

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

**Cretaceous-Palaeogene extinction does not affect
mammalian disparity. DISCLAIMER: THIS DRAFT IS
NOT FULLY COMPLETED AND HAS NOT BEEN
PROOF READ.**

THOMAS GUILLERME^{1,2*}, AND NATALIE COOPER^{1,2,3}

¹*School of Natural Sciences, Trinity College Dublin, Dublin 2, Ireland.*

²*Trinity Centre for Biodiversity Research, Trinity College Dublin, Dublin 2, Ireland.*

³*Department of Life Sciences, Natural History Museum, Cromwell Road, London, SW7 5BD, UK.*

***Corresponding author.** *Zoology Building, Trinity College Dublin, Dublin 2, Ireland; E-mail: guillert@tcd.ie; Fax: +353 1 6778094; Tel: +353 1 896 2571.*

Abstract

1

2

3 (Keywords: disparity, diversity, punctuated equilibrium, gradualism, time slicing)

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

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; 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. 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 for 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

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.

Here, 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. We measured the disparity of living and fossil mammals 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, to test whether mammals display significant changes in disparity after the K-Pg boundary, we tested whether there is significant changes in disparity through time. When an effect of time was detected, we ran post-hoc tests to measure if there is any significant difference between the disparity at the end of the Cretaceous and the disparity throughout the Cenozoic. We found 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
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 ≥ 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

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

(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 us to remove 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 two last eigenvector which 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 sub-sample 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). 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. In addition, 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 from centroid (similar but not equivalent to Wills et al. 1994; Korn et al. 2013; Huang et al. 2015) calculated as:

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

where:

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

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 n^{th} 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; 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 (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 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 occurs 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 where just dependant 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 Mya to the present resulting in 35 sub-samples of the cladisto-space. For each sub-sample, 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 re-sampling with replacement a new sub-sample of taxa from the observed taxa in the sub-sample 1000 times. We then calculated the median disparity value for each sub-sample along with the 50% and the 95% confidence intervals.

We also reported the number of phylogenetic elements (branches, nodes and tips) in each sub-sample representing the observed taxonomic diversity. Disparity may be higher in sub-samples with more phylogenetic elements simply because there are more taxa represented. To test whether our analyses were biased in this way, we rarefied our sub-samples during the bootstrap procedure by randomly re-sampling a

fix number of taxa across each sub-sample. In Slater (2013), the minimum number of taxa in each sub-sample from 170 to present was 8. In Beck and Lee (2014), the minimum number of taxa however was 3, however, from 150 Mya until the present, the minimum number of taxa is 8. To make both data sets comparable, we used 8 as a minimum number of taxa for the rarefied bootstrap measurements in Beck and Lee (2014) ignoring therefore the sub-sample between 170 and 150 Mya. We report both results of the bootstrapped measurements and the rarefied bootstrap measurements.

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 (***).

Finally, to assess if the K-Pg boundary had a significant effect on mammals disparity, we performed Anderson (2001)'s Permutational Analysis of Variance (also referred to as PERMANOVA or NPANOVA; e.g. Brusatte et al., 2008a; Ruta et al., 2013) to test whether there was a significant effect of time on our calculated disparity. We calculated the euclidean distance of the ordinated data with 1000 permutations on both data sets and on both evolutionary scenario using the `adonis` function from the R package `vegan` (Oksanen et al., 2015). When a significant effect of time on disparity was 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 both data sets, we measured similar changes in morphological disparity in the last 170 Million years for both the full data sets and the rarefied data sets (Figure 1 and 2) We

330 measured a significant effect of time on disparity in Eutherians under both gradual and
331 punctuated evolution model and in Mammaliaformes only under the gradual evolution
332 model only (table 1). For the Eutherians data set, we detected at least one significant
333 difference between the disparity in the last sub-sample of the Cretaceous and any
334 sub-sample of the Cenozoic suggesting an effect of the K-Pg boundary on disparity
335 (table 2). However, once corrected for taxonomic diversity, we did not detect any
336 significant difference, either under gradual or punctuated evolution model (table 3). For
337 the Mammaliaformes data set under gradual evolution model, there was no significant
338 difference between the disparity in the last sub-sample of the Cretaceous and any
339 sub-sample of the Cenozoic in both the raw and the rarefied data (table 4).

