

Species occurrence as a function of emergent biological traits and environmental context

Peter D. Smits^{1,*}

1. University of Chicago, Chicago, Illinois 60637.

* Corresponding author; e-mail: psmits@uchicago.edu.

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All the world's a stage, And all the men and women merely players; They have their
2 exits and their entrances...

(Shakespeare, *As You Like It*, Act II, Scene VII)

4 **Abstract**

The set of species in a region changes over time as new species enter through speciation or
6 immigration and as species leave the system as they go extinct. How a regional species pool
changes over time is the product of many processes acting across multiple levels of organization.
8 Changes in to the functional composition of a regional species pool are changes that occur
across all local communities drawn from that species pool. While a species being present in a
10 local community is due to the availability of the necessary biotic-biotic or biotic-abiotic
interactions that enable coexistence, a species being present in a regional species pool just
12 requires the possibility that is at least one local community that has that set of necessary
interactions. The goal of this analysis is to understand when, and possibly for what reasons, are
14 mammal ecotypes 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
16 million years). This analysis frames mammal diversity in terms of both their means of
interacting with both the biotic and abiotic environment (i.e. ecotype) as well as their regional
18 and global environmental context. Using two hierarchical Bayesian hidden Markov models of
diversity, I find that changes to mammal diversity is driven more by the influx of new species
20 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
22 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
24 origination of some mammal ecotypes but, in almost all cases, does not affect the extinction of
mammal ecotypes. The clear and direct translation of research question to statistical model
26 allows for precise and better contextualized results. By taking into account more of the
complexity surrounding and contributing to species diversity and the diversification process, the
28 idiosyncrasies of ecotype diversification histories are more clearly contextualized than before.

Introduction

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

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

A key question when comparing communities or regional species pools based their functional composition is whether a functional group is enriched or depleted and why; what are the processes that led to a species pool having the functional composition it does (Blois and Hadly, 2009; Brown and Maurer, 1989; McGill et al., 2006; Smith et al., 2008; Weber et al., 2017). Comparisons of contemporaneous regional species pools only determines if a functional group is enriched or

56 depleted relative to other species pools; this does not reveal if that functional group is enriched or
depleted relative to its diversity in the regional species pool over time (Blois and Hadly, 2009).

58 While a species pool may be 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
60 to its historical diversity. 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
62 Modern, paleontological data provides a unique opportunity to observe and estimate the changes to
functional diversity and how species functional traits and environmental context can shape the
64 enrichment or depletion of functional groups within a regional species pool (Blois and Hadly, 2009;
Smith et al., 2008).

66 The paleontological record of North American mammals for the Cenozoic (66 million years ago to
present) provides one of the best opportunities for understanding how regional species pool
68 functional diversity. The North American mammal record is a relatively complete temporal
sequence for the entire Cenozoic which primarily, but not exclusively, based on fossil localities from
70 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 that
72 functional traits like the dietary/trophic category of species are easy to estimate (Eronen et al.,
2010; Polly et al., 2011, 2015).

74 **Background**

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

82 et al., 2004; Janis, 2008; Janis et al., 2000; Janis and Wilhelm, 1993; Jernvall and Fortelius, 2004;
83 Pires et al., 2015), within/between clade comparisons (Cantalapiedra et al., 2017; Fraser et al.,
84 2015; Quental and Marshall, 2013; Silvestro et al., 2015; Slater, 2015), and estimating the impact of
85 environmental process on diversity (Alroy et al., 2000; Badgley and Finarelli, 2013; Badgley et al.,
86 2017; Blois and Hadly, 2009; Eronen et al., 2015; Fraser et al., 2015; Janis, 1993; Janis and
87 Wilhelm, 1993). Each of these individual perspectives provide a limited perspective on the
88 macroevolutionary and macroecological processes shaping diversity and diversification. Integration
89 across perspectives is necessary for producing a holistic and internally consistent picture of how the
90 North American mammal species pool has changed through time. One of the goals of this study is
91 to present a framework for approaching hypotheses about diversity and diversification through
92 multiple lenses simultaneously so that our inferences are better constrained and the relative
importance of various functional traits and environmental factors may be better elucidated.

93 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 major or sudden
95 cross-functional group or cross-taxonomic turnover events for the entire Cenozoic (Alroy, 1996, 2009;
Alroy et al., 2000; Eronen et al., 2015; Janis, 1993). Instead of being concentrated in time, turnover
96 has been found to be distributed through time. It is then expected then that, for this analysis,
turnover events or periods of rapid diversification or depletion should not occur simultaneously for
97 all functional groups under study. Additionally, changes to mammal diversification seem to be
primarily driven by changes to origination rate and not to extinction (Alroy, 1996, 2009; Alroy
98 et al., 2000). An unresolved aspect of the general history of mammal diversification is whether that
diversity is limited or somehow self-regulating; namely, to what extent is mammal diversification
99 diversity-dependent (Alroy, 2009; Harmon and Harrison, 2015; Rabosky, 2013; Rabosky and
Hurlbert, 2015). Similarly, this question can also be asked of specific functional groups (Jernvall
100 and Fortelius, 2004; Quental and Marshall, 2013; Silvestro et al., 2015; Valkenburgh, 1999).

101 Within the overall narrative of mammal diversity, the histories of a selection of taxonomic and
functional groups are better understood. These groups have particularly good fossil records and/or
102 have been the focus of previous analyses.

¹¹⁰ The diversity history of ungulate herbivores has been characterized by more recently originating
¹¹¹ taxa having longer legs, higher crowned teeth, and a shift from graze-dominated to
¹¹² browse-dominated diets than their earlier originating counterparts (Cantalapiedra et al., 2017;
¹¹³ Fraser et al., 2015; Janis et al., 2004; Janis, 2008; Janis et al., 2000; Janis and Wilhelm, 1993); all of
¹¹⁴ which has all been attributed to some combination of tectonic activity driving environmental
¹¹⁵ change or environmental change itself (Badgley et al., 2017; Blois and Hadly, 2009; Eronen et al.,
¹¹⁶ 2015; Janis, 2008).

In contrast, the origination of modern cursorial carnivore forms was not until much later in the
¹¹⁸ Cenozoic; this is not to say that carnivore diversity only grew in the late Cenozoic, but that those
forms were late entrants. Instead, the diversity history of carnivores is reflective of
¹²⁰ density-dependence or some other form of self-regulation (Silvestro et al., 2015; Slater, 2015;
Valkenburgh, 1999). Specifically, it has been proposed that different canid clades have replaced each
¹²² other as the dominate members of that macroecological role within the species pool (Silvestro et al.,
2015; Valkenburgh, 1999). It is then expected that for this analysis the diversity of digitigrade and
¹²⁴ plantigrade carnivores (i.e. the “carnivore” guild of Valkenburgh (1999)) should be relatively
constant for the Cenozoic, but possibly more so the Neogene than the Paleogene.

¹²⁶ 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, arborela taxa were found to
¹²⁸ 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
¹³⁰ 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
¹³² 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
¹³⁴ 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
¹³⁶ 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

¹³⁸ absent from the species pool during the Neogene.

The climate history of the Cenozoic can be broadly described as a gradual cooling trend, with polar
¹⁴⁰ ice-caps forming in the Neogene (Cramer et al., 2011; Zachos et al., 2008, 2001). There are of course exceptions to this pattern such as the Eocene climatic optimum, the mid-Miocene climatic
¹⁴² optimum, and the sudden drop in temperature at the Eocene/Oligocene boundary (Zachos et al., 2008, 2001). In terms of the biotic environment of North America, the Cenozoic is additionally
¹⁴⁴ characterized by major transition from having closed, partially forested biomes being common in the Paleogene to the landscape being dominated by savannah and grasslands biomes by the
¹⁴⁶ Neogene (Blois and Hadly, 2009; Janis, 1993; Janis et al., 2000; Strömberg, 2005); though this transition was not itself coincident with the transition within herbivores from browse-dominated to
¹⁴⁸ graze-dominated diets (Strömberg, 2005). Additionally, the fundamental landscape of North America changed substantially over the Cenozoic with mountain uplift and other tectonic actives in
¹⁵⁰ Western North America (Badgley and Finarelli, 2013; Blois and Hadly, 2009; Eronen et al., 2015; Janis, 2008). This type of geological activity affects both local climates as well as continental
¹⁵² weather patterns while also mobilizing increased grit into the environment, something which may be responsible for increasing trend of hypodonty (high crowned teeth) among herbivores (Damuth
¹⁵⁴ and Janis, 2011; Jardine et al., 2012; Jernvall and Fortelius, 2002).

The effect of climate on mammal diversity and its accompanying diversification process has been
¹⁵⁶ the focus of considerable research with a slight consensus favoring diversification being more biologically-mediated than climate-mediated (Alroy, 1996; Alroy et al., 2000; Clyde and Gingerich,
¹⁵⁸ 1998; Figueirido et al., 2012). However, differences in temporal and geographic scale seem to underly the contrast between these two perspectives. For example when the mammal fossil record
¹⁶⁰ analyzed at small temporal and geographic scales a correlation between diversity and climate are observable (Clyde and Gingerich, 1998). However, when the record is analyzed at the scale of the
¹⁶² continent and most of the Cenozoic there is no correlation with diversity and climate (Alroy et al., 2000). This results, however, does not go against the idea that there may be short periods of
¹⁶⁴ correlation and that the correlation between diversity and climate can change or even reverse direction over time; this type result means that there is no single direction of correlation between

¹⁶⁶ diversity and climate (Figueirido et al., 2012).

In the case of a fluctuating correlation between diversity and climate it is hard to make the
¹⁶⁸ argument for an actual causal link between the two without modeling the underlying ecological
differences between species; after all, species respond differently based on their individual ecologies
¹⁷⁰ (Blois and Hadly, 2009). When analysis is based on diversity or taxonomy alone no mechanisms are
possible to infer. Taxonomy, like body size, stands in for many important species traits to the point
¹⁷² that mechanistic or process based inference is impossible. While emergent patterns might
correspond to taxonomic grouping, this itself is an emergent phenomenon. Instead, by framing
¹⁷⁴ hypotheses in terms of species traits and their environmental context, these emergent phenomenon
can be observed rather than assumed.

¹⁷⁶ **Foreground**

Fourth-corner modeling is an approach to explaining the patterns of either species abundance or
¹⁷⁸ presence/absence as a product of species traits, environmental factors, and the interaction between
traits and environment (Brown et al., 2014; Jamil et al., 2013; Pollock et al., 2012; Warton et al.,
¹⁸⁰ 2015); effectively uniting species distribution modeling (SDMs) with trait-based community
assembly (CATS, MaxEnt). In modern ecological studies, what is being modeled is species
¹⁸² occurrences at localities distributed across a region (Jamil et al., 2013; Pollock et al., 2012). In this
study, what is being modeled is the pattern of species occurrence over time for most of the
¹⁸⁴ Cenozoic in North America (Fig. 1). By incorporating an additional dimension (time) to the
fourth-corner framework we can gain better inference of how an instantaneous species pool (i.e. the
¹⁸⁶ Modern) is assembled over time. These two approaches, modern and paleontological, are different
views of the same three-dimensional pattern: species at localities over time. The temporal
¹⁸⁸ limitations of modern ecological studies and difficulties with uneven spatial occurrences of fossils in
paleontological studies means that these approaches are complimentary but reveal different patterns
¹⁹⁰ of how species are distributed in time and space.

My approach to delimiting and assigning mammal functional groups is inspired on the ecocube

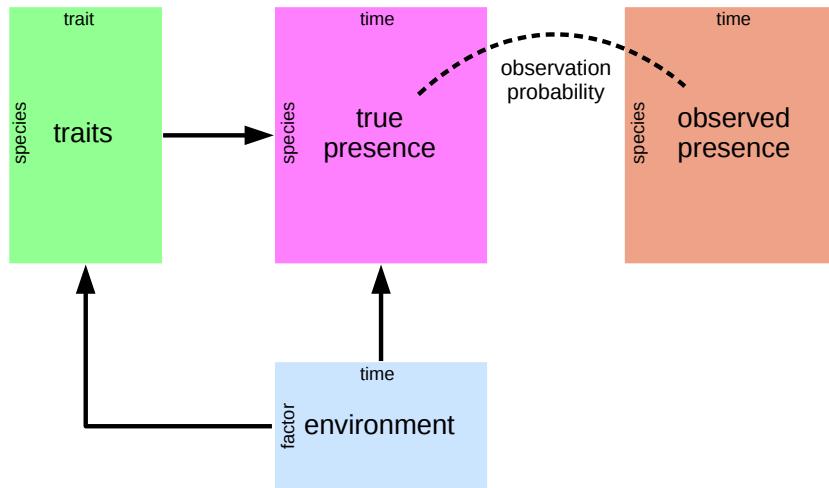


Figure 1: Conceptual diagram of the paleontological fourth corner problem. The observed presence matrix (orange) is the empirical presence/absence pattern for all species for all time points; this matrix is an incomplete observation of the “true” presence/absence pattern (purple). The estimated true presence matrix is modeled as a function of both environmental factors over time (blue) and multiple species traits (green). Additionally, the effect of environmental factors on 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).

192 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;
 194 Novack-Gottshall, 2007; Villéger et al., 2011). Unique combinations of traits represent ecotypes,
 which are equivalent to functional groups defined by functional traits instead of a holistic
 196 understanding how a taxon interacts with its environment. In this study, the two functional traits
 used to define a species’ ecotype are dietary (e.g. herbivore, carnivore, etc.) and locomotor category
 198 (e.g. arboreal, unguligrade, etc.). Species body mass was also included as a species trait in this
 analysis, but not as a functional trait for defining ecotypes; instead, its inclusion is principally to
 200 control for differences in species dynamics that are driven by mass and not ecotype.

