

Evolutionary paleoecology and the biology of extinction

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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 [71].
4 Ecological traits are expressed by a taxon which are involved in biotic–biotic or biotic–abiotic
5 interactions while ecological factors are the environmental conditions in which a taxon
6 exists (the set of all biotic and abiotic interactors). Diversification is the difference between
7 origination and extinction and is the net pattern of macroevolution. The study of evolutionary
8 paleoecology is therefore the link between environmental (biotic–biotic and biotic–abiotic)
9 interactions and macroevolution. As a corollary to Kitchell [71]’s definition, Allmon [2] states
10 that in order to correctly link ecological interactions to macroevolution, one must focus on
11 the specific traits and factors that may affect the speciation process. Tacitly included in this
12 is the study of how ecological traits are related to extinction [70].

13 It is expected that for the majority of geological time, extinction is non-random with respect
14 to biology [52]. Determining how different traits, both alone or in concert, influence extinction
15 risk is then extremely important for understanding the differential diversification of taxa over
16 the Phanerozoic. Periods of background extinction also represent the majority of geologic
17 time, remain relatively predictable and change slowly, thus providing a better opportunity to
18 study how traits are related to survival than periods of mass extinction [52, 102]. The Law of
19 Constant extinction [128] posits that extinction risk of taxa within a given adaptive zone is
20 age independent (memoryless), however the generality of this statement is possibly suspect
21 [29, 35, 100, 111]. By analyzing survival patterns within adaptive zones during periods of
22 background extinction, it should be possible to determine if extinction is best modeled as age
23 independent or dependent.

24 Organismal traits relating to environmental preference are good candidates for estimating
25 differences in extinction risk. A variety of organismal traits have been shown to be related
26 to differential extinction [11, 40, 75, 88], especially with regards to the relationship between
27 adaptation to variable environments and increased species longevity. A simple expectation
28 is that taxa with preference for rare environments will be more at risk than taxa which
29 prefer abundant environments based on purely stochastic grounds. As environments change
30 in availability, a taxon’s instantaneous risk of extinction would then be expected change in
31 concert. Taxa are also expected to be adapting to their environment, possibly increasing or
32 decreasing their environmental tolerance and thus changing their instantaneous extinction risk.
33 Related to environmental preference is species-level geographic range size. Species with larger
34 geographic ranges tend to have lower extinction rates than species with smaller geographic
35 ranges [47, 52, 58, 88, 109]. However, how range size is “formed” is different between clades
36 [53] and thus remains a black box for most taxa. Thus, the utility of focusing on organismal
37 traits related to environmental preference is that the black box can be “opened.”
38 In addition to understanding patterns of survival, how community composition changes
39 over time is extremely important for understanding how trophic structure changes or is
40 maintained over time. Additionally, community connectedness is important for understanding

the degree to which global, regional, or local scale processes are important for shaping the environment, or the set of all possible biotic and abiotic interactors. In addition to total community connectedness, the dynamics of taxa within various ecological categories are important for understanding whether different adaptive conditions are 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 [77]. 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 both 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 [82]. 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), also known as the duration of a taxon. Survival analysis has a long history in paleontology [118, 128], though these initial analyses differ from modern approaches [72]. 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 respectively. 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 [72], 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.

- 80 Survival analysis shares some similarities with linear and logistic regression. While these
 82 approaches use continuous (duration) or dichotomous (extinct/not extinct) responses, re-
 spectively, survival analysis combines these concepts by measuring the duration till event
 84 or follow-up time. In addition to using both duration and death/extinction information,
 86 censoring information can also be incorporated in analysis. Censoring is the term for when
 there is uncertainty of exact survival time. In a paleobiological context this would be when a
 taxon either originated or went extinct outside of a period of interest, or the exact duration
 is known only as a range and not a single value.
- 88 The Law of Constant extinction [128] predicts that extinction risk is random with respect
 90 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

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

. 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 [35], which
 could be modeled using, among many others, a Weibull distribution. In comparison to the
 96 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 $k > 1$
 100 then 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
 102 distributions, such as the log-logistic, extended Gamma, and log-normal distributions [72],
 all of which describe different patterns of age-dependent failure/extinction (monotonic and
 104 nonmonotonic).

1.1.1 Effect of heterogeneous preservation

- 106 While some amount of uncertainty is possible to incorporate in a survival analysis framework
 via censoring, this may be complicated when dealing with the fossil record. Because the
 108 observed duration 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
 110 homogeneous across taxa, space, and time, then this is expected to have a minimal and
 uniform effect on estimates of duration and survival [38, 41, 111].
- 112 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
 114 (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

the effect of systematic range truncation on one set of observations compared to another, I propose four different sets of simulations: (1) two groups with identical diversification and identical preservation, (2) two groups with identical diversification but different preservation, (3) two groups with different diversification but identical preservation, and (4) 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 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. 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 it is extremely simple, well understood, and is a common model used to model phylogenies [67, 86, 87, 103].

The simplest model of fossil preservation is a Poisson process [38, 41, 122, 123]. Following an exponential 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 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 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 survival time between both the “true” and the “fossilized” distributions. Any 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 diversification and fossilization models. Importantly, this approach may illuminate situations where survival may be biased away from being exponentially distributed.

1.2 Biogeographic networks

Community connectedness is the degree to which localities are composed of endemic versus cosmopolitan taxa, and how similar this relationship is across localities. If localities and taxa are defined as nodes in a bipartite network, different network measures can be used to measure the how nodes are linked and describe both how taxa are distributed among and between localities and how similar different localities are. A bipartite network is defined as a network where nodes can be divided into two disjoint sets such that connections are only between sets and not within sets [28], in this case meaning that taxa can only be linked to localities but not to taxa and *vice versa*.

Modified from Sidor et al. [114], community connectedness can be measured via four different summary statistics: average relative number of endemic taxa per locality (E , Eq. 2), average

¹⁵⁴ relative locality occupancy per taxon (Occ , Eq. 3), biogeographic connectedness (BC , Eq. 4),
 and code length [107, 108, 114]. These summary statistics describe how unique each locality
¹⁵⁶ is on average compared to all others during a time period, how relatively widespread taxa are
 on average during a time period, how evenly distributed taxa are amongst localities during a
¹⁵⁸ time period, and the degree of biogeographic provincially during a time period. Of course, the
 first three of these measures can be represented as distributions instead of means allowing for
¹⁶⁰ better understanding of the spread of taxa over the landscape. E is defined as

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

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

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

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

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

¹⁶⁶ where O is the total number of taxonomic occurrences. BC ranges from 0 to 1, with 0 meaning
 that each locality completely disconnected from all other localities and 1 indicating that all
¹⁶⁸ taxa are presents at all localities.