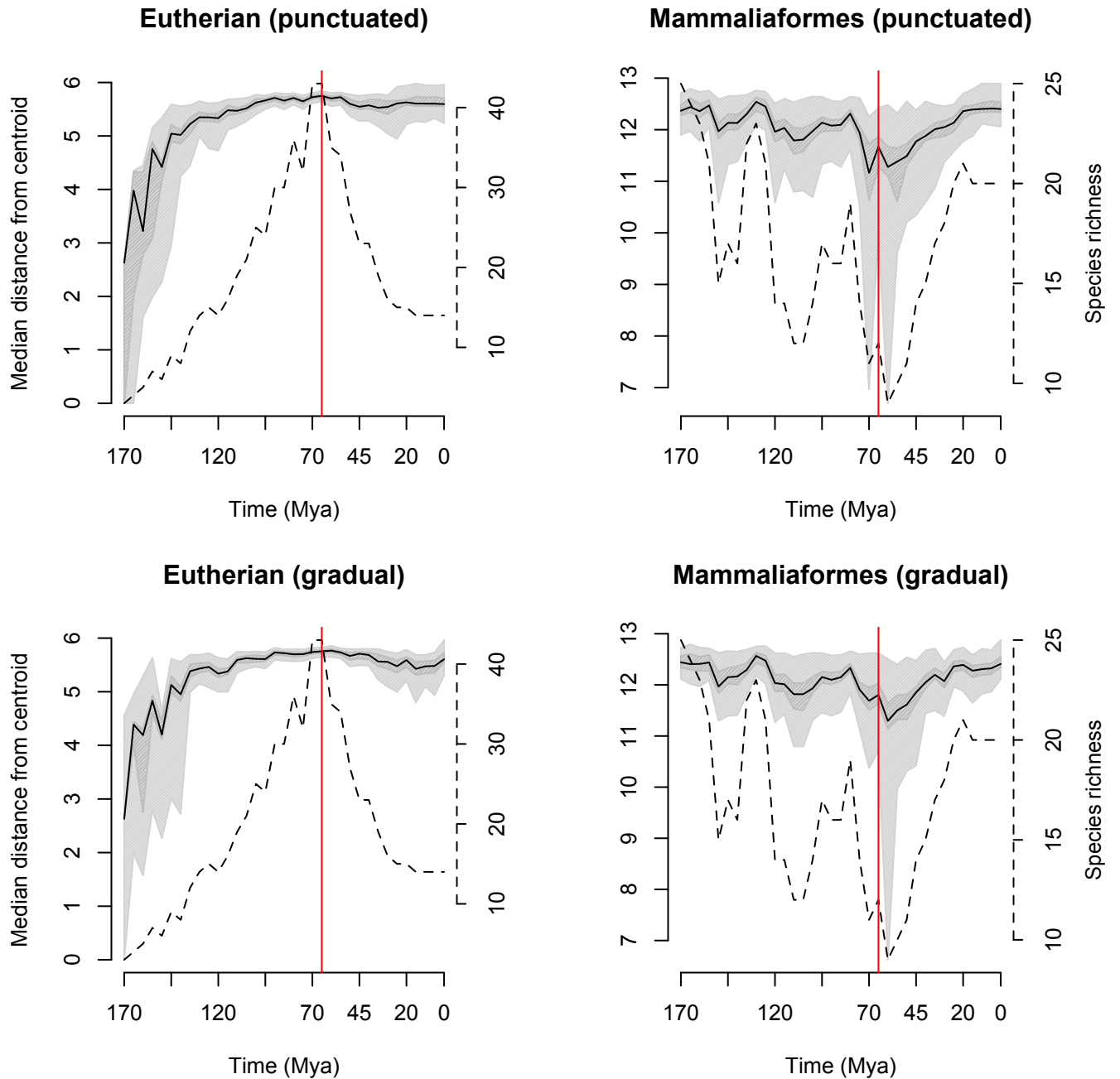


Figure 1: Observed variations of disparity through time among Eutherian and Mammaliaformes under punctuated or gradual evolution model. The x axis represents the time in Million of years ago (Mya). The y axis represents the disparity measured as the median distance from centroid per sub-sample. The solid black lines is the mean disparity from the bootstrapped pseudo-replicates, the confidence intervals (CI) are represented 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

