

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

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Introduction

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

⁴ (Shakespeare, *As You Like It*, Act II, Scene VII)

A regional species pool is the set of species which form communities in a specific region; local communities are subsets of the regional pool. The composition of a regional species pool changes over time due to speciation, migration, extinction. Local scale processes like resource competition only affect the regional species pool if all communities are affected.

How do species pools change over time as species are recruited or go extinct? When are specific
10 species ecologies enriched or depleted in the environment? How does global and regional environmental context affect the distribution of species ecotypes (e.g. guilds) in a regional species pool?
12 All of these questions fall under a single umbrella of analysis of ecotypic diversity and diversification.

¹⁴ Guilds are a set of species with similar sets of interactions and interactors (i.e. macroecology) (Bambach, 1977; Valentine, 1969). Species within a guild are expected to have more similar
¹⁶ macroecological dynamics than species in different guilds. Building on the framework of guilds, (Bush et al., 2007) presented an ecocube for describing the position, motility, and trophic role of
¹⁸ marine invertebrates. Unique combinations along the three ecological trait axes represent which among the possible ecotypes are observed. This approach has proven quite popular as it attempts
²⁰ to operationalize the guild in terms of shared characteristics (Bambach et al., 2007; Bush and Bambach, 2011; Bush et al., 2007), but the overall utility of this approach is limited due to its
²² condition as just a data type.

Analysis of mammal diversity and hypotheses as to the processes that have shaped it tend to fall
24 into one or more of the following categories: diversity of an entire system (e.g. continent) (Alroy,
1996; Alroy et al., 2000; Figueirido et al., 2012; Liow et al., 2008), guild based (Janis et al., 2004;
26 Janis, 2008; Janis et al., 2000; Janis and Wilhelm, 1993; Jernvall and Fortelius, 2004; Pires et al.,

2015), clade based (Quental and Marshall, 2013; Silvestro et al., 2015; Slater, 2015), climate based
28 (Blois and Hadly, 2009; Janis, 1993; Janis and Wilhelm, 1993), and location based (Badgley and
Finarelli, 2013; Eronen et al., 2015). Rarely are more than two of these categories considered
30 simultaneously, and instead integration of these diverse observations and hypotheses tends to be
based on coincidence. One of the goals of this study is to present a framework for simultaneously
32 analyzing a diversity of hypotheses by pulling information from multiple levels of organization by
integrating both species traits and environmental factors into a single analysis in order to infer a
34 more holistic picture of the processes which may have shaped mammal species diversity.

In the analyses done here, a few key covariates which describe species' macroecology and
36 environmental context are considered. Because of the complexity inherent in this question and
related analysis in terms of both number of covariates considered and structure of each model, it is
38 possible to consider and test a large number of possible hypotheses. The analytical approach used
here is appropriate for mitigating complications arising from this complexity (e.g. multiple
40 comparisons, garden of forking paths) CITATIONS.

The principle species trait considered in this study is a species' ecotype, defined here as the unique
42 combination of species dietary category and locomotor category (e.g. arboreal omnivore versus
unguligrade herbivore). This classification can be considered analogous to a guild or unique ecocube
44 combination as discussed above (Bambach et al., 2007; Bush and Bambach, 2011; Bush et al., 2007).
Species mass was also included as a species trait, but is mostly included in order to control for that
46 effect on species observation and occurrence.

There is no previous evidence of any major turnover events in history of North American mammal
48 diversity, unlike the Neogene record European mammals (Alroy, 1996, 2009; Alroy et al., 2000;
Eronen et al., 2015; Janis, 1993). There is also little evidence for simultaneous changes in
50 cross-ecotype or cross-guild diversity. Instead, turnover is distributed through time. It is then
expected then that turnover events or periods of rapid diversification or depletion should not occur
52 simultaneously for all ecotypes.

Translating previous work into hypotheses applicable to this analysis is difficult for a variety of

54 reasons. Taxonomic groupings such as order or family are frequently invoked as an important factor
in many proposed hypotheses for how mammal diversity is structured (Janis, 2008; Janis and
56 Wilhelm, 1993; Pires et al., 2015; Quental and Marshall, 2013; Slater, 2015). Because taxonomic
grouping conflates both species macroecology or guild membership with shared evolutionary history,
58 there are no clear hypotheses as to macroecological change viewed through the lens of species
interactions. Specifically, this issue arises when trying to generalize previous observations from
60 taxonomy-based to ecology-based hypotheses.

Jernvall and Fortelius (2004) found that for the Neogene of Europe the relative abundance of
62 mammal guilds was stable over time even in the face of high turnover rates, though they only
considered large bodied taxa from a small set of mammal orders. Similar results have been observed
64 for some taxonomic groups in North America CITATIONS.

Many discussions of the effects or associates of species ecology and diversity have focused on
66 ungulate herbivores (Janis et al., 2004; Janis, 2008; Janis et al., 2000; Janis and Wilhelm, 1993) and
carnivores (Janis and Wilhelm, 1993; Pires et al., 2015; Silvestro et al., 2015; Slater, 2015).

68 The diversity history of ungulate herbivores is characterized by more recently originating taxa
having longer legs, higher crowned teeth, and a shift from graze-dominated to browse-dominated
70 diets than their earlier originating counterparts (Janis et al., 2004; Janis, 2008; Janis et al., 2000;
Janis and Wilhelm, 1993); all of which have all been attributed to some combination of
72 environmental change and tectonic activity driving that environmental change (Blois and Hadly,
2009; Eronen et al., 2015; Janis, 2008). Additionally, it has been observed that ungulate cursorial
74 forms arose prior to cursorial carnivore forms, an observation attributed to the reorganization of
plant communities towards the end of the Cenozoic and the latter emergence of “modern”
76 environments and communities (Janis and Wilhelm, 1993).

Within the canid guild of North America (e.g. plantigrade and digitigrade carnivores) there is
78 evidence that their diversity is self-regulating or somehow limited. Specifically, it has been proposed
that different clades of “canids” have replaced each other as dominating that macroecological role
80 in the species pool (Silvestro et al., 2015). A pattern of generally constant diversity through time is

also observed within the canid carnivore subguilds of hypercarnivore, hypocarnivore, and
82 mesocarnivores even in the face of constant species turnover is consistent with limited possibility of
increased diversity, even though there was no evidence of diversity-dependence in trait (e.g. body
84 size) evolution (Slater, 2015).

There is some uncertainty as to the effect of species body size on mammal diversity and aspects of
86 the diversification processes, specifically extinction (Liow et al., 2008, 2009; Smits, 2015; Tomiya,
2013). Species body size is frequently framed as an important biological descriptor because of how
88 correlated this trait is with other traits such as metabolic rate and home range size CITATIONS. It
is also relatively easy to estimate the body mass of extinct species using proxy measures and
90 regression equations, as was done in this study (see below). However, body size is normally
considered in other studies without reference to other ecological descriptors of the species
92 CITATION, but see (Smits, 2015). Additionally, this high amount of correlation between life history
traits and body size limits process-based inference and hypothesis testing because the actual
94 mechanisms underlying any observed pattern are obscured.

Smits (2015) found several systematic differences in mammal species durations associated with
96 various species traits. Omnivorous taxa were found to have, on average, a greater duration than
other dietary categories. Additionally, arboreal taxa were found to have a shorter duration than
98 other locomotor categories. An unresolved question from Smits (2015) is whether the greater
extinction risk faced by arboreal is constant over time or if there was a change in extinction risk at
100 the Paleogene/Neogene boundary. Each of these possible explanations for the results of Smits
(2015) have clear and testable predictions for this analysis. Specifically, 1) the extinction risk
102 arboreal taxa increased in the Neogene compared to the Paleogene, driving the average extinction
risk of arboreal mammals up and leading to the loss of arboreal taxa from the species pool, or 2) if
104 arboreal taxa have just a generally higher extinction risk than other ecotypes but have maintained
a constant diversity for the Cenozoic.

106 Fundamentally, all species respond differently to climate and environmental change (Blois and
Hadly, 2009). Macroecological patterns are the similarities across species and the emergent

¹⁰⁸ properties of how species react to a similar “stimulus.”

The effect of climate on diversity and the diversification process has been the focus of considerable
¹¹⁰ research with many analyses favoring diversification being more biologically-mediated than
climate-mediated (Alroy, 1996; Alroy et al., 2000; Clyde and Gingerich, 1998; Figueirido et al.,
¹¹² 2012). Both temporal and geographic scale of analysis can make a big difference in the
interpretation of results. For example when the mammal fossil record analyzed at small temporal
¹¹⁴ and geographic scales a correlation between diversity and climate are observable (Clyde and
Gingerich, 1998). However, when the record is analyzed at the scale of the continent and most of
¹¹⁶ the Cenozoic there is no correlation with diversity and climate (Alroy et al., 2000). This results,
however, does not go against the idea that there may be short periods of correlation and that the
¹¹⁸ correlation between diversity and climate or even reverse direction over time; instead this result
means that there is no single direction of correlation between diversity and climate (Figueirido
¹²⁰ et al., 2012).

In the case of a fluctuating correlation between diversity and climate it is hard to make the
¹²² argument of an actual causal link between the two without modeling the underlying ecological
differences between species; when this analysis is based on diversity or taxonomy alone no
¹²⁴ mechanisms are possible to infer. Taxonomy, like body size, stands in for many important species
traits to the point that mechanistic or process based inference is impossible. While emergent
¹²⁶ patterns might correspond to taxonomic grouping, this itself is an emergent phenomenon. Instead,
by framing hypotheses in terms of species traits and their environmental context, these emergent
¹²⁸ phenomenon are actually being studied as opposed to be assumed.

The Cenozoic is generally characterized by a global cooling trend and the development of polar
¹³⁰ ice-caps during the Neogene, though there are a few notable exceptions to this broad
characterization (Cramer et al., 2011; Zachos et al., 2008, 2001). The Cenozoic of North America is
¹³² additionally characterized by an environmental transition from the closed, partially forested
environments of the Paleogene to the savannah and grasslands environments of the Neogene (Blois
¹³⁴ and Hadly, 2009; Janis, 1993; Janis et al., 2000; Strömberg, 2005).

A lot of the climate and environmental changes observed for North America have been attributed to
136 tectonic activity and uplift (Badgley and Finarelli, 2013; Blois and Hadly, 2009; Eronen et al., 2015;
Janis, 2008) CITATIONS. Additionally, tectonic activity and uplift is considered the causal
138 mechanism secondarily behind both the diversification process and trait evolution (Badgley and
Finarelli, 2013; Blois and Hadly, 2009) CITATIONS. Tectonic uplift changes weather patterns (e.g.
140 rain shadow) and mobilizes grit into the environment. Increased grit in the environment combined
with decreased rain fall is considered the primary reason behind the trend of increased hypsodonty,
142 or high crowned teeth, among herbivore groups over the Cenozoic of both North America and
Europe CITATIONS.

144 The Eocene-Oligocene transition is associated with high extinction amongst ungulate taxa (Janis,
2008). This period is also the transition from the Paleogene to the Neogene and from herbivores
146 being browsing dominated to grazing dominated CITATION. This transition is marked by WHAT?
This transition is associated globally with the appearance of ice caps WHERE? Additionally, this
148 transition is marked by GRASS? There is an observed stability in estimates of global temperature
from the E/O transition till the end of the Miocene; this is called the Mid-Miocene climatic
150 optimum (Zachos et al., 2008, 2001). The Mid-Miocene climatic optimum is bookended by periods
of temperature decline. We would then expect that, for the Miocene, turnover and other
152 diversification events would most likely be biologically mediated because of the constancy of
climate, and that for groups that are driven primarily by environmental factors, the Miocene would
154 be a period of marked by an absence of major changes to diversity or the diversification process.

