

Evolutionary paleoecology and the biology of extinction

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Dissertation Proposal Hearing
February 21, 2014
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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, along with global climatic context, provides a fantastic scenario to understand how long-term, large-scale processes away from mass extinctions proceed.

1.1 Survival analysis

Survival analysis is the analysis of time till event data. In the case of paleontological analysis 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 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 $h(t)$, 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 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 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 fully parametric methods are used here. Parametric techniques are favored because the shape of the hazard function is of interest.

Survival analysis shares some similarities with linear and logistic regression. While these

80 approaches use continuous (duration) or dichotomous (extinct/not extinct) responses, re-
spectively, survival analysis combines these concepts by measuring the duration till event
82 or follow-up time. In addition to using both duration and death/extinction information,
censoring information can also be incorporated in analysis. Censoring is the term for when
84 there is uncertainty of exact survival time and can come in three general forms: right-censored
(unknown extinction time), left-censored (unknown origination time), and interval censored
86 (range of possible extinction times). In the case of paleontological survival analysis, censoring
provides a framework for the inclusion of taxa ranging into/out of the time period of interest.
88 The Law of Constant extinction [117] predicts that extinction risk is random with respect
to taxon age. In the language of survival analysis, this means that $h(t) = \lambda$ where λ is a
90 constant. This only occurs when survival times are exponentially distributed, formulated as

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

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

There are many alternatives to constant extinction risk, however. For example, there is a
94 frequently observed inverse relationship between genus age and extinction risk [33] OTHERS,
which could be modeled using, among many others, a Weibull distribution. In comparison to
96 the exponential distribution which has only a single parameter λ , the Weibull distribution
has two parameters, λ and k . The λ of the Weibull distribution behaves as in the exponential
98 distribution while k is a shape parameter which describes how failure is proportional to a
power of time. If $k < 1$ then failure rate monotonically decreases with age, and if $k > 1$ then
100 failure rate monotonically increases with age. When $k = 1$ the Weibull distribution reduces to
the exponential distribution and failure rate is constant. Other potential survival distributions,
102 such as the log-logistic, extended Gamma, and log-normal distributions [65], describe different
patterns of age-dependent failure/extinction (monotonic and nonmonotonic).

104 1.1.1 Effect of heterogeneous preservation

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

However, a major concern is the systematic differential preservation of one group of organisms
112 compared to another, for example between taxa inhabiting open versus closed environments
(Section 3.2). Any systematic bias in estimation of survival times would affect estimating
114 model parameters of $S(t)$ and potentially lead to the wrong conclusions. In order to investigate
the effect of systematic range truncation on one set of observations compared to another,

¹¹⁶ I propose four different sets of simulations: two groups with identical diversification and
¹¹⁸ identical preservation, two groups with identical diversification but different preservation,
¹²⁰ two groups with different diversification but identical preservation, and two groups with
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.

Diversification will be simulated as a time-homogeneous birth-death process. This model has
¹²² only two parameters, birth (λ) and death (μ), which are the expected number of events per
unit time. Both events are memoryless and thus have no association with an observations age.
¹²⁴ When death is random with respect to age, the expected hazard function is constant and
survival is expected to be exponentially distributed (Eq. 1). This process was chosen because
¹²⁶ it is extremely simple, well understood, and is a common model used to model phylogenies
CITATIONS.

¹²⁸ The simplest preservation model is as a Poisson process CITATIONS. Following an exponential
distribution, preservation rate (ϕ) is defined as the number of expected observations per unit
¹³⁰ time. For a given observation (taxa), a series waiting times are randomly drawn until the
sum of these random times is equal to or greater than the duration of the observation. Each
¹³² of these waiting times represents a fossil occurrence. The time between the first occurrence
and the penultimate occurrence is then the duration of the “fossilized” observation.

¹³⁴ Varying λ , μ , and ϕ across a wide range of values, I will measure the deviance in median
survival time between the “true” distributions and from the “fossilized” distributions. Any
¹³⁶ systematic bias away from the range of deviances in median survival times of the “true”
distributions will represent the effect of differential preservation for the simplest possible
¹³⁸ diversification and fossilization models. Importantly, this approach may illuminate situations
where survival may be biased away from being exponentially distributed.

¹⁴⁰ 1.2 Biogeographic networks

Community connectedness is the degree to which localities are composed of endemic versus
¹⁴² cosmopolitan taxa, and how similar this ratio is across localities. If localities and taxa are
defined as nodes in a bipartite graph, different network measures can be used to measure the
¹⁴⁴ how nodes are linked. This then measures both how taxa are distributed among and between
localities and how similar different localities are. A bipartite network is defined as a network
¹⁴⁶ where nodes can be divided into two disjoint sets such that connections are only between
sets and not within sets CITATION, in this case meaning that taxa can only be linked to
¹⁴⁸ localities but not to taxa and *vice versa*.