¹⁷⁰ Code length is a measure of the information flow [113] of a graph as estimated from the
 behavior of a random surfer [16] on a graph and how often it visits each node and it's behavior
¹⁷² with regards to moving into and out of different regions of the graph. Code length is the
 minimum length of a binary code for describing the behavior the surfer and the community
¹⁷⁴ structure of the nodes and is estimated via the map equation [107, 108]. The logic of the
 map equation is that a good map compresses reality into as few symbols as possible thus we
¹⁷⁶ want to compress as many nodes as possible into as few symbols as possible. The goal is to
 compress a graph better than just assigning a unique Huffman code to each node [50, 107]. By
¹⁷⁸ compressing multiple nodes into a single code block, we decrease the minimum coding length
 of a network. A network with a low code length has more nodes compressed into distinct
¹⁸⁰ subunits/provinces without losing the underlying information flow of the graph. In the case
 of measuring community connectedness, a low code length means greater site distinctness
¹⁸² and provinciality than a graph with a high code length [114]. For further examples, visit
<http://mapequation.org/>.

¹⁸⁴ Analysis of these measures of community connectedness both within and between different
 regions across the globe allows for the expected relative importance of global versus regional
¹⁸⁶ versus local scale processes, and how this might change over time, to be estimated. If global pro-
 cesses are important to patterns of community connectedness and environmental interactions

than it is expected that these will be correlated with global climate measures. Additionally,
188 if two or more regions have similar or correlated patterns of community connectedness, it
is expected that global processes may play a role in shaping these environments. Regional
189 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 low, BC
190 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 and
191 environmental interactions. Importantly, which process scales are dominant may change over
time.

¹⁹⁶ **2 Australian Permian Brachiopods**

2.1 Traits and environmental preference

¹⁹⁸ Brachiopods are suspension feeders that are not actively motile, thus the availability of optimal environmental conditions is extremely important for both establishment and survival.
²⁰⁰ Brachiopod occurrence has been found to be strongly linked to the type ocean floor on which they occur [104, 105]. Environmental preference is estimated here using three traits,
²⁰² two environmental and one biological: substrate preference, habitat preference, and surface interface/affixing strategy. Each of these three traits relate to a different aspect of the environment and a taxon's specific adaptive zone. Importantly, the loss of suitable environments
²⁰⁴ may determine different trait associated extinction risk. While larval mode is considered
²⁰⁶ an important trait associated with geographic range and extinction risk [56, 57], it does not persevere in brachiopods and thus cannot be used to model survival [57]. Additionally,
²⁰⁸ 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 because of the
²¹⁰ distance required to reach a different shore line and the high latitude of the region.

²¹² Substrate preference is related to the chemical and physical processes present in a given environment. Substrate selection is mitigated via larval chemosensory abilities and thus may act as a weak proxy for larval dispersal ability [56, 57]. The three generally used states of
²¹⁴ substrate affinity are carbonate, clastic, or mixed [7, 39, 68, 85, 88]. The Pharenozoic is characterized by an overall decline in carbonates relative to clastics [39, 85]. Additionally,
²¹⁶ the Australian Permian is dominated by clastic beds [13, 31, 32, 91, 126]. It is expected then that the majority of brachiopod taxa will prefer clastic type substrates compared to the rarer
²¹⁸ carbonate type substrates.

²²⁰ Habitat preference is a description of the environment in which a taxon was found at the time of fossilization. Because brachiopods are sessil and frequently fixed to the environment, it is expected that the inferred environment is akin to that in which they lived. The range of environments are quite broad, representing many different marine settings. Because of the large range and difficulty of precisely inferring paleoenvironment a frequently used, albeit
²²⁴ coarse, classification is on-shore versus off-shore [15, 55, 59, 68, 112] along with the option of a taxon having no particular habitat preference. Importantly, habitat availability is broadly
²²⁶ related to sea-level which can change both dramatically and rapidly over time [89]. Because of this, on-shore type habitats are 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 [13, 30–32], which most likely strongly impacted sea-level as well
²³⁰ as the availability and constancy of on-shore versus off-shore habitats. Additionally, habitat preference might capture other factors relating to the environment not captured in substrate preference.

Affixing strategy is the manner by with an individual interfaces with the ocean floor. Unlike

²³⁴ bivalves which can burrow or snails which are motile, a brachiopod is sessil and has to maintain
²³⁶ their commissure at or above substrate level in order to expose their lophophore. Because of
²³⁸ this, brachiopods have evolved a variety of different methods to position themselves in various
²⁴⁰ different environmental conditions such as flow speed or mud depth [1, 73, 74, 104, 110].
²⁴² 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 [19] however these associations are weak as most assemblages are composed of
a heterogeneous mix of strategies.

Additionally, during the Permian there was a shift from an “ice house” to a “hot house” world
²⁴⁴ [13, 30, 32, 66, 94]. Australian 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, 30, 31, 66].
²⁴⁶ According to Olszewski and Erwin [89], however, sea-level and climate change do not wholly
explain the brachiopod ecological dynamics experienced in the Permian of Texas. It is then
²⁴⁸ 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.
²⁵⁰

2.2 Environmental preference and extinction

²⁵² 2.2.1 Questions

Which traits relating to environmental preference in brachiopods are predictors, either
²⁵⁴ 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?

²⁵⁶ 2.2.2 Hypotheses and predictions

Because of both the long-term decline in carbonates versus clastics [93] and the dominance of
²⁵⁸ Permian-age clastic beds [13, 31, 32, 91, 126] described above (Section 2.1), taxa with clastic
type affinities are expected to have longer durations than taxa with any other preference.
²⁶⁰ Additionally, this substrate dominance may have been a strong selection pressure for taxa
to adapt to the common clastic types and/or away of the rarer carbonates. Because of this,
²⁶² 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,
²⁶⁴ if it captures the same information as modern substrate type, will be a predictor in the best
model(s) of survival [104, 105]. However, if substrate affinity is not found to be important
²⁶⁶ 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
²⁶⁸ thus may act as a poor predictor of survival. Second, it may mean that because clastic type

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

While other environmental factors beyond substrate type, such as temperature or water depth,
272 have not been found to limit the distribution of modern brachiopods [104, 105] it is unknown
274 if 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.

During the Permian of Australia there were four major glaciation events where most of the
276 continent was covered [13, 30–32]. Because of this it is expected that off-shore adapted taxa
278 will have greater 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. If habitat preference is not found to be a predictor for modeling survival,
280 this may mean that sea-level mediated environmental availability does not determine long
term survival. Specifically, while sea-levels may have fluctuated greatly due to high latitude
282 glaciation [13, 31, 32] 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
284 from Texas that sea-level along with climate change do not wholly explain the observed
ecological dynamics [89], which may mean that habitat availability may not be the singly
286 dominate factor when modeling brachiopod survival.

Previous global level analysis of brachiopod durations showed that affixing strategy is
288 correlated with longevity [1] and that among endemic taxa, reclining taxa had longer durations
than other affixing strategies. Additionally, differential survival between affixing strategies has
290 been observed at the Cretaceous/Paleogene mass extinction [64]. Among cosmopolitan taxa,
however, pedunculate and cementing taxa had longer durations than all other taxa, both
292 cosmopolitan and endemic. This global analysis mixed taxa from many different geological
periods and geographic regions which may have led to unfair and biased comparisons. By
294 restricting analysis to a single continuous region and geological time period, I hope to
alleviate these concerns and instead focus on survival of an evolving taxonomic assemblage in
296 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 correlated with differential survival
298 [1], it may only be a minor factor. For example, this may indicate that the environmental
energetics of Australia were rather uniform or constant with respect to time.