The environmental factors included in this study are estimates of global temperature and the
156 changing floral groups present in North America across the Cenozoic. These covariates were chosen
because they provide high level characterizations of the environmental context of the entire North
158 American regional species pool for most of the Cenozoic. Importantly, the effects of a species
ecotype on diversity are themselves modeled as functions of environmental factors (Fig. 1) allowing
160 for inference as to how species ecology mediates environmental context.

Fourth-corner modeling is an approach to explaining the patterns of either species abundance or

¹⁶² presence/absence as a product of species traits, environmental factors, and the interaction between
traits and environment (Brown et al., 2014; Jamil et al., 2013; Pollock et al., 2012; Warton et al.,
¹⁶⁴ 2015) CITATION. In modern ecological studies, what 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
¹⁶⁶ being modeled is the pattern of species occurrence over time for most of the Cenozoic in North
America (Fig. 1). These two approaches, modern and paleontological, are different views of the same
¹⁶⁸ three-dimensional pattern: species at localities over time. The temporal limitations of modern
ecological studies and difficulties with uneven spatial occurrences of fossils in paleontological studies
¹⁷⁰ means that these approaches are complimentary but reveal different patterns of how species are
distributed in time and space.

¹⁷² All observations, paleontological or modern, are made with uncertainty CITATIONS. With
presence/absence data this uncertainty comes from now knowing if an absence is a “true” absence
¹⁷⁴ or just a failure to observe (Foote, 2001; Foote and Sepkoski, 1999; Lloyd et al., 2011; Royle and
Dorazio, 2008; Royle et al., 2014; Wang and Marshall, 2016). For paleontological data, the
¹⁷⁶ incomplete preservation of whatever species were present into fossil form combined with incomplete
sampling of what fossils are present means that the true times of origination or extinction may not
¹⁷⁸ be observed (Foote, 2001; Foote and Sepkoski, 1999; Wang et al., 2016; Wang and Marshall, 2016).

Ultimately, the goal of this analysis are to understand when are unique ecotypes enriched or
¹⁸⁰ depleted in the North American mammal regional species pool and how changes in ecotypic
diversity are related to changes in species’ environmental context.

¹⁸² Materials and Methods

Taxon occurrences and species-level information

¹⁸⁴ All fossil occurrence information used in this analysis was downloaded from the
Paleobiology Database (PBDB). The initial download restricted all occurrences to all Mammalia
¹⁸⁶ observed in North America between the Maastrichtian and Gelasian stages. Occurrences were then

further limited to those occurring between 64 and 2 million years ago (Mya). Taxonomic,
188 stratigraphic, and ecological metadata for each occurrence was included. A new download for a raw,
unfiltered PBDB datafile following the same criterion used here is available at
190 <http://goo.gl/2s1geU>. The raw datafiles used as a part of this study, along with all code for
filtering and manipulating this download is available at GITHUB.
192 After download, the raw occurrence data was then sorted, cleaned, and manipulated
programmatically prior to analysis. Many species taxonomic assignments as present in the raw
194 PBDB data were updated for accuracy and consistency. For example, species classified in the order
Artiodactyla were reclassified as Cetartiodactyla. These re-assignments follow Smits (2015) which
196 were based on taxonomies present in the Encyclopedia of Life WEBSITE and Janis et al. (2008,
1998). All taxa who's life habit was classified as either volant (i.e. Chiroptera) or aquatic (e.g.
198 Cetacea) were excluded from this analysis because of both differences in fossilization potential and
environmental context as well as their lack of direct applicability to the study of terrestrial species
200 pools.

Species ecotype is defined as the interaction between life habit and diet categories, the goal of
202 which is to classify species based on the manner they interact with their environment. Most species
records in the PBDB have life habit and dietary category assignemnts. In order to simplify
204 interpretation, analysis, and per ecotype sample size these classifications were coarsend in a similar
manner to (Smits, 2015) following Table 1. Additionally for this study, the life history category was
206 further broken up to better reflect the many locomotor modes employed by mammals. Specifically,
species were reassigned based on their ankle posture associated with their taxonomic group as
208 described in Table 2 (Carrano, 1999). Ecotype categories with less than 10 species havig ever been
that combination were excluded, yielding a total of 18 of 24 possible ecotypes.

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

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

Table 2: Ankle posture assignment as based on taxonomy. Assignments are based on (Carrano, 1999). Taxonomic groups are presented alphabetically and without reference for the nestedness of families in orders. As such, do not infer higher-order structure from this table.

Order	Family	Stance
	Ailuridae	plantigrade
	Allomyidae	plantigrade
	Amphicyonidae	plantigrade
	Amphilemuridae	plantigrade
	Anthracotheriidae	digitigrade
	Antilocapridae	unguligrade
	Apheliscidae	plantigrade
	Aplodontidae	plantigrade
	Apternodontidae	scansorial
	Arctocyonidae	unguligrade
	Barbourofelidae	digitigrade
	Barylambdidae	plantigrade
	Bovidae	unguligrade
	Camelidae	unguligrade
	Canidae	digitigrade

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Table 2 – continued from previous page

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

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Table 2 – continued from previous page

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

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Table 2 – continued from previous page

Order	Family	Stance
	Oromyctidae	unguligrade
	Oxyaenidae	digitigrade
	Palaeomerycidae	unguligrade
	Palaeoryctidae	plantigrade
	Pampatheriidae	plantigrade
	Pantolambdidae	plantigrade
	Periptychidae	digitigrade
Perissodactyla		unguligrade
	Phenacodontidae	unguligrade
Primates		plantigrade
	Procyonidae	plantigrade
	Proscalopidae	plantigrade
	Protoceratidae	unguligrade
	Reithroparamyidae	plantigrade
	Sciuravidae	plantigrade
	Sciuridae	plantigrade
	Simimyidae	plantigrade
	Soricidae	plantigrade
	Suidae	digitigrade
	Talpidae	fossorial
	Tayassuidae	unguligrade
	Tenrecidae	plantigrade
	Titanoideidae	plantigrade
	Ursidae	plantigrade
	Viverravidae	plantigrade

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Table 2 – continued from previous page

Order	Family	Stance
	Zapodidae	plantigrade

210

Estimates of species mass used as a covariate in this study were sources from multiple databases
 212 and papers, especially those focusing on similar macroevolutionary or macroecological questions; this
 is similar to what was done in Smits (2015). When species mass was not available, proxy measures
 214 were used and then transformed into estimates of mass. For example, given a measurement of a
 mammal tooth size, it is possible and routine to estimate its mass given some regression equation.
 216 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
 218 mean-centered and rescaled by dividing by two-times its standard deviation; this insures that the
 magnitude of effects for both continuous and discrete covariates are comparable (Gelman, 2008;
 220 Gelman and Hill, 2007).

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	?
General	$\log(m) = 3.68x - 3.83$	skull length	?
Carnivores	$\log(m) = 2.97x + 1.681$	lower m1 length	?
Insectivores	$\log(m) = 1.628x + 1.726$	lower m1 area	?
Insectivores	$\log(m) = 1.714x + 0.886$	upper M1 area	?
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	?
Marsupials	$\log(m) = 1.733x + 1.571$	upper M1 area	?
Rodentia	$\log(m) = 1.767x + 2.172$	lower m1 area	Legendre (1986)
Ungulates	$\log(m) = 1.516x + 3.757$	lower m1 area	?
Ungulates	$\log(m) = 3.076x + 2.366$	lower m2 length	?
Ungulates	$\log(m) = 1.518x + 2.792$	lower m2 area	?
Ungulates	$\log(m) = 3.113x - 1.374$	lower toothrow length	?

All fossil occurrences from 64 to 2 million years ago (Mya) were binned into 31 2 million year (My) bins. This temporal length was chosen because it is approximately the resolution of the North American mammal fossil record (Alroy, 1996; Alroy et al., 2000; Marcot, 2014).

224 Environmental and temporal covariates

The environmental covariates used in this study are collectively referred to as group-level covariates because they predict the response for a “group” of individual-level observations (i.e. species occurrences). Additionally, these covariates are defined for temporal bins and not the 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 phases” defined by Graham CITATION. Global temperature across most of the Cenozoic was calculated from Mg/Ca isotope record from deep sea carbonates (Cramer et al., 2011). Mg/Ca based temperature estimates are preferable to the frequently used $\delta^{18}\text{O}$ temperature proxy (Alroy et al., 2000; Figueirido et al., 2012; Zachos et al., 2008, 2001) because Mg/Ca estimates do not conflate temperature with ice sheet volume and depth/stratification changes. The former is particularly important to this analysis as the current polar ice-caps appeared and grew over the Cenozoic. These properties make Mg/Ca based temperature estimates preferable for macroevolutionary and macroecological studies (Ezard et al., 2016).

238 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 240 mean and range were then rescaled by subtracting the mean and then dividing by twice the standard deviation.

242 The other major set of environmental factors included in this study are the Cenozoic plant phases defined in Graham CITATION. Graham’s plant phases are holistic descriptors of the taxonomic 244 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 246 CITATION. Graham CITATION defines four intervals from the Cretaceous to the Pliocene, though

		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 4: Transition matrices for the pure-presence (4a) and birth-death (4b) 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).

only three of these intervals are included in this analysis. Graham’s plant phases CITATION was included as a series of “dummy variables” encoding the three phases included in this analysis. This means that the first phase is synonymous with the intercept and phases

250 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 hidden Markov model where the latent aspect of the process has an absorbing state (Allen, 2011). The difference between these two models is if the probabilities of a species originating or surviving are considered equal or different (Table 4). Something that is important to realize is that while there are only two state “codes” in a presence-absence matrix (i.e. 0/1), there are in fact three states in a birth-death model: never having originated, extant, and extinct. The last of these is the absorbing state, as once a species has gone extinct it cannot re-originate (Allen, 2011); this is made obvious in the transition matrices as the probability of an extinct species changing states is 0 (Table 4). See below for parameter explanations (Tables 6, and 7).

