

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 [75].
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 [75]’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 [74].

13 It is expected that for the majority of geological time, extinction is non-random with
14 respect to biology [1, 49, 56, 69, 76, 93, 98]. Determining how different traits, both alone
15 or in concert, influence extinction risk is then extremely important for understanding the
16 differential diversification of taxa over the Phanerozoic. Periods of background extinction also
17 represent the majority of geologic time, remain relatively predictable and change slowly, and
18 thus providing a better opportunity to study how traits are related to survival than periods
19 of mass extinction [56, 110]. The Law of Constant Extinction [136] posits that extinction risk
20 of taxa within a given adaptive zone is age independent (memoryless), however the generality
21 of this statement is possibly suspect [30, 37, 108, 119]. By analyzing survival patterns within
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 modeling
24 differences in extinction risk. A variety of organismal traits have been shown to be related
25 to differential extinction [11, 42, 80, 93], especially with regards to the relationship between
26 adaptation to variable environments and increased species longevity. A simple expectation
27 based purely on stochastic grounds is that taxa with a preference for rare environments will
28 be more at risk than taxa which prefer abundant environments. As environments change
29 in availability, a taxon’s instantaneous risk of extinction would then be expected change in
30 concert. Taxa are also expected to be adapting to their environment, possibly increasing or
31 decreasing their environmental tolerance and thus changing their instantaneous extinction risk.
32 Related to environmental preference is species-level geographic range size. Species with larger
33 geographic ranges tend to have lower extinction rates than species with smaller geographic
34 ranges [50, 56, 62, 93, 117]. However, how range size is “formed” is different between clades
35 [57] and thus remains a black box for most taxa. Thus, the utility of focusing on organismal
36 traits related to environmental 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 the environment,
42 or the set of all possible biotic and abiotic interactors. In addition to total community
connectedness, the dynamics of connectedness of taxa within various ecological categories are
44 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
46 during periods of environmental stability and is thus considered extremely difficult/impossible
to test [82]. However, if environmental shifts are incorporated into the analysis of survival
48 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
50 allow for illumination of what actual processes underly extinction during the majority of
geologic time.

52 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
54 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
56 fossil records able to reflect long term evolutionary patterns [87]. These two time periods were
chosen because they represent periods of approximately the same length (47 My and 65 My)
58 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
60 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
62 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
64 understand how long-term, large-scale processes away from mass extinctions proceed.

1.1 Survival analysis

66 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
68 of extinction (last appearance date; LAD), also known as the duration of a taxon. Survival
analysis has a long history in paleontology [126, 136], though these initial analyses differ from
70 modern approaches [77]. 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.
72 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,
74 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
76 Cox models [77], 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
78 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. 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
86 is known only as a range and not a single value.

The Law of Constant extinction [136] predicts that extinction risk is random with respect
88 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

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

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

92 There are many alternatives to constant extinction risk, however. For example, there is a
frequently observed inverse relationship between genus age and extinction risk [37], which
94 could be modeled using, among many others, a Weibull distribution. In comparison to the
exponential distribution which has only a single parameter λ , the Weibull distribution has
96 two parameters, λ and k . The λ of the Weibull distribution behaves as in the exponential
distribution while k is a shape parameter which describes how failure is proportional to a
98 power of time. If $k < 1$ then failure rate monotonically decreases with age, and if $k > 1$ then
failure rate monotonically increases with age. When $k = 1$ the Weibull distribution reduces to
100 the exponential distribution and failure rate is constant. Other potential survival distributions
such as the log-logistic, extended Gamma, and log-normal distributions [77] describe different
102 patterns of age-dependent failure/extinction (monotonic and nonmonotonic).

1.1.1 Effect of heterogeneous preservation

104 While some amount of uncertainty is possible to incorporate in a survival analysis framework
via censoring, this is may be complicated when dealing with the fossil record. Because the
106 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
108 homogeneous across taxa, space, and time, then this is expected to have a minimal and
uniform effect on estimates of duration and survival [40, 43, 119].

110 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
112 (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
114 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

116 identical preservation, (2) two groups with identical diversification but different preservation,
118 (3) two groups with different diversification but identical preservation, and (4) two groups
120 with different diversification and different preservation. Both diversification and preservation
122 will be simulated using very simple models in order to limit the complexity of interpreting
results. These simulations provide a bestiary of comparisons with the observed empirical
survival distributions. Specifically, how sampling may cause similar patterns to emerge from
very different parameter configurations.

124 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.
126 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
128 it is extremely simple, well understood, and is a common model used to model phylogenies
[71, 91, 92, 111].

130 The simplest model of fossil preservation is as a Poisson process [40, 43, 130, 131]. Following
an exponential distribution, preservation rate (ϕ) is defined as the number of expected
132 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
134 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”
136 observation.

138 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
140 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
142 be biased away from being exponentially distributed.

1.2 Biogeographic networks

144 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
146 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
148 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
150 between sets and not within sets [29], in this case meaning that taxa can only be linked to
localities but not to taxa and *vice versa*.

152 Modified from Sidor et al. [122], 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 [115, 116, 122]. These summary statistics describe, respectively, how
¹⁵⁶ unique each locality is on average compared to all others during a time period, how relatively
¹⁵⁸ widespread taxa are on average during a time period, how evenly distributed taxa are amongst
¹⁶⁰ localities during a 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 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 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.

Code length is a measure of information flow [121] as estimated from the behavior of a random
¹⁷⁰ surfer [16] on a graph, how often it visits each node, and it's behavior with regards to moving
¹⁷² into and out of different regions of the graph. Code length is the minimum binary code
¹⁷⁴ necessary to describe the behavior the surfer based on the relations between the nodes and is
¹⁷⁶ estimated via the map equation [115, 116]. The logic of the map equation is that a good map
¹⁷⁸ compresses reality into as few symbols as possible. The goal is to compress a graph better than just
¹⁸⁰ assigning a unique Huffman code to each node [54, 115]. By 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 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 and provinciality than a graph with a high code length [122]. For further examples, visit <http://mapequation.org/>.

Analysis of these measures of community connectedness both within and between different
¹⁸² 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 global processes
¹⁸⁶ are important to patterns of community connectedness and environmental interactions than it is expected that these will be correlated with global climate measures. Additionally, if two or more regions have similar or correlated patterns of community connectedness, it

is expected that global processes may play a roll in shaping these environments. Regional
188 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
192 environmental interactions. Importantly, which process scales are dominant may change over
time.

¹⁹⁴ **2 Australian Permian Brachiopods**

2.1 Traits and environmental preference

¹⁹⁶ Brachiopods are sessil suspension feeders, thus the availability of optimal environmental
¹⁹⁸ conditions is extremely important for both establishment and survival. Brachiopod occurrence
²⁰⁰ has been found to be strongly linked to the type ocean floor on which they occur [112, 113].
²⁰² Importantly, the loss of suitable environments may determine different trait associated
²⁰⁴ extinction risk. Environmental preference is estimated here using two environmental and
²⁰⁶ one biological traits: substrate preference, habitat preference, and surface interface/affixing
²⁰⁸ strategy. Each of these three traits relate to a different aspect of the environment and a
taxon's specific adaptive zone. While larval mode is considered an important trait associated
with geographic range and extinction risk [60, 61], it does not persevere in brachiopods and
thus cannot be estimated [61]. Additionally, taxa found on the east coast of Australia during
the Permian would have been facing the Panthalassic Ocean and would have had few "good"
areas to disperse to because of the distance required to reach a different shore line and the
high latitude of the region.

²¹⁰ Substrate preference is related to the chemical and physical processes present in a given
²¹² environment. Substrate selection is mitigated via larval chemosensory abilities and thus may
act as a weak proxy for larval dispersal ability [60, 61]. The three generally used states of
²¹⁴ substrate affinity are carbonate, clastic, or mixed [7, 41, 72, 90, 93]. The Pharenozoic is
characterized by an overall decline in carbonates relative to clastics [41, 90]. Additionally,
²¹⁶ the Australian Permian is dominated by clastic beds [13, 33, 34, 99, 134]. It is expected then
that the majority of brachiopod taxa will prefer clastic type substrates compared to the rarer
carbonate type substrates.