300 An important consideration is that taxonomic survival might not be linked to single environments *per se*, but the variability of environments [40, 48, 75] which has been found to relate
302 strongly with survival past origination. Adaptation to variability of environments may be
captured in taxa with mixed substrate preference and/or no habitat preference. Based on
304 this observation, it is predicted that taxa with mixed substrate preference and/or no habitat
preference will have longer durations than taxa with single preferences. However, this may
306 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 are predicted to have the longest
308 durations for their respective traits.

2.2.3 Proposed research

310 In order to investigate which traits best model survival and how, I propose a survival analysis
 311 approach (Section 1.1). I choose to restrict this analysis to Australia because it represents a
 312 relatively continually sampled and well worked area that preserves the majority of the entire
 313 Permian [8, 13, 21, 22, 32, 132]. The traits described above (Section 2.1) will be used as
 314 predictors of survival. The distribution of survival durations will be modeled using a variety
 315 of different distributions which are tied to different hypotheses of extinction risk (Section
 316 1.1).

Permian brachiopod occurrence information is available via the Paleobiology Database
 318 (PBDB; <http://fossilworks.org>) and is primarily sourced from the work of Clapham
 319 [19–23] and Waterhouse [132]. While lithological and paleoenvironmental information is
 320 available for some occurrences through the PBDB, this information is frequently missing or
 321 too coarse. Lithological information and paleoenvironmental reconstructions will be heavily
 322 supplemented using the extensive geological unit information from Geosciences Australia
 323 (<http://www.ga.gov.au/>) as well as the literature on the stratigraphy of Australian Permian
 324 basins [13, 30–33, 43, 66, 91, 131, 132].

Duration will be measured as the difference between FAD and LAD. If a taxon originates
 326 prior to the Permian or goes extinct within 5 million years of the Permo-Triassic (P/T) boundary
 327 or after the P/T it will be censored. The possibility of accounting for the affect
 328 of sampling on decreasing observed durations versus true durations may be done through
 329 interval censoring (Section 1.1). For example, a range of LAD values between the observed
 330 and that estimated via unbiased point estimation [6, 123] can be used. The unbiased point
 331 estimation of true extinction time is calculated using

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

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

The most probable genus substrate and habitat preferences are estimated from the distribution
 336 of occurrences. Preliminarily, the lithological setting of all occurrences will be classified into
 337 one of three substrate affinity categories following Foote [39] while paleoenvironmental settings
 338 will be classified following Kiessling et al. [69]. Both of these traits will be assigned to all
 339 taxa following the Bayesian approach of Simpson and Harnik [117] where assignments are
 340 determined as the posterior probability of a taxon’s occurrences in comparison to available
 341 options during the duration of said taxon. The probability that a genus prefers, for example,
 342 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.

344 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.

346 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
348 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
350 example, on-shore habitats, k , out of the total number of occurrences, n . The conditional
probability is calculated as

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

352 where p is the proportion of collections in on-shore habitats observed during a taxon's
duration.

354 In the case of the coarse classification schemes of Foote [39] and Kiessling et al. [69], the
following rules are used assign preference. For substrate affinity, if $P(H_1|E) > \frac{2}{3}$ then the taxon
356 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 affinity. For habitat
358 affinity, the posterior probability for each habitat (inshore, offshore, none) was calculated
using Eq. 6 and the preference with maximum of the three posterior 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
362 evolved will remain for future study.

Because there is no obvious single best model, multiple models will be compared in order to
364 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 [18]. Below are a list
366 of possible models of brachiopod survival, based solely on time-independent covariates and not
time-dependent covariates (below) nor distribution of survival, and the associated hypotheses
368 (Table 1). This does not represent an exhaustive list of plausible models or hypotheses.

Because the four major periods of glacial activity during the Permian of Australia may have
370 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: ice or no ice. The ages of the onset and
retreat for all of the glacial period are fairly well constrained [31, 32]. 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 [72], model comparison
and selection can be done via AICc scores [18, 51].

³⁷⁸ **2.2.4 Preliminary results**

The preliminary results presented here are based entirely on the data present in the PBDB.
³⁸⁰ Observations were censored following the procedure described above (Section 2.2.3). Uncertainty of duration was not taken into account via interval censoring. Substrate and habitat
³⁸² preference were the only covariates of survival and were classified coarsely following Foote [39] and Kiessling et al. [69] respectively. Model formulations with each covariate alone, additively
³⁸⁴ 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
³⁸⁶ (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
³⁹⁰ was closely followed by the second best model of survival which had both substrate and habitat
³⁹² 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
³⁹⁴ AIC ≈ 1.3), meaning that both models can be considered almost equivalent.

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)

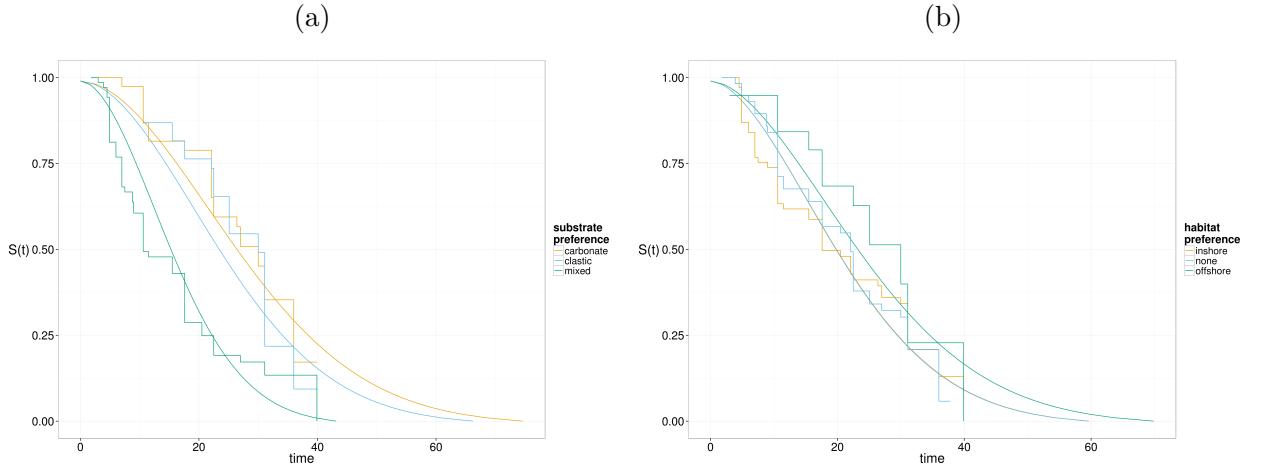


Figure 1: Survivorship curves of Australian Permian brachiopod genera based on substrate affinity (a) and habitat preference (b). The stepwise functions are nonparametric Kaplan–Meier survival curves for each of the three substrate affinities. The three smooth lines are the predicted survivorship probabilities 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 1.85 (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 are 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 22 between this model and
the AICc best model. There is a great degree of deviance between the nonparametric Kaplan–
406 Meier curves and model predictions (Fig. 1b). Additionally, this model is not significantly
different from the model with only an intercept ($\chi^2 = 1.14$, $df = 2$, $p = 0.57$). This means,
408 preliminarily, that habitat preference alone makes no difference in generic level survival.

