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# Palaeocene–Eocene evolution of beta diversity among ungulate mammals in North America

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## ABSTRACT

**Aim** The Palaeocene–late Eocene transition in North America marks a critical interval in the evolution and diversification of land mammals, including adaptive radiation in the Palaeocene, and repeated waves of immigration over habitat bridges at the Palaeocene–Eocene boundary. We investigate the fossil record of ungulate mammals over this period to understand the effects of immigration and faunal exchange on local (alpha), regional (gamma) and between-site (beta) diversity.

**Location** North America.

**Methods** We use Palaeocene and Eocene records of North American ungulate mammals taken from the Paleobiology Database (PBDB), and calculate beta diversity among families and genera within the seven stages of the Cenozoic. We reconstruct geographic ranges sizes for studied taxa, and test trends in these ranges against null models used to control for sampling biases. Finally, we use Mantel tests to quantify the relationship between geographic distance and faunal dissimilarity within each time slice, in order to visualize changes in the spatial complexity of mammal communities.

**Results** Gamma diversity increases over the studied interval, with varying contributions from alpha and beta diversity. Beta diversity increases from the Palaeocene to Eocene, reflected in decreasing range size and increased correlation between reconstructed distance and faunal similarity. Increase in beta diversity over the Palaeocene–Eocene transition is driven by smaller geographic ranges among putatively invasive ‘immigrant’ and secondarily endemic taxa; range contraction among these groups in the middle–late Eocene leads to a Bartonian peak in beta diversity.

**Main conclusions** High gamma diversity in the Eocene was driven by high beta diversity rather than alpha diversity, indicating that range contraction in both immigrant and secondarily endemic taxa restructured the spatial organization of mammal communities. These parallel trends suggest that factors such as tectonic uplift or climate change were responsible, as opposed to ecological differences. Increase in beta diversity over the Palaeocene–Eocene boundary suggests that over longer time-scales, mass immigration events can lead to greater overall richness and greater heterogeneity, rather than homogeneity, within regional assemblages.

## Keywords

**Beta diversity, fossil record, geographic range, mammals, mass immigration, North America.**

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## INTRODUCTION

Spatial patterns in biodiversity are profoundly influenced by large-scale ecological, historical and evolutionary processes (Ricklefs, 2004; Harrison & Cornell, 2008; Thomas *et al.*, 2008). This has led palaeontologists to emphasize processes such as continental drift, climate change and sea-level changes as sculpting global diversity patterns, stimulating both evolutionary radiations (Sepkoski, 1976) and mass extinction (Hallam & Wignall, 1999; Peters, 2008). Between-site (beta) diversity describes rates and patterns of ecological differentiation at any given scale, and is central to addressing the processes underlying the formation of local and regional biotas (McKnight *et al.*, 2007; Anderson *et al.*, 2011). Although studies have investigated ecological change over shorter temporal scales (i.e. 10–100 years; see Collins *et al.*, 2000; Korhonen *et al.*, 2010), the effects of regional-scale processes on beta diversity have only just begun to be investigated (see Davis, 2005; Gaston *et al.*, 2007; Belmaker *et al.*, 2008; Buckley & Jetz, 2008) and a long-term temporal perspective is still lacking.

Ecologists have rarely used the fossil record as a historical source of data due, in part, to the unequal temporal and spatial distribution of rock strata. The time-averaged nature of most fossil accumulations (such that fossil material represents a mix of organisms that did not live contemporaneously) has also been viewed as problematic. Processes that operate on organic remains after death (including decay, disarticulation, transport and burial) are referred to as 'taphonomic', and can obscure the original biological and ecological signals associated with fossil material. However, time averaging becomes an advantage when testing macroecological hypotheses on larger temporal scales; the taphonomic processes leading to time averaging filter out short-term variations and high-frequency ecological variability (such as seasonal fluctuations), such that local accumulations of fossils represent long-term habitat conditions (Olszewski, 1999; Tomasovych & Kidwell, 2010). In addition, studies (e.g. Davis, 2005; Powell, 2007; Miller, 2011) have shown that within appropriate time-scales and taxonomic groups, fossil material can provide a high-resolution spatial record, which can be used to test long-term evolution in the spatial fabric of communities. As a result, the appearance of georeferenced fossil databases, such as the Paleobiology Database (PBDB), has allowed palaeontologists to perform a wide variety of spatial analyses involving both beta diversity (e.g. Davis, 2005) and calculation of geographic range size (Payne & Finnegan, 2007). In this study we examine the spatial record of fossil ungulate mammals in North America over an externally dynamic period in order to understand the effects of immigration and faunal exchange on local- to continental-scale spatial organization of biota.

The Palaeocene–late Eocene transition in North America marks a critical interval in the evolution and diversification of land mammals, incorporating the recovery of terrestrial ecosystems after the Cretaceous–Palaeogene (K/Pg) extinction, rapid adaptive radiation (Alroy, 1999) and intense Cenozoic global warming during the Palaeocene–Eocene Thermal Maximum (PETM). Critically, this warming also led to the formation of

two high-latitude habitat bridges (Beringia and a North Atlantic bridge connecting Greenland and Scotland), which allowed dispersal and exchange of mammals between North America, Europe and Asia (Smith *et al.*, 2006; Beard, 2008). This exchange brought about a profound change in the nature of North American mammal faunas (see Maas *et al.*, 1995), with most family-level mammal taxa that appear in the lowermost Eocene of North America having originated in Asia (Beard & Dawson, 1999). Consequently, the earliest Eocene faunas in North America show a strong resemblance to contemporaneous faunas of both Asia and Europe (Krause & Maas, 1990; Maas & Krause, 1994).

Ungulates have an exceptionally rich Cenozoic fossil record in North America, which has been well studied in terms of taxonomy, palaeoecology and biogeography. Ungulate mammals possess several other advantages as a study group: first, they are generally large ('macromammals', possessing a body mass > 1 kg) so that skeletal material is more reliably preserved as fossils than in other, smaller groups (Janis *et al.*, 1998); and second, as larger mammals they were discovered earlier, have been studied for longer and consequently their taxonomy (and limitations) is better understood (Alroy, 2003). Ungulate mammals are thus both taxonomically and taphonomically ideally suited to testing macroecological hypotheses on evolutionary time-scales.