²¹⁸ Habitat preference is a description of the environment in which a taxon was found at the
²²⁰ time of fossilization. Because brachiopods are sessil and frequently fixed to the ocean floor, it
is expected that the inferred environment is at least akin to that in which they lived. The
²²² range of environments is quite broad, representing many different marine settings. Because of
this large range and difficulty of precisely inferring paleoenvironment a frequently used, albeit
²²⁴ coarse, classification is on-shore versus off-shore [15, 59, 63, 72, 120] 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 [94]. Because
of this, on-shore type habitats are potentially very volatile and unstable for long periods of
²²⁸ time. During the Permian of Australia there were four major glaciation events which covered
most of the entire continent [13, 32–34], 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 which an individual interfaces with the ocean floor. Unlike

²³² bivalves which can burrow or snails which are motile, a brachiopod is sessil and has to maintain
²³⁴ their commissure at or above substrate level in order to expose their lophophore. Because of
²³⁶ this, brachiopods have evolved a variety of different methods to position themselves in various
²³⁸ different environmental conditions such as flow speed or mud depth [1, 78, 79, 112, 118].
²⁴⁰ Broadly, these strategies 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.

²⁴² Additionally, during the Permian there was a shift from an “ice house” to a “hot house” world
²⁴⁴ [13, 32, 34, 70, 102]. 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, 32, 33, 70].
²⁴⁶ According to Olszewski and Erwin [94], 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
²⁴⁸ some combination of one or more the above organismal traits will be necessary to best model
survival.

2.2 Environmental preference and extinction

250 2.2.1 Questions

²⁵² 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?

254 2.2.2 Hypotheses and predictions

²⁵⁶ Because of both the long-term decline in carbonates versus clastics [101] and the dominance of
Permian-age clastic beds [13, 33, 34, 99, 134] described above (Section 2.1), taxa with clastic
²⁵⁸ 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 [112, 113]. 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
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
268 explained by other factors, either measured or unmeasured.

While other environmental factors beyond substrate type, such as temperature or water
270 depth, have not been found to limit the distribution of modern brachiopods [112, 113] it
is unknown how these factors affect survival. Predictions of differential survival based on
272 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 most of the
continent was covered [13, 32–34]. It is expected that off-shore adapted taxa will have greater
276 durations than on-shore adapted taxa because of the expected constancy and availability of
off-shore habitats and the expected high volatility of on-shore habitats. If habitat preference
278 is not found to be a predictor for modeling survival, this may mean that sea-level mediated
environmental availability may not determine long term survival. Specifically, while sea-levels
280 may have fluctuated greatly due to high latitude glaciation [13, 33, 34] it may be that the
long term continual availability of habitat over-shadows short term fluctuations. Also, it
282 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 [94], which may mean
284 that habitat availability may not be the singly dominate factor when modeling brachiopod
survival.

286 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 durations
288 than other affixing strategies. Additionally, differential survival between affixing strategies has
been observed at the Cretaceous/Paleogene mass extinction [68]. Among cosmopolitan taxa,
290 however, pedunculate and cementing taxa had longer durations than all other taxa, both
cosmopolitan and endemic. This global analysis mixed taxa from many different geological
292 periods and geographic regions which may have led to unfair and biased comparisons. By
restricting analysis to a single continuous region and geological time period, I hope to alleviate
294 these concerns and instead focus on survival of a single taxonomic series in a continuous
environmental context. If affixing strategy is found to not be a predictor in the best model(s)
296 of survival this would mean that, while it is correlated with differential survival [1, 68], it
may only be a minor factor. For example, this may indicate that the environmental energetics
298 of Australia were rather uniform or constant with respect to time.

An important consideration is that taxonomic survival might not be linked to single environments *per se*, but the variability of environments [42, 52, 80] which has been found to relate
300 strongly with survival past origination. Adaptation to variability of environments may be
302 captured in taxa with mixed substrate preference and/or no habitat preference. Based on
this observation, it is predicted that taxa with mixed substrate preference and/or no habitat
304 preference will have longer durations than taxa with single preferences. However, this may
also mean that taxa with mixed substrate and/or no habitat preferences will be of similar
306 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 (Section 1.1). I choose to restrict this analysis to Australia because it represents a relatively continually sampled and well worked area that preserves the majority of the entire
³¹² Permian [8, 13, 22, 23, 34, 140]. The traits described above (Section 2.1) will be used as predictors of survival. The distribution of survival durations will be modeled using a variety
³¹⁴ 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 [140]. 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 [13, 32–35, 45, 70, 99, 139, 140]. For example improvements to the initial PBDB
³²⁴ assignments, see Appendix A.

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 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 interval censoring (Section 1.1). For example, a range of LAD values between the observed
³³⁰ and that estimated via unbiased point estimation [6, 131] can be used. The unbiased point estimation of true extinction time is calculated using

$$r = \frac{R}{H - 1} \tag{5}$$

³³² where r is the average gap size between fossils, R is the stratigraphic range, and H is the number of fossil horizons. r can 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 sampled occurrences. Preliminarily, the lithological setting of all occurrences will be classified into one of three substrate affinity categories following Foote [41] while paleoenvironmental
³³⁸ settings will be classified following Kiessling et al. [73]. Both of these traits will be assigned to all taxa following the Bayesian approach of Simpson and Harnik [125] where assignments are
³⁴⁰ determined as the posterior probability of a taxon's occurrences in comparison to available options during the duration of said taxon. The probability that a genus prefers, for example,

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.
342 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.
344 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
346 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
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 [41] and Kiessling et al. [73], 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 [19]. 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 [33, 34]. 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 [77], model comparison
and selection can be done via AICc scores [19, 55].

³⁷⁸ **2.2.4 Preliminary results**

The preliminary results presented here are based entirely on the data present in the PBDB
³⁸⁰ without modification (Appendix A). Observations were censored following the procedure
described above (Section 2.2.3). Uncertainty of duration was not taken into account via
³⁸² interval censoring. Substrate and habitat preference were the only covariates of survival
and were classified coarsely following Foote [41] and Kiessling et al. [73] respectively. Model
³⁸⁴ formulations with each covariate alone, additively together, or interacting were used. Only
two different survival distributions were considered in this initial analysis: exponential and
³⁸⁶ Weibull. In total, 11 models were fit (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 distribution with
 $k > 1$. The difference between the AICc best model and the second best model was small (Δ
³⁹² AIC ≈ 1.3), meaning that both models can be considered almost equivalent.

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

The shape parameter (k) of the AICc best model (Fig. 1c) 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 means that the Law of Constant
³⁹⁸ Extinction may not hold when modeling generic level extinction in brachiopods.

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

The model with habitat preference being the sole predictor of survival following a Weibull
⁴⁰⁴ distribution was a poor estimate, with an approximate Δ AICc 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 elsewhere 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 similar at any given time and that changes, specifically decreases
426 in connectedness, would be expected during the four glacial periods [33, 34].

Dispersal ability of modern brachiopods appears to be most limited by availability and
428 proximity of substrate types [112, 113]. 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
 Occ (Eq. 3), low BC (Eq. 4), and low code length [115, 122] compared to the distribution of
432 clastic preferring taxa. However, if community connectedness is approximately equal between
carbonate and clastic preferring taxa this could be caused by approximately equal dispersal
434 ability in both groups, either high or low.

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
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
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
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
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.

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
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

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 [112, 113, 118].

452 **2.3.3 Proposed research**

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
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
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
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
of Australia because this represents a continuous coast line that faced the Panthalassic Ocean
462 during the Permian.