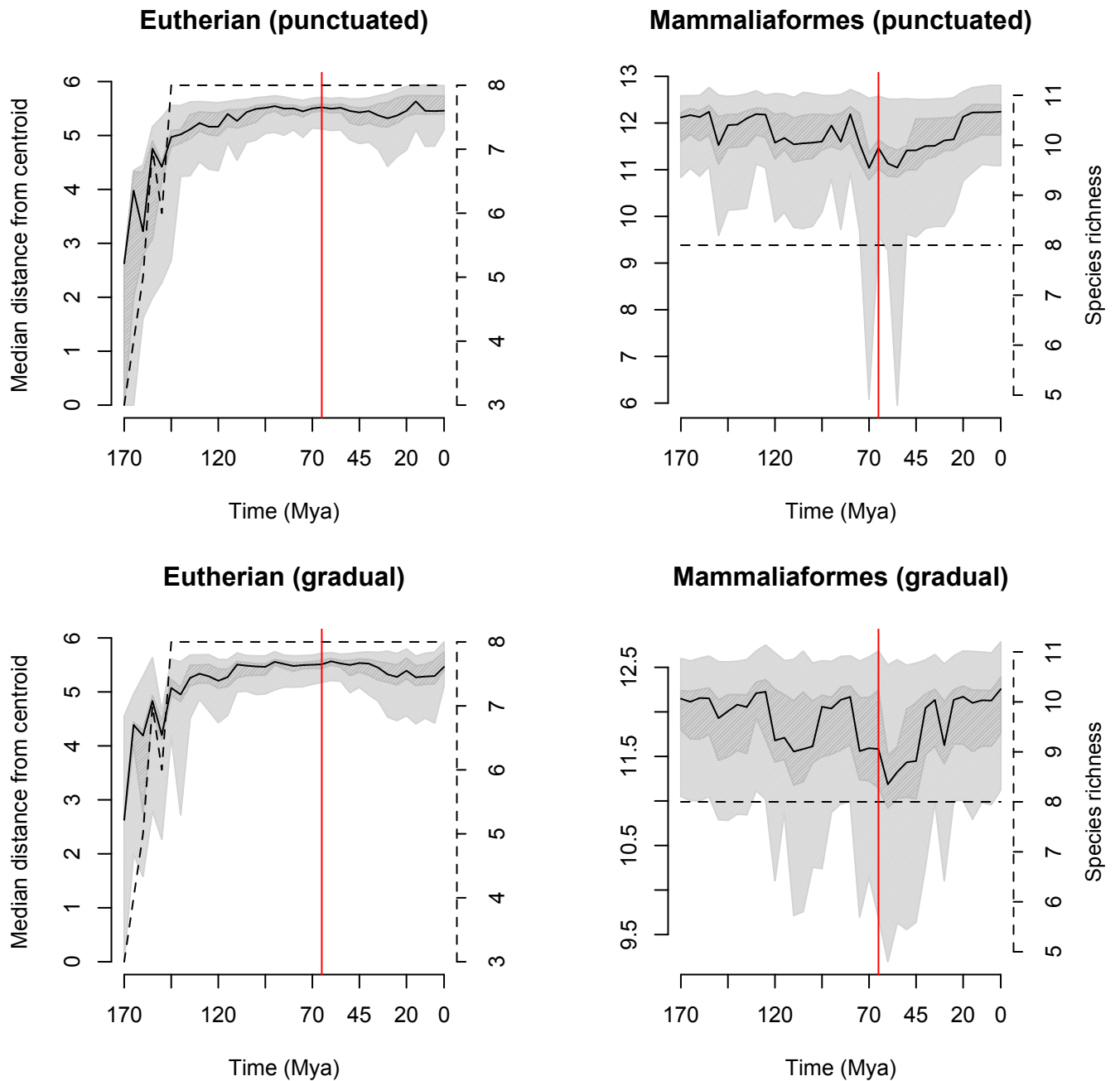


Figure 2: Rarefied variations of disparity through time among Eutherian and Mammaliaformes under punctuated or gradual evolution model. The x axis represents the time in Million of years ago (Mya). The y axis represents the disparity measured as the median distance from centroid per sub-sample. The solid 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 stars 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

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 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

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 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 were still high. Also, both data sets 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 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; Butler et al., 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 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 artefactually 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

use biostratigraphy and sometimes arbitrarily time bins of equal duration are used which also fix this caveat (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 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 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 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 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)).