There are two intervals of interest from the perspective of ungulate spatial ecology: (1) the initial Palaeocene adaptive radiation and (2) mass immigration of new taxa at the start of the Eocene. Both of these intervals contributed to an overall increase in gamma diversity over the Palaeocene and Eocene (Maas & Krause, 1994; Maas *et al.*, 1995); however, it is unclear how these profound changes in the diversity of North American mammal communities have affected spatial patterns of diversity at within-continent scales.

In particular, determining the effects of immigration on spatial patterns of diversity has important implications for present-day diversity. On human time-scales invasive/immigrant species have been implicated in both increases and decreases in biodiversity, but the extent to which introduced taxa are either spatially structured (i.e. narrow ranging) or unstructured (i.e. wide ranging) can determine their impacts on local and regional biotas (e.g. Rahel, 2002). Studying the history of mass immigration events using fossil material therefore provides valuable insight into the spatial effects and consequences of immigration, and on much longer time-scales than are typically available to ecologists.

We formulate two hypotheses to explain the overall increase in (gamma) diversity over the Palaeocene and Eocene. Our first hypothesis ('alpha') predicts an increase in alpha diversity with increasing gamma diversity. This increase in alpha diversity may be associated with the addition of wide-ranging taxa that are not structured spatially, either by *in situ* speciation or by immigration (see also Cornell & Lawton, 1992). Our second hypothesis ('beta') predicts an increase in beta diversity with increasing gamma diversity. The increase in beta diversity implies that increased regional diversity is associated with range

fragmentation and smaller geographic range sizes (e.g. Davis, 2005). This could arise due to increased habitat specialization of the groups examined, or due to environmental changes such as increased environmental heterogeneity or the formation of dispersal barriers (e.g. the rise of new mountain ranges; McKnight *et al.*, 2007).

## METHODS

Fossil records of ungulate mammals in North America from the earliest Palaeocene to the latest Eocene were obtained from the PBDB. Individual localities were coded for presence/absence with classification at the family and generic level. Although studies in beta diversity have typically used taxonomic datasets at species-level resolution, other studies have demonstrated that using higher-level taxa (such as genera and families) is a valid method for examining change in the structure of assemblages (e.g. Terlizzi *et al.*, 2009). Localities and taxonomic information were placed within time bins based on ICS official stratigraphic units (seven stages; Danian–Priabonian, see Fig. 1); as currently defined these seven stages vary in terms of chronological duration, from a maximum of 8.2 Myr (Ypresian) to a minimum of 2.4 Myr (Selandian). Palaeolatitude and palaeolongitude data from the PBDB were collated for all localities. To minimize the influence of isolated fossils, records from the same formation were combined when localities were within 0.5° of palaeolatitude or palaeolongitude of one another (for a full list

of localities and coordinates see Table S1 in Supporting Information). Localities without formal formation names (but possessing palaeolatitude and palaeolongitude data) were included. The resulting database collated 6661 individual occurrences representing 195 genera and 36 families (Table S1), from 114 individual localities within the first seven stages of the Cenozoic; all these records possessed both genus-level taxonomic data and locality palaeolatitude and palaeolongitude coordinates. Localities were plotted onto Cenozoic plate reconstructions (Scotese Paleomap Project, 2012; Fig. 2). All occurrences of ungulate genera appearing within the database were carefully checked against published stratigraphic ranges for these taxa (from Janis *et al.*, 1998); overall congruence between these two datasets was high.

Gamma diversity was taken as the total number of families/genera in North America within each time slice. We estimated alpha diversity within each time slice as the mean number of families/genera within each locality (see also Payne & Finnegan, 2007). We quantified patterns of beta diversity using the Simpson ( $\beta_{\text{sim}}$ ) dissimilarity index, which represents turnover independent of nestedness and is relatively robust to gradients in richness (Baselga, 2010). Beta diversity was calculated using both multisite and pair-wise analyses. Multisite analyses consider all localities simultaneously and thus produce a single value (see Diserud & Ødegaard, 2007), while pair-wise analyses produce a value for each pair of sites.

We first examined multisite  $\beta_{\text{sim}}$  within each time slice. As multisite indices are sensitive to the number of sites examined we rarefied the number of sites within each time slice to 24 (the minimum number of sites across all time period). This was done by randomly sampling 24 sites (without replacement), calculating multisite  $\beta_{\text{sim}}$  and using the mean value across 1000 iterations as the sample-size independent multisite  $\beta_{\text{sim}}$  value.

Using pair-wise  $\beta_{\text{sim}}$ , we also examined how the correlation between assemblage dissimilarity and spatial distance within each time slice (distance decay in similarity) changes through time. We used Mantel tests (based on Spearman rank correlation) to quantify the strength of the correlation between the spatial and community distance matrices within each time slice.

Observed changes in beta diversity could potentially reflect changes in spatial extent, because the overall geographic spread of localities changes between time slices (see Fig. 2). We therefore also recalculated multisite  $\beta_{\text{sim}}$  for a geographically consistent set of sites falling within a 30° (palaeolatitude and palaeolongitude) window centred on the Great Basin (dashed box in Fig. 2). The latitudinal bounds of this window were set to 30–60° N, but longitudinal bounds shift from 70–100° W to 90–120° W over the Palaeocene to Eocene to account for the westwards drift of North America during this interval.

