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Global patterns of β-diversity along the phylogenetic time-scale: The role of climate and plate tectonics

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Abstract

Aim: We aimed to assess the relative influence of the historical and contemporary processes determining global patterns of current β-diversity. Specifically, we quantified the relative effects of contemporary climate and historical plate tectonics on β-diversity at different phylogenetic scales.

Location: Global.

Time Period: Contemporaneous.

Major taxa studied: Mammals and birds.

Methods: We analysed the current β-diversity patterns of birds and mammal assemblages at sequential depths in the phylogeny, that is, from the tips to deeper branches. This was done by slicing bird and mammal phylogenetic trees into 66 time slices of 1 Ma (from 0 to 65 Ma) and recording the branches within each slice. Using global distribution data, we defined the branches' geographical distribution as the union of the corresponding downstream species distributions. For each time slice, we (a) computed pairwise β-diversity across all the grid cells for the whole world and (b) estimated the correlation between this β-diversity matrix and contemporary climatic and geographical distances, and past geological distances, a proxy for plate tectonics.

Results: Contemporary climate best explained the β-diversity of shallow branches (i.e., species). For mammals, the geographical isolation of landmasses generated by plate tectonics best explained the β-diversity of deeper branches, whereas the effect of past isolation was weaker for birds.

Main conclusions: Our study shows that the relative influence of contemporary climate and plate tectonics on the β-diversity of bird and mammal assemblages varies along the phylogenetic time-scale. Our phylogenetic time-scale approach is general and flexible enough to be applied to a broad spectrum of study systems and spatial scales.

KEYWORDS
biogeographical regions, biogeography, continental drift, geological time-scale, macroecology, taxonomic scale

1 | INTRODUCTION

Elucidating the determinants of broad-scale β-diversity between different regions of the world has long fascinated naturalists (e.g., Holt et al., 2013; Wallace, 1876). However, it is only recently that the ever-increasing availability of global distribution databases [e.g., International Union for Conservation of Nature (IUCN), Bird-Life, Map Of Life] has made it possible to produce a comprehensive synthesis of β-diversity patterns, especially for vertebrates (e.g., Holt et al., 2013; Kreft & Jetz, 2010). A wide variety of

potential processes may have generated these patterns. To unravel the relative importance of these processes, there is a need for a unification of multiple ecological and evolutionary approaches and theories.

Niche-based theory of species distributions posits that environmental conditions determine where species occur geographically, emphasizing the importance of environmental filtering (Chase & Leibold, 2003; Currie et al., 2004; Soininen, 2010). This would therefore mean that assemblages which experience similar climatic conditions would also exhibit similar species compositions (i.e., low β-diversity). There is, however, ample evidence that assemblages located in similar bioclimatic regions on different continents often differ not only in species composition, but also in phylogenetic composition (Holt et al., 2013). This apparent discrepancy may be explained by the history of lineage dispersal and diversification over evolutionary time (Flynn, 1998; Ronquist & Sanmartín, 2011; Simpson, 1980). If a given ancestor was constrained to a region of the globe (e.g., to a particular continent that was isolated in the past), its descendants might also be restricted to this particular region even if suitable climatic conditions exist elsewhere (Lomolino, Riddle, Whittaker, & Brown, 2010). In short, although both niche theory and dispersal history can predict how the structure of species assemblages might change over broad-scale climatic and geographical gradients, their respective influence is not fully understood and has not yet been properly tested.

By describing the historical flow of lineage diversification, phylogenies represent a window looking back through evolutionary time. Therefore, one potential avenue for assessing the relative influence of contemporary climate versus historical dispersal on diversity distribution is to study the geographical pattern of phylogenetic β-diversity (Davies & Buckley, 2012; Graham & Fine, 2008). It has been hypothesized that contemporary environmental filtering and historical dispersal limitations may have left an imprint on patterns of current β-diversity, but that their effects can be perceived only at certain depths along the phylogenetic time-scale (e.g., Duarte et al., 2014; Graham & Fine, 2008). However, global tests of this hypothesis are still lacking. Here, we aim to do so by asking a first question: do contemporary geographical distances (which cause dispersal limitation) and climatic gradients influence current patterns of β-diversity at different phylogenetic time-scales? One prediction is that the current β-diversity of deep branches correlates better with climatic distances, whereas the β-diversity of shallow branches might correlate with geographical distances (interpreted here as a legacy of past dispersal limitation). This prediction should be supported if evolutionary climatic niche divergence, driven by adaptation to past climate, has promoted the emergence of ancestral lineages (producing a correlation between β-diversity of deep branches and climatic distance; see, e.g., swallowtail butterflies, Condamine, Sperling, Wahlberg, Rasplus, & Kergoat, 2012). Then, in each of the climatic regimes, allopatric (geographical) speciation and climatic niche conservatism may have further driven diversification, producing a correlation between shallow branches and geographical distance. An alternative prediction stipulates that geographical distances correlate better with the current β-diversity of deep branches, whereas recent climatic and habitat distances correlate better with that of current shallow branches. This alternative prediction should be supported if dispersal events had brought an ancestral lineage to a new region where they further diversified into different climatic regimes or habitats [i.e., recent adaptation to local climate or habitat, e.g., tetragnatha spiders in Hawaï (Gillespie, 2004) or anoles lizards in the Caribbean (Losos, 2009)].