Data augmentation

All presence/absence observations are incomplete. The hidden Markov model at the core of this analysis allows for observed absences to be used meaningfully to estimate the number of unobserved

- 264 species. Of specific concern in this analysis is the unknown “true” size of the dataset; how many
 265 species could have actually been observed? While many species have been observed, the natural
 266 incompleteness of all observations, especially in the case of paleontological data, there are obviously
 267 many species which were never sampled (Royle and Dorazio, 2008; Royle et al., 2007).
- 268 Let N by the total number of observed species, M be the upper limit of possible species that could
 269 have existed given a model of species presence, and N^* is the all-zero histories where $N^* = M - N$.
 270 This approach assumes that $\hat{N} \sim \text{Binomial}(M, \psi)$ where \hat{N} is the estimated “true” number of
 271 species and ψ is the probability that any augmented species should actually be “present.” Because
 272 M is user defined, this approach effectively gives ψ a uniform prior over N to M (Royle and
 273 Dorazio, 2008). For this study, $M = \lfloor 1.35 \times N \rfloor$.
- 274 Data imputation is the process of estimating missing data for partially observed covariates (Gelman
 275 and Hill, 2007; Rubin, 1996), this is simple in a Bayesian context because data are also parameters
 276 (Gelman et al., 2013). Augmented species also have no known mass so a mass estimate must be
 277 imputed for each possible species (Royle and Dorazio, 2012). This procedure assumes that mass
 278 values for augmented species are from the same distribution as observed species. The distribution of
 279 observed mass values is estimated as part of the model, and new mass values are then generated
 280 from this distribution. This approach is an example of imputing data missing completely at random
 281 (Gelman and Hill, 2007; Royle and Dorazio, 2012). Because log mass values are rescaled as a part of
 282 this study, the body mass distribution is already known ($\mathcal{N}(0, 0.5)$) so the body mass of the
 283 augmented species are generated by simple random draws from this distribution.
- 284 In addition to body mass information, the augmented species need an ecotype classification. Because
 285 these species are completely unknown, they were all classified as “augmented,” an additional
 286 grouping indicating their unknown biology. This classification has no biological interpretation.

Observation process

- 288 The type of hidden Markov model used in this study has three characteristic probabilities:
 289 probability p of observing a species given that it is present, probability ϕ of a species surviving from

Table 5: Observation parameters

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

one time to another, and probability π of a species first appearing (Royle and Dorazio, 2008). In this formulation, the probability of a species going extinct is $1 - \pi$. For the pure-presence model $\phi = \pi$, while for the birth-death model $\phi \neq \pi$.

The probability of observing a species that is present p is modeled as a logistic regression was a time-varying intercept and species mass as a covariate. The effect of species mass on p was assumed 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. The parameters associated with this part of the model are described in Table 5.

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

298 Pure-presence process

For the pure-presence model there is only a single probability dealing with the presence of a species (Table 4a). This probability was modeled as multi-level logistic regression with both species-level and group-level covariates (Gelman et al., 2013; Gelman and Hill, 2007). The parameters associated with pure-presence model are presented in Table 6 and the full sampling statement in Equation 2.

The species-level of the model (Eq. 2) is a logistic regression where the intercept varies by ecotype.

Table 6: 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

304 Additionally, species mass was included as a covariate associated with two regression coefficients
 305 allowing a quadratic relationship with log-odds of occurrence. This assumption is based on the
 306 known distribution of mammal body masses where species with intermediate mass values are more
 307 common than either small or large bodied species. These assumptions are also reflected in the
 308 choice of priors for these regression coefficients.

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

314 All parameters not modeled elsewhere were given weakly informative priors (Gelman et al., 2013)
 315 CITATION STAN MANUAL STATISTICAL RETHINKING. Weakly informative means that
 316 priors do not necessarily encode actual prior information but instead help regularize or weakly
 317 constrain posterior estimates. These priors have a concentrated probability density around and near
 318 zero; this has the effect of tempering our estimates and help prevent overfitting the model to the
 319 data (Gelman et al., 2013) CITATION STAN MANUAL STATISTICAL RETHINKING. The
 320 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.

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

³²² Birth-death process

In the birth-death version of the model, $\phi \neq \pi$ and so each of these probabilities are modeled
³²⁴ separately but in a similar manner to how θ is modeled in the pure-presence model (Eq. 2, Table
4b). The parameters associated with the birth-death presence model are presented in Table 7 and
³²⁶ the full sampling statement, including observation (Eq. 1), is described in Equation 3.

Similar to the pure-presence model, both ϕ and π are modeled as logistic regressions with
³²⁸ varying-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
³³⁰ priors (Eq. 3).

The intercepts of ϕ and π both vary by species ecotype and those values are themselves the product
³³² of group-level regression using environmental factors as covariates (Eq. 3); this is identical to the

Table 7: 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).

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

³³⁴ **Posterior inference and model adequacy**

Programs that implement joint posterior inference for the above models (Eqs. 2, 3) were
³³⁶ implemented in the probabilistic programming language Stan CITATION. The models used here
both feature latent discrete parameters in the large matrix z (Tables 5, 6, 7; Eqs. 1, 2, 3). All
³³⁸ methods for posterior inference implemented in Stan are derivative based which causes
complications for actually implementing the above models because integers do not have derivatives.
³⁴⁰ Instead of implementing a latent discrete parameterization, the posterior probabilities of all possible
states of the latent parameters z were estimated (i.e. marginalized).

³⁴² Species durations at minimum range-through from the FAD to the LAD, but the incompleteness of
all observations means that the actual time of origination or extinction is unknown. The
³⁴⁴ marginalization approach used here means that the probabilities all possible histories for a species
are calculated, from the end members of the species having existed for the entire study interval and
³⁴⁶ the species having only existed between the directly observed FAD and LAD to all possible
intermediaries CITATION STAN MANUAL. This process is identical, language-wise, to assuming
³⁴⁸ range-through and then estimating the possibility of range extension due to incomplete sampling.

The combined size of the dataset and large number of parameters in both models (Eqs. 2, 3),
³⁵⁰ specifically the total number of latent parameters that are the matrix z , means that stochastic
approximate posterior inference is computationally very slow even using HMC. Instead, an
³⁵² approximate Bayesian approach was used: variational inference. A recently developed automatic
variational inference algorithm called “automatic differentiation variational inference” (ADVI) is
³⁵⁴ implemented in Stan and was used here CITATION. ADVI assumes that the posterior is Gaussian
but still yields a true Bayesian posterior; this assumption is similar to quadratic approximation of
³⁵⁶ the likelihood function used in maximum likelihood inference CITATION. The principal limitation
of assuming the joint posterior is Gaussian is that the true topology of the log-posterior isn’t
³⁵⁸ estimated; this is a particular burden for scale parameters which are bound to be positive (e.g.
standard deviation).

³⁶⁰ After fitting both models (Eqs. 2, 3) using ADVI, model adequacy and quality of fit was assessed

using a simple posterior predictive check CITATION CITATION. Because all Bayesian models are
 362 inherently generative, simulations of new data sets is “free” CITATION. By simulating many
 theoretical data sets using the observed covariate information the congruence between predictions
 364 made by the model and the observed empirical data can be assessed. By combining multiple
 posterior predictive tests of congruence between empirical and simulated values of interest, the
 366 holistic adequacy of the model can be analyzed CITATION. The ADVI assumption of a purely
 Gaussian posterior limits the utility and accuracy of the posterior predictive checks because
 368 parameter estimates do not reflect the true posterior distribution and are instead just an
 approximation. Because of this, posterior predictive estimates are themselves only approximate
 370 checks of model adequacy. The posterior predictive check that is used in this study focuses on mean
 occurrence and not to any scale parameters that might be most affected by the ADVI assumptions.
 372 An example posterior predictive check used in this study was comparing the observed average
 number of observations per species to a distribution of simulated averages; if the empirically
 374 observed value sits in the middle of the distribution than the model is adequate in reproducing the
 observed number of occurrences per species.
 376 Posterior simulations for time series are start with the values at $t = 1$ and then just simulating
 forward.
 378 Given parameter estimates, diversity and diversification rates are estimated through posterior
 predictive simulations. Given the observed presence-absence matrix y , estimates of the true
 380 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
 382 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

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

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

estimated as

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

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

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

388 Results

The posterior estimates and analysis in this study take one of two forms: direct inspection of
390 parameter estimates from both models, and downstream estimates of diversity and diversification
rates based on posterior predictive simulations from the birth-death model as explained below in
392 the comparison of the models' posterior predictive check results.

Comparing parameter estimates from the pure-presence and birth-death 394 models

Comparison of the posterior predictive results from the pure-presence and birth-death models
396 reveals a striking difference in the ability for the model to predict the structure of the underlying
data (Fig. 3). The simulated datasets generated from the birth-death model are clearly able to
398 better reproduce the observed average number of occurrence than the pure-birth model which
greatly underestimates the observed average number of occurrences. This result means that
400 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
402 parameter estimates from both models can provide further insight into the reasons for this difference
in posterior predictive results (Gelman et al., 2013).

404 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) as opposed to the estimates
406 of survival probability (Fig. 6). This result supports the idea that changes to the North American
regional species pool is more likely due to changes to origination than extinction, a result that is
408 returned to later in the discussion of per-capita diversification, origination, and extinction rates.

For most ecotypes, both estimated occurrence probabilities from the pure-presence model (Fig. 4)
410 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
412 had that occurrence by the last time point, so our certainty in a species occurring must increase
with time. Notably, ecotypes with arboreal components do not appear to follow a similar pattern;
414 instead, occurrence and origination probabilities appear relatively flat for most of the Cenozoic.

The dramatic differences in the estimates origination and survival probabilities are indicative of
416 how differently these processes affect the diversification process and may also be responsible for the
better posterior predictive performance of the birth-death model over the pure-presence model (Fig.
418 3a, and 3b). While the estimates at all points along both time series have high variance, what is
striking is how mean origination probability changes over time while most ecotype survival
420 probabilities have relatively stable means for the entire Cenozoic (Fig. 5, and 6).

For most ecotypes, the estimates of origination probabilities are with less uncertainty than similar
422 estimates of survival probabilities (Fig. 5, and 6). In logistic regression, high uncertainty in the
estimates of the underlying log-odds of occurrence, origination, or survival tends to be indicative of
424 extreme rarity or complete absence of the specific ecotype; the latter is called complete separation
which occurs when there is no uncertainty in the effect of a covariate on presence/absence, the
426 effect of which has been mitigated by the hierarchical modeling strategy used here (Gelman et al.,
2013; Gelman and Hill, 2007) CITATION Statistical Rethinking.

428 The pure-presence and birth-death models also differ in the estimated effect of mass on the
429 probability of sampling a species that is present (Fig. 7). For the pure-presence model, mass is
430 estimated to not have a great effect on the probability of sampling a species that is presence (Fig.
431 7a). Contrastingly, for the birth-death model mass is found to have a negative relationship with
432 observation such that larger species are less likely to be observed if present than smaller species
(Fig. 7b).

434 The result from the birth-death model may be considered unexpected given that it is generally
435 assumed that larger mammals are more likely to have been collected than smaller mammals
436 CITATION. However, collection is not preservation; similarities in preservation rate indicate
437 similarities in how gap-filled species records are. What this result means is that the record of large
438 bodied species is expected on average to have more gaps in sampling and less consistent from time
439 point to time point than smaller bodied species. Additionally, as this is presence/absence data
440 higher preservation and collection in terms of individual specimens at a location or a single
441 temporal horizon does not necessarily translate to high preservation over time.

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

The effect of species mass on probability of occurrence as estimated from the pure-presence (Fig. 8)
450 are most similar to the estimated effect of species mass on probability of origination for the
451 birth-death model (Fig. 9). The striking pattern observable in both sets of estimates is the higher
452 probability of occurrence for species with body sizes closer to the mean than either extremes. This
453 result is consistent with the canonically normal distribution of mammal body sizes CITATION; it is
454 then expected that the most likely to occur species would be those from the middle of the

distribution, and that species originating will on average be of average mass, especially considering
456 species shared common ancestry CITATION. Note that all variation in estimates between ecotypes
(Fig. 9) is due to differences in ecotype-specific survival probability and the associated effects of
458 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
460 model (Fig. 10) indicates little effect of mass on extinction; this is consistent with previous findings
from the North American mammal fossil record (Smits, 2015; Tomiya, 2013). Note that all variation
462 between ecotypes (Fig. 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.

