

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

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Manuscript elements:

Keywords: macroecology, macroevolution, paleobiology, species pool, community assembly

Manuscript type: Article

Prepared using the suggested L^AT_EX template for *Am. Nat.*

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. Using two hierarchical Bayesian hidden Markov models of diversity, I find that changes to mammal diversity are driven more by the influx of new species than by selective extinction. I also find that the only ecotypes which experience a near constant increase in diversity over time are digitigrade and unguligrade herbivores, while arboreal ecotypes become increasingly rare and in many cases disappear entirely from the species pool over the Cenozoic. Additionally, I find that global temperature is only associated with the origination of some mammal ecotypes but, in almost all cases, does not affect the extinction of mammal ecotypes.

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 all 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,
30 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
32 macroevolutionary and macroecological processes of speciation, extinction, migration, and
extirpation which, in turn, shape the downstream macroecological dynamics of the regional species
34 pool and its constituent local communities (Harrison and Cornell, 2008; Mittelbach and Schemske,
2015; Urban et al., 2008). In turn, the distribution of species within regional species pool represents
36 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.

38 Fundamentally, all species respond differently to climate and environmental change (Blois and
Hadly, 2009). Those species with similar ecological roles within a species pool can be described as
40 belonging to a guild or functional group (Bambach, 1977; Brown and Maurer, 1989; Simberloff and
Dayan, 1991; Valentine, 1969; Wilson, 1999). Species within the same functional group are expected
42 to have 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
44 interpretable as changes to the set of ways species within a species pool could interact with the
biotic and abiotic environment.

46 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
48 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;
50 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
52 CITATION. These types of comparison do 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
54 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.
56 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 the Recent, paleontological data
58 provides a unique opportunity to observe and estimate the changes to functional diversity and how
species functional traits and environmental context can shape the enrichment or depletion of
60 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 to their long term average
62 diversity in the species pool is particularly useful in conservation settings; species in depleted
groups are most likely more at risk of extinction than species in enriched groups, even if those
64 enriched groups are relatively rare when compared to the functional composition of other
contemporaneous species pools.

66 The paleontological record of North American mammals for the Cenozoic (\sim 66 million years ago to
the present) provides one of the best opportunities for understanding how regional species pool
68 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
70 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
72 that functional traits like the dietary/trophic category of species are easy to estimate (Eronen et al.,
2010; Polly et al., 2011, 2015).

74 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
76 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
78 species traits and environmental factors on these processes.

Background

80 The history of standing diversity for all mammals along with that some individual clades of North
American mammals for the Cenozoic has been the focus of considerable study (Alroy, 1996, 2009;
82 Alroy et al., 2000; 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, 84 2013; Silvestro 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 86 categories: total diversity (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 88 Wilhelm, 1993; Jernvall and Fortelius, 2004; Pires et al., 2015), within/between clade comparisons (Cantalapiedra et al., 2017; Fraser et al., 2015; Quental and Marshall, 2013; Silvestro et al., 2015; 90 Slater, 2015), and estimating the impact of environmental process on total diversity (Alroy et al., 2000; Badgley and Finarelli, 2013; Badgley et al., 2017; Blois and Hadly, 2009; Eronen et al., 2015; 92 Fraser et al., 2015; Janis, 1993; Janis and Wilhelm, 1993). Each of these studies provide a limited perspective on the macroevolutionary and macroecological processes shaping diversity and 94 diversification. Integration across perspectives is necessary for producing a holistic and internally consistent picture of how the North American mammal species pool has changed through time. One 96 of the goals of this study is to present a framework for approaching hypotheses about diversity and diversification through multiple lenses simultaneously through a joint model so that any inferences 98 are better constrained and the relative importance of species' ecological function, taxonomic affinities, and environmental context may be better elucidated.

100 The narrative of the diversification of North American mammals over the Cenozoic is one of gradual change. There is little convincing evidence that there have been any sudden 102 cross-functional or cross-taxonomic group turnover events in mammal diversity at any point in the Cenozoic record of North America (Alroy, 1996, 2009; Alroy et al., 2000; Eronen et al., 2015; Janis, 104 1993). Instead of being concentrated at specific time intervals, species turnover has been found to be distributed through time. It is then expected then that, for this analysis, turnover events or 106 periods of rapid diversification or depletion should not occur simultaneously for all functional groups under study. Additionally, changes to mammal diversification seem to be primarily driven by 108 changes to origination rate and not to extinction (Alroy, 1996, 2009; Alroy et al., 2000). An unresolved aspect of the general history of mammal diversification is whether that diversity is 110 limited or self-regulating; namely, to what extent is mammal diversification diversity-dependent

(Alroy, 2009; Harmon and Harrison, 2015; Rabosky, 2013; Rabosky and Hurlbert, 2015). Similarity,
112 this question can also be asked of specific functional groups (Jernvall and Fortelius, 2004; Quental
and Marshall, 2013; Silvestro et al., 2015; Van Valkenburgh, 1999).

114 The climate history of the Cenozoic can be broadly described as a gradual cooling trend, with polar
ice-caps forming in the Neogene (Cramer et al., 2011; Zachos et al., 2008, 2001). There are of course
116 exceptions to this pattern such as the Eocene climatic optimum, the mid-Miocene climatic
optimum, and the sudden drop in temperature at the Eocene/Oligocene boundary (Zachos et al.,
118 2008, 2001). In terms of the North American biotic environment, the Cenozoic is additionally
characterized by major transition from having closed, partially forested biomes being common in
120 the Paleogene to the landscape being dominated by savannah and grasslands biomes by the
Neogene (Blois and Hadly, 2009; Janis, 1993; Janis et al., 2000; Strömberg, 2005).

122 The Eocene-Oligocene transition has been observed to be associated with extinction of many
ungulate taxa (Janis, 2008). This boundary also marks the transition from the Paleogene to the
124 Neogene and from herbivores being browsing dominated to grazing dominated, though not
concurrently (Janis, 1993; Strömberg, 2005). Additionally, the Paleogene-Neogene boundary marks
126 the approximate start of Antarctic ice sheets, which were previously absent (Zachos et al., 2008).
There is an observed stability in estimates of global temperature from the E/O transition till the
128 end of the Miocene called the Mid-Miocene climatic optimum (Zachos et al., 2008, 2001). The
Mid-Miocene climatic optimum is bookended by periods of temperature decline. We would then
130 expect that, for the Miocene, turnover and other diversification events would most likely be due to
biological interactions or immigration and not biotic-abiotic interactions because of the constancy
132 of the climate, and that those groups that are driven primarily by environmental factors, the
Miocene would be a period of marked by an absence of major changes to diversity or the
134 diversification process.

In addition to the in the expansion of grasslands, the North American the landscape structure and
136 topology of North America was substantially changed from the beginning Cenozoic to the Recent
due mountain uplift and other tectonic actives in Western North America (Badgley and Finarelli,

¹³⁸ 2013; Badgley et al., 2017; Blois and Hadly, 2009; Eronen et al., 2015; Janis, 2008; ?). This type of geological activity affects both local climates as well as continental weather patterns while also
¹⁴⁰ mobilizing increased grit into the environment, something which may be responsible for increasing trend of hyposodony (high crowned teeth) among ungulate and rodent herbivores (Damuth and
¹⁴² Janis, 2011; Janis, 1993; Jardine et al., 2012; Jernvall and Fortelius, 2002). Tectonic processes and mountain uplift in particular have been implicated in the increasing diversification at the
¹⁴⁴ Mid-Miocene climatic optimum (Badgley and Finarelli, 2013; Finarelli and Badgley, 2010; Janis, 2008; ?; ?).

¹⁴⁶ The effect of (global) temperature on mammal diversity and its accompanying diversification process has been the focus of considerable research with a slight consensus favoring mammal
¹⁴⁸ diversification being more biologically-mediated than climate-mediated when considering the entire Cenozoic (Alroy et al., 2000; Clyde and Gingerich, 1998; Figueirido et al., 2012). However,
¹⁵⁰ differences in temporal and geographic scale seem to underly the contrast between these two perspectives. For example when the mammal fossil record analyzed at small temporal and
¹⁵² geographic scales a correlation between diversity and climate is observable (Clyde and Gingerich, 1998; ?). However, when the record is analyzed at the scale of the continent and most of the
¹⁵⁴ Cenozoic this correlation disappears (Alroy et al., 2000). This result, however, does not go against the idea that there may be short periods of correlation between diversity and climate and that this
¹⁵⁶ relationship can change or even reverse direction over time; this type result means that there is no single direction or longterm correlation between diversity and climate (Figueirido et al., 2012).

¹⁵⁸ In the case of a fluctuating correlation between diversity and climate it is hard to make the argument for an actual causal link between the two without modeling the underlying ecological
¹⁶⁰ differences between species; after all, species respond differently based on their individual ecologies (Blois and Hadly, 2009). When analysis is based on diversity or taxonomy alone no mechanisms are
¹⁶² possible to infer. Taxonomy, like body size, stands in for many important species traits to the point that mechanistic or process based inference is impossible. While emergent patterns might
¹⁶⁴ correspond to taxonomic grouping, this itself is an emergent phenomenon. Instead, by framing hypotheses in terms of species traits and their environmental context, these emergent phenomena

¹⁶⁶ can be observed and analyzed rather than assumed.

The diversity history of ungulate herbivores has been characterized by more recently originating
¹⁶⁸ taxa having longer legs, higher crowned teeth, and a shift from graze-dominated to
browse-dominated diets than their earlier originating counterparts (Cantalapiedra et al., 2017;
¹⁷⁰ Fraser et al., 2015; Janis et al., 2004; Janis, 1993, 2008; Janis et al., 2000). The mechanisms which
drive this pattern are theorized to be some combination of tectonic activity driving environmental
¹⁷² change such as the 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.,
¹⁷⁴ 2017; Blois and Hadly, 2009; Eronen et al., 2015; Janis, 2008).

In contrast, the origination of modern cursorial carnivore forms was not until later in the Cenozoic;
¹⁷⁶ this is not to say that carnivore diversity only grew in the late Cenozoic, but that those forms were
late entrants (Janis and Wilhelm, 1993). Instead, the diversity history of carnivores is reflective of
¹⁷⁸ density-dependence or some other form of self-regulation (Silvestro et al., 2015; Slater, 2015; Van
Valkenburgh, 1999). Specifically, it has been proposed that different canid clades have replaced each
¹⁸⁰ other as the dominate members of their functional group within the species pool (Silvestro et al.,
2015; Van Valkenburgh, 1999). It is then expected that, for this analysis, the diversity of digitigrade
¹⁸² and plantigrade carnivores (i.e. the “carnivore” guild of Van Valkenburgh (1999)) should be
relatively constant for the Cenozoic or at least have plateaued by the Neogene.

¹⁸⁴ In a relevant study, Smits (2015) found that functional traits such as a species dietary or locomotor
category structure differences in mammal extinction risk. In particular, arboreal taxa were found to
¹⁸⁶ have a shorter duration on average than species from other locomotor categories (Smits, 2015). Two
possible scenarios that could yield this pattern were proposed: the extinction risk faced by arboreal
¹⁸⁸ species is constant and high for the entire Cenozoic or the Paleogene and Neogene represent
different regimes and extinction risk increased in the Neogene, thus driving up the Cenozoic average
¹⁹⁰ extinction risk. These two possible explanations have clear and testable predictions with respect to
the diversity history of arboreal taxa: 1) if arboreal taxa always have an elevated extinction risk
¹⁹² when compared to other taxa, then the diversity history of arboreal taxa is expected to be constant

with time, albeit possibly at low diversity; and 2) if the Paleogene and Neogene represent difference
194 selective regimes with the former being associated with lower extinction risk than the latter, then
the diversity history of arboreal taxa are expected to be present in the Paleogene but depleted or
196 absent from the species pool during the Neogene.