ACKNOWLEDGMENTS

Thanks to Graeme Lloyd, Andrew Jackson, Gavin Thomas and Sive Finlay.

FUNDING

This work was funded by a European Commission CORDIS Seventh Framework Programme (FP7) Marie Curie CIG grant (proposal number: 321696).

547 References

- 548 Albert, J. S., D. M. Johnson, and J. H. Knouft. 2009. Fossils provide better estimates of
549 ancestral body size than do extant taxa in fishes. *Acta Zoologica* 90:357–384.
- 550 Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of
551 variance. *Austral Ecology* 26:32–46.
- 552 Anderson, P. S. and M. Friedman. 2012. Using cladistic characters to predict functional
553 variety: experiments using early gnathostomes. *Journal of Vertebrate Paleontology*
554 32:1254–1270.
- 555 Archibald, J. D. 2011. Extinction and radiation: how the fall of dinosaurs led to the rise
556 of mammals. JHU Press.
- 557 Arcila, D., R. A. Pyron, J. C. Tyler, G. Ort, and R. Betancur-R. 2015. An evaluation of
558 fossil tip-dating versus node-age calibrations in tetraodontiform fishes (teleostei:
559 Percomorphaceae). *Molecular Phylogenetics and Evolution* 82, Part A:131 – 145.
- 560 Beck, R. M. and M. S. Lee. 2014. Ancient dates or accelerated rates? Morphological
561 clocks and the antiquity of placental mammals. *Proceedings of the Royal Society B:*
562 *Biological Sciences* 281:1–10.
- 563 Benson, R. B. J. and P. S. Druckenmiller. 2014. Faunal turnover of marine tetrapods
564 during the Jurassic-Cretaceous transition. *Biological Reviews* 89:1–23.

- 565 Benton, M. J. 1985. Mass extinction among non-marine tetrapods. *Nature* 316:811–814.
- 566 Benton, M. J., J. Forth, and M. C. Langer. 2014. Models for the rise of the dinosaurs.
567 *Current biology* : CB 24:R87–R95.
- 568 Benton, M. J. and R. J. Twitchett. 2003. How to kill (almost) all life: the end-permian
569 extinction event. *Trends in Ecology and Evolution* 18:358 – 365.
- 570 Bininda-Emonds, O., R. Beck, and R. D. MacPhee. 2012. Rocking clocks and clocking
571 rocks: a critical look at divergence time estimation in mammals. From bone to clone:
572 the synergy of morphological and molecular tools in paleobiology Pages 38–82.
- 573 Bininda-Emonds, O. R., M. Cardillo, K. E. Jones, R. D. MacPhee, R. M. Beck, R. Grenyer,
574 S. A. Price, R. A. Vos, J. L. Gittleman, and A. Purvis. 2007. The delayed rise of
575 present-day mammals. *Nature* 446:507–512.
- 576 Brusatte, S., R. J. Butler, A. Prieto-Márquez, and M. A. Norell. 2012. Dinosaur
577 morphological diversity and the end-Cretaceous extinction. *Nature Communications*
578 3:804–804.
- 579 Brusatte, S. L., M. J. Benton, M. Ruta, and G. T. Lloyd. 2008a. The first 50 Myr of
580 dinosaur evolution: macroevolutionary pattern and morphological disparity. *Biology*
581 *Letters* 4:733–736.
- 582 Brusatte, S. L., M. J. Benton, M. Ruta, and G. T. Lloyd. 2008b. Superiority, competition,
583 and opportunism in the evolutionary radiation of dinosaurs. *Science* 321:1485–1488.

