

Evolutionary paleoecology and the biology of extinction

Peter D. Smits
psmits@uchicago.edu

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Committee on Evolutionary Biology
The University of Chicago

Committee
Dr. Michael J. Foote (co-advisor)
Dr. Kenneth D. Angielczyk (co-advisor)
Dr. Richard H. Ree
Dr. P. David Polly

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1 Introduction

- 2 Evolutionary paleoecology is the study of the effects of ecological traits and factors on
3 differential rate dynamics, particularly rates of faunal turnover and diversification [64].
4 Ecological traits are expressed by a taxon, at any level, and are involved in biotic–biotic or
5 biotic–abiotic interactions while ecological factors are the environmental conditions in which
6 a taxon exists (the set of all biotic and abiotic interactors). Diversification is the difference
7 between origination and extinction and is the net pattern of macroevolution. The study
8 of evolutionary paleoecology is therefore the link between environmental (biotic–biotic and
9 biotic–abiotic) interactions and macroevolution. As a corollary to Kitchell [64]’s definition,
10 Allmon [2] states that in order to correctly link ecological interactions to macroevolution, one
11 must focus on the specific traits and factors that may affect the speciation process. Tacitly
12 included in this is the study of how ecological traits are related to extinction [63].

13 It is expected that for the majority of geological time, extinction is non-random with
14 respect to biology [47] Determining how different traits, both alone or in concert, influence to
15 extinction risk is then extremely important for understanding the differential diversification
16 of taxa over the Phanerozoic. Periods of background extinction also represent the majority
17 of geologic time, remain relatively predictable and change slowly, thus providing a better
18 opportunity to study how traits are related to survival than periods of mass extinction
19 [47, 94]. The Law of Constant extinction [117] posits that extinction risk of taxa within a
20 given adaptive zone is age independent (memoryless), however the generality of this statement
21 is possibly suspect [28, 33, 91, 101]. By analyzing the survival patterns within different
22 adaptive zones during periods of background extinction, it should be possible to determine if
extinction is best modeled as age independent or dependent.

- 23 Organismal traits relating to environmental preference are good candidates for estimating
24 differences in extinction risk. Organismal traits have been shown to be related to differential
25 extinction [11, 37, 68, 79], especially the relationship between adaptation to variable envi-
26 ronments and increased species longevity. A simple expectation is that taxa with preference
27 for rare environments will be more at risk than taxa with abundant environments based on
28 purely stochastic grounds. As environments change in availability, a taxon’s instantaneous
29 risk of extinction would then be expected change in concert. Taxa are also expected to be
30 adapting to their environment, possibly increasing or decreasing their environmental tolerance
31 and thus changing their instantaneous extinction risk. Related to environmental preference is
32 species-level geographic range size. Species with larger geographic ranges tend to have lower
33 extinction rates than species with smaller geographic ranges [42, 47, 53, 79, 100]. However,
34 how range size is “formed” is different between clades [48] and thus remains a black box
35 for most taxa. Thus, the utility of focusing on organismal traits related to environmental
36 preference is that the black box can be “opened.”
- 37 In addition to understanding patterns of survival, how community composition changes over
38 time is extremely important for understanding how trophic structure changes or is maintained
39 over time. Additionally, community connectedness is important for understanding the degree

to which global, regional, or local scale processes are important for shaping environmental interactions, biotic–biotic and biotic–abiotic. In addition to total community connectedness, the dynamics of taxa within various ecological categories are important for understanding whether different adaptive zones may be differently affected by global, regional, or local scale processes. The Law of Constant extinction is theorized to hold during periods of environmental stability and is thus considered extremely difficult/impossible to test [70]. However, if environmental shifts are incorporated into the analysis of survival distributions, it may be possible to actually test the relationship between taxon age and extinction risk in the context of their adaptive zone and environment. Additionally, this may allow for illumination of what actual processes underly extinction during the majority of geologic time.

It is under this framework that I propose to study how ecological traits associated with environmental preference have affected differential survival and cosmopolitan-endemism dynamics. I will be studying two distantly related and biotically different groups: Permian brachiopods and Cenozoic mammals. Both of these groups are considered to have very good fossil records able to reflect massive long term evolutionary patterns [75]. These two time periods were chosen because they represent periods of approximately the same length (47 My and 65 My) and of climatic change, global warming and global cooling respectively. Also, these two groups are a marine and terrestrial system respectively and the traits associated with environmental preference and range size (described below) are fundamentally very different. Both patterns of survival (Section 1.1) and community connectedness (Section 1.2) will be measured for both of these groups. The differences between these two groups in terms of life-habit and environmental preference

Importantly, this comparison allows for a series of questions to be asked with regards to emergent properties and the Law of Constant extinction. Brachiopod and mammal survival can be analyzed at the generic level for different adaptive zones (combinations of traits). The age independence or dependence of extinction for these two groups can then be tested. However because there is a known potential bias towards age-dependent extinction when analyzing generic level survival curves [92, 93, 106], the mammalian survival will be further analyzed at the specific level and the differences between the two survival functions will be examined, specifically in whether different traits best model the two curves and if either is age-independent or not. Additionally, the importance of global climatic change in modeling both brachiopod and mammalian survival will be analyzed. In the case of mammalian survival, if global climatic change is found to not be important this does not mean that regional or local climatic changes are not important to survival. By analyzing mammalian community connectedness, it should be possible to estimate how disjoint communities are and if it is reasonable to expect global, regional, or local processes to have dominated and how this may have changed over time.

78 **1.1 Survival analysis**

Survival analysis is the analysis of time till event data. In the case of paleontological analysis
80 this is the time from the origination (first appearance date; FAD) of a taxon till the time
of extinction (last appearance date; LAD), or the duration of a taxon. Survival analysis
82 has a long history in paleontology [108, 117], though these initial analyses differ from many
of the modern approaches [65]. Survival is described primarily by two functions, $S(t)$ and
84 $h(t)$, or probability of survival at time (age) t and instantaneous failure rate at time t . The
survival function, and corresponding hazard function, can be parameterized in a variety of
86 different ways. Survival curves can also be estimated non-parametrically using, for example,
the Kaplan-Meier (K-M) estimator. This approach provides a useful method for graphically
88 representing the observed survival distribution. While other methods, such as semiparametric
Cox models [65], can be used to compare patterns of survival, only fully non-parametric and
90 fully parametric methods are used here. Parametric techniques are favored because the shape
of the hazard function is of interest.

92 Survival analysis shares some similarities with linear and logistic regression. While these
approaches use continuous (duration) or dichotomous (extinct/not extinct) responses, re-
94 spectively, survival analysis combines these concepts by measuring the duration till event
or follow-up time. In addition to using both duration and death/extinction information,
96 censoring information can also be incorporated in analysis. Censoring is the term for when
there is uncertainty of exact survival time and can come in three general forms: right-censored
98 (unknown extinction time), left-censored (unknown origination time), and interval censored
(range of possible extinction times). In the case of paleontological survival analysis, censoring
100 provides a framework for the inclusion of taxa ranging into/out of the time period of interest.

The Law of Constant extinction [117] predicts that extinction risk is random with respect
102 to taxon age. In the language of survival analysis, this means that $h(t) = \lambda$ where λ is a
constant. This only occurs when survival times are exponentially distributed, formulated as

$$S(t) = \exp^{-\lambda t} \tag{1}$$

104 . Importantly, this observation underlies the “validity” of birth-death models of population
and clade dynamics where death risk is memoryless.