There is a lack of consensus as to the effect of species body size on mammal diversity and aspects of
198 the diversification processes, specifically extinction (Liow et al., 2008, 2009; Smits, 2015; Tomiya,
2013). Species body size is frequently framed as an important biological descriptor because of its
200 correlation with other important and relevant ecological traits such as metabolic rate and home
range size (Brown, 1995). It is also relatively easy to estimate for extinct species using proxy
202 measures and regression equations, as was done in this study (see below). However, body size is
normally analyzed without simultaneous reference to other relevant species traits (Huang et al.,
204 2017; Liow et al., 2008; Raia et al., 2012; Smith et al., 2004), but see (Smits, 2015); this combined
with the high amount of correlation between life history traits and body size limits process-based
206 inference, because the actual causal mechanisms underlying an observed pattern are obscured or
missing.

208 **Foreground**

The fourth-corner problem is conceptual and statistical framework to explaining the patterns of
210 either species abundance or presence/absence in a community as a product of species traits,
environmental factors, and the interaction between traits and environment (Brown et al., 2014;
212 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
214 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
216 region (Jamil et al., 2013; Pollock et al., 2012).

This conceptual framework can be extended to include time when considering occurrence as a
218 three-dimensional: species at localities in space over time. This extension changes the goal of

predicting just occurrence to one of predicting species gain and loss at localities. However, the
220 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
222 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
224 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
226 problem than modern ecological data.

In this study, the fourth-corner problem is phrased as understanding how mammal functional
228 groups respond to environmental change in order to predict the origination and survival of species
over time (Fig. 1). Additionally, I also consider the incompleteness of the fossil record and the static
230 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
232 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;
234 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.
236 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
238 differences in species dynamics that driven by mass and not functional group.

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

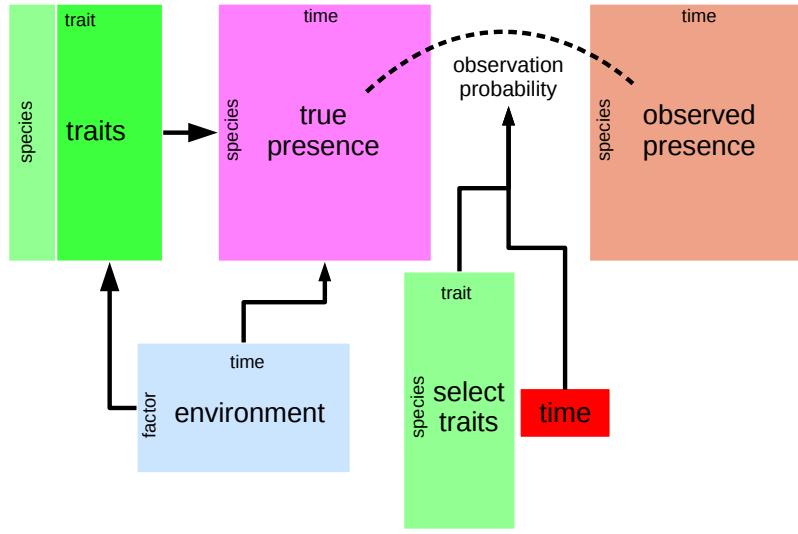


Figure 1: Conceptual diagram of the analysis at the center of this study. The observed presence matrix (orange) is the empirical presence/absence pattern for all species for all time points; this matrix is an incomplete observation of the “true” presence/absence pattern (purple). This observation process 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).

246 All observations, paleontological or modern, are made with uncertainty. With presence/absence
 247 data this uncertainty comes from not knowing if an absence is a “true” absence or just a failure to
 248 observe (Foote, 2001; Foote and Sepkoski, 1999; Lloyd et al., 2011; Royle and Dorazio, 2008; Royle
 249 et al., 2005; Wang and Marshall, 2016). For paleontological data, the incomplete preservation and
 250 sampling of species means that the true times of origination or extinction may not be observed
 (Foote, 2001; Foote and Sepkoski, 1999; Wang et al., 2016; Wang and Marshall, 2016). The model
 252 used in this analysis is a translation of the conceptual framework described above (Fig. 1) into a
 253 statistical model in order to estimate the relative diversity of mammal functional groups over time
 254 and how those functional groups respond to changes to environmental context while taking into
 account the fundamental incompleteness of the fossil record.

256 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
258 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
260 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
262 modeling approach with a model of an observation-occurrence or observation-origination-extinction
process.

264 Materials and Methods

Taxon occurrences and species-level information

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

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

280 Many species taxonomic assignments as present in the raw PBDB data were updated for accuracy

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

Species functional group is defined as the combination of locomotor and diet categories; the goal is
292 to classify species based on the manner with which they interact with their environment. Mammal
species records in the PBDB have life habit (i.e. locomotor category) and dietary category
294 assignments. In order to simplify interpretation, analysis, and per-functional group sample size
these classifications were coarsened in a similar manner to Smits (2015) (Table 1). Ground dwelling
296 species locomotor categories were then reassigned based on the ankle posture associated with their
taxonomic group, as described in Table 2 (Carrano, 1999). Ankle posture was assumed uniform for
298 all species within a taxonomic group except for those species assigned a non-ground dwelling
locomotor category in the PBDB, which retained their non-ground dwelling assignment. All species
300 for which it was possible to assign a locomotor category had one assigned, including species for
which post-cranaia are unknown but for which a taxonomic grouping is known. Ground dwelling
302 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
304 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
Apternodontidae	scansorial
Arctocyonidae	unguligrade
Barbourofelidae	digitigrade
Barylambdidae	plantigrade
Bovidae	unguligrade
Camelidae	unguligrade
Canidae	digitigrade

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Table 2 – continued from previous page

Family	Stance
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
Hapalodectidae	plantigrade
Heteromyidae	digitigrade
Hyaenidae	digitigrade

Continued on next page

Table 2 – continued from previous page

Family	Stance
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
Nimravidae	digitigrade
Nothrotheriidae	plantigrade
Notoungulata	unguligrade

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Table 2 – continued from previous page

Family	Stance
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
Titanoideidae	plantigrade
Ursidae	plantigrade
Viverravidae	plantigrade

Continued on next page

Table 2 – continued from previous page

Family	Stance
Zapodidae	plantigrade

306 Estimates of species mass used in this study were sourced from multiple databases and papers,
especially those focusing on similar macroevolutionary or macroecological questions (Brook and
308 Bowman, 2004; Freudenthal and Martín-Suárez, 2013; McKenna, 2011; Raia et al., 2012; Smith
et al., 2004; Tomiya, 2013); this is similar to Smits (2015). When a species' mass was not available,
310 proxy measures were used to estimate their mass. For example, given a measurement of a mammal
tooth size, it is possible and routine to estimate its mass given some regression equation (Table 3).
312 The PBDB has one or more body part measures for many species. These were used as body size
proxies for many species, as was the case in Smits (2015). Mass was log-transformed and then
314 rescaled by first subtracting mean log-mass from all mass estimates, then dividing by two-times its
standard deviation; this insures that the magnitude of effects for both continuous and discrete
316 covariates are directly comparable (Gelman, 2008; Gelman and Hill, 2007).

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

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

324 Environmental and temporal covariates

The environmental covariates used in this study are collectively referred to as group-level covariates
 326 because they predict the response of a “group” of individual-level observations (i.e. species). These

covariates are defined for temporal bins as they predict the individual parts of each species

328 occurrence history. The group-level covariates in this study are an estimate of global temperature
 and the Cenozoic “plant phases” defined by Graham (2011).

330 Global temperature across most of the Cenozoic was calculated from Mg/Ca isotope record from
 deep sea carbonates (Cramer et al., 2011). Mg/Ca based temperature estimates are preferable to

332 the frequently used $\delta^{18}\text{O}$ temperature proxy (Alroy et al., 2000; Figueirido et al., 2012; Zachos

et al., 2008, 2001) because Mg/Ca estimates do not conflate temperature with ice sheet volume and

334 depth/stratification changes (Cramer et al., 2011; Ezard et al., 2016). The former is particularly

important to this analysis as the current polar ice-caps appeared and grew during the second half of
 336 the Cenozoic. These properties make Mg/Ca based temperature estimates preferable for

macroevolutionary and macroecological studies (Ezard et al., 2016). Temperature was calculated as

338 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

was then rescaled by subtracting its mean from all values and then dividing by twice its standard

340 deviation.

The second set of environmental factors included in this study are the Cenozoic plant phases

342 defined in Graham (2011). Graham’s plant phases are holistic descriptors of the taxonomic
 343 composition of 12 ecosystem types, which plants are present at a given time, and the relative
 344 modernity of those plant groups with younger phases representing increasingly modern taxa
 (Graham, 2011). Graham (2011) defines four intervals from the Cretaceous to the Pliocene, though
 346 only three of these intervals take place during the time frame being analyzed. Graham’s plant
 347 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}	$1 - \pi$	π	0
	1	0	ϕ	$1 - \phi$
	$0_{extinct}$	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 π and survival ϕ .

348 analysis (Gelman and Hill, 2007); this means that the Miocene-Pleistocene phase is synonymous
with the intercept and other phases are defined by their differences from this baseline. The
350 temporal boundaries of these plant phases, their durations, and abbreviations are defined in Table 5.

Modelling species occurrence

352 At the core of the model used in this study is hidden Markov process where the latent process has
an absorbing state; also referred to as a discrete-time birth-death model (Allen, 2011) or a
354 capture-mark-recapture model CITATION. While there are only two state “codes” in a
presence-absence matrix (i.e. 0/1), there are in fact three states in a birth-death model: not having
356 originated yet, extant, and extinct. The last of these is the absorbing state, as once a species has
gone extinct it cannot re-originate (Allen, 2011). Thus, in the transition matrices the probability of
358 an extinct species changing states is 0 (Table 6); see below for extended parameter explanations
(Tables 7, 8, and 9).

360 **Basic model**

I will begin defining the model used in this study by focusing on the basic machinery of the hidden
362 Markov process at the model’s core. This aspect of the model is similar to the well-known
Jolly-Seber capture-mark-recapture model from ecology CITATION which has three characteristic
364 probabilities: probability p of observing a species given that it is present, probability π of a species
surviving from one time to another, and probability ϕ of a species first appearing (Royle and
366 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
ϕ	$N \times T$	probability of species originating from time t to $t + 1$ if it is not present
π	$N \times (T - 1)$	probability of species surviving at time t , given that it is already originated

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

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

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

374 **Expanding on the basics**

Expanding on the basic model involves modeling the observation, origination and survival
 376 probability as independent multi-level logistic regressions. Origination and survival probabilities
 share the same covariates and model structure, while observation probability is modeled as a
 378 function of a smaller selection of covariates.