584 Brusatte, S. L., R. J. Butler, P. M. Barrett, M. T. Carrano, D. C. Evans, G. T. Lloyd, P. D.
585 Mannion, M. A. Norell, D. J. Peppe, P. Upchurch, and T. E. Williamson. 2015. The
586 extinction of the dinosaurs. *Biological Reviews* 90:628–642.

587 Butler, R. J., S. L. Brusatte, B. Andres, and R. B. J. Benson. 2012. How do geological
588 sampling biases affect studies of morphological evolution in deep time? a case study
589 of pterosaur (reptilia: Archosauria) disparity. *Evolution* 66:147–162.

590 Cailliez, F. 1983. The analytical solution of the additive constant problem.
591 *Psychometrika* 48:305–308.

592 Cartmill, M. 2012. Primate origins, human origins, and the end of higher taxa.
593 *Evolutionary Anthropology: Issues, News, and Reviews* 21:208–220.

594 Ciampaglio, C. N. 2004. Measuring changes in articulate brachiopod morphology
595 before and after the permian mass extinction event: do developmental constraints
596 limit morphological innovation? *Evolution & Development* 6:260–274.

597 Ciampaglio, C. N., M. Kemp, and D. W. McShea. 2001. Detecting changes in
598 morphospace occupation patterns in the fossil record: characterization and analysis
599 of measures of disparity. *Paleobiology* 27:695–715.

600 Cisneros, J. C. and M. Ruta. 2010. Morphological diversity and biogeography of
601 procolophonids (amniota: Parareptilia). *Journal of Systematic Palaeontology*
602 8:607–625.

Clapham, M. E., D. J. Bottjer, C. M. Powers, N. Bonuso, M. L. Fraiser, P. J. Marenco,
S. Q. Dornbos, and S. B. Pruss. 2006. Assessing the ecological dominance of
phanerozoic marine invertebrates. *PALAIOS* 21:431–441.

Close, R., M. Friedman, G. Lloyd, and R. Benson. 2015. Evidence for a mid-jurassic
adaptive radiation in mammals. *Current Biology* .

Coxall, H. K., S. D'Hondt, and J. C. Zachos. 2006. Pelagic evolution and environmental
recovery after the cretaceous-paleogene mass extinction. *Geology* 34:297–300.

David Polly, P. 2001. Paleontology and the comparative method: Ancestral node
reconstructions versus observed node values. *The American Naturalist* 157:pp.
596–609.

D'Hondt, S., T. D. Herbert, J. King, and C. Gibson. 1996. Planktic foraminifera,
asteroids, and marine production: Death and recovery at the cretaceous-tertiary
boundary. *Geological Society of America Special Papers* 307:303–317.

dos Reis, M., P. C. J. Donoghue, and Z. Yang. 2014. Neither phylogenomic nor
palaeontological data support a palaeogene origin of placental mammals. *Biology*
Letters 10.

dos Reis, M., J. Inoue, M. Hasegawa, R. J. Asher, P. C. J. Donoghue, and Z. Yang. 2012.
Phylogenomic datasets provide both precision and accuracy in estimating the
timescale of placental mammal phylogeny. *Proceedings of the Royal Society of*
London B: Biological Sciences .

623 Douady, C. J. and E. J. Douzery. 2003. Molecular estimation of eulipotyphlan divergence
 624 times and the evolution of insectivora. *Molecular Phylogenetics and Evolution* 28:285
 625 – 296.

626 Eernisse, D. and A. Kluge. 1993. Taxonomic congruence versus total evidence, and
 627 amniote phylogeny inferred from fossils, molecules, and morphology. *Molecular*
 628 *Biology and Evolution* 10:1170–1195.

629 Erwin, D. H. 1998. The end and the beginning: recoveries from mass extinctions. *Trends*
 630 *in Ecology and Evolution* 13:344 – 349.

631 Erwin, D. H. 2007. Disparity: Morphological pattern and developmental context.
 632 *Palaeontology* 50:57–73.

633 Finarelli, J. A. and J. J. Flynn. 2006. Ancestral state reconstruction of body size in the
 634 caniformia (carnivora, mammalia): The effects of incorporating data from the fossil
 635 record. *Systematic Biology* 55:301–313.