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

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,
468 comparisons will be done between the different ecological traits both within and between
regions to determine which scale processes may be dominate. The approach and methodology
470 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.

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).

The summary statistics for community connectedness for all brachiopods show a qualitatively
482 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.
484 Importantly, this pattern is effectively the same as that seen in clastic preferring taxa (Fig. 3a).

These preliminary results are also demonstrate the predicted rarity of carbonate preferring
486 taxa (Fig. 3a)

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

490 Because these results are based on only preliminary substrate and habitat assignments, there
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.
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
periods are necessary in order to better understand what environmental factors may affect
496 brachiopod occurrence, and in term survival (Section 2.2). Additionally, given the difficulty in
measuring the four network summary statistics alternative methods for summarizing network
498 and taxon distributions will be explored, such as the analysis of just the locality x locality
network projection.

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 [112, 113].
~ 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: Example candidate models of brachiopod survival based on substrate affinity, habitat preference, and affixing strategy. Each model is presented with an associated biological hypothesis. 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	w
$\sim \text{aff}$	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 [19].

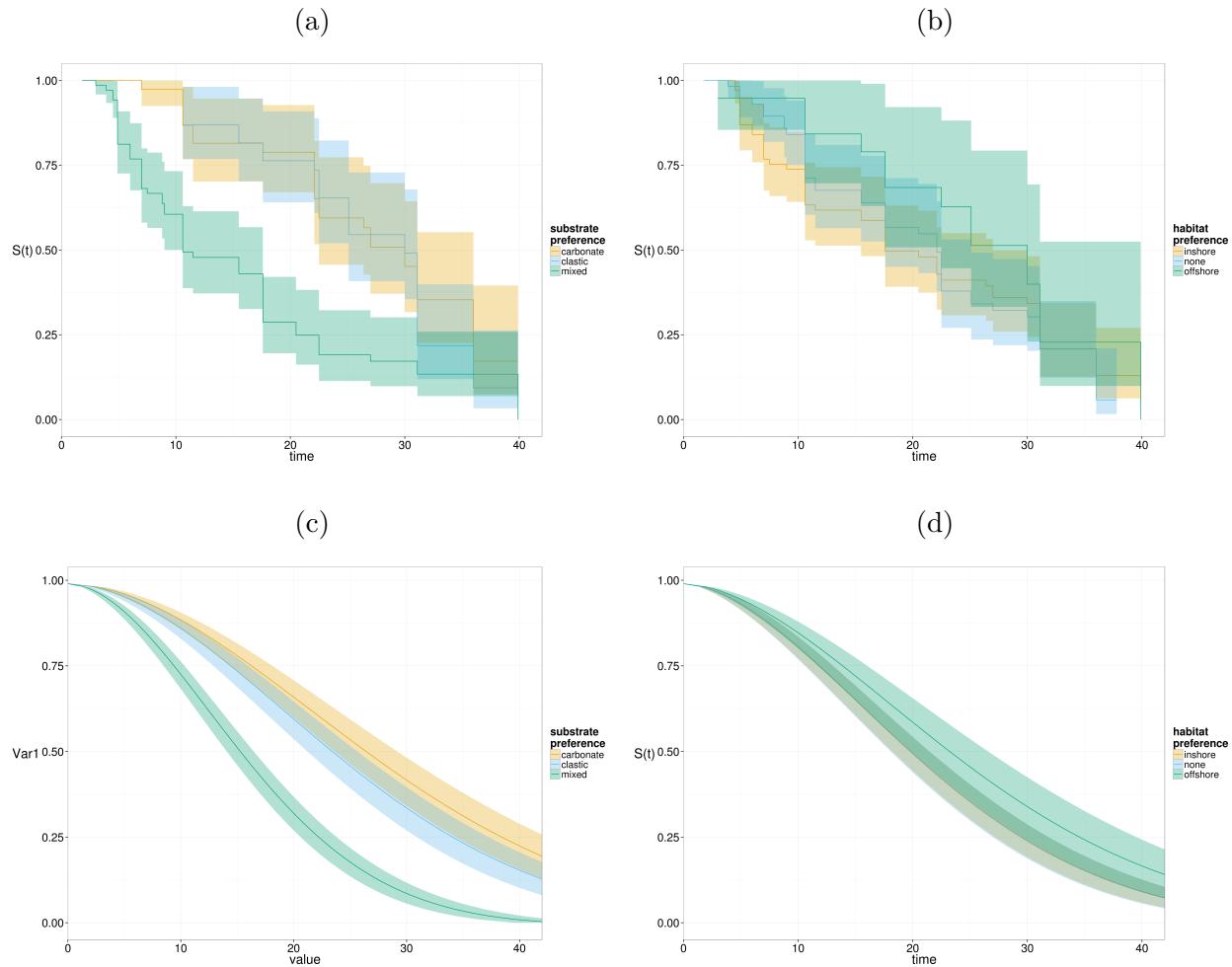


Figure 1: Nonparametric survivorship curves of Australian Permian brachiopod genera based on substrate affinity (a) and habitat preference (b). Curves are illustrated with 95% confidence intervals. Parametric survival curves based on the best parametric models with substrate (c) and habitat (d) as predictors are illustrated with the standard errors of prediction.

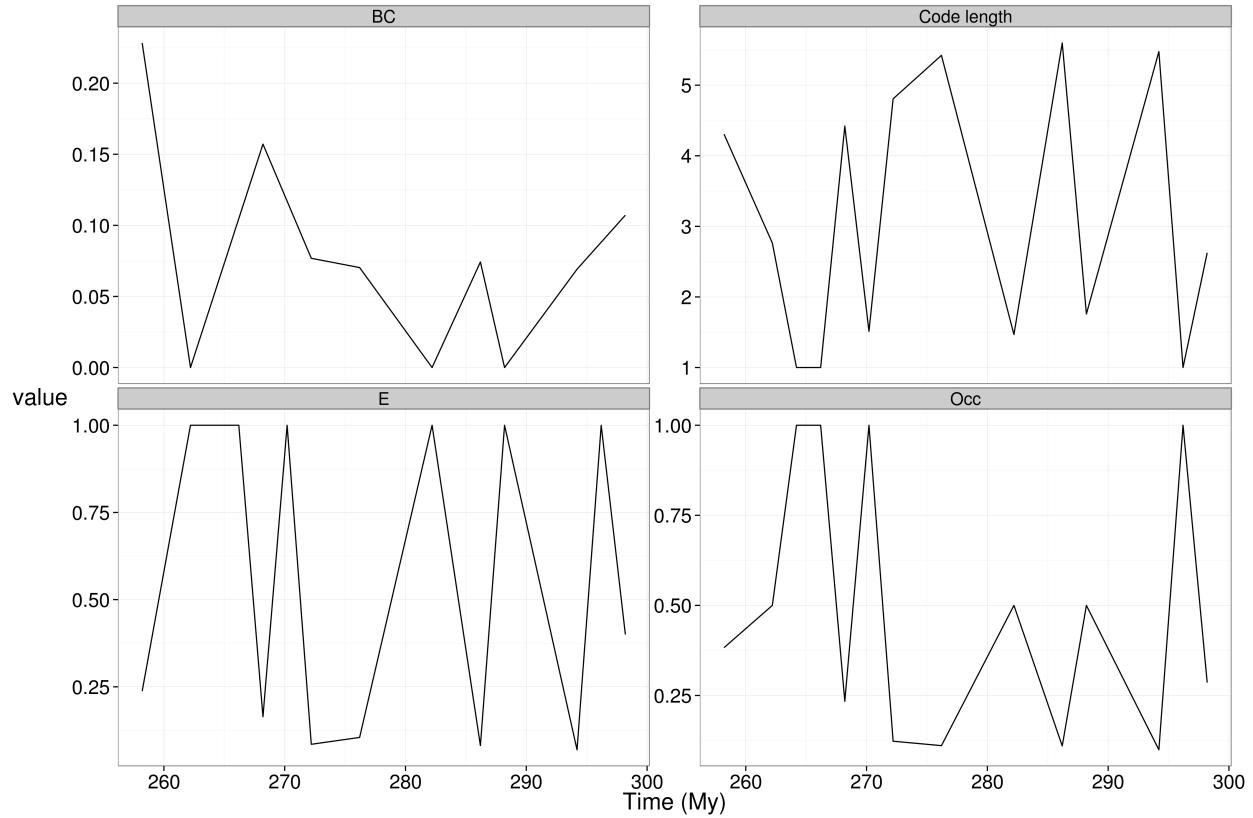


Figure 2: Summary statistics of community connectedness for brachiopods occurring on the east coast of Australia during the Permian. The summary statistics are, clockwise from top left: biogeographic connectedness (BC), code length, average relative locality occupancy per taxon (Occ), and average relative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