The environmental factors included in this study are estimates of global temperature and the
 202 changing floral groups present in North America across the Cenozoic (Cramer et al., 2011; Graham,

2011). These covariates were chosen because they provide high level characterizations of the
204 environmental context of the entire North American regional species pool for most of the Cenozoic.
Importantly, the effects of a species ecotype on diversity are themselves modeled as functions of
206 environmental factors (Fig. 1) allowing for inference as to how a species ecology can mediate
selective pressures due to its environmental context.

208 All observations, paleontological or modern, are made with uncertainty. With presence/absence
data this uncertainty comes from now knowing if an absence is a “true” absence or just a failure to
210 observe (Foote, 2001; Foote and Sepkoski, 1999; Lloyd et al., 2011; Royle and Dorazio, 2008; Royle
et al., 2005; Wang and Marshall, 2016). For paleontological data, the incomplete preservation of
212 whatever species were present into fossil form combined with incomplete sampling of what
organisms were actually fossilized means that the true times of origination or extinction may not be
214 observed (Foote, 2001; Foote and Sepkoski, 1999; Wang et al., 2016; Wang and Marshall, 2016).
The model(s) I propose below represent an attempt to translate the verbal/visual model described
216 here (Fig. 1) into a statistical model for estimating the relative diversity of mammal ecotypes over
time and how those ecotypes respond to changes to environmental context while taking into
218 account the fundamental incompleteness of the fossil record.

220 Ultimately, the goals of this analysis are to understand when unique ecotypes enriched or
depleted in the North American mammal regional species pool and how these changes in ecotypic
diversity are related to changes in species’ environmental context. In the analyses done here, many
222 covariates which describe both a species’ macroecology and its environmental context are considered.
In order to analyze this complex and highly structured data set, I developed a hierachal Bayesian
224 model combing the forth-corner modeling approach with a model of an observation-occurrence or
observation-origination-extinction process. The complexity and nuance inherent in questions that
226 are focus of this study, it is possible to consider and test a large number of possible hypotheses. The
hierarchical Bayesian modeling approach used here is appropriate for mitigating complications
228 arising from both this complexity and the plethora of testable hypotheses (e.g. multiple
comparisons, garden of forking paths) (Gelman et al., 2013, 2012; Gelman and Loken, 2014).

²³⁰ **Materials and Methods**

Taxon occurrences and species-level information

- ²³² All fossil occurrence information used in this analysis was downloaded from the Paleobiology Database (PBDB). The initial download restricted all occurrences to all Mammalia observed in ²³⁴ North America between the Maastrichtian (72-66 Mya) and Gelasian (2.58-1.8 Mya) stages (Cohen et al., 2015). Occurrences were then further limited to those occurring between 64 and 2 million ²³⁶ years ago (Mya); this age restriction was to insure that observation time series lines up with the temperature time series (Cramer et al., 2011). Taxonomic, stratigraphic, and ecological metadata ²³⁸ for each occurrence and species was also 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 ²⁴⁰ datafile used as a part of this study, along with all code for filtering and manipulating this download is available at <http://github.com/psmits/copings>.
- ²⁴² After being downloaded, the raw occurrence data was then sorted, cleaned, and manipulated programmatically before analysis. Many species taxonomic assignments as present in the raw ²⁴⁴ PBDB data were updated for accuracy and consistency. For example, species classified in the order Artiodactyla were reclassified as Cetartiodactyla. These re-assignments follow Smits (2015) which ²⁴⁶ were based on taxonomies present in the Encyclopedia of Life (<http://eol.org>) and Janis et al. (2008, 1998). All taxa who's life habit was classified as either volant (i.e. Chiroptera) or aquatic (e.g. ²⁴⁸ Cetacea) were excluded from this analysis because of their lack of direct applicability to the study of terrestrial species pools.
- ²⁵⁰ Species ecotype is defined here as the interaction between locomotor category and diet categories, the goal of which is to classify species based on the manner with which they interact with their ²⁵² environment. Most mammal species records in the PBDB have life habit (i.e. locomotor category) and dietary category assignments. In order to simplify interpretation, analysis, and per ecotype ²⁵⁴ sample size these classifications were coarsened in a similar manner to (Smits, 2015) following Table 1. Additionally for this study, the life history category was further broken up to better reflect the

256 diversity of mammal locomotor modes. Ground dwelling species locomotor categories were
 reassigned based on their ankle posture associated with their taxonomic group as described in Table
 258 2 (Carrano, 1999). Ankle posture was assumed uniform for all species within a taxonomic group
 except for those species assigned a non-ground dwelling locomotor category by the PBDB. All
 260 species for which it was possible to assign a locomotor category had one assigned, including species
 for which post-crana are unknown but for which a taxonomic grouping is known. Ground dwelling
 262 species which were unable to be reassigned based on posture were excluded from analysis. Finally,
 ecotype categories with less than 10 total species of that combination were excluded, yielding a
 264 total of 18 observed ecotypes out of a possible 24.

Table 1: Species trait assignments in this study are a coarser version of the information available in the PBDB. Information was coarsened to improve per category sample size and uniformity and followed this table.

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 the nestedness of families in orders. As such, do not infer higher-order structure from this table.

Order	Family	Stance
	Ailuridae	plantigrade
	Allomyidae	plantigrade
	Amphicyonidae	plantigrade
	Amphilemuridae	plantigrade
	Anthracotheriidae	digitigrade
	Antilocapridae	unguligrade

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Table 2 – continued from previous page

Order	Family	Stance
	Apheliscidae	plantigrade
	Aplodontidae	plantigrade
	Apternodontidae	scansorial
	Arctocyonidae	unguligrade
	Barbourofelidae	digitigrade
	Barylambdidae	plantigrade
	Bovidae	unguligrade
	Camelidae	unguligrade
	Canidae	digitigrade
	Cervidae	unguligrade
	Cimolodontidae	scansorial
	Coryphodontidae	plantigrade
	Cricetidae	plantigrade
	Cylindrodontidae	plantigrade
	Cyriacotheriidae	plantigrade
	Dichobunidae	unguligrade
Dinocerata		unguligrade
	Dipodidae	digitigrade
	Elephantidae	digitigrade
	Entelodontidae	unguligrade
	Eomyidae	plantigrade
	Erethizontidae	plantigrade
	Erinaceidae	plantigrade
	Esthonychidae	plantigrade
	Eutypomyidae	plantigrade

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Table 2 – continued from previous page

Order	Family	Stance
	Felidae	digitigrade
	Florentiamyidae	plantigrade
	Gelocidae	unguligrade
	Geolabididae	plantigrade
	Glyptodontidae	plantigrade
	Gomphotheriidae	unguligrade
	Hapalodectidae	plantigrade
	Heteromyidae	digitigrade
	Hyaenidae	digitigrade
	Hyaenodontidae	digitigrade
	Hypertragulidae	unguligrade
	Ischyromyidae	plantigrade
	Jimomyidae	plantigrade
Lagomorpha		digitigrade
	Leptictidae	plantigrade
	Leptochoeridae	unguligrade
	Leptomerycidae	unguligrade
	Mammutidae	unguligrade
	Megalonychidae	plantigrade
	Megatheriidae	plantigrade
	Mephitidae	plantigrade
	Merycoidodontidae	digitigrade
Mesonychia		unguligrade
	Mesonychidae	digitigrade
	Micropternodontidae	plantigrade

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Table 2 – continued from previous page

Order	Family	Stance
	Mixodectidae	plantigrade
	Moschidae	unguligrade
	Muridae	plantigrade
	Mustelidae	plantigrade
	Mylagaulidae	fossorial
	Mylodontidae	plantigrade
	Nimravidae	digitigrade
	Nothrotheriidae	plantigrade
Notoungulata		unguligrade
	Oromerycidae	unguligrade
	Oxyaenidae	digitigrade
	Palaeomerycidae	unguligrade
	Palaeoryctidae	plantigrade
	Pampatheriidae	plantigrade
	Pantolambdidae	plantigrade
	Peritychidae	digitigrade
Perissodactyla		unguligrade
	Phenacodontidae	unguligrade
Primates		plantigrade
	Procyonidae	plantigrade
	Proscalopidae	plantigrade
	Protoceratidae	unguligrade
	Reithroparamyidae	plantigrade
	Sciuravidae	plantigrade
	Sciuridae	plantigrade

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Table 2 – continued from previous page

Order	Family	Stance
	Simimyidae	plantigrade
	Soricidae	plantigrade
	Suidae	digitigrade
	Talpidae	fossorial
	Tayassuidae	unguligrade
	Tenrecidae	plantigrade
	Titanoideidae	plantigrade
	Ursidae	plantigrade
	Viverravidae	plantigrade
	Zapodidae	plantigrade

²⁶⁶ Estimates of species mass used as a covariate in this study were sourced from multiple databases and papers, especially those focusing on similar macroevolutionary or macrecological questions
²⁶⁸ (Brook and Bowman, 2004; Freudenthal and Martín-Suárez, 2013; McKenna, 2011; Raia et al., 2012; Smith et al., 2004; Tomiya, 2013); this is similar to what was done in Smits (2015). When species
²⁷⁰ mass was not available, proxy measures were used and then transformed into estimates of mass. For example, given a measurement of a mammal tooth size, it is possible and routine to estimate its
²⁷² mass given some regression equation. 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).
²⁷⁴ Mass was log-transformed and then mean-centered and rescaled by dividing by two-times its standard deviation; this insures that the magnitude of effects for both continuous and discrete
²⁷⁶ covariates are directly comparable (Gelman, 2008; Gelman and Hill, 2007).

All fossil occurrences from 64 to 2 million years long (Mya) were binned into 31 2 million year (My)
²⁷⁸ bins. This temporal length was chosen because it is approximately the resolution of the North

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)

American mammal fossil record (Alroy, 1996, 2009; Alroy et al., 2000; Marcot, 2014).

280 Environmental and temporal covariates

The environmental covariates used in this study are collectively referred to as group-level covariates
 282 because they predict the response of a “group” of individual-level observations (i.e. species
 occurrences of an ecotype). Additionally, these covariates are defined for temporal bins and not the
 284 species themselves; as such they predict the parts of each species occurrence history. The
 group-level covariates in this study are two global temperature estimates and the Cenozoic “plant
 286 phases” defined by Graham (2011). 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
 288 temperature estimates are preferable to 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
 290 temperature with ice sheet volume and depth/stratification changes. The former is particularly
 important to this analysis as the current polar ice-caps appeared and grew over the Cenozoic.
 292 These properties make Mg/Ca based temperature estimates preferable for macroevolutionary and

Table 4: Definitions of the start and stop times of the three plant phases used this study as defined by Graham (2011).

Plant phase	Phase number	Start	Stop
Paleocene-Eocene	1	66	50
Eocene-Miocene	2	50	16
Miocene-Pleistocene	3	16	2

macroecological studies (Ezard et al., 2016). Two aspects of the Mg/Ca-based temperature curve
 294 were included in this analysis: mean and range. Both were calculated as the mean of all respective
 estimates for each 2 My temporal bins. Both mean and range were then rescaled by subtracting the
 296 mean and then dividing by twice the standard deviation.

The second set of environmental factors included in this study are the Cenozoic plant phases
 298 defined in Graham (2011). Graham’s plant phases are holistic descriptors of the taxonomic
 composition of 12 ecosystem types, which plants are present at a given time, and the relative
 300 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
 302 only three of these intervals take place during the time frame being analyzed. Graham’s plant
 phases was included as a series of “dummy variables” encoding the three phases included in this
 304 analysis (Gelman and Hill, 2007); this means that the first phase is synonymous with the intercept
 and subsequent phases are defined by their differences from the first phase. The temporal
 306 boundaries of these plant phases are defined in Table 4.

Modelling species occurrence

308 Two different models were used in this study: a pure-presence model and a birth-death model. Both
 models at their core are a hidden Markov model where the latent process has an absorbing state
 310 (Allen, 2011). The difference between these two models is if the probabilities of a species originating
 or surviving are considered equal or different (Table 5). Something that is important to realize is
 312 that 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 originated yet, extant, and extinct. The last of these

		State at $t + 1$		
		0_{never}	1	$0_{extinct}$
State at t	0_{never}	$1 - \theta$	θ	0
	1	0	θ	$1 - \theta$
	$0_{extinct}$	0	0	1

(a) Pure-presence

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

(b) Birth-death

Table 5: Transition matrices for the pure-presence (5a) and birth-death (5b) models. Both of these models share the core machinery of discrete-time birth-death processes but make distinct assumptions about the equality of originating and surviving (Eq. 2, and 3). Note also 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).

Table 6: Parameters associated with the observation process part of the hidden Markov model.

Parameter	dimensions	explanation
y	$N \times T$	observed species presence/absence
z	$N \times T$	“true” species presence/absence
p	T	probability of observing a species that is present at time t
m	N	species log mass, rescaled
α_0	1	average log-odds of p
α_1	1	change in average log-odds of p per change mass
r	T	difference from α_0 associated with time t
σ	1	standard deviation of r

³¹⁴ is the absorbing state, as once a species has gone extinct it cannot re-originate (Allen, 2011); this is made obvious in the transition matrices as the probability of an extinct species changing states is 0

³¹⁶ (Table 5). See below for parameter explanations (Tables 6, 7, and 8).

Observation process

³¹⁸ The type of hidden Markov model used in this study has three characteristic probabilities: probability p of observing a species given that it is present, probability ϕ of a species surviving from ³²⁰ one time to another, and probability π of a species first appearing (Royle and Dorazio, 2008). In this formulation, the probability of a species going extinct is $1 - \pi$. For the pure-presence model ³²² $\phi = \pi$, while for the birth-death model $\phi \neq \pi$.

