

Species traits and environmental context: the changing functional composition of the North American species pool

Peter D. Smits^{1,*}

1. University of Chicago, Chicago, Illinois 60637.

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

Manuscript elements:

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

Manuscript type: Article

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

Abstract

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

Introduction

Changes to species diversity are the result of evolutionary and ecological processes acting 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). In turn, the distribution of species within
36 regional species pool represents the expected distribution of local communities under a purely
diffusive process of community assembly.

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

A key question when comparing communities or regional species pools based on their functional
46 composition is whether specific functional groups are enriched or depleted and why; what are the
processes that led to a species pool having the functional composition it does (Blois and Hadly,
48 2009; Brown and Maurer, 1989; McGill et al., 2006; Smith et al., 2008; Weber et al., 2017)?
Comparisons of contemporaneous regional species pools only determines if a functional group is
50 enriched or depleted in one species pool relative to other species pools CITATION. These types of
comparison do not take into account if a functional group is enriched or depleted relative to its
52 diversity over time (Blois and Hadly, 2009). While a species pool may be depleted of a functional
group relative to other contemporaneous species pools, that same functional group may be actually
54 be enriched in that species pool relative to its historical diversity. Because the processes which
56 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 opportunity
58 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 a regional
60 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 the species
62 pool is particularly useful in conservation settings; species in depleted groups are most likely more
at risk of extinction than species in enriched groups, even if those enriched groups are relatively
64 rare when compared to the functional composition of other contemporaneous species pools.

The paleontological record of North American mammals for the Cenozoic (~ 66 million years ago to
66 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
68 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).
70 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.,
72 2010; Polly et al., 2011, 2015).

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

76 **Background**

The history of standing diversity for all mammals along with that some individual clades of North
78 American mammals for the Cenozoic has been the focus of considerable study (Alroy, 1996, 2009;
Alroy et al., 2000; Badgley and Finarelli, 2013; Blois and Hadly, 2009; Figueirido et al., 2012;
80 Fraser et al., 2015; Janis, 1993; Janis and Wilhelm, 1993; Pires et al., 2015; Quental and Marshall,
2013; Silvestro et al., 2015; Slater, 2015; Smits, 2015). Previous approaches to understanding
82 mammal diversity, both in North America and elsewhere, fall into a number of overlapping

categories: total diversity (Alroy, 1996; Alroy et al., 2000; Figueirido et al., 2012; Liow et al., 2008),
 84 with/between guild comparisons (Janis et al., 2004; Janis, 2008; Janis et al., 2000; Janis and
 Wilhelm, 1993; Jernvall and Fortelius, 2004; Pires et al., 2015), within/between clade comparisons
 86 (Cantalapiedra et al., 2017; Fraser et al., 2015; Quental and Marshall, 2013; Silvestro et al., 2015;
 Slater, 2015), and estimating the impact of environmental process on total diversity (Alroy et al.,
 88 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 Wilhelm, 1993). Each of these individual perspectives
 90 provide an overall limited perspective on the macroevolutionary and macroecological processes
 shaping diversity and diversification. Integration across perspectives is necessary for producing a
 92 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 to present a framework for approaching
 94 hypotheses about diversity and diversification through multiple lenses simultaneously so that our
 inferences are better constrained and the relative importance of species' ecological function,
 96 taxonomic affinities, and environmental context may be better elucidated.

The narrative of the diversification of North American mammals over the Cenozoic is one of
 98 gradual change. There is little convincing evidence that there have been any major or sudden
 cross-functional or cross-taxonomic group turnover events in mammal diversity at any point in the
 100 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
 102 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
 104 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
 106 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
 108 (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
 110 and Marshall, 2013; Silvestro et al., 2015; Van Valkenburgh, 1999).

Within the overall narrative of mammal diversity, the histories of some functional and taxonomic groups are better understood than others. These groups include ungulate herbivores and Neogene carnivores which have particularly good fossil records and have been the focus of previous analyses.

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

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

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

the diversity history of arboreal taxa: 1) if arboreal taxa always have an elevated extinction risk when compared to other taxa, then the diversity history of arboreal taxa is expected to be constant with time, albeit possibly at low diversity; and 2) if the Paleogene and Neogene represent different selective regimes with the former being associated with lower extinction risk than the latter, then the diversity history of arboreal taxa are expected to be present in the Paleogene but depleted or absent from the species pool during the Neogene.

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

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 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). In terms of the North American biotic environment, the Cenozoic is additionally characterized by a major transition from having closed, partially forested biomes being common in the Paleogene to the landscape being dominated by savannah and grasslands biomes by the Neogene (Blois and Hadly, 2009; Janis, 1993; Janis et al., 2000; Strömberg, 2005). Additionally, the landscape structure and topology of North America changed substantially over the Cenozoic with mountain uplift and other tectonic activities in Western North America (Badgley and Finarelli, 2013; Blois and Hadly, 2009; Eronen et al., 2015; Janis, 2008). This type of geological activity affects both local climates as

well as continental weather patterns while also mobilizing increased grit into the environment, 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).

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

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 biologically-mediated than climate-mediated when considering the entire Cenozoic (Alroy et al., 2000; Clyde and Gingerich, 1998; Figueirido et al., 2012). However, differences in temporal and geographic scale seem to underly the contrast between these two perspectives. For example when the mammal fossil record analyzed at small temporal and geographic scales a correlation between diversity and climate is observable (Clyde and Gingerich, 1998). However, when the record is analyzed at the scale of the continent and most of the Cenozoic this correlation disappears (Alroy et al., 2000). This result, however, does not go against the idea that there may be short periods of correlation between diversity and climate and that this relationship can change or even reverse direction over time; this type result means that there is no single direction or longterm correlation between diversity and climate (Figueirido et al., 2012).