636 Foote, M. 1994. Morphological disparity in ordovician-devonian crinoids and the early
 637 saturation of morphological space. *Paleobiology* 20:320–344.

638 Foote, M. 1996. Ecological controls on the evolutionary recovery of post-paleozoic
 639 crinoids. *Science* 274:1492–1495.

640 Friedman, M. 2010. Explosive morphological diversification of spiny-finned teleost
 641 fishes in the aftermath of the end-Cretaceous extinction. *Proceedings of the Royal*
 642 *Society B: Biological Sciences* 277:1675–1683.

643 Garland, J., Theodore and A. R. Ives. 2000. Using the past to predict the present:
644 Confidence intervals for regression equations in phylogenetic comparative methods.
645 The American Naturalist 155:346–364.

646 Glor, R. E. 2010. Phylogenetic insights on adaptive radiation. Annual Review of
647 Ecology, Evolution, and Systematics 41:251–270.

648 Goswami, A., G. V. Prasad, P. Upchurch, D. M. Boyer, E. R. Seiffert, O. Verma,
649 E. Gheerbrant, and J. J. Flynn. 2011. A radiation of arboreal basal eutherian mammals
650 beginning in the late cretaceous of india. Proceedings of the National Academy of
651 Sciences of the United States of America 108:16333–16338.

652 Gould, S. J. and N. Eldredge. 1977. Punctuated equilibria: The tempo and mode of
653 evolution reconsidered. Paleobiology 3:pp. 115–151.

654 Gower, J. C. 1966. Some distance properties of latent root and vector methods used in
655 multivariate analysis. Biometrika 53:325–338.

656 Gower, J. C. 1971. A general coefficient of similarity and some of its properties.
657 Biometrics 27:pp. 857–871.

658 Grossnickle, D. M. and P. D. Polly. 2013. Mammal disparity decreases during the
659 cretaceous angiosperm radiation. Proceedings of the Royal Society of London B:
660 Biological Sciences 280.

661 Guillerme, T. and N. Cooper. 2015. Assessment of cladistic data availability for living
662 mammals. bioRxiv .

Guillerme, T. and N. Cooper. In review. Effects of missing data on topological inference
 using a total evidence approach,. *Molecular Phylogenetics and Evolution* .

Hetherington, A. J., E. Sherratt, M. Ruta, M. Wilkinson, B. Deline, and P. C. Donoghue.
 2015. Do cladistic and morphometric data capture common patterns of
 morphological disparity? *Palaeontology* 58:393–399.

Holm, S. 1979. A simple sequentially rejective multiple test procedure. *Scandinavian
 journal of statistics* Pages 65–70.

Hopkins, M. 2013. Decoupling of taxonomic diversity and morphological disparity
 during decline of the cambrian trilobite family ptercephaliidae. *Journal of
 Evolutionary Biology* 26:1665–1676.

Huang, S., K. Roy, and D. Jablonski. 2015. Origins, bottlenecks, and present-day
 diversity: Patterns of morphospace occupation in marine bivalves. *Evolution* .

Hughes, M., S. Gerber, and M. A. Wills. 2013. Clades reach highest morphological
 disparity early in their evolution. *Proceedings of the National Academy of Sciences*
 110:13875–13879.

Hunt, G. 2007. The relative importance of directional change, random walks, and stasis
 in the evolution of fossil lineages. *Proceedings of the National Academy of Sciences*
 104:18404–18408.

Hunt, G., M. J. Hopkins, and S. Lidgard. 2015. Simple versus complex models of trait

evolution and stasis as a response to environmental change. *Proceedings of the National Academy of Sciences* 112:4885–4890.

Korn, D., M. J. Hopkins, and S. A. Walton. 2013. Extinction spacea method for the quantification and classification of changes in morphospace across extinction boundaries. *Evolution* 67:2795–2810.

Lloyd, G. T. 2015. Claddis: Measuring Morphological Diversity and Evolutionary Tempo. R package version 0.1.

Losos, J. B. 2010. Adaptive radiation, ecological opportunity, and evolutionary determinism. *The American Naturalist* 175:pp. 623–639.