The probability of observing a species that is present p is modeled as a logistic regression was a ³²⁴ time-varying intercept and species mass as a covariate. The effect of species mass on p was assumed

Table 7: Parameters for the model of presence in the pure-presence model

Parameter	dimensions	explanation
z	$N \times T$	“true” species presence/absence
θ	$N \times T - 1$	probability of $z = 1$
a	$T - 1 \times D$	ecotype-varying intercept; mean value of log-odds of θ
m	N	species log mass, rescaled
b_1	1	effect of species mass on log-odds of θ
b_2	1	effect of species mass, squared, on log-odds of θ
U	$T \times D$	matrix of group-level covariates
γ	$U \times D$	matrix of group-level regression coefficients
Σ	$D \times D$	covariance matrix of a
Ω	$D \times D$	correlation matrix of a
τ	D	vector of standard deviations for each ecotype a_d

linear and constant over time and given a prior reflecting a possible positive relationship; these
326 assumptions are reflected in the structure of the model Equation 1, presented here:

$$\begin{aligned} y_{i,t} &\sim \text{Bernoulli}(p_{i,t} z_{i,t}) \\ p_{i,t} &= \text{logit}^{-1}(\alpha_0 + \alpha_1 m_i + r_t) \\ r_t &\sim \mathcal{N}(0, \sigma). \end{aligned} \tag{1}$$

The parameters associated with Equation 1 are described in Table 6.

328 **Pure-presence process**

For the pure-presence model there is only a single probability dealing with the presence of a species
330 θ (Table 5a). This probability was modeled as multi-level logistic regression with both species-level
and group-level covariates (Gelman et al., 2013; Gelman and Hill, 2007). The parameters associated
332 with pure-presence model are presented in Table 7 and the full sampling statement in Equation 2.

The species-level of the model (Eq. 2) is a logistic regression where the intercept varies by ecotype.
334 Additionally, species mass was included as a covariate associated with two regression coefficients
allowing a quadratic relationship with log-odds of occurrence. This assumption is based on the
336 known distribution of mammal body masses where species with intermediate mass values are more

common than either small or large bodied species. These assumptions are also reflected in the
 338 choice of priors for these regression coefficients.

The values of each ecotype's intercept are themselves modeled as regressions using the group-level
 340 covariates associated with environmental context. Each of these regressions has an associated
 variance of possible values of each ecotype's intercept (Gelman and Hill, 2007). In addition, the
 342 covariances between ecotype intercepts, given this group-level regression, are modeled (Gelman and
 Hill, 2007).

344 All parameters not modeled elsewhere were given weakly informative priors (Gelman et al., 2013;
 McElreath, 2016; Stan Development Team, 2016). Weakly informative means that priors do not
 346 necessarily encode actual prior information but instead help regularize or weakly constrain posterior
 estimates. These priors have a concentrated probability density around and near zero; this has the
 348 effect of tempering our estimates and help prevent overfitting the model to the data (Gelman et al.,
 2013; McElreath, 2016; Stan Development Team, 2016). The general line of thinking behind this
 350 approach is that a result of 0 or “no effect” is more preferable to a wrong or extremely weak result.

$$\begin{aligned}
 y_{i,t} &\sim \text{Bernoulli}(p_{i,t} z_{i,t}) & \alpha_0 &\sim \mathcal{N}(0, 1) \\
 p_{i,t} &= \text{logit}^{-1}(\alpha_0 + \alpha_1 m_i + r_t) & \alpha_1 &\sim \mathcal{N}(1, 1) \\
 r_t &\sim \mathcal{N}(0, \sigma) & \sigma &\sim \mathcal{N}^+(1) \\
 z_{i,1} &\sim \text{Bernoulli}(\rho) & b_1 &\sim \mathcal{N}(0, 1) \\
 z_{i,t} &\sim \text{Bernoulli}(\theta_{i,t}) & b_2 &\sim \mathcal{N}(-1, 1) \\
 \theta_{i,t} &= \text{logit}^{-1}(a_{t,j[i]} + b_1 m_i + b_2 m_i^2) & \gamma &\sim \mathcal{N}(0, 1) \\
 a &\sim \text{MVN}(u\gamma, \Sigma) & \tau &\sim \mathcal{N}^+(1) \\
 \Sigma &= \text{diag}(\tau)\Omega\text{diag}(\tau) & \Omega &\sim \text{LKJ}(2)
 \end{aligned} \tag{2}$$

Birth-death process

- 352 In the birth-death version of the model, $\phi \neq \pi$ and so each of these probabilities are modeled
 separately but each is handled in a similar manner to how θ is modeled in the pure-presence model
 354 (Eq. 2, Table 5b). The parameters associated with the birth-death presence model are presented in
 Table 8 and the full sampling statement, including observation (Eq. 1), is described in Equation 3:

$$\begin{aligned}
 y_{i,t} &\sim \text{Bernoulli}(p_{i,t} z_{i,t}) & \Sigma^\phi &= \text{diag}(\tau^\phi) \Omega^\phi \text{diag}(\tau^\phi) \\
 p_{i,t} &= \text{logit}^{-1}(\alpha_0 + \alpha_1 m_i + r_t) & \Sigma^\pi &= \text{diag}(\tau^\pi) \Omega^\pi \text{diag}(\tau^\pi) \\
 r_t &\sim \mathcal{N}(0, \sigma) & \rho &\sim U(0, 1) \\
 \alpha_0 &\sim \mathcal{N}(0, 1) & b_1^\phi &\sim \mathcal{N}(0, 1) \\
 \alpha_1 &\sim \mathcal{N}(1, 1) & b_1^\pi &\sim \mathcal{N}(0, 1) \\
 \sigma &\sim \mathcal{N}^+(1) & b_2^\phi &\sim \mathcal{N}(-1, 1) \\
 z_{i,1} &\sim \text{Bernoulli}(\phi_{i,1}) & b_2^\pi &\sim \mathcal{N}(-1, 1) \\
 z_{i,t} &\sim \text{Bernoulli} \left(z_{i,t-1} \pi_{i,t} + \sum_{x=1}^t (1 - z_{i,x}) \phi_{i,t} \right) & \gamma^\phi &\sim \mathcal{N}(0, 1) \\
 \phi_{i,t} &= \text{logit}^{-1}(a_{t,j[i]}^\phi + b_1^\phi m_i + b_2^\phi m_i^2) & \gamma^\pi &\sim \mathcal{N}(0, 1) \\
 \pi_{i,t} &= \text{logit}^{-1}(a_{t,j[i]}^\pi + b_1^\pi m_i + b_2^\pi m_i^2) & \tau^\phi &\sim \mathcal{N}^+(1) \\
 a^\phi &\sim \text{MVN}(U\gamma^\phi, \Sigma^\phi) & \tau^\pi &\sim \mathcal{N}^+(1) \\
 a^\pi &\sim \text{MVN}(U\gamma^\pi, \Sigma^\pi) & \Omega^\phi &\sim \text{LKJ}(2) \\
 && \Omega^\pi &\sim \text{LKJ}(2).
 \end{aligned} \tag{3}$$

- 356 Similar to the pure-presence model, both ϕ and π are modeled as logistic regressions with
 varying-intercept and one covariate associated with two parameters. The possible relationships
 358 between mass and both ϕ and π are reflected in the parameterization of the model and choice of
 priors (Eq. 3).
 360 The intercepts of ϕ and π both vary by species ecotype and those values are themselves the product
 of group-level regression using environmental factors as covariates (Eq. 3); this is identical to the

Table 8: Parameters for the model of presence in the pure-presence model

Parameter	dimensions	explanation
z	$N \times T$	“true” species presence/absence
ϕ	$N \times T$	probability of $z_{-,t} = 1 z_{-,t-1} = 0$; origination
π	$N \times T - 1$	probability of $z_{-,t} = 1 z_{-,t-1} = 1$; survival
a^ϕ	$T - 1 \times D$	ecotype-varying intercept; mean value of log-odds of θ
a^π	$T - 1 \times D$	ecotype-varying intercept; mean value of log-odds of θ
m	N	species log mass, rescaled
b_1^ϕ	1	effect of species mass on log-odds of ϕ
b_1^π	1	effect of species mass on log-odds of π
b_2^ϕ	1	effect of species mass, squared, on log-odds of ϕ
b_2^π	1	effect of species mass, squared, on log-odds of π
U	$T \times D$	matrix of group-level covariates
γ^ϕ	$U \times D$	matrix of group-level regression coefficients
γ^π	$U \times D$	matrix of group-level regression coefficients
Σ^ϕ	$D \times D$	covariance matrix of a^ϕ
Σ^π	$D \times D$	covariance matrix of a^π
Ω^ϕ	$D \times D$	correlation matrix of a^ϕ
Ω^π	$D \times D$	correlation matrix of a^π
τ^ϕ	D	vector of standard deviations for each ecotype a_d^ϕ
τ^π	D	vector of standard deviations for each ecotype a_d^π

³⁶² pure presence model (Eq. 2).

Posterior inference and model adequacy

³⁶⁴ Computer programs that implement joint posterior inference for the above models (Eqs. 2, 3) were
written in the probabilistic programming language Stan (Stan Development Team, 2016). The
³⁶⁶ models used here both feature latent discrete parameters in the large matrix z (Tables 6, 7, 8; Eqs.
1, 2, 3). All methods for posterior inference implemented in Stan are derivative based which causes
³⁶⁸ complications for actually implementing the above models because integers do not have derivatives.
Instead of implementing a latent discrete parameterization, the log posterior probabilities of all
³⁷⁰ possible states of the latent parameters z were calculated and summed (i.e. marginalized).

Species durations at minimum range-through from the FAD to the LAD, but the incompleteness of
³⁷² all observations means that the actual time of origination or extinction is unknown. The
marginalization approach used here means that the probabilities all possible histories for a species

374 are calculated, from the end members of the species having existed for the entire study interval and
 the species having only existed between the directly observed FAD and LAD to all possible
 376 intermediaries (Fig 2) (Stan Development Team, 2016). This process is identical, language-wise, to
 assuming range-through and then estimating the possibility of range extension due to incomplete
 378 sampling.

	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	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. The process of parameter marginalization described in the text

The combined size of the dataset and large number of parameters in both models (Eqs. 2, 3),
 380 specifically the total number of latent parameters that are the matrix z , means that stochastic
 approximate posterior inference is computationally very slow even using NUTS based HMC
 382 implemented. Instead, an approximate Bayesian approach was used: variational inference. A
 recently developed automatic variational inference algorithm called “automatic differentiation
 384 variational inference” (ADVI) is implemented in Stan and was used here (Kucukelbir et al., 2015;
 Stan Development Team, 2016). ADVI assumes that the posterior is Gaussian but still yields a true

386 Bayesian posterior; this assumption is similar to quadratic approximation of the likelihood function
commonly used in maximum likelihood based inference (McElreath, 2016). The principal limitation
388 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 bound to be positive (e.g.
390 standard deviation).

Of additionally concern for posterior inference is the partial identifiability of observation
392 parameters $p_{t=1}$ 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
394 no known “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
396 not already 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
398 pulling the values of $p_{t=1}$ and $p_{t=T}$ towards the overall mean of p (Gelman et al., 2013), and in fact
this approach might be more analytically sound than the more ad-hoc approaches that are
400 occasionally 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
402 estimates of θ , ϕ and survival pi at $t = T$ may suffer from similar edge effects. Again, the
hierarchical modeling approach used here may help correct for this reality by drawing these
404 estimates towards the overall means of those parameters.

After fitting both models (Eqs. 2, 3) using ADVI, model adequacy and quality of fit was assessed
406 using a posterior predictive check (Gelman et al., 2013). Because all Bayesian models are inherently
generative, simulations of new data sets is “free” (Gelman et al., 2013; McElreath, 2016). By
408 simulating 100 theoretical data sets from the posterior estimates of the model parameters and the
observed covariate information the congruence between predictions made by the model and the
410 observed empirical data can be assessed. These datasets are simulated by starting with the
observed states of the presence-absence matrix at $t = 1$; from their, the time series roll forward as
412 stochastic processes with covariate information given from the empirical observations. Importantly,
this is fundamentally different from observing the posterior estimates of the “true”

- 414 presence-absence matrix z . The posterior predictive check used in this study is to compare the
 observed average number of observations per species to a distribution of simulated averages; if the
 416 empirically observed value sits in the middle of the distribution than the model can be considered
 adequate in reproducing the observed number of occurrences per species.
- 418 The ADVI assumption of a purely Gaussian posterior limits the utility and accuracy of the
 posterior predictive checks because parameter estimates do not reflect the true posterior
 420 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
 422 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.
- 424 Given parameter estimates, diversity and diversification rates are estimated through posterior
 predictive simulations. Given the observed presence-absence matrix y , estimates of the true
 426 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
 428 possible occurrence history is estimated (Fig. 2).

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

$$N_t^{stand} = \sum_{i=1}^M z_{i,t}. \quad (4)$$

- 430 Given estimates of N_t^{stand} for all time points, the estimated number of originations O_t are be
 estimated as

$$O_t = \sum_{i=1}^M z_{i,t} = 1 | z_{i,t-1} = 0 \quad (5)$$

- 432 and number of extinctions E_t estimated as

$$E_t = \sum_{i=1}^M z_{i,t} = 0 | z_{i,t-1} = 1. \quad (6)$$

Per-capita growth D^{rate} , origination O^{rate} and extinction E^{rate} rates are then calculated as

$$\begin{aligned} O_t^{rate} &= \frac{O_t}{N_{t-1}^{stand}} \\ E_t^{rate} &= \frac{E_t}{N_{t-1}^{stand}} \\ D_t^{rate} &= O_t^{rate} - E_t^{rate}. \end{aligned} \quad (7)$$

434 Results

The results of the analyses described above take one of two forms: direct inspection of parameter
 436 posterior estimates from both models, and downstream estimates of diversity and diversification
 rates based on posterior predictive simulations from the birth-death model; the reason for which is
 438 explained below in the comparison of the models' posterior predictive check results.