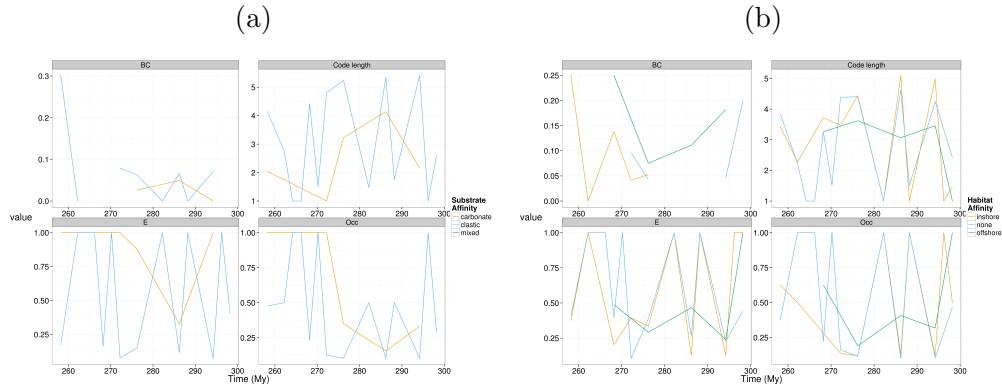


Figure 3: Community connectedness statistics for brachiopods separated by substrate (a) and habitat (b) preference. The summary statistics are, clockwise from top left: biogeographic connectedness (BC), code length, average relative locality occupancy per taxon (Occ), and average relative number of endemic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

500 **3 Cenozoic Mammals**

3.1 Traits and environmental context

502 Mammals are motile organisms which can track their preferred environmental context over
time and space. However, if a taxon requires rare or fragile environmental conditions, or is a
504 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
506 mammals and their environmental context are body size, dietary category, and locomotor
category [26, 27, 67, 83, 84, 128, 129]. Each of these traits describe different aspects of a
508 taxon's adaptive zone such as energetic cost, population density, expected home range size,
set of potential prey items, and dispersal ability among others.

510 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
512 was a shift from a predominately closed environment to a predominately open environment
[14, 64, 114]. This environmental shift was differently timed between continents [132, 133].
514 Because of the differential timing of environmental shift, along with the different biotic
context, the survival and community patterns are expected to vary between continents.

516 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
518 ecologies. For example, herbivores include both browsers and grazers which are known to have
had different diversification dynamics during the Cenozoic [65]. Dietary categories are roughly
520 linked with position in trophic hierarchy, with decreasing stability away from the “base.”
Stability here meaning trophic “distance” from primary productivity, with herbivores having
522 greater stability than carnivores because of the increased likelihood of prey item occurrence.
Additionally, with increased likelihood of prey item occurrence, abundance can increase
524 [18, 26, 65, 123, 138] which can effect both survival and increase occupancy [17, 44, 66, 67].

Locomotor categories describe the motility of a taxon, the plausibility of occurrence, and
526 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
528 tree cover. Locomotor categories are similar to dietary categories in that they represent coarse
groupings of taxa with similar life habits. Here, the categories are arboreal, ground dwelling,
530 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
532 [12, 46, 60] 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
534 stability associated with arboreal and ground dwelling taxa.

An organisms body size, here defined as (estimated) mass, has an associated energetic cost
536 in 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

538 range size, among others [18, 26, 100, 128]. While studies of body size dynamics are very
common [5, 25, 27, 69, 81], the interactions or processes that are correlated with body size
540 might better explain 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 better
542 understand what processes underly the patterns of survival and community connectedness.

3.2 Ecologically mediated survival

544 3.2.1 Questions

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

3.2.2 Hypotheses and predictions

550 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
552 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
554 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
556 major factor for determining species level survival and that other factors, such as body size,
may dominate.

558 Mammalian herbivores and carnivores have been found to have a greater diversification rate
than omnivores [103] which may indicate that these traits are better for survival. However
560 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)
562 impossible to determine from a phylogeny of only extant organisms [104] which means that
analysis of the fossil record is required. If survival is found to be similar between all dietary
564 categories, this may mean that the differential diversification patterns observed by Price et al.
[103] are due to differences in speciation and not extinction.

566 It is expected that arboreal taxa during the Paleogene will have a greater expected duration
than Neogene taxa while the opposite will be true for ground dwelling taxa. In comparison,
568 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 in
570 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 may or
572 may not affect mammalian survival. It may also be the case that other factors, measured or

unmeasured, may be of greater importance in determining differential survival. The difficulty
574 of a Paleogene–Neogene comparison, which is potentially undermined by heterogeneous
preservation, will be explored in simulation (Section 1.1.1).

576 Body size can possibly scale up to affect species level patterns because, for example, as
body size increases, home range size increases [26]. If individual home range size scales up
578 to reflect minimum 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
580 expectation, however, may not be right. As body size increases, reproductive rate decreases
[69], populations get smaller [142], and generations get longer [89] all of which can increase
582 extinction risk, as has been observed [28, 81]. However, the relationship between body size
and extinction rate at the generic level has been found to vary between continents [81, 135].
584 By expanding to include a third continent, South America, and analyzing specific level data
I hope to elucidate how differences in taxonomic diversity at a continental level might affect
586 body size mediated extinction rate. If body size is found to be unimportant for modeling
survival, as in the generic level analysis of Tomiya [135], this means that other biotic or
588 abiotic factors may dominate. This may also mean that individual level home range size does
not scale to increased species level range size, and there is therefore no correlated decrease in
590 extinction 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 [69].

592 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
594 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
596 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
598 respectively. Determining which factors dominate during the Paleogene, as well as other parts
of the Cenozoic, must be done empirically.

600 **3.2.3 Proposed research**

To analyze differential mammalian survival, I propose a survival analysis approach (Section
602 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
604 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
606 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,
608 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
610 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

612 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.

614 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
616 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.

618 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
620 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 [58]. While all three
622 of these traits may have evolved over a taxon’s duration, this will not be considered as part of this study.

624 While many analyses of survivorship are done using generic data [37, 41, 50, 81, 135], there are potential biases in accurately modeling a specific level process using generic level data
626 [108, 109, 119, 124, 137]. 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
628 approach similar to previous work on estimating specific level origination and extinction rates from generic level survival curves [39], I will measure the deviance between extinction
630 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
632 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
634 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.

636 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
638 important, however, that each model be well justified and be tied to a realistic biological hypothesis/prediction [19].

640 In order to account for environmental shifts, two different time-dependent covariates will be used. δO^{18} isotope information for the whole Cenozoic [144] will be used as a global climate
642 proxy. Additionally, the Paleogene–Neogene divide, which may reflect global environmental shift, will be modeled as a time-dependent step-function.

644 3.2.4 Preliminary results

Preliminary results are based solely on Cenozoic mammal occurrence data from the PBDB
646 for North America and Europe. Nonparametric Kaplan-Meier survival curves were estimated for both dietary and locomotor categories (Fig. 4). These are shown on a log-linear scale for
648 visual estimation of linearity [136, 137].