106 There are many alternatives to constant extinction risk, however. For example, there is a
frequently observed inverse relationship between genus age and extinction risk [33] OTHERS,
108 which could be modeled using, among many others, a Weibull distribution. In comparison to
the exponential distribution which has only a single parameter λ , the Weibull distribution
110 has two parameters, λ and k . The λ of the Weibull distribution behaves as in the exponential
distribution while k is a shape parameter which describes how failure is proportional to a
112 power of time. If $k < 1$ then failure rate monotonically decreases with age, and if $k > 1$ then
failure rate monotonically increases with age. When $k = 1$ the Weibull distribution reduces to
114 the exponential distribution and failure rate is constant. Other potential survival distributions,

such as the log-logistic, extended Gamma, and log-normal distributions [65], describe different
116 patterns of age-dependent failure/extinction (monotonic and nonmonotonic).

1.1.1 Effect of heterogeneous preservation

118 While some amount of uncertainty is possible to in a survival analysis framework via censoring,
this is may be complicated when dealing with the fossil record. Because the observed duration
120 of a taxon is virtually always shorter than the actual duration of that taxon, it is important
to understand how this affects models of survival. If preservation is homogeneous across taxa,
122 space, and time, then this is expected to have a minimal and uniform effect on estimates of
duration and survival [101].

124 However, a major concern is the systematic differential preservation of one group of organisms
compared to another, for example between taxa inhabiting open versus closed environments
126 (Section 3.2). Any systematic bias in estimation of survival times would affect estimating
model parameters of $S(t)$ and potentially lead to the wrong conclusions. In order to investigate
128 the effect of systematic range truncation on one set of observations compared to another,
I propose four different sets of simulations: two groups with identical diversification and
130 identical preservation, two groups with identical diversification but different preservation,
two groups with different diversification but identical preservation, and two groups with
132 different diversification and different preservation. Both diversification and preservation will
be simulated using very simple models in order to limit the complexity of interpreting results.

134 Diversification will be simulated as a time-homogeneous birth-death process. This model has
only two parameters, birth (λ) and death (μ), which are the expected number of events per
136 unit time. Both events are memoryless and thus have no association with an observations age.
When death is random with respect to age, the expected hazard function is constant and
138 survival is expected to be exponentially distributed (Eq. 1). This process was chosen because
it is extremely simple, well understood, and is a common model used to model phylogenies
140 CITATIONS.

The simplest preservation model is as a Poisson process CITATIONS. Following an exponential
142 distribution, preservation rate (ϕ) is defined as the number of expected observations per unit
time. For a given observation (taxa), a series waiting times are randomly drawn until the
144 sum of these random times is equal to or greater than the duration of the observation. Each
of these waiting times represents a fossil occurrence. The time between the first occurrence
146 and the penultimate occurrence is then the duration of the “fossilized” observation.

Varying λ , μ , and ϕ across a wide range of values, I will measure the deviance in median
148 survival time between the “true” distributions and from the “fossilized” distributions. Any
systematic bias away from the range of deviances in median survival times of the “true”
150 distributions will represent the effect of differential preservation for the simplest possible
diversification and fossilization models. Importantly, this approach may illuminate situations
152 where survival may be biased away from being exponentially distributed.

1.2 Biogeographic networks

- 154 Community connectedness is the degree to which localities are composed of endemic versus
 155 cosmopolitan taxa, and how similar this ratio is across localities. If localities and taxa are
 156 defined as nodes in a bipartite graph, different network measures can be used to measure the
 157 how nodes are linked. This then measures both how taxa are distributed among and between
 158 localities and how similar different localities are. A bipartite network is defined as a network
 159 where nodes can be divided into two disjoint sets such that connections are only between
 160 sets and not within sets CITATION, in this case meaning that taxa can only be linked to
 161 localities but not to taxa and *vice versa*.
- 162 Modified from Sidor et al. [104], community connectedness can be measured via four different
 163 summary statistics: average relative number of endemic taxa per locality (E , Eq. 2), average
 164 relative locality occupancy per taxon (Occ , Eq. 3), biogeographic connectedness (BC , Eq.
 165 4), and code length [98, 99, 104]. These summary statistics describe how unique each locality
 166 is on average compared to all others during a time period, how relatively widespread taxa are
 167 on average during a time period, how evenly distributed taxa are amongst localities during a
 168 time period, and the degree of biogeographic provincially during a time period. Of course,
 169 the first three of these measures can be represented as distributions instead of means allowing
 170 for better understanding of the spread of taxa over the landscape. Three measures are easily
 171 defined mathematically. E is defined as

$$E = \frac{\sum_{i=1}^L \frac{u_i}{n_i}}{L} \quad (2)$$

- 172 where L is as the number of localities, u is the number of taxa unique to a locality, and n is
 173 the number of taxa present at a locality. This is a measure of how unique localities are on
 174 average. Occ is the number of localities a taxon is, on average, found at and is defined

$$Occ = \frac{\sum_{i=1}^N \frac{l_i}{L}}{N} \quad (3)$$

- 175 where N is as the number of taxa present in the biogeographic network and l is the number
 176 of localities a taxon occurred in. BC is a measurement of the shared taxa between localities
 177 and is defined

$$BC = \frac{O - N}{LN - N} \quad (4)$$

- 178 where O is the total number of taxonomic occurrences. BC ranges from 0 to 1, with 0
 179 meaning that each locality completely disconnected from all other localities and 1 indicating
 180 that all taxa are presents at all localities.

181 Code length is a measure of the information flow [103] of a graph as estimated from the
 182 behavior of a random surfer [16] on a graph and how often it visits each node and it's behavior
 183 with regards to moving into and out of different regions of the graph. Code length is the
 184 minimum length of a binary code for describing the behavior the surfer and the community

structure of the nodes and is estimated via the map equation [98, 99]. The logic of the map
186 equation is that a good map compresses reality into as few symbols as possible thus we
want to compress as many nodes as possible into as few symbols as possible. Our goal is to
188 represent a graph better than just assigning a unique Huffman code to each node [45, 98]. By
compressing multiple nodes into a single code block, we decrease the minimum coding length
190 of a network and a network with a low code length has more nodes compressed into distinct
subunits/provinces without losing the underlying information flow of the graph. In the case
192 of measuring community connectedness, a low code length means greater site distinctness
and provinciality than a graph with a high code length [104]. For further examples of the
194 map equation, visit <http://mapequation.org/>.

Analysis of these measures of community connectedness both within and between different
196 regions across the globe allows for the expected relative importance of global versus regional
versus local scale processes, and how this might change over time, to be estimated. If
198 global processes are important to patterns of community connectedness and environmental
interactions than it is expected that these measures will be correlated with global climate
200 measures. Additionally, if two or more regions have similar or correlated patterns of community
connectedness, it is expected that global processes may play a roll in shaping the environment.
202 Regional processes are expected to dominate when E is low, Occ is high, BC is high, and code
length is high. In contrast, local processes are expected to dominate when E is high, Occ is
204 low, BC is low and code length is low. The different scales are not mutually exclusive, however,
and one or more scales might be involved in shaping patterns of community connectedness
206 and environmental interactions. Importantly, which process scales are dominant may change
over time.