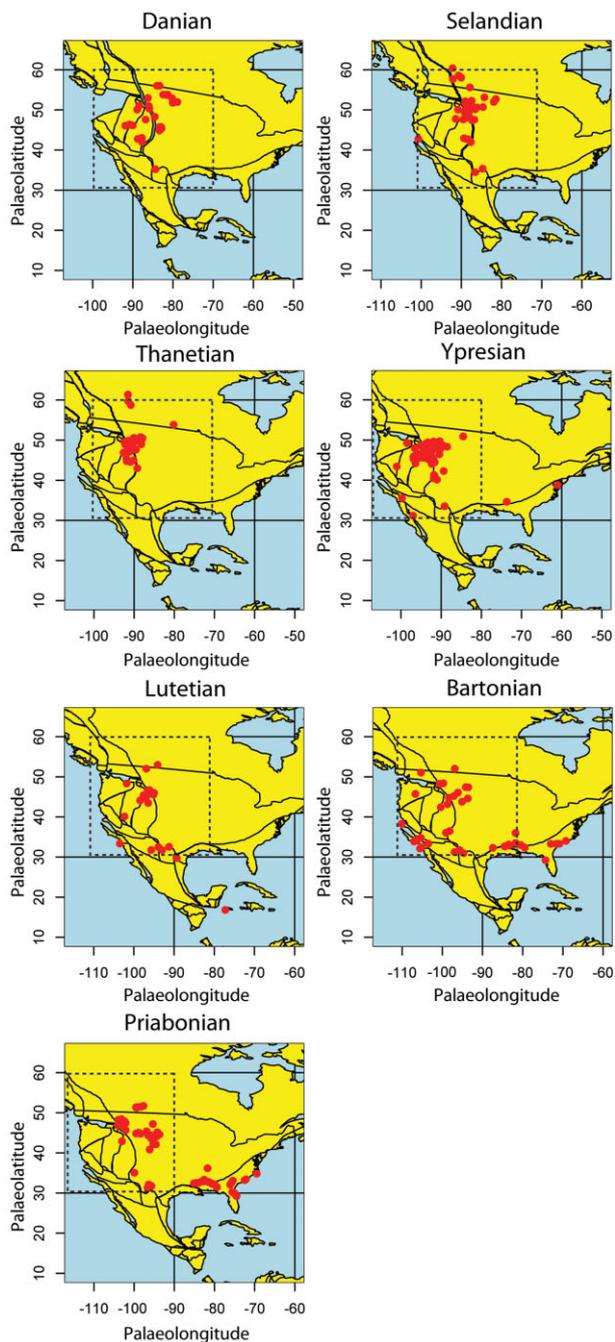
In addition, we tested whether changes in beta diversity are associated with changes in familial/generic geographic range size. Range size estimates were calculated after first projecting palaeolatitude and palaeolongitude data into the Behrmann equal-area projection. We reconstructed geographic range sizes for all families and genera with four or more occurrences for

ICS Stratigraphy		Radiometric dates (Ma)	
NEOG.	Olig.	Rupelian	
			33.9
PALEOGENE	Eocene	Priabonian	38.0
		Bartonian	41.3
		Lutetian	47.8
		Ypresian	56.0
		Thanetian	59.2
	Paleocene	Selandian	61.6
		Danian	66.0
CRET.	Upper	Maastrichtian	

PETM

K/Pg 

**Figure 1** Stratigraphic correlation; International Chronostratigraphic Chart (ICS) stage nomenclature and radiometric dates modified from Cohen *et al.* (2013). The positions of the Cretaceous/Palaeogene (K/Pg) mass extinction (bolide impact indicated with grey star) and the Palaeocene–Eocene thermal maximum (PETM) are marked.



**Figure 2** Palaeogeographic maps (Mercator projection) illustrating the location of sites within Palaeocene–Eocene stages. The 30° ‘window’ for geographically restricted analyses (see Fig. S1) is marked in dashed black square.

each time slice (range size estimates are unreliable when few sites are available) using a convex-hull algorithm. We excluded families and genera belonging to the Archaeoceti from range size analyses (equivalent to stem-group cetaceans, and potentially fully aquatic). Range size estimates are sensitive to changes in sampling effort (number of occurrences) and the geographical distribution of sampling locations through time. We therefore constructed a null model in which the observed number of

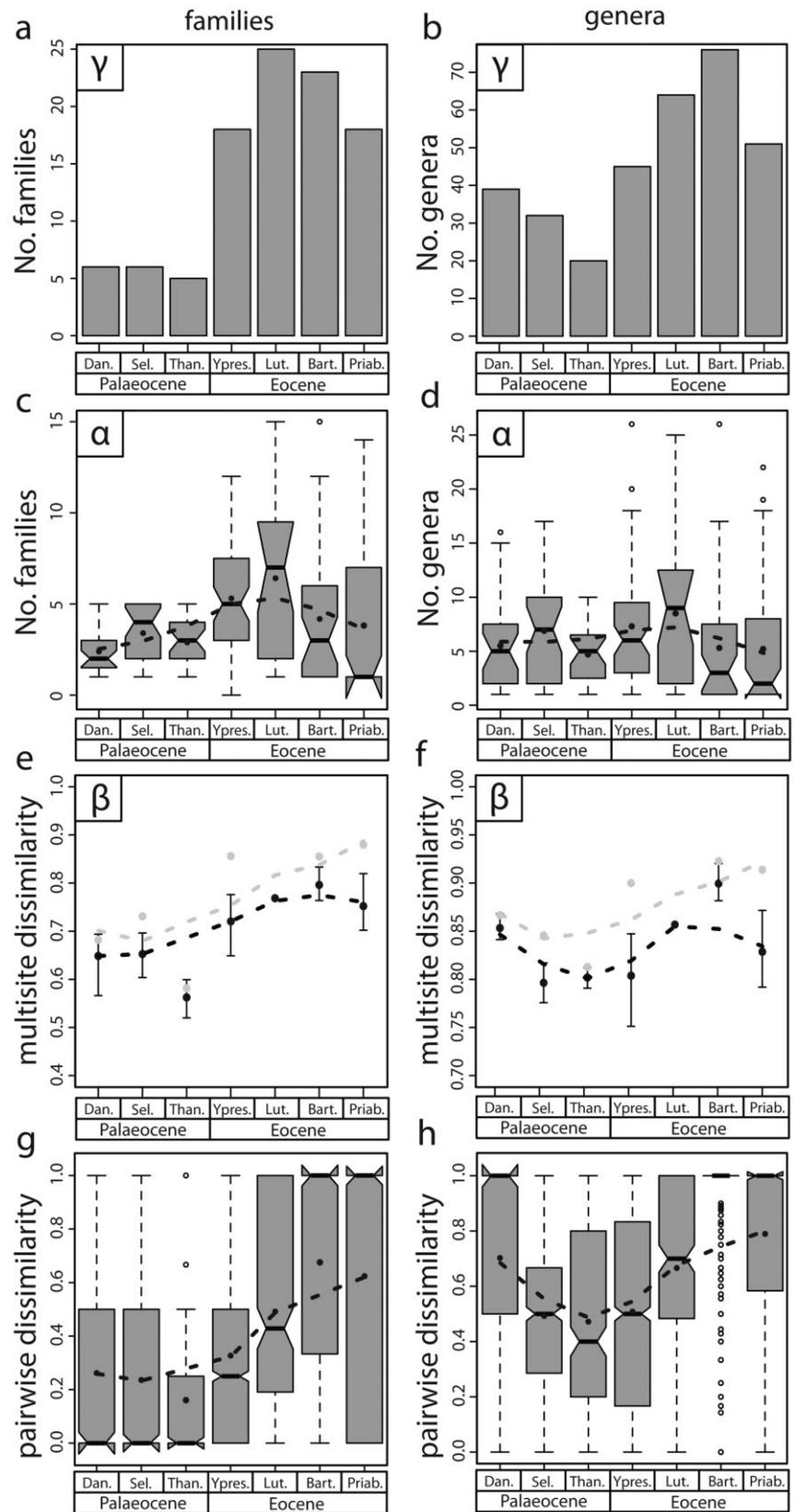
records for each family and genus within a time slice were randomly assigned to sites. Observed range size was then compared with the results of 1000 permutations of the null model and an effect size calculated as the standard normal deviate of observed values from the null; using this framework, range sizes that fall more than two standard deviates (either positive or negative) away from mean value of the null model can be designated as significant. We do not, however, take into account the sizes and distributions of freshwater lakes across North America at this time, which may introduce ‘gaps’ in ranges.