Modified from Sidor et al. [104], community connectedness can be measured via four different
¹⁵⁰ summary statistics: average relative number of endemic taxa per locality (E , Eq. 2), average
relative locality occupancy per taxon (Occ , Eq. 3), biogeographic connectedness (BC , Eq.
¹⁵² 4), and code length [98, 99, 104]. These summary statistics describe how unique each locality
is on average compared to all others during a time period, how relatively widespread taxa are

154 on average during a time period, how evenly distributed taxa are amongst localities during a
 155 time period, and the degree of biogeographic provincially during a time period. Of course,
 156 the first three of these measures can be represented as distributions instead of means allowing
 157 for better understanding of the spread of taxa over the landscape. Three measures are easily
 158 defined mathematically. E is defined as

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

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

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

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

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

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

168 Code length is a measure of the information flow [103] of a graph as estimated from the
 169 behavior of a random surfer [16] on a graph and how often it visits each node and it's behavior
 170 with regards to moving into and out of different regions of the graph. Code length is the
 171 minimum length of a binary code for describing the behavior the surfer and the community
 172 structure of the nodes and is estimated via the map equation [98, 99]. The logic of the map
 173 equation is that a good map compresses reality into as few symbols as possible thus we
 174 want to compress as many nodes as possible into as few symbols as possible. Our goal is to
 175 represent a graph better than just assigning a unique Huffman code to each node [45, 98]. By
 176 compressing multiple nodes into a single code block, we decrease the minimum coding length
 177 of a network and a network with a low code length has more nodes compressed into distinct
 178 subunits/provinces without losing the underlying information flow of the graph. In the case
 179 of measuring community connectedness, a low code length means greater site distinctness
 180 and provinciality than a graph with a high code length [104]. For further examples of the
 181 map equation, visit <http://mapequation.org/>.

182 Analysis of these measures of community connectedness both within and between different
 183 regions across the globe allows for the expected relative importance of global versus regional
 184 versus local scale processes, and how this might change over time, to be estimated. If
 185 global processes are important to patterns of community connectedness and environmental
 186 interactions than it is expected that these measures will be correlated with global climate

measures. Additionally, if two or more regions have similar or correlated patterns of community
188 connectedness, it is expected that global processes may play a roll in shaping the environment.
Regional processes are expected to dominate when E is low, Occ is high, BC is high, and code
190 length is high. In contrast, local processes are expected to dominate when E is high, Occ is
192 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
194 and environmental interactions. Importantly, which process scales are dominant may change
over time.

2 Australian Permian Brachiopods

196 2.1 Traits and environmental preference

Brachiopods are suspension feeders that are not actively motile, thus the availability of
198 optimal environmental conditions is extremely important for both establishment and survival.
Brachiopod occurrence has been found to be strongly linked to the type ocean floor on
200 which they occur [95, 96]. Environmental preference is esteemed here using three traits,
two environmental and one biological: substrate preference, habitat preference, and surface
202 interface/affixing strategy. Each of these three traits relates to a different aspect of the
environment and a taxon's specific adaptive zone. Importantly, it is possible that the loss of
204 suitable environments may determine different trait associated extinction risk. While larval
mode is considered an important trait associated with geographic range and extinction risk
206 [51, 52], it does not persevere in brachiopods and thus cannot be used to model survival [52].
Additionally, taxa found on the east coast of Australia during the Permian would have been
208 facing the Panthalassic Ocean and would have had few "good" areas to disperse to except in
the immediate region because of the distance required to reach a different shore line and the
210 high latitude of the region.

Substrate preference is related to the chemical and physical processes affecting a given
212 environment. Substrate selection is mitigated via larval chemosensory abilities and thus may
act as a weak proxy for larval dispersal ability [51, 52]. The three generally used states of
214 substrate affinity are carbonate, clastic, or mixed [7, 36, 61, 78, 79]. The Phanerozoic is
characterized by an overall decline in carbonates relative to clastics [36, 78]. Additionally,
216 the Australian Permian is dominated by clastic beds [13, 30, 31, 82, 115]. It is expected then
that the majority of brachiopod taxa will prefer clastic type substrates compared to the rarer
218 carbonate type substrates.

Habitat preference is a description of the depositional environment in which a taxon was
220 found at the time of fossilization. Because brachiopods are sessil and frequently fixed to
the environment, it is expected that the inferred depositional environment is akin to that
222 in which they lived. The range of depositional environments are quite broad, representing
many different marine settings. Because of the large range and difficulty of precisely inferring
224 depositional environment a frequently used, albeit coarse, classification is on-shore versus
off-shore [15, 50, 54, 61, 102] along with the option of a taxon having no particular habitat
226 preference. Importantly, habitat availability is broadly related to sea-level which can change
both dramatically and rapidly over time [80]. Because of this, on-shore type habitats are
228 potentially very volatile and unstable for long periods of time. During the Permian of
Australia there were four major glaciation events which covered most of the entire continent
230 [13, 29–31], which most likely strongly impacted sea-level as well as the availability and
constancy of on-shore versus off-shore habitats. Additionally, habitat might capture other
232 factors relating to the environment not captured in substrate preference.

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 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 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 (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 environments [20] however these associations are weak as most assemblages are composed of a heterogeneous mix of strategies.

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 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 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 of one or more the above organismal traits will be necessary to best model survival.

2.2 Environmental preference and extinction

2.2.1 Questions

Which traits relating to environmental preference in brachiopods are predictors, either 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?

2.2.2 Hypotheses and predictions

Because of both the long-term decline in carbonates versus clastics [84] and the dominance 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. 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 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, 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 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

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

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

274 During the Permian of Australia there were four major glaciation events where the most of the
continent was covered [13, 29–31], it is expected that off-shore adapted taxa will have greater
276 durations than on-shore adapted taxa. This prediction is based on the expected constancy
and availability of off-shore habitats and the expected high volatility of on-shore habitats.

278 If habitat preference is not found to be a predictor for modeling survival, this may mean
that sea-level mediated environmental availability does not determine long term survival.

280 Specifically, while sea-levels may have fluctuated greatly due to high latitude glaciation
[13, 30, 31] it may be that the long term continual availability of habitat over-shadows short
282 term fluctuations. Also, it has been found in the case of Permian brachiopods from Texas that
sea-level along with climate change do not wholly explain the observed ecological dynamics
284 [80], which may mean that habitat availability may not be the singly dominate factor when
modeling brachiopod survival. Additionally, in the case that habitat preference is a good
286 predictor of survival but not the “best” this may mean that other factors may be more
dominate factors related to survival.