440 Comparing parameter estimates from the pure-presence and birth-death models

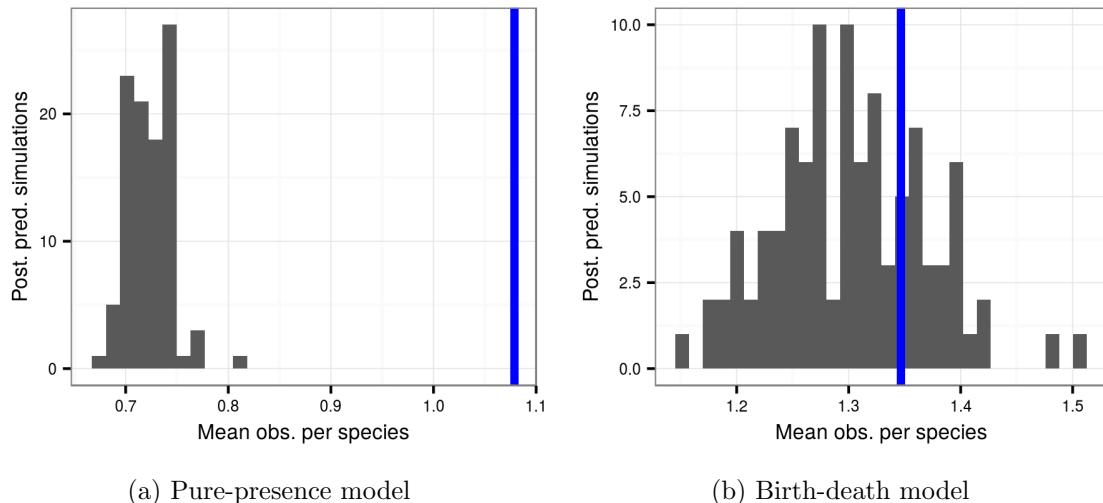


Figure 3: Comparison of the average observed number of occurrences per species (blue line) to the average number of occurrences from 100 posterior predictive datasets using the posterior estimates from the pure-presence and birth-death models.

Comparison of the posterior predictive results from the pure-presence and birth-death models

442 reveals a striking difference in performance of either model to predict the structure of the
underlying data (Fig. 3). The simulated datasets generated from the birth-death model are clearly
444 able to better reproduce the observed average number of occurrence than the pure-birth model
which greatly underestimates the observed average number of occurrences. This result means that
446 inferences based on the birth-death model are more likely to be representative of the underlying
data than inferences based on the pure-presence model. Further inspection of the posterior
448 parameter estimates from both models gives further insight into the reasons for this difference in
posterior predictive results (Gelman et al., 2013).

450 Occurrence probabilities estimated from the pure-presence model (Fig. 4) are broadly similar to the
estimates of origination probability from the birth-death model (Fig. 5) but not the survival
452 probability estimates (Fig. 6). This result supports the idea that changes to the North American
regional species pool is more likely due to changes in origination than extinction, a result that is
454 returned to later in the discussion of per-capita diversification, origination, and extinction rates.

For most ecotypes, both estimated occurrence probabilities from the pure-presence model (Fig. 4)
456 and origination probabilities estimated from the birth-death model (Fig. 5) increase with time. This
makes sense given that, over time, all species that have at least one observed occurrence must have
458 had that occurrence by the last time point, so our certainty in a species occurring must increase
with time. Importantly, there are potential issues surrounding the partial identifiability of the
460 observation parameters p which may contribute to edge effects in estimates of occurrence,
origination, and extinction (Royle and Dorazio, 2008). Notably, ecotypes with arboreal components
462 do not appear to follow a similar pattern; instead, occurrence and origination probabilities appear
relatively flat for most of the Cenozoic; this is most likely caused by those species of those ecotypes
464 no longer originating or originating very rarely.

The dramatic differences in the estimates origination and survival probabilities are indicative of
466 how differently these processes affect the diversification process and may also be responsible for the
better posterior predictive performance of the birth-death model over the pure-presence model (Fig.
468 3a, and 3b). While the estimates at all points along both time series have high variance, what is

striking is how mean origination probability changes over time while most ecotype survival
 470 probabilities have relatively stable means for the entire Cenozoic (Fig. 5, and 6).

For most ecotypes, the estimates of origination probabilities are with less uncertainty than similar
 472 estimates of survival probabilities (Fig. 5, and 6). In logistic regression, high uncertainty in the
 474 estimates of the underlying log-odds of occurrence, origination, or survival tends to be indicative of
 which occurs when there is no uncertainty in the effect of a covariate on presence/absence, the
 476 effect of which has been mitigated by the hierarchical modeling strategy used here (Gelman et al.,
 2013; Gelman and Hill, 2007; McElreath, 2016).

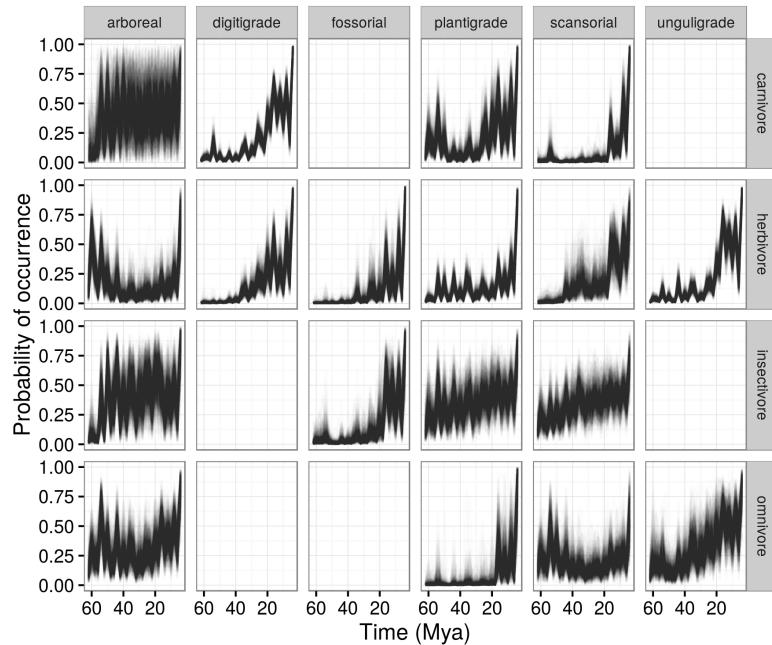


Figure 4: Probability of a mammal ecotype occurring over time as estimated from the pure-presence model. Each panel depicts 100 random samples from the model's posterior. The columns are by locomotor category and rows by dietary category; their intersections are the observed and analyzed ecotypes. Panels with no lines are ecotypes not observed in the dataset.

478 The pure-presence and birth-death models also differ in the estimated effect of mass on the
 probability of sampling a species that is present (Fig. 7). For the pure-presence model, mass is
 480 estimated to not have a strong effect on the probability of sampling a species that is presence (Fig.
 7a). Contrastingly, for the birth-death model mass is found to have a negative relationship with

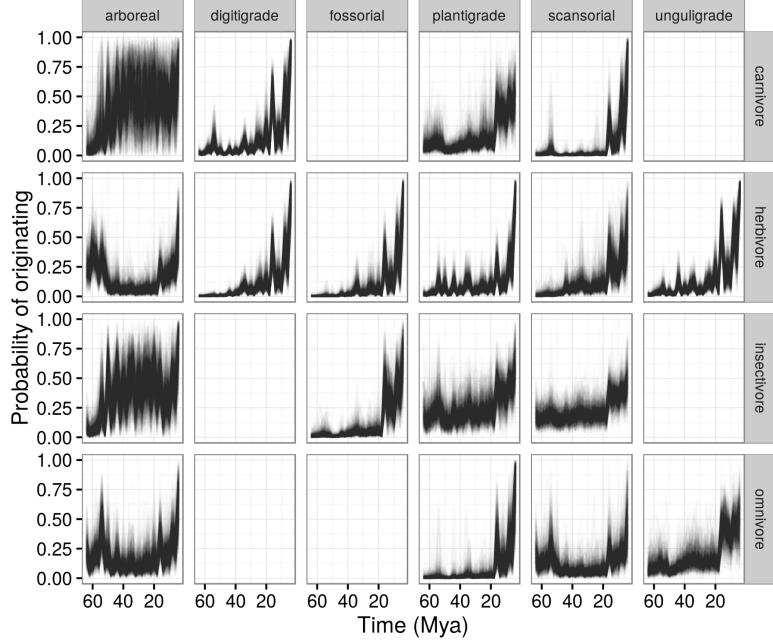


Figure 5: Probability of a mammal ecotype origination probabilities at each time point as estimated from the birth-death model. Each panel depicts 100 random samples from the model’s posterior. The columns are by locomotor category and rows by dietary category; their intersections are the observed and analyzed ecotypes. Panels with no lines are ecotypes not observed in the dataset.

482 observation such that larger species are less likely to be observed if present than smaller species
 (Fig. 7b). The result from the birth-death model is partially expected based on previous research
 484 (Damuth, 1982). What this result means is that the record of large bodied species is expected on
 average to have more gaps in sampling and a less consistent record from time point to time point
 486 than smaller bodied species. Additionally, as this is presence/absence data higher preservation and
 collection in terms of individual specimens at a location or a single temporal horizon does not
 488 necessarily translate to high preservation over multiple time points.

The average sampling probabilities for both the pure-presence model and birth-death model are
 490 both at the point where (rescaled log) mass equals 0; visual comparison indicates that, on average,
 sampling probability has greater posterior estimate in the pure-presence model than the birth-death
 492 model (Fig.7). The probability that one estimate is different from the other, however, are not
 directly calculable as they come from different models; what this tells us is how adding more
 494 information to the model (i.e. replacing occurrence with origination and extinction) changes

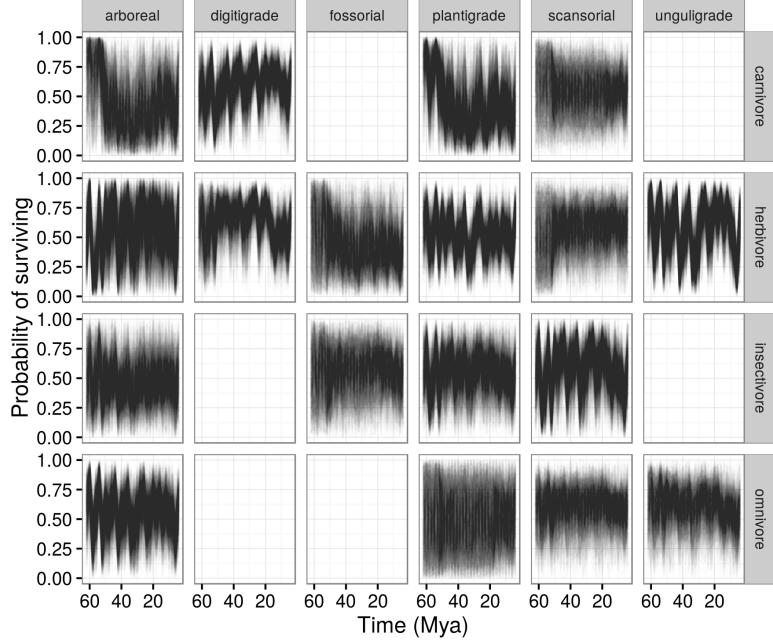


Figure 6: Probability of a mammal ecotype survival probabilities at each time point as estimated from the birth-death model. Each panel depicts 100 random samples from the model’s posterior. The columns are by locomotor category and rows by dietary category; their intersections are the observed and analyzed ecotypes. Panels with no lines are ecotypes not observed in the dataset.

parameter estimates in the model.

- 496 The effect of species mass on probability of occurrence as estimated from the pure-presence (Fig. 8)
 are most similar to the estimated effect of species mass on probability of origination for the
 498 birth-death model (Fig. 9). The striking pattern observable in both sets of estimates is the higher
 probability of occurrence for species with body sizes closer to the mean than either extremes. This
 500 result is consistent with the canonically normal distribution of mammal body sizes (Smith et al.,
 2004); it is then expected that the most likely to occur species would be those from the middle of
 502 the distribution, and that species originating will on average be of average mass, especially
 considering species shared common ancestry (Felsenstein, 1985). Note that all variation in estimates
 504 between ecotypes (Fig. 9) is due to differences in ecotype-specific survival probability and the
 associated effects of plant phase; the effect of mass was considered constant for all ecotypes.
 506 In contrast, the effect of species mass on probability of survival as estimated from the birth-death

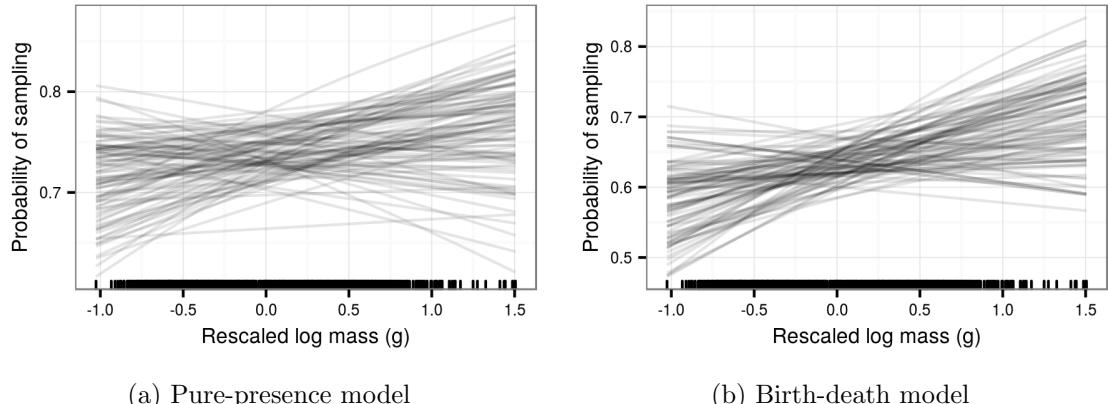


Figure 7: Estimates of the effect of species mass on probability of sampling a present species (p). Mass has been log-transformed, centered, and rescaled; this means that a mass of 0 corresponds to the mean of log-mass of all observed species and that mass is in standard deviation units. Estimates are from both the pure-presence and birth-death models.

model (Fig. 10) is consistent with previous findings that there is little effect of mass on extinction for North American mammals for the Cenozoic (Smits, 2015; Tomiya, 2013). Note that all variation between ecotypes depicted in Figure 10 is due to differences in ecotype-specific survival probability and the associated effects of plant phase; the effect of mass was considered constant for all ecotypes (Eqs. 2, 3).