Lovegrove, B. G., K. D. Lobban, and D. L. Levesque. 2014. Mammal survival at the cretaceous–palaeogene boundary: metabolic homeostasis in prolonged tropical hibernation in tenrecs. *Proceedings of the Royal Society of London B: Biological Sciences* 281.

Luo, Z.-X. 2007. Transformation and diversification in early mammal evolution. *Nature* 450:1011–1019.

KEY: luo2007

ANNOTATION: 10.1038/nature06277

Meredith, R., J. Janečka, J. Gatesy, O. Ryder, C. Fisher, E. Teeling, A. Goodbla, E. Eizirik, T. L. Simão, T. Stadler, D. Rabosky, R. Honeycutt, J. Flynn, C. Ingram, C. Steiner, T. Williams, T. Robinson, B. Angela, M. Westerman, N. Ayoub, M. Springer, and

W. Murphy. 2011. Impacts of the Cretaceous terrestrial revolution and KPg extinction on mammal diversification. *Science* 334:521–524.

Newham, E., R. Benson, P. Upchurch, and A. Goswami. 2014. Mesozoic mammaliaform diversity: The effect of sampling corrections on reconstructions of evolutionary dynamics. *Palaeogeography, Palaeoclimatology, Palaeoecology* 412:32 – 44.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2015. *vegan: Community Ecology Package*. R package version 2.3-0.

O'Leary, M. A., J. I. Bloch, J. J. Flynn, T. J. Gaudin, A. Giallombardo, N. P. Giannini, S. L. Goldberg, B. P. Kraatz, Z.-X. Luo, J. Meng, X. Ni, M. J. Novacek, F. A. Perini, Z. S. Randall, G. W. Rougier, E. J. Sargis, M. T. Silcox, N. B. Simmons, M. Spaulding, P. M. Velazco, M. Weksler, J. R. Wible, and A. L. Cirranello. 2013. The placental mammal ancestor and the postK-Pg radiation of placentals. *Science* 339:662–667.

Olson, M. E. and A. Arroyo-Santos. 2009. Thinking in continua: beyond the adaptive radiation metaphor. *BioEssays* 31:1337–1346.

OLEary, M. A., J. I. Bloch, J. J. Flynn, T. J. Gaudin, A. Giallombardo, N. P. Giannini, S. L. Goldberg, B. P. Kraatz, Z.-X. Luo, J. Meng, X. Ni, M. J. Novacek, F. A. Perini, Z. Randall, G. W. Rougier, E. J. Sargis, M. T. Silcox, N. B. Simmons, M. Spaulding, P. M. Velazco, M. Weksler, J. R. Wible, and A. L. Cirranello. 2013. Response to

comment on the placental mammal ancestor and the postk-pg radiation of placentals.

Science 341:613.

Paradis, E., J. Claude, and K. Strimmer. 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20:289–290.

Payne, J. L., N. A. Heim, M. L. Knope, and C. R. McClain. 2014. Metabolic dominance of bivalves predates brachiopod diversity decline by more than 150 million years. *Proceedings of the Royal Society B: Biological Sciences* 281.

Pearman, P. B., A. Guisan, O. Broennimann, and C. F. Randin. 2008. Niche dynamics in space and time. *Trends in Ecology and Evolution* 23:149 – 158.

Prentice, K. C., P. Ruta, and M. J. Benton. 2011. Evolution of morphological disparity in pterosaurs. *Journal of Systematic Palaeontology* 9:337–353.

R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing Vienna, Austria.

Raia, P., F. Carotenuto, F. Passaro, P. Piras, D. Fulgione, L. Werdelin, J. Saarinen, and M. Fortelius. 2012. Rapid action in the palaeogene, the relationship between phenotypic and taxonomic diversification in coenozoic mammals. *Proceedings of the Royal Society of London B: Biological Sciences* 280.

Raup, D. M. 1979. Size of the permo-triassic bottleneck and its evolutionary implications. *Science* 206:217–218.

Renne, P. R., A. L. Deino, F. J. Hilgen, K. F. Kuiper, D. F. Mark, W. S. Mitchell, L. E.
 Morgan, R. Mundil, and J. Smit. 2013. Time scales of critical events around the
 Cretaceous-Paleogene boundary. *Science* 339:684–687.