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

Foreground

204 The fourth-corner problem is conceptual and statistical framework to explaining the patterns of
either species abundance or presence/absence in a community as a product of species traits,
206 environmental factors, and the interaction between traits and environment (Brown et al., 2014;
Jamil et al., 2013; Pollock et al., 2012; Warton et al., 2015); effectively uniting climate-based species
208 distribution modeling (SDMs) with trait-based community assembly models (CATS, MaxEnt). The
fourth-corner problem is normally phrased in modern ecological studies as understanding how traits
210 and environment interact to predict the occurrence of species at localities distributed across a
region (Jamil et al., 2013; Pollock et al., 2012).

212 This conceptual framework can be extended to include time when considering occurrence as a
three-dimensional: species at localities in space over time. This extension changes the goal of
214 predicting just occurrence to one of predicting species gain and loss at localities. However, the
temporal limitations of modern ecological studies limit studying species over their entire durations,
216 where speciation and extinction govern the occurrence of species. By considering the patterns of
fossil occurrences in the geological record the macroevolutionary processes governing species'
218 (macro)ecology can be better understood. One limitation of the fossil record, however, is a lack of
spatial resolution for most taxonomic groups and periods of time. As such, paleontological data

”looks” at a different side of the three-dimensional occurrence matrix of the extended fourth-corner problem than modern ecological data.

In this study, the fourth-corner problem is phrased as understanding how mammal functional groups respond to environmental change in order to predict the origination and survival of species over time (Fig. 1). Additionally, I also consider the incompleteness of the fossil record and the static effect of other species descriptors not related to functional group on origination and survival.

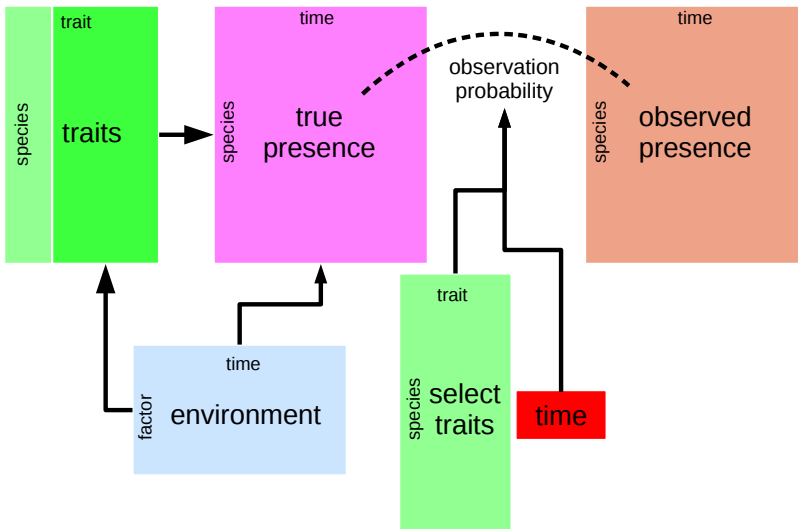


Figure 1: Conceptual diagram of the paleontological fourth corner problem. The observed presence matrix (orange) is the empirical presence/absence pattern for all species for all time points; this matrix is an incomplete observation of the “true” presence/absence pattern (purple). The estimated true 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).

My approach to delimiting and assigning mammal functional groups is inspired on the ecocube heuristic used to classify marine invertebrate species by three functional traits (Bambach et al., 2007; Bush and Bambach, 2011; Bush et al., 2007; Bush and Novack-Gottshall, 2012; Novack-Gottshall, 2007; Villéger et al., 2011). Unique combinations of traits represent functional groups, which are equivalent to functional groups defined by species functional traits instead of a

holistic understanding how a taxon interacts with its environment. In this study, the two functional traits used to define a species' functional group are dietary (e.g. herbivore, carnivore, etc.) and locomotor category (e.g. arboreal, unguligrade, etc.). Species body mass was also included as a species trait in this analysis, but not as a functional trait for defining functional groups; instead, its inclusion is principally to control for differences in species dynamics that driven by mass and not functional group.

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

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 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 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 used in this analysis is a translation of the conceptual framework described above (Fig. 1) into a statistical model in order to estimate the relative diversity of mammal functional groups over time and how those functional groups respond to changes to environmental context while taking into account the fundamental incompleteness of the fossil record.

Ultimately, the goals of this analysis are to understand when are different functional groups enriched or depleted in the North American mammal regional species pool and how these changes in ecotypic diversity are related to changes in species' environmental context. In the analyses done

here, I consider multiple covariates which describe a species' macroecology and its environmental context. In order to analyze this complex and highly structured question and accompanying data set, I developed a hierarchical Bayesian model combining the fourth-corner modeling approach with a model of an observation-occurrence or observation-origination-extinction process.

Materials and Methods

Taxon occurrences and species-level information

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

After being downloaded, the raw occurrence data was then sorted, cleaned, and manipulated programmatically before analysis. Occurrences were restricted to those occurring between 64 and 2 million years ago (Mya); this age restriction was to insure that observation time series lines up with the temperature time series (Cramer et al., 2011). 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 study of terrestrial species pools.

