

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

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Abstract

The set of species in a region changes over time as new species enter through speciation or immigration and as species leave the system through extinction and extirpation. How a regional species pool changes over time is the product of many processes acting at multiple levels of organization. Changes in the functional composition of a regional species pool are changes that occur across all local communities drawn from that species pool. While a species' presence in a local community is due to the availability of the necessary biotic-biotic or biotic-abiotic interactions that enable coexistence, a species' presence in a regional species pool just requires that at least one local community has that set of necessary interactions. The goal of this analysis is to understand when, and possibly for what reasons, mammal ecotypes are enriched or depleted relative to their average diversity. Here, I analyze the diversity history of North American mammals ecotypes for most of the Cenozoic (the last 65 million years). This analysis frames mammal diversity in terms of both their means of interacting with the biotic and abiotic environment (i.e. functional group or ecotype) as well as their regional and global environmental context. Using two hierarchical Bayesian hidden Markov models of diversity, I find that changes to mammal diversity are driven more by the influx of new species than by selective extinction. I also find that the only ecotypes which experience a near constant increase in diversity over time are digitigrade and unguligrade herbivores, while arboreal ecotypes become increasingly rare and in many cases disappear entirely from the species pool over the Cenozoic. Additionally, I find that global temperature is only associated with the origination of some mammal ecotypes but, in almost all cases, does not affect the extinction of mammal ecotypes.

Introduction

Changes to species diversity are the result of evolutionary and ecological processes acting 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
30 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
32 speciation, extinction, migration, and extirpation. The gain or loss of regional diversity is the result
of macroevolutionary dynamics which, in turn, shape the downstream macroecological dynamics of
34 the regional species pool and its constituent local communities (Harrison and Cornell, 2008;
Mittelbach and Schemske, 2015; Urban et al., 2008).

36 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
38 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
40 group are expected to have more similar macroecological dynamics to each other than to species of
a different functional group. By focusing on the relative diversity of functional groups, changes to
42 diversity are interpretable as changes to the set of ways species within a species pool could interact
with the biotic and abiotic environment.

44 A key question when comparing communities or regional species pools based on their functional
composition is whether specific functional groups are enriched or depleted and why; what are the
46 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)?
48 Comparisons of contemporaneous regional species pools only determines if a functional group is
enriched or depleted in one species pool relative to other species pools. This type of comparison
50 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). While a species pool may be depleted of a
52 functional group relative to other contemporaneous species pools, that same functional group may
be actually be enriched in that species pool relative to its historical diversity. Because the processes
54 which shape regional species pool diversity (e.g. origination, extinction) operate on much longer
time scales than is possible for studies of the Recent, paleontological data provides a unique
56 opportunity to observe and estimate the changes to functional diversity and how species functional

traits and environmental context can shape the enrichment or depletion of functional groups within
58 a regional species pool (Blois and Hadly, 2009; Smith et al., 2008). Being able to identify which if
the diversity of any functional groups are depleted relative to their long term average diversity in
60 the species pool is particularly useful in conservation settings; species in depleted groups are most
likely more at risk of extinction than species in enriched groups, even if the enriched groups is
62 relatively rare when compared to other contemporaneous species pools.

The paleontological record of North American mammals for the Cenozoic (\sim 66 million years ago to
64 present) provides one of the best opportunities for understanding how regional species pool
functional diversity changes over time. The North American mammal record is a relatively complete
66 temporal sequence for the entire Cenozoic which primarily, but not exclusively, based on fossil
localities from the Western Interior of North America (Alroy, 1996, 2009; Alroy et al., 2000).
68 Additionally, mammal fossils preserve a lot of important physiological information, such as teeth, so
that functional traits like the dietary/trophic category of species are easy to estimate (Eronen et al.,
70 2010; Polly et al., 2011, 2015).

The goals of this study are to understand when are unique functional groups, called ecotypes,
72 enriched or depleted in the North American mammal regional species pool and to estimate the
relationship between changes to regional ecotypic diversity and changes to their environmental
74 context.

Background

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

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

The narrative of the diversification of North American mammals over the Cenozoic is one of
96 gradual change. There is little convincing evidence that there have been any major or sudden
cross-functional group or cross-taxonomic turnover events in mammal diversity at any point in the
98 Cenozoic record of North America (Alroy, 1996, 2009; Alroy et al., 2000; Eronen et al., 2015; Janis,
1993). Instead of being concentrated at specific time intervals, species turnover has been found to
100 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 all functional
102 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 et al., 2000). An
104 unresolved aspect of the general history of mammal diversification is whether that diversity is
limited or self-regulating; namely, to what extent is mammal diversification diversity-dependent
106 (Alroy, 2009; Harmon and Harrison, 2015; Rabosky, 2013; Rabosky and Hurlbert, 2015). Similarity,
this question can also be asked of specific functional groups (Jernvall and Fortelius, 2004; Quental
108 and Marshall, 2013; Silvestro et al., 2015; Valkenburgh, 1999).

Within the overall narrative of mammal diversity, the histories of a selection of taxonomic and
110 functional groups are better understood. These groups have particularly good fossil records and/or

have been the focus of previous analyses.

112 The diversity history of ungulate herbivores has been characterized by more recently originating
113 taxa having longer legs, higher crowned teeth, and a shift from graze-dominated to
114 browse-dominated diets than their earlier originating counterparts (Cantalapiedra et al., 2017;
115 Fraser et al., 2015; Janis et al., 2004; Janis, 1993, 2008; Janis et al., 2000). The mechanisms which
116 drive this pattern are theorized to be some combination of tectonic activity driving environmental
117 change such as the drying of the western interior of North America due mountain building and
118 global temperature and environmental change such as the formation of polar icecaps (Badgley et al.,
119 2017; Blois and Hadly, 2009; Eronen et al., 2015; Janis, 2008).

120 In contrast, the origination of modern cursorial carnivore forms was not until later in the Cenozoic;
121 this is not to say that carnivore diversity only grew in the late Cenozoic, but that those forms were
122 late entrants (Janis and Wilhelm, 1993). Instead, the diversity history of carnivores is reflective of
123 density-dependence or some other form of self-regulation (Silvestro et al., 2015; Slater, 2015;
124 Valkenburgh, 1999). Specifically, it has been proposed that different canid clades have replaced each
125 other as the dominate members of their functional group within the species pool (Silvestro et al.,
126 2015; Valkenburgh, 1999). It is then expected that, for this analysis, the diversity of digitigrade and
127 plantigrade carnivores (i.e. the “carnivore” guild of Valkenburgh (1999)) should be relatively
128 constant for the Cenozoic or at least have plateaued by the Neogene.

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

¹³⁸ with time, albeit possibly at low diversity; and 2) if the Paleogene and Neogene represent difference
selective regimes with the former being associated with lower extinction risk than the latter, then
¹⁴⁰ the diversity history of arboreal taxa are expected to be present in the Paleogene but depleted or
absent from the species pool during the Neogene.

¹⁴² The climate history of the Cenozoic can be broadly described as a gradual cooling trend, with polar
ice-caps forming in the Neogene (Cramer et al., 2011; Zachos et al., 2008, 2001). There are of course
¹⁴⁴ exceptions to this pattern such as the Eocene climatic optimum, the mid-Miocene climatic optimum,
and the sudden drop in temperature at the Eocene/Oligocene boundary (Zachos et al., 2008, 2001).

¹⁴⁶ In terms of the North American biotic environment, the Cenozoic is additionally characterized by
major transition from having closed, partially forested biomes being common in the Paleogene to
¹⁴⁸ the landscape being dominated by savannah and grasslands biomes by the Neogene (Blois and
Hadly, 2009; Janis, 1993; Janis et al., 2000; Strömberg, 2005). Additionally, the landscape structure
¹⁵⁰ and topology of North America changed substantially over the Cenozoic with mountain uplift and
other tectonic actives in Western North America (Badgley and Finarelli, 2013; Blois and Hadly,
¹⁵² 2009; Eronen et al., 2015; Janis, 2008). This type of geological activity affects both local climates as
well as continental weather patterns while also mobilizing increased grit into the environment,
¹⁵⁴ something which may be responsible for increasing trend of hyposodony (high crowned teeth)
among herbivores (Damuth and Janis, 2011; Jardine et al., 2012; Jernvall and Fortelius, 2002).

¹⁵⁶ The effect of climate on mammal diversity and its accompanying diversification process has been the
focus of considerable research with a slight consensus favoring mammal diversification being more
¹⁵⁸ biologically-mediated than climate-mediated (Alroy, 1996; Alroy et al., 2000; Clyde and Gingerich,
1998; Figueirido et al., 2012). However, differences in temporal and geographic scale seem to underly
¹⁶⁰ the contrast between these two perspectives. For example when the mammal fossil record analyzed
at small temporal and geographic scales a correlation between diversity and climate is observable
¹⁶² (Clyde and Gingerich, 1998). However, when the record is analyzed at the scale of the continent and
most of the Cenozoic this correlation disappears (Alroy et al., 2000). This result, however, does not
¹⁶⁴ go against the idea that there may be short periods of correlation between diversity and climate and
that this relationship can change or even reverse direction over time; this type result means that

¹⁶⁶ there is no single direction of correlation between 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 phenomena
can be observed and analyzed rather than assumed.