Revell, L. J. 2012. phytools: An R package for phylogenetic comparative biology (and
 other things). *Methods in Ecology and Evolution* 3:217–223.

Ronquist, F., S. Klopstein, L. Vilhelmsen, S. Schulmeister, D. Murray, and A. Rasnitsyn.
 2012. A total-evidence approach to dating with fossils, applied to the early radiation
 of the Hymenoptera. *Systematic Biology* 61:973–999.

Ruta, M., K. D. Angielczyk, J. Fröbisch, and M. J. Benton. 2013. Decoupling of
 morphological disparity and taxic diversity during the adaptive radiation of
 anomodont therapsids. *Proceedings of the Royal Society of London B: Biological
 Sciences* 280.

Sepkoski, J., J. John. 1981. A factor analytic description of the phanerozoic marine fossil
 record. *Paleobiology* 7:pp. 36–53.

Slater, G. J. 2013. Phylogenetic evidence for a shift in the mode of mammalian body size
 evolution at the cretaceous-palaeogene boundary. *Methods in Ecology and Evolution*
 4:734–744.

Slater, G. J., S. A. Price, F. Santini, and M. E. Alfaro. 2010. Diversity versus disparity and
 the radiation of modern cetaceans. *Proceedings of the Royal Society of London B:
 Biological Sciences* .

760 Smith, A. J., M. V. Rosario, T. P. Eiting, and E. R. Dumont. 2014. Joined at the hip:
 761 Linked characters and the problem of missing data in studies of disparity. *Evolution*
 762 68:2386–2400.

763 Springer, M. S., R. W. Meredith, E. C. Teeling, and W. J. Murphy. 2013. Technical
 764 comment on the placental mammal ancestor and the postk-pg radiation of placentals.
 765 *Science* 341:613.

766 Stadler, T. 2011. Mammalian phylogeny reveals recent diversification rate shifts.
 767 *Proceedings of the National Academy of Sciences* 108:6187–6192.

768 Thorne, P. M., M. Ruta, and M. J. Benton. 2011. Resetting the evolution of marine
 769 reptiles at the Triassic-Jurassic boundary. *Proceedings of the National Academy of*
 770 *Sciences* 108:8339–8344.

771 Toljagic, O. and R. J. Butler. 2013. Triassic-Jurassic mass extinction as trigger for the
 772 mesozoic radiation of crocodylomorphs. *Biology Letters* 9.

773 Torgerson, W. S. 1965. Multidimensional scaling of similarity. *Psychometrika*
 774 30:379–393.

775 Wesley-Hunt, G. D. 2005. The morphological diversification of carnivores in north
 776 america. *Paleobiology* 31:35–55.

777 Wills, M. A., D. E. G. Briggs, and R. A. Fortey. 1994. Disparity as an evolutionary index:
 778 A comparison of cambrian and recent arthropods. *Paleobiology* 20:93–130.

- 779 Wilson, G. P. 2013. Mammals across the k/pg boundary in northeastern montana, u.s.a.:
780 dental morphology and body-size patterns reveal extinction selectivity and
781 immigrant-fueled ecospace filling. *Paleobiology* 39:429–469.
- 782 Wilson, G. P., A. R. Evans, I. J. Corfe, P. D. Smits, M. Fortelius, and J. Jernvall. 2012.
783 Adaptive radiation of multituberculate mammals before the extinction of dinosaurs.
784 *Nature* 483:457–460.
- 785 Wood, H. M., N. J. Matzke, R. G. Gillespie, and C. E. Griswold. 2013. Treating fossils as
786 terminal taxa in divergence time estimation reveals ancient vicariance patterns in the
787 palpimanoid spiders. *Systematic Biology* 62:264–284.
- 788 Yang, Z., S. Kumar, and M. Nei. 1996. A new method of inference of ancestral
789 nucleotide and amino acid sequences. *Genetics* 141:1641–50.
- 790 Zelditch, M. L., D. L. Swiderski, and H. D. Sheets. 2012. Geometric morphometrics for
791 biologists: a primer. Academic Press.

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 stars 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	$\frac{1}{46}$	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 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 (Mya)	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 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 (Mya)	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