The North American species-level survival curves, both based on dietary (Fig. 4a) and locomotor categories (Fig. 4b), are semi-log linear as expected under the Law of Constant Extinction [136]. All dietary categories have approximately equivalent patterns of survival while ground dwelling taxa have a qualitatively higher probability of long duration. In comparison, the species-level survival curves for European mammals, both dietary (Fig. 4c) and locomotor categories (Fig. 4d), are qualitatively not semi-log linear which is not consistent with the Law of Constant Extinction. Diet qualitatively appears to have little effect on European mammal survival, while locomotor category appears to differentiate arboreal taxa from both ground dwelling and scansorial taxa.

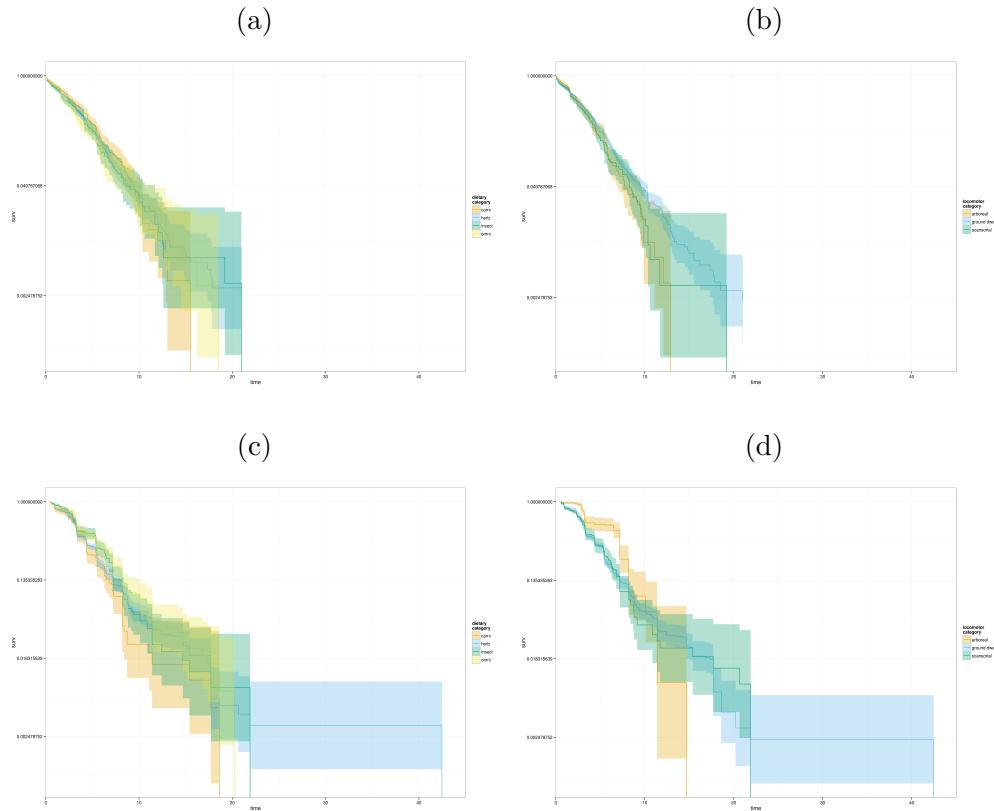


Figure 4: Nonparametric Kaplan-Meier species-level survival curves for North American and European mammals based on dietary category (a and c respectively, and locomotor category (b and d respectively). K-M curves are illustrated with 95% confidence intervals. The vertical axes are on a natural log scale.

These results are extremely preliminary and based solely on qualitative patterns present in the nonparametric K-M survival curves and without reference to estimated median survival times. Additionally, possible differences in survival based on body size were not estimated. Also, no comparison has been made with the climatic histories of either continent. By including all three time-independent covariates in a parametric survival framework it should be possible to

better understand the underlying process behind survival. The inclusion of a third continent,
664 South America, will also greatly improve the overall understanding of how extinction in
mammals proceeds and how this may differ across environments.

666 **3.3 Community connectedness: global, regional, local**

3.3.1 Questions

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

3.3.2 Background and Predictions

672 During the Cenozoic there was a global shift from a “hot house” environment to an “ice
house” environment [143, 144]. This transition was accompanied by major shifts in global
674 climatic envelopes and the reorganization of mammalian communities [5, 14, 36, 44, 64].
For mammalian community connectedness there are two possible scenarios. First, while the
676 environment was shifting, lineages may have adapted in place and overall trophic structure
and community connectedness would have remained relatively constant through time, as
678 observed during the Neogene of Europe [67]. Alternatively, species may have shifted ranges
and changed the average set of taxa present at a locality which would be associated with
680 non-stationary trophic structure and community connectedness.

Based on prior work, it is expected that the patterns of biogeographic community connect-
682 edness for herbivorous taxa in a region would be most similar to that for all regional taxa
combined and potentially “drive” the regional pattern, partially because on average this cate-
684 gory represents the majority or plurality of taxa [66]. In contrast, community connectedness
for carnivorous taxa is expected to remain constant over time or be correlated with herbivore
686 patterns. Finally, omnivorous taxa are not expected to be correlated with the patterns of
either herbivorous or carnivorous taxa and have either a relatively constant or random pattern
688 of connectedness over time. These predictions are based on the differences in resilience and
relationship to primary productivity, with herbivores being more resilient than carnivores
690 and omnivores being random in their resilience [67]. Resilience is defined here as the ability
for a taxon to increase in occupancy following a decline [67].

692 The Cenozoic global shift from closed, forested habitat in the Paleogene to open, savanna-like
habitat during the Neogene would have greatly affected the possible distributions of both
694 arboreal and ground dwelling taxa. Additionally, the timing of this environmental shift was
different between continents [132, 133], so patterns of community connectedness may not be
696 globally uniform and instead reflect regional differences. Generally this transitions would cause
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 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.

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 on North America [3–5, 9, 10, 14, 36, 47, 48, 126, 127]. However, the effect of global climate change on North American diversity remains unresolved and controversial [5, 10, 14, 36], 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.

The European mammalian fossil record is also well studied, though research has primarily focused on the Neogene [66, 67, 81, 105–107]. An important aspect about the European record is that during the Neogene there was little shift in relative dietary category abundance [67] and that the patterns within herbivores (browse–graze transition) were mostly driven by abundant, cosmopolitan taxa [66]. It is predicted then that herbivores will demonstrate the same patterns of community connectedness as Europe as a whole, while omnivores and carnivores will be different from that of herbivores and may demonstrate random or constant patterns of community connectedness through time.

Patterns of community connectedness for South American mammalian fauna are comparatively less synthesized than those of North America and Europe. Instead, cross-continental dynamics between North and South America during the Neogene are much more studied [88]. The South American mammalian faunal record reflects two distinct biotic provinces between the North and the South [38, 85, 86, 97]. Because of this, it is expected that South America will have a different pattern of community connectedness than either North America or Europe. Also, there is an expected dramatic increase occupancy in land-dwelling herbivores relative to arboreal and scansorial taxa related to the aridification of high-latitude South America. Additionally, because of this strong biome distinction, it is predicted that provinciality will be high but remain constant over time.

3.3.3 Proposed research

In order to estimate changes in community connectedness during the Cenozoic I will be using 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 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 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 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 analysis to large bodied and well studied groups such as Primates and Artiodactyls in order to

⁷³⁶ account for potential sampling and taxonomic biases, analysis will be done using all available
⁷³⁸ 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
as for the above analysis of mammalian survival (Section 3.2).

⁷⁴⁰ The degree of phylogenetic similarity between taxa at a locality may play an important
⁷⁴² role in community structuring [141]. For example, closely related taxa may be repulsed
“repulsed” due to competitive exclusion or “clumped” because of environmental filtering.
⁷⁴⁴ 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
⁷⁴⁶ as the structure of an informal phylogeny, it should be possible to estimate the distribution
of phylogenetic similarity across localities.

