

The macroecology behind macroevolution: North American  
mammal functional diversity and its relation to environmental  
change

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## Abstract

The set of species in a region changes over time as new species enter through speciation or immigration and as species leave the system through extinction and extirpation. How a regional species pool changes over time is the product of many processes acting at multiple levels of organization. Changes in the functional composition of a regional species pool are changes that occur across all local communities drawn from that species pool. While a species' presence in a local community is due to the availability of the necessary biotic-biotic or biotic-abiotic interactions that enable coexistence, a species' presence in a regional species pool just requires that at least one local community has that set of necessary interactions. The goal of this analysis is to understand when, and possibly for what reasons, mammal ecotypes are enriched or depleted relative to their average diversity. Here, I analyze the diversity history of North American mammals ecotypes for most of the Cenozoic (the last 65 million years). This analysis frames mammal diversity in terms of both their means of interacting with the biotic and abiotic environment (i.e. functional group or ecotype) as well as their regional and global environmental context.

## Introduction

Changes to species diversity are the result of evolutionary and ecological processes acting in concert and continually over time. Local communities are shaped by dispersal and local processes such as resource competition and predator-prey relationships. The constituent species of these communities are drawn from a regional species pool, the set of species that are present in any community within a region (Harrison and Cornell, 2008; Mittelbach and Schemske, 2015; Urban et al., 2008). Species dispersal from the regional species pool to the local communities is a sorting process shaped by biotic and abiotic environmental filters which are mediated by those species' traits (Cottenie, 2005; Elith and Leathwick, 2009; Harrison and Cornell, 2008; Loeuille and Leibold, 2008; Shipley et al., 2006; Urban et al., 2008). The gain or loss of regional diversity is the result of the macroevolutionary and macroecological processes of speciation, extinction, migration, and extirpation which, in turn, shape the downstream macroecological dynamics of the regional species

28 pool and its constituent local communities (Harrison and Cornell, 2008; Mittelbach and Schemske,  
29 2015; Urban et al., 2008). The distribution of species in the regional species pool then represents  
30 the expected distribution of local communities under a purely diffusive process of community  
assembly such as in the case of the neutral theory of biodiversity CITATION.

32 Fundamentally, all species respond differently to climate and environmental change (Blois and  
Hadly, 2009). Species with similar ecological roles within a species pool can be described as  
34 belonging to a guild or functional group (Bambach, 1977; Brown and Maurer, 1989; Simberloff and  
Dayan, 1991; Valentine, 1969; Wilson, 1999). Species within a functional group are expected to have  
36 more similar macroecological dynamics to each other than to species of a different functional group.  
By focusing on the relative diversity of functional groups, changes to diversity are interpretable as  
38 changes to the set of ways species within a species pool could interact with the biotic and abiotic  
environment.

40 A key question when comparing communities or regional species pools based on their functional  
composition is whether specific functional groups are enriched or depleted and why; what are the  
42 processes that led to a species pool having the functional composition it does (Blois and Hadly,  
2009; Brown and Maurer, 1989; Jernvall and Fortelius, 2004; McGill et al., 2006; Smith et al., 2008;  
44 Weber et al., 2017; ?) Comparisons of contemporaneous regional species pools can only determine  
if a functional group is enriched or depleted in one species pool relative to the other species pools  
46 CITATION. These types of comparison can not take into account if a functional group is enriched  
or depleted relative to its diversity over time (Blois and Hadly, 2009). While a species pool may be  
48 depleted of a functional group relative to other contemporaneous species pools, that same  
functional group may be actually be enriched in that species pool relative to its historical diversity.

50 Because the processes which shape regional species pool diversity (e.g. origination, extinction)  
operate on much longer time scales than is possible for studies of present day ecosystems,  
52 paleontological data provides a unique opportunity to observe and estimate the changes to  
functional diversity and how species functional traits and environmental context can shape the  
54 enrichment or depletion of functional groups within a regional species pool (Blois and Hadly, 2009;  
Smith et al., 2008). Being able to identify if the diversity of a functional group is depleted relative

56 to their long term average diversity in the species pool is particularly useful in conservation  
settings; species in depleted groups are potentially more at risk of extinction than species in  
58 enriched groups, even if those enriched groups are relatively rare when compared to the functional  
composition of other contemporaneous species pools.

60 The paleontological record of North American mammals for the Cenozoic (~ 66 million years ago to  
the present) provides one of the best opportunities for understanding how regional species pool  
62 functional diversity changes over time. The North American mammal record is a relatively complete  
temporal sequence for the entire Cenozoic which is primarily, but not exclusively, based on fossil  
64 localities from the Western Interior of North America (Alroy, 1996, 2009; Alroy et al., 2000).  
Additionally, mammal fossils preserve a lot of important physiological information, such as teeth, so  
66 that functional traits like the dietary/trophic category of species are easy to estimate (Eronen et al.,  
2010; Polly et al., 2011, 2015).

68 The goals of this study are to understand when are unique functional groups enriched or depleted  
in the North American mammal regional species pool and to estimate the relationship between  
70 these changes to regional ecotypic diversity and changes to their environmental context. My  
contribution is to develop a joint model of observation, origination, survival, as well as the effects of  
72 species traits and environmental factors on these processes.

## Background

74 The fossil record of mammals from the Cenozoic of North American has been the focus of  
considerable study, both in total and for specific clades (Alroy, 1996, 2009; Alroy et al., 2000;  
76 Badgley and Finarelli, 2013; Blois and Hadly, 2009; Figueirido et al., 2012; Fraser et al., 2015;  
Janis, 1993; Janis and Wilhelm, 1993; Pires et al., 2015; Quental and Marshall, 2013; Silvestro  
78 et al., 2015; Slater, 2015; Smits, 2015). Previous approaches to understanding mammal diversity,  
both in North America and elsewhere, fall into a number of overlapping categories: total diversity  
80 (Alroy, 1996; Alroy et al., 2000; Figueirido et al., 2012; Liow et al., 2008), with/between guild  
comparisons (Janis et al., 2004; Janis, 2008; Janis et al., 2000; Janis and Wilhelm, 1993; Jernvall

82 and Fortelius, 2004; Pires et al., 2015), within/between clade comparisons (Cantalapiedra et al.,  
83 2017; Fraser et al., 2015; Quental and Marshall, 2013; Silvestro et al., 2015; Slater, 2015), and  
84 estimating the impact of environmental process on total diversity (Alroy et al., 2000; Badgley and  
85 Finarelli, 2013; Badgley et al., 2017; Blois and Hadly, 2009; Eronen et al., 2015; Fraser et al., 2015;  
86 Janis, 1993; Janis and Wilhelm, 1993). Each of these studies provide a limited perspective on the  
87 macroevolutionary and macroecological processes shaping diversity and diversification. Integration  
88 across perspectives is necessary for producing a holistic and internally consistent picture of how the  
89 North American mammal species pool has changed through time. One of the goals of this study is  
90 to present a framework for approaching hypotheses about diversity and diversification through  
91 multiple lenses simultaneously through a joint model so that any inferences are better constrained  
92 and the relative importance of species' ecological function, taxonomic affinities, and environmental  
93 context may be better elucidated.

94 The narrative of the diversification of North American mammals over the Cenozoic is one of  
95 gradual change. Instead of being concentrated at specific time intervals, species turnover has been  
96 found to be distributed through time (Alroy, 1996, 2009; Alroy et al., 2000; Eronen et al., 2015;  
97 Janis, 1993). The basic expectation given this narrative is that turnover events or periods of rapid  
98 diversification or depletion should not occur simultaneously for all functional groups under study.  
99 Additionally, changes to mammal diversification seem to be primarily driven by changes to  
100 origination rate and not to extinction (Alroy, 1996, 2009; Alroy et al., 2000).

The climate history of the Cenozoic can be broadly described as a gradual cooling trend, the  
102 expansion of grasslands, and the formation of polar ice-caps during the Neogene (Cramer et al.,  
103 2011; Zachos et al., 2008, 2001). There are of course exceptions to this pattern such as the  
104 Paleocene-Eocene thermal maximum, the Early Eocene Climatic Optimum, cooling at the  
105 Eocene/Oligocene boundary, and the mid-Miocene climatic optimum (Zachos et al., 2008, 2001). In  
106 terms of the North American biotic environment, the Cenozoic is additionally characterized by  
107 major transition from having closed, partially forested biomes being common in the Paleogene to  
108 the landscape being dominated by savannah and grasslands biomes by the Neogene (Blois and  
Hadly, 2009; Janis, 1993; Janis et al., 2000; Strömberg, 2005).

110 The effect of (global) temperature on mammal diversity and its accompanying diversification process  
111 has been the focus of considerable research with a slight consensus favoring mammal diversification  
112 being more biologically-mediated than climate-mediated when considering the entire Cenozoic  
113 (Alroy et al., 2000; Clyde and Gingerich, 1998; Figueirido et al., 2012). However, differences in  
114 temporal and geographic scale seem to underly the contrast between these two perspectives. For  
115 example when the mammal fossil record analyzed at small temporal and geographic scales a  
116 correlation between diversity and climate is observable (Clyde and Gingerich, 1998; ?). However,  
117 when the record is analyzed at the scale of the continent and most of the Cenozoic this correlation  
118 disappears (Alroy et al., 2000). This result, however, does not go against the idea that there may be  
119 short periods of correlation between diversity and climate and that this relationship can change or  
120 even reverse direction over time; this type result means that there is no single direction or longterm  
121 correlation between diversity and climate (Figueirido et al., 2012). In the case of a fluctuating  
122 correlation between diversity and climate it is hard to make the argument for an actual causal link  
123 between the two without modeling the underlying ecological differences between species; after all,  
124 species respond differently based on their individual ecologies (Blois and Hadly, 2009).

The PETM and EECO are hypothesized to be major drivers behind changes in mammalian diversity  
126 and diversification (Clyde and Gingerich, 1998; ?). At local scales, the PETM is hypothesized to be  
127 causally related to an increase in diversity at the beginning of the Eocene. In contrast, the cooling  
128 at the end of the EECO is hypothesized to be a direct cause of a decrease in functional diversity  
129 and evenness (?). The onset of the PETM is characterized by an increase in diversity of creodonts,  
130 primates, Artiodactyla, and Perissodactyla; this time also hypothesized to be associated with a  
131 peak in diversity of browsing herbivores and terrestrial taxa and a drop in the diversity of  
132 insectivores (?). Additionally, phenacodonids and plesiadapids are hypothesized to be replaced by  
133 terrestrial herbivores and frugivores. In contrast the beginning of the EECO is hypothesized to  
134 coincide high species turnover and an increase in rodents, euprimates, and pholidotans. Similarly,  
135 the middle EECO is characterized by high turnover of euprimates, hypercarnivores, Artiodactyla,  
136 and Perrisodactyla. By the end of the EECO, however, both taxonomic and functional diversity are  
hypothesized to decrease dramatically, with increasingly uneven functional diversity. Temperature is

<sup>138</sup> hypothesized to be the causal mechanism behind these changes to diversity by facilitating migration  
and the expansion of ecological opportunity (?); temperature is specifically cited as the mechanism  
<sup>140</sup> because the authors did not find that plant diversity patterns mirrored the animal patterns.

The Eocene-Oligocene cooling event marks the transition from the Paleogene to the Neogene.  
<sup>142</sup> Additionally, this transition marks the approximate start of Antarctic ice sheets, which were  
previously absent (Zachos et al., 2008). This transition is hypothesized to be associated with  
<sup>144</sup> extinction of many ungulate taxa (Janis, 2008). The mechanisms which drive this pattern are  
theorized to be some combination of tectonic activity driving environmental change such as the  
<sup>146</sup> drying of the western interior of North America due mountain building and global temperature and  
environmental change such as the formation of polar icecaps (Badgley et al., 2017; Blois and Hadly,  
<sup>148</sup> 2009; Eronen et al., 2015; Janis, 2008).

In addition to the in the expansion of grasslands, the North American landscape changed  
<sup>150</sup> dramatically during the Cenozoic due mountain uplift and other tectonic actives in Western North  
America (Badgley and Finarelli, 2013; Badgley et al., 2017; Blois and Hadly, 2009; Eronen et al.,  
<sup>152</sup> 2015; Janis, 2008; ?). This type of geological activity affects both local climates as well as  
continental weather patterns while also mobilizing increased grit into the environment, something  
<sup>154</sup> which may be responsible for increasing trend of hyposodony (high crowned teeth) among ungulate  
and rodent herbivores (Damuth and Janis, 2011; Janis, 1993; Jardine et al., 2012; Jernvall and  
<sup>156</sup> Fortelius, 2002). Tectonic processes and mountain uplift in particular have been implicated in the  
increasing diversification at the MMCO (Badgley and Finarelli, 2013; Finarelli and Badgley, 2010;  
<sup>158</sup> Janis, 2008; ?; ?) and the differences in mammal diversity and diversification between North  
America and Eurasia CITATIONS. Given these observations, I hypothesize that fossorial functional  
<sup>160</sup> groups and unguiligrade and digitigrade herbivores would increase in standing and/or relative  
diversity following the MMCO. Which and how the other mammal functional groups change at or  
<sup>162</sup> following the MMCO events is unknown.

In a relevant study, Smits (2015) found that functional traits such as a species dietary or locomotor  
<sup>164</sup> category structure differences in mammal extinction risk. In particular, arboreal taxa were found to

have a shorter duration on average than species from other locomotor categories (Smits, 2015). Two  
166 possible scenarios that could yield this pattern were proposed: the extinction risk faced by arboreal  
species is constant and high for the entire Cenozoic or the Paleogene and Neogene represent  
168 different regimes and extinction risk increased in the Neogene, thus driving up the Cenozoic average  
extinction risk. These two possible explanations have clear and testable predictions with respect to  
170 the diversity history of arboreal taxa: 1) if arboreal taxa always have an elevated extinction risk  
when compared to other taxa, then the diversity history of arboreal taxa is expected to be constant  
172 with time, albeit possibly at low diversity; and 2) if the Paleogene and Neogene represent difference  
selective regimes with the former being associated with lower extinction risk than the latter, then  
174 the diversity history of arboreal taxa are expected to be present in the Paleogene but depleted or  
absent from the species pool during the Neogene.

176 There is a lack of consensus as to the effect of species body size on mammal diversity and aspects of  
the diversification processes, specifically extinction (Liow et al., 2008, 2009; Smits, 2015; Tomiya,  
178 2013). Species body size is frequently framed as an important biological descriptor because of its  
correlation with other important and relevant ecological traits such as metabolic rate and home  
180 range size (Brown, 1995). It is also relatively easy to estimate for extinct species using proxy  
measures and regression equations, as was done in this study (see below). However, body size is  
182 normally analyzed without simultaneous reference to other relevant species traits (Huang et al.,  
2017; Liow et al., 2008; Raia et al., 2012; Smith et al., 2004), but see (Smits, 2015); this combined  
184 with the high amount of correlation between life history traits and body size limits processed-based  
inference, because the actual causal mechanisms underlying an observed pattern are obscured or  
186 missing.

## Foreground

188 The fourth-corner problem is conceptual and statistical framework to explaining the patterns of  
either species abundance or presence/absence in a community as a product of species traits,  
190 environmental factors, and the interaction between traits and environment (Brown et al., 2014;

Jamil et al., 2013; Pollock et al., 2012; Warton et al., 2015); effectively uniting climate-based species distribution modeling (SDMs) with trait-based community assembly models (CATS, MaxEnt). The fourth-corner problem is normally phrased in modern ecological studies as understanding how traits and environment interact to predict the occurrence of species at localities distributed across a region (Jamil et al., 2013; Pollock et al., 2012).

This conceptual framework can be extended to include time when considering occurrence as a three-dimensional: species at localities in space over time. However, the temporal limitations of modern ecological studies limit studying species over their entire durations, where speciation and extinction govern the occurrence of species. By considering the patterns of fossil occurrences in the geological record the macroevolutionary processes governing species' (macro)ecology can be better understood. One limitation of the fossil record, however, is a lack of spatial resolution for most taxonomic groups and periods of time. As such, paleontological data "looks" at a different side of the three-dimensional occurrence matrix of the extended fourth-corner problem than modern ecological data.

In this study, I model how mammal functional groups respond to environmental change by estimating differences in origination and survival of species over time and how environmental context can affect these macroevolutionary processes (Fig. 1). Additionally, I also consider the incompleteness of the fossil record and the static effect of other species descriptors not related to functional group on origination and survival.

My approach to delimiting and assigning mammal functional groups is inspired on the ecocube heuristic used to classify marine invertebrate species by three functional traits (Bambach et al., 2007; Bush and Bambach, 2011; Bush et al., 2007; Bush and Novack-Gottshall, 2012; Novack-Gottshall, 2007; Villéger et al., 2011). In this study, the two functional traits used to define a species' functional group are dietary (e.g. herbivore, carnivore, etc.) and locomotor category (e.g. arboreal, unguligrade, etc.). Species body mass was also included as a species trait in this analysis, but not as a trait for defining a functional group; instead, its inclusion is principally to control for differences in species dynamics that driven by mass and not functional group.