¹⁷⁶ **Foreground**

Fourth-corner modeling is an approach to explaining the patterns of either species abundance or
¹⁷⁸ presence/absence in a community 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.,
¹⁸⁰ 2012; Warton et al., 2015); effectively uniting climate-based species distribution modeling (SDMs)
with trait-based community assembly models (CATS, MaxEnt). In modern ecological studies, what
¹⁸² is being modeled is species 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
¹⁸⁴ time for most of the Cenozoic record for North America (Fig. 1). By analyzing assemblages over
time instead of space in fourth-corner framework we can gain better inference of how an
¹⁸⁶ instantaneous species pool (i.e. the Recent) is assembled over time. These two approaches, modern
and paleontological, are different views of the same three-dimensional pattern: species at localities
¹⁸⁸ over time. The temporal limitations of modern ecological studies and difficulties with uneven spatial
occurrences of fossils in paleontological studies means that these approaches are complementary and
¹⁹⁰ reveal different patterns of how species are distributed in time and space.

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

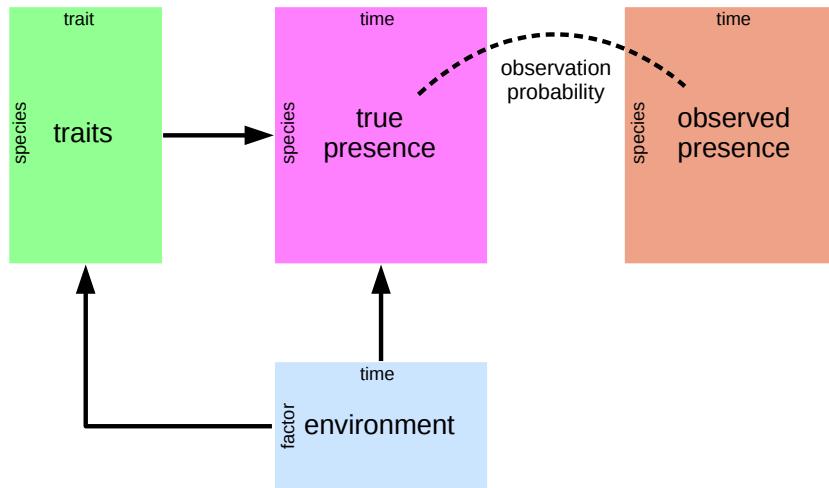


Figure 1: Conceptual diagram of the paleontological fourth corner problem. The observed presence matrix (orange) is the empirical presence/absence pattern for all species for all time points; this matrix is an incomplete observation of the “true” presence/absence pattern (purple). The estimated true presence matrix is modeled as a function of both environmental factors over time (blue) and multiple species traits (green). Additionally, the effects 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 species 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 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 not 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 and
212 sampling of species means that the true times of origination or extinction may not be observed
(Foote, 2001; Foote and Sepkoski, 1999; Wang et al., 2016; Wang and Marshall, 2016). The model(s)
214 I propose below represent an attempt to translate the verbal/visual model described here (Fig. 1)
into a statistical model for estimating the relative diversity of mammal ecotypes over time and how
216 those ecotypes respond to changes to environmental context while taking into account the
fundamental incompleteness of the fossil record.

218 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
220 diversity are related to changes in species’ environmental context. In the analyses done here, many
covariates which describe a species’ macroecology and its environmental context are considered. In
222 order to analyze this complex and highly structured data set, I developed a hierachal Bayesian
model combing the fourth-corner modeling approach with a model of an observation-occurrence or
224 observation-origination-extinction process.

Materials and Methods

226 Taxon occurrences and species-level information

All fossil occurrence information used in this analysis was downloaded from the Paleobiology
226 Database (PBDB). The initial download restricted occurrences to Mammalia observed in North
America between the Maastrichtian (72-66 Mya) and Gelasian (2.58-1.8 Mya) stages (Cohen et al.,
230 2015). Occurrences were then further limited to those occurring between 64 and 2 million years ago
(Mya); this age restriction was to insure that observation time series lines up with the temperature
232 time series (Cramer et al., 2011). Taxonomic, stratigraphic, and ecological metadata for each
occurrence and species was also downloaded. A new download for a raw, unfiltered PBDB datafile
234 following the same criterion used here is available at <http://goo.gl/2s1geU>. The raw datafile
used as a part of this study, along with all code for filtering and manipulating this download is
236 available at <http://github.com/psmits/copings>.

After being downloaded, the raw occurrence data was then sorted, cleaned, and manipulated
238 programmatically before analysis. Many species taxonomic assignments as present in the raw
PBDB data were updated for accuracy and consistency. For example, species classified in the order
240 Artiodactyla were reclassified as Cetartiodactyla. These re-assignments follow Smits (2015) which
were based on taxonomies present in the Encyclopedia of Life (<http://eol.org>) and Janis et al.
242 (2008, 1998). All taxa whose life habit was classified as either volant (i.e. Chiroptera) or aquatic
(e.g. Cetacea) were excluded from this analysis because of their lack of direct applicability to the
244 study of terrestrial species pools.

Species ecotype is defined based on a combination of locomotor and diet categories; the goal is to
246 classify species based on the manner with which they interact with their environment. Most
mammal species records in the PBDB have life habit (i.e. locomotor category) and dietary category
248 assignments. In order to simplify interpretation, analysis, and per-ecotype sample size these
classifications were coarsened in a similar manner to (Smits, 2015) following Table 1. Additionally
250 for this study, the life history category was further broken up to better reflect the diversity of

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

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

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.

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

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Table 2 – continued from previous page

Order	Family	Stance
	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
	Felidae	digitigrade

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Table 2 – continued from previous page

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

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Table 2 – continued from previous page

Order	Family	Stance
	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
	Simimyidae	plantigrade

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Table 2 – continued from previous page

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

260

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

All fossil occurrences from 64 to 2 million years ago (Mya) were binned into 31 2 million year (My)
274 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).

276 Environmental and temporal covariates

The environmental covariates used in this study are collectively referred to as group-level covariates
 278 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
 280 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
 282 phases” defined by Graham (2011).

Global temperature across most of the Cenozoic was calculated from Mg/Ca isotope record from
 284 deep sea carbonates (Cramer et al., 2011). Mg/Ca based temperature estimates are preferable to
 the frequently used $\delta^{18}\text{O}$ temperature proxy (Alroy et al., 2000; Figueirido et al., 2012; Zachos
 286 et al., 2008, 2001) because Mg/Ca estimates do not conflate temperature with ice sheet volume and
 depth stratification changes. The former is particularly important to this analysis as the current
 288 polar ice-caps appeared and grew over the Cenozoic. These properties make Mg/Ca based

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

temperature estimates preferable for macroevolutionary and macroecological studies (Ezard et al., 2016). Two aspects of the Mg/Ca-based temperature curve 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 mean and then dividing by twice the standard deviation.

The second set of environmental factors included in this study are the Cenozoic plant phases defined in Graham (2011). Graham's plant phases are holistic descriptors of the taxonomic composition of 12 ecosystem types, which plants are present at a given time, and the relative modernity of those plant groups with younger phases representing increasingly modern taxa (Graham, 2011). Graham (2011) defines four intervals from the Cretaceous to the Pliocene, though only three of these intervals take place during the time frame being analyzed. Graham's plant phases was included as a series of "dummy variables" encoding the three phases included in this 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 boundaries of these plant phases are defined in Table 4.

Modelling species occurrence

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 (Allen, 2011). The difference between these two models lies in whether the probabilities of a species originating or surviving are considered equal or different (Table 5). 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:

		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

310 not having originated yet, extant, and extinct. The last of these is the absorbing state, as once a species has gone extinct it cannot re-originate (Allen, 2011). Thus, in the transition matrices the
 312 probability of an extinct species changing states is 0 (Table 5). See below for parameter explanations (Tables 6, 7, and 8).

314 Observation process

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

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

time-varying intercept and species mass as a covariate. The effect of species mass on p was assumed
322 linear and constant over time and given a prior reflecting a possible positive relationship; these assumptions are reflected in the structure of the model Equation 1, presented here:

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

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

Pure-presence process

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

Presence is a logistic regression where the intercept varies by ecotype (Eq. 2). Species mass was
332 included as a covariate associated with two regression coefficients allowing a quadratic relationship

with log-odds of occurrence. Because the distribution of mammal species body mass is unimodal
 334 and approximately normal (Smith et al., 2004), I assume that species of intermediate body size will
 be more common than species of very large or very small mass. These assumptions are also
 336 reflected in the choice of priors for b_1 and b_2 where the latter is given a weakly informative prior
 with most of the density is below 0 (Eq. 2).

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

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

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

350 **Birth-death process**

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

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

Similar to the pure-presence model, both ϕ and π are modeled as logistic regressions with varying
 356 intercept and one covariate associated with two parameters. The possible relationships between
 mass and both ϕ and π are reflected in the parameterization of the model and choice of priors (Eq.
 358 3).

The intercepts of ϕ and π both vary by species ecotype and those values are themselves the product
 360 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

pure presence model (Eq. 2).

³⁶² Posterior inference and model adequacy

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 models used here 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; this causes 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 possible states of the latent parameters z were calculated and summed (i.e. marginalized). Species durations at minimum range through from their first appearance to their last appearance in the fossil record, but the incompleteness of all observations means that the actual times of origination and extinction are unknown. The marginalization approach used here means that the

probabilities of all possible histories for a species are calculated, from the end members of the
 374 species having existed for the entire study interval and the species having only existed between the
 directly observed FAD and LAD to all possible intermediaries (Fig 2) (Stan Development Team,
 376 2016). This process is identical, language-wise, to assuming range-through and then estimating the
 possibility of range extension due to incomplete 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. By marginalizing over all possible occurrence histories, the probability of each potential history is estimated. The process of parameter marginalization is described in the text.

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

Bayesian posterior; this assumption is similar to quadratic approximation of the likelihood function
386 commonly used in maximum likelihood based inference (McElreath, 2016). The principal limitation
of assuming the joint posterior is Gaussian is that the true topology of the log-posterior isn't
388 estimated; this is a particular burden for scale parameters which are bound to be positive (e.g.
standard deviation).