The probability of observing a species given that it is present p is modeled as a logistic regression
 380 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^ϕ	$J \times T - 1$	intercept of log-odds ϕ , varies by time and functional group
f^π	$J \times T$	intercept of log-odds π , varies by time and functional group
o^ϕ	K	effect of species' order on log-odds of ϕ
o^π	K	effect of species' order on log-odds of π
β^ϕ	1	effect of species' mass on log-odds of ϕ
β^π	1	effect of species' mass on log-odds of π
m	N	species' mass estimates

respectively. The effect of species mass was also included through a regression slope term β^p .

- 382 The log-odds of a species originating (logit π) or surviving (logit ϕ) are modeled independently but
 take the same form: a regression with an intercept that varies by both time and functional group,
 384 an additional taxonomic order varying-intercept term, and the slope term for species mass.
 Importantly, the time and functional group varying-intercept is itself modeled such that the
 386 intercept for each functional group is a time series predicted by the group-level covariates
 (described below).
- 388 The expanded model incorporating these regression models is written as

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

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

Complete model

- 392 The expanded model (Eq. 2) is still incomplete as it is missing the group-level covariates such as
 global temperature, and it is missing all of the necessary final generative priors.
- 394 Here I describe how the effects of mammal functional group on origination and survival are
 modeled. f^ϕ and f^π are modeled as the responses from a multivariate normal distribution, where
 396 each functional group is modeled by a time-series regression. Temporal autocorrelation is modeled
 as a random-walk prior for the varying intercept of the group-level regressions. The effects of the
 398 group-level covariates on origination and survival are included for each functional group through
 regression coefficients. The expansion to include these group-level regression is described in
 400 Equation 3, the parameters of which are described in Table 9.

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

- In hierarchical models like the one described here (Eq. 2, 3) it can be hard to distinguish between
 402 the likelihood and prior as data and structure can enter the model through many different
 parameters CITATION. For example, in Equation 2 the model of z can be considered a prior and
 404 statements in Equation 3 can be considered priors for the parameters which predict ϕ and π . The
 remaining priors necessary to this model, however, are not based on parameter expansion but are
 406 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
μ^ϕ	$J \times T$	time-series of the mean log-odds of ϕ for each functional group
μ^π	$J \times T$	time-series of the mean log-odds of π for each functional group
Σ^ϕ	$J \times J$	covariance matrix between functional groups for ϕ
Σ^π	$J \times J$	covariance matrix between functional groups for ϕ
α^ϕ	$J \times T$	time-varying intercept of μ^ϕ
α^π	$J \times T$	time-varying intercept of μ^π
σ^ϕ	J	scale of random-walk prior for α^ϕ
σ^π	J	scale of random-walk prior for α^π
γ^ϕ	D	group-level regression coefficients for μ^ϕ
γ^π	D	group-level regression coefficients for μ^π
U	T	matrix of group-level covariates

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

- 408 For the regression coefficients, such as β^ϕ and γ^ϕ , the chosen priors are considered weakly
- informative as they concentrate most of the probability density between -2 and 2. Similarly, the
- 410 scale parameters, such as τ^ϕ and σ^ϕ , are also given weakly informative half-Normal priors which
- concentrate most of the probability density between 0 and -2. The covariance matrices, such as Σ^ϕ ,
- 412 are decomposed into a vector of scale terms (e.g. τ^ϕ) and correlation matrices (e.g. Ω^ϕ) which were
- then given weakly informative priors. This approach and choice of LKJ priors for the correlation
- 414 matrices follows the Stan User Manual CITATION. For parameter vectors which are presented with

only a single prior (e.g. β^ϕ), that prior statement is for each of the elements of that vector.

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

- ⁴¹⁶ The model used in this study is the complete sampling statement expressed through the combination of equations 2, 3, and 4. These statements taken together form a complete generative
⁴¹⁸ model posterior inference is possible.

Posterior inference and model adequacy

420 A computer program that implements joint posterior inference the model described above (Eqs. 2,
421 3, and 4) was written in the probabilistic programming language Stan (Stan Development Team,
422 2016). All methods for posterior inference implemented in Stan are derivative-based; this causes
complications for actually implementing the above models, because integers do not have derivatives.
424 In order to infer the values of the matrix of latent discrete parameters z (Tables 7) the log posterior
probabilities of all possible states of the unknown values of z were calculated and summed (i.e.
426 marginalized) (Stan Development Team, 2016).

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

436 The combined size of the dataset and large number of parameters (Eqs. 2, 3, and 4), in specific the
total number of latent parameters that are the matrix z , means that MCMC based posterior
438 inference is computationally slow. Instead, an approximate Bayesian approach was used: variational
inference. A recently developed automatic variational inference algorithm called “automatic
440 differentiation variational inference” (ADVI) is implemented in Stan and is used here (Kucukelbir
et al., 2015; Stan Development Team, 2016). ADVI assumes that the posterior is Gaussian but still
442 yields a true Bayesian posterior; this assumption is similar to quadratic approximation of the
likelihood function commonly used in maximum likelihood based inference (McElreath, 2016). The
444 principal limitation of assuming the joint posterior is Gaussian is that the true topology of the
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.

446 be positive (e.g. standard deviation).

Of additional concern for posterior inference is the partial identifiability of observation parameters
 448 $p_{t=1}$ and $p_{t=T}$ (Royle and Dorazio, 2008). This issue means that the estimates of sampling
 probabilities at the “edges” of the time series cannot fully be estimated because there are no known
 450 “gaps” in species occurrence histories that are guaranteed to be filled. Instead, the values of the first
 and final columns of the “true” presence-absence matrix z for those observations that do not already
 452 have presences in the observed presence-absence matrix y cannot be estimated (Royle and Dorazio,
 2008). The hierarchical modeling approach used here helps mitigate this problem by pulling the
 454 values of $p_{t=1}$ and $p_{t=T}$ towards the overall mean of p (Gelman et al., 2013), and in fact this
 approach might be more analytically sound than the more ad-hoc approaches that are occasionally
 456 used to overcome this hurdle (Royle and Dorazio, 2008). Additionally, because $p_{t=1}$ and $p_{t=T}$ are
 only partially identifiable, estimates of occurrence θ and origination ϕ at $t = 1$ and estimates of θ , ϕ

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

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

474 The ADVI assumption of a purely Gaussian posterior limits the utility and accuracy of the
476 posterior predictive checks because parameter estimates do not reflect the true posterior
478 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
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.

480 Given parameter estimates, diversity and diversification rates are estimated through posterior
482 predictive simulations. Given the observed presence-absence matrix y , estimates of the true
484 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
possible occurrence history is estimated (Fig. 2), but now these occurrence histories are generated
relative to their estimated probabilities.

The posterior distribution of z gives the estimate of standing diversity N_t^{stand} for all time points as

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

486 Total regional standing diversity can also be partitioned into the standing diversity of each of the
functional groups.

488 Results

The results of the analyses described above take one of two forms: direct inspection of posterior
490 parameter estimates, and downstream estimates of diversity and diversification rates based on
posterior predictive simulations.

492 Posterior parameter estimates

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

Log-odds of observing a species given that it is present varies greatly with time (Fig. 4) with lowest
498 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
500 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
502 substantial difference in the probability of observation.

There is little variance in the effect of functional group on the log-odds of observing a species that
504 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 of this group is the least

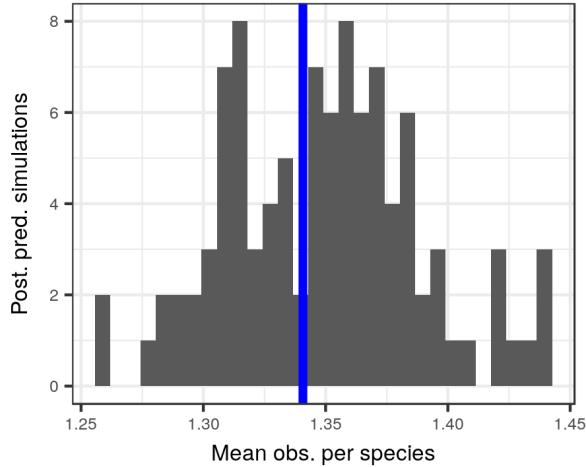


Figure 3: Comparison of the average observed number of occurrences per species (blue line) to the average number of occurrences from 100 posterior predictive datasets simulated from draws from the posterior parameter estimates from the model used in this study. The model is considered to have adequate 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.

506 complete of all the functional groups studied. Few functional groups have marginally better than
 expected log-odds of observation, the other insectivorous functional groups have marginally greater
 508 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 expected to be complete than
 510 most other functional groups. However, it is important to note that for many functional groups,
 their estimated log-odds of observation are poorly constrained with great uncertainty indicating
 512 little structure in how log-odds of observation varies between functional groups (Fig. 5).

Species mass is found to have a positive effect on probability of observing a species that is present
 514 (Fig. 6). This result indicates that species with greater than average mass are expected to have
 more complete observation histories than species with less than average mass. However, this
 516 estimate does not necessarily translate to substantial differences in the estimated probability of
 observation because observation probability is so high for most of the Cenozoic (Fig. 4). In fact, it
 518 is only when observation probability is low that the effect of mass is easily observable. It is
 important to remember the effect of mass on observation was considered constant over time and
 520 that all differences observation probability between land-mammal ages is driven by variation over

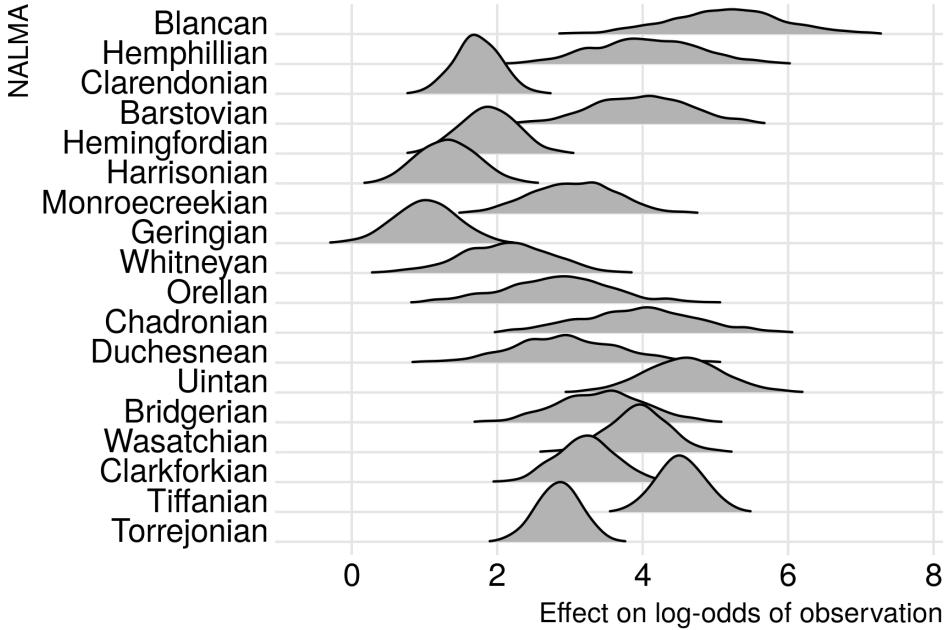


Figure 4: Ridgeline density plots of the estimates for the log-odds of observation from the time-varying intercept term. Each of the named time units are North American land-mammal ages. The oldest land-mammal age is at the bottom of the stack and the youngest is at the top. Higher values correspond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