For each locality, an informal phylogeny will be constructed based solely on available taxonomic
⁷⁴⁸ information such as order, family, and genus assignments with each of these levels being an
unresolved polytomy. Using this informal phylogeny, a number of measures of phylogenetic
⁷⁵⁰ similarity can be estimated. For example the relative mean pairwise distance between all
taxa at a locality [141] or the related phylogenetic species variability of a single locality [53].
⁷⁵² These values calculated for all localities can then be used as a partial correlates or covariates
when modeling changes in community connectedness.

⁷⁵⁴ As with the Permian brachiopods (Section 2.3), patterns of community connectedness will be
compared both within and between ecological categories. Additionally, the correspondence
⁷⁵⁶ of changes in environmental conditions and community connectedness will also be analysed.
The approach and methodology to accomplish these analyses is currently under development.
⁷⁵⁸ 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
⁷⁶⁰ general.

3.3.4 Preliminary results

⁷⁶² Preliminary analysis was done using only the occurrence information of both North American
and European fossil mammals available in the PBDB. Both regions have qualitatively different
⁷⁶⁴ 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.
⁷⁶⁶ However, some interesting qualitative patterns are present.

There is a qualitative decrease in *Occ* in Europe until approximately the start of the Neo-
⁷⁶⁸ gene (approximately 23 My), indicating that the average taxon is becoming generally less
cosmopolitan over time. In contrast, North American *Occ* is qualitatively stationary over the
⁷⁷⁰ entire Cenozoic and almost always lower than that observed for Europe. This means that, on
average, North American taxa are present in very few localities at any given point in time.

⁷⁷² In Europe there is a qualitative rise in *BC* in the first few million years of the Cenozoic, but

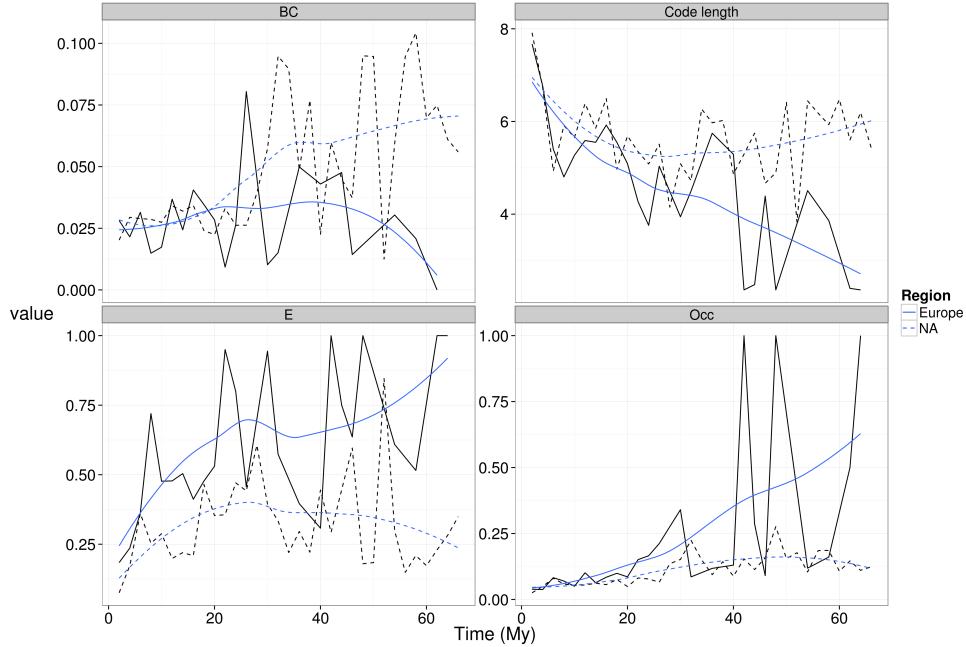


Figure 5: Biogeographic network summary statistics for mammalian communities in North America (dashed line) and Europe (solid line). The summary statistics are, clockwise from top left: biogeographic connectedness (BC), code length, average relative locality occupancy per taxon (Occ), and average relative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

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

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

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

When taxa are separated by dietary categories, the amount of noise associated with each

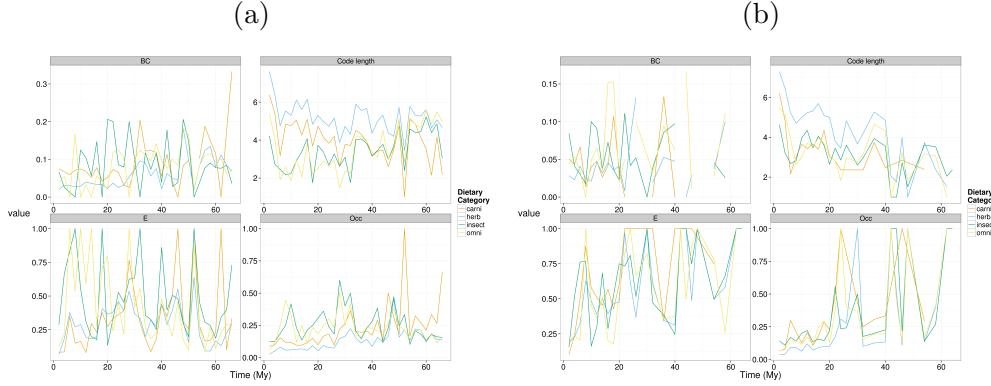


Figure 6: Time series of summary statistics for biogeographic networks determined by dietary category for North America (a) and Europe (b). The summary statistics are, clockwise from top left: biogeographic connectedness (BC), code length, average relative locality occupancy per taxon (Occ), and average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

statistic increases greatly (Fig. 6). In North America, *BC*, while variable, appears to qualitatively demonstrate no net change. Carnivores and herbivores to qualitatively become less volatile during the Neogene compared to the Paleogene (Fig. 6a). *BC* for Europe is also very volatile, though impossible to measure for dietary categories individually for much of the Paleogene (Fig. 6b).

- Code length for North American qualitatively shows a stationary pattern with an up-tick in the Recent and a major drop at approximately 50-55 My (Fig. 6a). Additionally, herbivore and carnivore patterns appear qualitatively similar. In comparison, the European record for code length shows a qualitatively slight increase over the entire Cenozoic (Fig. 6b). Also, the patterns of herbivore and carnivores appear qualitatively less similar than for North America. For both Europe and North America, herbivores have the over all highest code length. In North America, carnivores arguably have the second highest code length. In all other cases, the ranks are qualitatively ambiguous.
- E* for North American appears to qualitatively have two categories (Fig. 6a). Herbivore and carnivore patterns are qualitatively stationary and low during the Neogene, while the omnivore and insectivore patterns are qualitatively more variable and higher during the Neogene. In comparison, all four categories of European mammals demonstrate a slight decrease during the Cenozoic (Fig. 6b).

For North America, *Occ* are qualitatively stationary throughout the Cenozoic with one spike in carnivore *Occ* at approximately 50-55 My (Fig. 6a). In contrast, European values are highly volatile throughout the Paleogene and then less volatile during the Neogene (Fig. 6b).