288 Previous global level analysis of brachiopod durations showed that affixing strategy is
correlated with longevity [1] and that among endemic taxa, reclining taxa had longer
290 durations than other affixing strategies. Among cosmopolitan taxa, however, pedunculate
and cementing taxa had longer durations than all other taxa, both cosmopolitan and endemic.

292 This global analysis mixed taxa from many different geological periods and geographic
regions which may produce unfair and biased comparisons. By restricting analysis to a single
294 continuous region, I hope to alleviate these concerns and instead focus on survival of an
evolving taxonomic assemblage in a continuous environmental context. If affixing strategy is
296 found to not be a predictor in the best model(s) of survival this would mean that, while it is
correlated with differential survival [1], it may only be a minor factor. For example, this may
298 indicate that the environmental energetics of Australasia was rather uniform.

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 variability has been found to relate strongly with survival past origination [37]. Adaptation
300 to variability of environments may be captured in taxa with mixed substrate preference
and/or no habitat preference. Based on this observation, it is predicted that taxa with mixed
302 substrate preference and/or no habitat preference will have longer durations than taxa with
single preferences. However, this may also mean that taxa with mixed substrate and/or no
304 habitat preferences will be of similar duration to clastic type and off-shore preferences, which
are predicted to have the longest durations for their respective traits.

308 **2.2.3 Proposed research**

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

316 Permian brachiopod occurrence information is available via the Paleobiology Database (PBDB; <http://fossilworks.org>) and is primarily sourced from the work of Clapham
318 [20–24] and Waterhouse [120]. While lithological and paleoenvironmental information is available for some occurrences through the PBDB, this information is frequently missing or
320 too coarse. Lithological information and paleoenvironmental reconstructions will be heavily supplemented using the extensive geological unit information from Geosciences Australia
322 (<http://www.ga.gov.au/>) as well as the literature on the stratigraphy of Australian Permian basins CITATIONS.

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

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

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

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

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

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

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

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

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

360 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
 evolved will remain for future study.

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

370 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
 glacial activity as a time-dependent covariate. In the simplest case, it is possible to model
 372 glacial activity as a step-function with two states: no ice, ice. The ages of the onset and
 retreat for all of the glacial period are fairly well constrained [30, 31]. Other options for
 374 modeling climatic change are to use various Australian Permian isotope records [13] as more
 fine grained estimates of environmental change.

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

³⁷⁸ **2.2.4 Preliminary results**

The preliminary results presented here are based entirely on the data present in the PBDB.
³⁸⁰ Observations were either right or left censored following the procedure described above
 (Section 2.2.3). Uncertainty of duration was not taken into account via interval censoring.
³⁸² Substrate and habitat preference were the only covariates of survival and were classified
 coarsely following Foote [36] and Kiessling et al. [62] respectively. Model formulations with
³⁸⁴ 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
³⁸⁶ models were fit and compared (Table 2).

The best model of survival had substrate preference as the sole predictor of survival, which
³⁸⁸ followed a Weibull distribution with increasing risk of failure with age (Table 2). This model
 was closely followed by the second best model of survival which had both substrate and
³⁹⁰ habitat preference as additive predictors of survival, also following a Weibull ditribution with
 $k > 1$. The difference between the AICc best model and the second best model was small (Δ
³⁹² AIC ≈ 2.9), meaning that both models can be considered adequate.

The AICc best model is illustrated below (Fig. 1a) as well as the model with habitat as the
³⁹⁴ sole predictor of survival (Fig. 1b)

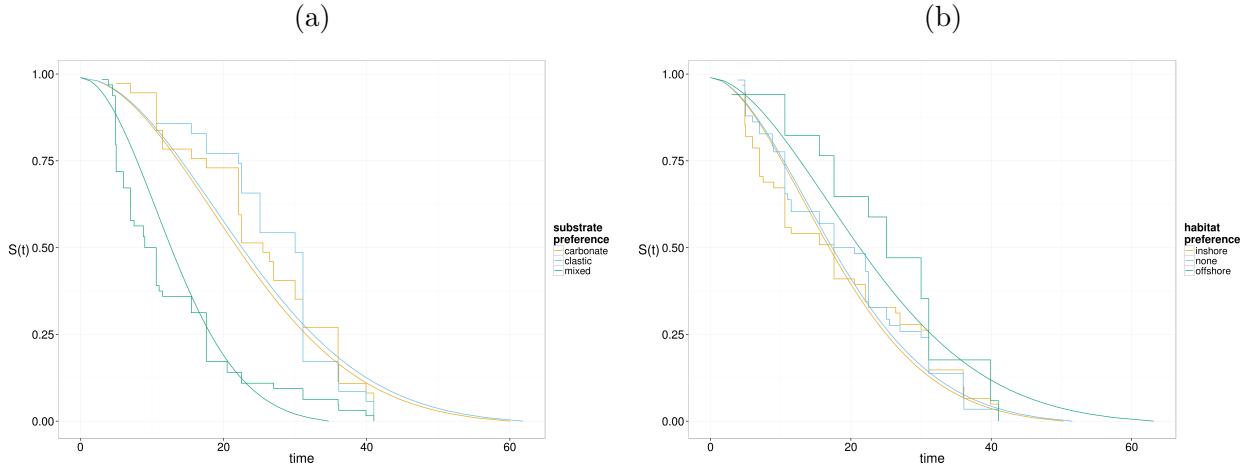


Figure 1: Survivorship curves of Australasian Permian brachiopod genera based on substrate affinity (a) and habitat preference (b). The stepwise functions are nonparametric Kaplan–Meier survival curves for each of the three substrate affinities. The three smooth lines are the predicted survivorship probabilities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

The shape parameter (k) of the AICc best model (Fig. 1a) is estimated to be approximately
³⁹⁶ 1.9 (Table 2). As described above (Section 1.1), values of k greater than 1 indicate that

failure (extinction) risk accelerates with taxon age, which may mean that the Law of Constant
398 Extinction does not hold when modeling generic level extinction in brachiopods.