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

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

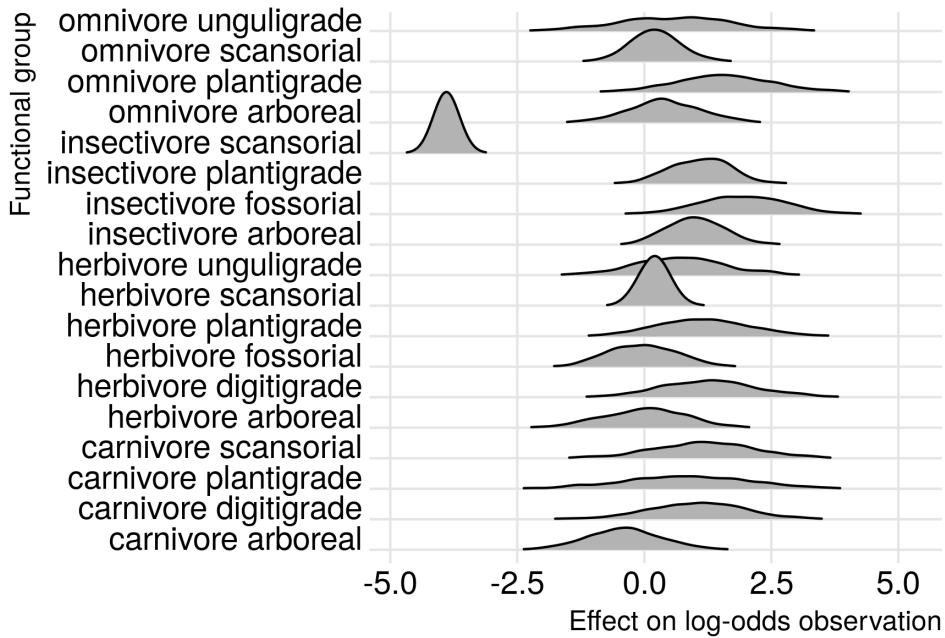


Figure 5: Ridgeline density plots of the estimated effects of species' functional group on log-odds of observing that species given that it is present. Each of the rows correspond to a different functional group as indicated by the dietary and locomotor category combination. Positive values correspond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

Most of the functional groups have peak origination probability at the present (Fig. 7); new species

534 in these functional groups are being added to the species pool through out the Cenozoic. In the case
of some functional groups, such as digitigrade carnivores and fossorial herbivores, this is the
536 culmination of those groups continued growth in the species pool. For other functional groups, such
as arboreal herbivores, this peak is a reversal from previously relatively low origination probability;
538 this indicates an expansion of these functional groups following a decline.

Five of the functional groups do not have peak origination probabilities at the end of the observed

540 period: arboreal carnivores, arboreal insectivores, plantigrade insectivores, scansorial insectivores,
and unguiligrade omnivores. All the arboreal functional groups reach peak origination probability in
542 the Paleogene, after which mean origination probabilities approach and remain at 0.50, reflecting
the loss of these functional groups from the species pool as origination probability never again
544 increases. Additionally, the uncertainty surrounding in the estimates of origination probability is

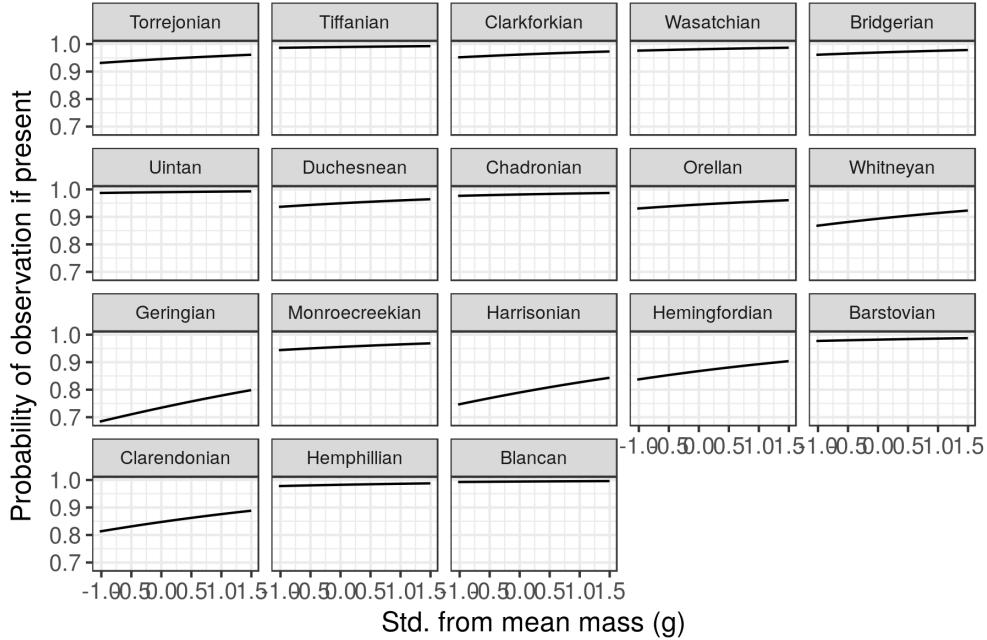


Figure 6: Estimates of the effect of species mass on probability of observing a species that is present (p). Mass has been log-transformed, centered, and rescaled; this means that a mass of 0 corresponds to the mean of log-mass of all observed species and that values are in units of standard deviations.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

very large, especially in the Neogene. Large uncertainty in probabilities can reflect complete separation which results from that functional group leaving the species pool and therefore it's absence is without ambiguity CITATION. The patterns evinced by the other functional groups have similar properties but reach peak origination probability early in the Neogene. Interestingly, origination probability of scansorial insectivores has effectively two peaks, once in the late Paleogene and again in the early Neogene. Additionally, as will be discussed later in the context of standing diversity, all five of these functional groups decrease in diversity through the Cenozoic.

Origination probability varies greatly amongst mammal orders (Fig. 8). These estimates reflect differences origination probability as well as the relative rarity of that order in the fossil record; if members of that order appear infrequently, they must have lower probability of origination. Orders with greater than average log-odds of origination include Multituberculata, Dinocerata, Didelphimorphia, Creodonta, Condylarthra, Cimolesta, and Acreodi; orders that are considered

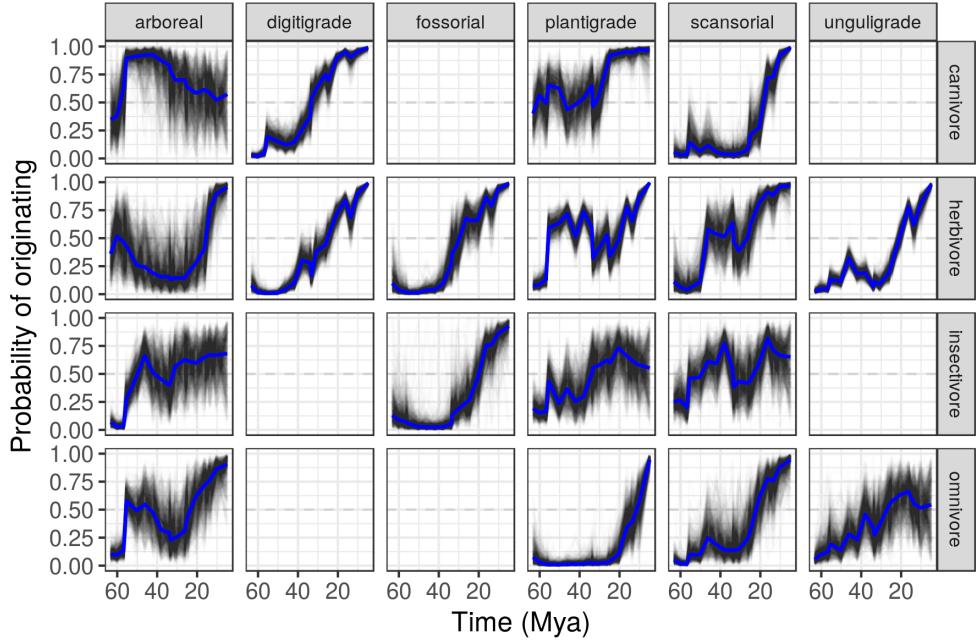


Figure 7: Probability of a species first originating based on functional group. Origination probability is graphed as 100 time-series drawn from the model’s posterior estimates. A greater density of the posterior estimates indicates increased certainty. The blue line is the mean origination probability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

major components of the Paleogene fossil record. Orders with lower than average log-odds of
 558 origination include Rodentia, Pilosa, Lagomorpha, Eulipotyphyla, Cingulata, Carnivora, and
 Artiodactyla; orders characterized by small body size or primarily Neogene records. Additionally,
 560 the variance between orders is vary large ranging from -2.5 to 2.5 log-odds of origination; this large
 of variance reflects how species within these orders have very different patterns of origination
 562 independent from their origination based on functional ecology (Fig. 7).

Species mass is estimated to have a negative relationship with origination probability (Fig. 9)
 564 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 the left-skewed
 566 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 body sized mammals.
 568 Interestingly, many of the orders with small body sizes (e.g. Rodentia, Lagomorpha) have below

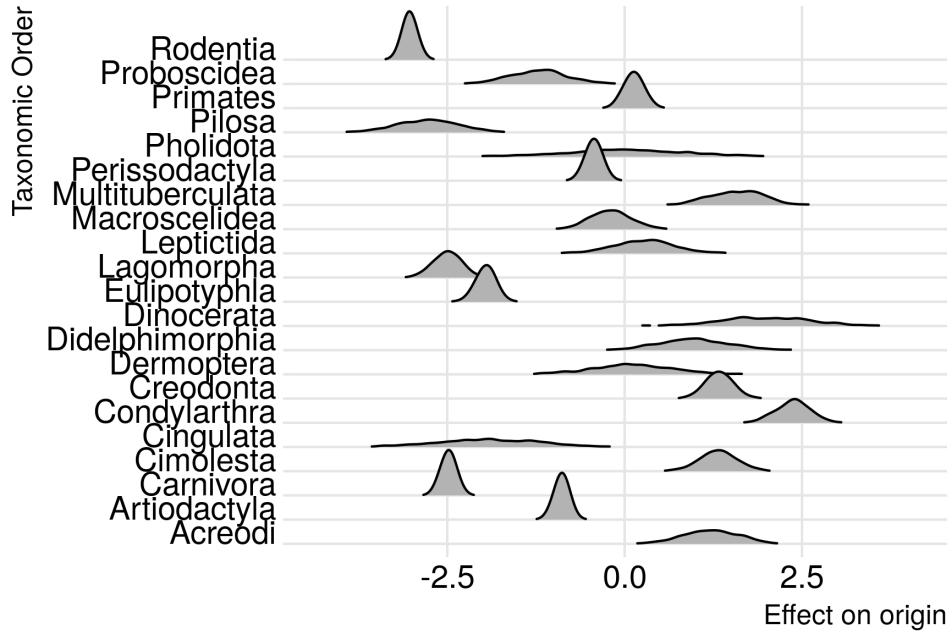


Figure 8: Ridgeline density plots of estimated log-odds of origination based on mammal orders. Positive values correspond to greater log-odds origination than average, while negative values correspond to lower log-odds of origination than average. Importantly, origination probability corresponds to the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

average origination probabilities (Fig. 8); while not completely statistically kosher, when this result
 570 is considered 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
 572 associated with species origination dynamics.