Further refinements to these models include modeling survival using other distributions of
410 survival such as a log-normal distribution. Additionally the inclusion of affixing strategy and
climate as predictors will increase the understanding of the biology underlying brachiopod
412 generic survival.

2.3 Brachiopod distribution and community connectedness

414 2.3.1 Questions

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

418 2.3.2 Hypotheses and predictions

During the Permian, the east coast of the Australian continent faced towards the massive
420 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
422 most likely too great. Additionally, individuals which settled across the ocean would have
been almost instantly genetically isolated and not increase community connectedness, *per*
424 *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
426 in connectedness, would be expected during the four glacial periods [31, 32].

Dispersal ability of modern brachiopods appears to be most limited by availability and
428 proximity of substrate types [104, 105]. The Permian of Australia is dominated by widespread
clastic beds compared to relatively few carbonate beds. The expectation is that the distribution
430 of taxa with a carbonate preference will be extremely patchy with a high E (Eq. 2), low

432 *Occ* (Eq. 3), low *BC* (Eq. 4), and low code length [107, 114] compared to the distribution of
433 clastic preferring taxa. However, if community connectedness is approximately equal between
434 carbonate and clastic preferring taxa this could be caused by approximately equal dispersal
ability in both groups, either high or low.

435 Habitat would be expected to influence community structure if there is an uneven distribution
436 of available habitats in space and time. Rarity of preferred habitat would be expected to lead
437 to high *E*, low *Occ*, low *BC*, and low code length compared to an abundance of preferred
438 habitat. Because of the four major glaciation events during the Permian of Australia, it is
439 expected that the availability of on-shore habitats would be highly variable. It is then expected
440 that during periods of glacial activity community connectedness of on-shore preferring taxa
441 would be extremely low because of rarity of environments in comparison to both periods of
442 non-glacial activity and off-shore habitats at all times. If habitat preference has no effect on
443 community connectedness this may mean that the dispersal ability of on-shore taxa is very
444 high and able to maintain gene flow between potentially isolated habitats.

445 It is expected that affixing strategy alone will have minimal effect on community connectedness
446 unless affixing strategy is highly correlated with substrate and/or habitat preference. If
447 community connectedness is found to be different between affixing strategies but affixing
448 strategy is not highly correlated with substrate or habitat preference this may be because of
449 spatial heterogeneity in energy levels which limits reclining versus fixed taxon distributions.
450 This scenario is highly unlikely given knowledge of modern and fossil brachiopod distributions
[104, 105, 110].

452 2.3.3 Proposed research

453 Using a biogeographic network approach (Section 1.2), I will construct networks between
454 brachiopod genera and localities defined as 2x2 latitude-longitude grid cells from an equal-area
455 map projection. Biogeographic networks will be constructed for the entire Permian using 2 My
456 bins. In addition to community wide networks, separate networks will be constructed for taxa
457 within ecological categories. This facilitates comparison of community connectedness patterns
458 during the Permian both within and between categories as well as with the community wide
459 pattern. The data necessary to complete this study is the same as for the above analysis of
460 brachiopod survival (Section 2.2). Importantly, sampling will be restricted to the east coast
461 of Australia because this represents a continuous coast line that faced the Panthalassic Ocean
462 during the Permian.

463 Trait assignment will follow the procedure outlined for analysis of brachiopod survival (Section
464 2.2.3).

465 The next step is to compare patterns of community connectedness both within and between
466 regions in order to understand if global, regional, or local scale processes dominate. Additionally,
467 comparisons will be done between the different ecological traits both within and between
468 regions to determine which scale processes may be dominate. The approach and methodology

to accomplish these analyses is currently under development. Additionally, the possibility
 470 of integrating locality–locality distance or some other measure of topology will be explored,
 especially how this relates to code length and provinciality in general.

472 2.3.4 Preliminary results

Preliminary results are based solely on the brachiopod occurrence information in the PBDB.
 474 Preliminary networks were constructed with taxa being defined as genera and localities
 defined from a 2x2 latitude-longitude grid from an equal area map projection. All localities
 476 were restricted to those occurring in basins not present in the state of Western Australia.
 Networks were also constructed for taxa divided by substrate and habitat preferences. No
 478 initial comparisons with the Permian glacial record have been made. These results are based
 on the lithological and paleoenvironmental data present in the PBDB which will be improved
 480 as discussed above (Section 2.3.3).