Many species taxonomic assignments as present in the raw PBDB data were updated for accuracy and consistency. Species present in the PBDB have some taxonomic information, including possible Family and Order assignments. In order to increase consistency between species and reflect more recent taxonomic assignments, each species taxonomic assignments updated as follows: 1) species family and order assignments as present in the Encyclopedia of life (<http://eol.org>) was

downloaded using the *taxize* package for R; 2) for species not present in the EoL or not assigned
order, their taxonomic information was further updated based on whatever family information was
recorded in the PBDB or EoL; 3) for species still missing order assignments, their genus
information was used to assign either an order or family, which was then used to assign an order.
This procedure is similar to that used in Smits (2015) and is detailed in the code repository
associated with this study.

Species ecotype is defined based on a combination of locomotor and diet categories; the goal is to
classify species based on the manner with which they interact with their environment. Mammal
species records in the PBDB have life habit (i.e. locomotor category) and dietary category
assignments. In order to simplify interpretation, analysis, and per-ecotype sample size these
classifications were coarsened in a similar manner to Smits (2015) (Table 1). The life history
category was then further edited to better reflect the diversity of mammal locomotor modes and
our knowledge of species' ecologies. Ground dwelling species locomotor categories were reassigned
based on 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 species assigned a non-ground dwelling locomotor category by the PBDB, which
retained their non-ground dwelling assignment. All species for which it was possible to assign a
locomotor category had one assigned, including species for which post-crania are unknown but for
which a taxonomic grouping is known. Ground dwelling species which were unable to be reassigned
based on ankle posture were excluded from analysis. Finally, ecotype categories with less than 10
total species were excluded, yielding a total of 18 observed ecotypes out of a possible 24.

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

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

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

Family	Stance
Ailuridae	plantigrade
Allomyidae	plantigrade
Amphicyonidae	plantigrade
Amphilemuridae	plantigrade
Anthracotheriidae	digitigrade
Antilocapridae	unguligrade
Apheliscidae	plantigrade
Aplodontidae	plantigrade
Apternodontidae	scansorial
Arctocyonidae	unguligrade
Barbourofelidae	digitigrade
Barylambdidae	plantigrade
Bovidae	unguligrade
Camelidae	unguligrade
Canidae	digitigrade
Cervidae	unguligrade
Cimolodontidae	scansorial
Coryphodontidae	plantigrade
Cricetidae	plantigrade
Cylindrodontidae	plantigrade
Cyriacotheriidae	plantigrade
Dichobunidae	unguligrade
Dinocerata	unguligrade
Dipodidae	digitigrade
Continued on next page	

Table 2 – continued from previous page

Family	Stance
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
Hyaenodontidae	digitigrade
Hypertragulidae	unguligrade
Ischyromyidae	plantigrade
Jimomyidae	plantigrade
Lagomorpha	digitigrade
Leptictidae	plantigrade
Leptochoeridae	unguligrade
Leptomerycidae	unguligrade
Mammutidae	unguligrade
Continued on next page	

Table 2 – continued from previous page

Family	Stance
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
Oromerycidae	unguligrade
Oxyaenidae	digitigrade
Palaeomerycidae	unguligrade
Palaeoryctidae	plantigrade
Pampatheriidae	plantigrade
Pantolambdidae	plantigrade
Periptychidae	digitigrade
Perissodactyla	unguligrade
Phenacodontidae	unguligrade
Continued on next page	

Table 2 – continued from previous page

Family	Stance
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
Zapodidae	plantigrade

304

Estimates of species mass used in this study were sourced from multiple databases and papers,
 306 especially those focusing on similar macroevolutionary or macroecological questions (Brook and
 Bowman, 2004; Freudenthal and Martín-Suárez, 2013; McKenna, 2011; Raia et al., 2012; Smith
 308 et al., 2004; Tomiya, 2013); this is similar to what was done in Smits (2015). When species mass was
 not available, proxy measures were used and then transformed into estimates of mass. For example,
 310 given a measurement of a mammal tooth size, it is possible and routine to estimate its 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). In total, 1400 mammal species occurrence histories were included in this study after applying all of the restrictions above.

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 tooththrow 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 tooththrow length	Mendoza et al. (2006)

All fossil occurrences from 64 to 2 million years ago (Mya) were binned into the 19 North American Land Mammal Ages (NALMA) covered by this interval CITATION. The choice of binning by NALMA reflects the belief that these represent distinct communities or periods of mammal evolution, something that is central to this study. Additionally, because of the inherently discrete nature of the fossil record it can be hard to re-bin fossils by temporal interval because of the inherent uncertainty in their ages CITATION.

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

Environmental and temporal covariates

The environmental covariates used in this study are collectively referred to as group-level covariates because they predict the response of a “group” of individual-level observations (i.e. species occurrences of an ecotype). 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 (2011).

Global temperature across most of the Cenozoic was calculated from Mg/Ca isotope record from deep sea carbonates (Cramer et al., 2011). Mg/Ca based 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 during the second half of the Cenozoic. These properties make Mg/Ca based 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 of the NALMA units. The distributions of the temperature mean and range estimates were then rescaled by subtracting their respective means from all values and then dividing by twice their respective standard deviations.

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

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

Table 5: Transition matrix for the birth-death model (Eq. 1). Note that while there are only two state “codes” (0, 1), there are in fact three states: never having originated 0_{never} , present 1, extinct $0_{extinct}$ (Allen, 2011).

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

At the core of the model used in this study is hidden Markov process where the latent process has an absorbing state; this can also be referred to as a discrete-time birth-death model (Allen, 2011). While there are only two state “codes” in a presence-absence matrix (i.e. 0/1), there are in fact three states in a birth-death model: not having originated yet, extant, and extinct. The last of these is the absorbing state, as once a species has gone extinct it cannot re-originate (Allen, 2011). Thus, in the transition matrices the probability of an extinct species changing states is 0 (Table 5). See below for parameter explanations (Tables 6, 7, and 8).