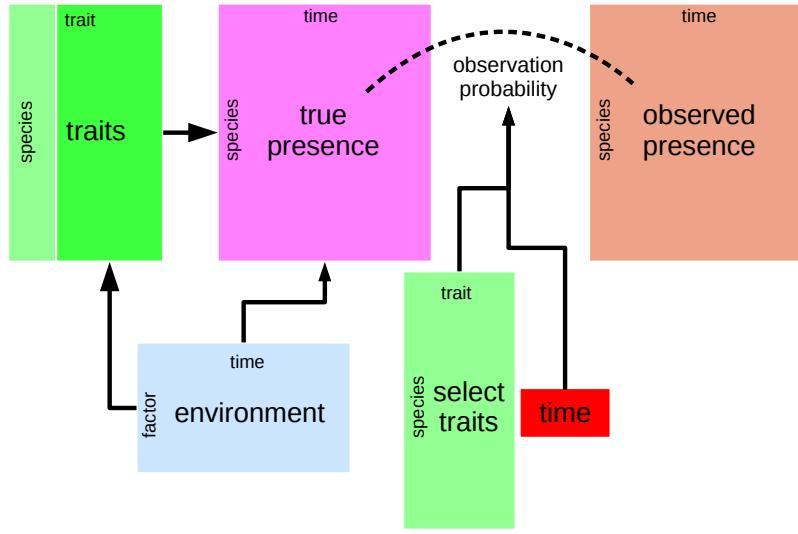


Figure 1: Conceptual diagram of the analysis at the center of this study. The observed presence matrix (orange) is the empirical presence/absence pattern for all species for all time points; this matrix is an incomplete observation of the “true” presence/absence pattern (purple). This observation process is modeled as a function of both time (red) and a selection of species traits (green). The estimated true presence matrix is modeled as a function of both environmental factors over time (blue) and multiple species traits (green). Additionally, the effects of environmental factors on some of those species traits are also modeled, as traits are expected to mediate the effects of a species environmental context. This diagram is based partially on material presented in Brown et al. (2014) and Warton et al. (2015).

218 The environmental covariates included in this study are estimates of global temperature as well as  
 which of three high-level North American plant taxonomic phases corresponds to that temporal  
 220 unit (Cramer et al., 2011; Graham, 2011). These covariates were chosen because they provide a  
 characterizations of the environmental context of the entire North American regional species pool  
 222 for most of the Cenozoic. Importantly, the effects of a species functional group on diversity are  
 themselves modeled as functions of environmental factors (Fig. 1) allowing for inference as to how a  
 224 species ecology can mediate selective pressures do to its environmental context.

All observations, paleontological or modern, are made with uncertainty. With presence/absence  
 226 data this uncertainty comes from not knowing if an absence is a “true” absence or just a failure to  
 observe (Foote, 2001; Foote and Sepkoski, 1999; Lloyd et al., 2011; Royle and Dorazio, 2008; Royle

<sup>228</sup> et al., 2005; Wang and Marshall, 2016). For paleontological data, the incomplete preservation and  
<sup>230</sup> sampling of species means that the true times of origination or extinction may not be observed  
<sup>232</sup> (Foote, 2001; Foote and Sepkoski, 1999; Wang et al., 2016; Wang and Marshall, 2016). The model  
used in this analysis is a translation of the conceptual framework described above (Fig. 1) into a  
<sup>234</sup> statistical model in order to estimate the relative diversity of mammal functional groups over time  
and how those functional groups respond to changes in environmental context while taking into  
account the fundamental incompleteness of the fossil record.

<sup>236</sup> Ultimately, the goals of this analysis are to understand when different functional groups  
enriched or depleted in the North American mammal regional species pool and how these changes  
<sup>238</sup> in functional diversity are related to changes in species' environmental context. In the analysis  
performed here, I consider multiple covariates which describe a species' macroecology and  
<sup>240</sup> environmental context. In order to analyze this complex, multi-level question and accompanying  
highly-structured data set, I developed a hierachal Bayesian model combing the fourth-corner  
modeling approach with a model of an observation-occurrence or observation-origination-extinction  
<sup>242</sup> process.

## Materials and Methods

### <sup>244</sup> Taxon occurrences and species-level information

All fossil occurrence information used in this analysis was downloaded from the Paleobiology  
<sup>246</sup> Database (PBDB). The initial download restricted occurrences to Mammalia observed in North  
America between the Maastrichtian (72-66 Mya) and Gelasian (2.58-1.8 Mya) stages (Cohen et al.,  
<sup>248</sup> 2015). Taxonomic, stratigraphic, and ecological metadata for each occurrence and species was also  
downloaded. A new download for a raw, unfiltered PBDB datafile following the same criterion used  
<sup>250</sup> here is available at <http://goo.gl/2s1geU>. The raw datafile used as a part of this study, along  
with all code for filtering, manipulating, and modeling is available at  
<sup>252</sup> <http://github.com/psmits/coping>.

After being downloaded, the raw occurrence data was then sorted, cleaned, and manipulated  
254 programmatically before analysis. Occurrences were restricted to those occurring between 64 and 2  
million years ago (Mya); this age restriction was to insure that observation time series lines up with  
256 the temperature time series described below (Cramer et al., 2011). All taxa whose life habit was  
classified as either volant (e.g. Chiroptera) or aquatic (e.g. Cetacea) were excluded from this  
258 analysis because of their lack of direct applicability to the study of terrestrial species pools.

Many species taxonomic assignments as present in the raw PBDB data were updated for accuracy  
260 and consistency. Species present in the PBDB have some taxonomic information, including possible  
Family and Order assignments. In order to increase consistency between species and reflect more  
262 recent taxonomic assignments, each species taxonomic assignments updated as follows: 1) species  
family and order assignemnts as present in the Encyclopedia of life (<http://eol.org>) was  
264 downloaded using the *taxize* package for R CITATION; 2) for species not present in the EoL or not  
assigned order, their taxonomic inforation was further updated based on whatever family  
266 information was recorded in the PBDB or EoL; 3) for species still missing order assignemnts, their  
genus information was used to assign either an order or family, which was then used to assign an  
268 order. This procedure is similar to that used in Smits (2015) and is detailed in the code repository  
associated with this study.

270 Species functional group is defined as the combination of locomotor and diet categories; the goal is  
to classify species based on the manner with which they interact with their environment. Mammal  
272 species records in the PBDB have life habit (i.e. locomotor category) and dietary category  
assignments. In order to simplify interpretation, analysis, and per-functional group sample size  
274 these classifications were coarsened in a similar manner to Smits (2015) (Table 1). Ground dwelling  
species locomotor categories were then reassigned based on the ankle posture associated with their  
276 taxonomic group, as described in Table 2 (Carrano, 1999). Ankle posture was assumed uniform for  
all species within a taxonomic group except for those species assigned a non-ground dwelling  
278 locomotor category in the PBDB, which retained their non-ground dwelling assignment. All species  
for which it was possible to assign a locomotor category had one assigned, including species for  
280 which post-crana are unknown but for which a taxonomic grouping is known. Ground dwelling

- species which were unable to be reassigned based on ankle posture were excluded from analysis.
- Finally, ecotype categories with less than 10 total species were excluded, yielding a total of 18 observed ecotypes out of a possible 24.

Table 1: Species trait assignments in this study are a coarser version of the information available in the PBDB. Information was coarsened to improve per category sample size. Assignments are considered uniform within that taxonomic group unless there is a non-ground dwelling assignment for a species in the PBDB.

This study		PBDB categories
Diet	Carnivore	Carnivore
	Herbivore	Browser, folivore, granivore, grazer, herbivore.
	Insectivore	Insectivore.
	Omnivore	Frugivore, omnivore.
Locomotor	Arboreal	Arboreal.
	Ground dwelling	Fossorial, ground dwelling, semifossorial, saltatorial.
	Scansorial	Scansorial.

Table 2: Ankle posture assignment as based on taxonomy. Assignments are based on (Carrano, 1999). Taxonomic groups are presented alphabetically and without reference for their relatedness.

Family	Stance
Ailuridae	plantigrade
Allomyidae	plantigrade
Amphicyonidae	plantigrade
Amphilemuridae	plantigrade
Anthracotheriidae	digitigrade
Antilocapridae	unguligrade
Apheliscidae	plantigrade
Aplodontidae	plantigrade
Aptenodontidae	scansorial
Arctocyonidae	unguligrade
Barbourofelidae	digitigrade
Barylambdidae	plantigrade

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**Table 2 – continued from previous page**

Family	Stance
Bovidae	unguligrade
Camelidae	unguligrade
Canidae	digitigrade
Cervidae	unguligrade
Cimolodontidae	scansorial
Coryphodontidae	plantigrade
Cricetidae	plantigrade
Cylindrodontidae	plantigrade
Cyriacotheriidae	plantigrade
Dichobunidae	unguligrade
Dinocerata	unguligrade
Dipodidae	digitigrade
Elephantidae	digitigrade
Entelodontidae	unguligrade
Eomyidae	plantigrade
Erethizontidae	plantigrade
Erinaceidae	plantigrade
Esthonychidae	plantigrade
Eutypomyidae	plantigrade
Felidae	digitigrade
Florentiamyidae	plantigrade
Gelocidae	unguligrade
Geolabididae	plantigrade
Glyptodontidae	plantigrade
Gomphotheriidae	unguligrade

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**Table 2 – continued from previous page**

Family	Stance
Hapalodectidae	plantigrade
Heteromyidae	digitigrade
Hyaenidae	digitigrade
Hyaenodontidae	digitigrade
Hypertragulidae	unguligrade
Ischyromyidae	plantigrade
Jimomyidae	plantigrade
Lagomorpha	digitigrade
Leptictidae	plantigrade
Leptochoeridae	unguligrade
Leptomerycidae	unguligrade
Mammutidae	unguligrade
Megalonychidae	plantigrade
Megatheriidae	plantigrade
Mephitidae	plantigrade
Merycoidodontidae	digitigrade
Mesonychia	unguligrade
Mesonychidae	digitigrade
Micropternodontidae	plantigrade
Mixodectidae	plantigrade
Moschidae	unguligrade
Muridae	plantigrade
Mustelidae	plantigrade
Mylagaulidae	fossorial
Mylodontidae	plantigrade

Continued on next page

**Table 2 – continued from previous page**

Family	Stance
Nimravidae	digitigrade
Nothrotheriidae	plantigrade
Notoungulata	unguligrade
Oromerycidae	unguligrade
Oxyaenidae	digitigrade
Palaeomerycidae	unguligrade
Palaeoryctidae	plantigrade
Pampatheriidae	plantigrade
Pantolambdidae	plantigrade
Peritychidae	digitigrade
Perissodactyla	unguligrade
Phenacodontidae	unguligrade
Primates	plantigrade
Procyonidae	plantigrade
Proscalopidae	plantigrade
Protoceratidae	unguligrade
Reithroparamyidae	plantigrade
Sciuravidae	plantigrade
Sciuridae	plantigrade
Simimyidae	plantigrade
Soricidae	plantigrade
Suidae	digitigrade
Talpidae	fossorial
Tayassuidae	unguligrade
Tenrecidae	plantigrade

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**Table 2 – continued from previous page**

Family	Stance
Titanoideidae	plantigrade
Ursidae	plantigrade
Viverravidae	plantigrade
Zapodidae	plantigrade

284

Estimates of species mass used in this study were sourced from multiple databases and papers,  
285 especially those focusing on similar macroevolutionary or macroecological questions (Brook and  
Bowman, 2004; Freudenthal and Martín-Suárez, 2013; McKenna, 2011; Raia et al., 2012; Smith  
286 et al., 2004; Tomiya, 2013); this is similar to Smits (2015). When a species' mass was not available,  
proxy measures were used to estimate their mass. For example, given a measurement of a mammal  
287 tooth size, it is possible and routine to estimate its mass given some regression equation (Table 3).

The PBDB has one or more body part measures for many species. These were used as body size  
288 proxies for many species, as was the case in Smits (2015). Mass was log-transformed and then  
rescaled by first subtracting mean log-mass from all mass estimates, then dividing by two-times its  
289 standard deviation; this insures that the magnitude of effects for both continuous and discrete  
covariates are directly comparable (Gelman, 2008; Gelman and Hill, 2007).

290 In total, 1400 mammal species occurrence histories were included in this study after applying all of  
the restrictions above.

291 All fossil occurrences from 64 to 2 million years ago (Mya) were binned into the 18 North American  
Land Mammal Ages (NALMA) covered by this interval CITATION. The choice of binning by  
292 NALMA reflects the belief that these represent distinct communities or periods of mammal  
evolution, something that is central to this study. The NALMA units in this study are listed in  
293 Table 4.

Table 3: Regression equations used in this study for estimating body size. Equations are presented with reference to taxonomic grouping, part name, and reference.

Group	Equation	log(Measurement)	Source
General	$\log(m) = 1.827x + 1.81$	lower m1 area	Legendre (1986)
General	$\log(m) = 2.9677x - 5.6712$	mandible length	Foster (2009)
General	$\log(m) = 3.68x - 3.83$	skull length	Luo et al. (2001)
Carnivores	$\log(m) = 2.97x + 1.681$	lower m1 length	Van Valkenburgh (1990)
Insectivores	$\log(m) = 1.628x + 1.726$	lower m1 area	Bloch et al. (1998)
Insectivores	$\log(m) = 1.714x + 0.886$	upper M1 area	Bloch et al. (1998)
Lagomorph	$\log(m) = 2.671x - 2.671$	lower toothrow area	Tomiya (2013)
Lagomorph	$\log(m) = 4.468x - 3.002$	lower m1 length	Tomiya (2013)
Marsupials	$\log(m) = 3.284x + 1.83$	upper M1 length	Gordon (2003)
Marsupials	$\log(m) = 1.733x + 1.571$	upper M1 area	Gordon (2003)
Rodentia	$\log(m) = 1.767x + 2.172$	lower m1 area	Legendre (1986)
Ungulates	$\log(m) = 1.516x + 3.757$	lower m1 area	Mendoza et al. (2006)
Ungulates	$\log(m) = 3.076x + 2.366$	lower m2 length	Mendoza et al. (2006)
Ungulates	$\log(m) = 1.518x + 2.792$	lower m2 area	Mendoza et al. (2006)
Ungulates	$\log(m) = 3.113x - 1.374$	lower toothrow length	Mendoza et al. (2006)

## Environmental and temporal covariates

304 The environmental covariates used in this study are collectively referred to as group-level covariates  
 because they predict the response of a “group” of individual-level observations (i.e. species). These  
 306 covariates are defined for temporal bins as they predict the individual parts of each species  
 occurrence history. The group-level covariates in this study are an estimate of global temperature  
 308 and the Cenozoic “plant phases” defined by Graham (2011).

Global temperature across most of the Cenozoic was calculated from Mg/Ca isotope record from  
 310 deep sea carbonates (Cramer et al., 2011). Mg/Ca based temperature estimates are preferable to  
 the frequently used  $\delta^{18}\text{O}$  temperature proxy (Alroy et al., 2000; Figueirido et al., 2012; Zachos  
 312 et al., 2008, 2001) because Mg/Ca estimates do not conflate temperature with ice sheet volume and  
 depth/stratification changes (Cramer et al., 2011; Ezard et al., 2016). The former is particularly  
 314 important to this analysis as the current polar ice-caps appeared and grew during the second half of  
 the Cenozoic. These properties make Mg/Ca based temperature estimates preferable for  
 316 macroevolutionary and macroecological studies (Ezard et al., 2016). Temperature was calculated as  
 the mean of all respective estimates for each of the NALMA units. The distributions of temperature

Table 4: Listed in order from oldest to youngest NALMA.:

NALMA	Start Age (Mya)
Torrejonian	63.3
Tiffanian	60.2
Clarkforkian	56.8
Wasatchian	55.4
Bridgerian	50.3
Uintan	46.2
Duchesnean	42
Chadronian	38
Orellan	33.9
Whitneyan	33.3
Geringian	30.8
Monroecreekian	26.3
Harrisonian	24.8
Hemingfordian	20.6
Barstovian	16.3
Clarendonian	13.6
Hemphillian	10.3
Blancan	4.9

Table 5: Definitions of the start and stop times of the three plant phases used this study as defined by Graham (2011).

Plant phase	Phase code	Start	Stop
Paleocene-Eocene	Pa-Eo	66	50
Eocene-Miocene	Eo-Mi	50	16
Miocene-Pleistocene	Mi-Pl	16	2

- 318 was then rescaled by subtracting its mean from all values and then dividing by twice its standard deviation.
- 320 The second set of environmental factors included in this study are the Cenozoic plant phases defined in Graham (2011). Graham’s plant phases are holistic descriptors of the taxonomic 322 composition of 12 ecosystem types, which plants are present at a given time, and the relative modernity of those plant groups with younger phases representing increasingly modern taxa 324 (Graham, 2011). Graham (2011) defines four intervals from the Cretaceous to the Pliocene, though only three of these intervals take place during the time frame being analyzed. Graham’s plant 326 phases was included as a series of “dummy variables” encoding the three phases included in this

		State at $t + 1$		
		$0_{never}$	1	$0_{extinct}$
State at $t$	$0_{never}$	$1 - \pi$	$\pi$	0
	1	0	$\phi$	$1 - \phi$
	$0_{extinct}$	0	0	1

Table 6: Transition matrix for the birth-death model (Eq. 1). Note that while there are only two state “codes” (0, 1), there are in fact three states: never having originated  $0_{never}$ , present 1, extinct  $0_{extinct}$  (Allen, 2011). The two modeled transition probabilities are origination  $\pi$  and survival  $\phi$ .

analysis (Gelman and Hill, 2007); this means that the Miocene-Pleistocene phase is synonymous

328 with the intercept and other phases are defined by their differences from this baseline. The temporal boundaries of these plant phases, their durations, and abbreviations are defined in Table 5.