390 Of additional concern for posterior inference is the partial identifiability of observation parameters
 $p_{t=1}$ and $p_{t=T}$ (Royle and Dorazio, 2008). This issue means that the estimates of sampling
392 probabilities at the “edges” of the time series cannot fully be estimated because there are no known
“gaps” in species occurrence histories that are guaranteed to be filled. Instead, the values of the first
394 and final columns of the “true” presence-absence matrix z for those observations that do not already
have presences in the observed presence-absence matrix y cannot be estimated (Royle and Dorazio,
396 2008). The hierarchical modeling approach used here helps mitigate this problem by pulling the
values of $p_{t=1}$ and $p_{t=T}$ towards the overall mean of p (Gelman et al., 2013), and in fact this
398 approach might be more analytically sound than the more ad-hoc approaches that are occasionally
used to overcome this hurdle (Royle and Dorazio, 2008). Additionally, because $p_{t=1}$ and $p_{t=T}$ are
400 only partially identifiable, estimates of occurrence θ and origination ϕ at $t = 1$ and estimates of θ , ϕ
and survival π at $t = T$ may suffer from similar edge effects. Again, the hierarchical modeling
402 approach used here may help correct for this reality by drawing these estimates towards the overall
means of those parameters.

404 After fitting both models (Eqs. 2, 3) using ADVI, model adequacy and quality of fit were assessed
using a posterior predictive check (Gelman et al., 2013). By simulating 100 theoretical data sets
406 from the posterior estimates of the model parameters and the observed covariate information the
congruence between predictions made by the model and the observed empirical data can be
408 assessed. These datasets are simulated by starting with the observed states of the presence-absence
matrix at $t = 1$; from there, the time series roll forward as stochastic processes with covariate
410 information given from the empirical observations. Importantly, this is fundamentally different from
observing the posterior estimates of the “true” presence-absence matrix z . The posterior predictive
412 check used in this study is to compare the observed average number of observations per species to a

distribution of simulated averages; if the empirically observed value sits in the middle of the
 414 distribution then the model can be considered adequate in reproducing the observed number of
 occurrences per species.
 416 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
 418 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
 420 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.
 422 Given parameter estimates, diversity and diversification rates are estimated through posterior
 predictive simulations. Given the observed presence-absence matrix y , estimates of the true
 424 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
 426 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

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

428 Given estimates of N_t^{stand} for all time points, the estimated number of originations O_t is estimated
 as

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

430 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

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

432 Results

The results of the analyses described above take one of two forms: direct inspection of parameter
 434 posterior estimates from both models, and downstream estimates of diversity and diversification
 rates based on posterior predictive simulations from the birth-death model because this model has a
 436 better fit to the observed occurrence information.

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

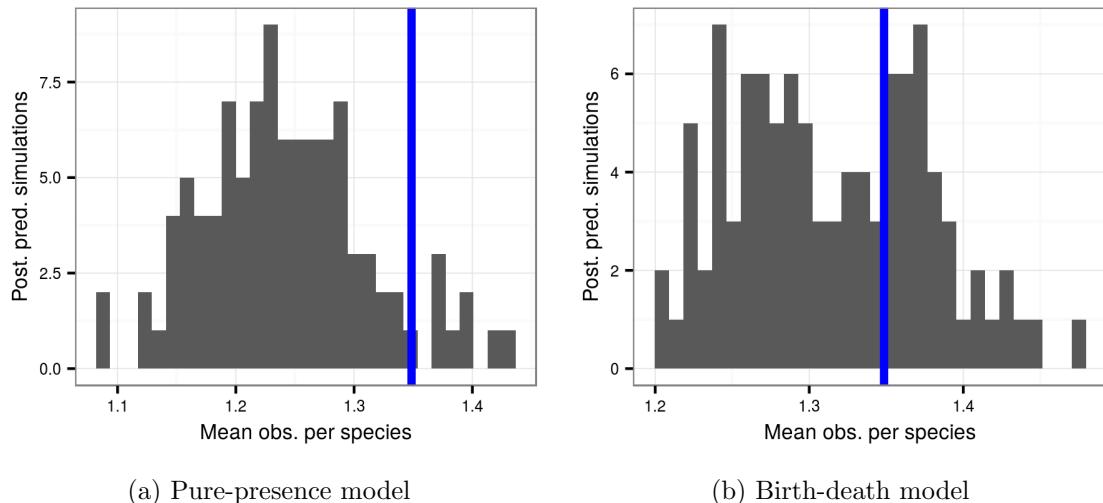


Figure 3: Comparison of the average observed number of occurrences per species (blue line) to the average number of occurrences from 100 posterior predictive datasets using the posterior estimates from the pure-presence and birth-death models.

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

440 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
442 able to better reproduce the observed average number of occurrence than the pure-presence model
which greatly underestimates the observed average number of occurrences. This result means that
444 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
446 parameter estimates from both models gives further insight into the reasons for this difference in
posterior predictive results (Gelman et al., 2013).

448 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
450 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 to which I
452 will return 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)
454 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
456 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
458 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
460 do not appear to follow a similar pattern; instead, occurrence and origination probabilities appear
relatively flat with high posterior variance for most of the Cenozoic.

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

probabilities have relatively stable means for the entire Cenozoic (Fig. 5, and 6).

- 468 For most ecotypes, the estimates of origination probabilities involve less uncertainty than similar
 469 estimates of survival probabilities (Fig. 5, and 6). In logistic regression, high uncertainty in the
 470 estimates of the underlying log-odds of occurrence, origination, or survival tends to indicate
 471 extreme rarity or complete absence of the specific ecotype. The latter is called complete separation
 472 and occurs when there is no uncertainty in the effect of a covariate on presence/absence. The
 473 problem of complete separation is mitigated by the hierarchical modeling strategy used here
 474 (Gelman et al., 2013; Gelman and Hill, 2007; McElreath, 2016).

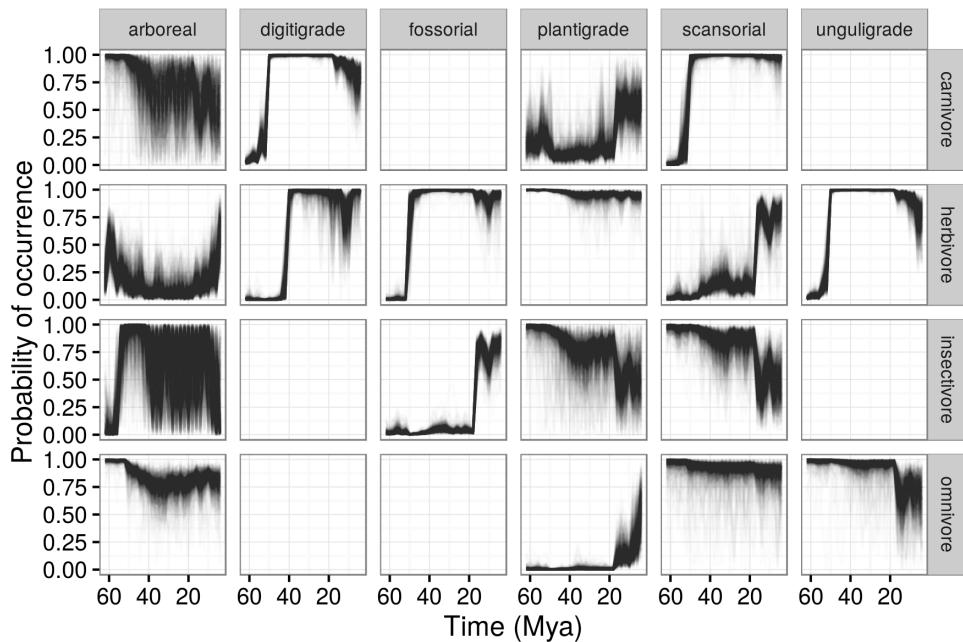


Figure 4: Probability of a mammal ecotype occurring over time as estimated from the pure-presence model. Each panel depicts 100 random samples from the model’s posterior. The columns are by locomotor category and rows by dietary category; their intersections are the observed and analyzed ecotypes. Panels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

The pure-presence and birth-death models also differ in the estimated effect of mass on the
 476 probability of sampling a species that is present (Fig. 7). For the pure-presence model, mass is
 477 estimated to not have a strong effect on the probability of sampling a species that is presence (Fig.
 478 7a). In contrast, for the birth-death model mass is found to have a negative relationship with
 observation such that larger species are less likely to be observed if present than smaller species

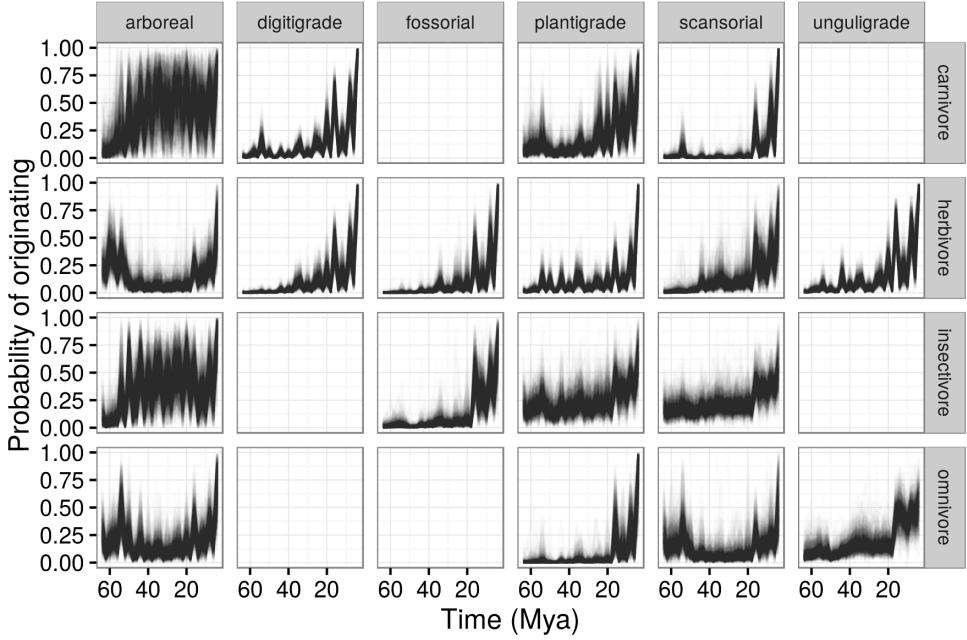


Figure 5: Probability of a mammal ecotype origination probabilities at each time point as estimated from the birth-death model. Each panel depicts 100 random samples from the model’s posterior. The columns are by locomotor category and rows by dietary category; their intersections are the observed and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