For brachiopod survival based on substrate affinity (Fig. 1a), survival was greater for both
400 carbonate and clastic affinities and lowest for taxa with mixed affinity. Visual inspection
402 of the estimated survival functions compared to the nonparametric Kaplan–Meier curves
indicates that they were adequate fits to the data.

The model with habitat preference being the sole predictor of survival following a Weibull
404 distribution was a poor estimate, with an approximate ΔAICc of 33 between this model
and the AICc best model. There is a great degree of deviance between the nonparametric
406 Kaplan–Meier curves and model predictions (Fig. 1b). Additionally, this model is not
significantly different from the model with only an intercept ($\chi^2 = 2.41$, $df = 2$, $p = 0.3$).
408 This means, preliminarily, that habitat preference alone makes no difference in generic level
survival.

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

2.3 Brachiopod distribution and community connectedness

416 2.3.1 Questions

Given the repeated major glacial activity during the Permian, how stable was community
418 connectedness in Permian brachiopods? Are patterns of community connectedness different
for taxa favoring different environments?

420 2.3.2 Hypotheses and predictions

During the Permian, the east coast of the Australian continent faced towards the massive
422 Panthalassic Ocean. Because of this, the establishment of populations was most likely limited
to within the local area because the amount of distance required to establish else was most
424 likely too great. This would also have made individuals which settled across the ocean would
have been almost instantly genetically isolated and not increase community connectedness,
426 *per se*. Because of this, it is expected that community connectedness in Australian Permian
brachiopods would be fairly high at any given time and that changes, specifically decreases
428 in connectedness, would be expected during the four glacial periods [30, 31].

Dispersal ability of modern brachiopods appears to be most limited by availability and
430 proximity of substrate types [95, 96]. The Permian of Australia is dominated by widespread

- clastic beds compared to relatively few and rare carbonate beds. The expectation is that
 432 the distribution of taxa with a carbonate preference will be extremely patchy with a high E
 (Eq. 2), low Occ (Eq. 3), low BC (Eq. 4), and low code length [98, 104] compared to the
 434 distribution of clastic preferring taxa. However, if community connectedness is approximately
 equal between carbonate and clastic preferring taxa this would could be caused by two
 436 different scenarios. If community similarity is high or low between all localities this could be
 caused by approximately equal dispersal ability in both groups, high and low respectively.
- 438 Habitat would be expected to influence community structure if there is an uneven distribution
 of available habitats in space and time. Rarity of preferred habitat would be expected to lead
 440 to high E , low Occ , low BC , and low code length compared to an abundance of preferred
 habitat. Because of the four major glaciation events during the Permian of Australia, it
 442 is expected that the availability of on-shore habitats would be highly variable. It is then
 expected that during periods of glacial activity community connectedness of on-shore would be
 444 extremely low because of rarity of environments in comparison to both periods of non-glacial
 activity and off-shore habitats at all times. If habitat preference has no effect on community
 446 connectedness this may mean that the dispersal ability of on-shore taxa is very high and able
 to maintain gene flow between potentially isolated habitats.
- 448 It is expected that affixing strategy alone will have minimal effect on community connectedness
 unless affixing strategy is highly correlated with substrate and/or habitat preference. If
 450 community connectedness is different between affixing strategies

2.3.3 Proposed research

- 452 Following the biogeographic network approach described above (Section 1.2), I will construct
 biogeographic networks between brachiopod genera and localities defined as 2x2
 454 latitude-longitude grid cells from an equal-area map projection. Biogeographic networks
 were constructed for the entire Permian using 2 My bins. In addition to community wide
 456 networks, seperate networks will be constructed for taxa within ecological categories. This
 facilitates comparison of community connectedness patterns during the Permian both within
 458 and between categories as well as with the community wide pattern. The data necessary to
 complete this study is the same as for the above analysis of brachiopod survival (Section 2.2).
 460 Importantly, sampling will be restricted to the east coast of Australia because this represents
 a continuous coast line that faced the Panthalassic Ocean during the Permian.
- 462 The next step is to compare patterns of community connectedness both within and between
 regions in order to understand if global, regional, or local scale processes dominate. Additionally,
 464 comparisons will be done between the different dietary and locomotor categories both
 within and between regions to determine which scale processes may be affecting either trait.
 466 The approach and methodology to accomplish these analyses is currently under development.
 Additionally, the possibility of integrating locality-locality distance or some other measure
 468 of topology will be explored, especially how this relates to code length and provinciality in

general.

⁴⁷⁰ **2.3.4 Preliminary results**

formulation	hypothesis
~ 1	No differential survival based on measured ecological traits.
$\sim \text{substrate}$	Substrate availability is the best predictor of survival as expected based on the distribution of modern taxa [95, 96].
$\sim \text{habitat}$	Habitat stability is the best predictor as expected by models of Phanerozoic diversification.
$\sim \text{affixing strategy}$	Environmental homogeneity/stability means that differentiation can only occur via differences in how a taxon interfaces with the ocean floor.
$\sim \text{substrate + habitat}$	Substrate and habitat combine to best describe the environmental context of a taxon and the availability of its adaptive zone.
$\sim \text{habitat + affixing strategy}$	By combining well adapted affixing strategy to the energetics of the habitat, survival increases.
$\sim \text{substrate + affixing strategy}$	By combining well adapted affixing strategy to the state of the ocean floor increases survival.
$\sim \text{substrate + habitat + affixing strategy}$	The adaptation of affixing strategy along with the environmental context represents the best approximation of the adaptive zone.