Basic model

I will begin defining the model used in this study by focusing on the basic machinery of the hidden Markov process at the model’s core. This basic model is similar to the Jolly-Seber capture-mark-recapture model CITATION. The basic model has three characteristic probabilities:

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	$N \times T$	probability of observing a species at time t if it is present
ϕ	$N \times T$	probability of species originating from time t to $t + 1$ if it is not present
π	$N \times T - 1$	probability of species surviving at time t , given that it is already originated

probability p of observing a species given that it is present, probability π of a species surviving
 366 from one time to another, and probability ϕ of a species first appearing (Royle and Dorazio, 2008)
 (Table 6). In this formulation, the probability of a species becoming extinct is $1 - \pi$. The inclusion
 368 of species and temporal information means that all three of these probabilities are defined for every
 species at every time point (Table 6; how this is accomplished is described below. Importantly, only
 370 origination can occur during the first time step as nothing is present in order to survive.

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

The parameters associated with Equation 1 are described in Table 6; this formulation is identical to
 372 that described in where individual covariates are included for all parameters (Royle and Dorazio,
 2008). The product term that appears when calculating values of z not at $t = 1$ ensures that once a
 374 species goes extinct it does not re-originate. The basic model described here (Eq. 1) does not
 include the additional, necessary prior information.

376 Expanding on the basics

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

The probability of observing a species given that it is present (logit p) is modeled as a logistic regression with a time-varying intercept with an additional zero-centered varying effect for species' functional group, respectively. The effect of species mass was also included through a slope term.

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

Importantly, the time and functional group varying-intercept is itself modeled such that each the intercept for each functional group is a time series with it's own group-level covariates (described below).

The expanded model incorporating these regression models is written as

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

How the priors for the varying-effects and coefficients in this expanded model are described below along with the complete model.

Complete model

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

Here I describe how the effects of mammal functional group on origination and survival are modeled. f^{ϕ} and f^{π} are modeled as the responses from a multivariate normal distribution, the

Table 7: Parameters for the first expansions

Parameter	dimensions	explanation
u	T	time-varying intercept
f	J	effect of functional group on observation
f^ϕ	$J \times T - 1$	intercept of log-odds ϕ , varies by time and functional group
f^π	$J \times T$	intercept of log-odds π , varies by time and functional group
o^ϕ	K	effect of species' order on log-odds of ϕ
o^π	K	effect of species' order on log-odds of π
β^ϕ	1	effect of species' mass on log-odds of ϕ
β^π	1	effect of species' mass on log-odds of π

means of which are modeled as independent regressions. The time-series structure of these regressions is represented as a random-walk prior for the time-varying intercept of these group-level regression. The effects of group-level covariates are included for each functional group as a vector regression coefficients. The expansion to include this group-level regression is described in Equation 3. The parameters for these group-level regressions are described in Table 8.

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

In hierarchical models like the one developed here (Eq. 2, 3) there is very little difference between the likelihood and prior as data can enter the model through many different parameters CITATION. For example, in Equation 2 the model of z can be considered a prior and the parameterizations in Equation 3 are priors on many of the parameters which predict ϕ and π . The remaining priors,

Table 8: Parameters for the group-level regressions.

Parameter	dimensions	explanation
μ^ϕ	$J \times T$	group-level time-series of the mean log-odds of ϕ for each functional group
μ^π	$J \times T$	group-level time-series of the mean log-odds of π for each functional group
Σ^ϕ	$J \times J$	covariance matrix of group-level time-series of the mean log-odds of ϕ for each functional group
Σ^π	$J \times J$	covariance matrix of group-level time-series of the mean log-odds of π for each functional group
α^ϕ	$J \times T$	time-varying intercept of μ^ϕ
α^π	$J \times T$	time-varying intercept of μ^π
σ^ϕ	J	scale of random-walk prior for α^ϕ
σ^π	J	scale of random-walk prior for α^π
γ^ϕ	D	group-level regression coefficients for μ^ϕ
γ^π	D	group-level regression coefficients for μ^π
U	$U \times J$	group-level covariates

however, are not based on parameter expansion but are prior estimates for the remaining

unmodeled parameters. These prior choices are expressed in Equation 4 and are explained below.

For the regression coefficients, such as β^ϕ and γ^ϕ , these priors are weakly informative and

concentrate most of their probability density between -2 and 2. Similarly, for the scale parameters,

such as τ^ϕ and σ^ϕ , are given weakly informative priors which concentrate of their probability

density between 0 and -2. The covariance matrices such as Σ^ϕ decomposed into a vector of scale

terms (e.g. τ^ϕ) and correlation matrices (e.g. Ω^ϕ which were then given weakly informative priors.

This approach and choice of LKJ priors for the correlation matrices follows the Stan User Manual

CITATION.

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

416 The total model is the sampling statement is expressed as the combination of equations 2, 3, and 4.
These statements form a complete generative model from which posterior inference of parameter
418 values is possible.

Posterior inference and model adequacy

420 A computer program that implements joint posterior inference the model described above (Eqs. 2,
3, and 4) was written in the probabilistic programming language Stan (Stan Development Team,
422 2016). All methods for posterior inference implemented in Stan are derivative-based; this causes
complications for actually implementing the above models, because integers do not have derivatives.
424 In order to infer the values of the matrix of latent discrete parameters z (Tables 6) the log posterior
probabilities of all possible states of the unknown values of z were calculated and summed (i.e.
426 marginalized) (Stan Development Team, 2016).