Regardless of which hypothesis may apply, there is a need to account for past geological events that have influenced past migration routes and, possibly, current β-diversity of deep branches. Continents have not been geographically stable over evolutionary time, and in some parts of the world their movement has created barriers, whereas in other parts it has facilitated dispersal among assemblages. Recent plate tectonic models based on magnetic anomalies and ocean seafloor spread reconstructions allow the accurate reconstruction of continental movements across geological times (Boyden et al., 2011; Seton et al., 2012; Williams, Müller, Landgrebe, & Whittaker, 2012). The development of such models offers a unique opportunity to test quantitatively the influence of plate tectonics on current global terrestrial β-diversity of vertebrates, but this has not yet been conducted (but see Leprieur et al. (2016) for a marine perspective). In particular, if ancient dispersal is more likely between continents that were close in the past, we expect higher deep branch similarity between these current assemblages compared with current assemblages whose geographical positions were further apart in the past. This is, for example, the case for the southern parts of Australia, Africa and South America that harbour some common deep branches because in the past they formed the supercontinent Gondwana (Lomolino et al., 2010). Here, we aim to test this prediction by asking our second question: does the past geographical configuration of continents better explain the current β-diversity of deep branches than the contemporary configuration of continents?

In order to answer our two questions, we coupled a recent framework [β-diversity through time (BDTT); Groussin et al. 2017] that breaks down conventional measures of phylogenetic β-diversity along the phylogenetic time-scale (producing a decomposed phylogenetic β-diversity profile called a BDTT profile) with palaeogeographical reconstructions. Using phylogenetic and current distributional data for most mammals and birds of the world (c. 4,600 mammals and c. 9,900 birds), as well as plate tectonic models, we found that contemporary climate and the contemporary and historical configuration of continents affect assemblage β-diversity at different phylogenetic time-scales, shedding light on our understanding of the factors determining the distribution of biological diversity.

2 | METHODS

2.1 | Distribution data

For mammals, we used the distribution maps provided by the Mammal Red List Assessment (http://www.iucnredlist.org/) for 4,616 species. For birds, breeding ranges distribution maps were extracted from

BirdLife (http://www.birdlife.org/) for 9,993 species. The best resolution at which these maps should be used is still under discussion in the literature, so we decided on the 200 km × 200 km resolution that is most commonly used at the global scale (Holt et al., 2013; Hurlbert & Jetz, 2007). The total number of grid cells was 3,646. Domestic and aquatic mammals were excluded from the analyses.

2.2 | Climatic and geographical data

We characterized global contemporary climate using the first two axes of a principal components analysis (PCA) applied to the 19 bioclimatic variables in the Worldclim database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). These axes together represented 80% of the total variability of the bioclimatic variables and were mainly related to mean annual temperature and precipitation seasonality, respectively. To quantify the effect of plate tectonics on β-diversity, we first derived the geographical positions of our grid cells along a geological time-scale using a global plate motion model derived from magnetic anomalies of the oceanic sea floor (Seton et al., 2012). This is possible because the global magnetic field has been reversed many times in the earth history, and the oceanic crust (that is created at mid-ocean ridges) has recorded these inversions, through the orientation of magnetic minerals in the newly formed crust. By measuring these recorded inversions (magnetic 'anomalies') and linking them to a geomagnetic polarity time-scale, it is possible to estimate the age of the sea floor to derive ocean sea-floor spreading dynamic and estimate relative motion between major tectonic plates. We used the GPLATE software program (Boyden et al., 2011; Williams et al., 2012), which implements this model, to obtain, for each million year from present back to 65 Ma, the past x and y coordinates of each grid cell. For both climate and geography, we then calculated the Euclidean distances between each pair of grid cells, based on the first two axes of the climatic PCA axes, and using the length of the shortest straight line between grid-cell positions (for both past and present), respectively.

2.3 | Phylogenies

For mammals, we used a recent, time-calibrated, ultrametric phylogenetic tree (Bininda-Emonds et al., 2007; Fritz, Bininda-Emonds, & Purvis, 2009). For birds, we used the Hackett back bone-based phylogeny used by Jetz, Thomas, Joy, and Mooers (2012). In order to assess the uncertainties associated with phylogenies, we used the first 100 trees proposed by Jetz et al. (2012) for birds, and the 100 trees proposed by Kuhn, Mooers, and Thomas (2011) for mammals. We updated the mammal phylogenetic trees by replacing the Carnivora group with a more recently published, highly resolved supertree (Nyakatura & Bininda-Emonds, 2012). As it was computationally too heavy to re-run the whole analysis for each of the 100 trees, the tree uncertainty analysis was performed on only a subset of 200 out of 3,646 grid cells. In order to sample the climatic and the geographical space in a representative manner, we used the cube method (Deville, 2004) based on the two climatic PCA axes and the contemporary geographical position of each grid cell (Supporting Information Appendix S1). The results

obtained with this subsampling design were similar to those based on the whole dataset (see Supporting Information Appendix S2), so we also present the subsampling results in the main text.

2.4 | β-Diversity

2.4.1 | Species β-diversity

To characterize the species β-diversity between two assemblages, we used the Simpson metric (Simpson, 1943):

$$\beta = \frac{\min(b, c)}{a + \min(b, c)} \tag{1}$$

where a is the number of species shared by the two grid cells, and b and c represent the number of species unique to each grid cell. The Simpson metric is the true turnover component (Baselga, 2010) of the classical Sørensen metric and is also known as 'spatial turnover' (Gaston & Blackburn, 2008). Importantly, this metric quantifies the degree of replacement of species between two sites, while being independent of species richness differences between assemblages (Baselga, 2010). In this paper, we will refer to it simply as species β-diversity.