Lastly, in order to examine the relative influences of endemic and immigrant taxa on overall trends in diversity, we examined the range size trajectories of individual ungulate families. We used published literature to putatively split families and genera into ‘endemic’ (i.e. those present in North America from the Palaeocene onwards), ‘immigrant’ (those that evolved outside North America and subsequently immigrated in the Eocene) and ‘secondarily endemic’ (originated in North America in the Eocene). Where no information could be found, these taxa are figured as ‘unknown’ (status information and references are given in Table S3). All analyses were performed in R (R Development Core Team, 2010).

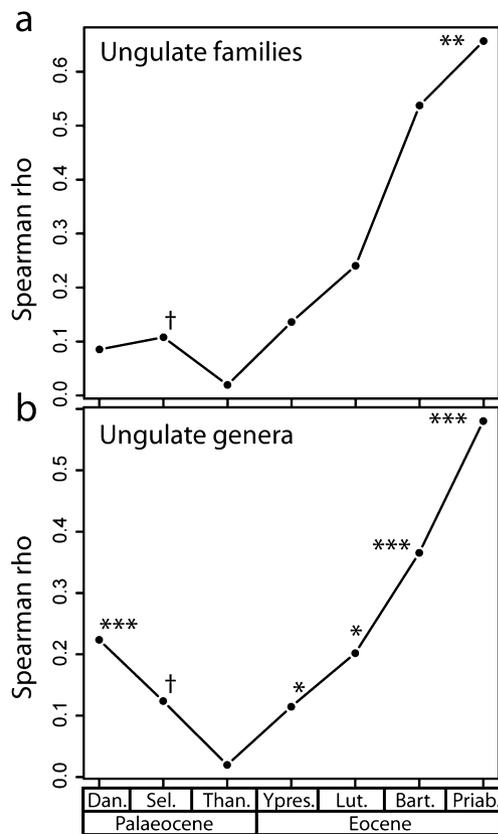
## RESULTS

Gamma diversity (Fig. 3a,b) among ungulate families is relatively low in the early Palaeocene, exhibits a marginal decrease in the late Palaeocene (Thanetian), increases rapidly through the lower to middle Eocene (Ypresian–Lutetian), and decreases in the late Eocene (Bartonian and Priabonian). At the generic level, gamma diversity decreases through the Palaeocene, and subsequently increases rapidly to the middle–late Eocene (Bartonian), before decreasing in the Priabonian. Trends in alpha diversity are similar for both families and genera; both exhibit a slow increase from the Palaeocene to early Eocene (with a dip in the Thanetian, albeit insignificant), peak in the middle Eocene (Lutetian), and then decrease in the Bartonian. However, at family level, significant increases (given by non-overlapping notches of box-plots; Chambers *et al.*, 1983) occur between the Danian and Selandian, and the Thanetian and Ypresian, with significant decrease from the Lutetian into the Bartonian. At genus level there are no statistically significant increases in alpha diversity between the Danian and Lutetian, but there is a significant decrease from the Lutetian into the Bartonian.

For beta diversity, both multisite  $\beta_{sim}$  and pair-wise  $\beta_{sim}$  indices show trends of overall increase over the Palaeocene and Eocene (with the notable exception of rarefied genus level  $\beta_{sim}$ , which exhibits a significant decrease in the Priabonian; Fig. 3e–h). This overall trend does not change when results are rarefied to control for varying number of sites within each time slice. Throughout all analyses,  $\beta_{sim}$  at family level exhibits decrease from the early to late Palaeocene, before dramatic increase from the Palaeocene to middle–late Eocene. At genus level, all analyses show decrease from the early to middle Palaeocene, increase from the late Palaeocene to middle Eocene, and then decrease from the middle to late Eocene. In general,



**Figure 3** Alpha, beta and gamma diversity for ungulate mammal families (left panels) and genera (right panels). (a), (b) Gamma ( $\gamma$ ) and (c), (d) alpha ( $\alpha$ ) diversity plotted against time over the studied interval. Note that alpha richness values for all localities with a time slice are plotted as box-plots; superimposed points (black) illustrate the mean alpha diversity within each time slice. (e), (f) Multisite ( $\beta_{sim}$ ) beta diversity, illustrating both raw (black) and rarefied (grey) data. (g), (h) Pair-wise beta diversity ( $\beta_{sim}$ ) illustrated as boxes with mean values (black) superimposed. The number of sites in each time slice is given in boxes. Trend lines in (c)–(h) are best-fit lowess (locally weighted scatterplot smoothing) lines.