464 Similarities in parameters estimates between ecotypes may be due to similar response to
environmental factors (Fig. 11, 12, and 13). As with previous comparisons between posterior
466 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
468 origination (Fig. 12) as opposed to survival (Fig. 13).

As demonstrated in the comparisons of the effect of mass on occurrence from the pure-presence
470 model (Fig. 8) with the effect of 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.
472 Plant phase is estimated to structure ecotype occurrence probability, specifically at least one phase
has a very different estimates from the others, for non-arboreal carnivores, arboreal and unguligrade
474 herbivores, arboreal and fossorial insectivores, and arboreal and unguligrade omnivores (Fig. 11).

For the other ecotypes, plant phase does not correspond to major differences in diversity over time.
476 The temperature covariates do not appear to strongly structure occurrence history for most
ecotypes (Fig. 11). Ecotypes for which at least one temperature covariate is estimated to have
478 strong effect on occurrence are digitigrade canivores (mean only), scansorial carnivores (mean only),
and non-arboreal herbivores. For the other ecotypes neither of the global temperature covariates are
480 expected to have strong effects on occurrence history.

Plant phase is estimated to at least partially structure ecotype origination probability for

482 non-arboreal carnivores, non-fossorial or plantigrade herbivores, arboreal and fossorial insectivores,
483 and plantigrade and scansorial omnivores (Fig. 12). In the case of the temperature covariates, at
484 least one of them is estimated to have strong effects on origination history for the following
485 ecotypes: digitigrade carnivores, and both digitigrade and unguligrade herbivores (Fig. 12). Neither
486 of the temperature covariates are estimate to have strong effects for the other ecotypes. Results like
487 these, assuming their accuracy, are probably responsible for many of the arguments over the effects
488 of climate on mammal diversity and diversification (Alroy, 1996; Alroy et al., 2000; Blois and Hadly,
489 2009; Figueirido et al., 2012; Janis and Wilhelm, 1993); because different ecotypes have different
490 responses, a myopic or limited view of mammal diversity can be misleading when attempting to
491 generalize for the entire system.

492 In contrast to both of the descriptions above of the group-level effects on origination (Fig. 11, and
493 Fig. 12), group-level covariates are estimate to have almost no effect on survival for all ecotypes (Fig.
494 13); this is the case for both the plant phases and temperature covariates.

Analysis of diversity

496 All of the following analyses of diversification and macroevolutionary rates has been done using
497 only the birth-death model; this is because of the models better posterior predictive check
498 performance (Fig. 3a, and 3b).

The general pattern of total estimated North American mammal diversity for the Cenozoic is
500 “stable” in that mean standing diversity does not fluctuate wildly and rapidly over the Cenozoic
501 (Fig. 14a). In broad strokes, the first 15 or so million years of the Cenozoic are characterized by a
502 gradual decline in standing diversity until approximately 45-50 million years ago (early-middle
503 Eocene). Following this decline, standing diversity is broadly constant from 45 to 18 Mya (early
504 Miocene). After this, there is a rapid spike in diversity followed by a slight decline in diversity up to
505 the Modern. This characterization of the estimated diversity history is knowingly broad strokes and
506 diversity time series is not without variation and vagaries.

When viewed through the lens of diversification rate, some of the structure behind the estimated

508 diversity history begins to take shape (Fig. 14b). For most of the Cenozoic, the diversification rate
hovers around zero, punctuated by both positive and negative spikes. The largest spike in
510 diversification rate is at 16 Mya, which is early Oligocene (Fig. 14b). Other notable increases in
diversification rate occur at 54, 44, 36, 26, and 20 Mya; other possible increases in diversification
512 rate are less certain (e.g. 8 Mya). Notable decreases in diversification rate occur at 52, 48, 42, 32,
14, 10, and 6 Mya.

514 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 origination
516 and survival probabilities, 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
518 pattern around a constant mean.

Now ask what origin or extinct are doing at the important time points indicated above.

520 Increases in diversification rate at 54, 44, 36, 26, 20, 16

Decreases in diversification rate at 52, 48, 42, 32, 14, 10, 6

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

524 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).

526 Arboreal herbivores and omnivores obtain peak diversity at the beginning of the Cenozoic then go
into decline while still possibly remaining a part of the species pool, while arboreal carnivores and
528 insectivores obtain peak diversity 52-50 Mya and then quickly decline and become extremely rare or
absent from the species pool.

530 The diversity of both digitigrade and unguligrade herbivores increase over the Cenozoic (Fig. 15).
In contrast, plantigrade herbivore diversity does not have a single, broad-strokes pattern; instead,
532 diversity increases, decreases, and may have then increased till the Modern. Contrastingly, fossorial
and scansorial herbivores demonstrate a much flatter history of diversity, with a slight increase in

534 diversity that over time is more pronounced among fossorial taxa than scansorial taxa.

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

540 There are some broad similarities in diversity histories of insectivorous and omnivorous taxa. The
diversity histories of arboreal, plantigrade, and scansorial insectivorous taxa all demonstrate a
542 decreasing pattern with time, while fossorial insectivores have a flat diversity history with a rapid
peak approximately 10 Mya (Fig. 15). Arboreal and scansorial omnivores decrease in diversity from
544 their initial peaks early in the Cenozoic, and plantigrade omnivores have a generally flat diversity
history with a sudden peak in diversity late in the Cenozoic (Fig. 15). Unguligrade omnivores also
546 demonstrate a possible decrease in diversity over the Cenozoic, but not as clearly as arboreal and
scansorial omnivores.

548 Many of the estimated ecotype specific diversity histories share a similar increases in diversity to
one degree or another at the late Cenozoic 16-14 Mya (Fig. 15); these increases are either sustained
550 or temporary: digitigrade carnivores, plantigrade carnivores, scansorial carnivores, unguligrade
herbivores, fossorial insectivores, and plantigrade omnivores.

552 Discussion

Both the composition of a species pool and its environmental context change over time, though not
554 necessarily at the same rate. Local communities, who's species are drawn from the regional species
pool, have "roles" in their communities defined by their interactions with a host of biotic and abiotic
556 interactors (i.e. species niche). For higher level ecological characterizations like ecotypes and guilds,
these roles are broadly defined and not defined by specific interactions but the genre of interactions
558 that 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; 560 Slater, 2015) CITATIONS. This implies that the size and scope of the role of an ecotype or guild is preserved even as the individual interactors change. This also implies the structure of regional 562 species pools can be constant over time despite a constantly changing set of “players.”

Comparison of the pure-presence model to the birth-death model support the conclusion that 564 regional species pool dynamics cannot simply be described by a single occurrence probability and is instead better modeled as the result of both origination and extinction. Additionally, changes to 566 ecotypic composition of the North American regional species pool are driven primarily by variation in origination rates. These aspects of how regional species pool diversity is shaped is not observable 568 from studies of the Modern CITATION.

Extinction rate for the entire regional species pool through time is highly variable and demonstrates 570 a saw-toothed pattern around an apparently constant mean. While a constant mean extinction rate is consistent with previous observation (Alroy, 1996; Alroy et al., 2000), the degree to which 572 extinction rate is actually variable may not have been equally appreciated. What is most consistent with previous observations (Alroy, 1996; Alroy et al., 2000), however, is that diversity seems to be 574 most structured by origination than extinction.

Arboreal taxa disappear over the Cenozoic, with massive disappearance by the Paleogene-Neogene 576 transition ~22 Mya. This is consistent with one of the two possible patterns that would result in arboreal taxa having a greater extinction risk than other ecotypes: Paleogene-Neogene are different 578 and while the earliest Cenozoic may have been neutral wrt arboreal taxa, they disappeared quickly over the Cenozoic which may account for their higher extinction risk.

580 Digitigrade carnivores have a relatively stable diversity history through the Cenozoic and could be characterized as varying around a constant mean diversity. The ecotypic has a large amount of 582 overlap with the carnivore guild which has been the focus of much research CITATIONS. This result is consistent with some form of “control” on the ecotype, such as environmental stability, 584 diversity-dependence, or similar Silvestro et al. (2015); Slater (2015).

Both digitigrade and unguligrade herbivores increase in diversity over the Cenozoic. The increase of

586 these cursorial forms is consistent with the gradual opening up of the North American landscape
CITATION. Only these herbivore from increase in diversity over the Cenozoic which may indicate a
588 long shift in the interactors associated with those ecotypes leading to increased contribution to the
regional species pool. This result may be comparable to the increasing percentage of hypsodont
590 (high-crowned teeth) mammals in the Neogene of Europe being due to an enrichment of hyposodont
taxa and not a depletion of non-hypsodont taxa.

592 What these results support is a gradual change to the ecotypic diversity of the regional species pool
for the Cenozoic. The rapidity of Cenozoic environmental change is worth discussing. If change is
594 rapid, ecotypic composition of species pool does not seem to track environmental change. If change
is gradual then there is the possibility that changes to ecotypic composition may be tracking
596 environmental change.

If plant phase is associated with differences in ecotype occurrence this is interpreted to mean that
598 ecotype enrichment or depletion is due to associations between that ecotype and whatever plants
are dominate at that time.

600 Temperature affects very few of the occurrence, origination, or survival probabilities of the mammal
ecotypes except for a negative relationship between temperature and the origination probabilities of
602 digitigrade carnivores, and both digitigrade and unguligrade herbivores. The origination
probabilities and diversity of these three groups all increase over the Cenozoic as average global
604 temperature decreased. This result coupled with the lack of relationship between temperature and
the other ecotypes may be responsible for the continued confusion surrounding the impact of
606 temperature on mammal diversity and diversification (Alroy, 1996; Alroy et al., 2000; Blois and
Hadly, 2009; Figueirido et al., 2012; Janis and Wilhelm, 1993).

608 What is the comparative size of the effects of plant phase and temperature? Both seem of “equal”
importance in the sense that they have similar effect sizes on the ecotypes. Perhaps focusing on
610 temperature and not considering other measures of environmental context has been a mistake and
perhaps led to increasing confusion in discussions of how “environment” effects mammal diversity
612 and diversification. The environment or climate is not just global or regional temperature, it is the

set of all possible biotic and abiotic interactions. By including more descriptors of species' 614 environmental context a more complete "picture" of the diversification process is inferred.

The effect of species mass on either occurrence or origination and extinction was not allowed to 616 vary by ecotype or environmental context even though it is not known if this is the case or not
CITATION. The primary reason for this modeling choice was that this study focuses on ecotypic 618 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 the overall complexity of the 620 model, something that I felt was not necessary because the overall scope of the study. Instead, body size was included in order to control for its possible underlying effects CITATION. A control means 622 that if there is variation due to body mass, having a term to "absorb" that effect is better than ignoring it which may affect other parameter estimates. Additionally, the effect of body size was 624 allowed to have a second-order polynomial form and no higher order polynomials were considered; this was done because it is hard to conceive of a more complex third- or higher-order relationship 626 between body size and the other parameters. Additionally, nonlinearity is rarely if ever considered in the first place, so the simple act of estimating a potential second-order relationship is an 628 opportunity to test more complex hypotheses of the effects of body size on macroevolutionary and macroecological processes.