2.4.2 | Decomposition through time (along the phylogenetic time-scale)

For a given metric, conventional measurements typically rely on a single number to describe the β-diversity between two assemblages. This number may reflect species β-diversity (Baselga, 2010, eq. 1; Simpson, 1943) or branch length β-diversity if a phylogeny is used (i.e., phylogenetic β-diversity; see, e.g., Leprieur et al., 2012). The analysis of species β-diversity patterns cannot establish the importance of factors influencing the current distribution of deep branches. For example, two regions that have no species in common (100% species β-diversity) can in reality be composed of the same deeper branches (i.e., 0% deeper branches β-diversity). Alternatively, phylogenetic β-diversity averages β-diversity across the temporal range spanned by the phylogeny, thus oversimplifying the temporal complexity of diversity patterns. Therefore, relying on a single metric to describe assemblage β-diversity may make it difficult to disentangle the relative influence of the factors in play on a different phylogenetic time-scale (Cavender-Bares & Reich, 2012; Duarte et al., 2014; Groussin et al., 2017; Levin, 1992; Mazel et al., 2016).

To overcome this issue, we use a framework to detect the phylogenetic time-scale at which a given factor had the greatest influence on the β-diversity of branches between assemblages (Groussin et al., 2017; and Figure 1). The framework computes β-diversity between assemblages at different time periods along the phylogenetic time-scale (Cavender-Bares & Reich, 2012). For example, if we consider a given time period S_T (e.g., one vertical grey line in Figure 1), initially, the phylogenetic tree is pruned to depth T by collapsing all descendent leaves of each of the branches encountered by S_T. The geographical distribution of these branches is calculated as the union of the distributions of their descending leaves (Borregaard et al., 2014). Importantly, this approach does not intend to estimate the geographical ranges of this branch in the past (i.e., its ancestral geographical range), but simply its current extent (as generally assumed when studying patterns of α or β

a. Phylogenetic tree   b. Assemblages

c. β-diversity throught time (BDTT)
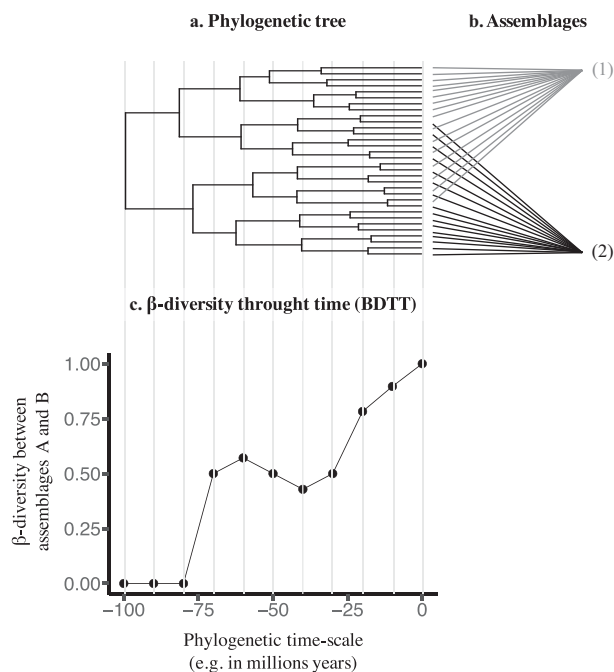
FIGURE 1 Theoretical example of the β-diversity through time (BDTT) framework. The figure presents (a) a balanced phylogenetic tree associated with (b) two hypothetical assemblages (1 and 2) composed of distinct species and (c) the resulting BDTT profile between 1 and 2 along the phylogenetic time-scale. The phylogenetic tree (a) contains 16 species, whose presence in assemblage 1 and/or 2 is depicted by a grey (assemblage 1) or black (assemblage 2) line in front of each tip (b). The BDTT profile and the phylogenetic tree are anchored in the same time-scale, with 11 vertical time periods represented in light grey

phylogenetic diversity). We thus obtain a branch × site matrix that can be used to quantify β-diversity (see Equation 1) for the period S_T. By dividing the phylogenetic tree into discrete time periods from the leaves to the root of the tree, the BDTT method provides a profile of β-diversity through time that makes it possible to separate shallow (e.g., species, genera) versus deep (e.g., families, orders) β-diversity, by breaking down conventional measurements of phylogenetic β-diversity (i.e., producing a decomposed phylogenetic β-diversity profile or BDTT profile). BDTT profiles were also computed for each order of the two groups independently, in order to explore the potential heterogeneity of responses across whole bird and mammal trees. The BDTT approach is conceptually similar to the classical analysis of β-diversity along the taxonomic scale (e.g., Kreft & Jetz, 2010; Lomolino et al., 2010), but it has the additional advantage of being anchored in an explicit geological time-scale.

2.4.3 | Visualizing assemblage composition through phylogenetic scales

In order to illustrate assemblage composition across the grid cells and along the phylogenetic time-scale, we used non-metric multidimensional scaling (hereafter NMDS; Minchin, 1987), a robust, nonparametric method for representing β-diversity in a low-dimensional space (Holt et al., 2013). We ran the NMDS for five different time periods (0,

15, 30, 45 and 65 Ma) using 20 starting points to avoid local minima, one unique phylogenetic tree and all 3,646 grid cells. To link the different ordination coordinates obtained for different phylogenetic time-scales, we started from the species (e.g., 0 Ma) ordination and rotated the 15 Ma time period ordination to maximize correspondence between these two ordinations (function *procrustes* of the vegan package; Oksanen et al., 2016). We iteratively performed this procedure until the last time period. This resulted in an illustration where a single grid cell has five sets of coordinates corresponding to five different phylogenetic time periods. With a view to providing a simple interpretation, we also grouped the grid cells according to 11 biogeographical realms (as in Holt et al., 2013). NMDS was calculated using the *metaMDS* function of the vegan R package.