**Figure 4** Mantel tests illustrating correlation (Spearman's rho) between geographic distance and taxonomic dissimilarity ( $\beta_{sim}$ ) for ungulate families and genera. Significance levels: † $P < 0.1$ ; \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

analyses at family and genus level behave in similar fashion, with a small difference in that beta decreases slightly earlier in the Palaeocene at family level (Danian–Selandian), than at genus level (Selandian–Thanetian).

The association between pairwise  $\beta_{sim}$  and geographical distance was quantified using Mantel tests (Fig. 4). We find that for both family and generic level the correlation between distance and faunal dissimilarity show increases in both strength and statistical significance in the middle–late Eocene.

Range-sizes (Fig. 5a,b) show broadly similar patterns for families and genera; in both cases ranges increase from the Danian to Selandian, decrease from the Selandian to Thanetian, reach a maximum in the lowermost Eocene (Ypresian) and subsequently show a general trend of decrease through to the end of the Eocene. Using null models, we find that at family level deviation from the null increases (becomes more negative indicating smaller range sizes) after the Ypresian, becoming significant in the Bartonian and Priabonian (Fig. 5c,d). At generic level, deviation from the null becomes slightly less significant over the course of the Palaeocene, before (as in the family-level data) decreasing in the Eocene and becoming significant in the Priabonian. Family and genus ranges in this interval are therefore smaller than expected from ranges constructed from random sampling of fossil-bearing sites.

All changes in beta diversity and geographic range size with time are therefore evident even after controlling for richness gradients, differences in the number of family/genus occurrences and the distribution of sampling location using null models (Figs 3e,f & 5). Although there is a notable latitudinal gradient in range sizes (Rapoport's rule), we determine that this is an unlikely explanation for our pattern (see Fig. S2).

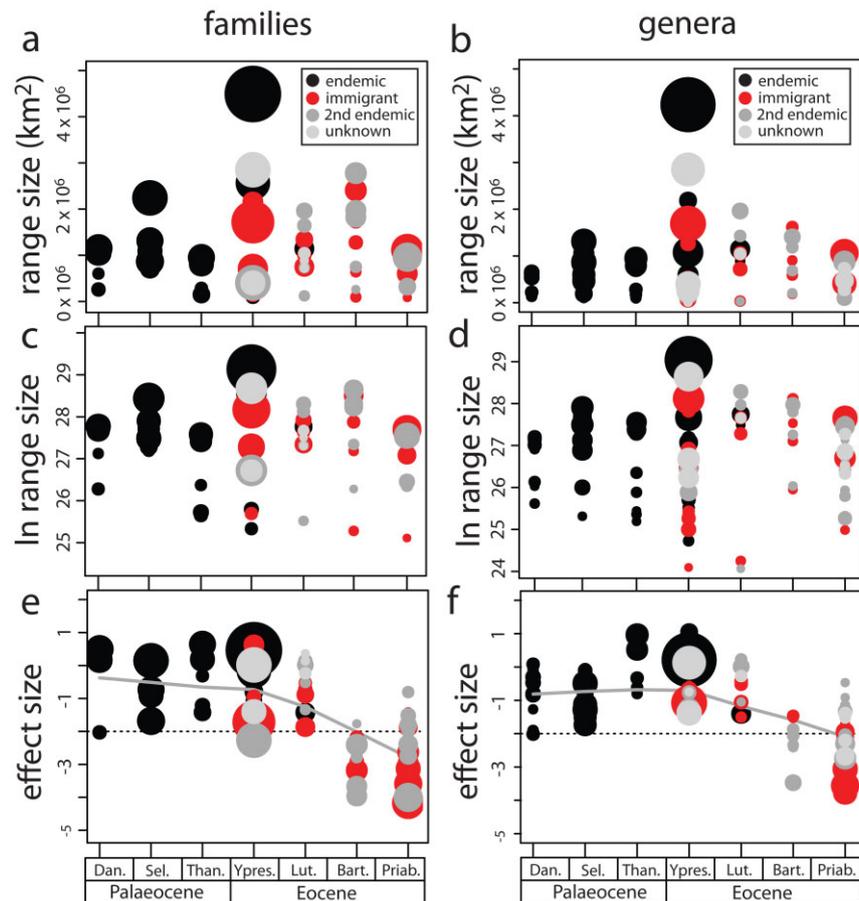
In order to quantify the contributions of endemic, immigrant and secondarily endemic taxa to these patterns, we plotted individual range size and effect size (standardized deviation from our null model) trajectories for families present in two or more time slices (Fig. 6; trajectories for all other families are given in Fig. S3). In terms of endemic families, there is no consistent pattern among Palaeocene taxa that persist into the Eocene; some families (e.g. Arctocyonidae, Mioclaenidae) undergo slight range contraction over the PETM, while others (Hyopsodontidae, Phenacodontidae) undergo more pronounced range expansion. Results are similarly mixed when using effect sizes, with both increase and decrease over the PETM, but none show significant deviation from the null. No endemic families persist into the Priabonian, when mean deviation from null range size becomes statistically significant (see Fig. 5). By contrast, early Eocene 'immigrant' families (those families that arrived via habitat bridges) show a consistent pattern (although only three appear in two or more time slices): all show an overall trend of decrease in range size and all develop significantly small ranges in the Bartonian and/or Priabonian. In similar fashion, effect sizes among secondarily endemic families all become more significant over time (exceeding two standard deviations in the Bartonian).

Across time slices, the relationship between alpha (local) and gamma (regional) diversity among families is positive, but with a relatively shallow slope (Fig. 7). When alpha and gamma diversities are split between endemic, secondarily endemic and 'immigrant' families for each time slice, endemic families show a much steeper slope than either the composite slope or secondarily endemic/immigrant families. Immigrant families show a slightly steeper slope than secondarily endemic, but both appear similar to the composite slope.