- Similarities in parameters estimates between ecotypes may be due to similar response to environmental factors (Fig. 11, 12, and 13). As with previous comparisons between posterior estimates from the pure-presence and birth-death models, the effects of the group-level covariates in the pure-presence model (Fig. 11) are more similar to those estimates of the group-level effects on origination (Fig. 12) as opposed to survival (Fig. 13). As demonstrated in the comparisons of the effect of body mass on occurrence from the pure-presence model (Fig. 8) with the effect of body mass on origination and survival from the birth-death model (Fig. 9, and 10), there is considerable variation in the effect of plant phases on ecotype-specific estimates.

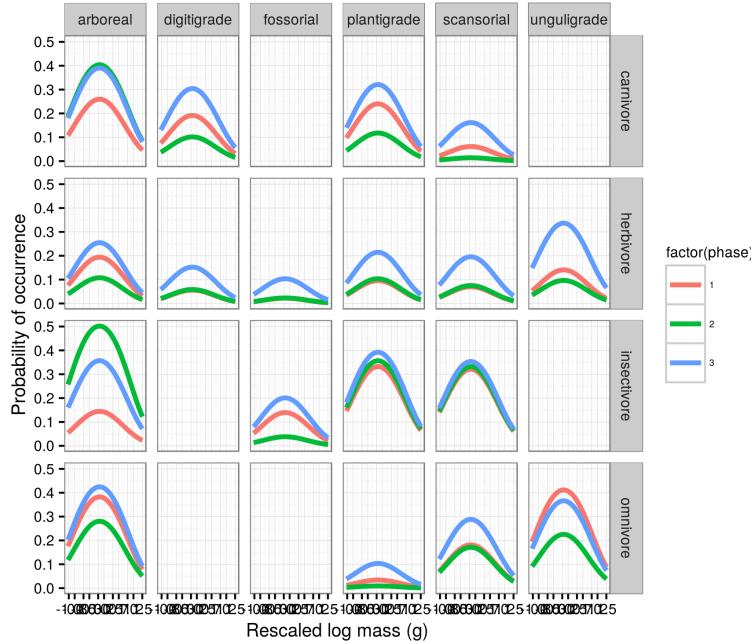


Figure 8: Mean estimate of the effect of species mass on the probability of a species occurrence for each of the three plant phases. The effect of mass is considered constant over time and that the only aspect of the model that changes with plant phase is the intercept of the relationship between mass and occurrence. 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. Only the mean estimates of the effects of both mass and plant phase are plotted for clarity; these estimates are obviously made with uncertainty.

524 for an ecotype may be indicative of an increasing number of possible and available mammal-plant
 525 interactions (e.g. ecological opportunity; Losos, 2010; Losos and Mahler, 2010; Yoder et al., 2010);
 526 while adverse conditions may translate to a decreasing set of interactions or loss of appropriate
 527 environmental context. Remember that favorable versus adverse condition of a plant phase is
 528 definitionally relative to the other two plant phases.

One of the limitations to this interpretation is the almost deterministic increase in probability of
 530 occurrence and origination for most ecotypes (Fig. 4, 5). This “pull of the Recent” means that
 531 interpreting the biological meaning of differences between the final plant phase and the two
 532 previous phases is difficult as the guaranteed occurrence of the later taxa increases the average
 533 probability for that phase, which in turn affects the other time bins in that phase.

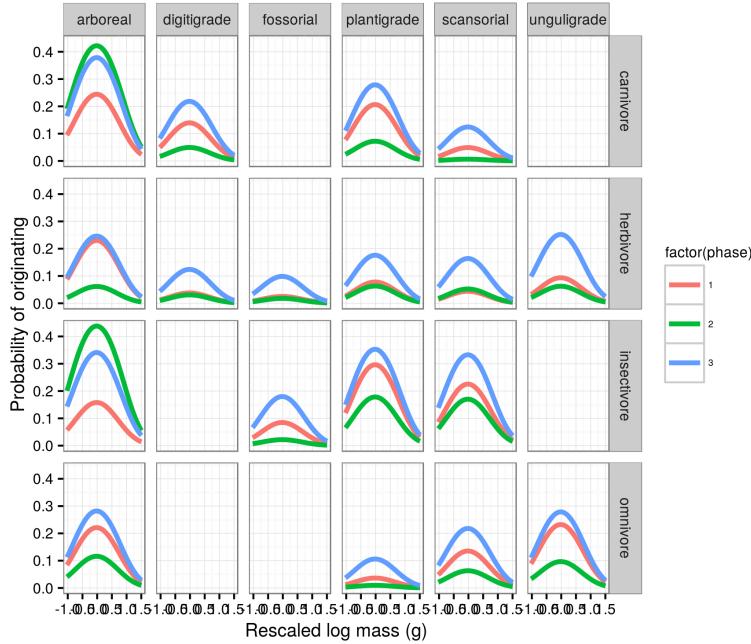


Figure 9: Mean estimate of the effect of species mass on the probability of a species originating for each of the three plant phases. The effect of mass is considered constant over time and that the only aspect of the model that changes with plant phase is the intercept of the relationship between mass 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. Only the mean estimates of the effects of both mass and plant phase are plotted for clarity; these estimates are obviously made with uncertainty.

534 Plant phases are associated with large differences in log-odds for occurrence and origination
 535 probabilities (Tables 9, 10), though there is little evidence of plant phase being an important
 536 distinguishing factor in species survival as only a few ecotypes demonstrate strong affinities with
 537 some plant phases (Table 11). As with previous comparisons between parameter estimates
 538 associated with species occurrence and species origination, parameters associated with probability
 539 of newly originating appear as a more “tempered” version of those associated with probability
 540 occurrence.

The almost universal pattern of the effect of plant phase on ecotype occurrence or origination is
 541 that the during first and last plant phases ecotypes have a greater log-odds of occurrence or
 542 origination than the second plant phase (Fig. 4, 5). The three ecotypes that do not follow this

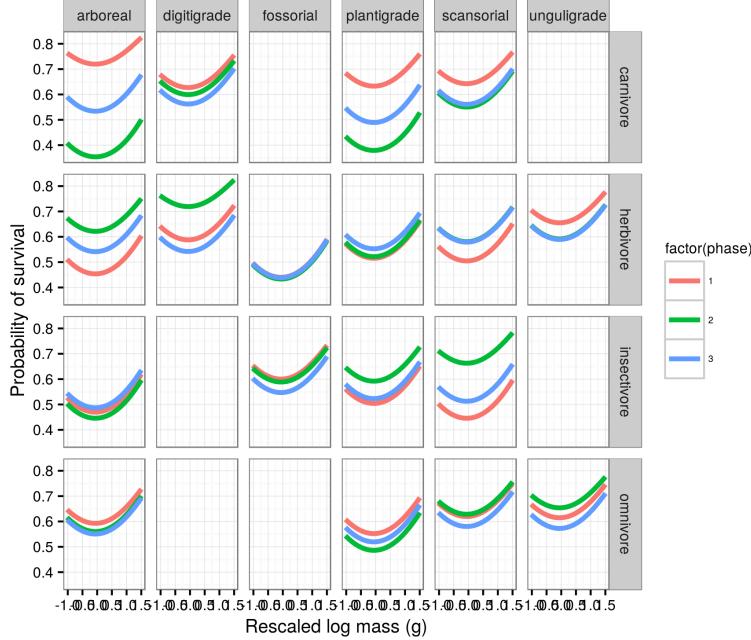


Figure 10: Mean estimate of the effect of species mass on the probability of a species survival for each of the three plant phases. The effect of mass is considered constant over time and that the only aspect of the model that changes with plant phase is the intercept of the relationship between mass 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. Only the mean estimates of the effects of both mass and plant plant are plotted for clarity; these estimates are obviously made with uncertainty.

544 pattern are fossorial herbivores, scansorial herbivores, and arboreal insectivores.

The difference between the third plant phase and the other two plant phases, for all ecotypes except
 546 arboreal carnivores, is obvious upon inspection the occurrence and origination time series as there
 is large up-tick in probability of occurring or originating towards the modern (Fig. 4, 5). The
 548 differences in mean probability of occurring or originating attributable to the plant phases are
 observable as shifts along the time series corresponding to the phase barriers (Table 4). For
 550 example, scansorial herbivore occurrence and origination probabilities demonstrate clear shifts at 50
 Mya and 16 Mya (Fig. 4, 5).

552 Both aspects of global temperature analyzed here are estimated to have strong effects on species
 occurrence and origination for most mammal ecotypes (Tables 12, 13). Similarity, temperature is

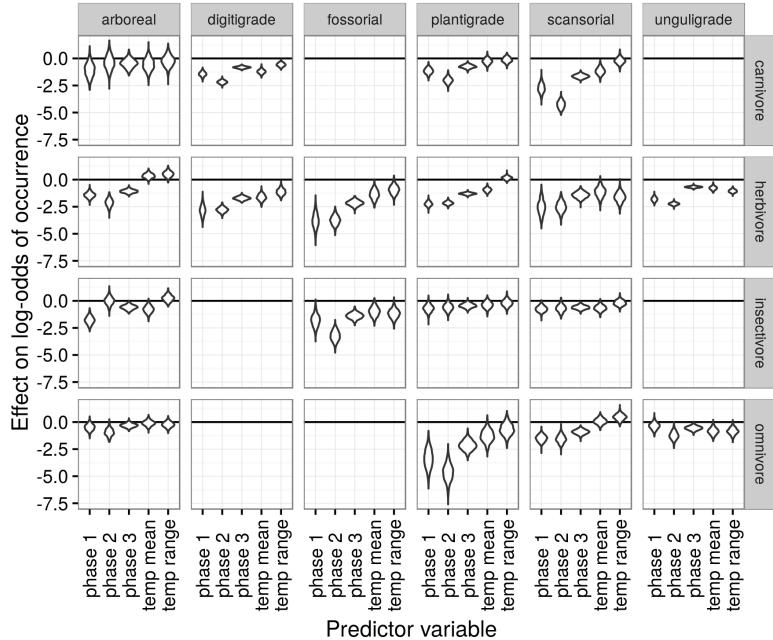


Figure 11: Estimated effects of the group-level covariates describing environmental context on log-odds of species occurrence. These estimates are from the pure-presence model. The effect of plant phase graphed here is calculated as Phase 1 = $\gamma_{phase\ 1}$, Phase 2 = $\gamma_{phase\ 1} + \gamma_{phase\ 2}$, and so on.

only expected to have a strong effect on species extinction for very few ecotypes (Table 14). For the occurrence and origination probabilities of many ecotypes, both temperature covariates have negative estimates which means that as temperature decreases, occurrence or origination are expected to increase. The only strongly positive estimate (e.g. temperature decrease, origination decrease) is for the effect of temperature range on arboreal herbivores. In the case of survival, the only strong ecotype associations for either of the temperature covariates are with plantigrade carnivores, plantigrade herbivores, and to a less certain extent arboreal herbivores and scansorial insectivores (Tab. 14). The effects of the temperature covariates on these ecotypes are all estimated to be positive (e.g. temperature range increase, increase in survival).

Analysis of diversity

All of the analyses of diversification and macroevolutionary rates has been done using only the birth-death model because of the model's better posterior predictive check performance (Fig. 3).

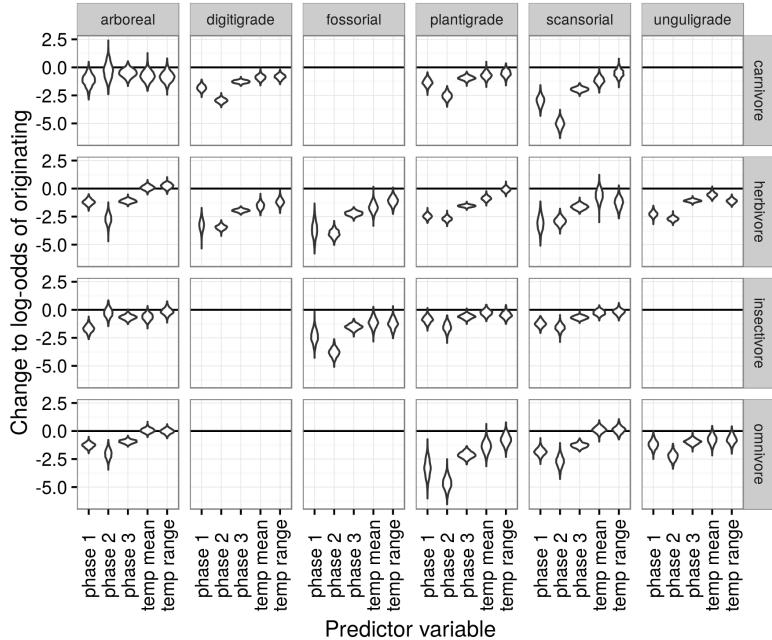


Figure 12: Estimated effects of the group-level covariates describing environmental context on log-odds of species origination. These estimates are from the birth-death model. The effect of plant phase graphed here is calculated as Phase 1 = $\gamma_{phase\ 1}$, Phase 2 = $\gamma_{phase\ 1} + \gamma_{phase\ 2}$, and so on.

