

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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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). 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

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; O’Leary 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

(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

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 combinatorial 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

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:

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

where:

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

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 n^{th} 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

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

results from (iii), although the ACCTRAN and DELTRAN results are available in the Supplementary Information @@@.

2. Gradual evolution. This model also selects the eigenvector score from either the ancestral node or the descendant node/tip of the branch, but the choice depends on the distance between the sampling time point and the end of the branch. If the sampling time point falls in the first half of the branch length the eigenvector score is taken from the ancestral node, conversely, if the sampling time point falls in the second half of the branch length the eigenvector score is taken from the descendant node/tip. This reflects a model of gradual evolution where changes in disparity are gradual and cumulative along the branch. Under this model, the gradual changes could be either directional or random, however, directional evolution have been empirically shown to be rare (only 5% of the time Hunt, 2007). We therefore considered that changes from a character state A to B were only dependent on the branch length.

We applied our time-slicing approach to the two cladisto-spaces calculated from Slater (2013) and Beck and Lee (2014), time-slicing the phylogeny every five million years from 170 Ma to the present resulting in 35 subsamples of the cladisto-space. For each subsample, we estimated its disparity assuming punctuated (ACCTRAN, DELTRAN and random) and gradual evolution as described above. To reduce the influence of outliers on our disparity estimates, we bootstrapped each disparity measurement by randomly resampling with replacement a new subsample of taxa from the observed

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).

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 were 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

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 @)