630 The only covariate allowed to affect sampling probability was mass and only as a linear predictor. Other covariates, such as the environmental factors considered here, could have affected the 632 underlying preservation process that limits sampling probability. Their exclusion as covariates of sampling/observation was the product of a few key decisions: model complexity, model 634 interpretability, the scope of this study, and a lack of good hypotheses related to these covariates to warrant their inclusion. It should be noted that in other similar studies that use a hidden 636 birth-death model to handle simultaneous estimation of sampling, origination, and extinction have not considered the possible effects of covariates, both species traits and environmental factors, on 638 sampling CITATION.

The time scale available with paleontological data is much greater than that obtainable from

640 modern ecological studies, even long running observations CITATION. Specifically, the temporal
scale of paleontological data allows for the complete turnover of a species pool to be observed,
642 something that is impossible in “real time.” However, paleontological data is very limited in its
spatial resolution, so the analysis of how the ecotypic diversity local communities change over time
644 and how that is also the product of larger scale regional turnover remains unanswered.

The potential effects of common ancestry (i.e. phylogeny) on origination and extinction are not
646 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
648 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;
650 Smits, 2015). One of the principle barriers to the inclusion of the effect of phylogeny in either the
pure-presence or birth-death models is computational; with well over 1000 tips, the calculation of
652 the scale parameter defining the phylogenetic effect would be very slow and further increase the
already slow computation time necessary for both the marginalization of the discrete occurrence
654 histories and data augmentation already included in both models.

Phylogenetic comparative community ecology and phylogenetic comparative biogeography also
656 discusses how the macroevolutionary processes helps structure an observed community, though it is
not necessarily phrased that way. However, that community did not form in isolation but it the
658 result of many factors interacting over time including incumbency, competition, limiting similarity,
etc.

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Database publication XXX.

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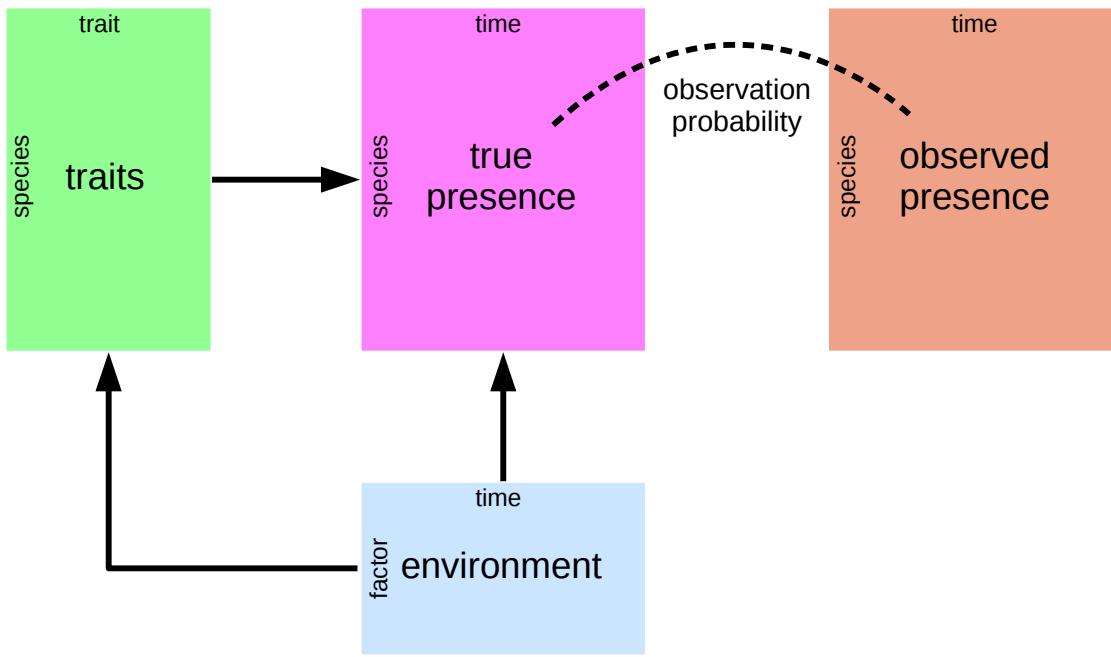


Figure 1: Conceptual diagram of the paleontological fourth corner problem. The observed presence matrix (orange) is the empirical presence/absence pattern for all species for all time points; this matrix is an incomplete observation of the “true” presence/absence pattern (purple). The estimated true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

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

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

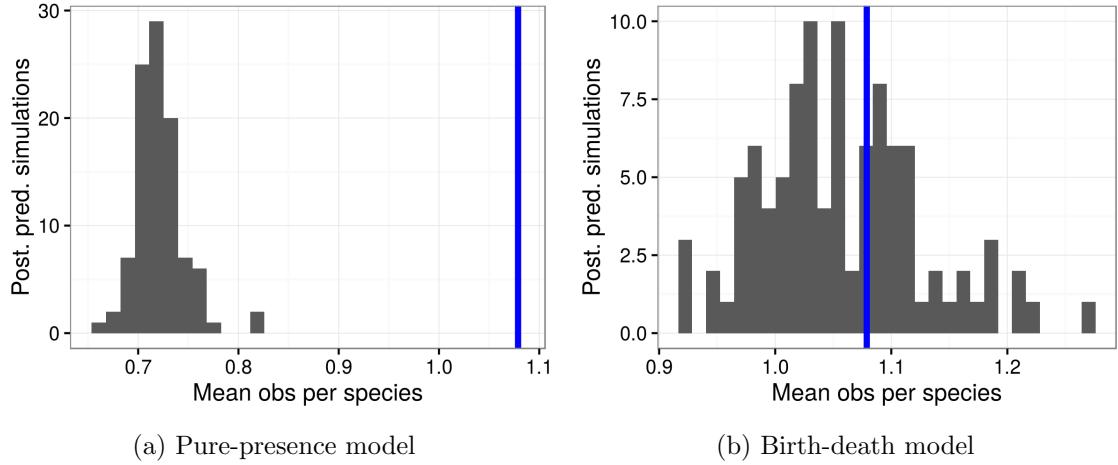


Figure 3: Comparison of the average observed number of occurrences per species (blue line) to the average number of occurrences from 100 posterior predictive datasets using the posterior estimates from the pure-presence and birth-death models.

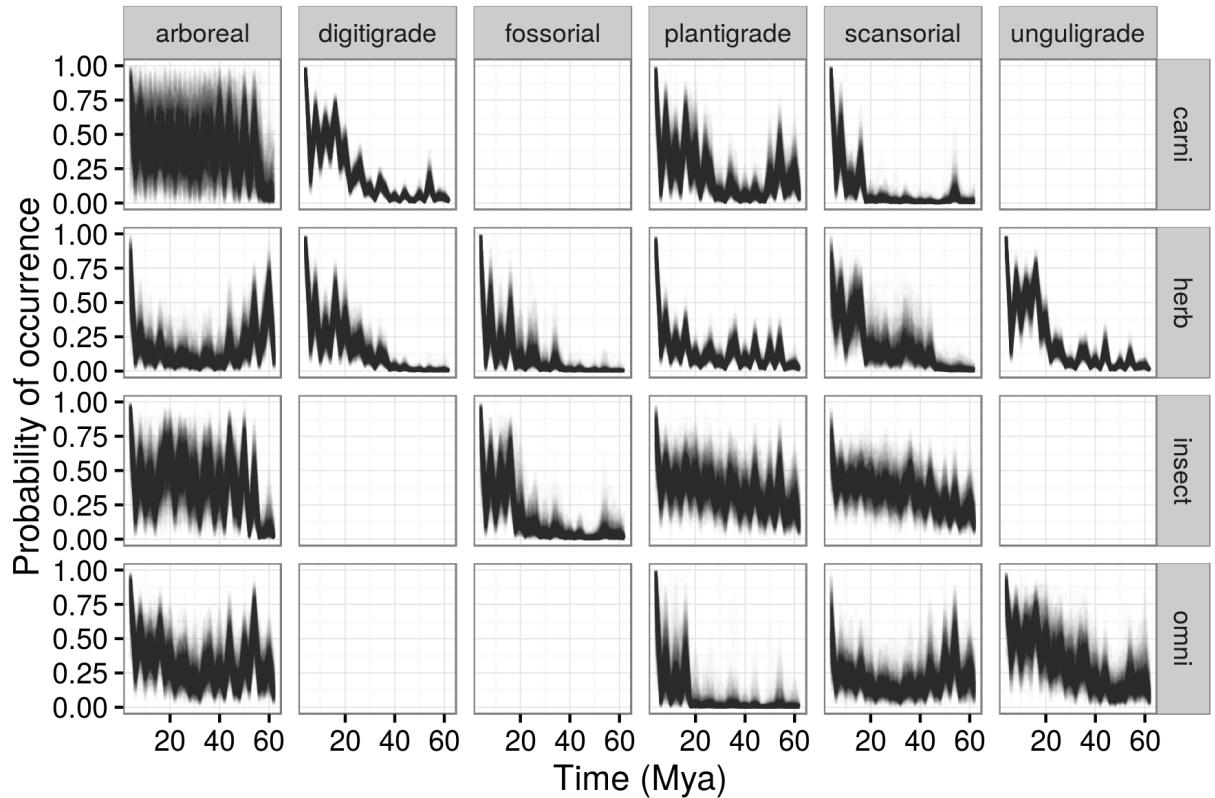


Figure 4: Probability of a mammal ecotype occurring over time as estimated from the pure-presence model. Each panel depicts 100 random samples from the model's posterior. The columns are by locomotor category and rows by dietary category; their intersections are the observed and analyzed ecotypes. Panels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

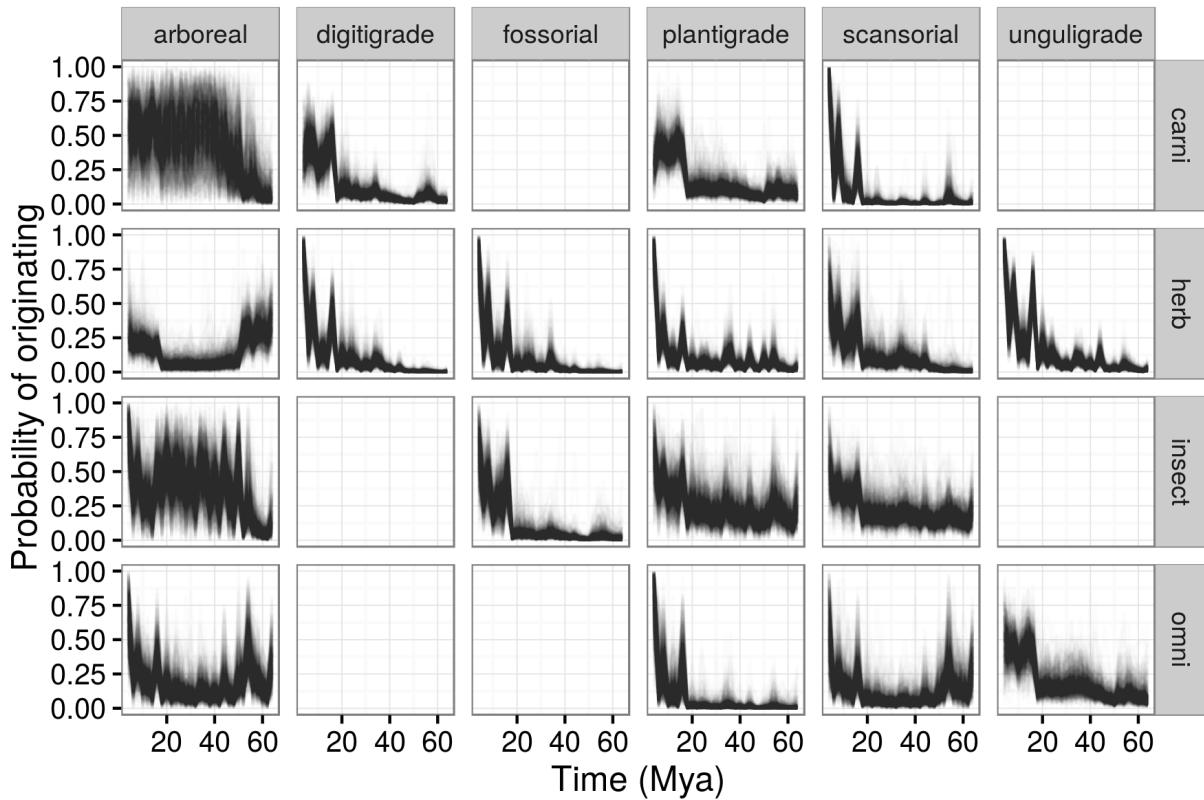


Figure 5: Probability of a mammal ecotype origination probabilities at each time point as estimated from the birth-death model. Each panel depicts 100 random samples from the model's posterior. The columns are by locomotor category and rows by dietary category; their intersections are the observed and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