330 **Modelling species occurrence**

At the core of the model used in this study is hidden Markov process where the latent process has

332 an absorbing state; also referred to as a discrete-time birth-death model (Allen, 2011) or a capture-mark-recapture model CITATION. While there are only two state “codes” in a

334 presence-absence matrix (i.e. 0/1), there are in fact three states in a birth-death model: not having originated yet, extant, and extinct. The last of these is the absorbing state, as once a species has 336 gone extinct it cannot re-originate (Allen, 2011). Thus, in the transition matrices the probability of an extinct species changing states is 0 (Table 6); see below for extended parameter explanations

338 (Tables 7, 8, and 9).

### Basic model

340 I will begin defining the model used in this study by focusing on the basic machinery of the hidden Markov process at the model’s core. This aspect of the model is similar to the well-known

342 Jolly-Seber capture-mark-recapture model from ecology CITATION which has three characteristic probabilities: probability  $p$  of observing a species given that it is present, probability  $\pi$  of a species 344 surviving from one time to another, and probability  $\phi$  of a species first appearing (Royle and

Dorazio, 2008) (Table 7). In this formulation, the probability of a species becoming extinct is  $1 - \pi$ .

Table 7: Parameters associated with the hidden Markov Model at core of this model (Eq. 1).  $N$  is the number of species tracked in this study, and  $T$  is the number of time units (NALMAs) covered by this study.

Parameter	dimensions	explanation
$y$	$N \times T$	observed species presence/absence
$z$	$N \times T$	“true” species presence/absence
$p$	$N \times T$	probability of observing a species at time $t$ if it is present
$\phi$	$N \times T$	probability of species originating from time $t$ to $t + 1$ if it is not present
$\pi$	$N \times (T - 1)$	probability of species surviving at time $t$ , given that it is already originated

- 346 The inclusion of species and temporal information means that all three of these probabilities are  
defined for every species at every time point (Table 7); how this is accomplished is described below.  
348 Importantly, only origination can occur during the first time step as nothing is already present to  
survive. This basic model is expressed as

$$\begin{aligned} y_{i,t} &\sim \text{Bernoulli}(p_{i,t} z_{i,t}) \\ z_{i,1} &\sim \text{Bernoulli}(\phi_{i,1}) \\ z_{i,t} &\sim \text{Bernoulli} \left( z_{i,t-1} \pi_{i,t} + \sum_{x=1}^t (1 - z_{i,x}) \phi_{i,t} \right) \end{aligned} \tag{1}$$

- 350 The parameters in Equation 1 are described in Table 7; this formulation is identical to that  
described in Royle and Dorazio (2008). The product term that appears when calculating values of  $z$   
352 not at  $t = 1$  ensures that once a species goes extinct it does not re-originate.

## Expanding on the basics

- 354 Expanding on the basic model involves modeling the observation, origination and survival  
probability as independent multi-level logistic regressions. Origination and survival probabilities  
356 share the same covariates and model structure, while observation probability is modeled as a  
function of a smaller selection of covariates.  
358 The probability of observing a species given that it is present  $p$  is modeled as a logistic regression  
with a time-varying intercept with an additional varying-intercept for species’ functional group,

Table 8: Parameters for the first expansions

Parameter	dimensions	explanation
$u$	$T$	time-varying intercept
$e$	$J$	effect of functional group on observation
$f^\phi$	$J \times T - 1$	intercept of log-odds $\phi$ , varies by time and functional group
$f^\pi$	$J \times T$	intercept of log-odds $\pi$ , varies by time and functional group
$o^\phi$	$K$	effect of species' order on log-odds of $\phi$
$o^\pi$	$K$	effect of species' order on log-odds of $\pi$
$\beta^\phi$	1	effect of species' mass on log-odds of $\phi$
$\beta^\pi$	1	effect of species' mass on log-odds of $\pi$
$m$	$N$	species' mass estimates

360 respectively. The effect of species mass was also included through a regression slope term  $\beta^p$ .

The log-odds of a species originating (logit  $\pi$ ) or surviving (logit  $\phi$ ) are modeled independently but  
362 take the same form: a regression with an intercept that varies by both time and functional group,  
an additional taxonomic order varying-intercept term, and the slope term for species mass.

364 Importantly, the time and functional group varying-intercept is itself modeled such that the  
intercept for each functional group is a time series predicted by the group-level covariates  
366 (described below).

The expanded model incorporating these regression models is written as

$$\begin{aligned}
y_{i,t} &\sim \text{Bernoulli}(p_{i,t} z_{i,t}) \\
p_{i,t} &= \text{logit}^{-1}(u_t + e_{j[i]} + \beta^p m_i) \\
z_{i,1} &\sim \text{Bernoulli}(\phi_{i,1}) \\
z_{i,t} &\sim \text{Bernoulli}\left(z_{i,t-1} \pi_{i,t} + \sum_{x=1}^t (1 - z_{i,x}) \phi_{i,t}\right) \\
\phi_{i,t} &= \text{logit}^{-1}(f_{j[i],t}^\phi + o_{k[i]}^\phi + \beta^\phi m_i). \\
\pi_{i,t} &= \text{logit}^{-1}(f_{j[i],t}^\pi + o_{k[i]}^\pi + \beta^\pi m_i)
\end{aligned} \tag{2}$$

368 How the group-level covariates are included in expanded model and the final choice of priors are  
described below.

370 **Complete model**

The expanded model (Eq. 2) is still incomplete as it is missing the group-level covariates such as  
 372 global temperature, and it is missing all of the necessary final generative priors.

Here I describe how the effects of mammal functional group on origination and survival are  
 374 modeled.  $f^\phi$  and  $f^\pi$  are modeled as the responses from a multivariate normal distribution, where  
 each functional group is modeled by a time-series regression. Temporal autocorrelation is modeled  
 376 as a random-walk prior for the varying intercept of the group-level regressions. The effects of the  
 group-level covariates on origination and survival are included for each functional group through  
 378 regression coefficients. The expansion to include these group-level regression is described in  
 Equation 3, the parameters of which are described in Table 9.

$$\begin{aligned}
 f^\phi &\sim \text{MVN}(\mu^\phi, \Sigma^\phi) \\
 f^\pi &\sim \text{MVN}(\mu^\pi, \Sigma^\pi) \\
 \mu_{j,t}^\phi &= \alpha_{j,t}^\phi + U * \gamma_j^\phi \\
 \mu_{j,t}^\pi &= \alpha_{j,t}^\pi + U * \gamma_j^\pi \\
 \alpha_{j,t}^\phi &\sim \begin{cases} \mathcal{N}(0, 1) & \text{if } t = 1 \\ \mathcal{N}(\alpha_{j,t-1}^\phi, \sigma_j^\phi) & \text{if } t > 1 \end{cases} \\
 \alpha_{j,t}^\pi &\sim \begin{cases} \mathcal{N}(0, 1) & \text{if } t = 1 \\ \mathcal{N}(\alpha_{j,t-1}^\pi, \sigma_j^\pi) & \text{if } t > 1 \end{cases}
 \end{aligned} \tag{3}$$

380 In hierarchical models like the one described here (Eq. 2, 3) it can be hard to distinguish between  
 the likelihood and prior as data and structure can enter the model through many different  
 382 parameters CITATION. For example, in Equation 2 the model of  $z$  can be considered a prior and  
 statements in Equation 3 can be considered priors for the parameters which predict  $\phi$  and  $\pi$ . The  
 384 remaining priors necessary to this model, however, are not based on parameter expansion but are  
 prior estimates for the remaining unmodeled parameters and are sampling statements where no new

Table 9: Parameters for the group-level regressions.  $J$  is the number of functional groups, and  $D$  is the number of group-level covariates.

Parameter	dimensions	explanation
$\mu^\phi$	$J \times T$	time-series of the mean log-odds of $\phi$ for each functional group
$\mu^\pi$	$J \times T$	time-series of the mean log-odds of $\pi$ for each functional group
$\Sigma^\phi$	$J \times J$	covariance matrix between functional groups for $\phi$
$\Sigma^\pi$	$J \times J$	covariance matrix between functional groups for $\phi$
$\alpha^\phi$	$J \times T$	time-varying intercept of $\mu^\phi$
$\alpha^\pi$	$J \times T$	time-varying intercept of $\mu^\pi$
$\sigma^\phi$	$J$	scale of random-walk prior for $\alpha^\phi$
$\sigma^\pi$	$J$	scale of random-walk prior for $\alpha^\pi$
$\gamma^\phi$	$D$	group-level regression coefficients for $\mu^\phi$
$\gamma^\pi$	$D$	group-level regression coefficients for $\mu^\pi$
$U$	$T$	matrix of group-level covariates

386 data enters the model. These prior choices are expressed in Equation 4 and are explained below.

For the regression coefficients, such as  $\beta^\phi$  and  $\gamma^\phi$ , the chosen priors are considered weakly  
 388 informative as they concentrate most of the probability density between -2 and 2. Similarly, the  
 scale parameters, such as  $\tau^\phi$  and  $\sigma^\phi$ , are also given weakly informative half-Normal priors which  
 390 concentrate most of the probability density between 0 and -2. The covariance matrices, such as  $\Sigma^\phi$ ,  
 are decomposed into a vector of scale terms (e.g.  $\tau^\phi$ ) and correlation matrices (e.g.  $\Omega^\phi$ ) which were  
 392 then given weakly informative priors. This approach and choice of LKJ priors for the correlation  
 matrices follows the Stan User Manual CITATION. For parameter vectors which are presented with

<sup>394</sup> only a single prior (e.g.  $\beta^\phi$ ), that prior statement is for each of the elements of that vector.

$$\begin{aligned}
e &\sim \mathcal{N}(0, \sigma^e) \\
\sigma^e &\sim \mathcal{N}^+(1) \\
\beta^p &\sim \mathcal{N}(0, 1) \\
o^\phi &\sim \mathcal{N}(0, v^\phi) \\
o^\pi &\sim \mathcal{N}(0, v^\pi) \\
v^\phi &\sim \mathcal{N}^+(1) \\
v^\pi &\sim \mathcal{N}^+(1) \\
\beta^\phi &\sim \mathcal{N}(0, 1) \\
\beta^\pi &\sim \mathcal{N}(0, 1) \\
\Sigma^\phi &= \text{diag}(\tau^\phi) \Omega^\phi \text{diag}(\tau^\phi) \\
\Sigma^\pi &= \text{diag}(\tau^\pi) \Omega^\pi \text{diag}(\tau^\pi) \\
\tau^\phi &\sim \mathcal{N}^+(1) \\
\tau^\pi &\sim \mathcal{N}^+(1) \\
\Omega^\phi &\sim \text{LKJ}(2) \\
\Omega^\pi &\sim \text{LKJ}(2) \\
\sigma^\phi &\sim \mathcal{N}^+(1) \\
\sigma^\pi &\sim \mathcal{N}^+(1) \\
\gamma^\phi &\sim \mathcal{N}(0, 1) \\
\gamma^\pi &\sim \mathcal{N}(0, 1)
\end{aligned} \tag{4}$$

The model used in this study is the complete sampling statement expressed through the  
<sup>396</sup> combination of equations 2, 3, and 4. These statements taken together form a complete generative model posterior inference is possible.

398 **Posterior inference and model adequacy**

A computer program that implements joint posterior inference the model described above (Eqs. 2,  
400 3, and 4) was written in the probabilistic programming language Stan (Stan Development Team,  
2016). All methods for posterior inference implemented in Stan are derivative-based; this causes  
402 complications for actually implementing the above models, because integers do not have derivatives.

In order to infer the values of the matrix of latent discrete parameters  $z$  (Tables 7) the log posterior  
404 probabilities of all possible states of the unknown values of  $z$  were calculated and summed (i.e.  
marginalized) (Stan Development Team, 2016).

406 Species durations at minimum range through from a species first appearance to their last  
appearance in the fossil record, but the incompleteness of all observations means that the actual  
408 times of origination and extinction are unknown. The marginalization approach used here means  
that the (log) probabilities of all possible histories for a species are calculated, from the end  
410 members of the species having existed for the entire study interval and the species having only  
existed between the directly observed first and last appearances to all possible intermediaries (Fig  
412 2) (Stan Development Team, 2016). Marginalization is identical, language-wise, to assuming  
range-through and then estimating the (log) probability of all possible range extension due to  
414 incomplete sampling.

The combined size of the dataset and large number of parameters (Eqs. 2, 3, and 4), in specific the  
416 total number of latent parameters that are the matrix  $z$ , means that MCMC based posterior  
inference is computationally slow. Instead, an approximate Bayesian approach was used: variational  
418 inference. A recently developed automatic variational inference algorithm called “automatic  
differentiation variational inference” (ADVI) is implemented in Stan and is used here (Kucukelbir  
420 et al., 2015; Stan Development Team, 2016). ADVI assumes that the posterior is Gaussian but still  
yields a true Bayesian posterior; this assumption is similar to quadratic approximation of the  
422 likelihood function commonly used in maximum likelihood based inference (McElreath, 2016). The  
principal limitation of assuming the joint posterior is Gaussian is that the true topology of the  
424 log-posterior isn’t estimated; this is a particular burden for scale parameters which are bounded to

	Time Bin							
	1	2	3	4	5	6	7	8
Observed	0	0	0	1	0	1	1	0
-----	-----	-----	-----	-----	-----	-----	-----	-----
Certain	?	?	?	1	1	1	1	?
.....	.....	.....	.....	.....	.....	.....	.....	.....
Potential	0	0	0	1	1	1	1	0
Potential	0	0	1	1	1	1	1	0
Potential	0	1	1	1	1	1	1	0
Potential	1	1	1	1	1	1	1	0
Potential	0	0	0	1	1	1	1	1
Potential	0	0	1	1	1	1	1	1
Potential	0	1	1	1	1	1	1	1
Potential	1	1	1	1	1	1	1	1

Figure 2: Conceptual figure of all possible occurrence histories for an observed species. The first row represents the observed presence/absence pattern for a single species at eight time points. The second row corresponds to the known aspects of the “true” occurrence history of that species. The remaining rows correspond to all possible occurrence histories that are consistent with the observed data. By marginalizing over all possible occurrence histories, the probability of each potential history is estimated. The process of parameter marginalization is described in the text.

be positive (e.g. standard deviation).

- 426 Of additional concern for posterior inference is the partial identifiability of observation parameters  
 $p_{t=1}$  and  $p_{t=T}$  (Royle and Dorazio, 2008). This issue means that the estimates of sampling  
428 probabilities at the “edges” of the time series cannot fully be estimated because there are no known  
“gaps” in species occurrence histories that are guaranteed to be filled. Instead, the values of the first  
430 and final columns of the “true” presence-absence matrix  $z$  for those observations that do not already  
have presences in the observed presence-absence matrix  $y$  cannot be estimated (Royle and Dorazio,  
432 2008). The hierarchical modeling approach used here helps mitigate this problem by pulling the  
values of  $p_{t=1}$  and  $p_{t=T}$  towards the overall mean of  $p$  (Gelman et al., 2013), and in fact this  
434 approach might be more analytically sound than the more ad-hoc approaches that are occasionally  
used to overcome this hurdle (Royle and Dorazio, 2008). Additionally, because  $p_{t=1}$  and  $p_{t=T}$  are  
436 only partially identifiable, estimates of occurrence  $\theta$  and origination  $\phi$  at  $t = 1$  and estimates of  $\theta$ ,  $\phi$

and survival  $\pi$  at  $t = T$  may suffer from similar edge effects. Again, the hierarchical modeling  
438 approach used here may help correct for this reality by drawing these estimates towards the overall  
means of those parameters.

440 Finally, after obtaining approximate estimation of the model posterior using ADVI, model  
adequacy and quality of fit were assessed using a posterior predictive check (Gelman et al., 2013).  
442 By simulating 100 theoretical data sets from the posterior estimates of the model parameters and  
the observed covariate information the congruence between predictions made by the model and the  
444 observed empirical data can be assessed. These datasets are simulated by starting with the  
observed states of the presence-absence matrix at  $t = 1$ ; from there, the time series roll forward as  
446 stochastic processes with covariate information given from the empirical observations. Importantly,  
this is fundamentally different from observing the posterior estimates of the “true”  
448 presence-absence matrix  $z$ . The posterior predictive check used in this study is to compare the  
observed average number of observations per species to a distribution of simulated averages; if the  
450 empirically observed value sits in the middle of the distribution then the model can be considered  
adequate in reproducing the observed number of occurrences per species.