For many of the functional groups, the group-level covariates are estimated with high probability
 574 (> 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 probabilities over time.

576 At least two of the three plant phases are associated with differences in origination probability for
 714 14 of the 18 functional groups (> 0.85 probability; Table 10). The Paleocene-Eocene phase is found
 578 to be associated with differences in origination probability from the Miocene-Pleistocene for ten of
 the functional groups, all of which are expected to have lower origination probability than the latter
 580 (Table 10). The Eocene-Miocene phase is found to be associated with differences in origination

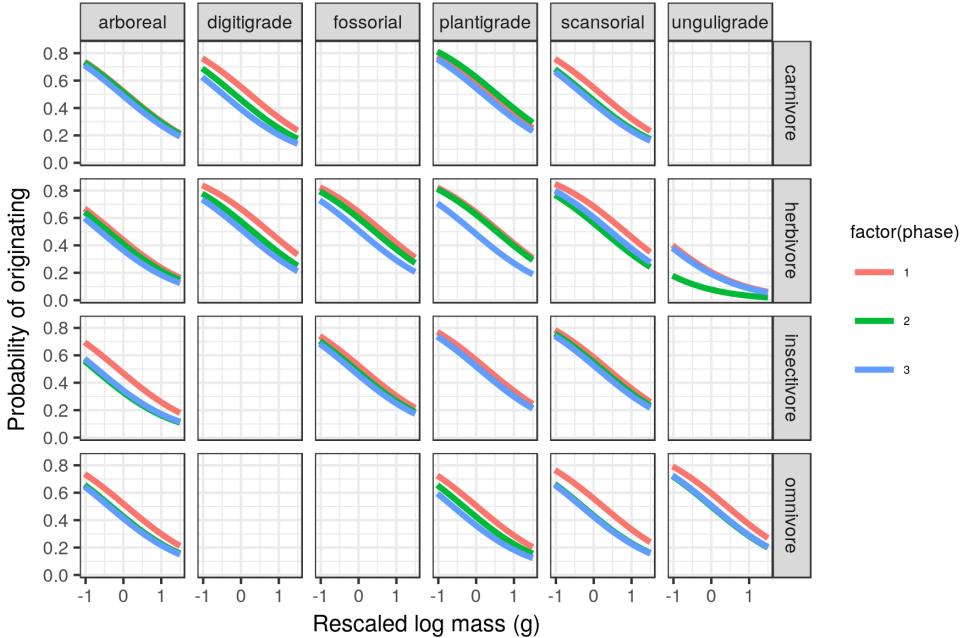


Figure 9: Mean estimates of the effect of species' mass on the probability of a species originating, plotted for each of the three plant phases. While the effect of mass is considered constant over time, each plant phases corresponds to a different intercept of the relationship between mass and origination. 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.

probability from the Miocene-Pleistocene for nine of functional groups: eight with a greater
 582 origination probability than the latter, and one with a lower origination probability than the latter
 (Table 10). The Eocene-Miocene phase is expected to be associated with a greater origination
 584 probability than the Paleocene-Eocene for 13 of the functional groups (Table 10).

Temperature is estimated with probability > 0.85) to have an affect origination probability for ten
 586 of the 18 functional groups (Table 11). In all cases this relationship is estimated to be negative,
 meaning that an increase in temperature is associated with a decrease in origination probability.
 588 Considering that, on average, temperature decreases through the Cenozoic CITATION, this implies
 that the origination probability of these ten functional groups may be tracking this long-term trend
 590 as opposed to the other functional groups which increase in origination probability independently of
 temperature.

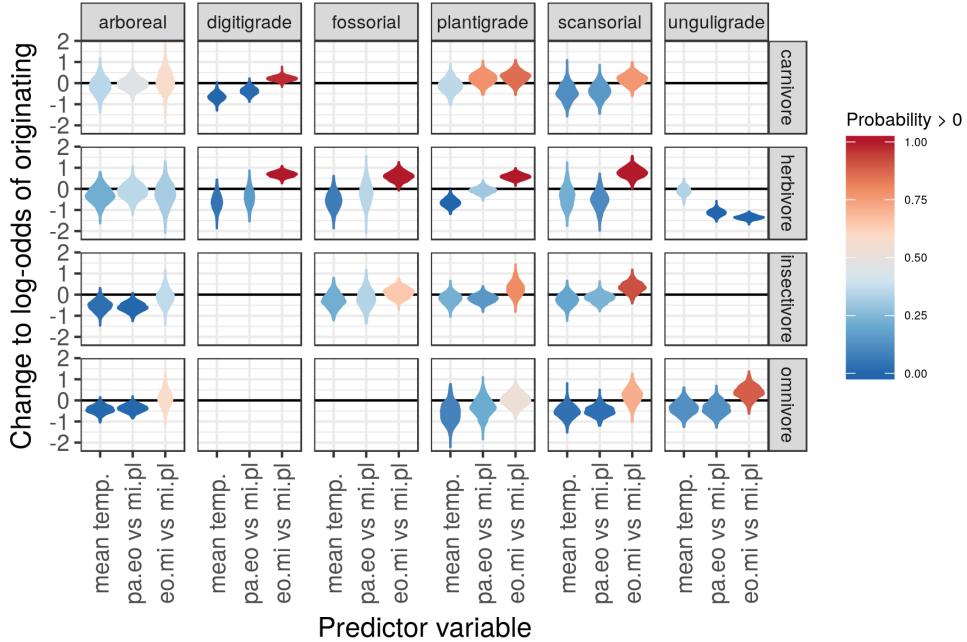


Figure 10: Estimated effects of the group-level covariates describing environmental context on log-odds of species origination. The violin densities that are plotted are based on 1000 samples from the approximate posterior. The color of the violin corresponds to the probability that the covariates effect 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.

- 592 The origination probabilities of the functional groups are not estimated to be correlated (Fig. 11).
 This result indicates that functional groups have independent origination histories for the Cenozoic.
 594 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. Additionally, if the
 596 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. Finally, it is
 598 important to remember that these correlation estimates is based on origination probability and not
 origination rate or diversity.
- 600 The survival probability time-series vary greatly between each of the functional groups with each
 exhibiting unique patterns (Fig. 12). Interestingly, unlike origination probability (Fig. 7), survival
 602 probability is 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

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 greater than 0.50 species can be expected to survive to the next time unit. Finally, when survival probability is approximately 0.50 then survival and extinction are equally likely. For 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 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 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 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, and plantigrade omnivores though all three of these groups have sudden drops in survival

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

616 probability by the Hemphillian 10.3 Mya.

Arboreal herbivores are the only functional group for which survival probability is approximately
 618 above 0.50 for the entire Cenozoic (Fig. 12). This result indicates that when an arboreal herbivore
 species is present it is expected to survive from one time unit to the next. However, it is important
 620 to note that arboreal herbivores are estimated to have an origination probability below 0.50 for
 most of the Cenozoic. Together, these results mean that arboreal herbivore species are rare but are
 622 expected to survive from one time point to the next.

A common feature of multiple functional group's survival probability time-series is a peak in
 624 survival during the Neogene (Fig. 12). In most cases, these peaks are estimated with little
 uncertainty which indicates how apparent this event is. Digitigrade carnivores, digitigrade
 626 herbivores, plantigrade herbivores, scansorial insectivores, unculigrade herbivores, and unculigrade
 omnivores all peak in survival probability by the Monrocreaekian 26.3Mya. This peak in survival

means that species of these functional groups which are unlikely to go extinct at this point, 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 another (Table 5).

The effect of order on survival probability has much lower variance (Fig. 13) than the effect of order on origination probability (Fig. 8). Primates, Multituberculata, Eulipotyphla, Dermoptera, Creodonta, Condylarthra, Carnivora, and Artiodactyla are estimated to have a lower than average 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 survival probability of all orders. The orders expected to have greater than average survival probability are Rodentia, Lagomorpha, and Didelphimorphia.

Species mass is estimated to have no relationship, or at best a weakly positive relationship, with survival probability (Fig. 14). This result means that differences in mass do not lead to differences in species survival. This result is consistent with previous studies of North American species and genus survival dynamics CITATION SMITS TOMIYA, and implies that other ecological factors have greater importance on survival than mass alone. GET PROBABILITY ESTIMATE

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 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, 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 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 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% probability of having lower survival probability during the Paleocene-Eocene than the

Miocene-Pleistocene. For digitgrade herbivores, and unguligrade omnivores, the Eocene-Miocene phase have an approximately 90% probability of having greater survival probability than during the Miocene-Pleistocene phase. In contrast, unguligrade herbivores are estimated to have lower 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 probability during the Paleocene-Eocene than the Eocene-Miocene.

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

None of the time-series of functional group survival probability are estimated to be either positively or negatively correlated (Fig. 16); this mirrors the estimated correlations between functional group

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

origination probabilities (Fig. 11). This result indicates that functional groups probably have
 668 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
 670 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
 672 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
 674 extinction rate or diversity.

Analysis of diversity

676 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

678 which there is a marked increase till approximately the Barstovian 15Mya after which it decreases
 680 slightly till it is equal to the overall mean diversity of the Cenozoic (Fig. 18). Per-unit standing
 680 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,
 682 Hemingfordian, Barsotvian, and Clarendonian while diversity is lower than average during the
 Duchesnean, Chadronian, Orellan, Whitneyan, Geringian, Monroecreekian, and Harrisonian. The
 684 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
 686 estimated to have any temporary dips in diversification for that entire approximately 15 million
 year period.

Table 14: Probability that diversity during one NALMA N_t^{stand} is greater than average standing diversity for the whole Cenozoic $\overline{N^{\text{stand}}}$. 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	$P(N_t^{\text{stand}} > \overline{N^{\text{stand}}})$
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

688 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

690 diversity history, there are some broad similarities as is similar to the estimates origination and
survival probability (Fig. 7, 12).

692 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).

694 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

696 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

698 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

700 proposed by Smits (2015).

The diversity of plantigrade insectivores, scansorial insectivores, and scansorial omnivores are
702 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
704 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
706 the Cenozoic till approximately Orelan and Whitneyan, after which diversity drops and remaining
below average diversity for the rest of the Cenozoic.

708 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
710 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
712 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
714 Barstovian 16.3 Mya, after which this group declines in diversity.

Plantigrade carnivores, scansorial herbivores and unguligrade omnivores are estimated to maintain
716 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
718 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
720 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
722 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,
724 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
726 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
728 after the Barstovian approximately 16.3 Mya.

Scansorial carnivores and plantigrade herbivores have below average standing diversity from the
730 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
732 (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
734 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.

736 Digitigrade carnivores, plantigrade herbivores, and unguligrade herbivores functional groups
maintain relatively high standing diversity through out the entire Cenozoic though each exhibits
738 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
740 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
742 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.
744 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
746 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
748 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.

750 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
752 decrease in the standing diversity of digitigrade herbivores: from the start of the study period will the Wasatchian 55.4 Mya, and a sudden decrease at the Clarendonian 13.6 Mya. Beyond these two
754 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
756 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
758 relative log-mean of 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
760 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,
762 plantigrade herbivores, and scansorial omnivores are their functional groups maintained as relatively constant proportions of the species pool (Fig. 20).