2.5 | Linking β-diversity profiles with geography and climate

We used multiple regression on distance matrices (MRM; Lichstein, 2006) with randomization tests to link the BDTT profiles statistically to geographical (past and contemporary) and climatic (contemporary) distances between grid cells and to assess the significance of the relationships. We used both Pearson and Spearman rank correlation coefficients to assess the strength of the correlation, at each time period T, to obtain correlation profiles through time. We then used variance partitioning to extract the unique and shared effects of climate and geography (Legendre, 2007). When presenting the results, we focused on the unique effect of geography and the total effect for climate (unique climate plus shared affect), because geographically structured climate effects should be considered as indirect climatic effects (as climatic variables are strongly structured geographically at large scales). Furthermore, in order to test the extent to which these results were driven by a specific continent, we computed these correlation profiles while removing each continent one by one.

2.6 | Effects of the hierarchical nature of phylogenies on BDTT profiles

With the BDTT approach, the branches used to compute β-diversity progressively delineate larger groups of species when moving towards the root of the phylogeny (Figure 1). Larger groups of species have naturally larger geographical ranges, so they may not differ much in terms of climate, which inevitably means that the climatic correlation profile will increase towards the leaves of the tree. A null model approach was used to assess the impact of this effect on our results. We shuffled species identity on the phylogenetic trees of the two taxa (mammals and birds), then recomputed the BDTT profiles and their correlation with climate and geography. By repeating this procedure 100 times, we obtained a distribution of correlation values under the null hypothesis. Comparing the observed and null profiles of correlation made it possible to distinguish between biological and statistical effects (Leprieur et al., 2012; Weinstein et al., 2014). For each time period, comparisons between observed correlations and the correlations under the null hypothesis were summarized using standard effect sizes [SES,
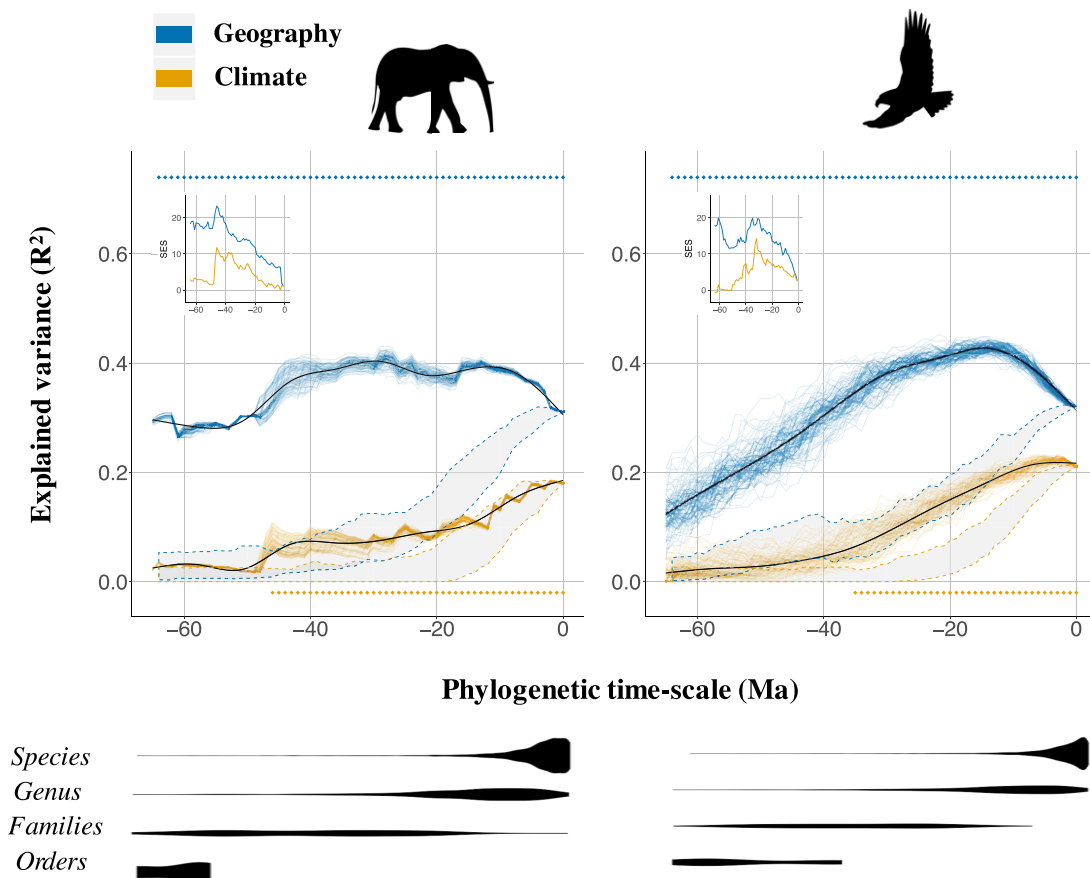
FIGURE 2 The relative effect of contemporary geographical and climatic distances on the β-diversity of branches through a phylogenetic time-scale. The figure presents, for mammals (left) and birds (right), the variation of the strength of the squared Pearson's correlation (R^2; y axis) between branch β-diversity and contemporary geographical (blue, 'unique' effect of geography) or climatic (yellow, 'total' effect for climate (unique climate plus shared effect with geography)) distances along the phylogenetic time-scale at which branches are defined (x axis). The uncertainty associated with the 100 phylogenetic trees used for the analyses is represented by the multiple correlation profiles. Black lines correspond to a smoothed fit across all profiles. The distribution of stem ages for four standard taxonomic ranks (species, genera, families and orders) is given along the same time-scale as the one used to define branches. Significant correlations for a given time period (i.e., > 90% of the phylogenetic trees support a significant relationship at the 5% level) are indicated with a coloured dot below (for climate) or above (for geography) the plots. The shaded area corresponds to the 95% confidence interval of a null model that randomizes phylogenetic relationships but keeps species composition constant. The inset panels present the standard effect sizes (SES) across phylogenetic scales (y axis = SES; x axis = phylogenetic scale, same as main plots)