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. A formulation of ~ 1 is a model with only an intercept and no covariates. Formulations are without reference to the distribution of survival.

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

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

3 Cenozoic Mammals

472 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.

482 Environmental availability, along with stability, is crucial for both establishment and persistence of a species. During the Cenozoic, primarily between the Paleogene–Neogene, there
484 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
486 environmental shift was differently timed between continents [113, 114]. Because of the differential timing of environmental shift between continents, along with the different biotic
488 context of each continent, the community and survival patterns are expected to vary between continents.

490 Dietary category are coarse groupings of similar dietary ecologies: carnivores, herbivores,
492 omnivores, and insectivores. Each of these categories is composed of taxa with a variety of
494 ecologies. For example, herbivores include both browsers and grazers which are known to
496 have had different diversification dynamics during the Cenozoic [56]. Dietary categories are
498 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
increase [18, 25, 56, 105, 119].

Locomotor category describes the motility of a taxon, the plausibility of occurrence, and the
500 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
502 tree cover. Locomotor categories are similar to dietary categories as they represent coarse
504 groupings of taxa with similar life habits. Here, the categories are arboreal, ground dwelling,
506 and scansorial. Similar to dietary category, this trait is considered constant at the specific
508 level. Dispersal ability is important for determining the extent of a taxon's geographic range
[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
in stability associated with arboreal and ground dwelling taxa.

Body size, here defined as (estimated) mass, has an associated energetic cost in order to
510 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
512 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
514 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
516 what processes underly patterns of survival and community connectedness.

3.2 Ecologically mediated survival

518 3.2.1 Questions

Which ecological traits relating to environmental selection in mammals are predictors, either
520 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
522 survival different?

3.2.2 Hypotheses and predictions

524 Because dietary category describes, roughly, the trophic position of a taxon and its related
stability, it is predicted that more stable categories will have longer durations than less stable
526 categories. Stability here being “distance” from primary productivity, thus it is expected that
herbivores will have greater duration than carnivores. Specifically, herbivores are expected to
528 have greatest survival and carnivores the lowest survival. Omnivorous taxa are expected to
have average taxon durations compared to the other two categories. If dietary category is
530 not found to be important for modeling survival it may mean that trophic category is not a
major factor for determining species level survival and that other factors, such as body size,
532 may dominate.

Mammalian herbivores and carnivores have been found to have a greater diversification rate
534 than omnivores [86] which may indicate that these traits are better for survival. However
diversification can be caused either by an increase in origination relative to extinction or
536 a decrease in extinction relative to origination. If the latter scenario occurred, this would
agree with the predictions from Price et al. [86] that herbivorous and carnivorous taxa would
538 be more successful and have had greater average survival than omnivores. Which scenario
occurred, however, is (currently) impossible to determine from a phylogeny of only extant
540 organisms [87] which means that analysis of the fossil record is necessary to estimate which
scenario was most likely. If survival is found to be similar between all dietary categories, this
542 may mean that the differential diversification patterns observed by Price et al. [86] are due
to differences in speciation and not extinction.

544 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
546 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 be
548 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 dispersal ability
550 which may or may not affect mammalian survival. However, it may be the case that other
factors, measured or unmeasured, may be of greater importance in determining differential
552 survival. The difficulty of a Paleogene–Neogene comparison, which is potentially undermined
by heterogeneous preservation potential, will be explored in simulation as described above
554 (Section 1.1.1).

Body size can possibly scale up to affect species extinction because as body size increases,
556 home range size increases [25]. If individual home range size scales up to reflect minimum
total species geographic range, we would expect that taxa with larger body sizes would
558 have lower extinction rates than species with smaller body sizes. This expectation, however,
may not be right. As body size increases, reproductive rate decreases [59], populations get
560 smaller [122], generations get 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
562 generic level has been found to vary between continents [69, 116]. By expanding to include a
third continent, South America, and analyzing specific level data I hope to elucidate how
564 differences in taxonomic diversity 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
566 generic level analysis of Tomiya [116], this means that other biotic or abiotic factors may
dominate. Also, this may mean that individual level home range size does not scale into
568 increased species level range size, and there is therefore no correlated decrease in extinction
rate.

570 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
572 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
574 locomotion, as well as an increased availability of resources. Together this would mean that
relative survival would be expected to be less than, greater than, and greater than average
576 respectively. Determining which factors dominate during the Paleogene, as well as other
parts of the Cenozoic, must be done empirically.

578 3.2.3 Proposed research

To analyze differential mammalian survival, I propose a survival analysis approach (Section
580 1.1) similar to that described above for Permian brachiopods (Section 2.2). Mammalian
occurrence data will be collected primarily through a combination of the PBDB, Neogene Old
582 World Database (NOW; <http://www.helsinki.fi/science/now/>), and museum collections.