208 **2 Australian Permian Brachiopods**

2.1 Traits and environmental preference

- 210 Brachiopods are suspension feeders that are not actively motile, thus the availability of
optimal environmental conditions is extremely important for both establishment and survival.
212 Brachiopod occurrence has been found to be strongly linked to the type ocean floor on
which they occur [95, 96]. Environmental preference is esteemed here using three traits,
214 two environmental and one biological: substrate preference, habitat preference, and surface
interface/affixing strategy. Each of these three traits relates to a different aspect of the
216 environment and a taxon's specific adaptive zone. Importantly, it is possible that the loss of
suitable environments may determine different trait associated extinction risk. While larval
218 mode is considered an important trait associated with geographic range and extinction risk
[51, 52], it does not persevere in brachiopods and thus cannot be used to model survival [52].
220 Additionally, taxa found on the east coast of Australia during the Permian would have been
facing the Panthalassic Ocean and would have had few "good" areas to disperse to except in
222 the immediate region because of the distance required to reach a different shore line and the
high latitude of the region.
- 224 Substrate preference is related to the chemical and physical processes affecting a given
environment. Substrate selection is mitigated via larval chemosensory abilities and thus may
226 act as a weak proxy for larval dispersal ability [51, 52]. The three generally used states of
substrate affinity are carbonate, clastic, or mixed [7, 36, 61, 78, 79]. The Phanerozoic is
228 characterized by an overall decline in carbonates relative to clastics [36, 78]. Additionally,
the Australian Permian is dominated by clastic beds [13, 30, 31, 82, 115]. It is expected then
230 that the majority of brachiopod taxa will prefer clastic type substrates compared to the rarer
carbonate type substrates.
- 232 Habitat preference is a description of the depositional environment in which a taxon was
found at the time of fossilization. Because brachiopods are sessil and frequently fixed to
234 the environment, it is expected that the inferred depositional environment is akin to that
in which they lived. The range of depositional environments are quite broad, representing
236 many different marine settings. Because of the large range and difficulty of precisely inferring
depositional environment a frequently used, albeit coarse, classification is on-shore versus
238 off-shore [15, 50, 54, 61, 102] along with the option of a taxon having no particular habitat
preference. Importantly, habitat availability is broadly related to sea-level which can change
240 both dramatically and rapidly over time [80]. Because of this, on-shore type habitats are
potentially very volatile and unstable for long periods of time. During the Permian of
242 Australia there were four major glaciation events which covered most of the entire continent
[13, 29–31], which most likely strongly impacted sea-level as well as the availability and
244 constancy of on-shore versus off-shore habitats. Additionally, habitat might capture other
factors relating to the environment not captured in substrate preference.

- ²⁴⁶ Affixing strategy is the manner by which an individual interfaces with the environment. Unlike bivalves which can burrow or snails which are motile, a brachiopod is sessile and has to
²⁴⁸ maintain their commissure at or above substrate level in order to expose their lophophore. Because of this, brachiopods have evolved a variety of different methods to position themselves
²⁵⁰ in various different environmental conditions such as flow speed or mud depth [1, 66, 67, 95]. Broadly, these methods can be classified as pedunculate (presence of a pedicle), reclining
²⁵² (absence of pedicle), and cementing. During the Permian, pedunculate taxa are associated with shallow on-shore environments while reclining taxa are associated with deep off-shore
²⁵⁴ environments [20] however these associations are weak as most assemblages are composed of a heterogeneous mix of strategies.
- ²⁵⁶ Additionally, the Permian shift from an “ice house” to a “hot house” world [13, 29, 31, 60, 85]. Australasian taxa are of particular interest because of their proximity to the south pole
²⁵⁸ during the Permian and the repeated glacial activity in the region [13, 29, 30, 60]. According to Olszewski and Erwin [80], however, sea-level and climate change do not wholly explain the
²⁶⁰ brachiopod ecological dynamics experienced in the Permian of Texas. It is then predicted that climate will not be the best sole predictor of brachiopod survival, and that some combination
²⁶² of one or more the above organismal traits will be necessary to best model survival.

2.2 Environmental preference and extinction

²⁶⁴ 2.2.1 Questions

Which traits relating to environmental preference in brachiopods are predictors, either
²⁶⁶ separate or together, of differential survival? Do Permian glacial periods relate to differences in trait-correlated extinction? What is the distribution of brachiopod generic survival?

²⁶⁸ 2.2.2 Hypotheses and predictions

Because of both the long-term decline in carbonates versus clastics [84] and the dominance
²⁷⁰ of Permian-age clastic beds [13, 30, 31, 82, 115] described above (Section 2.1), it is taxa with clastic type affinities will have longer durations than taxa with any other preference.
²⁷² Additionally, this substrate dominance may have been a heavy selection pressure for taxa to adapt to common clastic types and/or away of the rarer carbonates. Because of this, it
²⁷⁴ is expected that taxa with clastic or mixed affinities will have greater survival than taxa associated with carbonate substrates. Additionally, it is predicted that substrate preference,
²⁷⁶ if it captures the same information as modern substrate type, will be a predictor in the best model(s) of survival [95, 96]. However, if substrate affinity is not found to be important
²⁷⁸ for modeling survival this may be due to one or more reasons. First, substrate affinity, as quantified here, may not be capturing the same information as modern substrate type and thus may act as a poor predictor of survival. Second, it may mean that because clastic type

substrate were so dominate during the Permian of Australia that differential survival may be
282 better explained by other factors, either measured or unmeasured.

While other environmental factors beyond substrate type, such as temperature or water depth,
284 have not been found to limit the distribution of modern brachiopods [95, 96] it is unknown if
these traits affect survival. Predictions of differential survival based on habitat preference
286 and affixing strategy can be made on the basis of environmental preference and availability.

During the Permian of Australia there were four major glaciation events where the most of the
288 continent was covered [13, 29–31], it is expected that off-shore adapted taxa will have greater
durations than on-shore adapted taxa. This prediction is based on the expected constancy
290 and availability of off-shore habitats and the expected high volatility of on-shore habitats.
If habitat preference is not found to be a predictor for modeling survival, this may mean
292 that sea-level mediated environmental availability does not determine long term survival.
Specifically, while sea-levels may have fluctuated greatly due to high latitude glaciation
294 [13, 30, 31] it may be that the long term continual availability of habitat over-shadows short
term fluctuations. Also, it has been found in the case of Permian brachiopods from Texas that
296 sea-level along with climate change do not wholly explain the observed ecological dynamics
[80], which may mean that habitat availability may not be the singly dominate factor when
298 modeling brachiopod survival. Additionally, in the case that habitat preference is a good
predictor of survival but not the “best” this may mean that other factors may be more
300 dominate factors related to survival.

Previous global level analysis of brachiopod durations showed that affixing strategy is
302 correlated with longevity [1] and that among endemic taxa, reclining taxa had longer
durations than other affixing strategies. Among cosmopolitan taxa, however, pedunculate
304 and cementing taxa had longer durations than all other taxa, both cosmopolitan and endemic.
This global analysis mixed taxa from many different geological periods and geographic
306 regions which may produce unfair and biased comparisons. By restricting analysis to a single
continuous region, I hope to alleviate these concerns and instead focus on survival of an
308 evolving taxonomic assemblage in a continuous environmental context. If affixing strategy is
found to not be a predictor in the best model(s) of survival this would mean that, while it is
310 correlated with differential survival [1], it may only be a minor factor. For example, this may
indicate that the environmental energetics of Australasia was rather uniform.

312 An important consideration is that taxonomic survival might not be linked to single environments *per se*, but the variability of environments [37, 43, 68]. Adaptation to environmental
314 variability has been found to relate strongly with survival past origination [37]. Adaptation
to variability of environments may be captured in taxa with mixed substrate preference
316 and/or no habitat preference. Based on this observation, it is predicted that taxa with mixed
substrate preference and/or no habitat preference will have longer durations than taxa with
318 single preferences. However, this may also mean that taxa with mixed substrate and/or no
habitat preferences will be of similar duration to clastic type and off-shore preferences, which
320 are predicted to have the longest durations for their respective traits.

2.2.3 Proposed research

322 In order to investigate which traits best model survival and how, I propose a survival analysis
approach as described above (Section 1.1). I choose to restrict this analysis to Australasia
324 because it represents a relatively continually sampled and well worked area that preserves the
majority of the entire Permian [8, 13, 22, 23, 31, 120]. The traits described above (Section
326 2.1) will be used as predictors of survival. The distribution of survival durations will be
modeled using a variety of different distributions which are tied to different hypotheses of
328 extinction risk (Section 1.1).