452 The ADVI assumption of a purely Gaussian posterior limits the utility and accuracy of the  
posterior predictive checks because parameter estimates do not reflect the true posterior  
454 distribution and are instead just an approximation (Gelman et al., 2013). Because of this, posterior  
predictive estimates are themselves only approximate checks of model adequacy. The posterior  
456 predictive check that is used in this study focuses on mean occurrence and not to any scale  
parameters that might be most affected by the ADVI assumptions.

458 Given parameter estimates, diversity and diversification rates are estimated through posterior  
predictive simulations. Given the observed presence-absence matrix  $y$ , estimates of the true  
460 presence-absence matrix  $z$  can be simulated and the distribution of possible occurrence histories  
can be analyzed. This is conceptually similar to marginalization where the probability of each  
462 possible occurrence history is estimated (Fig. 2), but now these occurrence histories are generated  
relative to their estimated probabilities.

<sup>464</sup> The posterior distribution of  $z$  gives the estimate of standing diversity  $N_t^{stand}$  for all time points as

$$N_t^{stand} = \sum_{i=1}^M z_{i,t}. \quad (5)$$

<sup>466</sup> Total regional standing diversity can also be partitioned into the standing diversity of each of the functional groups.

## Results

### <sup>468</sup> Posterior parameter estimates

<sup>469</sup> The model used here in this study has an approximately adequate fit to the data based on the results of the posterior predictive check (Fig. 3). Simulated datasets as estimated from the models' <sup>470</sup> posterior appears similar in terms of average number of occurrences per species to the observed number of occurrences in the empirical mammal dataset.

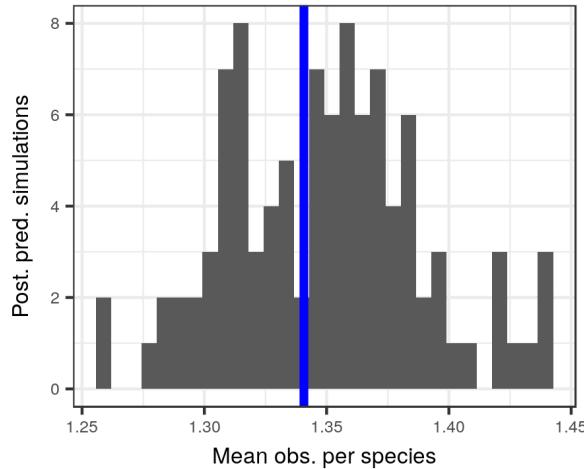


Figure 3: Comparison of the average observed number of occurrences per species (blue line) to the average number of occurrences from 100 posterior predictive datasets simulated from draws from the posterior parameter estimates from the model used in this study. The model is considered to have adequate fit to this aspect of the data if the observed value of the test statistic is approximately centered in the simulated distribution of test statistic values.

<sup>472</sup>

Log-odds of observing a species given that it is present varies greatly with time (Fig. 4) with lowest  
 474 log-odds of observation being during the Gerigian and Harrisonian land-mammal ages. It is  
 important to note, however, that all land-mammal ages with log-odds of observation greater than 2  
 476 correspond to high probabilities of observation, which means that while there may be large  
 differences in log-odds of observation between land-mammal ages this may not translate to  
 substantial difference in the probability of observation.

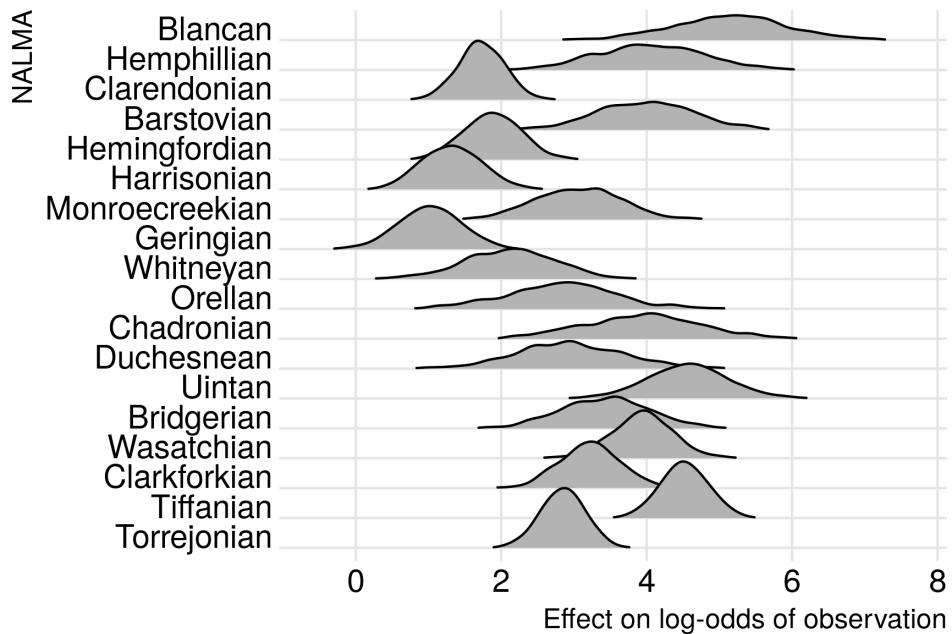


Figure 4: Ridgeline density plots of the estimates for the log-odds of observation from the time-varying intercept term. Each of the named time units are North American land-mammal ages. The oldest land-mammal age is at the bottom of the stack and the youngest is at the top. Higher values correspond to a greater log-odds of observation than lower values.

478

In comparison to temporal variation, there is little variance in the effect of functional group on the  
 480 log-odds of observing a species that is present (Fig. 5). The only functional group with substantially  
 less than expected log-odds of observation is scansorial insectivores, indicating that the fossil record  
 482 of this group is the least complete of all the functional groups studied. A few functional groups have  
 marginally better than expected log-odds of observation, the other insectivorous functional groups  
 484 have marginally greater than average log-odds of observation; this is also the case for plantigrade  
 omnivores. These results indicate that the observation histories of these functional groups are

486 expected to be relatively more complete than most other functional groups. However, it is  
 487 important to note that for many functional groups, their estimated log-odds of observation are  
 488 poorly constrained with great uncertainty indicating little structure in how observation probability  
 varies by functional groups (Fig. 5).

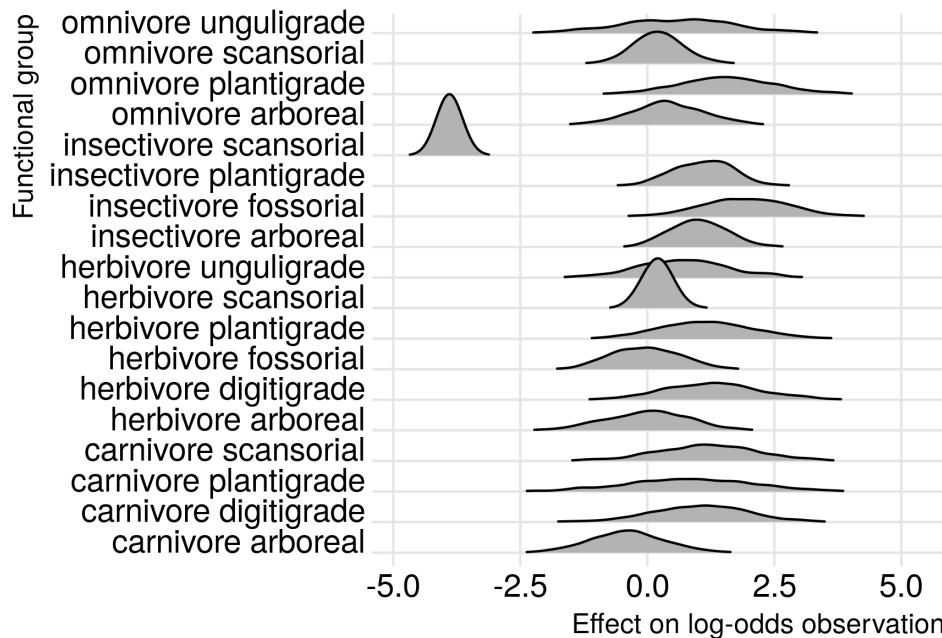


Figure 5: Ridgeline density plots of the estimated effects of species' functional group on log-odds of observing that species given that it is present. Each of the rows correspond to a different functional group as indicated by the dietary and locomotor category combination. Positive values correspond to greater than average log-odds of observation, while negative values indicate lower than average log-odds of observation.

490 Species mass is found to have a possible positive effect on probability of observing a species that is  
 491 present ( $P(\beta^p 0) = 0.849$ ; Fig. 6). This result indicates that species with greater than average mass  
 492 are expected to have more complete observation histories than species with less than average mass.  
 493 However, this estimate does not necessarily translate to substantial differences in the estimated  
 494 probability of observation because observation probability is so high for most of the Cenozoic (Fig.  
 495 4). In fact, it is only when observation probability is low that the effect of mass is easily observable.  
 496 It is important to remember the effect of mass on observation was considered constant over time  
 and that all differences in observation probability between land-mammal ages is driven by variation

498 over time. When log-odds of observation is high, differences due to covariate effects translate to  
very small differences in actual probability.

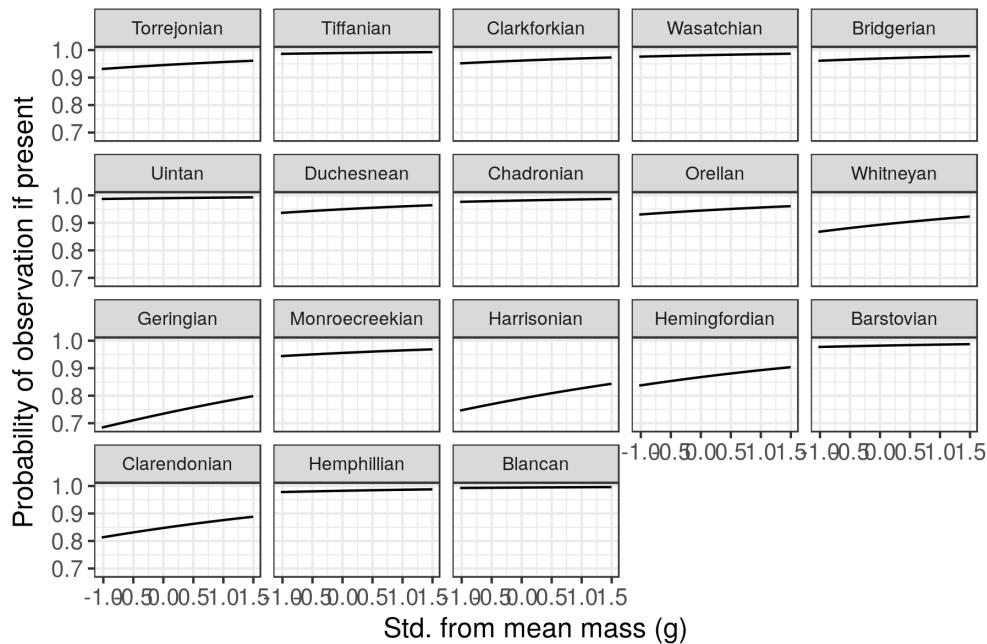


Figure 6: Estimates of the effect of species mass on probability of observing a species that is present ( $p$ ). Mass has been log-transformed, centered, and rescaled; this means that a mass of 0 corresponds to the mean of log-mass of all observed species and that values are in units of standard deviations. The effect of mass on observation was considered constant over time, and variation in observation probability is due to the temporal effect (Fig. ??).

500 Origination probability varies greatly among functional groups with each functional group  
exhibiting a unique time series with a few shared features (Fig. 7). When origination probability is  
502 below 0.50 this means that a new species of that functional group most likely will not enter the  
species pool, and when origination probability is greater than 0.50 then a new species of that  
504 functional group will probably entering the species pool. Finally, if origination probability is  
approximately 0.50, this indicates that it is equally likely that a new species will enter the species  
506 pool as it will not. The slope of origination probability time-series is also very revealing; when the  
slope of the time series is positive then new species are being added to the species pool, and when  
508 the slope is negative it is expected that the number of new species entering the pool is decreasing  
with time.

510 Most of the functional groups have peak origination probability at the present (Fig. 7); new species  
511 in these functional groups are being added to the species pool through out the Cenozoic. In the case  
512 of some functional groups, such as digitigrade carnivores and fossorial herbivores, this is the  
513 culmination of those groups continued growth in the species pool. For other functional groups, such  
514 as arboreal herbivores, this peak is a reversal from previously relatively low origination probability;  
this indicates an expansion of these functional groups following a decline.

516 Five of the functional groups do not have peak origination probabilities at the end of the observed  
517 period: arboreal carnivores, arboreal insectivores, plantigrade insectivores, scansorial insectivores,  
518 and unguligrade omnivores. All the arboreal functional groups reach peak origination probability in  
519 the Paleogene, after which mean origination probabilities approach and remain at 0.50, reflecting  
520 the loss of these functional groups from the species pool as origination probability never again  
521 increases. Additionally, the uncertainty surrounding in the estimates of origination probability is  
522 very large, especially in the Neogene. Large uncertainty in probabilities can reflect complete  
523 separation which results from that functional group leaving the species pool and therefore it's  
524 absence is without ambiguity CITATION. The patterns evinced by the other functional groups have  
525 similar properties but reach peak origination probability early in the Neogene. Of note is that  
526 origination probability of scansorial insectivores has effectively two peaks, once in the late  
527 Paleogene and again in the early Neogene. Additionally, as will be discussed later in the context of  
528 standing diversity, all five of these functional groups decrease in diversity through the Cenozoic.

530 Origination probability varies greatly amongst mammal orders (Fig. 8). These estimates reflect  
531 differences origination probability as well as the relative rarity of that order in the fossil record; if  
532 there are few members of that order and they are distributed through time then they would have  
533 an inherently lower probability of origination. Orders with greater than average log-odds of  
534 origination include Multituberculata, Dinocerata, Didelphimorphia, Creodonta, Condylarthra,  
535 Cimolesta, and Acreodi; orders that are considered major components of the Paleogene fossil record.  
Orders with lower than average log-odds of origination include Rodentia, Pilosa, Lagomorpha,  
536 Eulipotyphyla, Cingulata, Carnivora, and Artiodactyla; orders characterized by small body size or  
primarily Neogene records. Additionally, the variance between orders is vary large ranging from -2.5

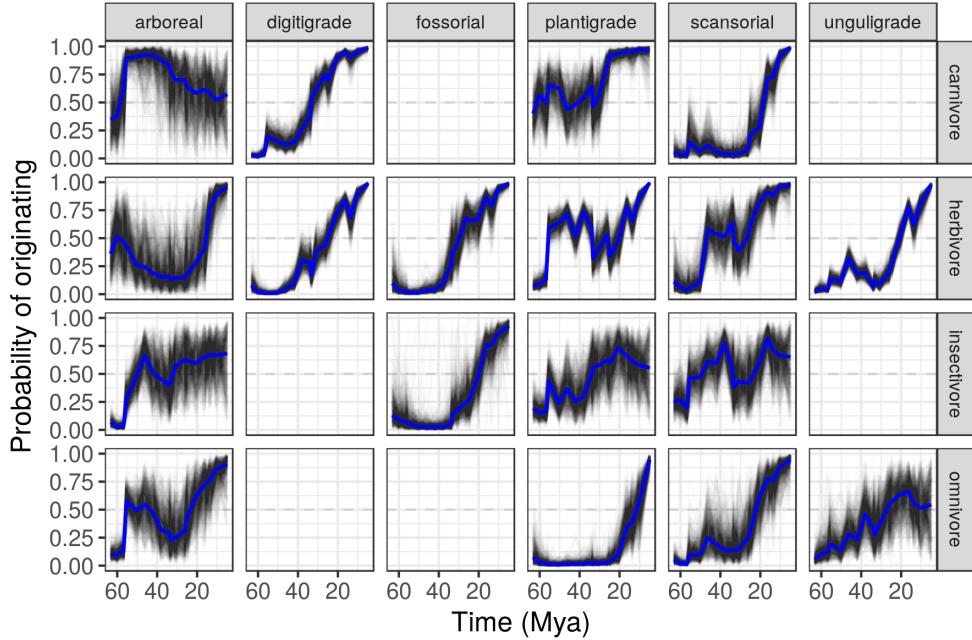


Figure 7: Probability of a species first originating based on functional group. Origination probability is graphed as 100 time-series drawn from the model’s posterior estimates. A greater density of the posterior estimates indicates increased certainty. The blue line is the mean origination probability as predicted by just the group-level predictors. The columns are by locomotor category and rows by dietary category.

538 to 2.5 log-odds of origination; this large of variance reflects how species within these orders have  
 very different patterns of origination independent from their origination based on functional ecology  
 540 (Fig. 7).