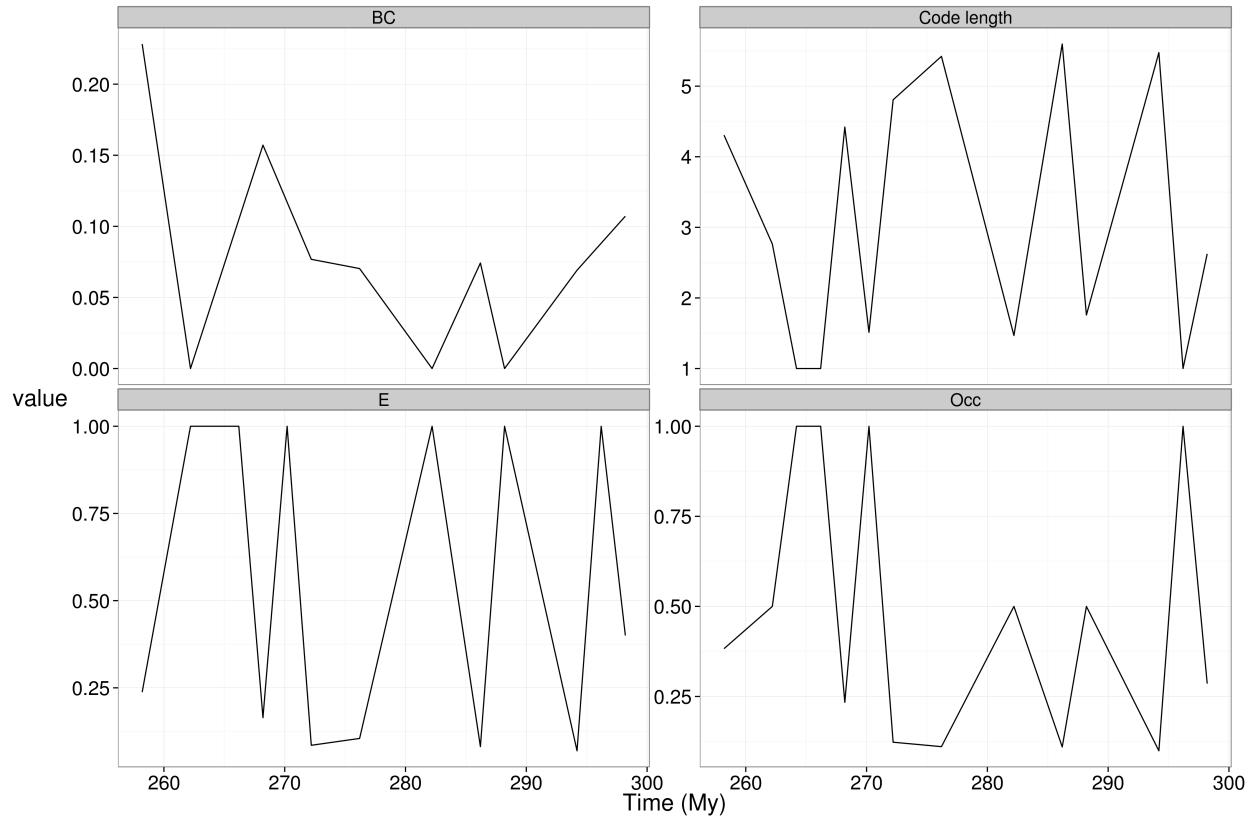


Figure 2: Summary statistics of community connectedness for all brachiopods occurring on the East coast of Australia during the Permian. The summary statistics are, clockwise from top left: biogeographic connectedness (BC), code length, average relative locality occupancy per taxon (Occ), and average relative number of endemic taxa per locality (E).

The summary statistics for community connectedness for all brachiopods show a qualitatively random pattern (Fig. 2) with no observable trends. Three of four summary statistics fluctuate continually (E , Occ , code length) while BC is qualitatively stationary throughout the Permian.
 482 Importantly, this pattern is effectively the same as that seen in clastic preferring taxa (Fig. 3a).
 484 These preliminary results are also demonstrate the predicted rarity of carbonate preferring
 486 taxa (Fig. 3a)

Additionally, taxa with both in-shore and no habitat preference have approximately identical
 488 patterns that are also qualitatively random in contrast to the qualitatively stable off-shore
 preferring taxa (Fig. 3b).

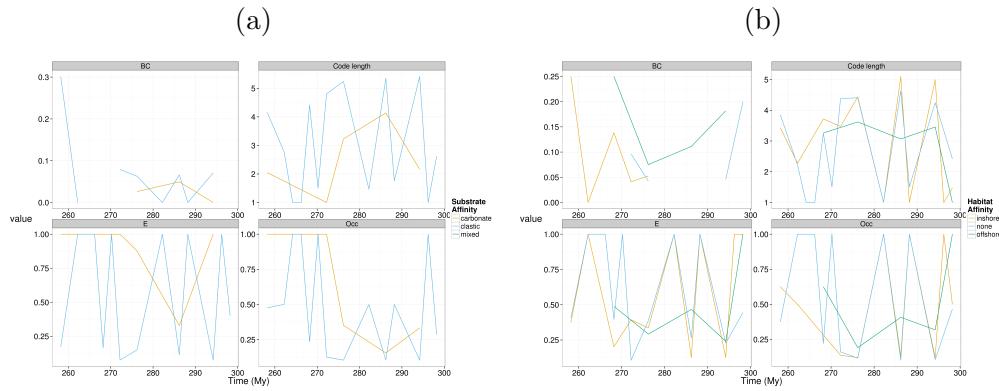


Figure 3: Community connectedness statistics for brachiopods separated by substrate (a) and habitat (b) preference. The summary statistics are, clockwise from top left: biogeographic connectedness (BC), code length, average relative locality occupancy per taxon (Occ), and average relative number of endemic taxa per locality (E).

490 Because these results are based on only preliminary substrate and habitat assignments, there
 491 is still major room for improvement. Additionally, patterns have not been explored for taxa
 492 based on affixing strategy, which may or may not follow the same pattern as substrate (Fig.
 493 3a). There are many further analyses to accomplish. Most importantly, comparisons both
 494 within and between the different ecological traits as well as with the timing of the four glacial
 496 periods are necessary in order to better understand what environmental factors may affect
 brachiopod occurrence, and in term survival (Section 2.2).

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 [104, 105].
~ habitat	Habitat stability is the best predictor as expected by models of Phanerozoic diversification.
~ affixing strategy	Environmental homogeneity/stability means that differentiation can only occur via differences in how a taxon interfaces with the ocean floor.
~ substrate + habitat	Substrate and habitat combine to best describe the environmental context of a taxon and the availability of its adaptive zone.
~ habitat + affixing strategy	By combining well adapted affixing strategy to the energetics of the habitat, survival increases.
~ substrate + affixing strategy	By combining well adapted affixing strategy to the state of the ocean floor increases survival.
~ 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.

formula	distribution	shape	df	AICc	weight
$\sim \text{aff}$	weibull	1.85	4	941.6757	0.65
$\sim \text{aff} + \text{hab}$	weibull	1.87	6	942.9977	0.34
$\sim \text{aff} * \text{hab}$	weibull	1.89	10	949.0816	0.02
~ 1	weibull	1.74	2	960.2550	0.00
$\sim \text{hab}$	weibull	1.75	4	963.3091	0.00
$\sim \text{aff}$	exponential		3	993.1724	0.00
$\sim \text{aff} + \text{hab}$	exponential		5	996.4089	0.00
~ 1	exponential		1	1000.2592	0.00
$\sim \text{aff} * \text{hab}$	exponential		9	1003.7639	0.00
$\sim \text{hab}$	exponential		3	1003.9227	0.00

Table 2: Model selection table for the preliminary 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 [18].

3 Cenozoic Mammals

498 3.1 Traits and environmental context

Mammals are motile organisms which can track their preferred environmental context over time. However, if a taxon requires rare or fragile environmental conditions, or is a poor disperser, this would limit the availability of suitable environments or ability to track the preferred environment. Three important traits that describe the relationship between mammals and their environmental context are body size, dietary category, and locomotor category [25, 26, 63, 78, 79, 120, 121]. 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 fossils.

508 Environmental availability, along with stability, is crucial for both the establishment and persistence of a species. During the Cenozoic, primarily between the Paleogene–Neogene, there was a shift from a predominately closed environment to a predominately open environment [14, 60, 106]. This environmental shift was differently timed between continents [124, 125]. Because of the differential timing of environmental shift, along with the different biotic context, the community and survival patterns are expected to vary between continents.

514 Dietary categories are coarse groupings of similar dietary ecologies: carnivores, herbivores, omnivores, and insectivores. Each of these categories is composed of taxa with a variety of 516 ecologies. For example, herbivores include both browsers and grazers which are known to have had different diversification dynamics during the Cenozoic [61]. Dietary categories are 518 roughly linked with position in trophic hierarchy, with decreasing stability away from the “base.” Stability here meaning trophic “distance” from primary productivity, with herbivores 520 having greater stability than carnivores because of the increased likelihood of prey item occurrence. Additionally, with increased likelihood of prey item occurrence, abundance can 522 increase [17, 25, 61, 115, 130].

Locomotor categories describe the motility of a taxon, the plausibility of occurrence, and the 524 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 526 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, 528 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 530 [12, 44, 56] and affects both the taxon's extinction risk and regional community evenness. With the transition from primarily closed to open environments, there is an expected shift in 532 stability associated with arboreal and ground dwelling taxa.