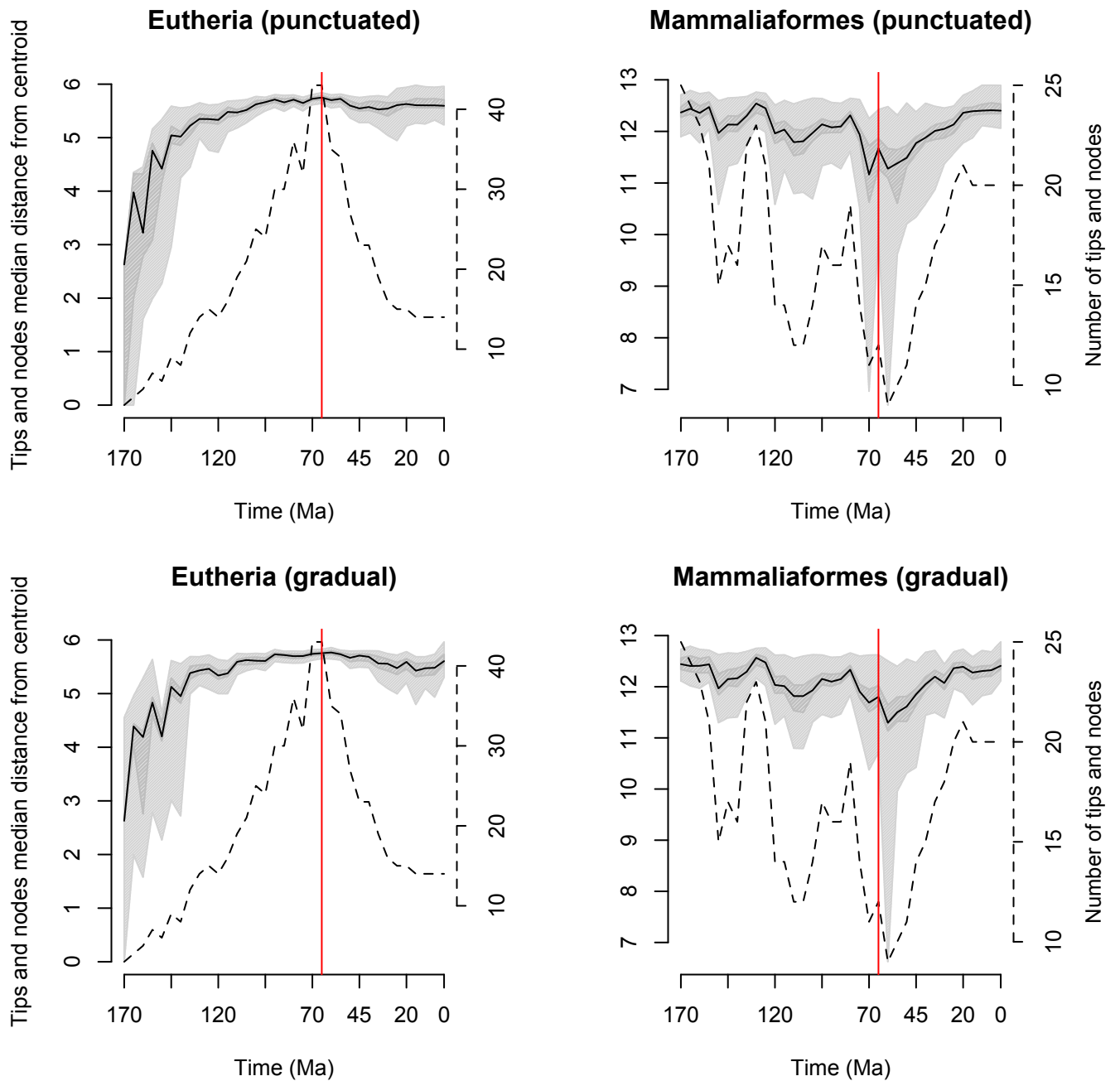


Figure 1: Disparity through time in Eutheria and Mammaliaformes calculated using a model of punctuated or gradual evolution. The x axis represents time in millions of years before the present (Ma). The y axis represents disparity, measured as the median distance from centroid at each time slice. The 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-