Species mass is estimated to have a negative relationship with origination probability ( $P(\beta^\phi < 0) =$   
 542 1; Fig. 9) meaning that species with greater than average mass have a lower probability of  
 originating at any point in time than species with below average mass. This result is sensible given  
 544 the left-skewed distribution of mammal species body sizes where large body sizes form the  
 right-hand tail. There are fewer large body-sized mammals which have ever originated than small  
 546 body sized mammals. Interestingly, many of the orders with small body sizes (e.g. Rodentia,  
 Lagomorpha) have below average origination probabilities (Fig. 8); when this result is considered  
 548 together with the effect of mass on origination these effects could be counteracting each other.

These results continue to add to the understanding of the heterogeneity and nuance associated with

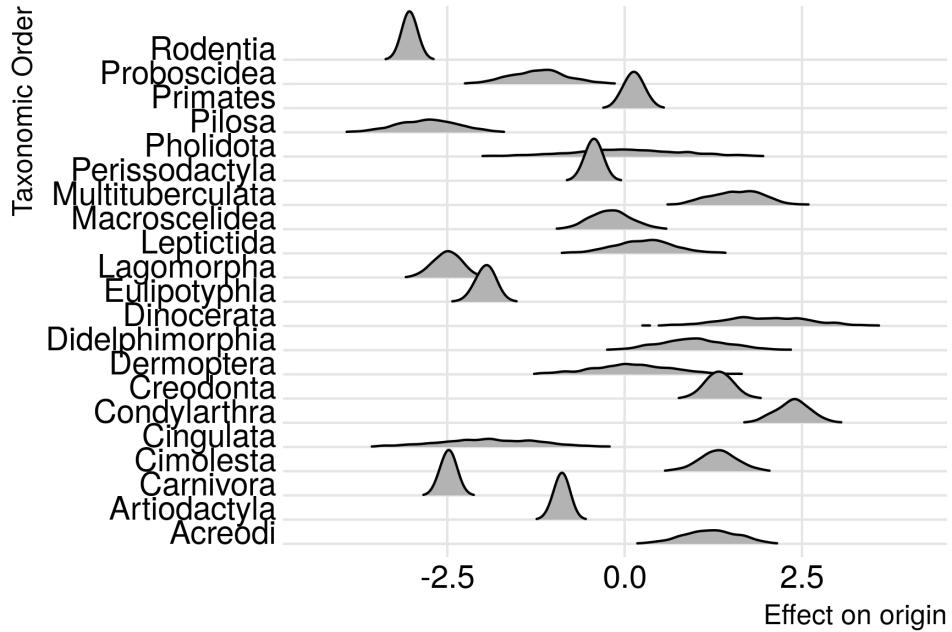


Figure 8: Ridgeline density plots of estimated log-odds of origination based on mammal orders. Positive values correspond to greater log-odds origination than average, while negative values correspond to lower log-odds of origination than average. Importantly, origination probability corresponds to the rarity of that order in the fossil record as well as differences in origination due to species' order (rare orders have few originations)

550 species origination dynamics.

For many of the functional groups, the group-level covariates for origination probability are  
 552 estimated with high probability ( $> 0.80$ ) of being different from 0 (Fig. 10). These results mean  
 that the environmental factors analyzed here are expected to shape changes in origination  
 554 probabilities over time.

At least two of the three plant phases are possibly associated with differences in origination  
 556 probability for 14 of the 18 functional groups ( $> 0.85$  probability; Table 10). The Paleocene-Eocene  
 phase is found to be associated with differences in origination probability from the  
 558 Miocene-Pleistocene for ten of the functional groups, all of which are expected to have lower  
 origination probability than the latter (Table 10). The Eocene-Miocene phase is found to be  
 560 associated with differences in origination probability from the Miocene-Pleistocene for nine of  
 functional groups: eight with a greater origination probability than the latter, and one with a lower

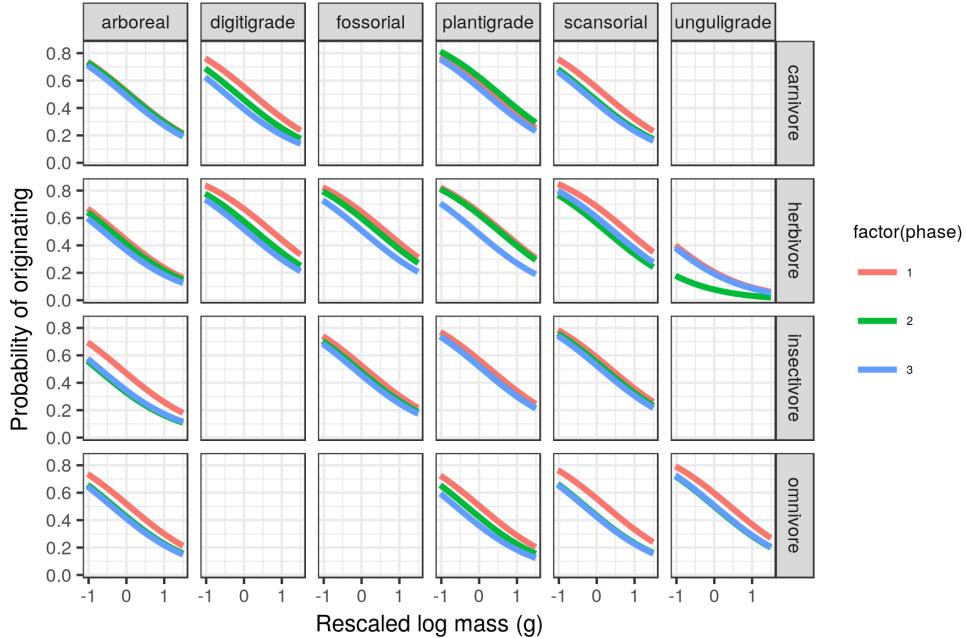


Figure 9: Mean estimates of the effect of species' mass on the probability of a species originating, plotted for each of the three plant phases. While the effect of mass is considered constant over time, each plant phases corresponds to a different intercept of the relationship between mass and origination. The three plant phases are indicated by the color of the line. Mass has been log-transformed, centered, and rescaled; this means that a mass of 0 corresponds to the mean of log-mass of all observed species and that mass is in standard deviation units. For clarity, only the mean of these estimates is plotted.

562 origination probability than the latter (Table 10). The Eocene-Miocene phase is expected to be  
 563 associated with a greater origination probability than the Paleocene-Eocene for 13 of the functional  
 564 groups (Table 10).

Temperature is estimated with probability greater than 0.85 to have negative relationship with  
 565 origination probability for ten of the 18 functional groups (Table 11). This result means that for an  
 566 increase in temperature it is a plausible expectation that origination probability decreases.

567 Considering that, on average, temperature decreases through the Cenozoic CITATION, this implies  
 568 that the origination probability of these ten functional groups may be tracking this long-term trend  
 569 as opposed to the other functional groups which increase in origination probability independently of  
 570 temperature.

571 The origination probabilities of the functional groups are not estimated to be correlated (Fig. 11).

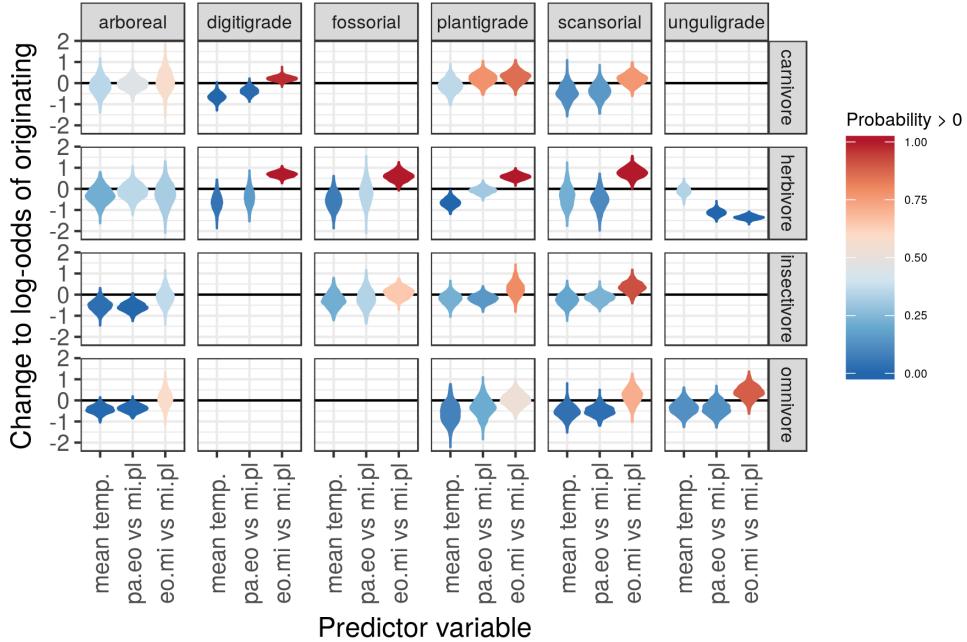


Figure 10: Estimated effects of the group-level covariates describing environmental context on log-odds of species origination. The violin densities that are plotted are based on 1000 samples from the approximate posterior. The color of the violin corresponds to the probability that the covariates effect is estimated to be greater than 0; red values correspond to greater than 0.50 probability of being positive, blue values correspond to less than 0.50 probability of being positive.

This result indicates that functional groups have independent origination probability histories for

574 the Cenozoic. This result does not preclude the possibility of short term similarities in the increase or decrease of origination probability or shared peaks and troughs of origination probability.

576 Additionally, if the relationship between two functional groups changes over time (e.g. from positive correlation to negative correlation), then it would yield no overall correlation for the Cenozoic.

578 Finally, it is important to remember that these correlation estimates is based on origination probability and not origination rate or diversity.

580 The survival probability time-series vary greatly by functional groups with each exhibiting a unique pattern (Fig. 12). Interestingly, unlike origination probability (Fig. 7), survival probability is

582 frequently estimated with considerable uncertainty. When survival probability is below 0.50 then a species that is present is unlikely to survive from one time unit to the next, while when survival

584 probability is greater than 0.50 species can be expected to survive to the next time unit. Finally,

Table 10: Probability of a plant phase having greater log-odds of originating than another. The first two columns are comparisons of that posterior estimate to zero, which corresponds to the probability of that plant phase having a greater log-odds of originating when compared to the Miocene-Pleistocene. The final columnn corresponds to the comparison in log-odds of originating between the Eocene-Miocene and the Paleocene-Eocene.

	P(Eo.Mi > 0)	P(Pa.Eo > 0)	P(Eo.Mi > Pa.Eo)
arboreal carnivore	0.575	0.447	0.598
digitigrade carnivore	0.976	0.017	0.998
plantigrade carnivore	0.857	0.780	0.578
scansorial carnivore	0.768	0.154	0.889
arboreal herbivore	0.318	0.357	0.428
digitigrade herbivore	1.000	0.161	0.995
fossorial herbivore	0.999	0.353	0.926
plantigrade herbivore	1.000	0.304	0.998
scansorial herbivore	0.999	0.108	0.998
unguligrade herbivore	0.000	0.000	0.100
arboreal insectivore	0.364	0.003	0.857
fossorial insectivore	0.645	0.341	0.708
plantigrade insectivore	0.794	0.148	0.881
scansorial insectivore	0.916	0.235	0.940
arboreal omnivore	0.590	0.006	0.882
plantigrade omnivore	0.524	0.209	0.762
scansorial omnivore	0.713	0.027	0.938
unguligrade omnivore	0.888	0.127	0.960

when survival probability is approximately 0.50 then survival and extinction are equally likely. For

586 most mammal functional groups, survival probability is rarely estimated to be greater than 0.50  
 with any certainty. This result is consistent with the average occurrence being <1.35 time units per  
 588 species which means that a plurality of species have only a single temporal occurrence (Fig. 3).

The survival probability for many functional groups is frequently estimated to be approximately

590 0.50, indicating extinction is frequently random with respect to functional group (Fig. 12). For  
 example, the survival probability scansorial carnivores is approximately 0.50 for the entire time  
 592 series which indicates that there is no best or worst time for this functional groups survival. Similar  
 patterns can be observed for mean survival probability of arboreal omnivores, fossorial insectivores,  
 594 and plantigrade omnivores though all three of these groups have sudden drops in survival  
 probability by the Hemphillian 10.3 Mya.

Table 11: Probability that the two temperature covariates have an effect on the log-odds of functional group origination. Values greater than 0.50 correspond to the probability of that effect having positive relationship with origination, while values less than 0.5 correspond increasing certainty that that covariate has a negative relationship with origination.

	$P(\gamma_{temp\ mean} > 0)$
arboreal carnivore	0.355
digitigrade carnivore	0.001
plantigrade carnivore	0.358
scansorial carnivore	0.121
arboreal herbivore	0.219
digitigrade herbivore	0.045
fossorial herbivore	0.067
plantigrade herbivore	0.000
scansorial herbivore	0.221
unguligrade herbivore	0.339
arboreal insectivore	0.027
fossorial insectivore	0.219
plantigrade insectivore	0.224
scansorial insectivore	0.192
arboreal omnivore	0.009
plantigrade omnivore	0.087
scansorial omnivore	0.035
unguligrade omnivore	0.129

- 596 Arboreal herbivores are the only functional group for which survival probability is approximately  
 above 0.50 for the entire Cenozoic (Fig. 12). This result indicates that when an arboreal herbivore  
 598 species is present it is expected to survive from one time unit to the next. However, it is important  
 to note that arboreal herbivores are estimated to have an origination probability below 0.50 for  
 600 most of the Cenozoic. Together, these results mean that arboreal herbivore species are rare but are  
 expected to survive from one time point to the next.
- 602 A common feature of multiple functional group's survival probability time-series is a peak in  
 survival during the Neogene (Fig. 12). In most cases, these peaks are estimated with little  
 604 uncertainty which indicates how apparent this event is. Digitigrade carnivores, digitigrade  
 herbivores, plantigrade herbivores, scansorial insectivores, unguiligrade herbivores, and unguiligrade  
 606 omnivores all peak in survival probability by the Monroecreekian 26.3 Mya. This peak in survival  
 means that species of these functional groups which are unlikely to go extinct at this point,

608 potentially indicating favorable environmental conditions for these groups at the Paleogene-Neogene  
transition. Additionally, this peak does not coincide with the change from one plant phase to  
610 another (Table 5).

The effect of order on survival probability has much lower variance (Fig. 13) than the effect of order  
612 on origination probability (Fig. 8). Primates, Multituberculata, Eulipotyphla, Dermoptera,  
Creodonta, Condylarthra, Carnivora, and Artiodactyla are estimated to have a lower than average  
614 survival probability which implies that species of these orders are expected to be present for a  
single time unit. Of these orders, Primates and Multituberculata are expected to have the lowest  
616 survival probability of all orders. The orders expected to have greater than average survival  
probability are Rodentia, Lagomorpha, and Didelphimorphia.

618 Species mass is estimated to possibly have a positive relationship with survival probability  
 $(P(\beta^\pi > 0) = 0.88$ ; Fig. 14). This result means that it is plausible that species with greater than  
620 average mass have a greater extinction risk than those of average or below average mass. This  
relationship is the opposite of that predicted by CITATION and is in contrast to those from  
622 CITATION. However, because of the marginal plausibility of this result, it is not a strong refutation  
of these previous results. Instead, it points to why there has been confusion as to the effect of mass  
624 on survival; this effect might be very small relative to other factors such as functional ecology and  
thus difficult to estimate the nature of this relationship with high certainty.

626 In contrast to the origination probability, there is little evidence that the group-level covariates  
have large effects on functional group survival probabilities (Fig. 15). In fact, only the plant phases  
628 are associated with differences in survival probability and only for a relatively small number of  
functional groups. These results combined with those from the individual-level covariates (Fig. 12,  
630 13, 14) imply that direct interactions (e.g. species-species) are potentially more important to long  
term species survival than ambient environment (e.g. temperature tolerance). However, because the  
632 estimate of temperature is global in nature, this interpretation is inherently speculative.

Average functional group survival probability is rarely estimated to be different between the three  
634 plant phases (Table 12) with only five pair-wise comparisons having greater than 89% probability of

differences in survival between phases. Unuligrade herbivores have an approximately 89%  
636 probability of having lower survival probability during the Paleocene-Eocene than the  
Miocene-Pleistocene. For digitgrade herbivores, and unguligrade omnivores, the Eocene-Miocene  
638 phase have an approximately 90% probability of having greater survival probability than during the  
Micocene-Pleistocene phase. In contrast, unguligrade herbivores are estimated to have lower  
640 survival probability in the Eocene-Miocene phase than the Miocene-Pleistocene phase. Finally,  
unguligrade herbivores have an approximately 99% probability of having a lower survival  
642 probability during the Paleocene-Eocene than the Eocene-Miocene.

As stated earlier, temperature is not estimated to have an effect on survival probability for any of  
644 the functional group (Table 13). This is congruent with previous studies which found no association  
between extinction and global temperature CITATION ALROY or no consistent, unidirectional  
646 relationship between extinction and global temperature CITATION.

Table 12: Probability of one plant phase having greater log-odds of survival than another. The first two columns are comparisons of that posterior estimate to zero, which corresponds to the probability of that plant phase having a greater log-odds of survival when compared to the Miocene-Pleistocene. The final column corresponds to the comparison in log-odds of survival between the Eocene-Miocene and the Paleocene-Eocene.