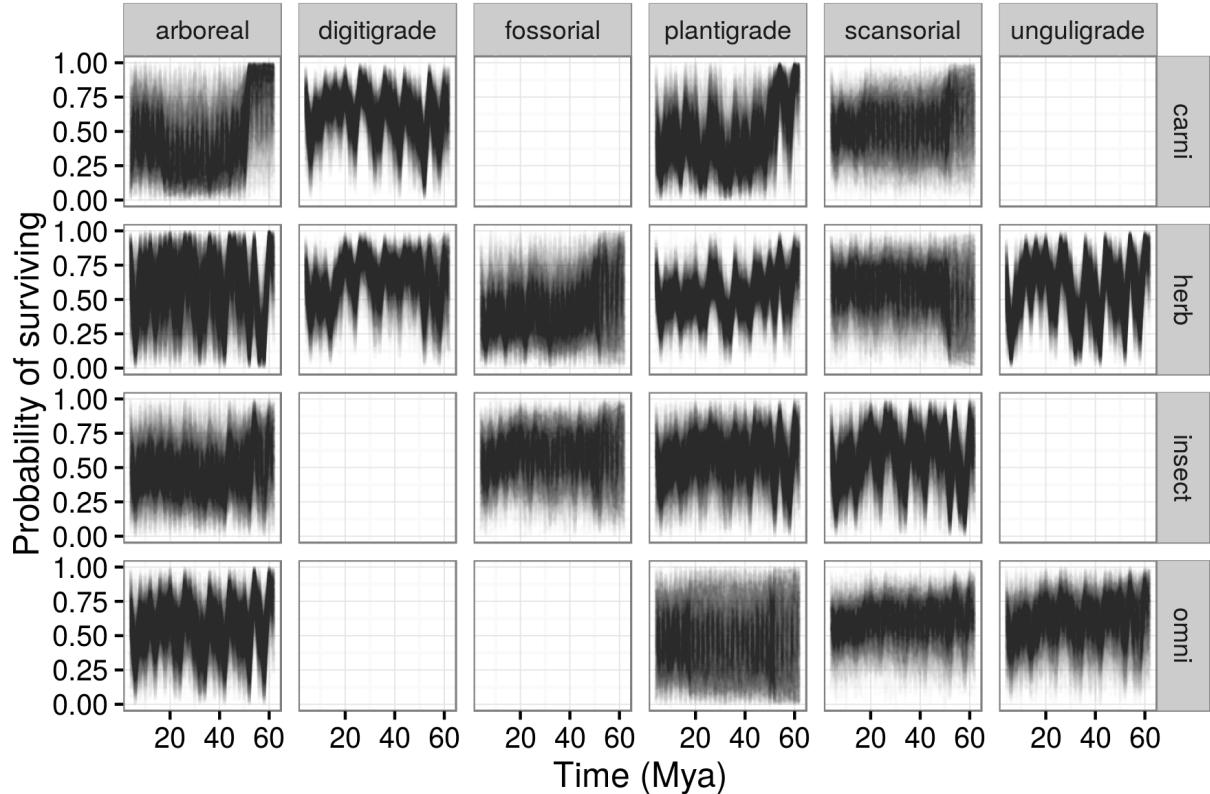


Figure 6: Probability of a mammal ecotype survival probabilities at each time point as estimated from the birth-death model. Each panel depicts 100 random samples from the model’s posterior. The columns are by locomotor category and rows by dietary category; their intersections are the observed and analyzed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

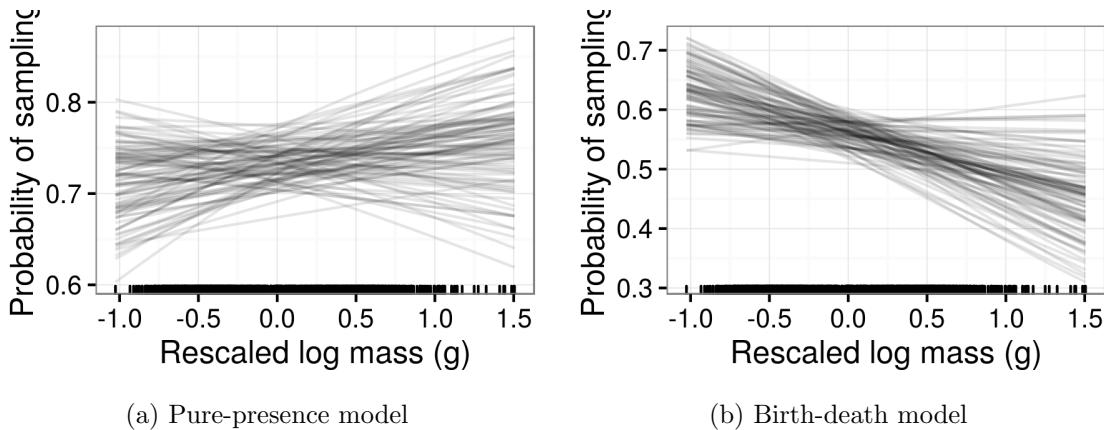


Figure 7: Estimates of the effect of species mass on probability of sampling a present species (p). Mass has been log-transformed, centered, and rescaled; this means that a mass of 0 corresponds to the mean of log-mass of all observed species and that mass is in standard deviation units. Estimates are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

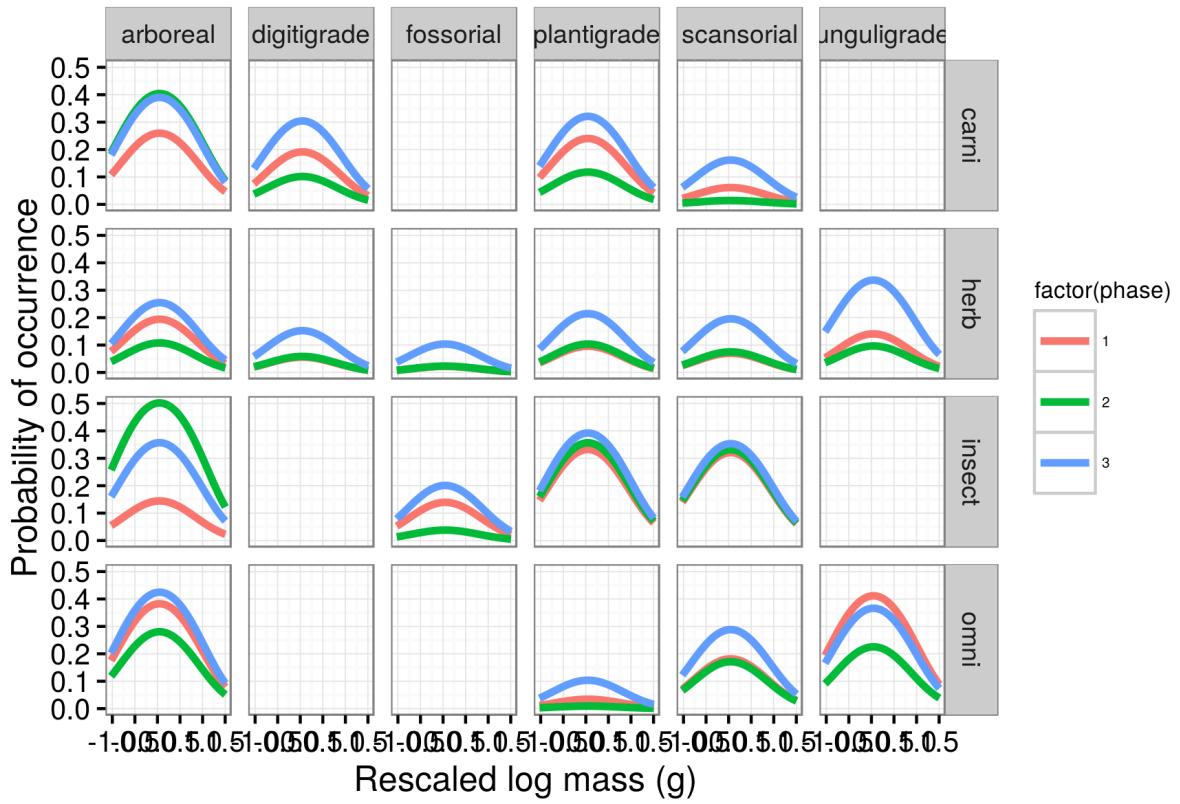


Figure 8: Mean estimate of the effect of species mass on the probability of a species occurrence for each of the three plant phases. The effect of mass is considered constant over time and that the only aspect of the model that changes with plant phase is the intercept of the relationship between mass and occurrence. The three plant phases are indicated by the color of the line. Mass has been log-transformed, centered, and rescaled; this means that a mass of 0 corresponds to the mean of log-mass of all observed species and that mass is in standard deviation units. Only the mean estimates of the effects of both mass and plant phase are plotted for clarity; these estimates are obviously made with uncertainty.