## DISCUSSION

### Changing contributions of alpha and beta to increasing gamma diversity

Our patterns of alpha, beta and gamma diversity illustrate evolving spatial structure among ungulate mammals over the Palaeocene and Eocene (the first c. 34 million years of the Cenozoic). Whereas changes in alpha diversity can reflect the filling and emptying of ecological niches on local scales (Cornell & Lawton, 1992), changes in beta diversity quantify the geographic heterogeneity in the taxonomic make-up of communities. We find that both alpha and beta diversity contribute to changes in overall increase in gamma diversity, and that the relative importance of these two diversity metrics differs from stage to stage, suggesting that the mechanisms shaping gamma diversity are



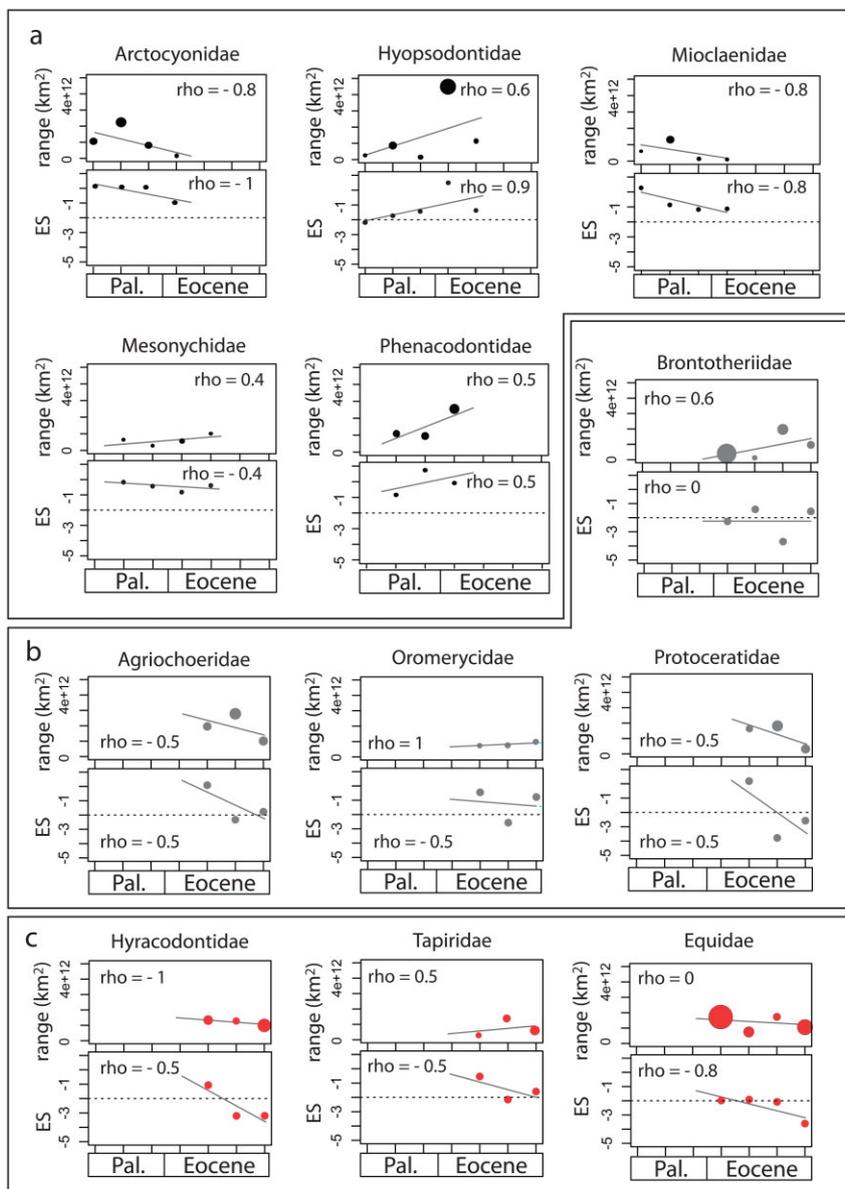
**Figure 5** Reconstructed geographic range sizes for ungulate families and genera, present in four or more sites: (a), (b) range sizes, point size is proportional to the number of localities occupied by each family/genus; (c), (d) range sizes plotted on logged axes; (e), (f) standardized deviation from range size null models (effect size). Dashed lines indicate statistical significance at the 95% confidence interval. Trend lines in (e) and (f) are best-fit lowess lines.

changing over time. Therefore, in terms of our original two hypotheses we find support for both ‘alpha’ and ‘beta’, but within different time periods. Importantly, we find the relative contribution of alpha and beta diversity to differ between endemic and both ‘secondarily endemic’ and ‘immigrant’ taxa. The marked increase in beta diversity in the Eocene, in contrast to low/decreasing levels in the Palaeocene (see Fig. 3) suggests a pivotal role played by both secondarily endemic and immigrant groups in restructuring the spatial fabric of mammal communities.

In support of this, the shallower alpha–gamma (local–regional) slope among immigrants and secondary endemics than in endemics (Fig. 7) suggests that across time slices, increases in gamma diversity among endemics is primarily associated with increasing alpha, while among immigrants and secondary endemics increases in gamma are more strongly associated with increasing beta. It has been previously shown that the strength of the associations between local and regional richness varies within assemblages (e.g. resident versus transient species; Belmaker, 2009). This study extends this observation and shows that the relative contribution of alpha and beta diversity to regional diversity may also change across time. Thus, certain periods are marked by regional richness changing primarily due to local processes such as niche filling, while others periods display stasis in local richness, as regional richness is shaped by dynamic spatial processes associated with connectivity and range changes.

We identify three intervals with distinct diversity patterns: (1) the Palaeocene – within the Palaeocene, gamma diversity (especially among genera) shows a slight decrease, concomitant with decreases in both alpha and beta diversity; (2) the early Eocene – a dramatic increase in all three (alpha, beta and gamma) diversity components; and (3) the middle–late Eocene – decreasing alpha diversity and increasing in beta diversity.