	P(Eo.Mi > 0)	P(Pa.Eo > 0)	P(Eo.Mi > Pa.Eo)
arboreal carnivore	0.297	0.560	0.328
digitigrade carnivore	0.786	0.367	0.743
plantigrade carnivore	0.411	0.744	0.273
scansorial carnivore	0.428	0.445	0.486
arboreal herbivore	0.256	0.768	0.174
digitigrade herbivore	1.000	0.400	0.942
fossorial herbivore	0.696	0.563	0.565
plantigrade herbivore	0.659	0.508	0.596
scansorial herbivore	0.616	0.539	0.531
unguligrade herbivore	0.000	0.102	0.012
arboreal insectivore	0.289	0.483	0.368
fossorial insectivore	0.532	0.420	0.592
plantigrade insectivore	0.499	0.361	0.605
scansorial insectivore	0.443	0.252	0.634
arboreal omnivore	0.651	0.597	0.591
plantigrade omnivore	0.417	0.549	0.393
scansorial omnivore	0.486	0.525	0.487
unguligrade omnivore	0.929	0.521	0.844

Table 13: Probability that the two temperature covariates have an effect on the log-odds of functional group survival. Values greater than 0.50 correspond to the probability of that effect having positive relationship with survival, while values less than 0.5 correspond increasing certainty that that covariate has a negative relationship with survival.

	$P(\gamma_{temp\ mean} > 0)$
arboreal carnivore	0.665
digitigrade carnivore	0.453
plantigrade carnivore	0.618
scansorial carnivore	0.380
arboreal herbivore	0.761
digitigrade herbivore	0.395
fossorial herbivore	0.429
plantigrade herbivore	0.279
scansorial herbivore	0.345
unguligrade herbivore	0.818
arboreal insectivore	0.489
fossorial insectivore	0.452
plantigrade insectivore	0.435
scansorial insectivore	0.384
arboreal omnivore	0.600
plantigrade omnivore	0.639
scansorial omnivore	0.512
unguligrade omnivore	0.396

None of the time-series of functional group survival probability are estimated to be either positively  
648 or negatively correlated (Fig. 16); this mirrors the estimated correlations between functional group  
origination probabilities (Fig. 11). This result indicates that functional groups probably have  
650 ultimately independent survival histories for the entire study period. As with origination  
probability, this result does not preclude the possibility of short term similarities in expansion and  
652 decline of origination probability or shared peaks and troughs of survival probability. Additionally,  
if the relationship between two functional groups changes over time (e.g. from positive correlation  
654 to negative correlation), then it would yield no overall correlation for the Cenozoic. Finally, it is  
important to remember that this estimate correlation is based on survival probability and not  
656 extinction rate or diversity.

## Analysis of diversity

- 658 Standing diversity of the North American mammal species pool estimated from this model exhibits  
an initial increase in diversity followed by a decrease till approximately the Whitneyan 30Mya, after  
660 which there is a marked increase till approximately the Barstovian 15Mya after which it decreases  
slightly till it is equal to the overall mean diversity of the Cenozoic (Fig. 18). Per-unit standing  
662 diversity is found to be different from average standing diversity for 12 of 18 time-units ( $> 85$   
probability; Table 14). Diversity is greater than average during the Tiffanian, Wasatchian,  
664 Hemingfordian, Barsotvian, and Clarendonian while diversity is lower than average during the  
Duchesnean, Chadronian, Orellan, Whitneyan, Geringian, Monroecreekian, and Harrisonian. The  
666 nadir of diversity is the Orellan while the apex is the Barstovian (Fig. 18). Interestingly, the rise in  
diversity among the sampled species from the Orellan to the Barstovian is unidirectional and is not  
668 estimated to have any temporary dips in diversification for that entire approximately 15 million  
year period.
- 670 Standing diversity when partitioned by ecotype reveals a lot of the complexity behind the pattern  
of mammal diversity for the Cenozoic (Fig. 19). While each functional group has its own unique  
672 diversity history, there are some broad similarities as is similar to the estimates origination and  
survival probability (Fig. 7, 12).
- 674 Arboreal ecotypes obtain peak diversity early in the Cenozoic and then decline for the rest of the  
time series, becoming increasingly rare or absent as diversity approaches the Recent (Fig. 19).
- 676 Arboreal herbivores and omnivores obtain peak diversity at the beginning of the Cenozoic then go  
into decline while remaining a small part of the species pool, while arboreal carnivores and  
678 insectivores obtain peak diversity by the WAsatchian 55.4 Mya and then quickly decline and  
become extremely rare or entirely absent from the species pool. The only arboreal functional group  
680 estimated to not experience a complete disappearance from the species pool are arboreal herbivores.  
This is consistent with increasing extinction risk in the Neogene compared to the Paleogene as  
682 proposed by Smits (2015).

The diversity of plantigrade insectivores, scansorial insectivores, and scansorial omnivores are

Table 14: Probability that diversity during one NALMA  $N_t^{stand}$  is greater than average standing diversity for the whole Cenozoic  $\overline{N^{stand}}$ . NALMA is a North American Land Mammal age and is the temporal unit for this study. Values greater than 0.50 indicate support for the diversity at that NALMA being greater than average, while values less than 0.50 indicate support for diversity being less than average. These are listed from oldest to youngest NALMA.

NALMA	$P(N_t^{stand} > \overline{N^{stand}})$
Torrejonian	0.79
Tiffanian	0.95
Clarkforkian	0.50
Wasatchian	1.00
Bridgerian	0.69
Uintan	0.75
Duchesnean	0.00
Chadronian	0.01
Orellan	0.00
Whitneyan	0.00
Geringian	0.00
Monroecreekian	0.01
Harrisonian	0.11
Hemingfordian	0.96
Barstovian	1.00
Clarendonian	0.93
Hemphillian	0.63
Blancan	0.73

- 684 estimated to decrease through the Cenozoic (Fig. 19). Plantigrade herbivores and scansorial  
 omnivores have peak diversity at the early Cenozoic and reach low diversity by the Orelan and  
 686 Whitneyan approximately approximately 33 Mya, after which diversity never increases again. In  
 contrast, scansorial omnivores have nearly constant, above average diversity for the beginning of  
 688 the Cenozoic till approximately Orelan and Whitneyan, after which diversity drops and remaining  
 below average diversity for the rest of the Cenozoic.
- 690 The fossorial functional groups included in this study are estimated to be rare or absent absent for  
 the first half of the Cenozoic, fossorial herbivores probably having lower diversity than fossorial  
 692 insectivores (Fig. 19). After fossorial herbivores increase in diversity till the Orelan and Whitneyan  
 approximately 33 Mya, this functional group is estimated to quickly reach approximately constant  
 694 standing diversity for the rest of the Cenozoic. In contrast, fossorial insectivores increase in  
 diversity starting approximately at the Orelan and Whitneyan and reach max diversity at the

696 Barstovian 16.3 Mya, after which this group declines in diversity.

Plantigrade carnivores, scansorial herbivores and unguligrade omnivores are estimated to maintain  
698 near constant standing diversity for most of the Cenozoic (Fig. 19). Of these three functional  
groups, plantigrade carnivores have the greatest variance in standing diversity. Plantigrade  
700 carnivores have greater than average standing diversity from the beginning of the Cenozoic till the  
Bridgerian 50.3 Mya and from the Harrisonian 24.8 Mya till the Barstovian 16.3 Mya. This  
702 functional group is estimated to be below average standing diversity from the Bridgerian till the  
Orelan and Whitneyan approximately 30Mya, and then from the Hemphillian 10.3 Mya till the end  
704 of the studied time period. Scansorial herbivores exhibit a similar patterns but with a reversed  
diversity pattern for the first 30My of the studied period. Instead of near constant diversity,  
706 scansorial herbivores are estimated to have lower than average diversity from the beginning of the  
Cenozoic till the Bridgerian approximately 50.3 Mya, after which this group has approximately  
708 average standing diversity for the rest of the Cenozoic. The unguligrade omnivore functional group  
has slightly elevated diversity at the beginning of the Cenozoic and a possible decrease in diversity  
710 after the Barstovian approximately 16.3 Mya.

Scansorial carnivores and plantigrade herbivores have below average standing diversity from the  
712 beginning of the Cenozoic till the Hemingfordian approximately 20.6 Mya, after which both  
functional groups increase in diversity till being well above average by the end of the study period  
714 (Fig. 19). Plantigrade omnivores are estimated to be absent or extremely rare in the species pool,  
only increasing in standing diversity beginning at the Hemingfordian approximately 24.8 Mya. In  
716 contrast, scansorial carnivores are estimated to have been a rare but constant part of the species  
pool diversity for the entire Cenozoic with an increase at the Hemingfordian.

718 Digitigrade carnivores, plantigrade herbivores, and unguligrade herbivores functional groups  
maintain relatively high standing diversity through out the entire Cenozoic though each exhibits  
720 periods of greater than average and below average standing diversity (Fig. 19). Digitigrade  
carnivore diversity is estimated to begin the study period below average and then quickly rise to  
722 the first peak in diversity at the Wasatchian 55.4 Mya. After this, ditigrade carnivore diversity

decreases to below average diversity till the Orellan and Whitneyan approximately 33 Mya, after  
724 which diversity increases till a second greater peak in diversity at the Barstovian 16.3 Mya. After  
this second peak in diversity, ditigrade carnivore diversity declines until the end of the study period.  
726 Unguligrade herbivores exhibit a similar pattern though with considerably less uncertainty. In  
contrast, while plantigrade herbivores have a similar increase and peak in diversity during the first  
728 half of the Cenozoic, the functional group does not experience a second peak in functional diversity  
till the end of the study period. Additionally, plantigrade herbivores have a longer period of above  
730 average standing diversity during the first half of the Cenozoic, only experiencing a decrease in  
diversity starting at the Orellan and Whitneyan approximately 33 Mya.

732 The digitigrade herbivore functional group is estimated to be the only group with a near constant  
increase in standing diversity through most of the Cenozoic (Fig. 19). There are two periods of  
734 decrease in the standing diversity of digitigrade herbivores: from the start of the study period till  
the Wasatchian 55.4 Mya, and a sudden decrease at the Clarendonian 13.6 Mya. Beyond these two  
736 decreases, this functional group exhibits a remarkable increase in diversity from relative rarity at  
the Wasatchian and Bridgerian till peak diversity at the Hemingfordian and Barstovian. Diversity  
738 even appears to begin to rebound after the sudden decrease at the Clarendonian 13.6 Mya.

The waxing and waning of the mammal ecotypes is obvious when comparing changes to estimated  
740 relative log-mean diversity (Fig. 20). While the relative diversity of functional groups changes  
gradually over time, there are definite patterns associated with a few functional groups and axes of  
742 functional diversity that are interesting. There are many expansions and retractions of functional  
group relative diversity, some of which are coincidental. Only in the case of digitigrade carnivores,  
744 plantigrade herbivores, and scansorial omnivores are their functional groups maintained as  
relatively constant proportions of the species pool (Fig. 20).

746 Eight of the 18 functional groups expand in relative diversity over the Cenozoic (Fig. 20).  
Digitigrade herbivores have an obvious increase in relative diversity at the Uintan 46.2 Mya, after  
748 which it remains a substantial part of the species pool. Fossiliferous herbivores, and fossiliferous  
insectivores increase in relative diversity at the Orellan and Whitneyan approximately 33 Mya,

750 after which these groups are maintained as parts of the species pool. Plantigrade omnivores, and  
scansorial carnivores are both a relatively small fraction of the species pool until the Hemingfordian  
752 20.6 Mya where these functional groups increase in relative diversity for the rest of the time  
analyzed. Scansorial herbivores expand their relative diversity starting at the Harrisonian 24.8 Mya,  
754 after which this functional group has an approximately constant relative diversity. Scansorial  
insectivores experience an increase in relative diversity after the Bridgerian 50.3 Mya. Finally, unlike  
756 other functional groups, unguligrade herbivores slowly increase in their relative diversity for the  
entire Cenozoic.

758 Six of the 18 functional groups are estimated to experience a decrease in relative diversity over the  
Cenozoic (Fig. 20). As expected from the diversity time-series for the functional groups (Fig. 19),  
760 the relative diversity of all four arboreal functional groups declines from the beginning of the  
Cenozoic until the Orellan and Whitneyan approximately 33 Mya, after which only arboreal  
762 herbivores remain in any capacity (Fig. 20). In addition to the arboreal groups, there are other  
functional groups which decrease in relative diversity over the Cenozoic (Fig. 20). Plantigrade  
764 carnivores are a relatively constant portion of the species pool until after the Barstovian 16.3 Mya,  
after which this functional group decreases in relative diversity. Plantigrade insectivores decrease in  
766 their relative diversity, experience greatest winnowing starting approximately at the Geringian till  
the Barstovian, after which this functional group becomes absent from the species pool. Finally,  
768 unguligrade omnivores begin to decrease in relative diversity starting at the Hemingfordian 20.6  
Mya, after which they continue to decrease until they are only a small portion of the relative  
770 diversity of the species pool.

## Discussion

772 The goal of this study has been to understand how macroevolutionary processes are affected by  
species ecology as well as environmental context, and how these interactions shape macroecological  
774 patterns such as regional functional diversity that we observe in the fossil record and the present.  
The composition of a species pool as well as its environmental context change over time, though not

776 necessarily at the same rate or concurrently. Local communities, whose species are drawn from the  
777 regional species pool, have “roles” in their communities defined by their interactions with a host of  
778 biotic and abiotic interactors (i.e. a species’ niche). For higher level ecological characterizations like  
779 ecotypes and guilds, these roles are broad and not defined by specific interactions but by the genre  
780 of interactions species within that grouping participate in. The diversity of species within an  
781 functional group can be stable over millions of years despite constant species turnover (Jernvall and  
782 Fortelius, 2004; Slater, 2015; Van Valkenburgh, 1999). This implies that the size and scope of the  
783 role of an ecotype or guild in local communities, and the regional species pool as a whole, is  
784 preserved even as the individual interactors change. This also implies that the structure of regional  
785 species pools can be constant over time despite a constantly changing set of “players.” There is  
786 even evidence that functional groups are at least partially self-organizing and truly emergent  
(Scheffer and van Nes, 2006).

788 By analyzing mammals species in the context of their functional ecologies, how species response to  
789 environmental change can be better contextualized and interpreted. A major result from this study  
790 is that functional groups have independent responses to changes in their environmental context, and  
791 that most functional groups are estimated to respond through changes in environmental context by  
792 changes to origination probability and not survival probability. Additionally, the functional groups’  
793 origination probability time-series are not estimated to be cross-correlated; this is also true for the  
794 functional groups’ survival probability time-series. Instead, there are individual periods in time that  
795 are characterized by similar changes to absolute or relative diversity. Importantly, it is not always  
796 the same functional groups that appear to experience changes in absolute or relative diversity at  
797 these time points. The results of the analysis presented here add considerable nuance to our  
798 understanding of mammal macroevolution and macroecology over the Cenozoic.

The environmental covariates are found to effect the origination probability of some functional  
800 groups, but only effect the survival probability of relatively few groups. Plant phases: biggest  
801 difference is higher origination probability in the Eocene-Miocene phase than the Paleocene-Eocene  
802 phase (13 of 18 with  $P > 0.85$ ). Lower origination probability in the Paleocene-Eocene than the  
803 Miocene-Pleistocene (10 of 18 with  $P < 0.85$ ). Higher origination in the Eocene-Miocene than

804 Miocene-Pleistocene (8 of 18 P $\geq$ 0.85) exception that 1 of 18 P $\geq$ 0.85 has lower.

806 There is no evidence that the estimate of global temperature used in this study is not estimated to  
be a strong predictor of survival probability. Additionally, there is very little evidence (3 of 18 for  
min 1 phase comparison) of survival probability being different between two plant phases.

808 Temperature is estimated to be a predictor of origination probability for many functional groups  
which either decrease or increase in diversity over the Cenozoic. For example, arboreal and  
810 digitigrade herbivores have close opposite diversity histories, but there are similarities in origination  
probability for which temperature is estimated to be a good predictor. The contrast between these  
812 two groups appears in their survival histories; arboreal herbivores have flat survival probabilities for  
the Cenozoic while digitigrade herbivores have peak in survival approximately 33 Mya.

814 The result that temperature does not affect the survival probability of most functional groups is  
consistent with previous analysis of mammal diversity (Alroy et al., 2000). The result that  
816 temperature affects origination probability, on the other hand, is in strong contrast to the results  
Alroy et al. (2000). An important difference between the analyses presented here and that of Alroy  
818 et al. (2000) is I am considering the effect of temperature on the probability of a species originating,  
assuming it hasn't originated yet while Alroy et al. (2000) analyzes the correlation between the first  
820 differences of the origination and extinction rates with an oxygen isotope curve (Zachos et al., 2001).  
Origination or extinction rates have very different properties than the origination probabilities  
822 estimated here brought upon by the difference both in definition and units. Origination probability  
is the expected probability that a species that has never been present and is not present at time  $t$   
824 will be present at time  $t + 1$ ; origination probability is defined for a single species. In contrast, per  
capita rates are defined (for origination) as the expected number of new species to have originated  
826 between time  $t$  and  $t + 1$  given the total number of species present at time  $t$ ; per capita rates are  
defined for the standing diversity. It is also important to note that even though there is an edge  
828 effect at the last time interval that causes an increase in the occurrence and origination probabilities  
of some functional groups (Fig. 7. However, it is still possible that the finding that temperature has  
830 an effect on origination may simply be because as time approaches the present the number of

species which have originated increases and not because of climatic forcing of origination.