North American fossil mammal data are well represented and vetted in the PBDB because
584 of the extensive work of Alroy [3–5]. European fossil mammal data is also well represented
between the PBDB and NOW. South American fossil mammal data is available through
586 the PBDB, but is not particularly well vetted and has poor overall coverage. Because of
this, South American fossil mammal data will be gathered via various museums such as the
588 Field Museum of Natural History and the American Museum of Natural History as well as
published occurrence compilations. With the South American taxa, taxonomy and sampling
590 may not be as well resolved as for North and South America and it may be necessary to
restrict analysis to the most taxonomically resolved and sampled groups such as Notoungulata,
592 Marsupials, Carnivora, and Primates.

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

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

604 While many analyses of survivorship are done using generic data [33, 36, 42, 69, 116], there
are potential biases in accurately modeling specific level processes using generic level data
606 [91, 93, 101, 106, 118]. In order to assess some of the differences between generic and specific
level survival, I will estimate specific and generic level survival models. Using an approach
608 similar to previous work on estimating specific level origination and extinction rates from
generic level survival curves [35], I will measure the deviance between extinction rate directly
610 estimated from the specific survivorship and the specific level extinction rates estimated from
the generic level survival data. In addition to empirical comparison between generic and
612 specific level survival, simulations of diversification with varying levels of cryptic speciation
(anagenesis). This may also act as a proxy for generic level diversification because a lineage
614 having a long duration because it is not correctly broken up can be considered analogous to
a genus persisting because it continues to speciate.

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

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

both biotic and abiotic, will be modeled as a time-dependent step-function.

624 3.2.4 Preliminary results

Preliminary analysis was performed solely on mammal occurrence data from North America
626 and South America during the Cenozoic from the PBDB. Nonparametric Kaplan-Meier survival curves were estimated for both dietary and locomotor categories (Fig. 2).

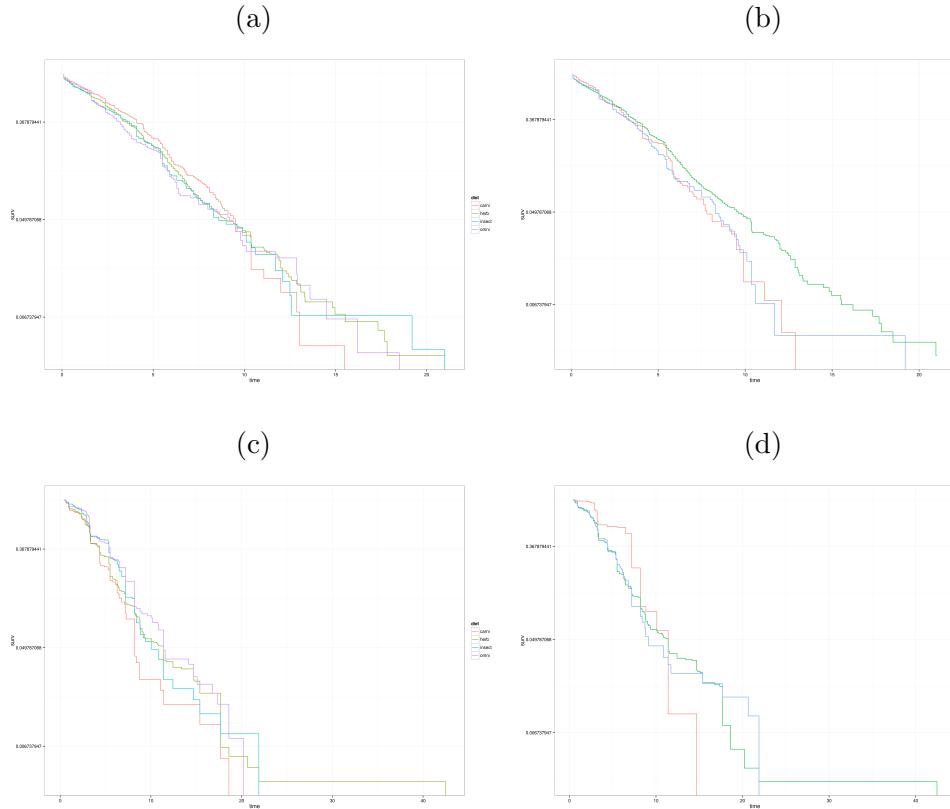


Figure 2: Nonparametric Kaplan-Meier survival curves for North American and European mammals based on dietary category (a and c respectively, and locomotor category (b and d respectively). The vertical axes are on a natural log scale.

628 3.3 Community connectedness: global, regional, local

3.3.1 Questions

- 630 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

632 local processes?

3.3.2 Background and Predictions

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

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

654 The Cenozoic global shift from closed, forested habitat in the Paleogene to open, savanna-like
655 habitat during the Neogene would have greatly affected the possible distributions of arboreal
656 and ground dwelling taxa. Additionally, the timing of this environmental shift was different
657 between continents [113, 114], so patterns of community connectedness may not be globally
658 uniform and could instead reflect regional differences. Generally this transitions would
659 cause forested environments to become increasingly patchily in their distributions while
660 transitioning from the Paleogene to the Neogene. The global prediction then is that there
661 would have been a relative increase in E (Eq. 2) and code length accompanied by a decrease
662 in BC (Eq. 4) and Occ (Eq. 3) in arboreal taxa over time. The opposite is expected for
663 terrestrial taxa.
664 At a regional scale, North American community connectedness is expected to follow the
665 global predictions described above because the vast amount of prior synthesis has focused
666 on North America [3–5, 9, 10, 14, 32, 40, 41, 108, 109]. However, the effect of global climate
667 change on North American diversity remains unresolved and controversial [5, 10, 14, 32],
668 thus it is necessary to determine empirically when global versus regional versus local scale
669 processes may have dominated and how that may have changed over time.