In the earliest Palaeocene, high beta diversity (specifically at genus level, but also to a lesser extent at the family level) may reflect aspects of both the mechanism of extinction itself (i.e. bolide impact) as well as subsequent ecomorphological evolution and niche filling. Diversity dynamics in mammalian faunas over the K/Pg boundary have been well studied at both local and regional scales. On local scales Wilson (2013) found that the effects of extinction in North America were severe and selectively removed both larger taxa and those with specialized diets. Recovery faunas in the earliest Palaeocene may have mostly comprised generalist survivors, perhaps also those possessing the ability to burrow and thus escape the secondary effects of extinction (see Robertson *et al.*, 2004). High beta and low alpha diversity in the earliest Palaeocene, on the longer time-scales being considered, may therefore reflect the patchy nature of communities in the aftermath of K/Pg mass extinction (the Danian stage in particular may include elements of a post-extinction recovery fauna that may have been highly aggregated



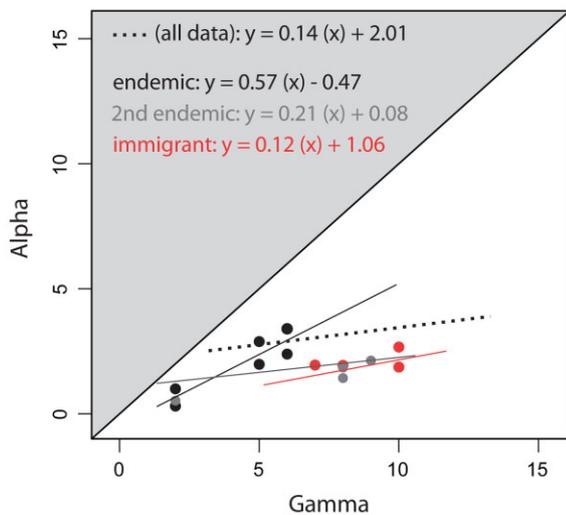
**Figure 6** Individual range size/effect size trajectories for ungulate families appearing in four or more sites over two or more time slices, showing (a) 'endemic', (b) 'secondarily endemic', and (c) 'immigrant' taxa. Point size is proportional to the number of localities occupied by each family. (Negative) significance lines at two standard deviations are given in dashed black lines on effect size plots. Trend lines (grey) represent ordinary least squares regressions. Correlation statistics are nonparametric Spearman rho values.

within geographic refugia), as well as newly evolved elements of an adaptive radiation that was already under way c. 1 Myr into the Palaeogene (Wilson, 2013).

Throughout the Selandian and Thanetian, both ungulate families and genera show a slight decrease in overall gamma diversity concomitant with decreasing beta, while alpha remains at similar levels. Mean alpha diversity does show small decrease from the Selandian to Thanetian in both families and genera, although differences between median values across all sites are insignificant (given by overlapping notches in box-plots). Lower beta diversity and larger range sizes among middle-late Palaeocene taxa further suggest that these animals were becoming wider ranging, leading to lower disparity between communities separated in space; this observation is supported by Maas & Krause (1994), who note little evidence for faunal provinciality among Palaeocene localities.

In the early Eocene (subsequent to the mass immigration of European and Asian taxa at the PETM), gamma diversity in both families and genera increases dramatically, mirrored by increases in both alpha and beta (see Figs 3 & 5). Although range sizes increase, most ranges do not deviate from null expectations, indicating that large ranges in the Ypresian perhaps reflects a sampling bias brought about by the appearance of new localities on the eastern coast of North America (see Fig. 2). Increase in beta diversity (significant in families, but equivocal in genera) over the Palaeocene–Eocene transition suggests that (on the time-scales being considered) biological invasion proceeded in tandem with habitat specialization.

Within the middle-late Eocene (Lutetian–Bartonian), changes in gamma diversity seem better correlated with changes in beta than with changes in alpha; alpha diversity shows significant decrease from the Lutetian–Priabonian, while gamma diversity



**Figure 7** Mean local (alpha) versus regional (gamma) diversity for ungulate families. Note that points cannot fall in the top left of plots (where alpha would be higher than gamma). Regression statistics are plotted for endemic, secondarily endemic and immigrant families. Regression parameters for all three groups are given in the panel, as well as for the combined dataset (i.e. where richness values for both endemic and immigrant families are combined within each time slice).

remains high. Correspondingly, beta diversity continues to rise (or remains high) during this interval. High beta diversity in the late Eocene also shows good correlation with decreasing range sizes, with the majority of both families and genera showing significant deviation from null models from the Bartonian onwards. The important contribution played by beta diversity in maintaining high gamma diversity in the late Eocene is also reflected in the results of Mantel tests, which illustrate increasing statistical correlation (associated with increasing statistical significance) between geographic distance and faunal dissimilarity.

Our results therefore comprise three lines of evidence (increasing beta diversity, strengthening correlation between distance and faunal dissimilarity, and decreasing range sizes) that indicate increasing spatial complexity among North American ungulate mammals over the entire interval, and in the late Eocene in particular. Although change in these three parameters could potentially be an artefact of the changing spatial distribution of sampling sites over time (e.g. the apparent increase in range size over the Palaeocene–Eocene transition), our distribution of sites shows little change over the course of the Eocene (and in particular from the Lutetian onwards), indicating that increase in spatial complexity among mammal communities most likely represents a genuine palaeoecological signal. In the next section, we attempt to explain the processes underlying patterns of decreasing Eocene range sizes and increased beta diversity.

### Macroecological/macroevolutionary dynamics of Eocene communities

In the middle–late Eocene, increasing beta diversity matches well with decreasing range sizes among studied taxa while overall

gamma diversity remains high after repeated immigration events. We suggest two major processes that may have contributed to the increase in the importance of beta diversity for gamma diversity throughout the Eocene: specialization and vicariance.

**1. Specialization:** the replacement of putatively generalist endemic taxa by specialized immigrants may have resulted in increased overall habitat specialization. Although very little is known about the ecology of archaic ungulates beyond their dental morphology (e.g. Janis *et al.*, 1998), they are thought to represent a polyphyletic assemblage of primarily omnivorous or generalist feeders (Rensberger, 1986; Janis, 2000). In contrast to these endemic forms, workers have suggested that immigrant ungulates were in general more ecologically specialized than archaic Palaeocene forms, and comprised a broader diversity of herbivorous, frugivorous and carnivorous taxa (Rensberger, 1986; Collinson & Hooker, 1987; Stucky, 1990; Janis, 2000). Some of the profound morphological differences between archaic Palaeocene, and more ‘modern’ Eocene ungulates are illustrated by contrasting the Selandian genus *Arctocyon* (likely omnivorous, jackal-sized and scansorial), with the Priabonian genus *Megacerops* (herbivorous, browsing and estimated to be around 3000 kg in weight). Invading immigrants would therefore most likely have occupied very different ecological niches to those from endemics, which may in part explain why there is little evidence for competition between the two faunas (and, by extension, perhaps why gamma diversity increases so dramatically over the Palaeocene–Eocene boundary). Geographic range size has been shown in many cases to correlate with niche breadth (Pyrone, 1999; Gaston & Spicer, 2001); ecological generalists tend to have large environmental and resource tolerances allowing a broad geographic distribution, with the opposite being true for ecological specialists (Gaston & Spicer, 2001). Smaller range sizes among middle–late Eocene immigrants may therefore in part reflect the profound ecological differences between endemic (generalist) and immigrant (specialized) families.