All environmental factors are found to affect the occurrence and origination probabilities for most, but not all, mammal ecotypes (Fig. 10). In contrast, the environmental factors probably do not affect differences in ecotype survival probability (Fig. 15). The focus in previous research on temperature and major climatic or geological events without other measures of environmental context may have led to confusion in discussions of how the “environment” affects mammal diversity and diversification (Alroy et al., 2000; Figueirido et al., 2012). The environment or climate are more than just global or regional temperature, it is also the set of all possible biotic and abiotic interactions that can be experienced by a member of the species pool. By including more descriptors of species’ environmental context than simple an estimate of global temperature a more complete “picture” of the diversification process is inferred.

The results of my model suggest that there are three moments of exceptionally high or low mammal species diversity in the Cenozoic: the Wasatchian, Orellan/Whitneyan, and the Barstovian. The Wasatchian and Barstovian NALMA mark the two major peaks in mammal diversity as estimated by my model, while the Orellan/Whitneyan are estimated to be time lowest diversity during the Cenozoic. Each of these time units mark changes in absolute and relative diversity; for example, the Wasatchian marks peak relative diversity of arboreal carnivores and scansorial herbivores increase in relative diversity after this time point. Here I discuss which functional groups are associated with important changes to the regional species pool at these three periods of time as well as their environmental context.

The Wasatchian brackets the PETM and the EECO. In terms of standing diversity, the Wasatchian marks peak diversity of all arboreal functional groups; peak diversity of digitigrade carnivores, plantigrade carnivores, plantigrade herbivores; high diversity of plantigrade insectivores and scansorial carnivores; and the subsequent expansion of diversity of digitigrade herbivores following this time point. In terms of relative diversity, the Wasatchian marks peak arboreal carnivore, a low amount of fossorial herbivores, and the expansion of scansorial herbivores after this time point.

MEANING? COMPARE TO HYPOTHESES FROM INTRO In general, these findings are

858 consistent with many of the hypothesized changes to mammal diversity described in ?.

Orellan and Whitneyan is lowest diversity, and is a major moment in changes to functional  
860 diversity. Marks the loss of some, marks the expansion of others. This also marks a peak in survival  
probability for six functional groups WHICH. These time units also mark the Eocene/Oligocene  
862 boundary. In terms of standing diversity, these time units mark the complete loss or the nadir in  
diversity of all the arboreal functional groups; a dip in diversity of unguligrade herbivores, a drop  
864 off in diversity of plantigrade insectivores, scansorial insectivores, and scansorial omnivores; and  
marks the expansion fossorial functional groups as well as plantigrade omnivores. In terms of  
866 relative diversity, the Orellan and Whitneyan are associated with an increase in digitigrade  
carnivores, digitigrade herbivores, fossorial herbivores and fossorial insectivores; the beginning of an  
868 increase in scansorial omnivores; a decrease in diversity of scansorial insectivores; and the loss of  
arboreal insectivores as a meaningful component of relative diversity. MEANING? COMPARE TO  
870 HYPOTHESES FROM INTRO

The near complete loss of arboreal functional groups from the regional species pool is not  
872 specifically hypothesized in previous studies of the Eocene-Oligocene transition, but is none the less  
predictable given the long standing narrative describing the loss of closed, forested environments  
874 from North America. What is remarkable, however, is the simultaneous near complete loss of these  
groups which is one of the most obvious shared changes to functional diversity. This pattern implies  
876 a single, shared mechanism underlying the loss of arboreal diversity.

The third moment of particular interest is the Barstovian which marks the second peak in mammal  
878 standing diversity as estimated from my model. This time unit also marks the Mid-Miocene  
Climatic Optimum, a period of relative warmth and stability in global temperature compared to  
880 the rest of the Neogene. In terms of standing diversity, the Barstovian marks peak diversity of  
unguligrade herbivores, digitigrade carnivores, digitigrade herbivores, and fossorial insectivores. In  
882 contrast, relative diversity is much more varied in terms of changes to functional diversity. The  
Barstovian marks an increase in relative diversity of arboreal insectivores, plantigrade omnivores; a  
884 decrease in relative diversity of digitigrade herbivores; and the loss of the contribution of

unguligrade omnivores and plantigrade insectivores to the species pool. MEANING? COMPARE  
886 TO HYPOTHESES FROM INTRO

Mammal species are short lived with average duration being only slightly more than one NALMA.  
888 This short a duration means that observation probability is very high for most of the Cenozoic,  
with it being greater than 0.50 for the entire Cenozoic while also being greater than 0.80 for most of  
890 the Cenozoic. Time is associated with greater variation in observation probability than functional  
group. Scansorial insectivores are estimated to have a substantially lower observation probability  
892 than the other functional groups.

Mass is estimated with XX percent probability of having a TYPE effect on species observation, XX  
894 percent probability of having a TYPE effect on species origination, and an XX percent probability  
of having a TYPE effect on species survival.

896 What do all these results mean? This is the nuance we've needed to actually understand species  
response to changes in environmental context. Is origination driven by ecological opportunity while  
898 survival is driven by differences in species-level fitness?

## Conclusions

900 Is origination driven by ecological opportunity while survival is driven by differences in species-level  
fitness?  
902 These results add a considerable degree of nuance to the narrative of changes to North American  
diversity being gradual. My results support the conclusions that functional diversity is shaped more  
904 by changes to origination than extinction and that major changes to total diversification rate can  
be attributed to increases in origination of only some ecotypes. There are a number of interesting  
906 estimated ecotype diversity patterns. While arboreal ecotypes are diverse in the Paleogene, by the  
Neogene all arboreal ecotypes dramatically decreased in diversity and became either rare or absent  
908 from the regional species pool. The other ecotypes that decrease in diversity over the Cenozoic are  
plantigrade and scansorial insectivores and scansorial omnivores. The only ecotypes that

910 demonstrate a sustained pattern of increasing diversity are digitigrade and unguligrade herbivores.  
When the environmental covariates analyzed here are inferred to affect the diversification of an  
912 ecotype, this effect is virtually always on origination and not survival. This analysis provides a  
much more complete picture of North American mammal diversity and diversification, specifically  
914 the dynamics of the ecotypic composition of that diversity. By increasing the complexity of analysis  
while precisely translating research questions into a statistical model, the context of the results is  
916 much better understood. Future studies of diversity and diversification should incorporate as much  
information as possible into their analyses in order to better understand or at least contextualize  
918 the complex processes underlying that diversity.

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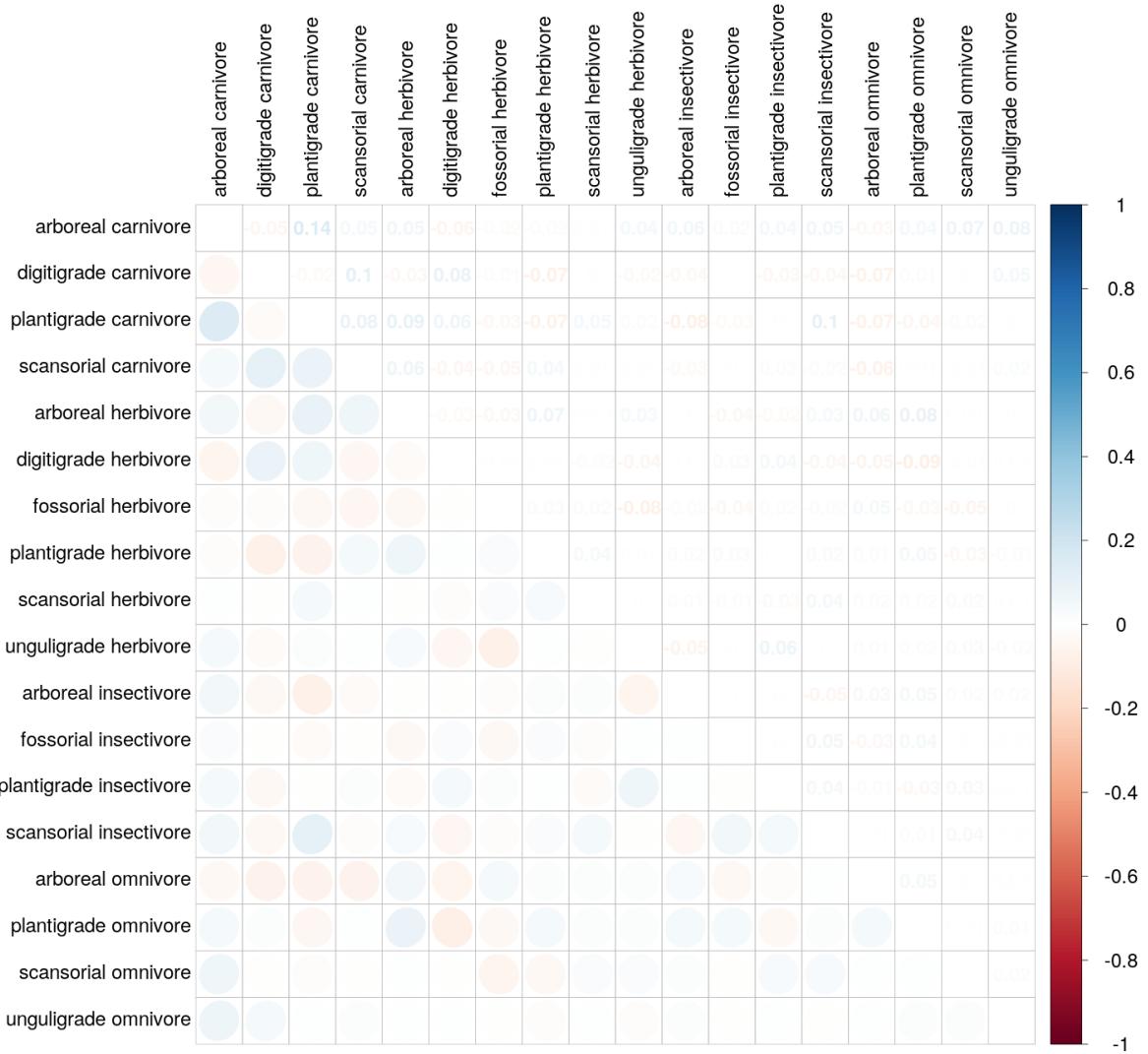


Figure 11: Posterior estimate of mean correlations in origination probability between the mammal functional groups. The lower triangle of the matrix is populated with ellipses corresponding to the level of correlation between the two functional groups, while the upper triangle of the matrix corresponds to the mean estimate of the correlation between functional groups. Darker values correspond to a greater magnitude of correlation with blue values corresponding to a positive correlation and red values a negative correlation.

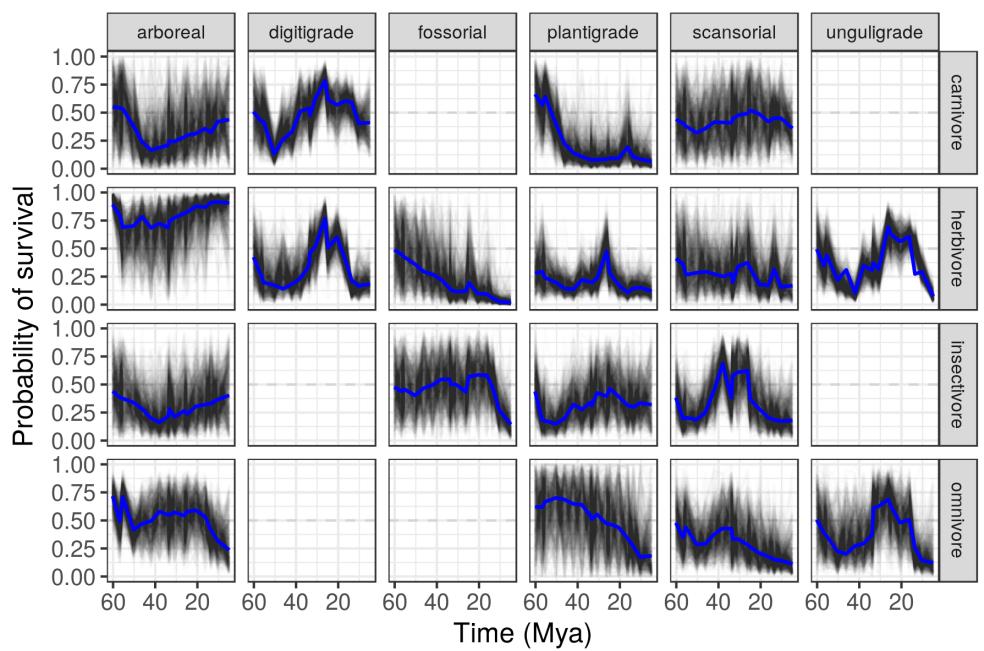


Figure 12: Probability of a species continued survival based on functional groups. Survival probability is graphed as 100 time-series drawn from the model's posterior estimates. A greater density of the posterior estimates indicates increased certainty. The blue line is the mean survival probability as predicted by just the group-level predictors. The columns are by locomotor category and rows by dietary category.

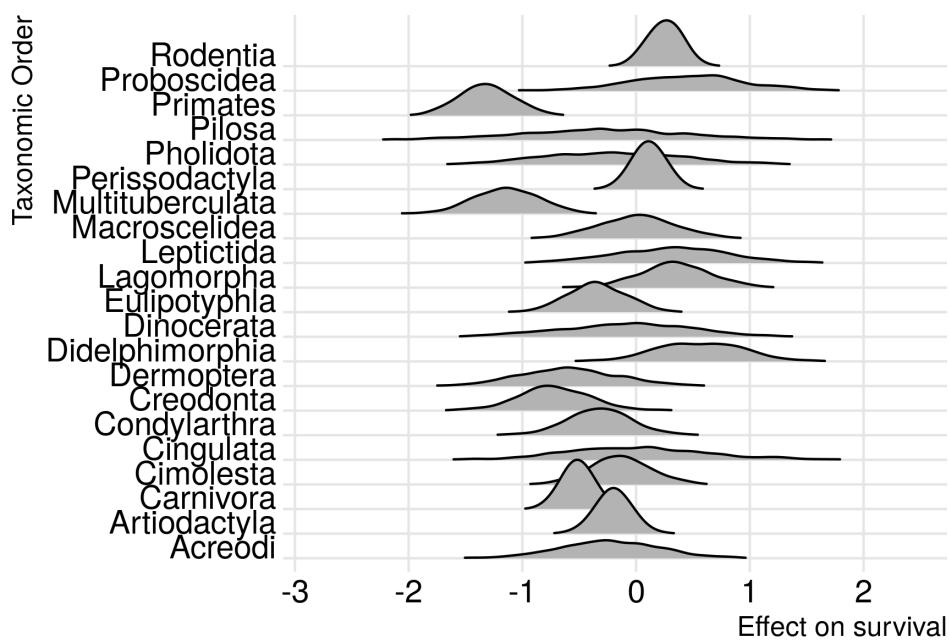


Figure 13: Differences in log-odds of survival based on mammal orders. Positive values correspond to greater log-odds survival than average, while negative values correspond to lower log-odds of survival than average.

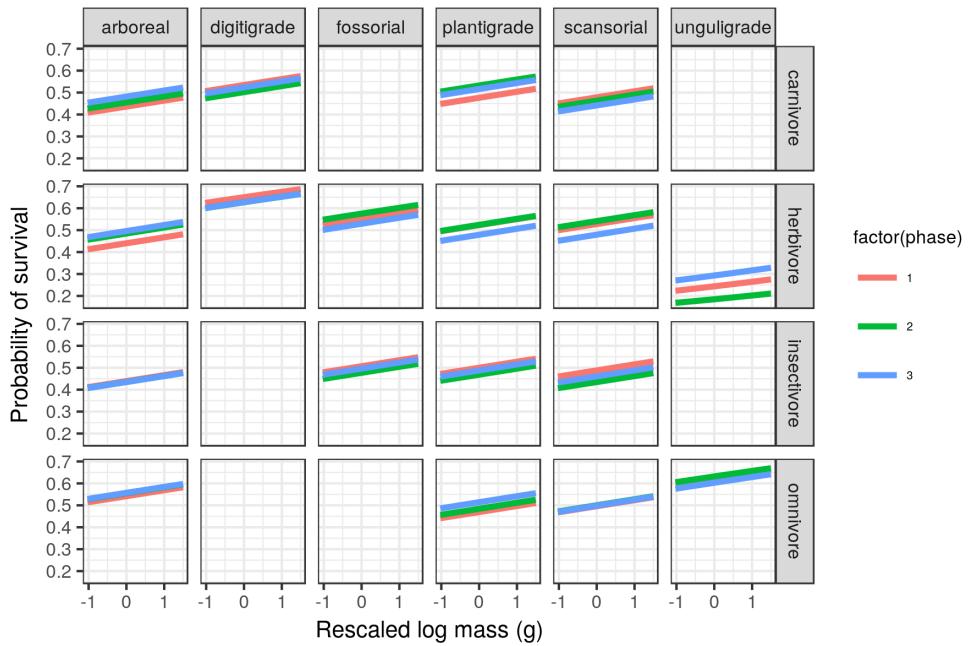


Figure 14: Mean estimates of the effect of species' mass on the probability of a species surviving, plotted for each of the three plant phases. While the effect of mass is considered constant over time, each plant phases corresponds to a different intercept of the relationship between mass and survival. The three plant phases are indicated by the color of the line. Mass has been log-transformed, centered, and rescaled; this means that a mass of 0 corresponds to the mean of log-mass of all observed species and that mass is in standard deviation units. For clarity, only the mean of these estimates.