An organisms body size, here defined as (estimated) mass, has an associated energetic cost in 534 order to maintain homeostasis which in turn necessitates a supply of prey items. Many life

history traits are associated with body size: reproductive rate, metabolic rate, home range
536 size, among many others [17, 25, 92, 120]. While studies of body size dynamics are very
common [5, 24, 26, 65, 76], the interactions or processes that are correlated with body size
538 might be underlying the observed diversity pattern more than body size itself. By combining
analysis of body size and both dietary and locomotor categories, it should be possible to
540 better understand what processes underly patterns of survival and community connectedness.

3.2 Ecologically mediated survival

542 3.2.1 Questions

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

3.2.2 Hypotheses and predictions

548 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
550 categories. Stability here being “distance” from primary productivity, thus it is expected
that herbivores will have greater duration than carnivores. Omnivorous taxa are expected to
552 have average taxon durations compared to the other two categories. If dietary category is
not found to be important for modeling survival it may mean that trophic category is not a
554 major factor for determining species level survival and that other factors, such as body size,
may dominate.

556 Mammalian herbivores and carnivores have been found to have a greater diversification rate
than omnivores [95] which may indicate that these traits are better for survival. However
558 diversification can be caused either by an increase in origination relative to extinction or a
decrease in extinction relative to origination. Which scenario occurred, however, is (currently)
560 impossible to determine from a phylogeny of only extant organisms [96] which means that
analysis of the fossil record is required. If survival is found to be similar between all dietary
562 categories, this may mean that the differential diversification patterns observed by Price et al.
[95] are due to differences in speciation and not extinction.

564 It is expected 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 comparison,
566 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 viable
568 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 which

570 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 survival.

572 The difficulty of a Paleogene–Neogene comparison, which is potentially undermined by heterogeneous preservation, will be explored in simulation (Section 1.1.1).

574 Body size can possibly scale up to affect species level patterns because as body size increases, home range size increases [25]. If individual home range size scales up to reflect minimum

576 total species geographic range, we would expect that taxa with larger body sizes would have lower extinction rates than species with smaller body sizes. This expectation, however, may

578 not be right. As body size increases, reproductive rate decreases [65], populations get smaller

580 [134], and generations get longer [84] all of which can increase extinction risk, as has been

582 observed [27, 76]. However, the relationship between body size and extinction rate at the generic level has been found to vary between continents [76, 127]. By expanding to include a

584 third continent, South America, and analyzing specific level data I hope to elucidate how

586 differences in taxonomic diversity at a continental level might affect body size mediated

588 extinction rate. If body size is found to be unimportant for modeling survival, as in the generic level analysis of Tomiya [127], this means that other biotic or abiotic factors may

590 dominate. Also, this may mean that individual level home range size does not scale into increased species level range size, and there is therefore no correlated decrease in extinction

592 rate. If increase in body size increases extinction risk, this may be due to traits correlated with body size and not necessarily body size itself [65].

594 The interaction of body size, locomotor category, and dietary category is also extremely

596 important. For example, a small bodied arboreal taxon of any trophic category during 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 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 parts of the Cenozoic, must be done empirically.

598 3.2.3 Proposed research

To analyze differential mammalian survival, I propose a survival analysis approach (Section

600 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

602 World Database (NOW; <http://www.helsinki.fi/science/now/>), and museum collections. North American fossil mammal data are well represented in the PBDB because of the

604 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 the PBDB,

606 but has poor overall coverage. Because of this, South American fossil mammal data will be gathered via various museums such as the Field Museum of Natural History and the

608 American Museum of Natural History as well as 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 restrict analysis to the most taxonomically resolved and sampled groups such as Notoungulata, Marsupials, Carnivora, and Primates.

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

Dietary category, locomotor category, and body size will be considered constant throughout the duration of a taxon and will be 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 mean body size as an aggregate trait in studies of clade-wise dynamics [54]. While all three of these traits may have evolved over a taxon's duration, this will not be considered as part of this study.

While many analyses of survivorship are done using generic data [35, 39, 47, 76, 127], there are potential biases in accurately modeling a specific level process using generic level data [100, 101, 111, 116, 129]. 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 similar to previous work on estimating specific level origination and extinction rates from generic level survival curves [37], I will measure the deviance between extinction rate directly 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 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 having a long duration because it is not correctly broken up can be considered analogous to 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, so multiple models must be compared in order to determine which is the most likely. It is important, however, that each model be well justified and be tied to a realistic biological hypothesis/prediction [18].

In order to account for environmental shifts, two different time-dependent covariates will be used. δO^{18} isotope information for the whole Cenozoic [136] will be used as a global climate proxy. Additionally, the Paleogene–Neogene divide, which may reflect global environmental shift, will be modeled as a time-dependent step-function.

3.2.4 Preliminary results

Preliminary results are based solely on Cenozoic mammal occurrence data from North America and Europe from the PBDB. Nonparametric Kaplan-Meier survival curves were estimated for both dietary and locomotor categories (Fig. 4). These are shown on a log-linear scale for

646 more direct visual comparison with linearity [128, 129].

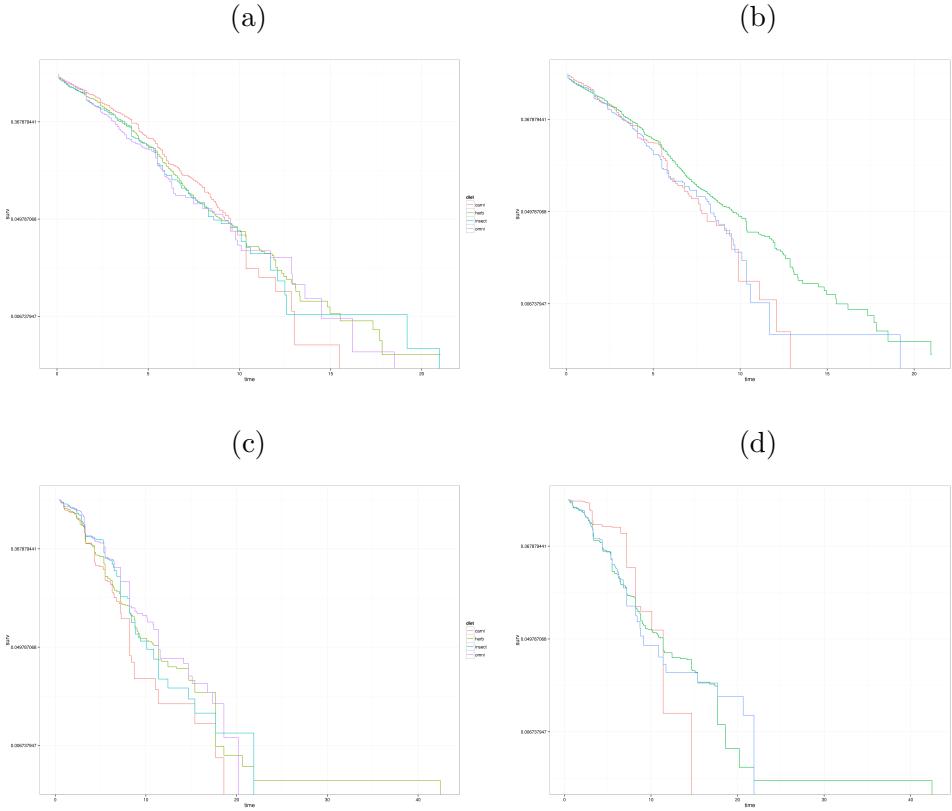


Figure 4: Nonparametric Kaplan-Meier survival curves for North American and European mammals based on dietary category (a and c respectively, and locomotor category (b and d respectively). The vertical axes are on a natural log scale.