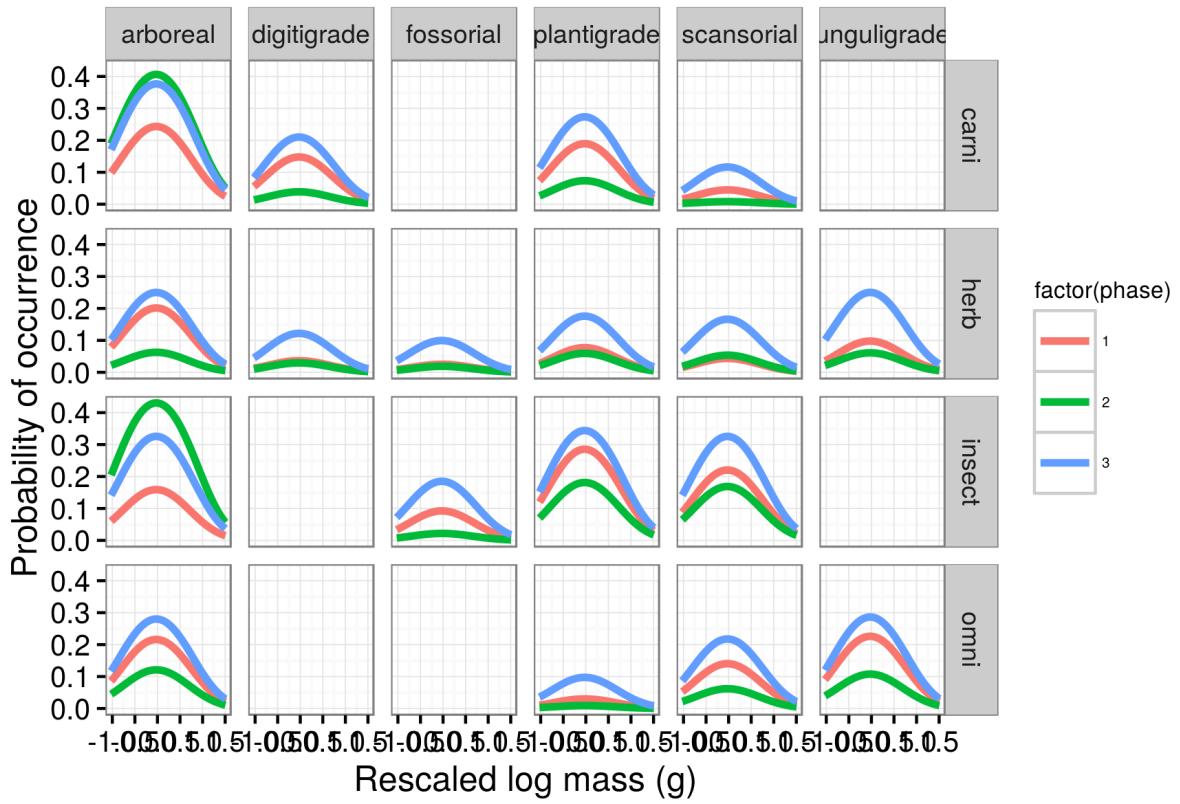


Figure 9: Mean estimate of the effect of species mass on the probability of a species originating for each of the three plant phases. The effect of mass is considered constant over time and that the only aspect of the model that changes with plant phase is the intercept of the relationship between mass and origination. The three plant phases are indicated by the color of the line. Mass has been log-transformed, centered, and rescaled; this means that a mass of 0 corresponds to the mean of log-mass of all observed species and that mass is in standard deviation units. Only the mean estimates of the effects of both mass and plant phase are plotted for clarity; these estimates are obviously made with uncertainty.

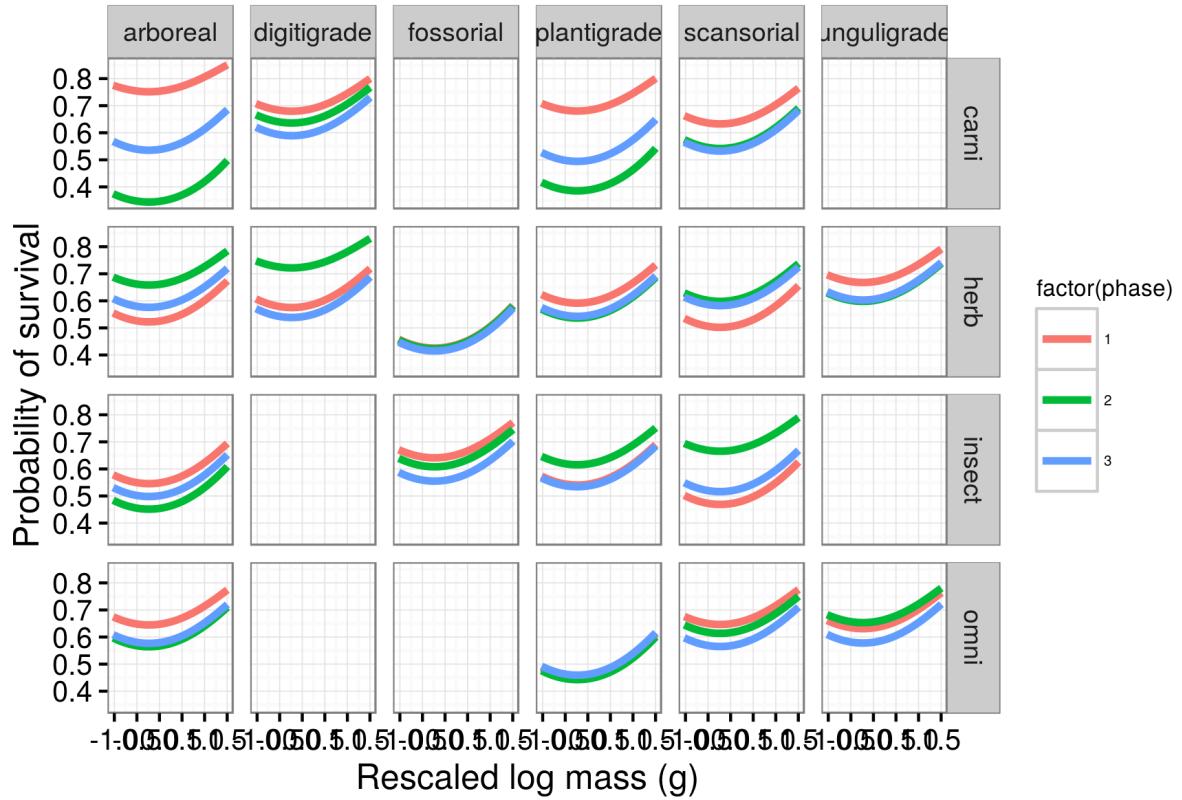


Figure 10: Mean estimate of the effect of species mass on the probability of a species survival for each of the three plant phases. The effect of mass is considered constant over time and that the only aspect of the model that changes with plant phase is the intercept of the relationship between mass and survival. The three plant phases are indicated by the color of the line. Mass has been log-transformed, centered, and rescaled; this means that a mass of 0 corresponds to the mean of log-mass of all observed species and that mass is in standard deviation units. Only the mean estimates of the effects of both mass and plant plant are plotted for clarity; these estimates are obviously made with uncertainty.

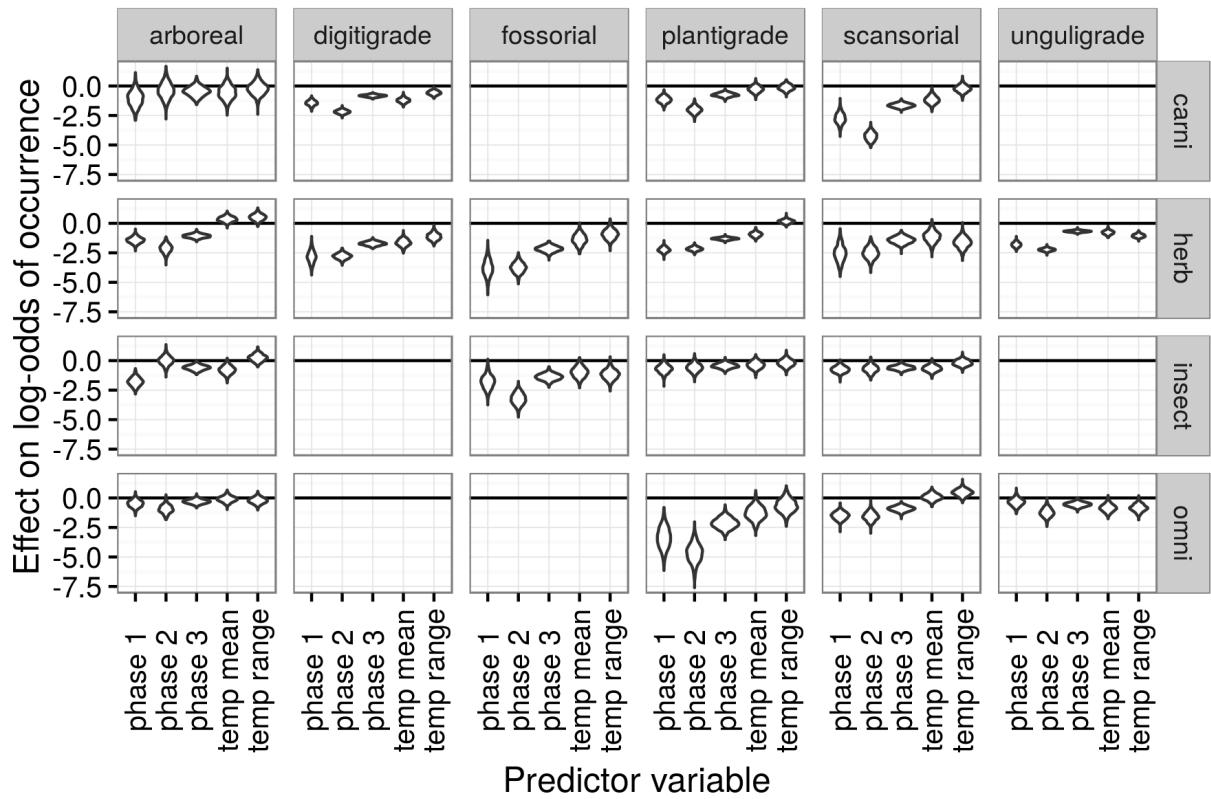


Figure 11: Estimated effects of the group-level covariates describing environmental context on log-odds of species occurrence. These estimates are from the pure-presence model.

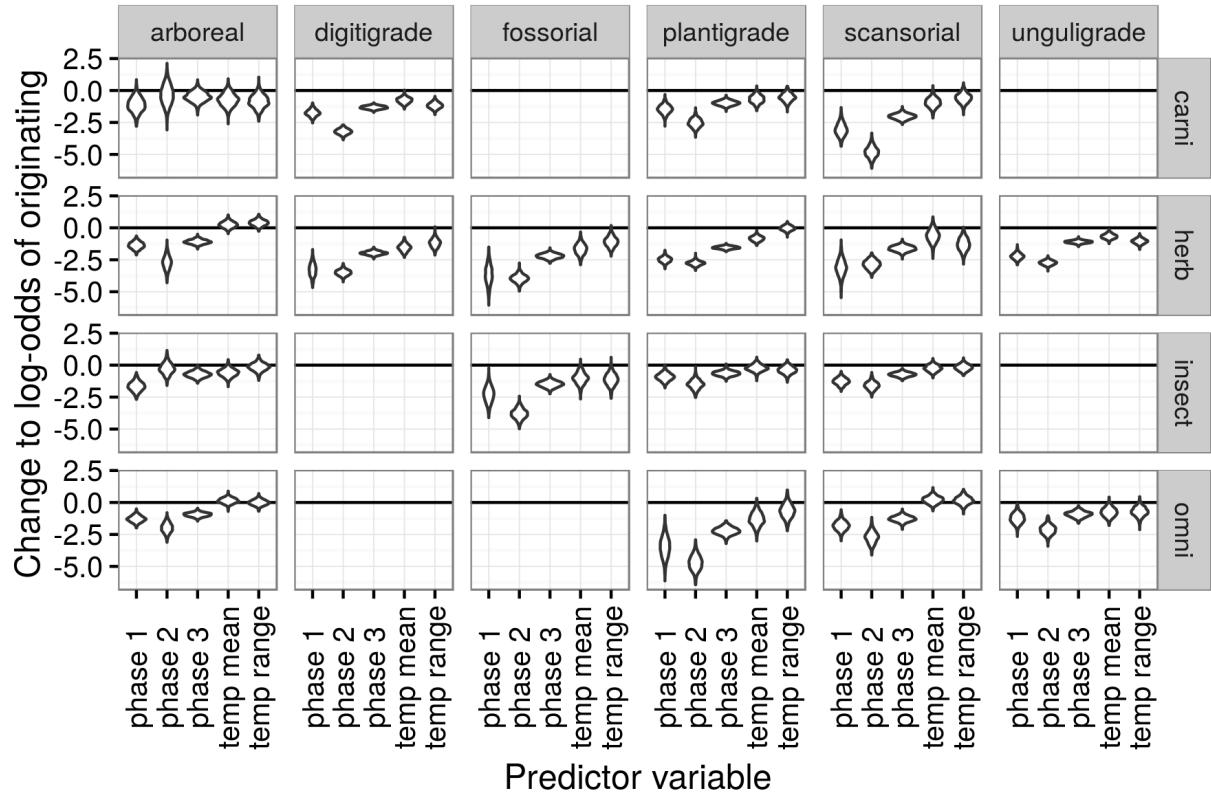


Figure 12: Estimated effects of the group-level covariates describing environmental context on log-odds of species origination. These estimates are from the birth-death model.