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

678 Patterns of community connectedness for South American mammalian fauna are comparatively
679 less synthesized than those of North America and Europe. Instead, cross-continental
680 dynamics between North and South America during the Neogene are much more studied
681 [76]. The South American mammalian faunal record reflects two distinct biotic provinces
682 between the North and the South [34, 73, 74, 81]. Because of this, it is expected that
683 South America will have a different pattern of community connectedness than either North
684 America or Europe. Also, there is an expected dramatic increase occupancy in land-dwelling
685 herbivores relative to arboreal and scansorial taxa related to the aridification of high-latitude
686 South America. Additionally, because of this strong biome distinction, it is predicted that
687 provinciality will be high but remain constant over time.

688 3.3.3 Proposed research

In order to estimate changes in community connectedness during the Cenozoic I will be using
690 the network-based approach described above (Section 1.2). Biogeographic networks will be
691 constructed for each region (North America, Europe, South American) between species and
692 localities defined as 2x2 latitude-longitude grid cells from an equal-area map projection.
693 Networks will be made for every 2 My span of the Cenozoic. This bin width was chosen to in
694 order to maximize the chance that two localities are present at the same time. Networks will
695 also be constructed for subsets of taxa defined by dietary and locomotor categories order to
696 compare patterns both within and between categories, as well as to the combined regional and
697 global patterns. Because previous studies of mammalian occurrence patterns have restricted
698 analysis to large bodied and well studied groups such as Primates and Artiodactyls in order to
699 account for potential sampling and taxonomic biases, analysis will be done using all available
700 taxa and with a restricted sample of just major groups in order to observe any differences in
701 patterns of community connectedness. The data necessary to complete this study is the same
702 as for the above analysis of mammalian survival (Section 3.2).

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

of phylogenetic similarity across localities.

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

As with the Permian brachiopods (Section 2.3), patterns of community connectedness will be
718 compared both within and between ecological categories. Additionally, the correspondence
719 of changes in environmental conditions and community connectedness will also be analysed.
720 The approach and methodology to accomplish these analyses is currently under development.
721 Additionally, the possibility of integrating locality–locality distance or some other measure
722 of topology will be explored, especially how this relates to code length and provinciality in
723 general.

724 3.3.4 Preliminary results

Preliminary analysis was done using only the occurrence information of both North American
726 and European fossil mammals available in the PBDB. Both regions have qualitatively different
727 patterns of community connectedness, primarily during the Paleogene (Fig. 3). Almost all
728 four of the summary statistics are extremely volatile over the Cenozoic, especially for Europe.
729 However, some interesting qualitative patterns are present.

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

In Europe there is a qualitative rise in *BC* in the first few million years of the Cenozoic, but
736 afterwards remains relatively stationary meaning that the average proportion of shared taxa
737 remained qualitatively stationary. In comparison, North American *BC* remains stationary
738 with a greater amount of shared taxa than Europe for the first half of the Cenozoic followed
739 by a decrease and another plateau at the end of the Cenozoic.

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

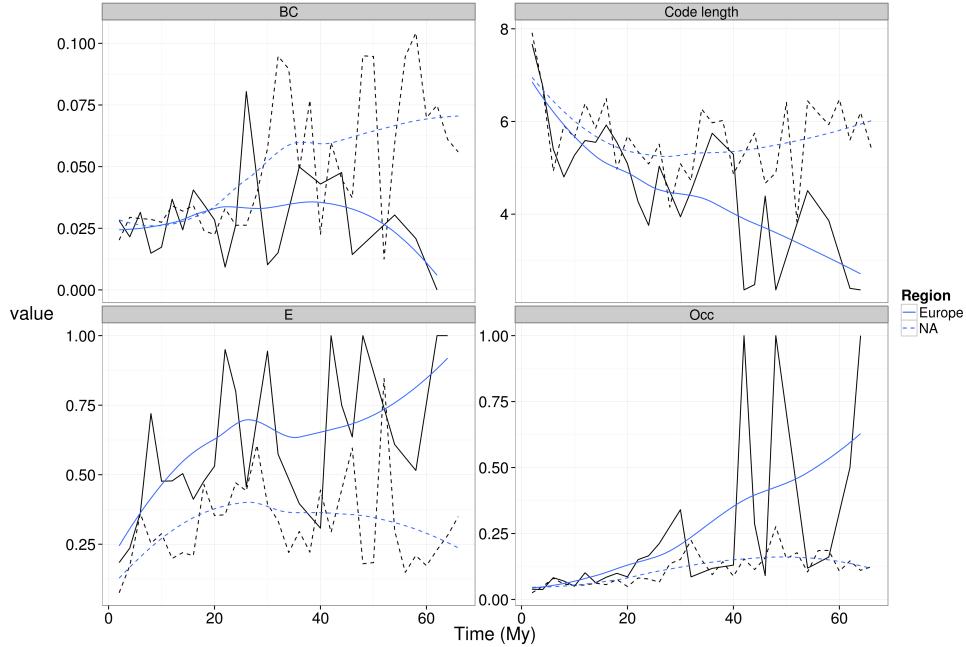


Figure 3: Biogeographic network summary statistics for mammalian communities in North America (dashed line) and Europe (solid line). The summary statistics are, clockwise from top left: biogeographic connectedness (BC), code length, average relative locality occupancy per taxon (Occ), and average relative 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.