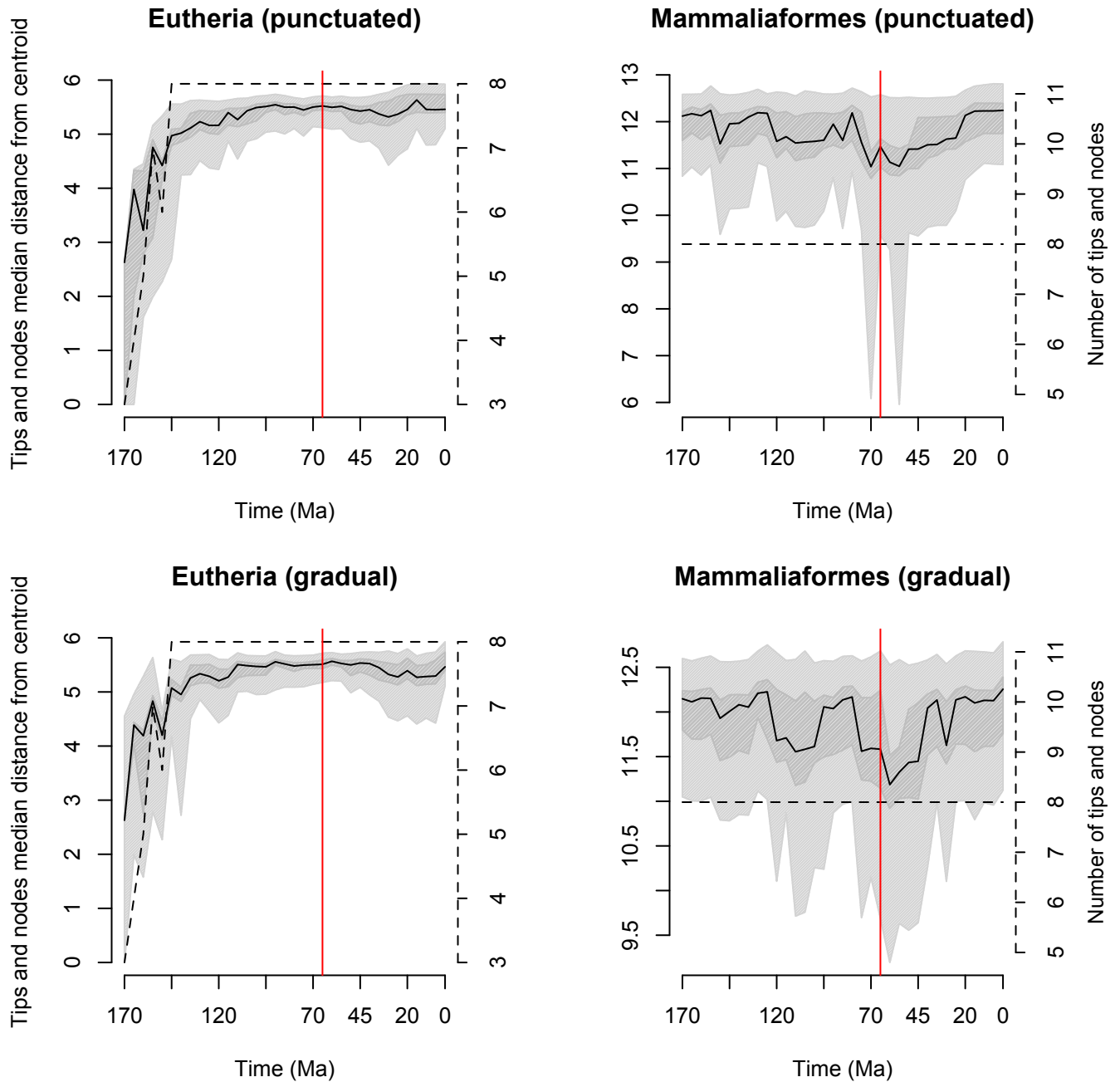


Figure 2: Disparity through time in Eutheria and Mammaliaformes calculated using a model of punctuated or gradual evolution, but controlling for variations in species richness at each time slice using rarefaction. The x axis represents time in millions of years before the present (Ma). The y axis represents 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

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 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 subsample and any of the Cenozoic subsamples (Fig 2). In fact the disparity seems to reach a plateau at the end of the Jurassic (150 Ma) for Eutherians and during the late Triassic (Norian; 220 Ma) for the Mammaliaformes and stays relatively constant after that (see Fig 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

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 an 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 Foth et al. 2012; 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 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 traits (the 446 morphological 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 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 datasets (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 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, 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 Ma; 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 were still high. Also, both datasets contains cladistic data for only a few living mammals which can also have an effect of topological accuracy (Guillerme and Cooper, In review, 2015). However, both original phylogenies were built using strong topological constraint to avoid such a caveat (Slater, 2013; Beck and Lee, 2014).

Secondly, the core of the debate in mammalian evolution is whether *placental* mammals originated before or after the K-Pg boundary (dos Reis et al., 2012; O’Leary et al., 2013; Springer et al., 2013; O’Leary et al., 2013; dos Reis et al., 2014). The infraclass Placentalia can be defined as “the least inclusive clade that includes all extant placentals” (Beck and Lee, 2014). However, part of the dating debate might be due to the lack of clear characters that can be used to define early placental mammals (Bininda-Emonds et al., 2012; Beck and Lee, 2014). Cartmill (2012) also argues that the use of higher taxa definition in general might be obsolete since “there is only a long, geologically slow cascade of accumulating small apomorphies”. Therefore, in this study, we made the deliberate choice to focus on the taxonomic levels (genus *vs.* family) rather than on the higher clades definitions. We argue that if a significant change in disparity occurred at the K-Pg boundary in any of such infraclass (Placentalia, Marsupialia, etc...) it would be detectable even at a higher level (i.e. changes in Placentalia correspond by definition to changes in Eutheria and Mammaliaformes). Also, using Total Evidence tip-dated trees provides more accurate estimates of diversification times (Ronquist et al. 2012; Wood et al. 2013; Beck and Lee 2014; but see Arcila et al. 2015) and allows the opportunity to look at changes in disparity for both living and fossil species.

Methodology improvements for measuring disparity

Additionally, throughout this paper, we propose several incremental changes to the classic ways to measure disparity. This is how we believe they improve disparity

through time analysis:

1. **Using all the axis of the cladisto-space.** Previous studies focusing on disparity have used various ways to select a subsample of the the full cladisto-space (i.e. a subsample 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

(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 Figs @@@).

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 artefactually emphasize disparity differences between time intervals because the same time intervals are based on notable differences in fossil fauna and flora (see supplementary Figs @@@ 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

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.** Finally, 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 datasets shows also no significant effect of time when using the time bin method (including nodes) or when assuming that disparity evolves under an ACCTAN 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

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 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)

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 whether 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](https://github.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 stars between 0.005 and 0.0005 and three stars < 0.0005.

Subsamples	Gradual				Punctuated			
(Ma)	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 46	0.30	55	3.377	0.0176 *
65:0	0.14	55	1.818	0.9692	0.17	55	2.250	0.3705

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 (Ma)	Gradual				Punctuated			
	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 (Ma)	Raw data				Rarefied data			
	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