Alternatively, the observed decrease in range size (and increase in beta diversity) could be caused by individual groups (both endemic and immigrant) becoming more specialized over time. Evidence for smaller range sizes among taxa first appearing in the Eocene would support a scenario whereby smaller-ranged immigrant taxa are driving the increases in beta diversity, whereas finding decreasing range sizes within endemic, immigrant and secondarily endemic families would suggest increasing habitat specialization or exogenous forces as the more likely drivers.

We find a number of key differences between the individual trajectories of endemic and both immigrant and secondarily endemic ungulate families: whereas endemic families show no consistent trend in range size over the Palaeocene–Eocene boundary, both immigrant and secondarily endemic families appearing in North America in the earliest Eocene have smaller ranges, and further show a pronounced contraction in the late Eocene (Figs 5 & 6). The similar trajectories of immigrant and secondarily endemic families in this key Lutetian–Bartonian interval (when beta diversity reaches a maximum, and range sizes show significant deviation from null expectations) therefore suggest that newly immigrant taxa were not any more spatially

restricted than endemics, and that decreasing range sizes was likely driven by some other process that had similar impacts across families.

2. Vicariance events, such as tectonic uplift, may also have a profound effect on patterns of diversity. Uplift associated with the Laramide orogeny was a significant influence on the landscape of western North America from the Cretaceous onwards (e.g. Prothero, 1988). However, a period of relatively rapid uplift began in the Eocene (Mix *et al.*, 2011) and continued rapidly until c. 5 Ma (Davis, 2005). The fossil localities examined here are largely concentrated in uplifted areas (i.e. the Great Basin), and so the observed changes may have been driven in part by tectonic changes leading to range fragmentation. In turn this can lead to allopatric speciation, higher beta and gamma diversities and stronger patterns of distance decay in assemblage similarity. Alternatively, increasing beta diversity and decreasing range sizes among late Eocene ungulate mammals could also have been driven by fragmentation associated with rapid cooling in the latest Eocene and Oligocene (Janis, 1993; Salamy & Zachos, 1999), which would have had a profound effect on patterns of vegetation and the spatial distribution of biomes.

In summary, although we are unable to distinguish between 'specialization' and 'vicariance' hypotheses for decrease in range size and increase in beta diversity, we establish that both secondarily endemic and immigrant taxa behave in similar fashion in the middle–late Eocene. Increase in spatial complexity among ungulate mammal faunas during this period therefore resulted from either (1) parallel ecological specialization in these groups or (2) exogenous change which affected both groups equally.

## SUMMARY

Our data demonstrate that beta diversity can make varying contributions to overall (gamma) richness at any given time, reflecting dynamic changes in macroevolutionary and macroecological processes that operate on geological time-scales. Our observation that high gamma diversity in the late Eocene is driven by increased beta, rather than alpha, illustrates the role of beta diversity in driving overall diversity patterns on continental scales. In addition, our finding that increasing beta diversity was associated with range contraction in both immigrant and secondarily endemic taxa suggests an exogenous change, and reinforces the critical role played by regional-scale processes (operating on geological time-scales) in shaping the spatial fabric of biotas.

In the context of previous studies, other authors (e.g. Anthony & Maas, 1990; Stucky, 1990; Maas *et al.*, 1995) found little evidence for faunal provinciality in Palaeocene and Eocene North American mammal faunas. Our data suggest a different picture. We find: (1) relatively high levels of provinciality in the earliest Palaeocene (especially among ungulate genera); (2) decreasing provinciality in the middle–late Palaeocene; and (3) dramatic increase in the middle–late Eocene as the appearance of immigrant taxa coincided with considerable spatial restructuring of mammal communities. In ungulate families in particular, the Palaeocene–Eocene boundary coincides with a

large jump in beta diversity, coinciding with dramatic increase in gamma. Our results therefore provide strong evidence for the increasing contribution of beta diversity to total diversity throughout the Eocene.

Comparatively few studies have examined the effects of biological invasions on alpha, beta and gamma diversity. Some studies have suggested that most introduced species simply establish self-sustaining populations and cause few (if any) indigenous species to go extinct (Williamson, 1996; Davis *et al.*, 2011), other studies suggest that episodes of continued mass biological invasion can replace endemic species with high numbers of wide-ranging, cosmopolitan taxa (Rahel, 2002). Here we show that a period of mass immigration into North America over the Palaeocene–Eocene boundary elevated overall familial and generic richness, but importantly also led to greater heterogeneity, rather than homogeneity, within regional assemblages. The range sizes of endemic families do not appear to have been affected in a consistent fashion by the appearance of new taxa, nor were immigrants wider ranging and/or less spatially structured than endemic taxa.

Lastly, these findings reinforce the utility of the fossil record as a valuable source of spatial data which can be brought to bear when examining the processes responsible for assembling local and regional biotas on evolutionary time-scales.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

**Figure S1** Multisite  $\beta_{sim}$  analyses (raw data) for a geographically restricted dataset.

**Figure S2** Mean range size versus mean latitude for each time slice.

**Figure S3** Individual genus and family range size/effect size trajectories.

**Table S1** Presence/absence matrices for ungulate families (excel file).

**Table S2** Presence/absence matrices for ungulate genera (excel file).

**Table S3** Range size and null model data (excel file).

## BIOSKETCH

**Simon Darroch** is a graduate student at Yale University; his research broadly focuses on the spatial palaeoecology of mass extinction events.

Author contributions: S.A.F.D. conceived the project, S.A.F.D. and N.L. collected the data; S.A.F.D., A.E.W. and J.B. analysed the data and S.A.F.D. and J.B. led the writing.

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