Species durations at minimum range through from a species first appearance to their last

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 species having existed for the entire study interval and the species having only existed between
the directly observed first and last appearances to all possible intermediaries (Fig 2) (Stan

Development Team, 2016). This process is identical, language-wise, to assuming range-through and
then estimating the possibility of all possible 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	0	1	1	1	1	1	1	0
Potential	1	1	1	1	1	1	1	0
Potential	0	0	0	1	1	1	1	1
Potential	0	0	1	1	1	1	1	1
Potential	0	1	1	1	1	1	1	1
Potential	1	1	1	1	1	1	1	1

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

The combined size of the dataset and large number of parameters (Eqs. 2, 3, and 4), specifically the
total number of latent parameters that are the matrix z , means that stochastic approximate
posterior inference is computationally slow even using NUTS based HMC as implemented in Stan
(Stan Development Team, 2016). Instead, an approximate Bayesian approach was used: variational

inference. A recently developed automatic variational inference algorithm called “automatic
 440 differentiation variational inference” (ADVI) is implemented in Stan and was used here (Kucukelbir
 et al., 2015; Stan Development Team, 2016). ADVI assumes that the posterior is Gaussian but still
 442 yields a true Bayesian posterior; this assumption is similar to quadratic approximation of the
 likelihood function commonly used in maximum likelihood based inference (McElreath, 2016). The
 444 principal limitation of assuming the joint posterior is Gaussian is that the true topology of the
 log-posterior isn’t estimated; this is a particular burden for scale parameters which are bounded to
 446 be positive (e.g. standard deviation).

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

After obtaining approximate posterior inference using ADVI, model adequacy and quality of fit
 462 were assessed using a posterior predictive check (Gelman et al., 2013). By simulating 100 theoretical
 data sets from the posterior estimates of the model parameters and the observed covariate
 464 information the congruence between predictions made by the model and the observed empirical
 data can be assessed. These datasets are simulated by starting with the observed states of the
 466 presence-absence matrix at $t = 1$; from there, the time series roll forward as stochastic processes

with covariate information given from the empirical observations. Importantly, this is fundamentally
 468 different from observing the posterior estimates of the “true” presence-absence matrix z . The
 posterior predictive check used in this study is to compare the observed average number of
 470 observations per species to a distribution of simulated averages; if the empirically observed value
 sits in the middle of the distribution then the model can be considered adequate in reproducing the
 472 observed number of occurrences per species.

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

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

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

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

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

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

488 and number of extinctions E_t estimated as

$$E_t = \sum_{i=1}^M z_{i,t} = 0 | z_{i,t-1} = 1. \quad (7)$$

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

$$\begin{aligned} O_t^{rate} &= \frac{O_t}{N_{t-1}^{stand}} \\ E_t^{rate} &= \frac{E_t}{N_{t-1}^{stand}} \\ D_t^{rate} &= O_t^{rate} - E_t^{rate}. \end{aligned} \quad (8)$$

490 Acknowledgements

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

496 References

- Allen, L. J. S. 2011. An introduction to stochastic processes with applications to biology. 2nd ed.
498 Chapman and Hall/CRC, Boca Raton, FL.
- Alroy, J. 1996. Constant extinction, constrained diversification, and uncoordinated stasis in North
500 American mammals. *Palaeogeography, Palaeoclimatology, Palaeoecology* 127:285–311.
- . 2009. Speciation and extinction in the fossil record of North American mammals. Pages
502 302–323 *in* R. K. Butlin, J. R. Bridle, and D. Schluter, eds. *Speciation and patterns of diversity*.
Cambridge University Press, Cambridge.

- 504 Alroy, J., P. L. Koch, and J. C. Zachos. 2000. Global climate change and North American
mammalian evolution. *Paleobiology* 26:259–288.
- 506 Badgley, C., and J. A. Finarelli. 2013. Diversity dynamics of mammals in relation to tectonic and
climatic history: comparison of three Neogene records from North America. *Paleobiology*
508 39:373–399.
- Badgley, C., T. M. Smiley, R. Terry, E. B. Davis, L. R. G. Desantis, D. L. Fox, S. S. B. Hopkins,
510 T. Jezkova, M. D. Matocq, N. Matzke, J. L. McGuire, A. Mulch, B. R. Riddle, V. L. Roth, J. X.
Samuels, C. A. E. Strömberg, and B. J. Yanites. 2017. Biodiversity and Topographic Complexity:
512 Modern and Geohistorical Perspectives. *Trends in Ecology & Evolution* pages 1–16.
- Bambach, R. K. 1977. Species richness in marine benthic habitats through the Phanerozoic.
514 *Paleobiology* 3:152–167.
- Bambach, R. K., A. M. Bush, and D. H. Erwin. 2007. Autecology and the filling of ecospace: Key
516 metazoan radiations. *Palaeontology* 50:1–22.
- Bloch, J. I., K. D. Rose, and P. D. Gingerich. 1998. New species of *Batodonoides* (Lipotyphla,
518 *Geolabididae*) from the Early Eocene of Wyoming: smallest known mammal? *Journal of*
Mammalogy 79:804–827.
- 520 Blois, J. L., and E. A. Hadly. 2009. Mammalian Response to Cenozoic Climatic Change. *Annual*
Review of Earth and Planetary Sciences 37:181–208.
- 522 Brook, B. W., and D. M. J. S. Bowman. 2004. The uncertain blitzkrieg of Pleistocene megafauna.
Journal of Biogeography 31:517–523.
- 524 Brown, A. M., D. I. Warton, N. R. Andrew, M. Binns, G. Cassis, and H. Gibb. 2014. The
fourth-corner solution - using predictive models to understand how species traits interact with
526 the environment. *Methods in Ecology and Evolution* 5:344–352.
- Brown, J. H., and B. A. Maurer. 1989. Macroecology: the division of food and space among species
528 on continents. *Science* 243:1145–1150.