480 (Fig. 7b). The result from the birth-death model is partially expected based on previous research
 (Damuth, 1982). What this result means is that the record of large bodied species is expected on
 482 average to have more gaps in sampling and a less consistent record from time point to time point
 than smaller bodied species. Additionally, as this is presence/absence data higher preservation and
 484 collection in terms of individual specimens at a location or a single temporal horizon does not
 necessarily translate to high preservation over multiple time points.
 486 The average sampling probabilities for both the pure-presence model and birth-death model are
 both at the point where (rescaled log) mass equals 0; visual comparison indicates that, on average,
 488 sampling probability has greater posterior estimate in the pure-presence model than the birth-death
 model (Fig.7). The probability that one estimate is different from the other, however, is not directly
 490 calculable as they come from different models; what this tells us is how adding more information to
 the model (i.e. replacing occurrence with origination and extinction) changes parameter estimates
 492 in the model.

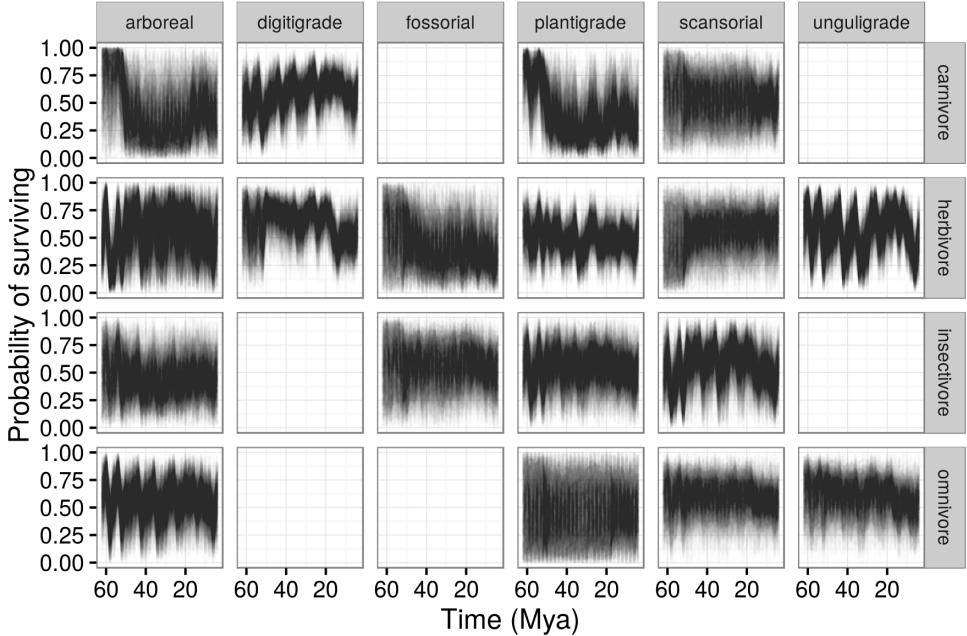


Figure 6: Probability of a mammal ecotype survival probabilities at each time point as estimated from the birth-death model. Each panel depicts 100 random samples from the model’s posterior. The columns are by locomotor category and rows by dietary category; their intersections are the observed and analyzed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

The effect of species mass on probability of occurrence as estimated from the pure-presence model

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

In contrast, the effect of species mass on probability of survival as estimated from the birth-death
 504 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

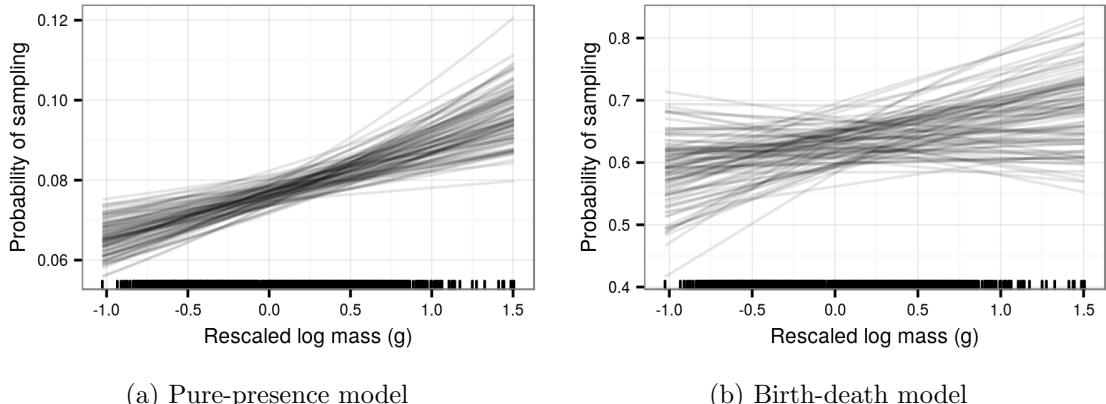


Figure 7: Estimates of the effect of species mass on probability of sampling a present species (p). Mass has been log-transformed, centered, and rescaled; this means that a mass of 0 corresponds to the mean of log-mass of all observed species and that mass is in standard deviation units. Estimates are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

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 parameter estimates between ecotypes may be due to a 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.

An association between plant phase and differences in the log-odds of occurrence (Fig. 11),
518 origination (Fig. 12), or extinction (Fig. 13) is interpreted to mean that the set of possible
mammal-plant interactions was relatively more favorable (positive association) or less so (negative
520 association) to those ecotypes. In the case of species origination, for example, more favorable
conditions for an ecotype may indicate an increasing number of possible and available
522 mammal-plant interactions (e.g. ecological opportunity; Losos, 2010; Losos and Mahler, 2010; Yoder

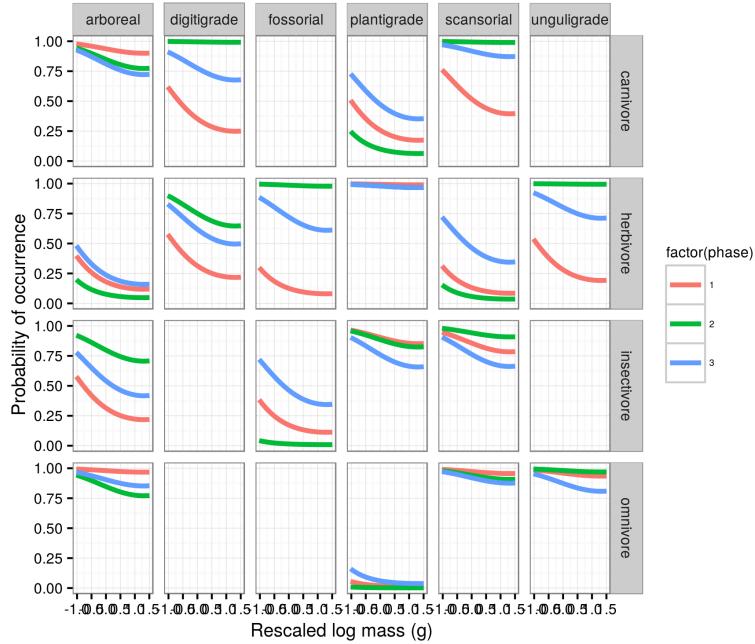


Figure 8: Mean estimate of the effect of species mass on the probability of a species occurrence for each of the three plant phases. The effect of mass is considered constant over time and that the only aspect of the model that changes with plant phase is the intercept of the relationship between mass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

et al., 2010); while adverse conditions may translate to a decreasing set of interactions or loss of

appropriate environmental context. Remember that favorable versus adverse condition of a plant phase is definitionally relative to the other two plant phases.

