, disparity increases rapidly but then seems to reach a plateau at the end of the Jurassic (150 Ma@) for Eutheria, and during the late Triassic (Anisian; 245 Ma@) for the Mammaliaformes, and remains relatively constant after approximatively 12%@ and 25%@ of their evolutionary history respectively. Our observed global patterns of mammalian disparity are consistent with previous mammalian studies (Close et al. 2015 but see Grossnickle and Polly 2013) as well as with patterns of disparity in metazoans more generally (e.g. Hughes et al., 2013). Additionally, our analyses did not detect any short- or long-term effect of the K-Pg extinction event on mammalian disparity. This suggests that the numerous extinctions of terrestrial vertebrates, including the dominant non-avian dinosaur group, at the K-Pg boundary did not directly affect mammalian morphological evolution during the Cenozoic.

There has been mixed evidences for what happened to mammalian evolution after the K-Pg boundary (Stadler, 2011; Meredith et al., 2011; O'Leary et al., 2013; dos Reis et al., 2014). Our results underline that using both living and fossil species as well as different proxy for measuring diversity (i.e. disparity) can give a new approach to help solving this debate. Our findings might change the long-lasting idea that the non-avian dinosaurs where restraining mammal evolution (Lovegrove et al., 2014) or that their extinction liberate ecology niches for mammals to evolve in (Archibald, 2011).

Our results varies from previous studies (Grossnickle and Polly, 2013; Wilson, 2013, see below) but most interestingly 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 dataset 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 446 traits (i.e. cladistic characters) in opposition of one continuous trait (body mass in 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. Our results might show more robustness than Slater (2013)'s since we detected the same absence effect of the K-Pg boundary from a second independent datasets (i.e. Beck and Lee, 2014). Nonetheless, even though our results suggest that cladistic disparity is not affected by the K-Pg boundary, 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 datasets are limited. They do not represent the full known mammalian taxonomic diversity, especially during the Neogene (23–2.58 Ma) where no fossils were represented in both datasets. However, our study focuses on the changes in disparity around the K-Pg boundary and not during the whole Cenozoic. Besides, this might not cause a serious under-estimation of disparity, at least for the Mammaliaformes dataset, since their diversity peaked during the late Cretaceous (Campanian; 72.1–83.6 Ma; Newham et al.,

₃₆₆ 2014). Additionally Raia et al. (2012) have shown that mammalian diversification rates

₃₆₇ declined throughout the whole Cenozoic, suggesting therefore, that an effect of the

₃₆₈ K-Pg boundary would be more likely detected during the Paleogene.

₃₆₉ *Methodology improvements for measuring disparity*

₃₇₀ It is also worth noticing that our results might differ from previous studies because or

₃₇₁ our specific methodological choices (e.g. compared to Grossnickle and Polly, 2013;

₃₇₂ Wilson, 2013). In fact, throughout this paper, we propose several incremental changes

₃₇₃ to the classic ways to measure disparity.

₃₇₄ Firstly we used all the axis of the cladisto-space, as opposed to previous studies

₃₇₅ which selected a subsample of the the full cladisto-space arguing that the *m* first axis of

₃₇₆ the cladisto-space usually bear most of the data-set's variance (e.g Brusatte et al., 2008a;

₃₇₇ Cisneros and Ruta, 2010; Prentice et al., 2011; Anderson and Friedman, 2012; Hughes

₃₇₈ et al., 2013; Benton et al., 2014). We argue that even if the last dimensions of the

₃₇₉ cladisto-space bears a trivial amount of variance, there is no statistical justification to

₃₈₀ exclude them. However, by doing so, we included dimensions of the cladisto-space

₃₈₁ with a near 0 variance and range (variance of 2×10^{-14} and 1.15×10^{-15} and range of

₃₈₂ 7.31×10^{-7} and 3.33×10^{-7} in respectively Slater 2013 and Beck and Lee 2014). An

₃₈₃ alternative method allows to avoid this problem by simply not ordinating the data and

₃₈₄ just using the raw distance matrix (e.g. Benson and Druckenmiller, 2014; Close et al.,

₃₈₅ 2015) yet, in both cases, it makes the calculation of the products of ranges and variances

₃₈₆ impossible.

24

387   Secondly, we used median distance from centroid as a disparity metric. This

388 metric is not affected by the last dimensions of the cladisto-space problem (see above)

389 and therefore gave use several advantages upon the four classic sum and products of

390 ranges and variance. Additionally, this metric comes with no special statistical

391 assumptions and seems less coupled with taxonomic diversity (especially for the

392 products of ranges and variance and the sum of ranges, see supplementary Figs @@@).

393   Thirdly, we used a time-slicing method instead of binning the data into time

394 intervals (e.g in: Cisneros and Ruta, 2010; Prentice et al., 2011; Hughes et al., 2013;

395 Hopkins, 2013; Benton et al., 2014; Benson and Druckenmiller, 2014). Instead we used a

396 continuous method, that allows to avoid two caveats:

397 (i) using time intervals based on biostratigraphy is tautologic. In fact, this is likely to

398   artefactualy emphasize disparity differences between time intervals since the same

399   time intervals are based on notable differences in fossil fauna and flora. Note

400   however that some studies used arbitrarily time bins of equal duration rather than

401   biostratigraphy (Butler et al., 2012; Hopkins, 2013; Benson and Druckenmiller,

402   2014).

403 (ii) in both cases (time bins based on biostratigraphy or on arbitrary durations), such

404   methods are based on the underlying assumption that disparity changes in a

405   punctuated evolution manner (i.e. changes occurring only between time intervals).

406   However, gradual (i.e. random walk) evolution have been shown to be relatively

407   common in the fossil record (Hunt, 2007; Hunt et al., 2015).

Finally, using the time slicing method, allows use to crudely specify the evolutionary model for changes in disparity such as punctuated or gradual evolution and therefore test macroevolutionary hypotheses (such as in this paper) without assuming only one evolutionary model. For example, we find differences in disparity with such and such model ... or no difference at all with all of these models... However, 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, the time-slicing 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 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

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confidence intervals (e.g. when only three phylogenetic elements are sampled see Fig 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)

Conclusion

The majority of attempts to solve the debate on whether 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

27

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 subsample of the Cretaceous (65 Ma) to all the subsamples of the Cenozoic for the Eutherians (data from Beck and Lee, 2014). Subsamples: reference sample (65 Million years ago; Ma) to Cenozoic sample (from 60 Ma to present). Gradual: gradual evolution; punctuated: punctuated evolution. Difference: mean subsample 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.

Subsamples (Ma)	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	

42

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

Subsamples	Gradual				Punctuated			
(Ma)	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 subsample of the Cretaceous (65 Ma) to all the subsamples 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.

Subsamples	Raw data				Rarefied data			
(Ma)	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