Permian brachiopod occurrence information is available via the Paleobiology Database
330 (PBDB; <http://fossilworks.org>) and is primarily sourced from the work of Clapham
[20–24] and Waterhouse [120]. While lithological and paleoenvironmental information is
332 available for some occurrences through the PBDB, this information is frequently missing or
too coarse. Lithological information and paleoenvironmental reconstructions will be heavily
334 supplemented using the extensive geological unit information from Geosciences Australia
(<http://www.ga.gov.au/>) as well as the literature on the stratigraphy of Australian Permian
336 basins CITATIONS.

Duration will be measured as the difference between FAD and LAD. If a taxon originates prior
338 to the Permian it will be left censored. If a taxon goes extinct within 5 million years of the
Permo-Triassic (P/T) boundary or after the P/T it will be right censored. The possibility of
340 accounting for the effect of sampling on decreasing observed durations versus true durations
may be done through interval censoring (Section 1.1). For example, a range of LAD values
342 between the observed and that estimated via unbiased point estimation [6, 112] can be used.
The unbiased point estimation of true extinction time is calculated using

$$r = \frac{R}{H - 1} \quad (5)$$

344 where r is the average gap size between fossils, R is the stratigraphic range, and H is the
number of fossil horizons. r is then added to the LAD value for an estimate of the true
346 extinction time.

The most probable genus substrate and habitat preferences are estimated from the distribution
348 of occurrences. Preliminarily, the lithological setting of all occurrences will be classified into
one of the three substrate affinity categories following Foote [36] while paleoenvironmental
350 settings will be classified following Kiessling et al. [62]. Both of these traits will be assigned to
all taxa following the Bayesian approach of Simpson and Harnik [107] where assignments are
352 determined as the posterior probability of a taxon’s occurrences in comparison to available
options during the duration of said taxon. The probability that a genus prefers, for example,
354 on-shore habitat ($P(H_1|E)$) is calculated as

$$P(H_1|E) = \frac{P(E|H_1)P(H_1)}{P(E|H_1)P(H_1) + P(E|H_2)P(H_2)} \quad (6)$$

where the prior probability $P(E)$ is the proportion of all occurrences that are on-shore.

356 The null hypotheses, $P(H_1)$ and $P(H_2)$, differ for assignments of substrate and habitat. For
 substrate, $P(H_1) = P(H_2) = 0.5$, meaning that the null is that a genus has no preference.
 358 For habitat preference, probability of assignment is calculated three times with $P(H_1) = \frac{1}{3}$
 and $P(H_2) = \frac{2}{3}$, meaning that the null is that there is an equal chance that a genus prefers
 360 on-shore, off-shore, or neither habitat. The conditional probabilities, $P(E|H_1)$ and $P(E|H_2)$,
 are calculated using the binomial probability of observing the number of occurrences in, for
 362 example, on-shore habitats, k , out of the total number of occurrences, n . The conditional
 probability is calculated as

$$P(E|H_1) = \binom{n}{k} p^k (1-p)^{n-k} \quad (7)$$

364 where p is the proportion of collections in on-shore habitats.

In the case of the coarse classification schemes of Foote [36] and Kiessling et al. [62], the
 366 following rules are used assign preference. For substrate affinity, if $P(H_1|E) > \frac{2}{3}$ then
 the taxon was considered of carbonate affinity while if $P(H_1|E) < \frac{1}{3}$ then the taxon was
 368 considered to have a clastic affinity. Otherwise, the taxon was considered to have mixed
 affinity. For habitat affinity, the posterior probability for each habitat (inshore, offshore,
 370 none) was calculated using Eq. 6 and the preference with maximum of the three posterior
 probabilities was assigned.

372 Each of the three traits will be considered constant throughout the duration of a genus and
 will be modeled as time-independent covariates of survival. If and how these traits may have
 374 evolved will remain for future study.

Because there is no obvious single best model, multiple models will be compared in order to
 376 determine which is the most likely model of survival. It is important, however, that each
 model be well justified and be tied to a realistic biological hypothesis/prediction [19]. Below
 378 are a list of possible candidate models of survival, based solely on time-independent covariates
 and not time-dependent covariates (below) nor distribution of survival, and the associated
 380 hypotheses (Table 1). This does not represent an exhaustive list of plausible models or
 hypotheses.

382 Because the four major periods of glacial activity during the Permian of Australia may have
 had dramatic impacts on survival and environmental availability, it is necessary to model
 384 glacial activity as a time-dependent covariate. In the simplest case, it is possible to model
 glacial activity as a step-function with two states: no ice, ice. The ages of the onset and
 386 retreat for all of the glacial period are fairly well constrained [30, 31]. Other options for
 modeling climatic change are to use various Australian Permian isotope records [13] as more
 388 fine grained estimates of environmental change.

Because survival models are fit in a maximum likelihood framework [65], model comparison
 390 and selection was done via AICc values [19, 46].

formulation	hypothesis
~ 1	No differential survival based on measured ecological traits.
~ substrate	Substrate availability is the best predictor of survival as expected based on the distribution of modern taxa [95, 96].
~ habitat	Habitat stability is the best predictor as expected by models of Phanerozoic diversification.
~ affixing strategy	
~ substrate + habitat	
~ substrate + affixing strategy	
~ habitat + affixing strategy	Substrate availability as expected by the modern, as well as the method by which a taxon is associated with that substrate as expected by Alexander [1]. By combining well adapted affixing strategy to the energetics of the habitat, survival increases.
~ substrate + habitat + affixing strategy	

Table 1: Some example candidate models of brachiopod survival based on substrate affinity, habitat preference, and affixing strategy. Each model is presented with an associated hypothesis of biological meaning. Formulations are without reference to the distribution of survival.

2.2.4 Preliminary results

- 392 The preliminary results presented here are based entirely on the data present in the PBDB. Observations were either right or left censored following the procedure described above
 394 (Section 2.2.3). Uncertainty of duration was not taken into account via interval censoring.
 396 Substrate and habitat preference were the only covariates of survival and were classified
 398 coarsely following Foote [36] and Kiessling et al. [62] respectively. Model formulations with each covariate alone, additively together, or interacting were used. Only two different survival distributions were considered in this initial analysis: exponential and Weibull. In total, 11 models were fit and compared (Table 2).
- 400 This model is illustrated below (Fig. 1a). While this is the preliminarily best model of survival, the model with both substrate affinity and habitat preference as additive effects
 402 and a Weibull survival distribution may also be considered a good model of survival ($\Delta\text{AICc} \approx 2.9$). Additionally, as illustrated by the difference between the nonparametric Kaplan–Meier
 404 survival curves and the predictions of the parametric model of survival (Fig. 1a) and there is room for improvement in model specification.

formula	distribution	k	df	AICc	w
~ substrate	Weibull	1.91	4	1003.4543	0.81
~ substrate + habitat	Weibull	1.92	6	1006.3618	0.19
~ substrate * habitat	Weibull	1.94	10	1013.3003	0.01
~ 1	Weibull	1.76	2	1034.4234	0.00
~ habitat	Weibull	1.76	4	1036.2236	0.00
~ substrate	exponential		3	1071.9199	0.00
~ substrate + habitat	exponential		5	1075.6211	0.00
~ 1	exponential		1	1083.8734	0.00
~ substrate * habitat	exponential		9	1084.0485	0.00
~ habitat	exponential		3	1086.7439	0.00

Table 2: Model selection table for the preliminary parametric models of brachiopod survival. A formula of ~ 1 is a model with only an intercept and no covariates. The $*$ symbol corresponds to covariate interaction. w are Akaike weights [19].