746 The code length of European biogeographic networks increases qualitatively over the entire
 748 Cenozoic, while code length of North American networks remains relatively constant until the
 750 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

752 Biogeographic networks of taxa of similar locomotor category

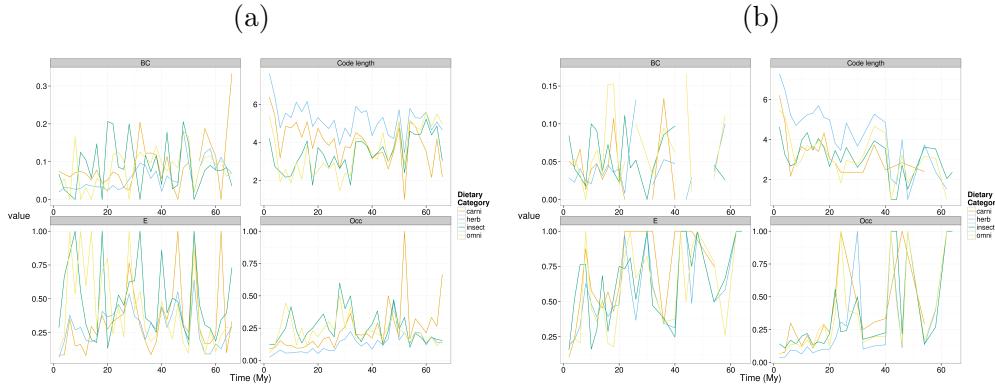


Figure 4: Time series of summary statistics for biogeographic networks determined by dietary category. The summary statistics are, clockwise from top left: biogeographic connectedness (BC), code length, average relative locality occupancy per taxon (Occ), and average relative number of endemic taxa per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

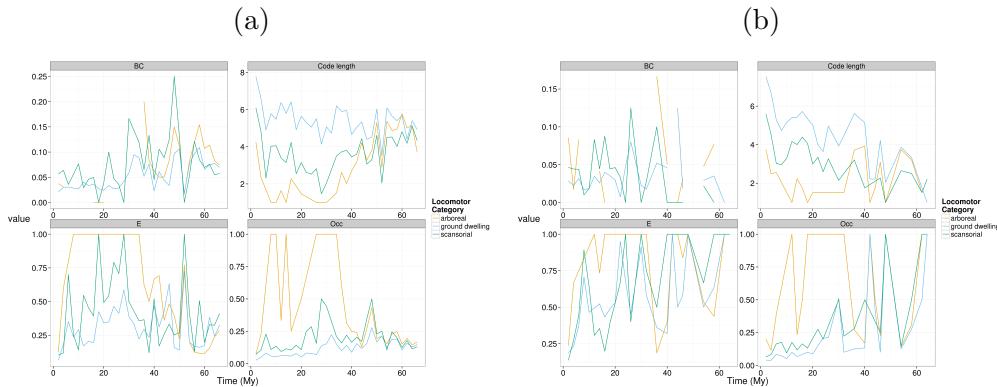


Figure 5: Time series of summary statistics for biogeographic networks determined by locomotor category. The summary statistics are, clockwise from top left: biogeographic connectedness (BC), code length, average relative locality occupancy per taxon (Occ), and average relative number of endemic taxa per locality (E).

4 Synthesis of proposed research

- 754 Underlying all of the above is a foundational question in paleobiology: why do certain taxa
755 go extinct while others do not? In the context of evolutionary paleoecology, this question can
756 be rephrased as “how do the set of all biotic–biotic and biotic–abiotic interactions a taxon
757 experiences over time (i.e. adaptive zone 108) affect extinction risk?” Related to this is the
758 Law of Constant Extinction which states that extinction risk for a given adaptive zone is
759 taxon–age independent [117]. It is asserted that the Law of Constant Extinction only holds
760 during periods of relatively constant environment even though this was not the context for
761 the initial observation [68, 117] which can be interpreted as the set of dominant non-organism
762 mediated processes do not fluctuate or fluctuate in a known manner. By understanding which
763 non-organism mediated processes may be shaping the environment (set of all possible biotic
764 and abiotic interactors) and how they change over time and phrasing analysis of extinction
765 in this context, it may be possible to “test” the Law of Constant Extinction.
- 766 The first two studies proposed above investigate how organismal traits potentially related
767 to environmental preference affect extinction rate. In effect, these traits may determine
768 the “bounds” of a taxon’s adaptive zone by limiting the total set of interactions to just
769 those for which the taxon is adapted. The final proposed study aims to estimate what
770 non-organism mediated processes (global, regional, and/or local) may be dominate in shaping
771 the environment and the related set of adaptive zones. Between these studies, as well the
772 use of two desperate groups, it should be possible to determine when, what, and if certain
773 variables matter for survival and potentially how they matter.

⁷⁷⁴ 5 Timeline

Spring/Summer 2014

- ⁷⁷⁶
- Evolution Meeting: preliminary brachiopod survival results
 - South American fossil mammal data from Field Museum of Natural History collections

⁷⁷⁸ Fall 2014/Winter 2015

- GSA: survivorship simulation for anagenesis and sampling
- Doctoral Dissertation Improvement Grant

Spring/Summer 2015

- ⁷⁸²
- Evolution Meeting: mammalian survivorship analysis for North America and Europe
 - South American fossil mammal data from American Museum of Natural History collections
 - write and submit survivorship simulation paper

⁷⁸⁶ Fall 2015/Winter 2016

- SVP or GSA: mammalian biogeographic connectedness
- write and submit mammal connectedness paper

Spring/Summer 2016

- ⁷⁹⁰
- Evolution Meeting: brachiopod survival analysis results
 - write and submit brachiopod survival paper

⁷⁹² Fall 2016/Winter 2017

- SVP or GSA: mammalian survivorship analysis
- write and submit mammal survival paper

Spring/Summer 2017

- ⁷⁹⁶
- Evolution Meeting
 - write and submit review/philosophy paper
 - **Defend**

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