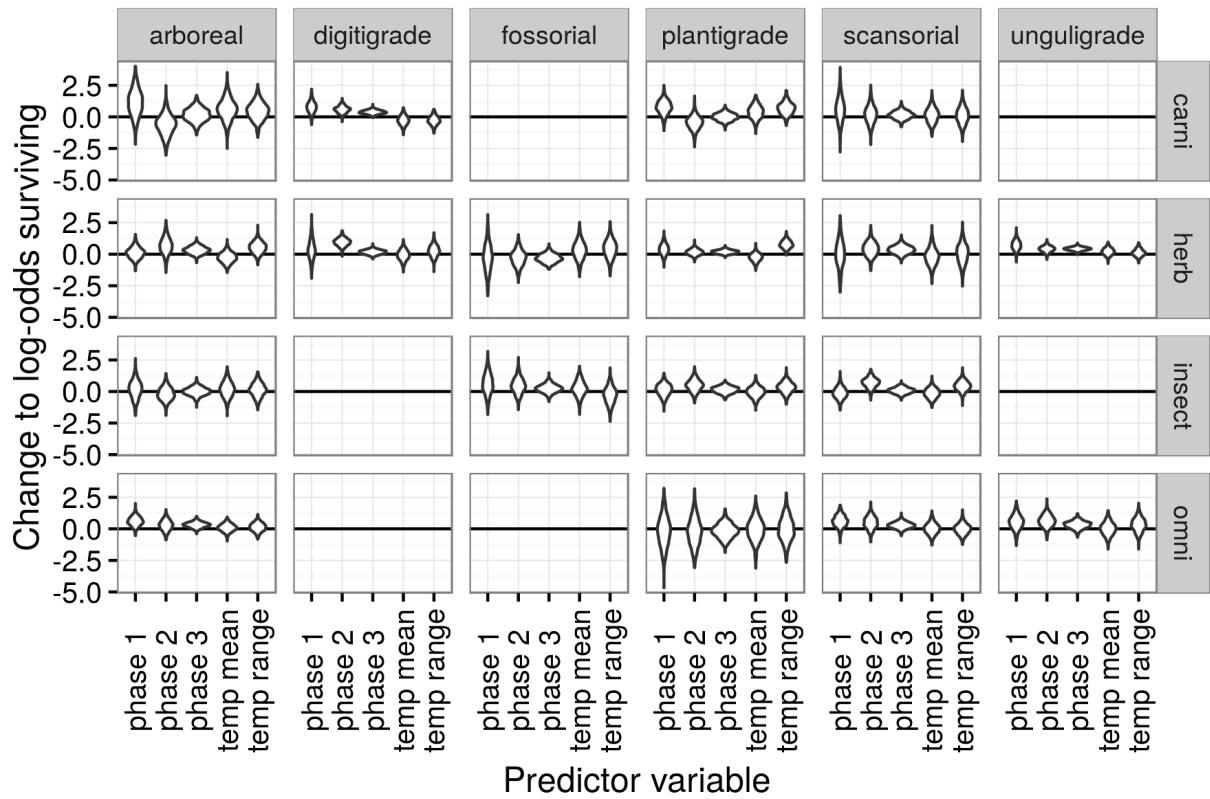


Figure 13: Estimated effects of the group-level covariates describing environmental context on log-odds of species survival. These estimates are from the birth-death model.

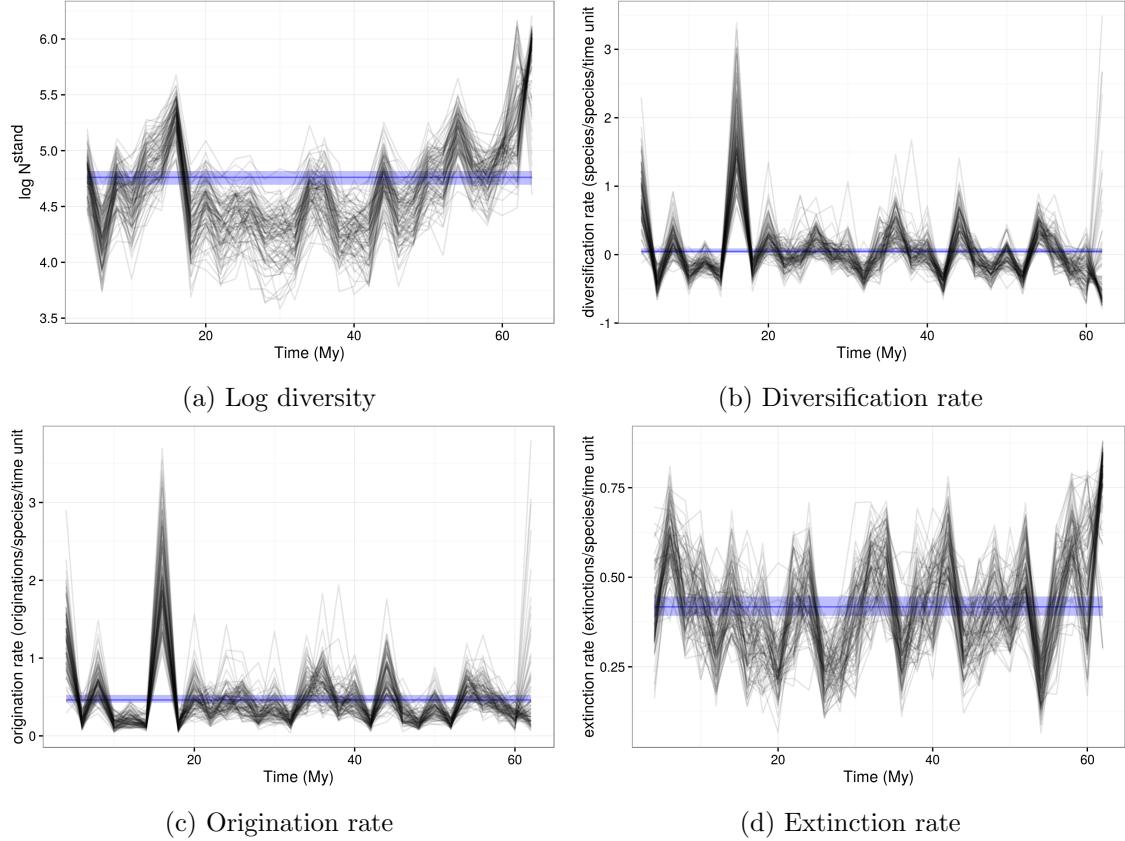


Figure 14: Posterior estimates of the time series of Cenozoic North American mammal diversity and its characteristic macroevolutionary rates; all estimates are from the birth-death model and 100 posterior draws are plotted to indicate the uncertainty in these estimates. The dramatic differences between 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.

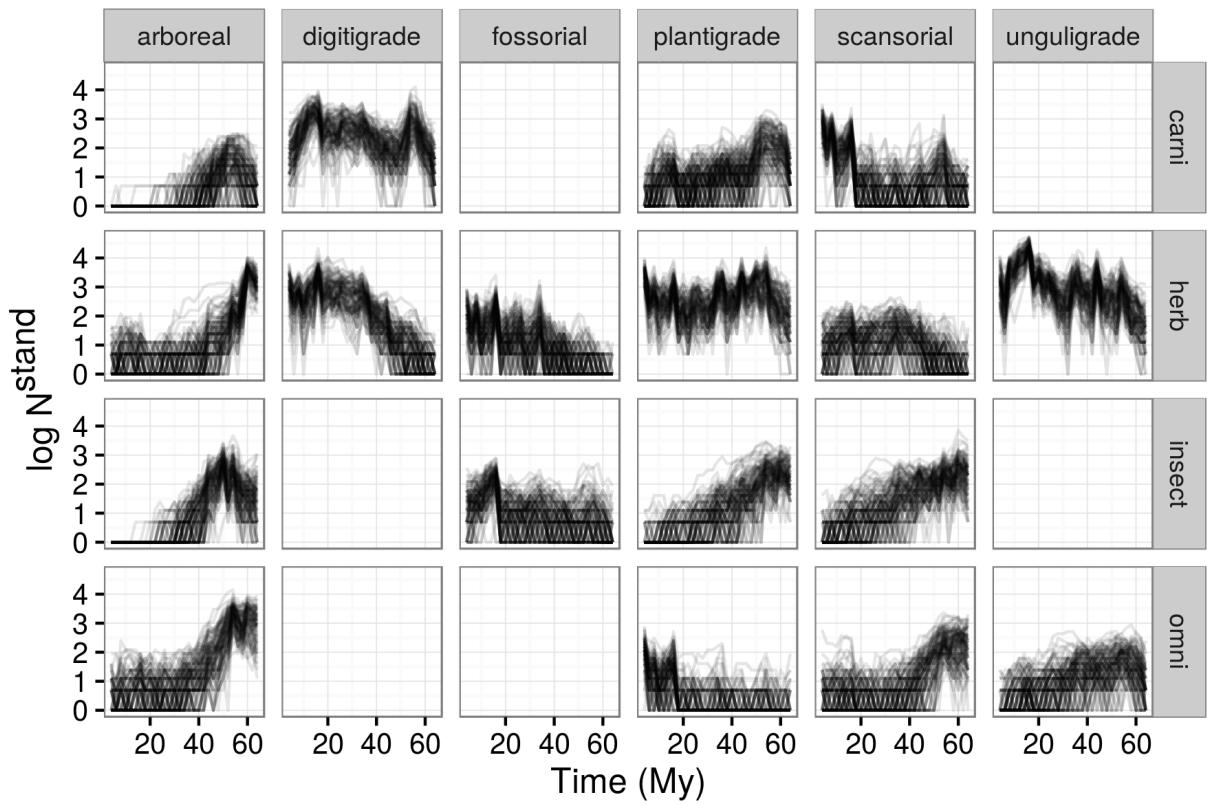


Figure 15: Posterior of standing log-diversity of North American mammals by ecotype for the Cenozoic as estimated from the birth-death model; 100 posterior draws are plotted to indicate the uncertainty in these estimates and what is technically plotted is log of diversity plus 1.