(observed correlation minus mean null correlations)/(SD of null correlations)]. In addition, β-diversity was computed here with progressively fewer and fewer units (i.e., using fewer internal phylogenetic branches than tips), which might bias our results of correlation with climate and geography. To test the sensitivity of our results to this potential bias, we compared the R^2 of climatic and spatial models at different depths, but by keeping the same number of units when computing β-diversity. Specifically, when we compared the R^2 of the relationship between climatic (or geographical) distances and β-diversity computed at depth d versus species β-diversity, we subsampled species (100 repetitions) in order to have the same number of species as branches at depth d. This procedure should prove whether our results were biased or not by the difference in the number of units used to compute β-diversity at different depths. All the statistical analyses were carried out using the R software program (R Development Core Team, 2015).

3 | RESULTS

Relating BDTT profiles of mammals and birds to contemporary climatic and geographical distances shows that species β-diversity is significantly and positively related to both climatic and geographical distances ($p < .001$; Figure 2). Conversely, deep branch β-diversity is always significantly (and positively) related to contemporary geographical distances, but not to climatic distances (Figure 2). For both mammals and birds, the correlation between contemporary geographical distance and β-diversity is hump shaped along the phylogenetic time-scale, meaning that geographical distances explain the β-diversity of deep branches better than the β-diversity of species (Figure 2). This result is not attributable to the spurious effect of the difference in the number of units used to compute β-diversity at different depths of the tree (Supporting Information Appendix S3). However, because of the non-

independence of the distribution of branches at different depths, it is not possible to compare the correlation values directly between different depths. Rather, difference of correlations between depths has to be compared with a null expectation, given the tree shape. We found that, with such a null expectation, geographical distances never explain the β-diversity of deep branches better than species β-diversity (compare observed and null correlation profiles in Figure 2). In other words, there is a significant geographical signal on deep branches (SES are highly positive and > 2; see inset panels in Figure 2). Interestingly, in deep mammalian phylogenetic branches, β-diversity is more related to geographical distance compared with deep bird phylogenetic branches (e.g., for time slices > 40 Ma), in terms of either raw correlation (Figure 2) or SES (insets of Figure 2). Note that the phylogenetic time-scale used here is related to the standard taxonomic scale (i.e., on average species are younger than genera, genera are younger than families, etc.; see distributions of taxonomic rank ages on the phylogenetic time-scale in Figure 2).

The positive correlations between climatic distances and β-diversity are similar for both groups and increase from deep to shallow branches, meaning that climate distances explain the β-diversity of species better than that of deep branches (Figure 2). This is expected under our null model, which shuffles species identities on the phylogenetic tree (compare null and observed profiles in Figure 2), but the observed profiles lie significantly higher than the null profiles, showing that our results are not merely statistical bias [i.e., standard effect sizes are (sometimes significantly) positive; see inset panels of Figure 2]. These results are also robust to tree uncertainty (comparison of multiple observed profiles in Figure 2), to the relaxation of the assumption of a linear relationship between branch β-diversity and geographical or climatic distances (Supporting Information Appendix S4), and are also observed when some continents are removed from the analysis (Supporting Information Appendix S5). Nevertheless, the overall trends obscure some of the varied responses across the different parts of each phylogenetic tree. Indeed, the breakdown of β-diversity within orders shows that the geographical correlation profiles along the phylogenetic time-scale are more variable through time than their climatic counterparts. Climatic correlation profiles often increase the closer they get to a recent phylogenetic time-scale, whereas geographical effects show distinct shapes across orders (Supporting Information Appendix S6). For example, bats show an increasingly strong correlation profile, meaning that deep bat branches have less geographical structure than shallow branches, whereas the opposite pattern is found for rodents.

When using tectonic plate models to assess the effects of contemporary versus past geographical distances on branch β-diversity, we find past geographical distances to be the best predictor of the β-diversity of deep branches for mammals, but not for birds (Figure 3 and Supporting Information Appendix S7). Interestingly, the results for mammals hold only when all continents are included in the analysis. When Australia is excluded, the overwhelming effect of past distances on deep branch β-diversity disappears (Supporting Information Appendix S8). Australia represents an important zoogeographical realm

because it contains a unique set of species and deep branches (Figure 4). It should be noted that the compositional uniqueness of deep branches is, by default, expected to be lower than that of species owing to the hierarchical structure of the phylogenetic tree. However, it appears that Australia shows relatively greater uniqueness in deep branches than in shallow ones (the Australian arrow in Figure 4 points to the centre of the graph). Compared with other continents, Australia was geographically more isolated in the past, which explains why this continent drives the overall pattern of congruence between BDDT and past distances.