764 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
766 which it remains a substantial part of the species pool. Fossilorial herbivores, and fossilorial insectivores increase in relative diversity at the Orellan and Whitneyan approximately 33 Mya,
768 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
770 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,

772 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
774 other functional groups, unguligrade herbivores slowly increase in their relative diversity for the
entire Cenozoic.

776 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),
778 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
780 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
782 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
784 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,
786 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
788 diversity of the species pool.

Discussion

790 Both the composition of a species pool and its environmental context change over time, though not
necessarily at the same rate or concurrently. Local communities, whose species are drawn from the
792 regional species pool, have “roles” in their communities defined by their interactions with a host of
biotic and abiotic interactors (i.e. a species’ niche). For higher level ecological characterizations like
794 ecotypes and guilds, these roles are broad and not defined by specific interactions but by the genre
of interactions species within that grouping participate in. The diversity of species within an
796 functional group can be stable over millions of years despite constant species turnover (Jernvall and
Fortelius, 2004; Slater, 2015; Van Valkenburgh, 1999). This implies that the size and scope of the

798 role of an ecotype or guild in local communities, and the regional species pool as a whole, is
800 preserved even as the individual interactors change. This also implies that the structure of regional
800 species pools can be constant over time despite a constantly changing set of “players.” There is
even evidence that functional groups are at least partially self-organizing and truly emergent
802 (Scheffer and van Nes, 2006).

The goal of this study has been to understand how macroevolutionary processes are affected by
804 species ecology as well as environmental context, and how these interactions shape macroecological
patterns such as regional functional diversity that we observe in the fossil record and the present.

806 The results of the analysis presented here add considerable nuance to our understanding of mammal
macroevolution and macroecology over the Cenozoic.

808 This analysis reveals how functional groups respond differently to environmental factors through
changes to origination probability but not survival probability.

810 I focus on functional diversity because of its importance to macroecological patterns McGill
CITATION. By analyzing mammals species in the context of their functional ecologies, the
812 complexity of species response to environmental change can be better elucidated. Additionally, by
analyzing all of them simultaneously these results are all directly comparable as they are estimated
814 relative to each other.

Over the entity of the studied period, each functional group demonstrates its own origination and
816 survival history with no evidence of any longterm cross-correlations. Of course, lack of correlation
over the Cenozoic does not preclude similarities in response to individual events; it is just that
818 these correlations are ephemeral and indicate that there is no one relationship between climate and
diversity.

820 Not always the same functional group associated. That's why breaks down over entire cenozoic.
individual events aren't series. can affect moments, but not time. sudden shifts vs long term
822 patterns. Respond sometimes, but not others; thus no correlation for Cenozoic; doesn't preclude
process association.

824 Instead, there are individual periods in time that are characterized by similar changes to absolute
825 or relative diversity. Additionally, it is not always the same functional groups that appear to
826 experience changes in abundance at these time points.

The environmental covariates are found to effect the origination probability of some functional
828 groups, but only effect the survival probability of relatively few groups.

Plant phases: biggest difference is higher origination probability in the Eocene-Miocene phase than
830 the Paleocene-Eocene phase (13 of 18 with $P \geq 0.85$). Lower origination probability in the
831 Paleocene-Eocene than the Miocene-Pleistocene (10 of 18 with $P \geq 0.85$). Higher origination in the
832 Eocene-Miocene than Miocene-Pleistocene (8 of 18 $P \geq 0.85$) exception that 1 of 18 $P \geq 0.85$ has lower.

There is no evidence that the estimate of global temperature used in this study is not estimated to
834 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.

836 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
838 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
840 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.

842 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
844 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
846 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
848 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
850 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
852 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
854 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
856 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
858 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.

860 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
862 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
864 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
866 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
868 descriptors of species’ environmental context than simple an estimate of global temperature a more
complete “picture” of the diversification process is inferred.

870 Mass affects observation and origination probability, but not survival probability.

There are three major time units during the Cenozoic important points in time stick out: the
872 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
874 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
876 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

878 the regional species pool at these three periods of time as well as their environmental context.

The Wasatchian

880 - peak in all arboreal, peak in digitigrade carnivores, expansion digitigrade herbivores after, peak
881 plantigrade carnivore, peak plantigrade herbivores, high plantigrade insectivores, high scansorial
882 carnivores

- Changes at 55: peak arboreal carnivore, low fossorial herbivore, expansion scansorial herbivores
884 after

Orellan and Whitneyan is lowest diversity, but is a moment of change in diversity. Marks the loss of
886 some, marks the expansion of others. This also marks a peak in survival for some groups. Are these
887 the groups that expand in the Neogene? Six functional groups are estimated to have peaks in
888 survival probability at these points. Eocene/Oligocene boundary

- loss/bottom out of all arboreal groups, dip unguiligrade herbivore, mark expansion of fossorial
890 groups + plantigrade omnivores, drop off of plantigrade insectivore, scansorial insectivore,
891 scansorial omnivore

892 - Changes at 33: increase digitigrade carnivores, digitigrade herbivores, fossorial herbivores, fossorial
893 insectivores, start of increase scansorial omnivores; decrease scansorial insectivores, loss arboreal
894 insectivore

The Barstovian Mid-Miocene Climatic Optimum

896 - peak unguiligrade herbivore, peak digitigrade carnivore, peak digitigrade herbivore, peak fossorial
897 insectivore

898 - Changes at 15: increase arboreal insectivore, plantigrade omnivores, decrease digitigrade
899 herbivores, loss unguiligrade omnivore, loss plantigrade insectivore.

900 Mammal species are short lived with average duration being only slightly more than one NALMA.
901 This short a duration means that observation probability is very high for most of the Cenozoic,
902 with it being greater than 0.50 for the entire Cenozoic while also being greater than 0.80 for most of

the Cenozoic. Time is associated with greater variation in observation probability than functional
904 group. Scansorial insectivores are estimated to have a substantially lower observation probability
than the other functional groups.

906 Conclusions

Is origination driven by ecological opportunity while survival is driven by differences in species-level
908 fitness?

These results add a considerable degree of nuance to the narrative of changes to North American
910 diversity being gradual. My results support the conclusions that functional diversity is shaped more
by changes to origination than extinction and that major changes to total diversification rate can
912 be attributed to increases in origination of only some ecotypes. There are a number of interesting
estimated ecotype diversity patterns. While arboreal ecotypes are diverse in the Paleogene, by the
914 Neogene all arboreal ecotypes dramatically decreased in diversity and became either rare or absent
from the regional species pool. The other ecotypes that decrease in diversity over the Cenozoic are
916 plantigrade and scansorial insectivores and scansorial omnivores. The only ecotypes that
demonstrate a sustained pattern of increasing diversity are digitigrade and unguligrade herbivores.
918 When the environmental covariates analyzed here are inferred to affect the diversification of an
ecotype, this effect is virtually always on origination and not survival. This analysis provides a
920 much more complete picture of North American mammal diversity and diversification, specifically
the dynamics of the ecotypic composition of that diversity. By increasing the complexity of analysis
922 while precisely translating research questions into a statistical model, the context of the results is
much better understood. Future studies of diversity and diversification should incorporate as much
924 information as possible into their analyses in order to better understand or at least contextualize
the complex processes underlying that diversity.

926 **Acknowledgements**

I would like to thank K. Angielczyk, M. Foote, P. D. Polly, R. Ree, and G. Slater for helpful
928 discussion and advice. This entire study would not have been possible without the Herculean
effort of the many contributors to the Paleobiology Database. In particular, I would like to thank J.
930 Alroy and M. Uhen for curating most of the mammal occurrences recorded in the PBDB. This is
Paleobiology Database publication XXX.

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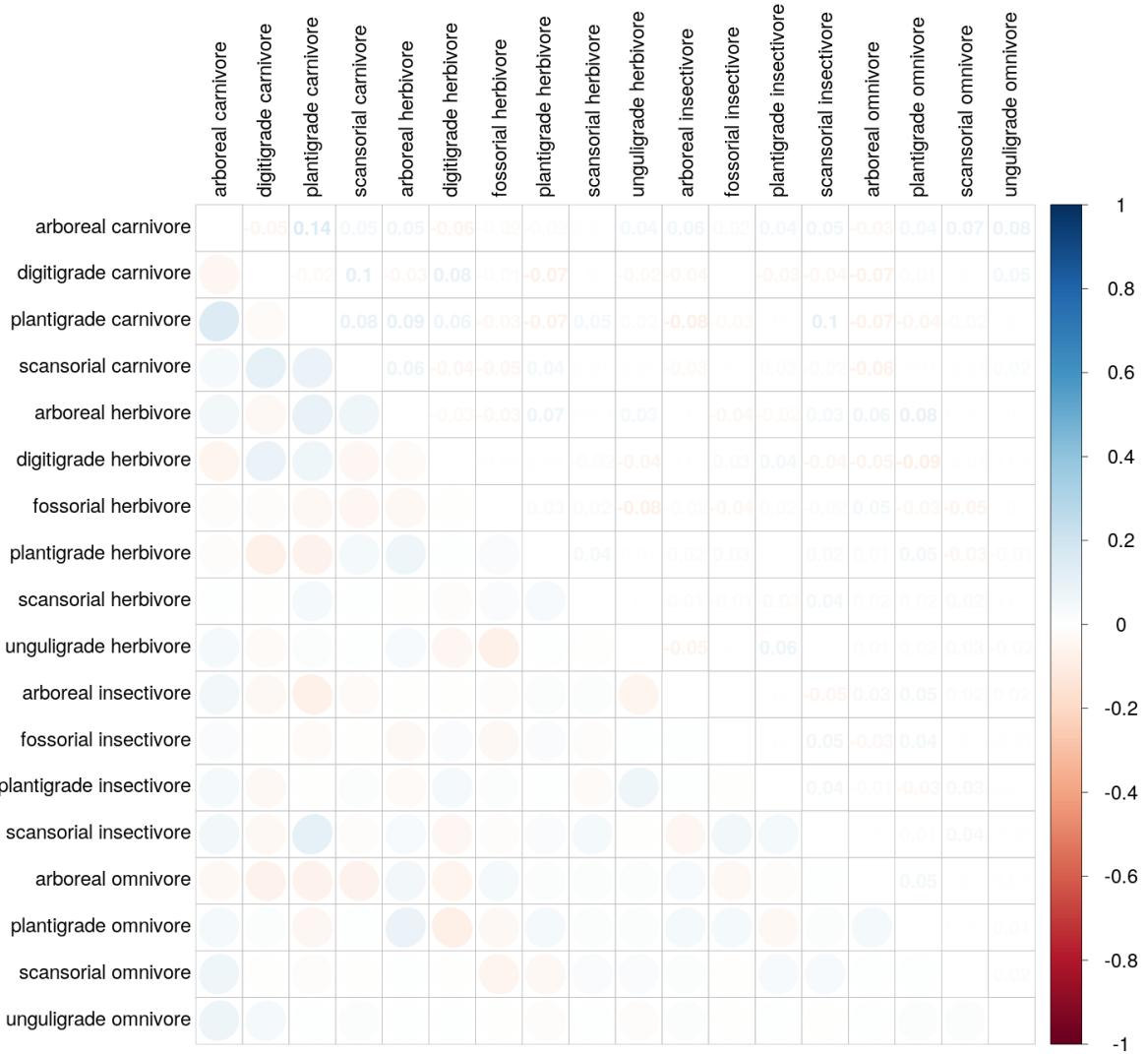


Figure 11: Posterior estimate of mean correlations in origination probability between the mammal functional groups. The lower triangle of the matrix is populated with ellipses corresponding to the level of correlation between the two functional groups, while the upper triangle of the matrix corresponds 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.