566 The general pattern of the estimated North American total mammal diversity for the Cenozoic is
 567 “stable” in that diversity fluctuates around a constant mean standing diversity, does not fluctuate
 568 wildly and rapidly over the Cenozoic, and demonstrates no sustained directional trends (Fig. 14a).
 570 In broad strokes, the first 15 or so million years of the Cenozoic are characterized by a gradual
 572 decline in standing diversity until approximately 45-50 million years ago (early-middle Eocene).
 Following this decline, standing diversity is broadly constant from 45 to 18 Mya (early Miocene).
 574 After this, there is a rapid spike in diversity followed by a slight decline in diversity up to the
 Modern. This characterization of the estimated diversity history is knowingly broad strokes and
 diversity time series is not without variation and vagaries.

The pattern exhibited by the diversity history estimated in this study (Fig. 14a) has some major
 576 similarities with previous mammal diversity curves (Alroy, 2009): both curves begin with an
 increase in diversity most of the major increases in diversity are retained including the large
 578 diversity spike during the Miocene. Note that my time series begins at a different point than that

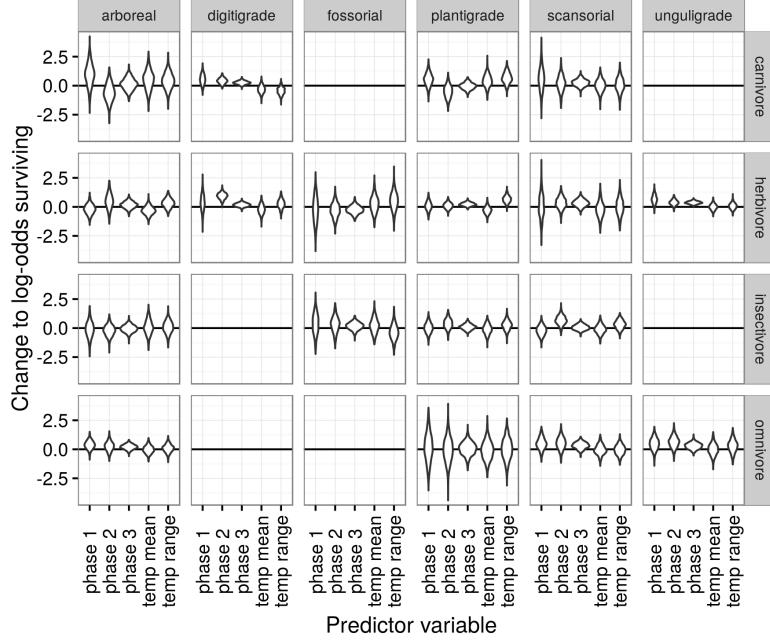


Figure 13: Estimated effects of the group-level covariates describing environmental context on log-odds of species survival. These estimates are from the birth-death model. The effect of plant phase graphed here is calculated as Phase 1 = $\gamma_{phase\ 1}$, Phase 2 = $\gamma_{phase\ 1} + \gamma_{phase\ 2}$, and so on.

Alroy (2009) and I'm able to interpolate over unsampled/poorly sampled time periods. Additionally,
 580 the time intervals used by Alroy (2009) are slightly shorter than those used here, so this may cause
 some of the minor differences between the curves. Also, please note that the diversity values are
 582 plotted at the “ceiling” of each temporal interval and not at the midpoint (Fig. 14a).

When viewed through the lens of diversification rate, some of the structure behind the estimated
 584 diversity history begins to take shape (Fig. 14b). For most of the Cenozoic, the diversification rate
 hovers around zero, punctuated by both positive and negative spikes. The largest spike in
 586 diversification rate is at 18 Mya, which is early Oligocene (Fig. 14b). Other notable increases in
 diversification rate occur 56, 46, 38, and 6 Mya (Table 15), though the last of these may be due
 588 to edge effects surrounding the partial-identifiability of $p_{t=T}$. Notable decreases in diversification rate
 occur 60, 54, 50, 44, 34, 20, 16, 12, and 8 Mya (Table 15), meaning that diversification rate has
 590 more major decreases than increases. Given that diversification rate more closely resembles
 origination rate than extinction rate (Fig. 14b, 14c, 14d), these decreases in diversification rate may

Table 9: Posterior probability of the differences in the log-odds of an ecotype occurring based on plant phase. These probabilities are calculated as $P(\text{Phase 1} > 2) = (\sum \gamma_{\text{phase1}} > \gamma_{\text{phase1}} + \gamma_{\text{phase2}})/100$ and similarly for the other comparisons. These estimates are from the pure-presence model.

	P(Phase 1 > Phase 2)	P(Phase 2 > Phase 3)	P(Phase 1 > Phase 3)
arboreal carnivore	0.460	0.776	0.866
digitigrade carnivore	1.000	0.000	1.000
plantigrade carnivore	1.000	0.040	1.000
scansorial carnivore	1.000	0.001	1.000
arboreal herbivore	1.000	0.540	1.000
digitigrade herbivore	1.000	0.995	1.000
fossorial herbivore	1.000	0.920	1.000
plantigrade herbivore	1.000	0.998	1.000
scansorial herbivore	0.999	0.754	1.000
unguligrade herbivore	1.000	0.000	1.000
arboreal insectivore	0.028	1.000	0.999
fossorial insectivore	1.000	0.161	1.000
plantigrade insectivore	0.706	0.774	0.985
scansorial insectivore	0.630	0.937	1.000
arboreal omnivore	0.981	0.165	0.944
plantigrade omnivore	1.000	0.325	1.000
scansorial omnivore	0.987	0.746	1.000
unguligrade omnivore	0.990	0.344	0.997

592 be indicative of “depletions” (failure to replace extinct taxa) rather than pulses of extinction.

The comparison between per capita origination and extinction rate estimates reveals how
594 diversification rate is formed (Fig. 14c, 14d). As expected given previous inspection of the ecotype
specific estimates of origination and survival probabilities from the birth-death model,

596 diversification rate seems most driven by changes in origination rate as opposed to extinction rate.
Extinction rate, on the other hand, demonstrates an almost saw-toothed pattern around a constant
598 mean (Fig. 14d). These results are broadly consistent with those from previous analyses of North
American mammals diversity and diversification (Alroy, 1996, 2009; Alroy et al., 2000).

600 Diversity partitioned by ecotype reveals a lot of the complexity behind the pattern of mammal
diversity for the Cenozoic (Fig. 15).

602 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 Modern (Fig. 15).

Table 10: Posterior probability of the differences in the log-odds of an ecotype originating based on plant phase. These probabilities are calculated as $P(\text{Phase 1} > \text{2}) = (\sum \gamma_{\text{phase1}} > \gamma_{\text{phase1}} + \gamma_{\text{phase2}})/100$ and similarly for the other comparisons. These estimates are from the birth-death model.

	P(Phase 1 > Phase 2)	P(Phase 2 > Phase 3)	P(Phase 1 > Phase 3)
arboreal carnivore	0.460	0.776	0.866
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scansorial carnivore	1.000	0.001	1.000
arboreal herbivore	1.000	0.540	1.000
digitigrade herbivore	1.000	0.995	1.000
fossorial herbivore	1.000	0.920	1.000
plantigrade herbivore	1.000	0.998	1.000
scansorial herbivore	0.999	0.754	1.000
unguligrade herbivore	1.000	0.000	1.000
arboreal insectivore	0.028	1.000	0.999
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scansorial omnivore	0.987	0.746	1.000
unguligrade omnivore	0.990	0.344	0.997

- 604 Arboreal herbivores and omnivores obtain peak diversity at the beginning of the Cenozoic then go
 605 into decline while remaining a small part of the species pool, while arboreal carnivores and
 606 insectivores obtain peak diversity 52-50 Mya and then quickly decline and become extremely rare or
 607 entirely absent from the species pool. This is consistent with increasing extinction risk in the
 608 Neogene compared to the Paleogene as proposed by Smits (2015).

The diversity of both digitigrade and unguligrade herbivores increase over the Cenozoic (Fig. 15).
 610 In contrast, plantigrade herbivore diversity does not have a single, broad-strokes pattern; instead,
 611 diversity increases, decreases, and may have then increased till the Modern. Contrastingly, fossorial
 612 and scansorial herbivores demonstrate a much flatter history of diversity, with a slight increase in
 613 diversity that over time is more pronounced among fossorial taxa than scansorial taxa. The
 614 expansion of digitigrade and unguligrade herbivores over the Cenozoic is consistent with the
 615 gradual expansion of grasslands which these ecotypes are better adapted to than closed

Table 11: Posterior probability of the differences in the log-odds of an ecotype surviving based on plant phase. These probabilities are calculated as $P(\text{Phase 1} > \text{2}) = (\sum \gamma_{\text{phase1}} > \gamma_{\text{phase1}} + \gamma_{\text{phase2}})/100$ and similarly for the other comparisons. These estimates are from the birth-death model.

	P(Phase 1 > Phase 2)	P(Phase 2 > Phase 3)	P(Phase 1 > Phase 3)
arboreal carnivore	0.904	0.121	0.382
digitigrade carnivore	0.181	0.248	0.004
plantigrade carnivore	0.857	0.195	0.519
scansorial carnivore	0.477	0.438	0.310
arboreal herbivore	0.278	0.510	0.140
digitigrade herbivore	0.001	0.978	0.175
fossorial herbivore	0.480	0.723	0.816
plantigrade herbivore	0.558	0.192	0.111
scansorial herbivore	0.444	0.286	0.133
unguligrade herbivore	0.548	0.022	0.002
arboreal insectivore	0.691	0.359	0.492
fossorial insectivore	0.334	0.488	0.221
plantigrade insectivore	0.189	0.677	0.308
scansorial insectivore	0.017	0.918	0.375
arboreal omnivore	0.549	0.196	0.074
plantigrade omnivore	0.528	0.537	0.618
scansorial omnivore	0.326	0.442	0.125
unguligrade omnivore	0.191	0.487	0.145

environments (Blois and Hadly, 2009; Strömberg, 2005).

Digitigrade carnivores have a multi-modal diversity history, with peaks 54-52 and 12-10 Mya (Fig.15). Between these two peaks digitigrade carnivore diversity dips below average diversity following the first peak and then grows slowly until the second peak. Plantigrade carnivores obtain peak diversity in the early Cenozoic and then maintain a relatively stable diversity until another peak at the end of the Cenozoic. The generally flat diversity history digitigrade carnivores lacks any sustained temporal trends and seems to reflect previous findings of limited diversity in spite of constant turnover and morphological evolution (Silvestro et al., 2015; Slater, 2015; Valkenburgh, 1999)

There are some broad similarities in diversity histories of insectivorous and omnivorous taxa. The diversity histories of arboreal, plantigrade, and scansorial insectivorous taxa all demonstrate a decreasing pattern with time, while fossorial insectivores have a flat diversity history with a peak approximately 10 Mya (Fig. 15). Arboreal and scansorial omnivores decrease in diversity from their

Table 12: Posterior probability the effects of the two temperature covariates on the log-odds of an ecotype occurring are greater than 0. What is estimated is the probability that these estimates are greater than 0; high or low probabilities indicate the “strength” of the covariate in that direction (positive and negative, respectively). These estimates are from the pure-presence model.

	$P(\gamma_{temp\ mean} > 0)$	$P(\gamma_{temp\ range} > 0)$
arboreal carnivore	0.169	0.317
digitigrade carnivore	0.000	0.000
plantigrade carnivore	0.168	0.304
scansorial carnivore	0.000	0.206
arboreal herbivore	0.943	0.969
digitigrade herbivore	0.000	0.000
fossorial herbivore	0.001	0.022
plantigrade herbivore	0.000	0.832
scansorial herbivore	0.009	0.003
unguligrade herbivore	0.000	0.000
arboreal insectivore	0.006	0.783
fossorial insectivore	0.016	0.003
plantigrade insectivore	0.127	0.260
scansorial insectivore	0.009	0.238
arboreal omnivore	0.337	0.191
plantigrade omnivore	0.012	0.120
scansorial omnivore	0.597	0.935
unguligrade omnivore	0.002	0.002

initial peaks early in the Cenozoic, and plantigrade omnivores have a generally flat diversity history

630 with a sudden peak in diversity late in the Cenozoic (Fig. 15). Unguligrade omnivores also demonstrate a possible decrease in diversity over the Cenozoic, but not as clearly as arboreal and
632 scansorial omnivores.

Many of the estimated ecotype specific diversity histories share a similar increases in diversity to

634 one degree or another at the late Cenozoic 16-14 Mya (Fig. 15); these increases are either sustained or temporary: digitigrade carnivores, plantigrade carnivores, scansorial carnivores, unguiligrade
636 herbivores, fossorial insectivores, and plantigrade omnivores.