4 | DISCUSSION

On the species scale, β-diversity relates to contemporary geographical and climatic distances. The strong relationship between geographical distance and β-diversity reflects the existence of biogeographical realms (Holt et al., 2013; Wallace, 1876). It is also consistent with the hypothesis that biogeographical realms are, at least in part, the outcome of historical factors, such as past dispersal limitations (e.g., Flynn, 1998; Lomolino et al., 2010; Woodburne, 2010). The significant positive relationship between β-diversity and climatic distances most probably indicates that climatic filtering has a strong influence. Climatic filtering implies that ambient climatic conditions determine which species can and cannot persist in a specific region, given their inherent climatic tolerance (Buckley & Jetz, 2008; Currie et al., 2004). However, our results indicate that contemporary geographical distances explain β-diversity better than climate for both birds and mammals, suggesting that, at this scale, dispersal limitations have a greater influence than climatic filtering. This is in line with the argument that, at the global scale, faunas of different continents are often very dissimilar because they have been isolated for a long time, with relatively few dispersal events (Flynn, 1998; Holt et al., 2013; Lomolino et al., 2010; Penone et al., 2016; Simpson, 1980). One alternative explanation is that the climatic variables used here do not perfectly describe the climatic conditions actually experienced by animals, and that geographical distances incorporate differences in additional climatic or ecological conditions that potentially constrain branches to different regions (Anderson et al., 2011). However, it remains complicated to tease apart these two explanations using a correlative approach as used here.

In this study, we predicted that the relative influence of recent climate filtering and historical dispersal legacies (e.g., biogeographical history; Ronquist & Sanmartín, 2011) on β-diversity patterns might vary along the phylogenetic time-scale. Breaking phylogenetic β-diversity down along a phylogenetic time-scale (i.e., producing BDTT profiles) reveals the relative influence of geography and climate on branch distributions. For mammals and birds, contemporary geographical distances explain the β-diversity of deep branches better than the β-diversity of shallow branches, whereas climatic distances explain the β-diversity of species better than that of deep branches, compared with a null expectation. This result might be caused by ancient dispersal events followed by species diversifying in relative isolation across climatic gradients. Similar sequences of events have already been
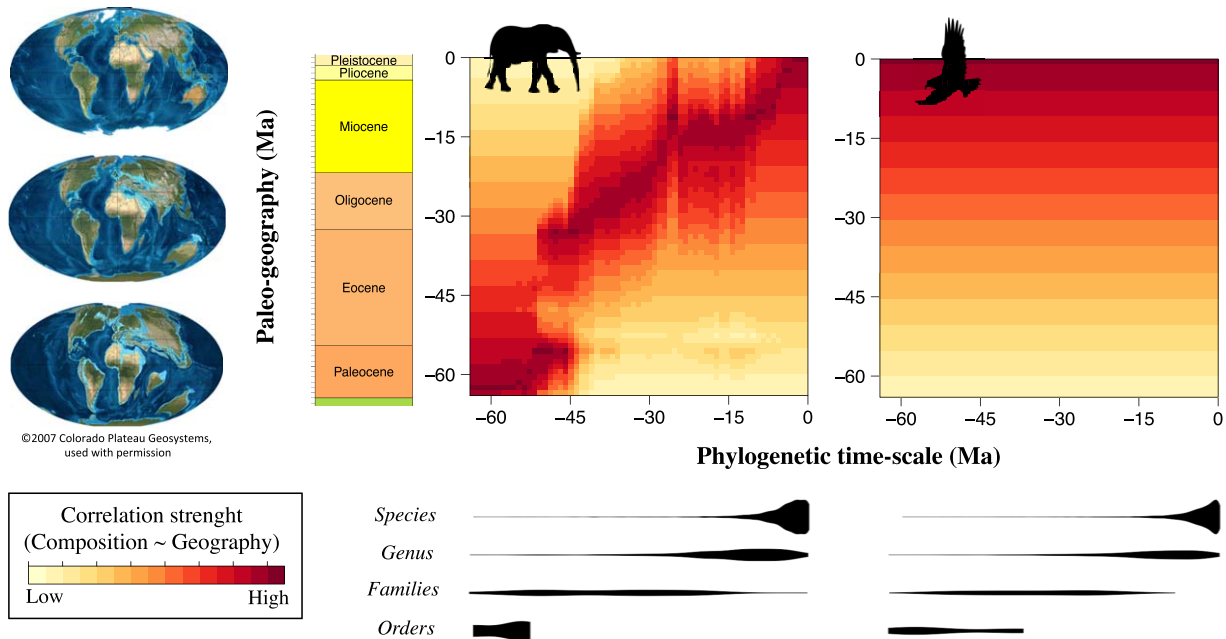
FIGURE 3 The imprint of plate tectonics on β-diversity. The figure shows the variation of the ranks of the squared Pearson's correlation (see the colours in the legend) between branch β-diversity and geographical distances ('unique' effect of geography, without contemporary climatic effect) along the phylogenetic time-scale at which branches are defined (x axis) and the date at which geographical distances are computed (y axis). More specifically, for each phylogenetic time period for which β-diversity is computed (x axis), we ranked the different past geographical distances (i.e., from 0 to 65 Ma) according to their squared Pearson correlation. The ranks presented are the median over 100 phylogenetic trees, with the red colour indicating a better relative fit. Note that ranks are computed across time-scales of geographical distances (y axis), for a given phylogenetic time period for which β-diversity is computed (x axis), so the colours should be compared within a given x coordinate (i.e., vertically). Palaeogeographical positions of continents are depicted to the left of the y axis (Blakey, 2008), along with epochs of the geological time-scale. The distribution of stem ages from four standard taxonomic ranks (species, genera, families and orders) is given along the time-scale used to define branches below the x axis