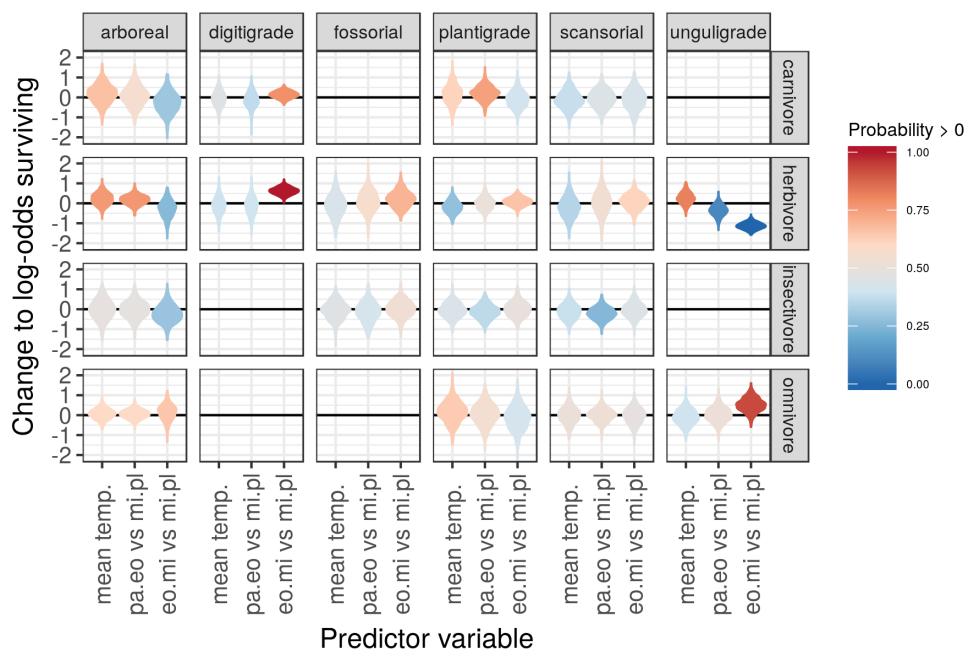


Figure 15: Estimated effects of the group-level covariates describing environmental context on log-odds of species survival. The violin densities that are plotted are based on 1000 samples from the approximate posterior. The color of the violin corresponds to the probability that the covariates effect is estimated to be greater than 0; red values correspond to greater than 0.50 probability of being positive, blue values correspond to less than 0.50 probability of being positive.

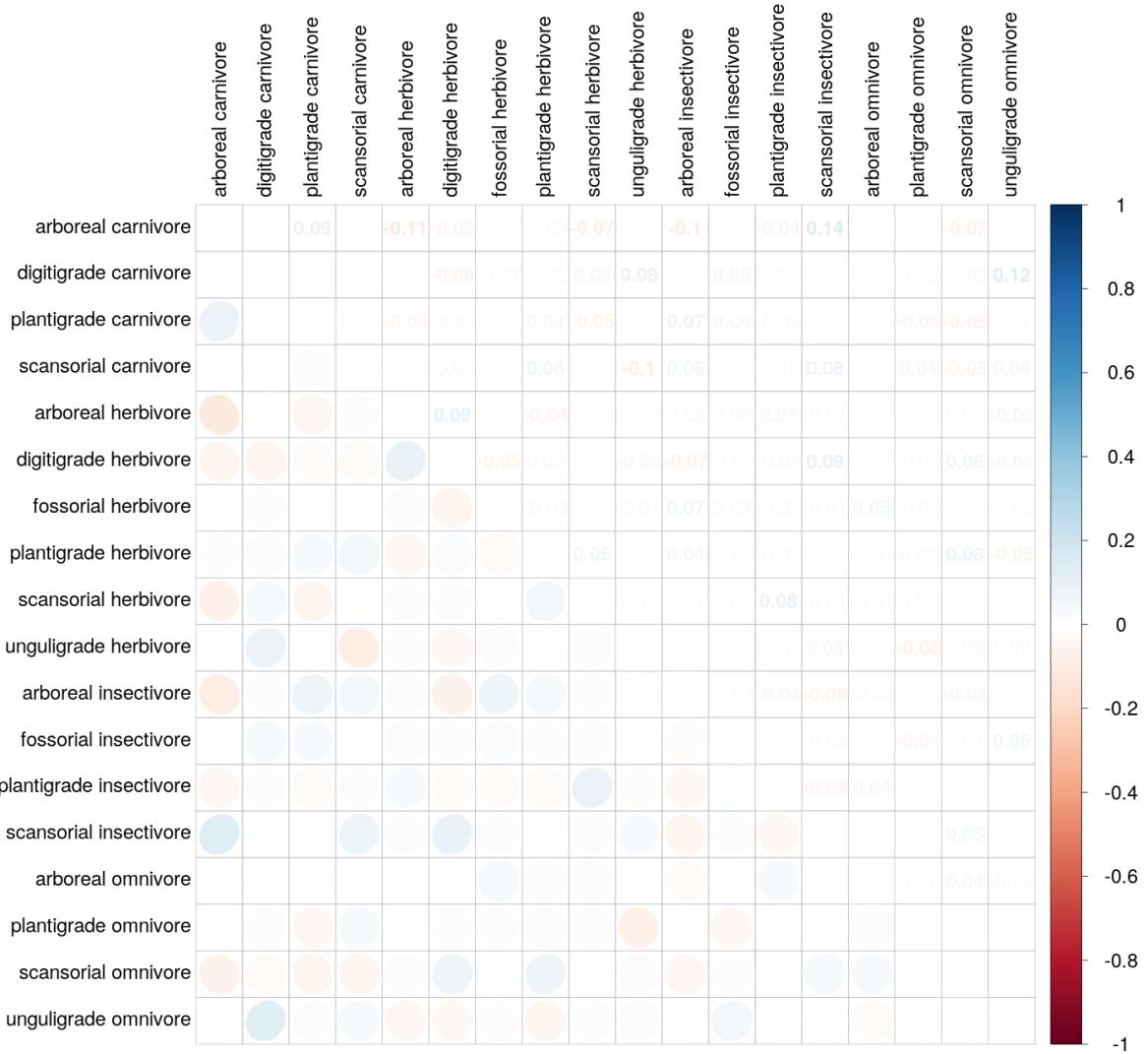


Figure 16: Posterior estimate of mean correlations in survival probability between the mammal functional groups. The lower triangle of the matrix is populated with ellipses corresponding to the level of correlation between the two functional groups, while the upper triangle of the matrix corresponds to the mean estimate of the correlation between functional groups. Darker values correspond to a greater magnitude of correlation with blue values corresponding to a positive correlation and red values a negative correlation.

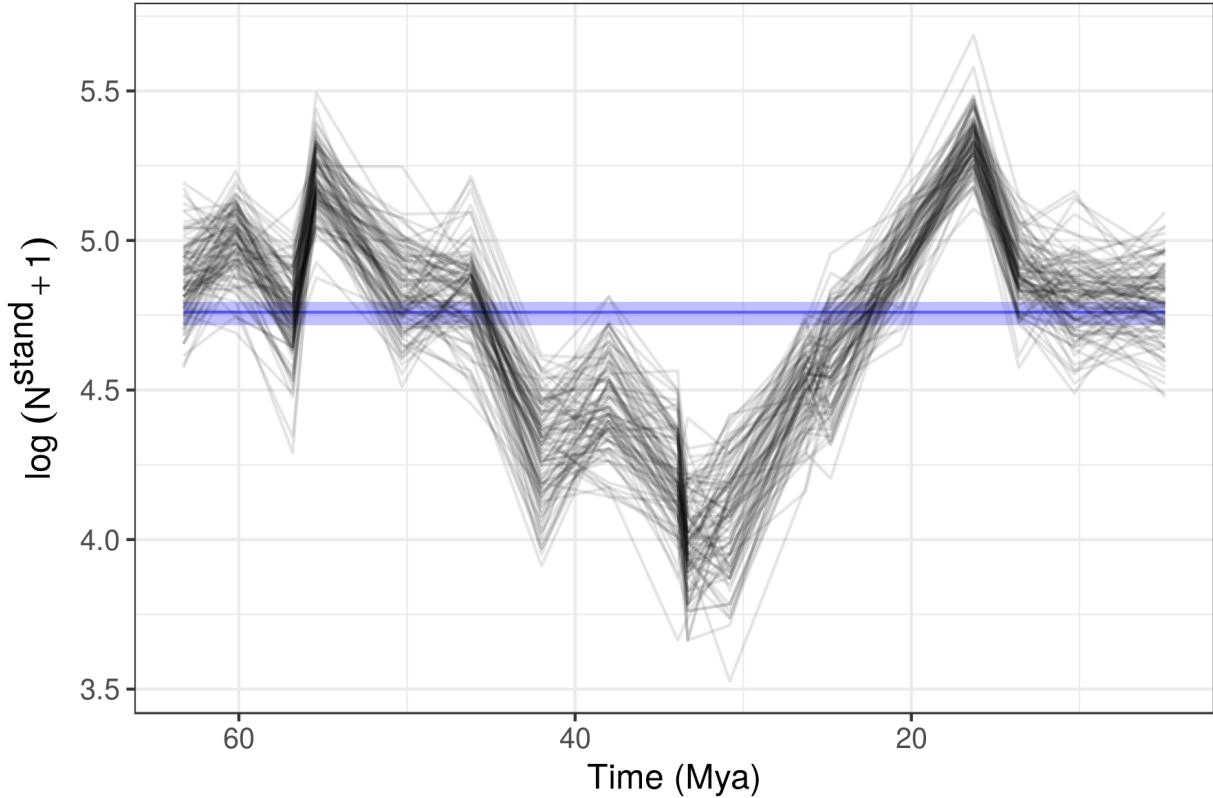


Figure 17: Log diversity

Figure 18: Estimated standing diversity of Cenozoic mammals based on the 1400 species analyzed in this study. Estimates are based on 100 posterior draws of the “true” occurrence matrix  $z$  (Table 7). The blue horizontal strip corresponds to the median and 80% credible interval of estimated mean standing diversity for the entire time period studied.

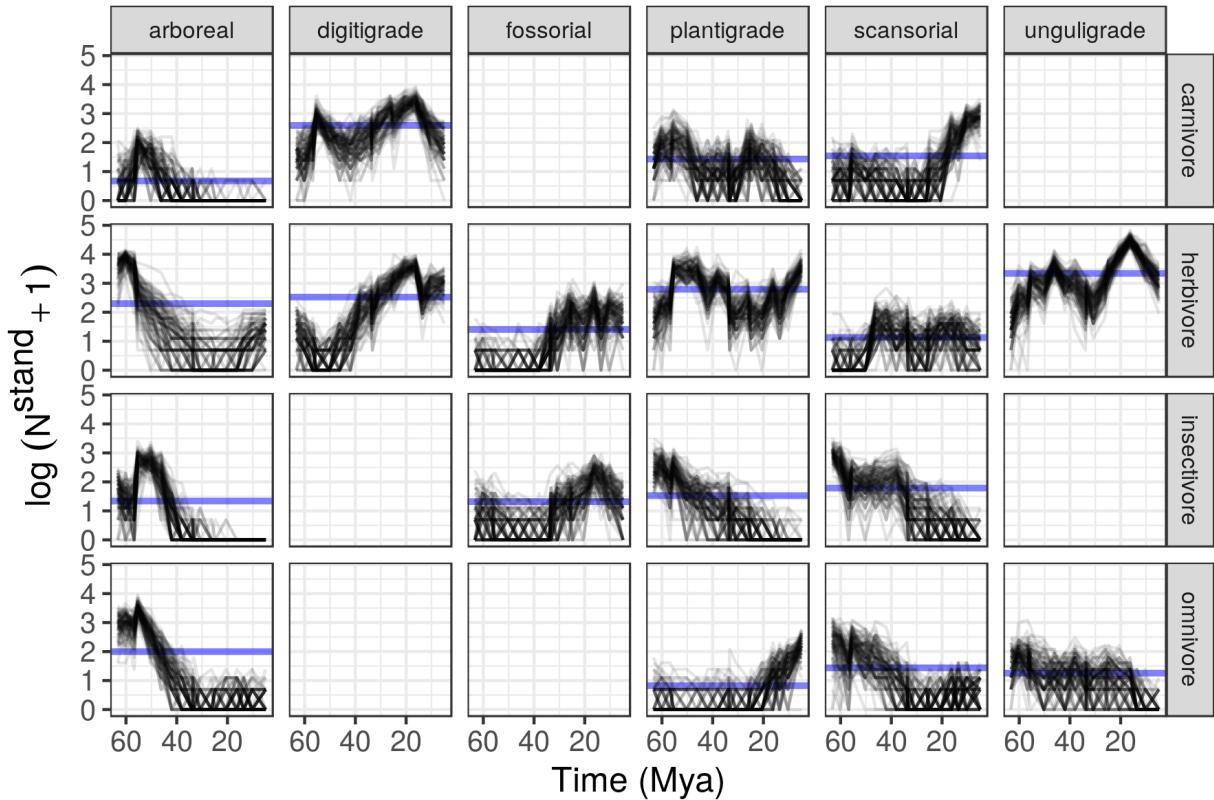


Figure 19: Estimated standing log-diversity of North American mammals by functional group for the Cenozoic. Diversity is represented as 100 posterior draws plotted over time. Density of time-series indicates congruence in estimates. The blue line corresponds to average standing diversity for that functional group for the entire Cenozoic.

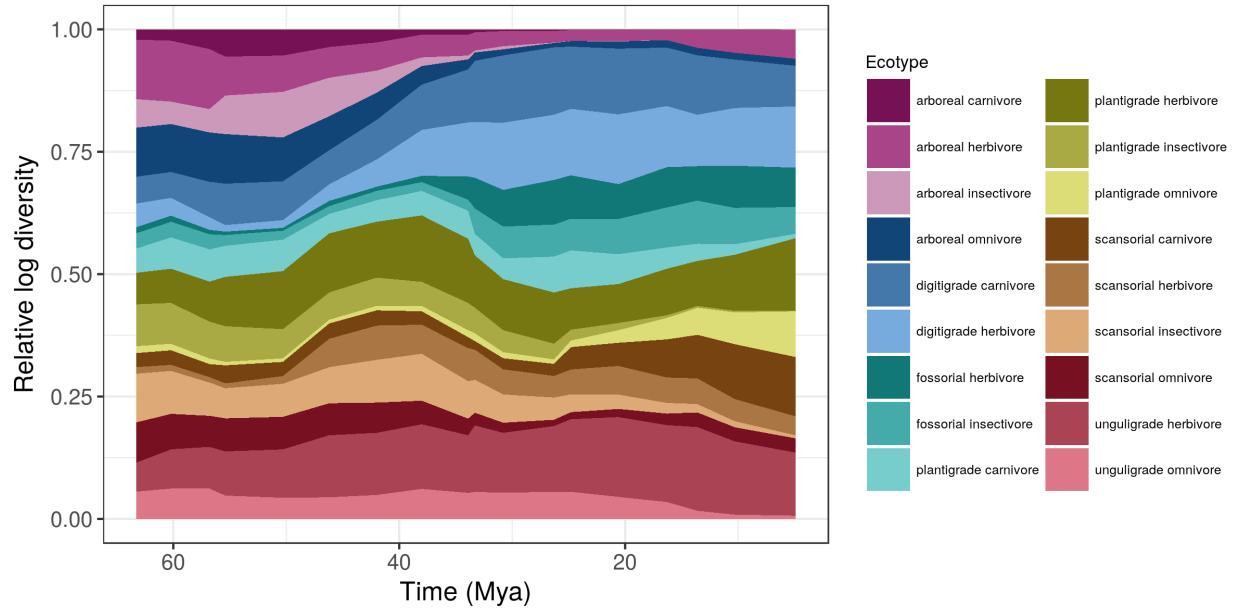


Figure 20: Relative diversity of the mammal functional groups for the Cenozoic. Relative diversity was calculated from the mean posterior estimate of standing diversity (Fig. 19) and is plotted here without uncertainty. These estimates are calculated from 100 posterior estimates of the true occurrence matrix  $z$  (Table 7).