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

Plant phases are associated with large differences in log-odds for occurrence and origination probabilities (Tables 9, 10), though there is little evidence of plant phase being an important distinguishing factor in species survival, as only a few ecotypes demonstrate strong affinities with

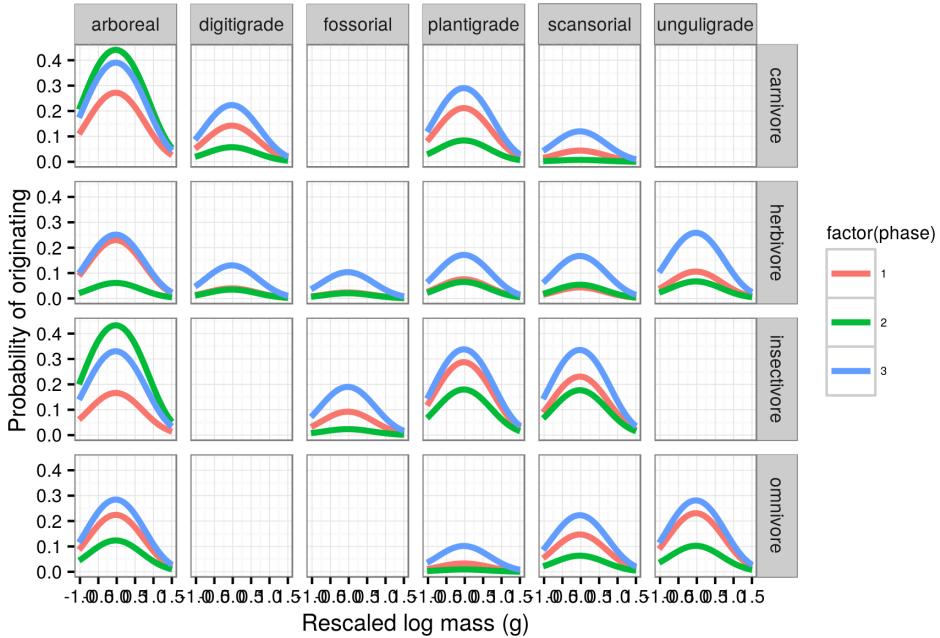


Figure 9: Mean estimate of the effect of species mass on the probability of a species originating for each of the three plant phases. The effect of mass is considered constant over time and that the only aspect of the model that changes with plant phase is the intercept of the relationship between mass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

- 534 some plant phases (Table 11). As with previous comparisons between parameter estimates
 associated with species occurrence and species origination, parameters associated with probability
 536 of newly originating appear as a more “tempered” version of those associated with probability
 occurrence.
- 538 The almost universal pattern of the effect of plant phase on ecotype occurrence or origination is
 that the during first and last plant phases ecotypes have a greater log-odds of occurrence or
 540 origination than the second plant phase (Fig. 4, 5). The three ecotypes that do not follow this
 pattern are fossorial herbivores, scansorial herbivores, and arboreal insectivores.
- 542 The difference between the third plant phase and the other two plant phases, for all ecotypes except
 arboreal carnivores, is obvious upon inspection of the occurrence and origination time series as
 544 there is large up-tick in probability of occurring or originating towards the modern (Fig. 4, 5). The

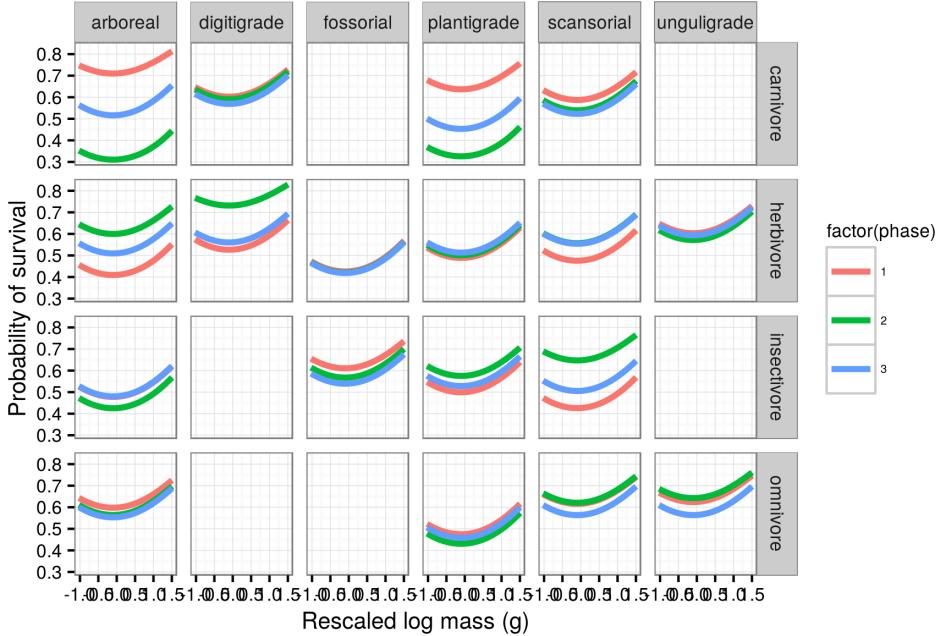


Figure 10: Mean estimate of the effect of species mass on the probability of a species survival for each of the three plant phases. The effect of mass is considered constant over time and that the only aspect of the model that changes with plant phase is the intercept of the relationship between mass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

differences in mean probability of occurring or originating attributable to the plant phases are

546 observable as shifts along the time series corresponding to the phase barriers (Table 4). For
example, scansorial herbivore occurrence and origination probabilities demonstrate clear shifts at 50
548 Mya and 16 Mya (Fig. 4, 5).

Both aspects of global temperature analyzed here are estimated to have strong effects on species
550 occurrence and origination for most mammal ecotypes (Tables 12, 13). Similarity, temperature is
only expected to have a strong effect on species extinction for very few ecotypes (Table 14). For the
552 occurrence and origination probabilities of many ecotypes, both temperature covariates have
negative estimates which means that as temperature decreases, occurrence or origination are
554 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

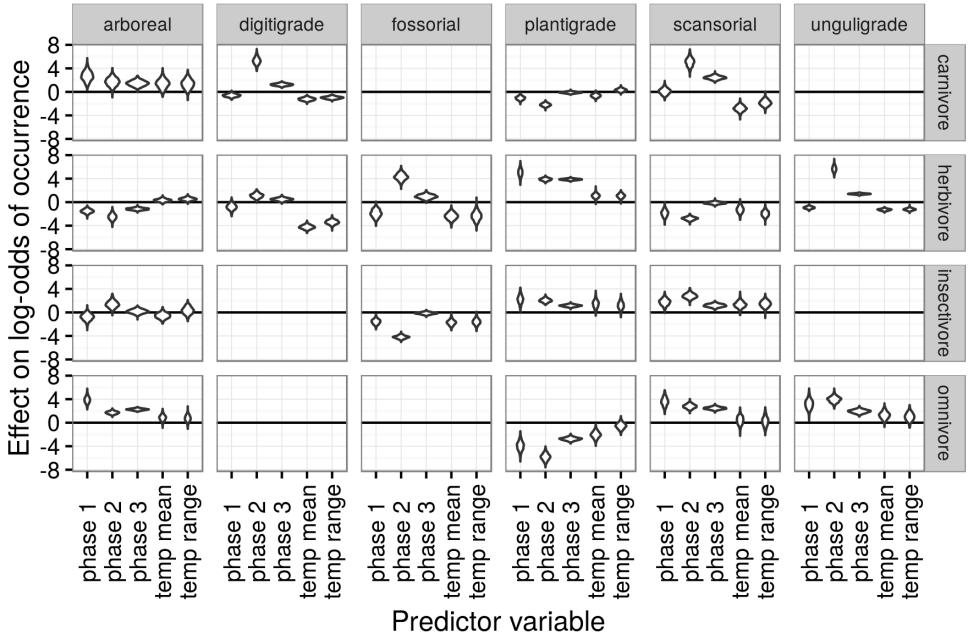


Figure 11: Estimated effects of the group-level covariates describing environmental context on log-odds of species occurrence. These estimates are from the pure-presence model. The effect of plant phase graphed here is calculated as Phase 1 = $\gamma_{phase\ 1}$, Phase 2 = $\gamma_{phase\ 1} + \gamma_{phase\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

556 only strong ecotype associations for either of the temperature covariates are with plantigrade
 carnivoroes, plantigrade herbivores, and to a less certain extent arboreal herbivores and scansorial
 558 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).

560 Analysis of diversity

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

The general pattern of the estimated North American total mammal diversity for the Cenozoic is
 564 "stable" in that diversity fluctuates around a constant mean standing diversity, does not fluctuate
 wildly and rapidly over the Cenozoic, and demonstrates no sustained directional trends (Fig. 14a).
 566 In broad strokes, the first 15 or so million years of the Cenozoic are characterized by a gradual
 decline in standing diversity until approximately 45-50 million years ago (early-middle Eocene).

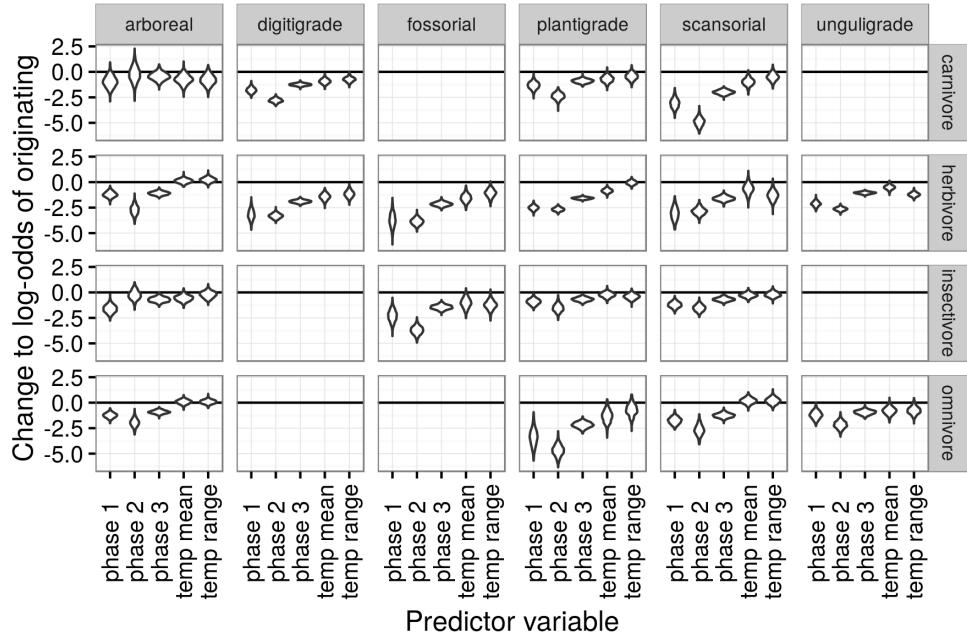


Figure 12: Estimated effects of the group-level covariates describing environmental context on log-odds of species origination. These estimates are from the birth-death model. The effect of plant phase graphed here is calculated as Phase 1 = $\gamma_{phase\ 1}$, Phase 2 = $\gamma_{phase\ 1} + \gamma_{phase\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

568 Following this decline, standing diversity is broadly constant from 45 to 18 Mya (early Miocene).
 After this, there is a rapid spike in diversity followed by a slight decline in diversity up to the
 570 Modern.