When ecotype diversity is decomposed into the number of origination events per time bin (Fig. 16)

638 and the number of extinction events per time bin (Fig. 17) the estimates are clearly similar; there are no obvious major cross-ecotype origination or extinction events, and there is no evidence of a
640 sudden turnover as expected peaks in originations proceed peaks in peaks in the number of

Table 13: Posterior probability that the effects of the two temperature covariates on the log-odds of an ecotype origination are greater than 0. What is estimated is the probability that these estimates are greater than 0; high or low probabilities indicate the “strength” of the covariate in that direction (positive and negative, respectively). These estimates are from the birth-death model.

	$P(\gamma_{temp\ mean} > 0)$	$P(\gamma_{temp\ range} > 0)$
arboreal carnivore	0.086	0.045
digitigrade carnivore	0.001	0.000
plantigrade carnivore	0.013	0.054
scansorial carnivore	0.007	0.062
arboreal herbivore	0.853	0.957
digitigrade herbivore	0.000	0.001
fossorial herbivore	0.000	0.002
plantigrade herbivore	0.000	0.428
scansorial herbivore	0.106	0.003
unguligrade herbivore	0.000	0.000
arboreal insectivore	0.028	0.314
fossorial insectivore	0.010	0.006
plantigrade insectivore	0.188	0.090
scansorial insectivore	0.182	0.224
arboreal omnivore	0.749	0.482
plantigrade omnivore	0.007	0.117
scansorial omnivore	0.765	0.699
unguligrade omnivore	0.016	0.023

extinctions. Also, it is clear that the sustained increases in digitigrade and unguligrade herbivore

642 diversity observed above (Fig. 15) is driven by an increase in the average number of originations as
with a relatively constant number of extinctions over time (Fig. 16, 17).

644 Discussion

Both the composition of a species pool and its environmental context changes over time, though not

646 necessarily at the same rate or concurrently. Local communities, who’s species are drawn from the
regional species pool, have “roles” in their communities defined by their interactions with a host of
648 biotic and abiotic interactors (i.e. a species’ niche). For higher level ecological characterizations like
ecotypes and guilds, these roles are broad and not defined by specific interactions but by the genre
650 of interactions species within that grouping participate in. The diversity of species within an

Table 14: Posterior probability that the effects of the two temperature covariates on the log-odds of an ecotype survival are greater than 0. What is estimated is the probability that these estimates are greater than 0; high or low probabilities indicate the “strength” of the covariate in that direction (positive and negative, respectively). These estimates are from the birth-death model.

	$P(\gamma_{temp\ mean} > 0)$	$P(\gamma_{temp\ range} > 0)$
arboreal carnivore	0.777	0.745
digitigrade carnivore	0.236	0.211
plantigrade carnivore	0.763	0.929
scansorial carnivore	0.596	0.554
arboreal herbivore	0.261	0.878
digitigrade herbivore	0.438	0.720
fossorial herbivore	0.676	0.731
plantigrade herbivore	0.215	0.997
scansorial herbivore	0.377	0.535
unguligrade herbivore	0.768	0.655
arboreal insectivore	0.614	0.610
fossorial insectivore	0.673	0.337
plantigrade insectivore	0.470	0.787
scansorial insectivore	0.364	0.879
arboreal omnivore	0.620	0.645
plantigrade omnivore	0.476	0.484
scansorial omnivore	0.514	0.494
unguligrade omnivore	0.513	0.729

ecotype or guild can be stable over millions of years despite constant species turnover (Jernvall and

652 Fortelius, 2004; Slater, 2015; Valkenburgh, 1999). This implies that the size and scope of the role of
 654 an ecotype or guild in local communities, and the regional species pool as a whole, is preserved even
 as the individual interactors change. This also implies the structure of regional species pools can be
 constant over time despite a constantly changing set of “players.” This result supports the
 656 hypothesis that ecotypes or guilds are at least partially self-organizing and truly emergent (Scheffer
 and van Nes, 2006).

658 Comparison of the posterior predictive check results for the pure-presence and birth-death models
 supports the conclusion that regional species pool dynamics cannot simply be described by a single
 660 occurrence probability and is instead the result of the interplay between origination and extinction.
 Additionally, changes to the ecotypic composition and diversification rate for the North American
 662 regional species pool are driven primarily by variation in origination rates. These aspects of how

regional species pool diversity is shaped is not directly observable in studies of the Modern where
664 time scales are short and macroevolutionary dynamics are inferable solely from phylogeny (Fritz
et al., 2013).

666 Extinction rate for the entire regional species pool through time is highly variable and demonstrates
a saw-toothed pattern around an apparently constant mean. While a constant mean extinction rate
668 is consistent with previous observation (Alroy, 1996; Alroy et al., 2000), the degree to which
extinction rate is actually variable may not have been equally appreciated. What is most consistent
670 with previous observations, however, is that diversity seems to be most structured by changes to
origination rather than changes to extinction (Alroy, 1996; Alroy et al., 2000).

672 Comparison of the ecotype specific diversity histories supports the conclusion that there were no
major, simultaneous changes in diversity between the functional groups of the regional speies pool;
674 instead these results support a more gradual and idiosyncratic shifts in relative ecotypic diversity
over time (Fig. 15). The closest examples to a sudden increase or decrease of a specific ecotype is
676 the jump in standing diversity of scansorial carnivores and, to a lesser extent, fossorial insectivores
at 16 Mya (i.e. the start of the third plant phase). However, this result may not reflect the
678 dynamics of individual local communities as this is an analysis of the entire North American
mammal regional species pool.

680 Arboreal taxa disappear from the regional species pool over the Cenozoic, with long term decline
over the Paleogene leading to the disappearance by start of Neogene ~22 Mya. This is consistent
682 with one of the two possible patterns presented here and in Smits (2015) that would result in
arboreal taxa having a greater extinction risk than other ecotypes: the Paleogene and Neogene were
684 different selective regimes and while the earliest Cenozoic may have been neutral wrt arboreal taxa,
they disappeared quickly over the Cenozoic which may account for their higher extinction risk. In
686 addition to all arboreal taxa, the diversity of plantigrade and scansorial insectivores decreases with
time (Fig. 15).

688 Digitigrade carnivores have a relatively stable diversity history through the Cenozoic and can be
characterized as varying around a constant mean diversity. This ecotype has a large amount of

overlap with the carnivore guild which has been the focus of much research (Janis and Wilhelm, 1993; Pires et al., 2015; Slater, 2015; Valkenburgh, 1999). This result is consistent with some form of “control” on the diversity of this ecotype, such as diversity-dependent diversification (Silvestro et al., 2015; Slater, 2015; Valkenburgh, 1999).

Both digitigrade and unguligrade herbivores increase in diversity over the Cenozoic. The increase of these cursorial forms is consistent with the gradual opening up of the North American landscape (Blois and Hadly, 2009; Graham, 2011; Strömberg, 2005). These herbivore increase in diversity over the Cenozoic which may be indicative of a long-term shift in the interactors associated with those ecotypes leading to increased contribution to the regional species pool. This result may be comparable to the increasing percentage of hypsodont (high-crowned teeth) mammals in the Neogene of Europe being due to an enrichment of hyposodont taxa and not a depletion of non-hypsodont taxa. Smaller scale increases in fossorial herbivore species, and a lesser extent plantigrade herbivores, suggests that the increase of interactors may be associated mostly with the herbivore dietary category with locomotor category tempering that relationship. These results support the conclusion that the increase in digitigrade and unguligrade herbivores is the result of an enrichment of these ecotypes as opposed to being caused by the depletion of other herbivorous ecotypes; this is further supported by the lack of major changes to the number of extinctions of all herbivore ecotypes (Fig. 17).

An association between plant phase and differences in ecotype occurrence or origination-extinction probabilities is interpreted to mean that an ecotype enrichment or depletion is due to associations between that ecotype and whatever plants are dominate at that time and are thus a contributing factor to the constancy of an ecotype, or the lack thereof. Plant phase clearly structures the occurrence and origination probability time series (Fig. 4, 5). These differences in occurrence or origination translate opaquely to the estimates of diversity and diversification rate; the largest spike in both diversity, diversification rate, and origination rate all correspond to the onset of the last plant phase (Fig. 14). The clearest example of the diversity of an ecotype increasing at this particular transition is in scansorial carnivores (Fig. 15); similar shifts in other ecotypes are much more subtle, as was previously noted for fossorial insectivores.

718 Interestingly, all of the ecotypes with sudden changes to diversity at this transition increase in
719 diversity, even if only temporarily. There are two interpretations of these results. A biological
720 interpretation of this result is that, because plant phase associations are only with occurrence or
721 origination probabilities and not survival, these ecotypes were well suited for the newly available
722 mammal-plant interactions due to the increased modernization of their floral context (Graham,
723 2011). Alternatively, the increase in diversity associated with the third plant phase may be
724 caused by the edge effect in origination probability that is artificially inflating the number of
725 origination events (Fig. 5). However, the estimated number of origination events does not have a
726 tremendous spike at this transition, nor is a major increase in the number of origination events
727 sustained (Fig. 16).

728 There are fewer, less obvious shifts in diversity surrounding the transition from the first to second,
729 with the following ecotypes having apparent shifts in diversity at 50 My: digitigrade carnivores
730 (down), plantigrade carnivores (down), plantigrade herbivores (up), arboreal omnivores (down), and
731 scansorial omnivores (down). Because plant phase has been found to structure
732 occurrence/origination (Fig. 4, 5), but not survival (Fig. 6. My interpretation of these results is that
733 new species were not entering the system because there were fewer available mammal-plant
734 interactions available for those ecotypes. Instead, these ecotypes were poorly suited for the newly
735 available mammal-plant interactions brought upon by the changing environmental context
736 (Graham, 2011).

The estimated effects of temperature on occurrence and origination-extinction probabilities are
737 similar to those of the plant phases. The occurrence and origination probabilities of many mammal
738 ecotypes have strong relationships with the two temperature covariates (Tables 12, 13). In most
739 cases, there is a negative association between temperature and probability of occurring or first
740 originating; this means that if temperature decreases, we would then expect the probability of
741 occurring or first originating would increase. Contrastingly, only temperature range are estimated
742 to be good predictors of survival in four mammal ecotypes and only marginally for two of those
743 (Table 14). Additionally, in all four of these cases are expected to have positive relationships,
744 meaning that if temperature decreases it is expected that species survival will also decrease.

746 The result that temperature does not affect the extinction probability of most ecotypes is consistent
with previous analysis of mammal diversity (Alroy et al., 2000). The result that temperature affects
748 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 et al. (2000) is I am
750 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 differences of the
752 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 estimated here
754 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 will be present at
756 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 between time t
758 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 the occurrence and origination
760 probabilities increase over time because of the increasingly deterministic occurrence of those species
which had not yet originated (Fig. 4, 5, the corresponding rates and population level birth/death
762 dynamics do not share that pattern (Fig. 14, 16, 17). In effect, the finding that temperature has an
effect on origination simply because as time approaches the present the number of species which
764 have originated increases and not because of climatic forcing of origination.

Analysis of relationship between temperature and origination rate is probably better suited for a
766 continuous-time birth-death model instead of a discrete-time model because the former estimates
rates while the latter estimates probabilities (Allen, 2011). The PyRate model(s) are based on a
768 continuous-time birth-death process (Silvestro et al., 2015, 2014). Unfortunately, a continuous-time
model may be unsuited for most paleontological data as the fossil record is naturally discrete; fossils
770 are assigned to temporal units, such as stages, which have age ranges. Fossils are not assigned
individual numeric ages. This reality was in fact my one of motivations for using discrete-time
772 birth-death model instead of one in continuous-time.

The comparative size of the effects of plant phase and temperature are approximately equal in

774 importance in the sense that they have similar effect sizes on the ecotypes. The focus in previous
research on temperature and major climatic or geological events without other measures of
776 environmental context may have been a mistake and perhaps led to increasing confusion in
discussions of how the “environment” affects mammal diversity and diversification. The
778 environment or climate is not just global or regional temperature, it is the set of all possible biotic
and abiotic interactions that can be experienced by a member of the species pool. By including
780 more descriptors of species’ environmental context a more complete “picture” of the diversification
process is inferred.

782 The effect of species mass on either occurrence or origination and extinction was not allowed to
vary by ecotype or environmental context. The primary reason for this modeling choice was that
784 this study focuses on ecotypic based differences in either occurrence, or origination and extinction.
Allowing the effect of body size to vary by ecotype, time, and environmental factors would increase
786 the overall complexity of the model, something that I felt was not necessary because the overall
scope of the study. Instead, body size was included in order to control for its possible underlying
788 effects (McElreath, 2016). A control means that if there is variation due to body mass, having a
term to “absorb” that effect is better than ignoring it which may affect other parameter estimates.
790 Additionally, the effect of body size was allowed to have a second-order polynomial form and no
higher order polynomials were considered; this was done because it is hard to conceive of a more
792 complex third- or higher-order relationship between body size and the other parameters. Finally,
parametric forms of nonlinearity have not previously been considered, so the simple act of
794 estimating a potential second-order relationship is an opportunity to test more complex hypotheses
of the relationship between body size and both macroevolutionary and macroecological processes.

796 The only covariate allowed to affect sampling probability was mass and only as a linear predictor.
Other covariates, such as the environmental factors considered here, could have affected the
798 underlying preservation process that limits sampling probability; their exclusion as covariates of
sampling/observation was the product of a few key decisions: model complexity, model
800 interpretability, the scope of this study, and a lack of good hypotheses related to these covariates to
warrant their inclusion.