Brown, J. J. 1995. *Macroecology*. University of Chicago Press, Chicago.

530 Bush, A. M., and R. K. Bambach. 2011. Paleoeologic Megatrends in Marine Metazoa. *Annual Review of Earth and Planetary Sciences* 39:241–269.

532 Bush, A. M., R. K. Bambach, and G. M. Daley. 2007. Changes in theoretical ecospace utilization in marine fossil assemblages between the mid-Paleozoic and late Cenozoic. *Paleobiology* 33:76–97.

534 Bush, A. M., and P. M. Novack-Gottshall. 2012. Modelling the ecological-functional diversification of marine Metazoa on geological time scales. *Biology Letters* 8:151–155.

536 Cantalapiedra, J. L., J. L. Prado, and M. T. Alberdi. 2017. Decoupled ecomorphological evolution and diversification in Neogene-Quaternary horses. *Science* 355:627–630.

538 Carrano, M. T. 1999. What, if anything, is a cursor? Categories versus continua for determining locomotor habit in mammals and dinosaurs. *Journal of Zoology* 247:29–42.

540 Clyde, W. C., and P. D. Gingerich. 1998. Mammalian community response to the latest Paleocene thermal maximum: an isotaphonomic study in the northern Bighorn Basin, Wyoming. *Geology* 26:1011–1014.
542

Cohen, K. M., S. C. Finney, P. L. Gibbard, and J.-X. Fan. 2015. The ICS International Chronostratigraphic Chart.
544

Cottenie, K. 2005. Integrating environmental and spatial processes in ecological community dynamics. *Ecology Letters* 8:1175–1182.
546

Cramer, B. S., K. Miller, P. Barrett, and J. Wright. 2011. Late Cretaceous-Neogene trends in deep ocean temperature and continental ice volume: Reconciling records of benthic foraminiferal geochemistry ($\delta^{18}\text{O}$ and Mg/Ca) with sea level history. *Journal of Geophysical Research: Oceans* 116:1–23.
548
550

Damuth, J., and C. M. Janis. 2011. On the relationship between hypsodonty and feeding ecology in ungulate mammals, and its utility in palaeoecology. *Biological Reviews* 86:733–758.
552

Elith, J., and J. R. Leathwick. 2009. Species distribution models: ecological explanation and

prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics* 40:677–697.

Eronen, J. T., C. M. Janis, C. P. Chamberlain, and A. Mulch. 2015. Mountain uplift explains differences in Palaeogene patterns of mammalian evolution and extinction between North America and Europe. *Proceedings of the Royal Society B: Biological Sciences* 282:20150136.

Eronen, J. T., P. D. Polly, M. FRED, J. Damuth, D. C. FRANK, V. Mosbrugger, C. SCHEIDEGGER, N. C. Stenseth, and M. Fortelius. 2010. Ecometrics: The traits that bind the past and present together. *Integrative Zoology* 5:88–101.

Ezard, T. H. G., A. Purvis, and H. Morlon. 2016. Environmental changes define ecological limits to species richness and reveal the mode of macroevolutionary competition. *Ecology Letters* 19:899–906.

Figueirido, B., C. M. Janis, J. A. Pérez-Claros, M. De Renzi, and P. Palmqvist. 2012. Cenozoic climate change influences mammalian evolutionary dynamics. *Proceedings of the National Academy of Sciences* 109:722–727.

Foote, M. 2001. Inferring temporal patterns of preservation, origination, and extinction from taxonomic survivorship analysis. *Paleobiology* 27:602–630.

Foote, M., and J. J. Sepkoski. 1999. Absolute measures of the completeness of the fossil record. *Nature* 398:415–7.

Foster, J. R. 2009. Preliminary body mass estimates for mammalian genera of the Morrison Formation (Upper Jurassic, North America). *PaleoBios* 28:114–122.

Fraser, D., R. Gorelick, and N. Rybczynski. 2015. Macroevolution and climate change influence phylogenetic community assembly of North American hoofed mammals. *Biological Journal of the Linnean Society* 114:485–494.

Freudenthal, M., and E. Martín-Suárez. 2013. Estimating body mass of fossil rodents. *Scripta Geologica* 145:1–130.

Gelman, A. 2008. Scaling regression inputs by dividing by two standard deviations. *Statistics in Medicine* pages 2865–2873.

Gelman, A., J. B. Carlin, H. S. Stern, D. B. Dunson, A. Vehtari, and D. B. Rubin. 2013. *Bayesian data analysis*. 3rd ed. Chapman and Hall, Boca Raton, FL.

Gelman, A., and J. Hill. 2007. *Data Analysis using Regression and Multilevel/Hierarchical Models*. Cambridge University Press, New York, NY.

Gordon, C. L. 2003. A First Look at Estimating Body Size in Dentally Conservative Marsupials. *Journal of Mammalian Evolution* page 21.

Graham, A. 2011. *A natural history of the New World: the ecology and evolution of plants in the Americas*. University of Chicago Press, Chicago.

Harmon, L. J., and S. Harrison. 2015. Species Diversity Is Dynamic and Unbounded at Local and Continental Scales. *The American Naturalist* 185:000–000.