- 406 The shape parameter (k) of the AICc best model (Fig. 1a) is estimated to be approximately
 407 1.9. As described above, values of k greater than 1 indicate that failure (extinction) rate is
 408 accelerating with respect to taxon age, which may mean that the Law of Constant Extinction
 409 does not hold when modeling generic level extinction in brachiopods.
- 410 For brachiopod survival based on substrate affinity (Fig. 1a), survival was greater for both
 411 carbonate and clastic affinities and lowest for taxa with mixed affinity. Visual inspection
 412 of the estimated survival functions compared to the nonparametric Kaplan–Meier curves
 413 indicates that they were adequate fits to the data.
- 414 Brachiopod survival with the sole predictor being environmental and a Weibull distribution
 415 of survival was not a good model of survival, with an approximate ΔAICc of 33 between
 416 this model and the AICc best model. There is a great degree of deviance between the
 417 nonparametric Kaplan–Meier curves and model predictions (Fig. 1b). Additionally, this
 418 model is not significantly different from the model with only an intercept ($\chi^2 = 2.41$, $df = 2$,
 419 $p = 0.3$). This means, preliminarily, that habitat preference alone makes no difference in
 420 generic level survival.

Further refinements to these models include modeling survival using other distributions of
 421 survival such as a log-normal distribution. Additionally the inclusion of affixing strategy and
 422 climate as predictors will increase the understanding of the biology underlying brachiopod
 423 generic survival. Additionally, the effects of sampling and uncertain durations will be explored
 424 in simulations described below in the context of generic versus specific survival.

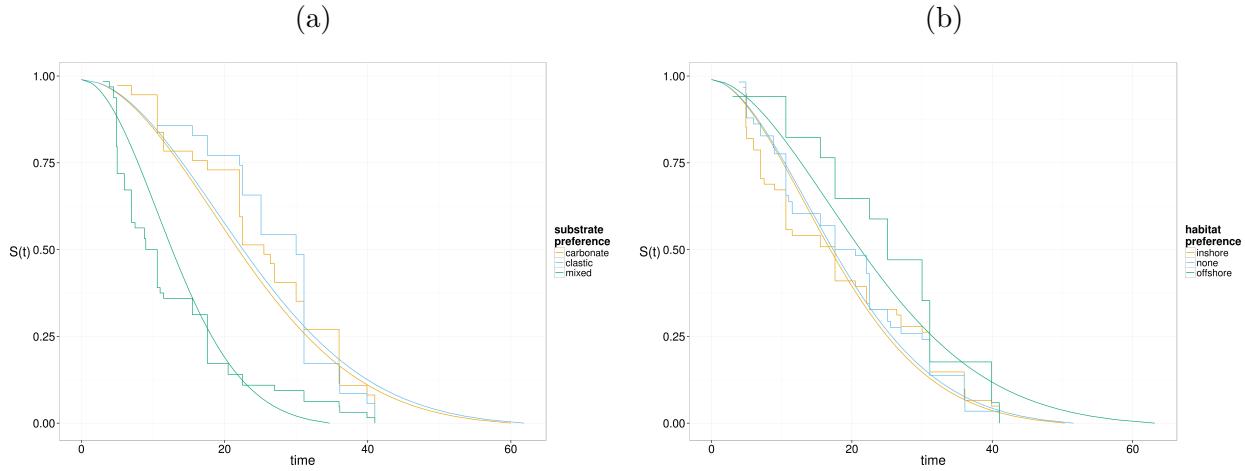


Figure 1: Survivorship curves of Australasian Permian brachiopod genera based on substrate affinity (a) and habitat preference (b). The stepwise functions are nonparametric Kaplan–Meier survival curves for each of the three substrate affinities. The three smooth lines are the predicted survivorship probabilities for taxon of the given age from parametric survival models.

426 2.3 Brachiopod distribution and community connectedness

2.3.1 Questions

428 2.3.2 Hypotheses and predictions

2.3.3 Proposed research

430 2.3.4 Preliminary results

3 Cenozoic Mammals

432 3.1 Traits and environmental context

Mammals are motile organisms which can track their preferred environmental context over time. However, if an organism requires a rare or fragile environmental conditions or is a poor disperser this would limit both the availability of suitable environments and ability to track the preferred environment over time. Three important traits that describe the relationship between mammals and their environmental context are body size, dietary category, and locomotor category [25, 26, 58, 71, 72, 110, 111]. Each of these traits describe different aspects of a taxon's adaptive zone such as energetic cost, population density, expected home range size, set of potential prey items, and dispersal ability among others. Additionally, these three traits are relatively easy to estimate from fossilized remains.

442 Environmental availability, along with stability, is crucial for both establishment and persistence of a species. During the Cenozoic, primarily between the Paleogene–Neogene, there
444 was a shift from a predominately closed environment to a predominately open environment [14, 55, 97] representing a major destabilizing of environments over the Cenozoic. This
446 environmental shift was differently timed between continents [113, 114]. Because of the differential timing of environmental shift between continents, along with the different biotic
448 context of each continent, the community and survival patterns are expected to vary between continents.

450 Dietary category are coarse groupings of similar dietary ecologies: carnivores, herbivores,
452 omnivores, and insectivores. Each of these categories is composed of taxa with a variety of
454 ecologies. For example, herbivores include both browsers and grazers which are known to
have had different diversification dynamics during the Cenozoic [56]. Dietary categories are
456 roughly linked with position in trophic hierarchy, with decreasing stability away from the
“base.” Stability here meaning trophic “distance” from primary productivity, with herbivores
having greater stability than carnivores because of the increased likelihood of prey item
occurrence. Additionally, with increased likelihood of prey item occurrence, abundance can
458 increase [18, 25, 56, 105, 119].

Locomotor category describes the motility of a taxon, the plausibility of occurrence, and the
460 dispersal ability. For example, an obligate arboreal taxon can only occur in locations with a
minimum of tree cover and can most likely only disperse to other environments with suitable
462 tree cover. Locomotor categories are similar to dietary categories as they represent coarse
groupings of taxa with similar life habits. Here, the categories are arboreal, ground dwelling,
464 and scansorial. Similar to dietary category, this trait is considered constant at the specific
level. Dispersal ability is important for determining the extent of a taxon's geographic range
466 [12, 39, 51] and affects both the taxon's extinction risk and regional community evenness.
With the transition from primarily closed to closed environments, there is an expected shift
468 in stability associated with arboreal and ground dwelling taxa.

Body size, here defined as (estimated) mass, has an associated energetic cost in order to
470 maintain homeostasis and in turn necessitates a supply of prey items. Many important life
history traits are associated with body size: reproductive rate, metabolic rate, home range
472 size, among many others [18, 25, 83, 110]. While the study of body size dynamics is very
common CITATIONS, the interactions or processes that are correlated with body size might
474 be underlying the observed pattern more than body size itself. By combining analysis of body
size and both dietary and locomotor categories, it should be possible to better understand
476 what processes underly patterns of survival and community connectedness.

3.2 Ecologically mediated survival

478 3.2.1 Questions

Which ecological traits relating to environmental selection in mammals are predictors, either
480 separately or together, of differential survival? How does both regional and global envi-
ronmental shift relate to differential survival? Are the distributions of generic and specific
482 survival different?