documented in several groups; for example, lemur primates occur only in Madagascar because of ancient dispersal events followed by diversification into different climatic regimes of the island (Ganzhorn, Goodman, Nash, & Thalmann, 2006). Our study generalizes these case-specific findings by demonstrating that contemporary geographical and climatic distances do not influence branch distributions at the same phylogenetic time-scale. Although contemporary climate best explains the β-diversity of shallow, but not deep branches, we also found that the correlation between deep branch β-diversity and climatic distance was higher than expected under our null model. This is probably because species climatic niches harbour some degree of phylogenetic signal (Cooper, Freckleton, & Jetz, 2011). However, the two PCA axes used here represent strong but complex climatic gradients. Two regions may have the same broad climate but still harbour non-null climatic distance from the PCA axes. These relatively fine-scale climatic species affinities may not be conserved at deep phylogenetic scales, which might partly explain why climatic distances mainly explain species β-diversity. Although beyond the scope of this study, an interesting avenue for future research could be to analyse correlation profiles across phylogenetic scales and climatic scales (e.g., using biomes instead of the climatic variables used here; see Penone et al., 2016).

The second question we asked was whether past geographical distances, as shaped by plate tectonics, can explain the β-diversity of

deep branches better than contemporary distances. This is true for mammals, but not for birds (Figure 2). This mammalian particularity is driven by the singular evolution of Australian fauna, which shows the greatest geographical and branch isolation when we go back in time. When Australia was removed from our analyses, past geographical distances no longer strongly influenced the β-diversity of deep branches. One possibility is that the overall dispersal along geological time-scales was not constrained by past geographical distances; for example, when land bridges reconnected land masses that had remained isolated for millions of years and/or extinction events erased the signal of tectonic isolation. For instance, this is the case for the Great American Biotic Interchange (GABI) that recently brought new mammalian orders, such as cetartiodactyls and carnivorans, to South America (i.e., in the last 3–15 Ma; Bacon et al., 2015; Webb, 2006; Woodburne, 2010) or during the complex biogeographical history of horses (e.g., Cantalapiedra, Prado, Hernández Fernández, & Alberdi, 2017). As a result of these recent events, the β-diversity of deep (e.g., at a time slice of 30 Ma in the current phylogeny) mammalian branches that we observe today between, for example South and North America does not actually represent what the β-diversity looked like 30 Ma between these continents. Indeed, South America harboured a unique set of high taxonomic ranks in the past (and so a high β-diversity with, e.g., North America) because it has been isolated for most of its history (Flynn,
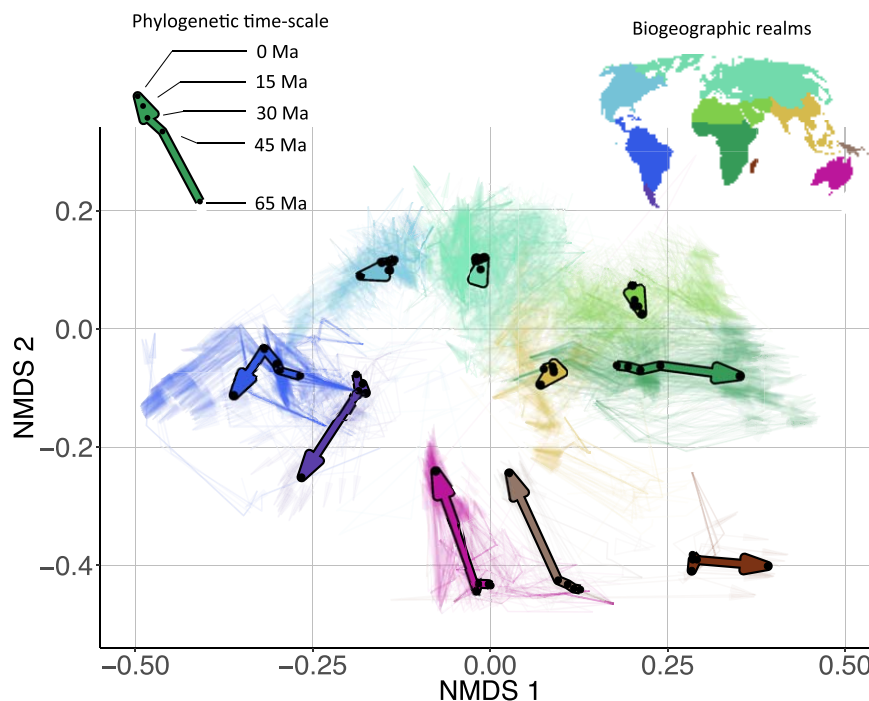
FIGURE 4 Mammalian assemblage compositions along a phylogenetic time-scale. The figure presents the non-metric multidimensional scaling (NMDS) ordination coordinates for mammalian assemblage compositions defined at different phylogenetic time-scales. Each assemblage is represented by a small arrow that links the five coordinates through time (0, −15, −30, −45 and −65 Ma; see key). Arrows are coloured according to the biogeographical realm to which they belong (cf. inset map), and ordination coordinates averaged across biogeographical realms are shown as large arrows