3.3 Community connectedness: global, regional, local

648 3.3.1 Questions

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

652 3.3.2 Background and Predictions

During the Cenozoic there was a global shift from a “hot house” environment to an “ice
654 house” environment [135, 136]. This transition was accompanied by major shifts in global

climatic envelopes and the reorganization of mammalian communities [5, 14, 34, 42, 60].
656 For mammalian community connectedness there are two possible scenarios. First, while the
environment was shifting, lineages may have adapted in place and overall trophic structure
658 and community connectedness would have remained relatively constant through time, as
observed during the Neogene of Europe [63]. Alternatively, species may have shifted ranges
660 and changed the average set of taxa present at a locality which would be associated with
non-stationary trophic structure and community connectedness.
662 Based on prior work, it is expected that the patterns of biogeographic community connected-
ness for herbivorous taxa in a region would be most similar to that for all regional taxa and
664 potentially “drive” the regional pattern, partially because on average this category represents
the majority or plurality of taxa [62]. In contrast, community connectedness for carnivorous
666 taxa is expected to remain constant over time or be correlated with herbivore patterns. Finally,
omnivorous taxa are not expected to be correlated with the patterns of either herbivorous or
668 carnivorous taxa and have either a relatively constant or random pattern of connectedness
over time. These predictions are based on the differences in resilience and relationship to
670 primary productivity, with herbivores being more resilient than carnivores and omnivores
being random in their resilience [63]. Resilience is defined here as the ability for a taxon to
672 increase in occupancy following a decline [63].

The Cenozoic global shift from closed, forested habitat in the Paleogene to open, savanna-like
674 habitat during the Neogene would have greatly affected the possible distributions of both
arboreal and ground dwelling taxa. Additionally, the timing of this environmental shift was
676 different between continents [124, 125], so patterns of community connectedness may not be
globally uniform and instead reflect regional differences. Generally this transitions would cause
678 forested environments to become increasingly patchier in distribution while transitioning
from the Paleogene to the Neogene. The global prediction then is that there would have been
680 a relative increase in E (Eq. 2) and code length accompanied by a decrease in BC (Eq. 4)
and Occ (Eq. 3) in arboreal taxa over time. The opposite is expected for terrestrial taxa.

682 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
684 on North America [3–5, 9, 10, 14, 34, 45, 46, 118, 119]. However, the effect of global climate
change on North American diversity remains unresolved and controversial [5, 10, 14, 34],
686 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.

688 The European mammalian fossil record is also well studied, though research has primarily
focused on the Neogene [62, 63, 76, 97–99]. An important aspect about the European record
690 is that during the Neogene there was little shift in relative dietary category abundance [63]
and that the patterns within herbivores (browse–graze transition) were mostly driven by
692 abundant, cosmopolitan taxa [62]. It is predicted then that herbivores will demonstrate
the same patterns of community connectedness as Europe as a whole, while omnivores and
694 carnivores will be different from that of herbivores and may demonstrate random or constant

patterns of community connectedness through time.

- 696 Patterns of community connectedness for South American mammalian fauna are comparatively
less synthesized than those of North America and Europe. Instead, cross-continental
698 dynamics between North and South America during the Neogene are much more studied [83].
The South American mammalian faunal record reflects two distinct biotic provinces between
700 the North and the South [36, 80, 81, 90]. Because of this, it is expected that South America
will have a different pattern of community connectedness than either North America or Europe.
702 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 South America.
704 Additionally, because of this strong biome distinction, it is predicted that provinciality will
be high but remain constant over time.

706 **3.3.3 Proposed research**

In order to estimate changes in community connectedness during the Cenozoic I will be using
708 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
710 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
712 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
714 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
716 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
718 taxa and with a restricted sample of just major groups in order to observe any differences in
patterns of community connectedness. The data necessary to complete this study is the same
720 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
722 role in community structuring [133]. For example, closely related taxa may be repulsed
“repulsed” due to competitive exclusion or “clumped” because of environmental filtering.
724 While it is infeasible to create an explicit phylogenetic hypothesis for all taxa sampled on all
continents, almost all taxa have some hierarchical taxonomic information. Using taxonomy as
726 the structure of an information phylogeny, it should be possible to estimate the distribution
of phylogenetic similarity across localities.

728 For each locality, an informal phylogeny will be constructed based solely on available taxonomic
information such as order, family, and genus assignments with each of these levels being a
730 completely unresolved polytomy. Using this informal phylogeny, a number of measures of
phylogenetic similarity can be estimated. For example the relative mean pairwise distance
732 between all taxa at a locality [133] or the related phylogenetic species variability of a single

locality [49]. These values calculated for all localities can then be used as a partial correlates
734 or covariates when modeling changes in community connectedness.

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

742 3.3.4 Preliminary results

Preliminary analysis was done using only the occurrence information of both North American
744 and European fossil mammals available in the PBDB. Both regions have qualitatively different
746 patterns of community connectedness, primarily during the Paleogene (Fig. 5). Almost all
four of the summary statistics are extremely volatile over the Cenozoic, especially for Europe.
However, some interesting qualitative patterns are present.

748 There is a qualitative decrease in *Occ* in Europe until approximately the start of the Neogene
(approximately 23 My), indicating that the average taxon is becoming generally less
750 cosmopolitan over time. In contrast, North American *Occ* is qualitatively stationary over the
entire Cenozoic and almost always lower than that observed for Europe. This means that, on
752 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
754 afterwards remains relatively stationary meaning that the average proportion of shared taxa
remained qualitatively stationary. In comparison, North American *BC* remains stationary
756 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.

758 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
760 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.
762 While the pattern of the European record shows a qualitatively nonmonotonic decrease in
locality uniqueness.

764 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
766 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
768 has a qualitatively decreasing degree of provinciality.