802 The potential effects of common ancestry (i.e. phylogeny) on origination and extinction are not
directly considered in this analysis. While a birth-death process approximates the
804 speciation-extinction process underlying the phylogeny (Silvestro et al., 2014) this is not same as
considering how the similarity between closely related species may affect the estimates of the effects
806 of species traits to environmental factors on both origination and extinction (Harnik et al., 2014;
Smits, 2015). The inclusion of phylogeny can help disentangle if the functional composition of
808 species diversity is shaped either by many closely related species occurring at the same time or if
closely related species are more evenly distributed in time; this is analogous to if species within
810 local communities are clumped or dispersed relative to their relatedness (Cavender-Bares et al.,
2009; Kraft et al., 2007; Webb et al., 2002). One of the principle barriers to the inclusion of the
812 effect of phylogeny in either the pure-presence or birth-death models is computational; with well
over 1000 tips, the calculation of the scale parameter defining the phylogenetic effect would be very
814 slow and further increase the already slow computation time necessary for the marginalization of all
possible discrete occurrence histories for z .

816 **Conclusions**

These results support the conclusion that the relative ecotypic diversity of the North American
818 mammal species pool has changed gradually over time. While there is constant species turnover for
the entire Cenozoic, there is little evidence of major cross-ecotype upheaval and sudden
820 reorganization of the functional composition of the regional species pool. The results of this study
also support the conclusion that mammal diversification over the Cenozoic is driven primarily by
822 changes to origination rate and not extinction rate. There are a number of interesting estimated
ecotype diversity patterns. While arboreal ecotypes are diverse in the Paleogene, by the Neogene all
824 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
826 plantigrade and scansorial insectivores and scansorial omnivores. Contrastingly, the only ecotypes
that demonstrate a sustained pattern of increasing diversity are digitigrade and unguligrade
828 herbivores. Interestingly, when the environmental covariates analyzed here are inferred to affect the

diversification of an ecotype, this effect is virtually always for origination and not survival. This
830 analysis provides a much more complete picture of North American mammal diversity and
diversification, specifically the dynamics of the ecotypic composition of that diversity. By increasing
832 the complexity of analysis while precisely translating research questions into a statistical model, the
context of the results is much better understood. Future studies of diversity and diversification
834 should incorporate as much information as possible into their analyses in order to better
understand or at least contextualize the complex processes underlying that diversity.

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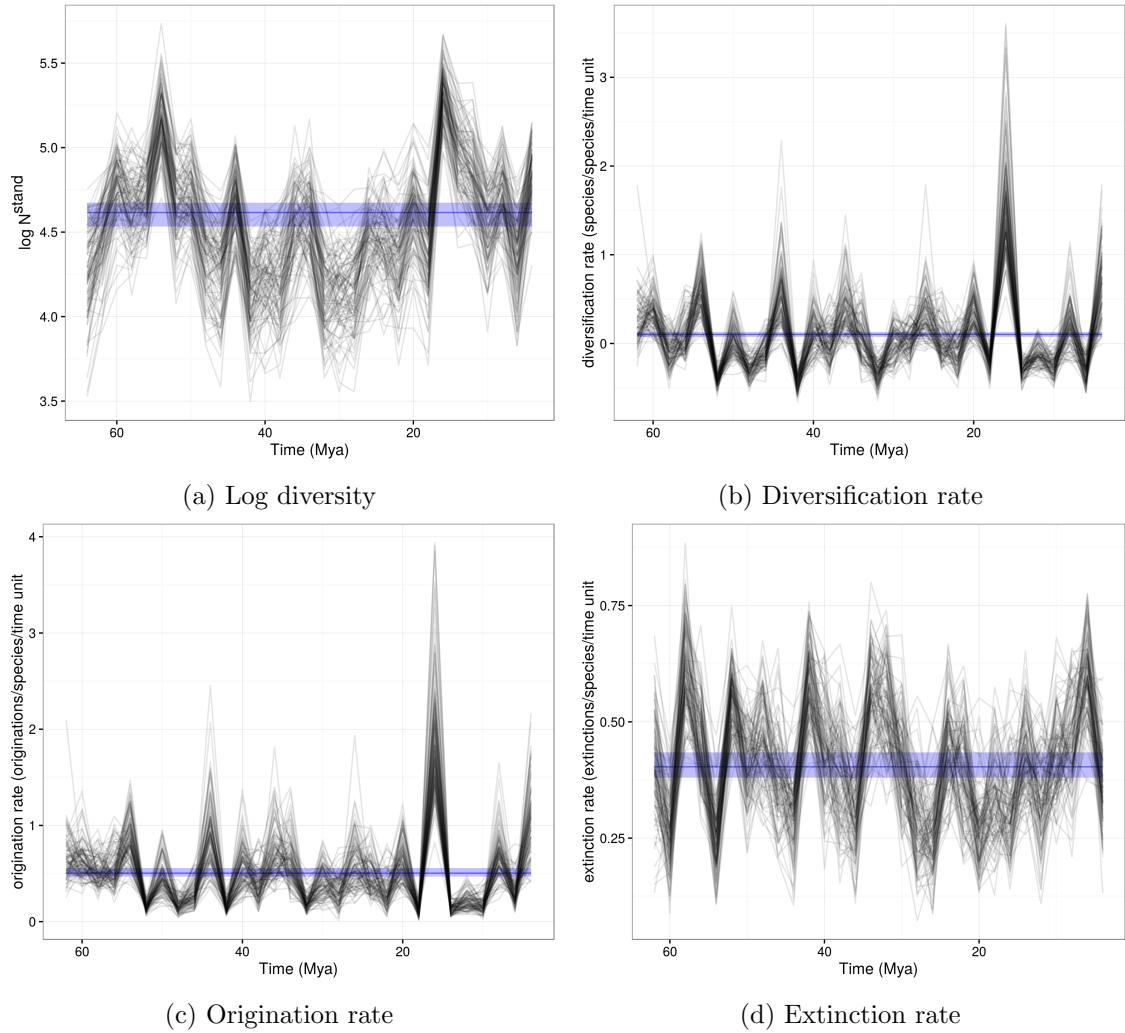


Figure 14: Posterior estimates of the time series of Cenozoic North American mammal diversity and its characteristic macroevolutionary rates; all estimates are from the birth-death model and 100 posterior draws are plotted to indicate the uncertainty in these estimates. The blue horizontal strip corresponds to the 80% credible interval of estimated mean standing diversity, diversification rate, origination rate, and extinction rate respectively; the median estimate is also indicated. What is also plotted is the The dramatic differences between diversity estimates at the first and second time points and the penultimate and last time points in this series are caused by well known edge effects in discrete-time birth-death models caused by $p_{-,t=1}$ and $p_{-,t=T}$ being partially unidentifiable (Royle and Dorazio, 2008); the hierarchical modeling strategy used here helps mitigate these effects but they are still present (Gelman et al., 2013; Royle and Dorazio, 2008). Diversification rate is in units of species gained per species present per time unit (2 My), origination rate is in units of species originating per species present per time unit, and extinction rate is in units of species becoming extinct per species present per time unit.

Table 15: Posterior probabilities of diversity N_t^{stand} or diversification rate D_t^{rate} being greater than average standing diversity \bar{N}^{stand} or average diversification rate \bar{D}^{rate} for the whole Cenozoic. The “Time” column corresponds to the top of each of the temporal bins. Diversification rate can not be estimated for the last time point because it is unknown how many more species originated or went extinct following this temporal bin. The estimates are from the birth-death model.

Time (Mya)	$P(N_t^{stand} > \bar{N}^{stand})$	$P(D_t^{rate} > \bar{D}^{rate})$
64.00	0.99	0.18
62.00	0.93	0.15
60.00	0.93	0.04
58.00	0.53	0.59
56.00	0.72	0.99
54.00	0.99	0.00
52.00	0.59	0.45
50.00	0.57	0.01
48.00	0.05	0.27
46.00	0.04	0.92
44.00	0.53	0.00
42.00	0.01	0.44
40.00	0.00	0.37
38.00	0.01	0.94
36.00	0.23	0.46
34.00	0.22	0.01
32.00	0.00	0.31
30.00	0.00	0.33
28.00	0.00	0.83
26.00	0.03	0.32
24.00	0.02	0.25
22.00	0.01	0.89
20.00	0.15	0.02
18.00	0.02	1.00
16.00	1.00	0.00
14.00	0.83	0.11
12.00	0.67	0.01
10.00	0.11	0.79
8.00	0.40	0.02
6.00	0.00	0.98
4.00	0.59	

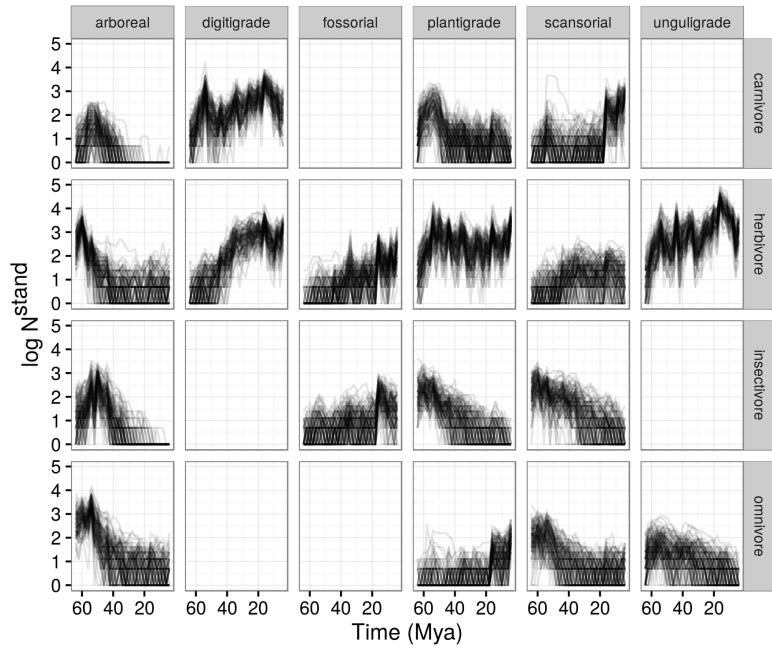


Figure 15: Posterior of standing log-diversity of North American mammals by ecotype for the Cenozoic as estimated from the birth-death model; 100 posterior draws are plotted to indicate the uncertainty in these estimates and what is technically plotted is log of diversity plus 1.

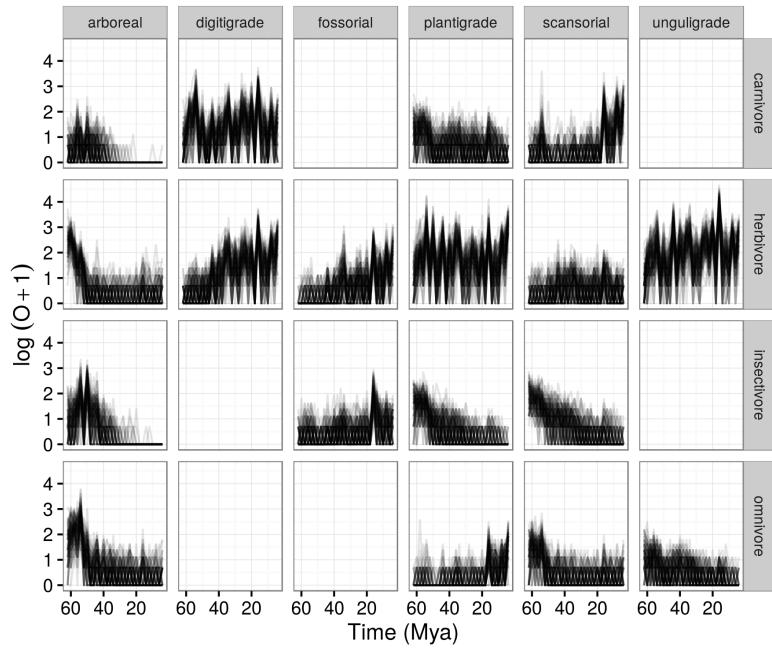


Figure 16: Posterior estimates of the number of origination events from one temporal bin to another, plotted at the bin they originate from. 100 posterior draws are plotted to indicate the uncertainty in these estimates. Also, what is plotted is log of the number of originations plus 1.

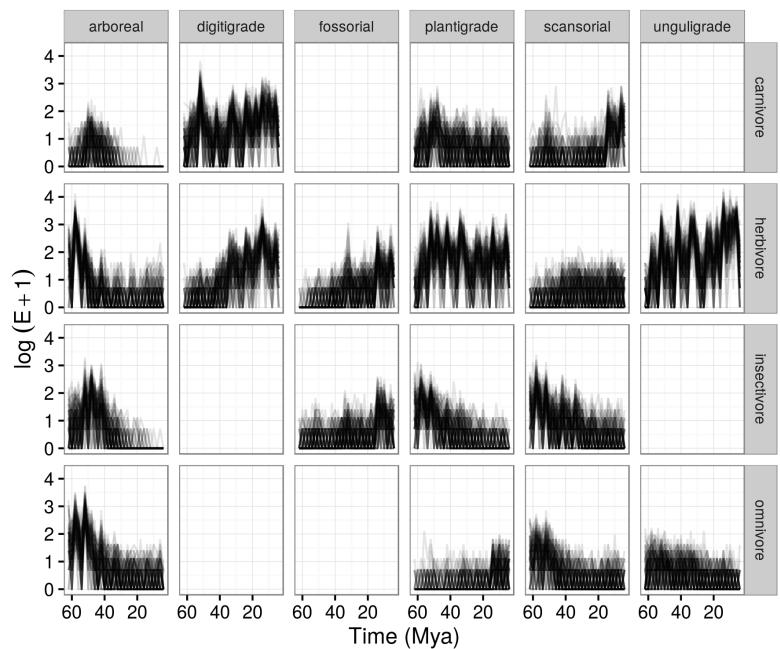


Figure 17: Posterior estimates of the number of extinction events from one temporal bin to another, plotted at the bin they go extinct from. 100 posterior draws are plotted to indicate the uncertainty in these estimates. Also, what is plotted is log of the number of extinctions plus 1.