3.2.2 Background and Predictions

484 Abundance is correlated with occupancy, or the number of localities at which a taxon is found
[17, 38, 57]. It follows then that the limits on abundance imposed by resource availability
486 would affect the possible range size of a taxon. Because dietary categories are fundamentally
linked to primary productivity and trophic hierarchy, it is expected that the most stable
488 categories would have the greatest survival and the least stable would have the lowest survival.
Stability is used here to mean number of “steps” from primary productivity and the related
490 relative requirement of other biotic interactors. As such, herbivores are expected to have
greatest survival and carnivores the lowest survival. Omnivorous taxa are expected to have
492 average taxon durations compared to the other two categories. Mammalian herbivores and
carnivores have been found to have a greater diversification rate than omnivores [86] which
494 may indicate that these traits are better for survival. However diversification can be caused
either by an increase in origination relative to extinction or a decrease in extinction relative
496 to origination. If the latter scenario occurred, this would agree with the predictions from
Price et al. [86] that herbivorous and carnivorous taxa would be more successful and have had
498 greater average survival than omnivores. Which scenario occurred, however, is (currently)
impossible to determine from a phylogeny of only extant organisms [87] which means that
500 analysis of the fossil record is necessary to estimate which scenario was most likely. If dietary
category is not found to be important for modeling survival it may mean that trophic category
502 is not a major factor for determining species level survival and that other factors, such as
body size, may dominate.

- 504 It is expected then that arboreal taxa during the Paleogene will have a greater expected
duration than Neogene taxa, and the opposite will be true for ground dwelling taxa. In
506 comparison, taxon duration of scansorial taxa is expected to remain relatively similar between
the two time periods because it represents a mixed environmental preference that may
508 be viable in either closed or open environments. If locomotor category is not included in
the best model of survival this may mean that it is either a poor descriptor of potential
510 dispersal ability or range size or that other factors, both measured or unmeasured, may be of
greater importance. The difficulty of a Paleogene–Neogene comparison, which is potentially
512 undermined by heterogeneous preservation potential, will be explored in simulation as
described below.
- 514 It is then expected that, because taxa with larger range sizes have been found to have lower
extinction rates, that species with higher average body sizes will have a lower extinction rate
516 than taxa with smaller body sizes. This expectation, however, may not be right. As body
size increases, reproductive rate decreases [59], populations are smaller [122], generations are
518 longer [77] all of which can increase extinction risk, as has been observed [27, 69]. However,
the relationship between body size and extinction rate at the generic level has been found to
520 vary between continents [69, 116]. By expanding to include a third continent, South America,
and analyzing specific level data I hope to elucidate how differences in taxonomic diversity
522 at a continental level might affect body size mediated extinction rate. If body size is found
to be unimportant for modeling survival, as in the generic level analysis of Tomiya [116],
524 this means that other biotic or abiotic factors may dominate. This may also mean that
individual level home range size does not scale into increased species level range size, and
526 there is therefore no correlated decrease in extinction rate.

528 The interaction of body size, locomotor category, and dietary category is also extremely
important. For example, a small bodied arboreal taxon of any trophic category during
530 the heavily forested and warm time of the Paleogene would be expected at once to have
both a small body size determined range, a large potential geographic range determined by
locomotion, as well as an increased availability of resources. Together this would mean that
532 relative survival would be expected to be less than, greater than, and greater than average
respectively. Determining which factors dominate during the Paleogene, as well as other
534 parts of the Cenozoic, must be done empirically.

3.2.3 Proposed research

- 536 To analyze differential mammalian survival, I propose a survival analysis approach (Section
1.1) similar to that described above for Permian brachiopods (Section 2.2). Mammalian
538 occurrence data will be collected primarily through a combination of the PBDB, Neogene Old
World Database (NOW; <http://www.helsinki.fi/science/now/>), and museum collections.
540 North American fossil mammal data are well represented and vetted in the PBDB because
of the extensive work of Alroy [3–5]. European fossil mammal data is also well represented
542 between the PBDB and NOW. South American fossil mammal data is available through

the PBDB, but is not particularly well vetted and has poor overall coverage. Because of
544 this, South American fossil mammal data will be gathered via various museums such as the
Field Museum of Natural History and the American Museum of Natural History as well as
546 published occurrence compilations. With the South American taxa, taxonomy and sampling
may not be as well resolved as for North and South America and it may be necessary to
548 restrict analysis to the most taxonomically resolved and sampled groups such as Notoungulata,
Marsupials, Carnivora, and Primates.

550 As described above (Section 2.2.3), duration is measured as the difference between the
observed FAD and LAD of every taxon. Taxa which originated prior to the Cenozoic will be
552 left censored while all taxa that are either extant or went extinct within 2 My of the present
will be right censored. This threshold is to limit the effect of the improved record of the
554 recent.

Dietary category, locomotor category, and body size were considered constant throughout
556 the duration of a taxon and were modeled as time-independent covariates of survival. While
body size is actually a distribution of values, it is quite common to use a single estimate of
558 mean body size as an aggregate trait [49] in studies of clade-wise dynamics CITATIONS.
Additionally, while all three of these traits may evolve over the duration of a taxon, this will
560 not be considered as part of this study.

While many analyses of survivorship are done using generic data [33, 36, 42, 69, 116], there
562 are potential biases in accurately modeling specific level processes using generic level data
[91, 93, 101, 106, 118]. In order to assess some of the differences between generic and specific
564 level survival, I will estimate specific and generic level survival models. Using an approach
similar to previous work on estimating specific level origination and extinction rates from
566 generic level survival curves [35], I will measure the deviance between extinction rate directly
estimated from the specific survivorship and the specific level extinction rates estimated from
568 the generic level survival data. In addition to empirical comparison between generic and
specific level survival, simulations of diversification with varying levels of cryptic speciation
570 (anagenesis). This may also act as a proxy for generic level diversification because a lineage
having a long duration because it is not correctly broken up can be considered analogous to
572 a genus persisting because it continues to speciate.

As with the brachiopods (Section 2.2.3), there is no obvious single best model of survival,
574 so multiple models must be compared in order to determine which is the likely. It is
important, however, that each model be well justified and be tied to a realistic biological
576 hypothesis/prediction [19].

In order to account for environmental shifts, two different time-dependent covariates will be
578 used. δO^{18} isotope information for the whole Cenozoic [124] will be as a global climate proxy.
Additionally, the Paleogene–Neogene divide which may reflect global environmental shift,
580 both biotic and abiotic, will be modeled as a time-dependent step-function.

3.2.4 Preliminary results

582 3.3 Community connectedness: global, regional, local

3.3.1 Questions

- 584 How does the ratio between endemic and cosmopolitan taxa change over time? Is this pattern
different between ecological categories? Does this pattern reflect global, regional, and/or
586 local processes?

3.3.2 Background and Predictions

- 588 During the Cenozoic there was a global shift from a “hot house” environment to an “ice
house” environment [123, 124]. This transition was accompanied by major shifts in global
590 climatic envelopes and the reorganization of mammalian communities [5, 14, 32, 38, 55].
For mammalian community connectedness there are two possible scenarios. First, while the
592 environment was shifting, lineages may have adapted in place and overall trophic structure
and community connectedness would have remained relatively constant through time, as
594 observed during the Neogene of Europe [58]. Alternatively, species may have shifted ranges
and changed the average set of taxa present at a locality which would be associated with
596 non-stationary trophic structure and community connectedness.

Based on prior work, it is expected that the patterns of biogeographic community connect-
598 edness for herbivorous taxa in a region would be most similar to that for all regional taxa
and potentially “drive” the regional pattern, partially because on average this category
600 represents the majority or plurality of taxa [57]. In contrast, community connectedness for
carnivorous taxa is expected to remain constant over time or be correlated with herbivore
602 patterns. Finally, omnivorous taxa are not expected to be correlated with the patterns of
either herbivorous or carnivorous taxa and have either relatively consant or random patterns
604 of community connectedness over time. These predictions are based on the differences in
resilience and relationship to primary productivity, with herbivores being more resilient than
606 carnivores and omnivores being random in their resilience [58]. Resilience is defined here as
the ability for a taxon to increase in commonness (occupancy) after a decline [58].