- When taxa are separated by locomotor category, there is qualitatively less noise then is the case for by dietary category (Fig. 7). *BC* for North America has qualitative differences

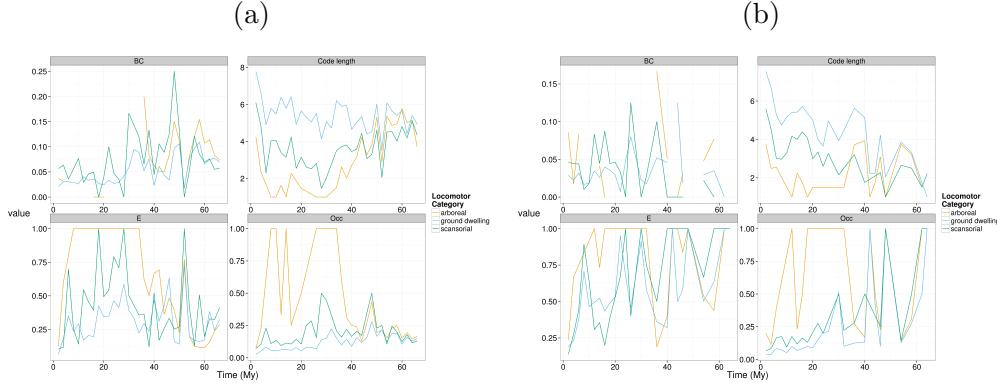


Figure 7: Time series of summary statistics for biogeographic networks determined by locomotor category for North America (a) and Europe (b). The summary statistics are, clockwise from top left: biogeographic connectedness (BC), code length, average relative locality occupancy per taxon (Occ), and average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

812 between each of the three categories (Fig. 7a). Arboreal taxa can only be measured for
 814 BC predominately during the Paleogene where there is no qualitative pattern beyond high
 816 variance. Scansorial taxa have a qualitative decline in volatility and was stationary during the
 818 European values of BC were generally more volatile and very difficult to measure
 820 during the Paleogene because of the paucity of geographically spaced localities (Fig. 7b). Qualitatively,
 822 values of BC for scansorial taxa are more volatile than for ground dwelling
 824 taxa.

For North American values of code length, there are a few clear qualitative patterns (Fig. 7a).
 820 Ground dwelling taxa have generally the highest code length values, followed by scansorial
 822 and arboreal taxa. Interestingly, all three of these categories have almost identical code length
 824 values until approximately 50 My. Following this, arboreal taxa have a qualitative decrease
 826 in code length, while scansorial taxa are qualitatively stationary with a slight decrease, and
 ground dwelling taxa have a slight increase though are mostly stationary. European code
 length values show a general increase during the entire Cenozoic, though this is mostly
 confined to scansorial and ground dwelling taxa (Fig. 7b).

The *E* series for North America demonstrates qualitatively distinct patterns for the three
 828 locomotor categories (Fig. 7a). *E* increases dramatically for arboreal taxa, has a moderate
 increase for scansorial taxa, and is qualitatively stationary for ground dwelling taxa during
 830 the Cenozoic. In comparison for Europe, values of *E* are generally high throughout the entire
 Cenozoic and vary with much greater volatility (Fig. 7b). Qualitatively there is a decrease in
 832 *E* for ground dwelling and scansorial taxa during the Neogene.

Values of *Occ* for both North America and Europe show respectively qualitatively similar
 834 patterns to patterns of *E*, though are less volatile. *Occ* increases in North American arboreal

taxa at approximately 40 My years ago while both scansorial and ground dwelling taxa
836 are qualitatively stationary (Fig. 7a). The pattern of *Occ* for scansorial taxa appears to
qualitatively be a more exaggerated version of the pattern for ground dwelling taxa. All three
838 appear correlated during the earliest Cenozoic. As with *E*, European patterns of *Occ* are
volatile, particularly during the early Cenozoic (Fig. 7b). At approximately 40 My, patterns
840 of *Occ* become less volatile and qualitatively decrease for ground dwelling and scansorial taxa.
In comparison, *Occ* values for arboreal taxa become qualitatively much higher during the
842 late Cenozoic with a massive decrease near the Recent.

These analyses will be greatly improved by varying locality “size”, comparison with South
844 American patterns, comparison of major orders, and other ideas stated above (Section
3.3.3). Additionally, quantitatively analysis of these patterns and what correlations might
846 exist, especially in a phylogenetic context, are necessary in order to better understand what
processes might dominate and when.

848 **4 Synthesis of proposed research**

Underlying all of the above is a foundational question in paleobiology: why do certain taxa
850 go extinct while others do not? In the context of evolutionary paleoecology, this question can
be rephrased as “how do the set of all biotic–biotic and biotic–abiotic interactions a taxon
852 experiences over time (i.e. adaptive zone 126) affect extinction risk?” Related to this is the
Law of Constant Extinction which states that extinction risk for a given adaptive zone is
854 taxon–age independent [136]. It is asserted that the Law of Constant Extinction only holds
during periods of relatively constant environment, even though this was not the context for
856 the initial observation [80, 136], which can be interpreted as the set of dominant non-organism
mediated processes do not fluctuate or fluctuate in a known manner. By understanding which
858 non-organism mediated processes may be shaping the environment (set of all possible biotic
and abiotic interactors) and how they change over time and phrasing analysis of extinction
860 in this context, it may be possible to “test” the Law of Constant Extinction.

The two studies proposed above (Sections 2.2 and 3.2) investigate how organismal traits
862 potentially related to environmental preference affect extinction rate. In effect, these traits
may determine the “bounds” of a taxon’s adaptive zone by limiting the total set of interactions
864 to just those for which the taxon is adapted. The other two proposed studies (Sections 2.3 and
3.3) aim to estimate what non-organism mediated processes (global, regional, and/or local)
866 may be dominate in shaping the environment and the related set of adaptive zones. Between
these studies, as well the use of two disparate groups, it should be possible to determine
868 when, what, and if certain variables matter for survival and, potentially, how they matter.

5 Timeline

- 870 Spring/Summer 2014
- Evolution Meeting: mammalian survivorship analysis for North America and Europe
- 872 South American fossil mammal data from American Museum of Natural History collections
- 874 Fall 2014/Winter 2015
- GSA: survivorship simulation for anagenesis and sampling
 - Doctoral Dissertation Improvement Grant
- Spring/Summer 2015
- 878
- Evolution Meeting: preliminary brachiopod survival results
 - write and submit survivorship simulation paper
- 880
- possible South American fossil mammal data from American Museum of Natural History collections
- 882 Fall 2015/Winter 2016
- SVP: mammalian biogeographic connectedness
 - write and submit mammal connectedness paper
- Spring/Summer 2016
- 886
- Evolution Meeting: brachiopod survival analysis
 - write and submit brachiopod community paper
- 888 Fall 2016/Winter 2017
- GSA: brachiopod community connectedness
 - write and submit brachiopod survival paper
- Spring/Summer 2017
- 892
- Evolution Meeting: survival and communities together
 - write and submit mammal survival paper
- 894
- write and review/philosophy paper
 - **Defend**

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A Permian lithology and paleoenvironment

1382 Lithological and paleoenvironmental assignments available in the PBDB may be poorly resolved or missing, as is frequently the case for paleoenvironment. Because these assignments
1384 are critical in the proposed study of brachiopod survival and distribution (Section 2), it is necessary to improve these values with more precise information available in the paleontological
1386 and geological literature. Currently, no improved assignments have been included in any of the preliminary analyses (Section 2).