The pattern exhibited by the diversity history estimated in this study (Fig. 14a) has some major
 572 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
 574 diversity spike during the Miocene. Note that my time series begins at a different point than that
 Alroy (2009) and I'm able to interpolate over unsampled/poorly sampled time periods. Additionally,
 576 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
 578 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
 580 diversity history begins to take shape (Fig. 14b). For most of the Cenozoic, the diversification rate

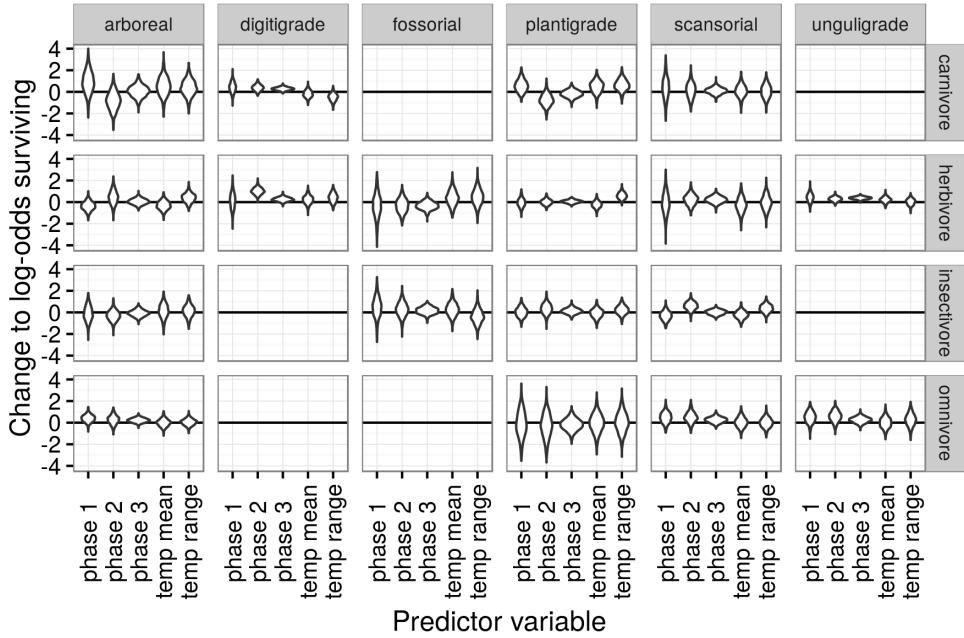


Figure 13: Estimated effects of the group-level covariates describing environmental context on log-odds of species survlval. These estimates are from the birth-death model. The effect of plant phase graphed here is calculated as Phase 1= $\gamma_{phase\ 1}$, Phase 2= $\gamma_{phase\ 1} + \gamma_{phase\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

hovers around zero, punctuated by both positive and negative spikes. The largest spike in
 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 to
 edge effects surrounding the partial-identifiability of $p_{t=T}$. Notable decreases in diversification rate
 occur at 60, 54, 50, 44, 34, 20, 16, 12, and 8 Mya (Table 15), meaning that diversification rate has
 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
 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
 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,
 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

Table 9: Posterior probability of the differences in the log-odds of an ecotype occurring based on plant phase. These probabilities are calculated as $P(\text{Phase 1} > \text{2}) = (\sum \gamma_{\text{phase1}} > \gamma_{\text{phase1}} + \gamma_{\text{phase2}})/100$ 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	0.315	0.043	0.000
digitigrade carnivore	0.000	1.000	0.000
plantigrade carnivore	1.000	0.000	0.793
scansorial carnivore	0.000	0.618	0.000
arboreal herbivore	0.997	0.367	1.000
digitigrade herbivore	0.023	0.654	0.024
fossorial herbivore	0.000	1.000	0.001
plantigrade herbivore	0.475	0.000	0.000
scansorial herbivore	1.000	0.000	0.778
unguligrade herbivore	0.000	1.000	0.000
arboreal insectivore	0.007	0.961	0.309
fossorial insectivore	1.000	0.000	0.796
plantigrade insectivore	0.001	0.189	0.000
scansorial insectivore	0.000	0.845	0.000
arboreal omnivore	0.999	0.000	0.000
plantigrade omnivore	1.000	0.289	1.000
scansorial omnivore	0.141	0.000	0.000
unguligrade omnivore	0.000	0.592	0.000

- 594 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).
- 596 Diversity partitioned by ecotype reveals a lot of the complexity behind the pattern of mammal
diversity for the Cenozoic (Fig. 15).
- 598 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).
- 600 Arboreal herbivores and omnivores obtain peak diversity at the beginning of the Cenozoic then go
into decline while remaining a small part of the species pool, while arboreal carnivores and
- 602 insectivores obtain peak diversity 52-50 Mya and then quickly decline and become extremely rare or
entirely absent from the species pool. This is consistent with increasing extinction risk in the
- 604 Neogene compared to the Paleogene as proposed by Smits (2015).

The diversity of digitigrade and unguligrade herbivores increases over the Cenozoic (Fig. 15). In

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	0.373	0.810	0.873
digitigrade carnivore	1.000	0.066	1.000
plantigrade carnivore	1.000	0.036	1.000
scansorial carnivore	1.000	0.019	1.000
arboreal herbivore	1.000	0.134	1.000
digitigrade herbivore	1.000	0.985	1.000
fossorial herbivore	1.000	0.919	1.000
plantigrade herbivore	1.000	0.996	1.000
scansorial herbivore	1.000	0.843	1.000
unguligrade herbivore	1.000	0.001	1.000
arboreal insectivore	0.096	0.996	1.000
fossorial insectivore	1.000	0.019	1.000
plantigrade insectivore	0.993	0.331	1.000
scansorial insectivore	1.000	0.293	1.000
arboreal omnivore	0.998	0.378	1.000
plantigrade omnivore	1.000	0.277	1.000
scansorial omnivore	0.999	0.353	1.000
unguligrade omnivore	1.000	0.224	1.000

606 contrast, plantigrade herbivore diversity does not have a single, broad-strokes pattern; instead,
 607 diversity increases, decreases, and may have then increased till the Recent. In contrast, fossorial and
 608 scansorial herbivores demonstrate a much flatter history of diversity, with a slight increase in
 609 diversity that over time is more pronounced among fossorial taxa than scansorial taxa. The
 610 expansion of digitigrade and unguligrade herbivores over the Cenozoic is consistent with the
 611 gradual expansion of grasslands which these ecotypes are better adapted to than closed
 612 environments (Blois and Hadly, 2009; Strömberg, 2005).

Digitigrade carnivores have a multi-modal diversity history, with peaks at 54-52 and 12-10 Mya
 614 (Fig.15). Between these two peaks digitigrade carnivore diversity dips below average diversity
 615 following the first peak and then grows slowly until the second peak. Plantigrade carnivores obtain
 616 peak diversity in the early Cenozoic and then maintain a relatively stable diversity until another
 617 peak at the end of the Cenozoic. The generally flat diversity history digitigrade carnivores lacks any

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	0.919	0.128	0.439
digitigrade carnivore	0.358	0.238	0.029
plantigrade carnivore	0.898	0.244	0.702
scansorial carnivore	0.462	0.480	0.373
arboreal herbivore	0.244	0.707	0.436
digitigrade herbivore	0.002	0.939	0.080
fossorial herbivore	0.491	0.696	0.822
plantigrade herbivore	0.593	0.331	0.343
scansorial herbivore	0.489	0.335	0.228
unguligrade herbivore	0.699	0.016	0.003
arboreal insectivore	0.735	0.370	0.610
fossorial insectivore	0.417	0.472	0.324
plantigrade insectivore	0.295	0.560	0.303
scansorial insectivore	0.034	0.935	0.464
arboreal omnivore	0.435	0.317	0.133
plantigrade omnivore	0.541	0.514	0.623
scansorial omnivore	0.286	0.493	0.176
unguligrade omnivore	0.212	0.534	0.189

618 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,
 620 1999)

There are some broad similarities in diversity histories of insectivorous and omnivorous taxa. The
 622 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
 624 approximately 10 Mya (Fig. 15). Arboreal and scansorial omnivores decrease in diversity from their
 initial peaks early in the Cenozoic, and plantigrade omnivores have a generally flat diversity history
 626 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
 628 scansorial omnivores.

Many of the estimated ecotype-specific diversity histories share a similar increase in diversity in the
 630 late Cenozoic, 16-14 Mya (Fig. 15). These increases are either sustained or temporary and are seen

Table 12: Posterior probabilities that 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	0.954	0.955
digitigrade carnivore	0.000	0.000
plantigrade carnivore	0.012	0.883
scansorial carnivore	0.000	0.001
arboreal herbivore	0.907	0.984
digitigrade herbivore	0.000	0.000
fossorial herbivore	0.000	0.003
plantigrade herbivore	0.998	0.996
scansorial herbivore	0.010	0.000
unguligrade herbivore	0.000	0.000
arboreal insectivore	0.117	0.684
fossorial insectivore	0.000	0.002
plantigrade insectivore	0.986	0.975
scansorial insectivore	0.989	0.997
arboreal omnivore	0.955	0.911
plantigrade omnivore	0.000	0.143
scansorial omnivore	0.708	0.607
unguligrade omnivore	0.978	0.944

in digitigrade carnivores, plantigrade carnivores, scansorial carnivores, unculigrade herbivores,

632 fossorial insectivores, and plantigrade omnivores.