- 608 The Cenozoic global shift from closed, forested habitat in the Paleogene to open, savanna-like
habitat during the Neogene would have greatly affected the possible distributions of arboreal
610 and ground dwelling taxa. Additionally, the timing of this environmental shift was different
between continents [113, 114], so patterns of community connectedness may not be globally
612 uniform and could instead reflect regional differences. Generally this transitions would
cause forested environments to become increasingly patchily in their distributions while
614 transitioning from the Paleogene to the Neogene. The global prediction then is that there
would have been a relative increase in E (Eq. 2) and code length accompanied by a decrease

616 in *BC* (Eq. 4) and *Occ* (Eq. 3) in arboreal taxa over time. The opposite is expected for
terrestrial taxa.

618 At a regional scale, North American community connectedness is expected to follow the
global predictions described above because the vast amount of prior synthesis has focused
620 on North America [3–5, 9, 10, 14, 32, 40, 41, 108, 109]. However, the effect of global climate
change on North American diversity remains unresolved and controversial [5, 10, 14, 32],
622 thus it is necessary to determine empirically when global versus regional versus local scale
processes may have dominated and how that may have changed over time.

624 The European mammalian fossil record is also well studied, though research has primarily
focused on the Neogene [57, 58, 69, 88–90]. An important aspect about the European record
626 is that during the Neogene there was little shift in relative dietary category abundance [58]
and that the patterns within herbivores (browse–graze transition) were mostly driven by
628 abundant, cosmopolitan taxa [57]. It is predicted then that herbivores will demonstrate
the same patterns of community connectedness as Europe as a whole, while omnivores and
630 carnivores will be different from that of herbivores and may demonstrate random or constant
patterns of community connectedness through time.

632 Patterns of community connectedness for South American mammalian fauna are comparatively
less synthesized than those of North American and Europe. Instead, cross–continental
634 dynamics between North and South America during the Neogene are much more studied
[76]. The South American mammalian faunal record reflects two distinct biotic provinces
636 between the North and the South [34, 73, 74, 81]. Because of this, it is expected that
South America will have a different pattern of community connectedness than either North
638 America or Europe. Also, there is an expected dramatic increase occupancy in land-dwelling
herbivores relative to arboreal and scansorial taxa related to the aridification of high-latitude
640 South America. Additionally, because of this strong biome distinction, it is predicted that
provinciality will be high but remain constant over time.

642 3.3.3 Proposed research

In order to estimate changes in community connectedness during the Cenozoic I will be using
644 the network-based approach described above (Section 1.2). Biogeographic networks will be
constructed for each region (North America, Europe, South American) between species and
646 localities defined as 2x2 latitude–longitude grid cells from an equal-area map projection.
Networks will be made for every 2 My span of the Cenozoic. This bin width was chosen to in
648 order to maximize the chance that two localities are present at the same time. Networks will
also be constructed for subsets of taxa defined by dietary and locomotor categories order to
650 compare patterns both within and between categories, as well as to the combined regional and
global patterns. Because previous studies of mammalian occurrence patterns have restricted
652 analysis to large bodied and well studied groups such as Primates and Artiodactyls in order to
account for potential sampling and taxonomic biases, analysis will be done using all available

654 taxa and with a restricted sample of just major groups in order to observe any differences in
655 patterns of community connectedness. The data necessary to complete this study is the same
656 as for the above analysis of mammalian survival (Section 3.2).

657 The degree of phylogenetic similarity between taxa at a locality may play an important
658 role in community structuring [121]. For example, closely related taxa may be repulsed
659 “repulsed” due to competitive exclusion or “clumped” because of environmental filtering.
660 While it is infeasible to create an explicit phylogenetic hypothesis for all taxa sampled on all
661 continents, almost all taxa have some hierarchical taxonomic information. Using taxonomy as
662 the structure of an information phylogeny, it should be possible to estimate the distribution
663 of phylogenetic similarity across localities.

664 For each locality, an informal phylogeny will be constructed based solely on available taxonomic
665 information such as order, family, and genus assignments with each of these levels being a
666 completely unresolved polytomy. Using this informal phylogeny, a number of measures of
667 phylogenetic similarity can be estimated. For example the relative mean pairwise distance
668 between all taxa at a locality [121] or the related phylogenetic species variability of a single
669 locality Helmus et al. [44]. These values calculated for all localities can then be used as a
670 partial correlates or covariates when modeling changes in community connectedness.

671 The next step is to compare patterns of community connectedness both within and between
672 regions in order to understand if global, regional, or local scale processes dominate. Additionally,
673 comparisons will be done between the different dietary and locomotor categories both
674 within and between regions to determine which scale processes may be affecting either trait.
675 The approach and methodology to accomplish these analyses is currently under development.
676 Additionally, the possibility of integrating locality–locality distance or some other measure
677 of topology will be explored, especially how this relates to code length and provinciality in
678 general.

3.3.4 Preliminary results

680 Preliminary analysis was done using only the occurrence information of both North American
681 and European fossil mammals available in the PBDB. Both regions have qualitatively different
682 patterns of community connectedness, primarily during the Paleogene (Fig. 2). Almost all
683 four of the summary statistics are extremely volatile over the Cenozoic, especially for Europe.
684 However, some interesting qualitative patterns are present.

685 There is a qualitative decrease in *Occ* in Europe until approximately the start of the Neo-
686 gene (approximately 23 My), indicating that the average taxon is becoming generally less
687 cosmopolitan over time. In contrast, North American *Occ* is qualitatively stationary over the
688 entire Cenozoic and almost always lower than that observed for Europe. This means that, on
689 average, North American taxa are present in very few localities at any given point in time.

690 In Europe there is a qualitative rise in *BC* in the first few million years of the Cenozoic, but

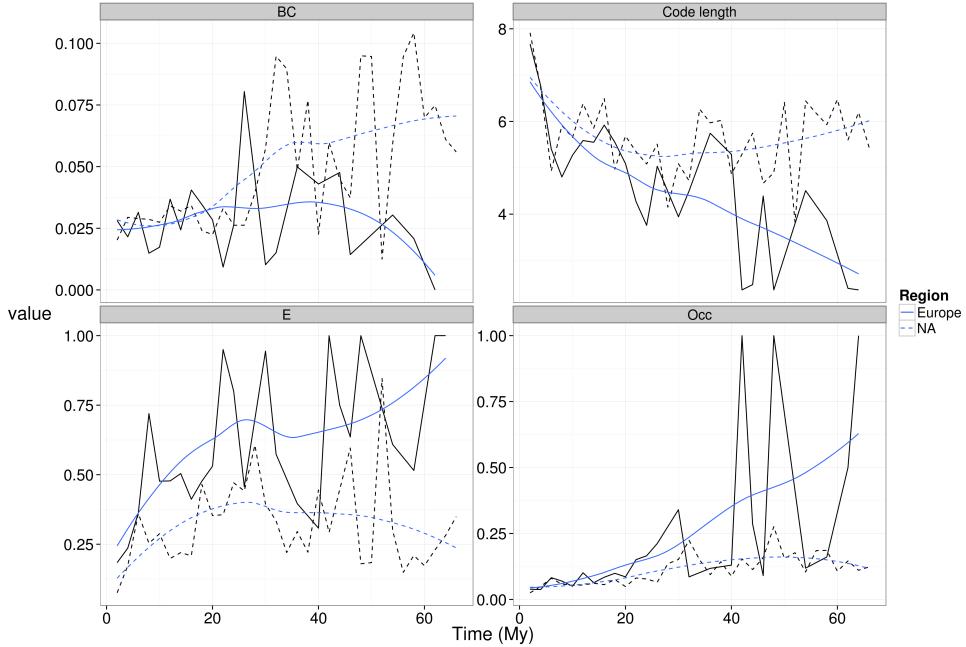


Figure 2: Biogeographic network summary statistics for mammalian communities in North America (dashed line) and Europe (solid line). The summary statistics are, clockwise from top left: biogeographic connectedness (BC), code length, average relative locality occupancy per taxon (Occ), and average relative number of endemic taxa per locality (E). Blue lines are generalized additive model smooths and are presented to illustrate the overall pattern for each region.

afterwards remains relatively stationary meaning that the average proportion of shared taxa remained qualitatively stationary. In comparison, North American *BC* remains stationary with a greater amount of shared taxa than Europe for the first half of the Cenozoic followed by a decrease and another plateau at the end of the Cenozoic.