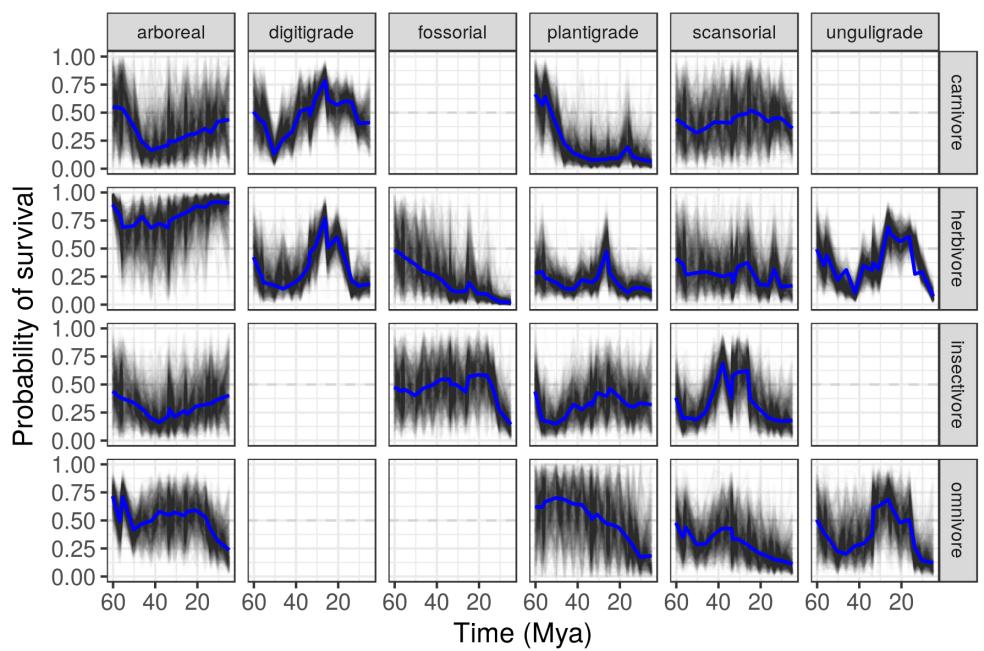


Figure 12: Probability of a species continued survival based on functional groups. Survival probability is graphed as 100 time-series drawn from the model's posterior estimates. A greater density of the posterior estimates indicates increased certainty. The blue line is the mean survival probability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

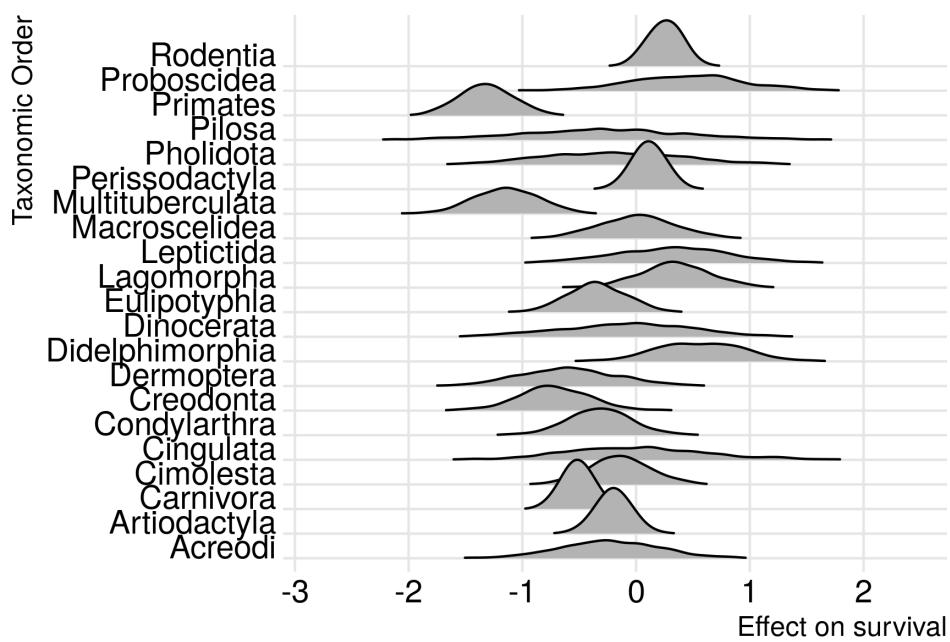


Figure 13: Differences in log-odds of survival based on mammal orders. Positive values correspond to greater log-odds survival than average, while negative values correspond to lower log-odds of survival.

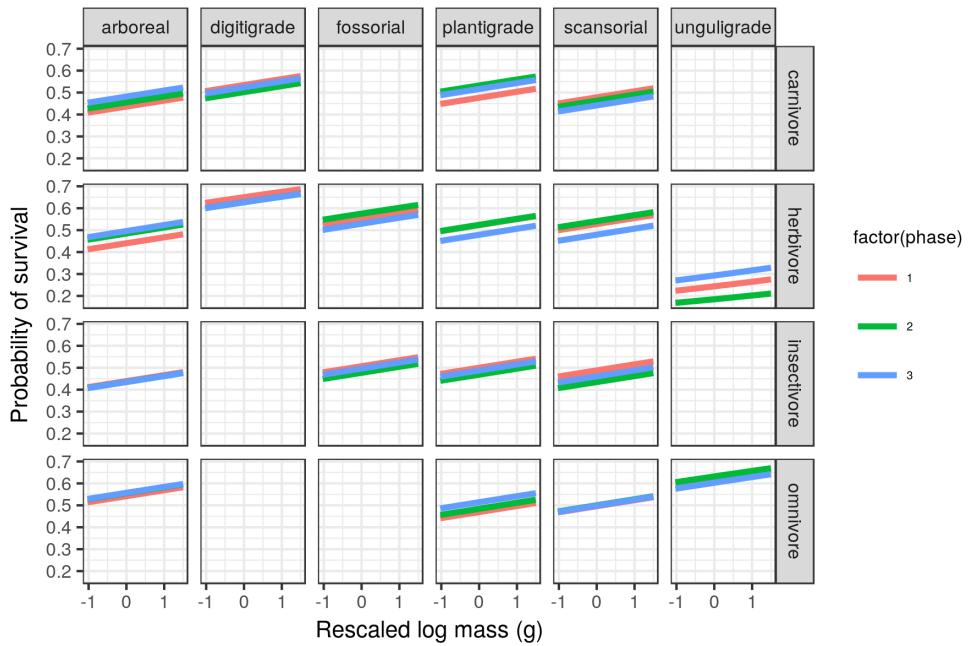


Figure 14: Mean estimates of the effect of species' mass on the probability of a species surviving, plotted for each of the three plant phases. While the effect of mass is considered constant over time, each plant phases corresponds to a different intercept of the relationship between mass and survival. 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.

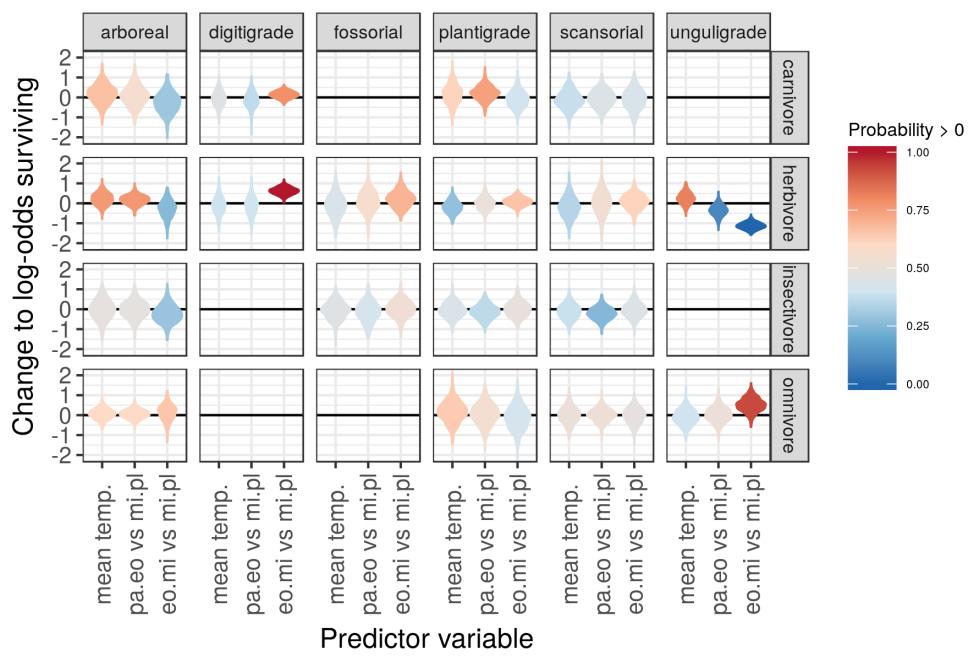


Figure 15: Estimated effects of the group-level covariates describing environmental context on log-odds of species survival. The violin densities that are plotted are based on 1000 samples from the approximate posterior. The color of the violin corresponds to the probability that the covariates effect 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.