Biogeographic networks of taxa of similar dietary category

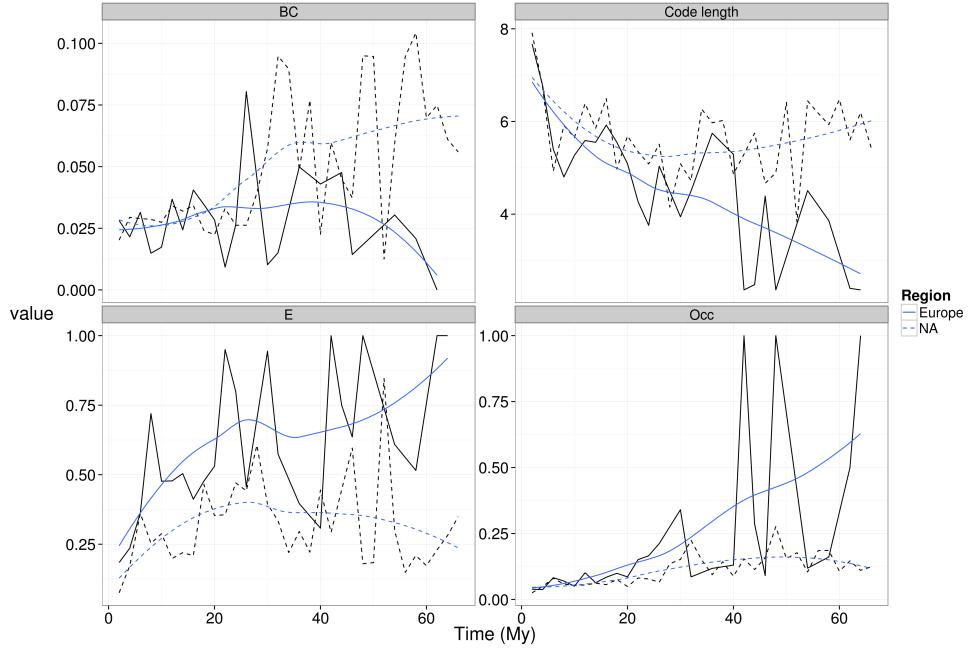


Figure 5: Biogeographic network summary statistics for mammalian communities in North America (dashed line) and Europe (solid line). The summary statistics are, clockwise from top left: biogeographic connectedness (BC), code length, average relative locality occupancy per taxon (Occ), and average relative 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.

770 Biogeographic networks of taxa of similar locomotor category

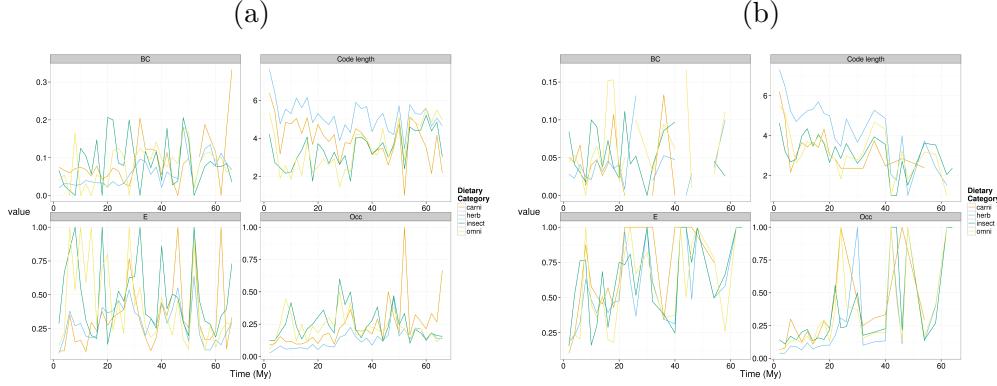


Figure 6: Time series of summary statistics for biogeographic networks determined by dietary category for North America (a) and Europe (b). The summary statistics are, clockwise from top left: biogeographic connectedness (BC), code length, average relative locality occupancy per taxon (Occ), and average relative number of endemic taxa per locality (E).

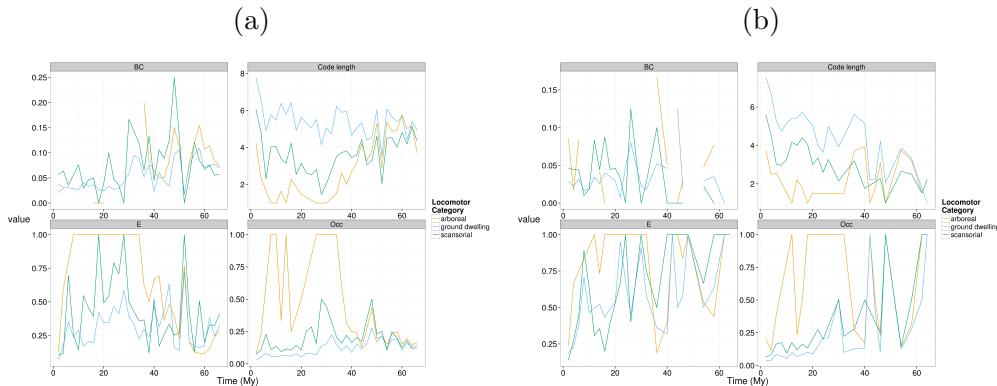


Figure 7: Time series of summary statistics for biogeographic networks determined by locomotor category for North America (a) and Europe (b). The summary statistics are, clockwise from top left: biogeographic connectedness (BC), code length, average relative locality occupancy per taxon (Occ), and average relative number of endemic taxa per locality (E).

4 Synthesis of proposed research

- 772 Underlying all of the above is a foundational question in paleobiology: why do certain taxa
go extinct while others do not? In the context of evolutionary paleoecology, this question can
774 be rephrased as “how do the set of all biotic–biotic and biotic–abiotic interactions a taxon
experiences over time (i.e. adaptive zone 118) affect extinction risk?” Related to this is the
776 Law of Constant Extinction which states that extinction risk for a given adaptive zone is
taxon–age independent [128]. It is asserted that the Law of Constant Extinction only holds
778 during periods of relatively constant environment, even though this was not the context for
the initial observation [75, 128], which can be interpreted as the set of dominant non-organism
780 mediated processes do not fluctuate or fluctuate in a known manner. By understanding which
non-organism mediated processes may be shaping the environment (set of all possible biotic
782 and abiotic interactors) and how they change over time and phrasing analysis of extinction
in this context, it may be possible to “test” the Law of Constant Extinction.
- 784 The two studies proposed above (Sections 2.2 and 3.2) investigate how organismal traits
potentially related to environmental preference affect extinction rate. In effect, these traits
786 may determine the “bounds” of a taxon’s adaptive zone by limiting the total set of interactions
to just those for which the taxon is adapted. The other two proposed studies (Sections 2.3 and
788 3.3) aim to estimate what non-organism mediated processes (global, regional, and/or local)
may be dominate in shaping the environment and the related set of adaptive zones. Between
790 these studies, as well the use of two disparate groups, it should be possible to determine
when, what, and if certain variables matter for survival and, potentially, how they matter.

₇₉₂ 5 Timeline

Spring/Summer 2014

- ₇₉₄
- Evolution Meeting: preliminary brachiopod survival results
 - South American fossil mammal data from American Museum of Natural History collections

Fall 2014/Winter 2015

- ₇₉₈
- GSA: survivorship simulation for anagenesis and sampling
 - Doctoral Dissertation Improvement Grant

₈₀₀ Spring/Summer 2015

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

Fall 2015/Winter 2016

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

₈₀₈ Spring/Summer 2016

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

Fall 2016/Winter 2017

- GSA: brachiopod community connectedness
- write and submit mammal survival paper

₈₁₄ Spring/Summer 2017

- Evolution Meeting: survival and communities together
- write and submit brachiopod community paper
- write and review/philosophy paper
- **Defend**

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