1998; Simpson, 1980). However, the combined effect of recent migration (i.e., the GABI) and high extinction rates of native lineages (Simpson, 1980) removed the signal of deep branch β-diversity (i.e., the current β-diversity of deep branches between North and South America is relatively lower today). Conversely, Australia did not experience these secondary connections with other continents followed by massive migration and extinction events, so it retained most of its unique deep branches and thus drove the observed pattern in mammals. The BDTT framework is a descriptive approach that aims to quantify contemporary β-diversity along the phylogenetic scale, and thus does not explicitly incorporate past extinctions or dispersal events. However, it could be extended to determine the relative importance of recent versus ancient dispersal by taking into account inferred dispersal events (e.g., using ancestral range reconstruction methods; Matzke, 2014; Ronquist & Sanmartín, 2011).

One noteworthy limitation of our approach is that our proxy for historical connectivity measures only past geographical proximity and ignores the location of dispersal barriers (e.g., oceans or mountains). For example, connectivity may be significantly different between pairs of grid cells at the same crow-fly distance, if one pair is separated by a dispersal barrier, whereas there are no barriers for the second pair. Future studies could test alternative measures of connectivity, such as least cost distances (Weinstein et al., 2014), considering the different barrier effects of oceans or regions with unsuitable climatic conditions (e.g., deserts or sea-level variations). Another avenue for future research would be to account for the past distribution of climates to

track back the potential corridors of suitable climate for lineages through time. However, maps of past climates are scarce and highly uncertain, even for relatively recent time periods (Mauri, Davis, Collins, & Kaplan, 2014). Moreover, estimating the habitat suitability of potential corridors over time for > 15,000 species is challenging, as a priori we do not know the climatic affinities of deep branches, nor their migrating abilities. Consequently, although our approach has some limitations, it represents an important step towards integrating deep geological factors into our understanding of extant global diversity patterns (see also Svenning, Eiserhardt, Normand, Ordonez, and Sandel, 2015) for the effect of more recent geological and climatic processes on diversity distribution).

We found some differences between mammalian and avian decomposed phylogenetic β-diversity patterns, which are probably attributable to their different dispersal abilities. The effect of contemporary geographical distance on deep branches is relatively greater for mammals than for birds, and this is even greater when past distances are considered (see SES values in Figure 2). This may suggest that high dispersal abilities and repeated colonization events in bird lineages have limited (a) the geographical signal of in situ diversification and (b) the signal of past plate tectonics over evolutionary time. However, this is not always the case. It is well known that some avian groups of species harbour a Gondwanian distribution (e.g., Palaeognathae: ratites and tinamous). In our main analysis, we assumed that geographical and climatic effects could act differently along the phylogenetic time-scale, but not on different parts of the tree, thus neglecting heterogeneity

within the tree. Repeating our analyses separately for all major mammalian and avian orders showed that orders with a clear disjoint distribution between continents harboured similar correlation patterns between BDTT and contemporary geography. For example, the strength of the relationship between primate β-diversity and geography showed a clear decrease from deep to shallow β-diversity, a pattern that matches the geographical disjunction of major primate branches (New versus Old World monkeys) and that is potentially linked to dispersal limitation legacies. In addition, the geographical effect varied more through phylogenetic scales than the climatic effect, a pattern that is potentially explained by highly variable dispersal capacity between orders (e.g., bats versus rodents). The fact that the climatic profiles were more similar than geographical ones, both amongst orders and between birds versus mammals, is consistent with the deterministic nature of niche factors and the similar climatic niche conservatism across the different groups.

In conclusion, our global analysis reveals the importance of considering the phylogenetic time-scale to describe and understand macroecological patterns. While the phylogenetic time-scale is related to the conventional taxonomic scale, the continuous BDTT approach offers several key advantages compared with a taxonomic scale approach, because it is transparent, not subject to arbitrary taxonomic assignments (to genera, families or higher levels) and anchored in an explicit and absolute geological time-scale. Importantly, the BDTT approach is highly flexible and can be extended in several ways and used in multiple fields. In macroecology, it could be interesting to study the link between the decomposed phylogenetic β-diversity and geography and climate across geographical and climatic scales, as it is known that processes shaping diversity patterns also vary along these two scales. To gain a better understanding of the importance of historical events on the current distribution of biological diversity, the BDTT approach could be coupled with ancestral area reconstruction or palaeoclimatic data. For example, ancestral area reconstructions could be used to measure the relative role of in situ diversification versus dispersal in shaping the patterns of phylogenetic diversity across major landmasses. Finally, the BDTT approach is not only useful for studying broad geographical patterns, but could also be applied to local plant–animal interaction networks (e.g., plants and their pollinators) or even to microscopic systems.

DATA ACCESSIBILITY

BDTT has been implemented in R. All codes needed to run BDTT, as well as illustrative examples are available here: https://github.com/FloMazel/BDTT. All datasets used in this study are freely available (see Methods).

AUTHOR CONTRIBUTIONS

F.M., S.L. and W.T. conceived the study. J.R. formatted the distribution data. F.M. conducted the analyses, with help from R.O.W. F.M., R.O.W., S.L. and W.T. analysed the results. F.M. and W.T. wrote the first version of the manuscript, and all authors contributed to the revisions.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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