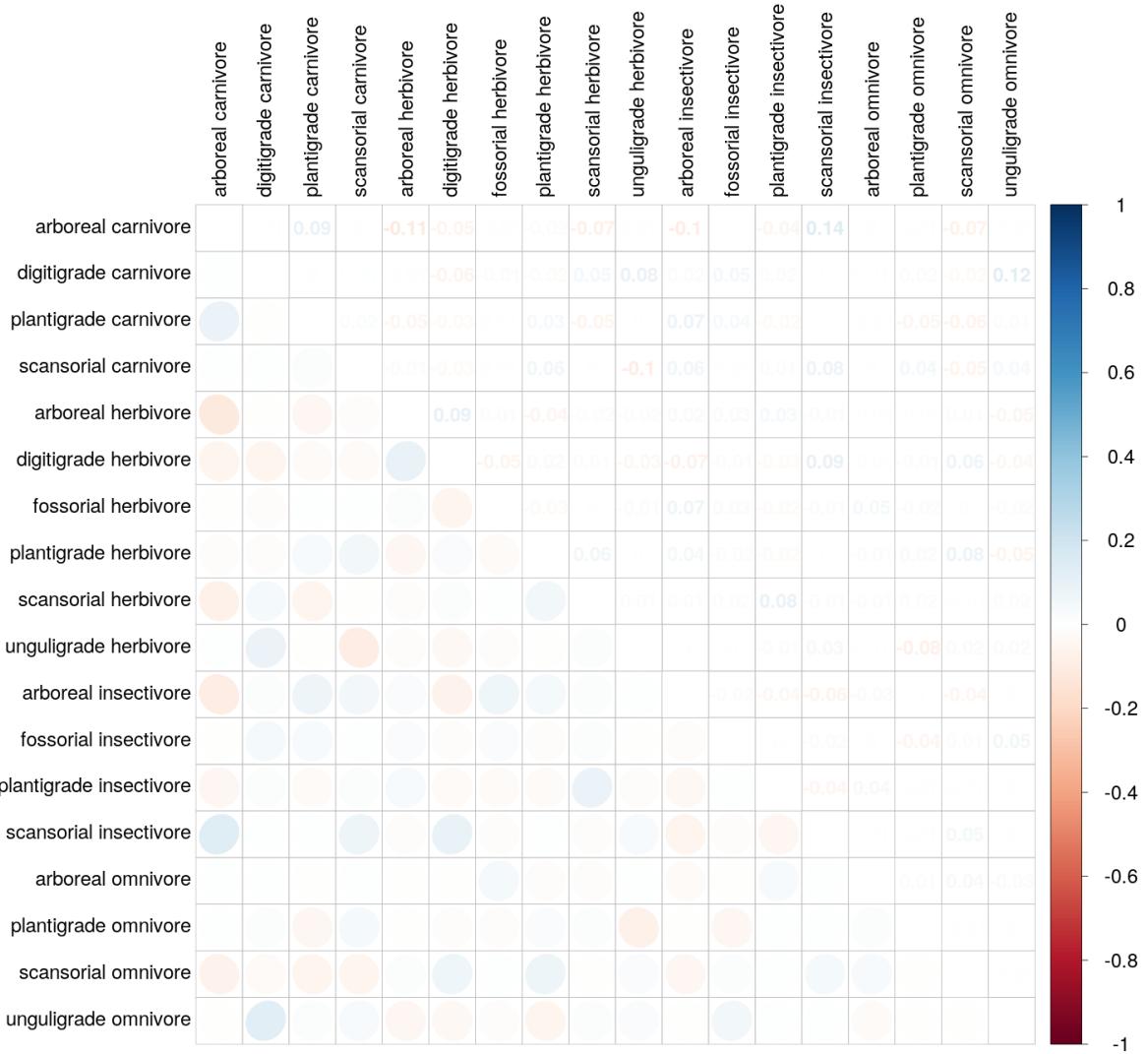


Figure 16: Posterior estimate of mean correlations in survival probability between the mammal functional groups. The lower triangle of the matrix is populated with ellipses corresponding to the level of correlation between the two functional groups, while the upper triangle of the matrix corresponds 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.

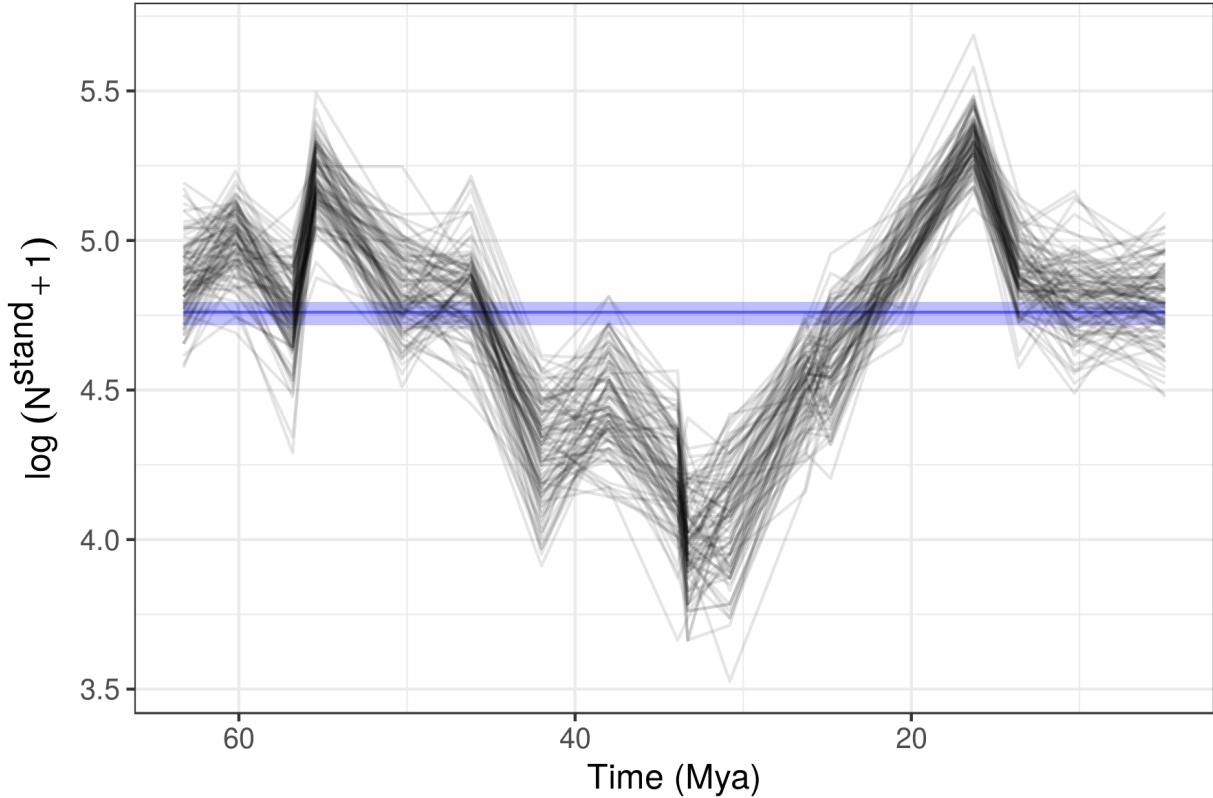


Figure 17: Log diversity

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.

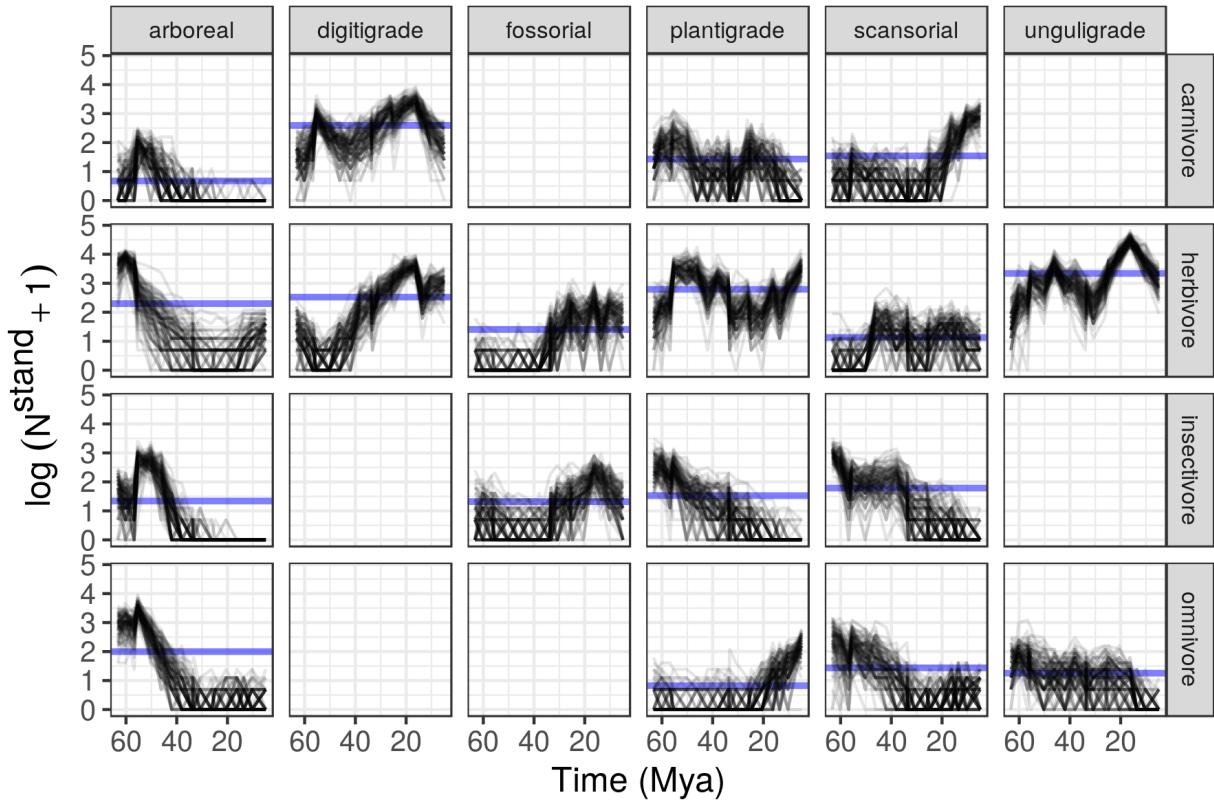


Figure 19: Estimated standing log-diversity of North American mammals by functional group for the Cenozoic. Diversity is represented as 100 posterior draws plotted over time. Density of time-series indicates congruence in estimates. The blue line corresponds to average standing diversity for that functional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

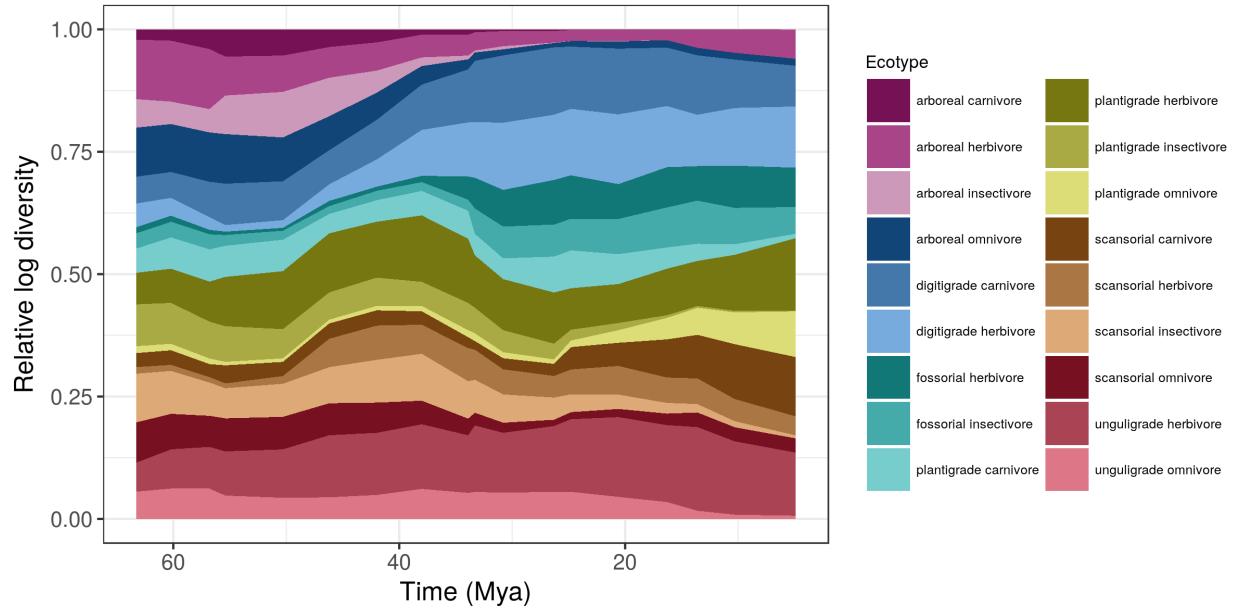


Figure 20: Relative diversity of the mammal functional groups for the Cenozoic. Relative diversity was calculated from the mean posterior estimate of standing diversity (Fig. 19) and is plotted here without uncertainty. These estimates are calculated from 100 posterior estimates of the true occurrence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