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

634 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

636 sudden turnover as expected peaks in originations preceed peaks in the number of extinctions. Also,

it is clear that the sustained increases in digitigrade and unculigrade herbivore diversity observed

638 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).

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	0.060	0.062
digitigrade carnivore	0.000	0.001
plantigrade carnivore	0.014	0.098
scansorial carnivore	0.003	0.101
arboreal herbivore	0.709	0.833
digitigrade herbivore	0.000	0.000
fossorial herbivore	0.000	0.002
plantigrade herbivore	0.000	0.393
scansorial herbivore	0.100	0.003
unguligrade herbivore	0.006	0.000
arboreal insectivore	0.030	0.260
fossorial insectivore	0.014	0.003
plantigrade insectivore	0.173	0.055
scansorial insectivore	0.107	0.207
arboreal omnivore	0.659	0.649
plantigrade omnivore	0.015	0.104
scansorial omnivore	0.743	0.720
unguligrade omnivore	0.014	0.034

640 Discussion

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

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	0.716	0.704
digitigrade carnivore	0.289	0.071
plantigrade carnivore	0.800	0.902
scansorial carnivore	0.557	0.529
arboreal herbivore	0.241	0.831
digitigrade herbivore	0.725	0.828
fossorial herbivore	0.704	0.733
plantigrade herbivore	0.223	0.979
scansorial herbivore	0.328	0.458
unguligrade herbivore	0.809	0.545
arboreal insectivore	0.592	0.616
fossorial insectivore	0.675	0.276
plantigrade insectivore	0.437	0.697
scansorial insectivore	0.262	0.836
arboreal omnivore	0.490	0.576
plantigrade omnivore	0.487	0.507
scansorial omnivore	0.527	0.503
unguligrade omnivore	0.500	0.682

- 652 hypothesis that ecotypes or guilds are at least partially self-organizing and truly emergent (Scheffer
and van Nes, 2006).
- 654 Comparison of the results from the posterior predictive checks for the pure-presence and
birth-death models supports the conclusion that regional species pool dynamics cannot simply be
656 described by a single occurrence probability and are instead the result of the interplay between
origination and extinction. Additionally, changes to the ecotypic composition and diversification
658 rate for the North American regional species pool are driven primarily by variation in origination
rates. These aspects of how regional species pool diversity is shaped are not directly observable in
660 studies of the Recent where time scales are short and macroevolutionary dynamics are inferable
solely from phylogeny (Fritz et al., 2013).
- 662 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

- 664 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
666 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).
- 668 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;
670 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
672 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
674 dynamics of individual local communities, as this is an analysis of the entire North American
mammal regional species pool.
- 676 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
678 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
680 different selective regimes and, while the earliest Cenozoic may have been neutral with respect to
arboreal taxa, they disappeared quickly over the Cenozoic which may account for their higher
682 extinction risk. In addition to all arboreal taxa, the diversity of plantigrade and scansorial
insectivores decreases with time (Fig. 15).
- 684 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
686 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
688 of “control” on the diversity of this ecotype, such as diversity-dependent diversification (Silvestro
et al., 2015; Slater, 2015; Valkenburgh, 1999).
- 690 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
692 (Blois and Hadly, 2009; Graham, 2011; Strömberg, 2005) and may indicate a long-term shift in the
interactors associated with those ecotypes leading to increased contribution to the regional species
694 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
696 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
698 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
700 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
702 extinctions of all herbivore ecotypes (Fig. 17).

An association between plant phase and differences in ecotype occurrence or origination-extinction
704 probabilities is interpreted to mean that an ecotype enrichment or depletion is due to associations
between that ecotype and whatever plants are dominant at that time. Plant phase clearly
706 structures the occurrence and origination probability time series (Fig. 4, 5). These differences in
occurrence or origination translate to the estimates of diversity and diversification rate; the largest
708 spike in 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
710 particular transition is in scansorial carnivores (Fig. 15); similar shifts in other ecotypes are much
more subtle, as was previously noted for fossorial insectivores.

712 Interestingly, for all of the ecotypes with sudden changes in diversity at this transition the change is
an increase, even if only temporarily. There are two interpretations of these results. A biological
714 interpretation of this result is that, because plant phase associations are only with occurrence or
origination probabilities and not survival, these ecotypes were well suited for the newly available
716 mammal-plant interactions due to the increased modernization of their floral context (Graham,
2011). Alternatively, the increase in diversity associated with the third plant phase may be caused
718 by the edge effect in origination probability that is artificially inflating the number of origination

events (Fig. 5). However, the estimated number of origination events does not have a tremendous spike at this transition, nor is a major increase in the number of origination events sustained (Fig. 16).

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

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

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 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 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

746 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
748 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
750 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
752 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
754 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
756 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
758 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
760 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
762 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
764 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
766 birth-death model instead of one in continuous-time.

The effects of plant phase and temperature on ecotypes are approximately equal in importance. The
768 focus in previous research on temperature and major climatic or geological events without other
measures of environmental context may have led to confusion in discussions of how the
770 “environment” affects mammal diversity and diversification. The environment or climate is not just
global or regional temperature, it is the set of all possible biotic and abiotic interactions that can be
772 experienced by a member of the species pool. By including more descriptors of species’
environmental context a more complete “picture” of the diversification process is inferred.

774 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
776 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
778 the overall complexity of the model beyond the scope of the study. Instead, body size was included
in order to control for its possible underlying effects (McElreath, 2016). A control means that if
780 there is variation due to body mass, having a term to “absorb” that effect is better than ignoring it.

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

The potential effects of common ancestry (i.e. phylogeny) on origination and extinction are not
788 directly considered in this analysis. While a birth-death process approximates the
speciation-extinction process underlying the phylogeny (Silvestro et al., 2014) this is not same as
790 considering how the similarity between closely related species may affect the estimates of the effects
of species traits to environmental factors on both origination and extinction (Harnik et al., 2014;
792 Smits, 2015). The inclusion of phylogeny can help disentangle if the functional composition of
species diversity is shaped either by many closely related species occurring at the same time or if
794 closely related species are more evenly distributed in time; this is analogous to if species within
local communities are clumped or dispersed relative to their relatedness (Cavender-Bares et al.,
796 2009; Kraft et al., 2007; Webb et al., 2002). One of the principal barriers to the inclusion of the
effect of phylogeny in either the pure-presence or birth-death models is computational; with well
798 over 1000 tips, the calculation of the scale parameter defining the phylogenetic effect would be very
slow and further increase the already slow computation time necessary for the marginalization of all
800 possible discrete occurrence histories for z .

Conclusions

802 These results support the conclusion that the ecotypic diversity of the North American mammal
species pool has changed gradually over time. While there is constant species turnover for the entire
804 Cenozoic, there is little evidence of major cross-ecotype upheaval and sudden reorganization of the
functional composition of the regional species pool. The results of this study also support the
806 conclusion that mammal diversification over the Cenozoic is driven primarily by changes to
origination rate and not extinction rate. There are a number of interesting estimated ecotype
808 diversity patterns. While arboreal ecotypes are diverse in the Paleogene, by the Neogene all
arboreal ecotypes dramatically decreased in diversity and became either rare or absent from the
810 regional species pool. The other ecotypes that decrease in diversity over the Cenozoic are
plantigrade and scansorial insectivores and scansorial omnivores. The only ecotypes that
812 demonstrate a sustained pattern of increasing diversity are digitigrade and unguligrade herbivores.
When the environmental covariates analyzed here are inferred to affect the diversification of an
814 ecotype, this effect is virtually always for origination and not survival. This analysis provides a
much more complete picture of North American mammal diversity and diversification, specifically
816 the dynamics of the ecotypic composition of that diversity. By increasing the complexity of analysis
while precisely translating research questions into a statistical model, the context of the results is
818 much better understood. Future studies of diversity and diversification should incorporate as much
information as possible into their analyses in order to better understand or at least contextualize
820 the complex processes underlying that diversity.