1388 Using the geological unit reference data set available through Geosciences Australia (<http://www.ga.gov.au/>), lithological information for many of the Permian brachiopod occurrences
1390 can be improved and made more precise (Table 3). The lithological assignments below are based on the order with which rock types are named in the lithological description of a
1392 geological unit and were extracted automatically using a very simple algorithm. While more than two rock types may be listed for a geological unit, only the first two are reported below.
1394 Duplicates of the same rock type for a geological unit result from it occurring twice in a lithological description before any other named rock types. These formations represent 2956 of 4432 (67%) total Permian occurrences across all of Australia.
1396

Table 3: Australian formations included in the study of brachiopod survival and distribution (Section 2) and improvements based on lithological descriptions from Geosciences Australia (<http://www.ga.gov.au/>).

geological unit	PDBD lithology 1	PBDB lithology 2	my lithology 1	my lithology 2
Aldebaran Sandstone	sandstone		conglomerate	siltstone
Allandale Formation	siliciclastic		conglomerate	sandstone
Alum Rock Conglomerate	siliciclastic		tuff	limestone
Bon-donga/Pikedale/Silver Spur and beds	Bon-donga/Pikedale/Silver Spur and beds			
Baker Formation	siltstone		siltstone	quartz
Bakers Blue Granite	siltstone		granodiorite	
Bakers Creek Diorite	siltstone		diorite	quartzbiotite
Bakers Creek Suite	siltstone		gabbros	diorites
Bakerville Granodiorite	siltstone		granodiorite	
Barfield Formation	sandstone		tuff	conglomerate
Beekeeper Formation	not reported		carbonatesiliciclastic	carbonatesiliciclastic
Berserker Group	siliciclastic		conglomerates	breccia
Billidee Formation	sandstone		siltstone	shale
Black Alley Shale	shale		shale	siltstone
Black Jack Granodiorite	siliciclastic		granite	granodiorite
Black Jack Group	siliciclastic		sandstone	
Blenheim Formation	sandstone		sandstone	coquinite
Broughton River Granodiorite	sandstone		granodiorite	granite
Broughton River Suite	sandstone		granodiorite	
Buffel Formation	siliciclastic		limestone	limestone
Bulgadoo Shale	shale		shale	siltstone
Burnett Formation	sandstone		arenite	siltstone
Callytharra Formation			calcarenite	conglomerate
Carmila beds	siliciclastic		siltstone	basalt
Carolyn Formation	sandstone	claystone	sandstone	sandstone
Carrandibby Formation	siliciclastic		claystone	siltstone
Catherine Sandstone	sandstone		siltstone	mudstone
Cattle Creek Formation	siliciclastic		mudstone	quartzose
Condamine beds	mudstone		conglomerate	tuff
Cookilya Sandstone	sandstone		quartz	siltstone
Coyrie Formation	siliciclastic		shale	siltstone
Crocker Well Suite	siliciclastic		granodiorite	
Cundlego Formation			siltstone	shale
Darlington Limestone	limestone		limestones	calcirudites
Eight Mile Creek beds	siliciclastic		conglomerate	sandstone
Eight Mile Creek Granite	siliciclastic		granite	
Eight Mile Creek Granodiorite	siliciclastic		granite	
Flat Top Diorite	sandstone		diorite	diorite
Flat Top Formation	sandstone		tuff	sandy
Freitag Formation	sandstone		sandstone	sandstone
Gilgurra Mudstone	mudstone		mudstone	sandstone
Glencoe Gabbro	mudstone		gabbro	gabbro
Glencoe Limestone Member	mudstone		limestone	
Glenmore Creek Granite	siliciclastic		monzogranite	
Gray Creek Complex	siltstone		metagabbro	
Hardman Formation	sandstone		sandstone	limestone
Hickman Creek Granite	siliciclastic		monzogranite	
High Cliff Sandstone	sandstone		siltstone	shale
Holmwood Shale	siliciclastic		limestone	shale
Ingelara Formation	siliciclastic		sandy	siltstone
Inglinton Granite	siliciclastic		granite	
Lakes Creek Formation	not reported		volcanics	sandstones
Lizzie Creek Volcanic Group/Mount Wickham Rhyolite	sandstone		andesite	rhyolite
Lochinvar Formation	limestone		basalt	siltstone
Manning Group	siliciclastic		mudstone	conglomerate
Maria Formation	siliciclastic		mudstone	shale
Maria Island Granite	siliciclastic		granite	
Marra Creek Formation	siliciclastic		sandy	carbonate
Marra Formation	siliciclastic		sandstone	siltstone
Marrangaroo Conglomerate	siliciclastic		sandstone	conglomerate
Marrar Dyke	siliciclastic		monzogabbro	
Mistletoe Granite	siliciclastic		granite	
Moonlight Valley Tillite	sandstone		conglomerate	sandstone
Mooraback beds	siliciclastic		sandstone	siltstone
Mount Poole Monzogranite	siliciclastic		monzogranite	
Muggleton Formation	siliciclastic		shale	quartzose
Mulbring Siltstone	sandstone		claystone	sandstone
Muree Sandstone	siltstone		sandstone	conglomerate
Narayen beds	siliciclastic		conglomerate	siltstone
Nowra Sandstone	sandstone		siltstone	quartzose
Oxtrack Formation	siltstone		conglomerate	
Peawaddy Formation	siliciclastic		chert	siltstone
Poole Sandstone	siliciclastic		siltstone	siltstone
Porcupine Creek Granodiorite	siliciclastic		conglomerate	quartzose
Porcupine Creek rhyolite	siliciclastic		granodiorite	
Porcupine Formation	siliciclastic		ignimbrite	
Quinnanie Shale	shale		conglomerate	sandstone
			shale	siltstone

Rammutt Formation	siliciclastic	mudstone	basaltic
Rhyolite Range beds	siliciclastic	sandstone	siltstone
Risdon Stud Formation	sandstone	tuff	arenite
Rutherford Formation	siliciclastic	marl	sandstone
Silver Spur beds	siliciclastic	conglomerate	mudstone
Snapper Point Formation/Wandrawandian Siltstone	siltstone	sandstone	siltstone
South Curra Limestone	limestone	grainstone	calcareous
Tamby Creek Formation	siliciclastic	andesite	breccia
Tomago Coal Measures	siliciclastic	tuff	siltstone
Towgon Grange Tonalite	mudstone	granodiorite	diorite
Wandagee Formation		siltstone	quartz
Wandrawandian Siltstone	siltstone	siltstone	quartzlithic
Watermark Formation	siliciclastic	siltstone	claystone
Werrie Basalt	siliciclastic	basaltic	tuffs
Yessabah Limestone	limestone	limestone	mudstone

Below is a set of PBDB environmental assignments for formations and my preliminary improvements based on key papers and maps [31, 32, 51, 95, 96, 99]. There are a total of 4432 Permian Australian brachiopod occurrences in the PBDB, from both eastern and Western Australia. Within is, there are 3407 occurrences that are not from Western Australia. The geological units listed in Table 4, which are from eastern Australia, account for 1897 of the 1398 1400 1402 Permian brachiopod occurrences which is about 43% of the total samples and 56% of the east Australian samples.

formation	PBDB paleoenvironment	my paleoenvironment 1	my paleoenvironment 2
Aldebaran	offshore	deltaic/coastal plain	nearshore marine
Allandale	coastal indet	sublittoral strand	marine shelf
Barfield	coastal indet	prograding shelf	deep shelf
Berry	marine indet	offshore marine	
Black Alley	offshore	alluvial plain	delta
Black Jack	marine indet	alluvial	delta
Branxton	coastal indet	fan delta	delta plain
Buffel	coastal indet	delta	shallow shelf/coastal
Camboon	coastal indet	alluvial	lacustrine
Catherine	coastal indet	prograding shelf	nearshore marine
Cattle Creek	coastal indet	delta	nearshore marine
Farley	marine indet	delta plain	delta front
Flat Top	coastal indet	prograding shelf	deep shelf
Freitag	marine indet	coastal plain	offshore marine
Ingelara	marine indet	prograding shelf	offshore marine
Lizzie Creek	coastal indet	alluvial	lacustrine
Lochinvar	marine indet	sublittoral strand	marine shelf
Mulbring	marine indet	marine shelf	
Muree	coastal indet	alluvial fan	fan delta
Nowra	coastal indet	nearshore marine	coastal
Oxtrack	coastal indet	deltaic/coastal plain	shallow shelf/coastal
Peawaddy	marine indet	prograding shelf	nearshore marine
Porcupine	marine indet	marine shelf	
Rutherford	coastal indet	delta front	marine shelf
Snapper Point	shoreface	fluvial coastal	nearshore marine
Wandrawandian	offshore	offshore marine	
Wasp Head	shoreface	alluvial valley fill	nearshore marine
Watermark	marine indet	delta	marine shelf

Table 4: Paleoenvironmental assignments for Australian geological units included in the study of brachiopod survival and distribution (Section 2). Both PBDB assignments and those sourced from the literature are included.