Harrison, S., and H. Cornell. 2008. Toward a better understanding of the regional causes of local community richness. *Ecology Letters* 11:969–979.

Huang, S., J. T. Eronen, C. M. Janis, J. J. Saarinen, D. Silvestro, and S. A. Fritz. 2017. Mammal body size evolution in North America and Europe over 20 Myr: similar trends generated by different processes. *Proceedings of the Royal Society B: Biological Sciences* 284:20162361.

Jamil, T., W. A. Ozinga, M. Kleyer, and C. J. F. Ter Braak. 2013. Selecting traits that explain species-environment relationships: A generalized linear mixed model approach. *Journal of Vegetation Science* 24:988–1000.

Janis, C., J. Damuth, and J. M. Theodor. 2004. The species richness of Miocene browsers, and implications for habitat type and primary productivity in the North American grassland biome. *Palaeogeography, Palaeoclimatology, Palaeoecology* 207:371–398.

Janis, C. M. 1993. Tertiary mammal evolution in the context of changing climates, vegetation, and tectonic events. *Annual Review of Ecology and Systematics* 24:467–500.

- 604 ———. 2008. An evolutionary history of browsing and grazing ungulates. Pages 21–45 *in* I. J. Gordon and H. H. T. Prins, eds. *The Ecology of Browsing and Grazing*. Springer-Verlag.
- 606 Janis, C. M., J. Damuth, and J. M. Theodor. 2000. Miocene ungulates and terrestrial primary productivity: where have all the browsers gone? *Proceedings of the National Academy of Sciences* 97:7899–904.
- 608 Janis, C. M., and P. B. Wilhelm. 1993. Were there mammalian pursuit predators in the tertiary? *Dances with wolf avatars. Journal of Mammalian Evolution* 1:103–125.
- Jardine, P. E., C. M. Janis, S. Sahney, and M. J. Benton. 2012. Grit not grass: concordant patterns of early origin of hypsodonty in Great Plains ungulates and Glires. *Palaeogeography, Palaeoclimatology, Palaeoecology* 365–366:1–10.
- 612 Jernvall, J., and M. Fortelius. 2002. Common mammals drive the evolutionary increase of hypsodonty in the Neogene. *Nature* 417:538–40.
- 614 ———. 2004. Maintenance of trophic structure in fossil mammal communities: site occupancy and taxon resilience. *The American Naturalist* 164:614–624.
- 616 Kucukelbir, A., R. Ranganath, A. Gelman, and D. M. Blei. 2015. Automatic Variational Inference in Stan. Pages 568–576 *in* NIPS. Vol. 28.
- 618 Legendre, S. 1986. Analysis of mammalian communities from the Late Eocene and Oligocene of Southern France. *Paleovertebrata* 16:191–212.
- 620 Liow, L. H., M. Fortelius, E. Bingham, K. Lintulaakso, H. Mannila, L. Flynn, and N. C. Stenseth. 2008. Higher origination and extinction rates in larger mammals. *Proceedings of the National Academy of Sciences* 105:6097–6102.
- 622 Liow, L. H., M. Fortelius, K. Lintulaakso, H. Mannila, and N. C. Stenseth. 2009. Lower Extinction Risk in SleeporHide Mammals. *The American Naturalist* 173:264–272.
- 624 Lloyd, G. T., J. R. Young, and A. B. Smith. 2011. Taxonomic Structure of the Fossil Record is Shaped by Sampling Bias. *Systematic Biology* 61:80–89.

Loeuille, N., and M. a. Leibold. 2008. Evolution in metacommunities: on the relative importance of
species sorting and monopolization in structuring communities. *The American naturalist*
171:788–99.

Luo, Z.-X., A. W. Crompton, and A.-L. Sun. 2001. A New Mammaliaform from the Early Jurassic
and Evolution of Mammalian Characteristics. *Science* 292:1535–1540.

McElreath, R. 2016. *Statistical rethinking: a Bayesian course with examples in R and Stan*. CRC
Press, Boca Raton, FL.

McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology
from functional traits. *TRENDS in Ecology and Evolution* 21:178–185.

McKenna, R. T. 2011. *Potential for Speciation in Mammals Following Vast , Late Miocene Volcanic
Interruptions in the Pacific Northwest*. Masters. Portland State University.

Mendoza, M., C. M. Janis, and P. Palmqvist. 2006. Estimating the body mass of extinct ungulates:
a study on the use of multiple regression. *Journal of Zoology* 270:90–101.

Mittelbach, G. G., and D. W. Schemske. 2015. Ecological and evolutionary perspectives on
community assembly. *Trends in Ecology and Evolution* 30:241–247.

Novack-Gottshall, P. M. 2007. Using a theoretical ecospace to quantify the ecological diversity of
Paleozoic and modern marine biotas Using a theoretical ecospace to quantify the ecological
diversity of Paleozoic and modern marine biotas. *Paleobiology* 33:273–294.

Pires, M. M., D. Silvestro, and T. B. Quental. 2015. Continental faunal exchange and the
asymmetrical radiation of carnivores. *Proceedings of the Royal Society B: Biological Sciences*
282:20151952.

Pollock, L. J., W. K. Morris, and P. A. Vesk. 2012. The role of functional traits in species
distributions revealed through a hierarchical model. *Ecography* 35:716–725.

Polly, P., J. Eronen, M. Fred, G. P. Dietl, V. Mosbrugger, C. Scheidegger, D. C. Frank, J. Damuth,

N. C. Stenseth, and M. Fortelius. 2011. History matters: ecometrics and integrative climate
change biology. *Proceedings of the Royal Society B: Biological Sciences* 278:1131–1140.