In Europe, there is a over all qualitative decrease in *E* while in North America there is a qualitatively constant *E* over the Cenozoic with a slight decrease in the Neogene. As discussed above, *E* is a measure of relative uniqueness of a locality on average. Qualitatively, North America retained approximately the same amount of site uniqueness through out the Cenozoic. While the pattern of the European record shows a qualitatively nonmonotonic decrease in locality uniqueness.

The code length of European biogeographic networks increases qualitatively over the entire Cenozoic, while code length of North American networks remains relatively constant until the Neogene when there is a qualitative increase. Initial interpretation of these results indicates that North America maintains a relatively stationary degree of provinciality while Europe has a qualitatively decreasing degree of provinciality.

Biogeographic networks of taxa of similar dietary category

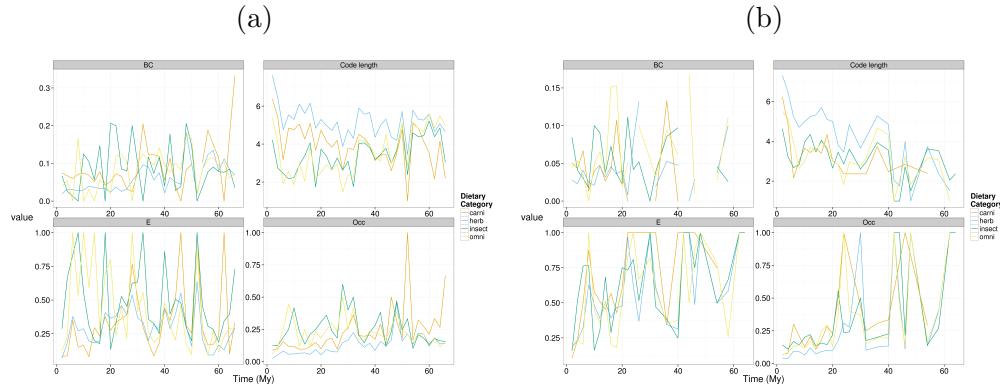


Figure 3: Time series of summary statistics for biogeographic networks determined by dietary category. The summary statistics are, clockwise from top left: biogeographic connectedness (BC), code length, average relative locality occupancy per taxon (Occ), and average relative number of endemic taxa per locality (E).

Biogeographic networks of taxa of similar locomotor category

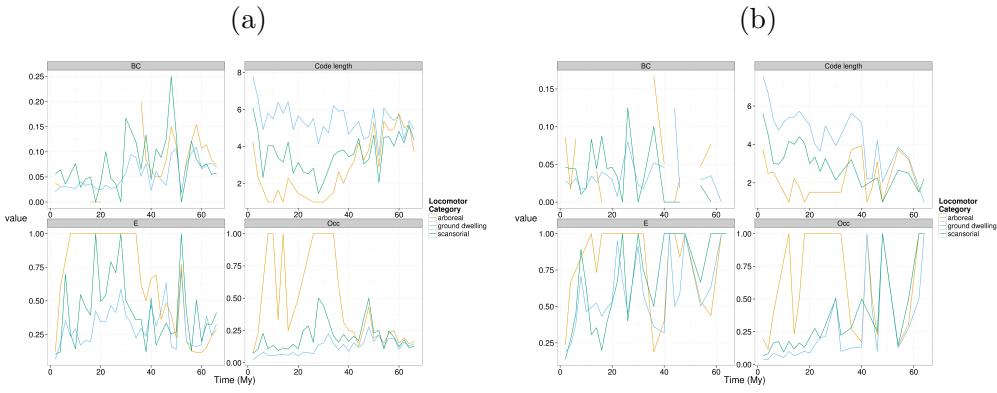


Figure 4: Time series of summary statistics for biogeographic networks determined by locomotor category. The summary statistics are, clockwise from top left: biogeographic connectedness (BC), code length, average relative locality occupancy per taxon (Occ), and average relative number of endemic taxa per locality (E).

708 **4 Synthesis of proposed research**

Underlying all of the above is a foundational question in paleobiology: why do certain taxa
710 go extinct while others do not? In the context of evolutionary paleoecology, this question can
be rephrased as “how do the set of all biotic–biotic and biotic–abiotic interactions a taxon
712 experiences over time (i.e. adaptive zone 108) affect extinction risk?” Related to this is the
Law of Constant Extinction which states that extinction risk for a given adaptive zone is
714 taxon–age independent [117]. It is asserted that the Law of Constant Extinction only holds
during periods of relatively constant environment even though this was not the context for
716 the initial observation [68, 117] which can be interpreted as the set of dominant non-organism
mediated processes do not fluctuate or fluctuate in a known manner. By understanding which
718 non-organism mediated processes may be shaping the environment (set of all possible biotic
and abiotic interactors) and how they change over time and phrasing analysis of extinction
720 in this context, it may be possible to “test” the Law of Constant Extinction.

The first two studies proposed above investigate how organismal traits potentially related
722 to environmental preference affect extinction rate. In effect, these traits may determine
the “bounds” of a taxon’s adaptive zone by limiting the total set of interactions to just
724 those for which the taxon is adapted. The final proposed study aims to estimate what
non-organism mediated processes (global, regional, and/or local) may be dominate in shaping
726 the environment and the related set of adaptive zones. Between these studies, as well the
use of two desperate groups, it should be possible to determine when, what, and if certain
728 variables matter for survival and potentially how they matter.

5 Timeline

- ⁷³⁰ Spring/Summer 2014
- Evolution Meeting: preliminary brachiopod survival results
- ⁷³² South American fossil mammal data from Field Museum of Natural History collections
- Fall 2014/Winter 2015
- ⁷³⁴
- GSA: survivorship simulation for anagenesis and sampling
 - Doctoral Dissertation Improvement Grant
- ⁷³⁶ Spring/Summer 2015
- Evolution Meeting: mammalian survivorship analysis for North America and Europe
- ⁷³⁸ South American fossil mammal data from American Museum of Natural History collections
- ⁷⁴⁰
- write and submit survivorship simulation paper
- Fall 2015/Winter 2016
- ⁷⁴²
- SVP or GSA: mammalian biogeographic connectedness
 - write and submit mammal connectedness paper
- ⁷⁴⁴ Spring/Summer 2016
- Evolution Meeting: brachiopod survival analysis results
- ⁷⁴⁶
- write and submit brachiopod survival paper
- Fall 2016/Winter 2017
- ⁷⁴⁸
- SVP or GSA: mammalian survivorship analysis
 - write and submit mammal survival paper
- ⁷⁵⁰ Spring/Summer 2017
- Evolution Meeting
 - write and submit review/philosophy paper
- ⁷⁵²
- **Defend**

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