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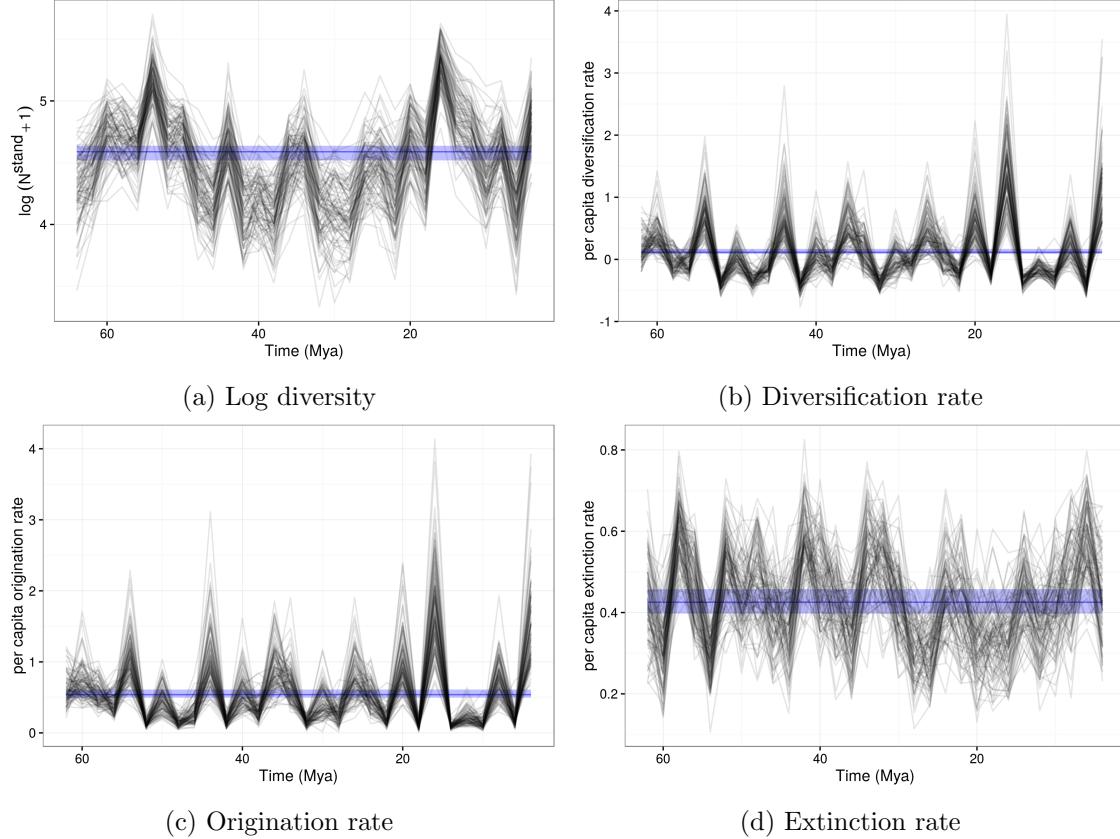


Figure 14: Posterior estimates of the time series of Cenozoic North American mammal diversity and its characteristic macroevolutionary rates; all estimates are from the birth-death model and 100 posterior draws are plotted to indicate the uncertainty in these estimates. The blue horizontal strip corresponds 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	0.07	0.63
62.00	0.28	0.94
60.00	0.86	0.13
58.00	0.68	0.18
56.00	0.62	0.99
54.00	1.00	0.00
52.00	0.68	0.41
50.00	0.80	0.00
48.00	0.12	0.04
46.00	0.01	0.98
44.00	0.64	0.00
42.00	0.02	0.47
40.00	0.03	0.08
38.00	0.00	0.89
36.00	0.40	0.46
34.00	0.52	0.00
32.00	0.02	0.27
30.00	0.06	0.09
28.00	0.02	0.88
26.00	0.22	0.39
24.00	0.38	0.03
22.00	0.09	0.96
20.00	0.81	0.00
18.00	0.29	1.00
16.00	1.00	0.00
14.00	0.95	0.02
12.00	0.80	0.01
10.00	0.13	0.83
8.00	0.67	0.00
6.00	0.02	1.00
4.00	0.91	

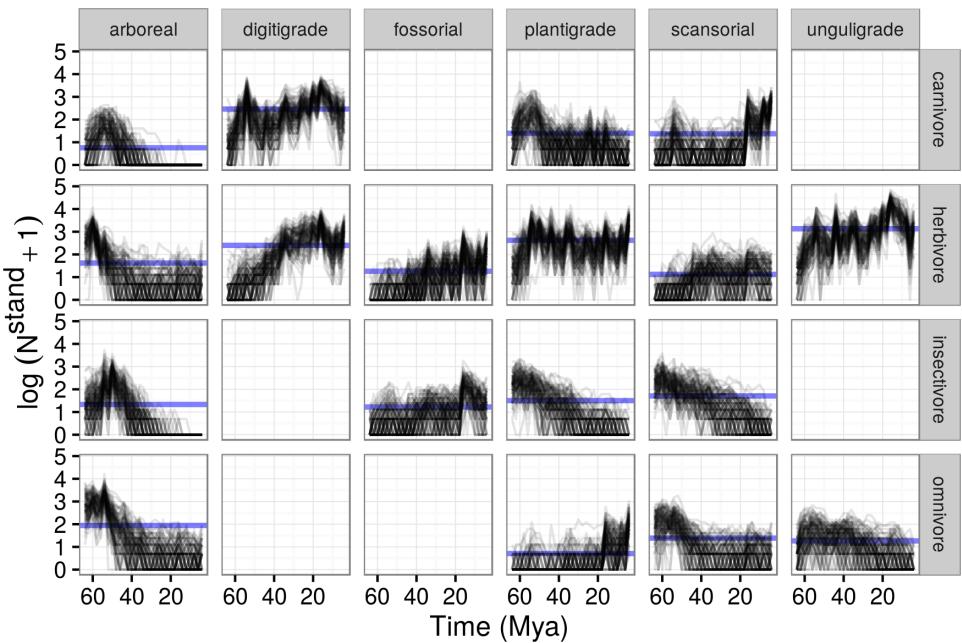


Figure 15: Posterior of standing log-diversity of North American mammals by ecotype for the Cenozoic as estimated from the birth-death model; 100 posterior draws are plotted to indicate the uncertainty in these estimates and what is technically plotted is log of diversity plus 1.

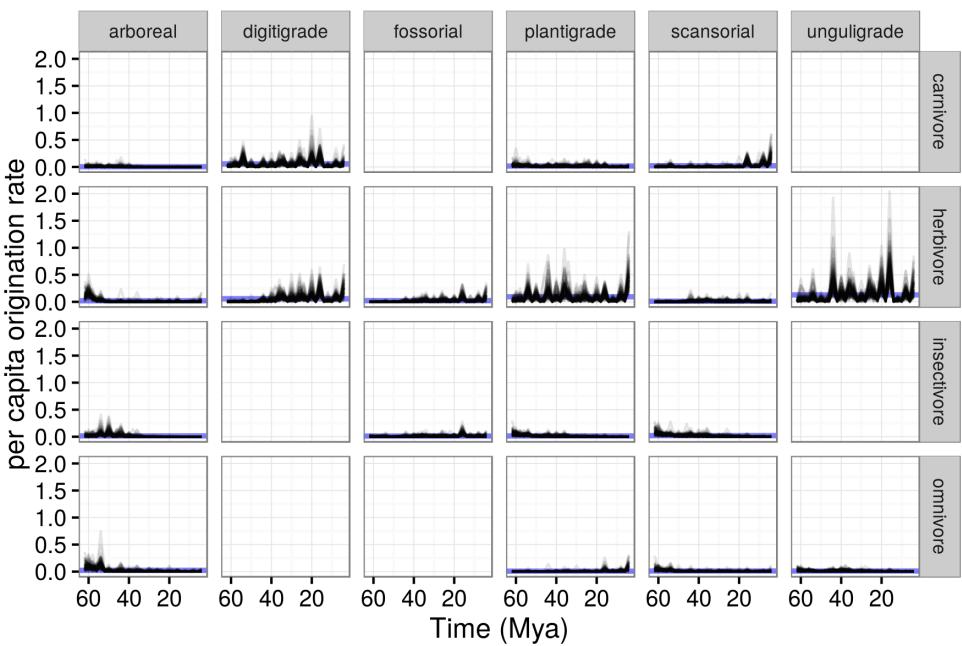


Figure 16: Posterior estimates of the number of origination events from one temporal bin to another, plotted at the bin they originate from. 100 posterior draws are plotted to indicate the uncertainty in these estimates. Also, what is plotted is log of the number of originations plus 1.

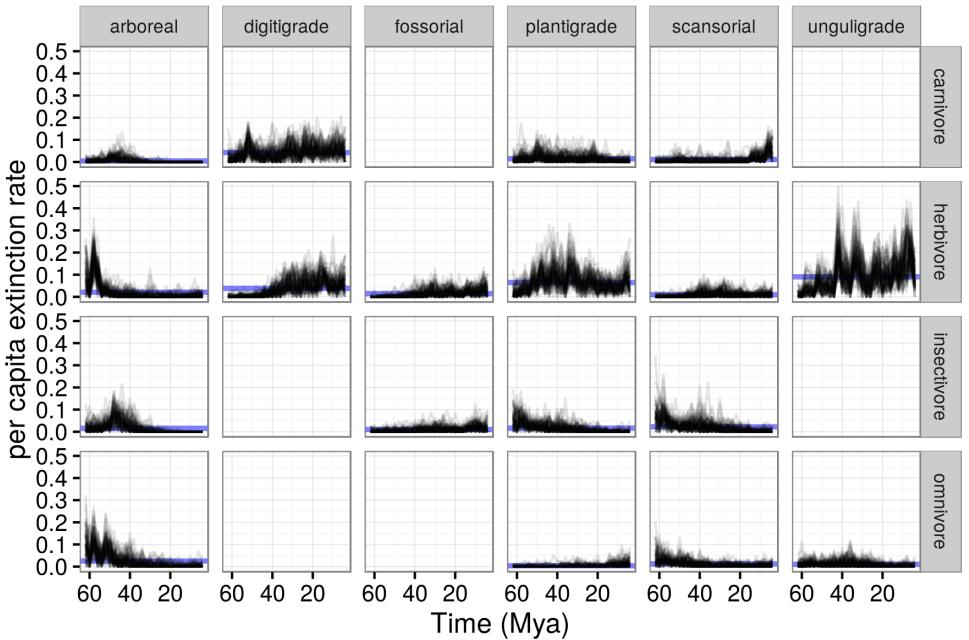


Figure 17: Posterior estimates of the number of extinction events from one temporal bin to another, plotted at the bin they go extinct from. 100 posterior draws are plotted to indicate the uncertainty in these estimates. Also, what is plotted is log of the number of extinctions plus 1.