Polly, P. D., A. M. Lawing, J. T. Eronen, and J. Schnitzler. 2015. Processes of ecometric patterning:
modelling functional traits, environments, and clade dynamics in deep time. *Biological Journal of
the Linnean Society* pages n/a–n/a.

Quental, T. B., and C. R. Marshall. 2013. How the Red Queen Drives Terrestrial Mammals to
Extinction. *Science* 341:290–292.

Rabosky, D. L. 2013. Diversity-Dependence, Ecological Speciation, and the Role of Competition in
Macroevolution. *Annual Review of Ecology, Evolution, and Systematics* 44:1–22.

Rabosky, D. L., and A. H. Hurlbert. 2015. Species Richness at Continental Scales Is Dominated by
Ecological Limits. *The American Naturalist* 185:000–000.

Raia, P., F. Carotenuto, F. Passaro, D. Fulgione, and M. Fortelius. 2012. Ecological specialization
in fossil mammals explains Cope’s rule. *The American Naturalist* 179:328–37.

Royle, J. A., and R. M. Dorazio. 2008. Hierarchical modeling and inference in ecology: the analysis
of data from populations, metapopulations and communities. Elsevier, London.

Royle, J. A., J. D. Nichols, and M. Kéry. 2005. Modelling occurrence and abundance of species
when detection is imperfect. *Oikos* 110:353–359.

Shipley, B., D. Vile, and E. Garnier. 2006. From plant traits to plant communities: a statistical
mechanistic approach to biodiversity. *Science* 314:812–814.

Silvestro, D., A. Antonelli, N. Salamin, and T. B. Quental. 2015. The role of clade competition in
the diversification of North American canids. *Proceedings of the National Academy of Sciences of
the United States of America* 112:8684–9.

Simberloff, D., and T. Dayan. 1991. The Guild Concept and the Structure of Ecological
Communities. *Annual Review of Ecology and Systematics* 22:115–143.

Slater, G. J. 2015. Iterative adaptive radiations of fossil canids show no evidence for

diversity-dependent trait evolution. *Proceedings of the National Academy of Sciences* 112:4897–4902.

Smith, F. A., J. Brown, J. Haskell, and S. Lyons. 2004. Similarity of mammalian body size across the taxonomic hierarchy and across space and time. *The American Naturalist* 163:672–691.

Smith, F. A., S. K. Lyons, S. Morgan Ernest, and J. H. Brown. 2008. Macroecology: more than the division of food and space among species on continents. *Progress in Physical Geography* 32:115–138.

Smits, P. D. 2015. Expected time-invariant effects of biological traits on mammal species duration. *Proceedings of the National Academy of Sciences* 112:13015–13020.

Stan Development Team. 2016. Stan Modeling Language Users Guide and Reference Manual.

Strömberg, C. A. E. 2005. Decoupled taxonomic radiation and ecological expansion of open-habitat grasses in the Cenozoic of North America. *Proceedings of the National Academy of Sciences of the United States of America* 102:11980–4.

Tomiya, S. 2013. Body Size and Extinction Risk in Terrestrial Mammals Above the Species Level. *The American Naturalist* 182:196–214.

Urban, M. C., M. A. Leibold, P. Amarasekare, L. De Meester, R. Gomulkiewicz, M. E. Hochberg, C. A. Klausmeier, N. Loeuille, C. de Mazancourt, J. Norberg, J. H. Pantel, S. Y. Strauss, M. Vellend, and M. J. Wade. 2008. The evolutionary ecology of metacommunities. *Trends in Ecology and Evolution* 23:311–317.

Valentine, J. W. 1969. Patterns of taxonomic and ecological structure of the shelf benthos during Phanerozoic time. *Paleontology* 12:684–709.

Van Valkenburgh, B. 1990. Skeletal and dental predictors of body mass in carnivores. Pages 181–205 *in* J. Damuth and B. J. Macfadden, eds. *Body size in mammalian paleobiology: estimation and biological implications*. Cambridge University Press, Cambridge.

- 702 ———. 1999. Major patterns in the history of carnivorous mammals. *Annual Review of Earth and Planetary Sciences* 27:463–493.
- 704 Villéger, S., P. M. Novack-Gottshall, and D. Mouillot. 2011. The multidimensionality of the niche reveals functional diversity changes in benthic marine biotas across geological time. *Ecology letters* 14:561–8.
- 706 Wang, S. C., P. J. Everson, H. J. Zhou, D. Park, and D. J. Chudzicki. 2016. Adaptive credible intervals on stratigraphic ranges when recovery potential is unknown. *Paleobiology* 42:240–256.
- 708 Wang, S. C., and C. R. Marshall. 2016. Estimating times of extinction in the fossil record. *Biology Letters* 12:20150989.
- Warton, D. I., B. Shipley, and T. Hastie. 2015. CATS regression - a model-based approach to studying trait-based community assembly. *Methods in Ecology and Evolution* 6:389–398.
- 712 Weber, M. G., C. E. Wagner, R. J. Best, L. J. Harmon, and B. Matthews. 2017. Evolution in a Community Context: On Integrating Ecological Interactions and Macroevolution. *Trends in Ecology & Evolution* xx:1–14.
- 714 Wilson, J. B. 1999. Guilds, functional types and ecological groups. *Oikos* 86:507–522.
- 716 Zachos, J. C., G. R. Dickens, and R. E. Zeebe. 2008. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature* 451:279–283.
- 718 Zachos, J. C., M. Pagani, L. Sloan, E. Thomas, and K. Billups. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292:686–693.
- 720