

Evolutionary paleoecology and the biology of extinction

Peter D. Smits
psmits@uchicago.edu

Dissertation Proposal Hearing
December 28, 2013
Committee on Evolutionary Biology
The University of Chicago

Committee

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

Introduction and Theory

Paleobiology is the study of life over time and the inference of what processes generate the observed patterns in diversity and disparity. Intimately related to paleobiology is the concept of macroevolution here defined as the pattern of speciation and extinction over time [44]. The study of macroevolution is the estimation of the processes underlying these observed patterns. The term origination is frequently used in place of speciation because it includes both speciation and migration and depending on both the spatial scale and quality of the fossil record it may be impossible to distinguish between the two.

Evolutionary paleoecology is defined as the study of the effects of ecological traits and factors on differential rate dynamics, particularly rates of faunal turnover and diversification [58]. Ecological traits and factors are traits expressed by a taxon, at any level, that are involved with biotic–biotic or biotic–abiotic interactions. Diversification is the difference between origination and extinction and is the net pattern of macroevolution. The study of evolutionary paleoecology is therefore the link between environmental (biotic–biotic and biotic–abiotic) interactions and macroevolution. As a corollary to Kitchell [58]’s definition, Allmon [3] states that in order to correctly link ecological interactions to macroevolution, one must focus on the specific traits and factors that may affect the speciation process. Tacitly included in this is the study of how ecological traits are related to extinction [57].

Survival can be considered the fundamental measure evolutionary success because ultimately, a successful lineage is not one that speciated greatly but one that never went extinct [25, 73]. Because during periods of background extinction, extinction is most likely non-random with respect to biology [42], it should be possible to estimate how various ecological traits are correlated with survival [57, 58]. Periods of background extinction also represent the majority of geologic time and remain relatively predictable and change slowly, providing a better opportunity to study how traits affect survival than during mass extinctions [42, 85]. Additionally, the Law of Constant extinction [102] states that extinction rate within an adaptive zone is taxon-age independent. Van Valen [102] came to this conclusion by observing survival curves across many different taxonomic groups and developed the Red Queen hypothesis in order to explain this perceived phenomenon. Survival curves are the estimated probability of survival of an observation given a certain length of survival.

It is under this framework that I propose to study how ecological traits associated with environmental preference and adaptive zone have affected the differential survival and cosmopolitan–endemism dynamics. I will be studying two distantly related and biotically different groups: Cenozoic mammals and Permian brachiopods. Both of these groups are considered to have very good fossil records able to reflect massive long term evolutionary patterns [68]. These two time periods were chosen because they represent periods of climatic change, global cooling and global warming respectively. Also, these two groups are a terrestrial and marine system respectively and the traits associated with range size and environmental preference (described below) are fundamentally very different.

Importantly, these two groups allow for a hierarchy of questions to be asked. Both the brachiopod and mammal data allows for generic level survival curves of different adaptive zones (combinations of traits) to be estimated and for age independent or dependent extinction to be tested. However because there is a known biasing factor towards age-dependent extinction in generic level survival [83, 84, 93], the mammalian survival will be further analyzed at the specific level. Additionally, the importance of global climatic change in modeling mammalian survival will be analyzed. If global climatic change is found to not be important for mammalian survival, this does not mean that regional or local climatic change may not be important to survival. Analysis of mammalian community connectedness is then to estimate how disjoint taxa are across the landscape and if it is reasonable expect global, regional, or local environmental factors to dominate and how this might change over time.

The relationship between geographic range and extinction risk is well understood. Species with larger geographic ranges tend to have lower extinction rates than species with smaller geographic ranges [39, 42, 48, 71, 88]. Range size is considered emergent because no one property of an organism can explain this trait and instead it is a combination of multiple properties which determines range size. However the effect of various organismal traits, such as body size or environmental preference, remains much less well understood. It has been shown that ecological traits can be related to differential extinction [12, 33, 62, 71], especially the relationship of adaptation to variable environments and increased species longevity. While some research has focused on the indirect effect of organismal traits on longevity [38], the interaction between organismal traits and its relationship to survival remains understudied especially during periods of background extinction. Here I propose to study the individual and combined effects of organismal traits related to range size on survival.

Permian brachiopods, extinction and environmental preference

Questions: In Australasian Permian brachiopods, do traits directly related to environmental preference relate to differential survival? Are certain traits more explanatory of survival than others? Does changing climate, habitat or substrate availability affect survival?

Background and Predictions: In brachiopods, three important ecological traits potentially involved in determining environmental preference are affixing strategy, substrate preference, and habitat preference. While larval mode is considered important in determining range size in marine invertebrates [46, 47], this does not preserve in brachiopods and thus cannot be used to directly model survivorship [47]. Substrate preference is statement of the chemical and physical processes affecting the environment and acts as a limiting factor on the range of possible environments in which an organism can optimally survive. This then limits the possible geographic extent of a taxon. Substrate selection is mitigated via larval chemosensory abilities and thus may be a weak proxy for larval dispersal ability [46, 47].

Affixing strategy and habitat preference relate to range size by means of limiting the possible geographic extent of a taxon. Affixing strategy is the manner by which an individual interfaces with the substrate. Different strategies are optimal for certain environmental conditions such as flow speed or mud depth [2, 60, 61]. Because brachiopods are obligate filter feeders, flow speed and environmental energetics are important in prey capture and individual survival. Thus, the availability of optimal environments becomes a limiting factor on the possible geographic extent of a taxon. Habitat preference is a statement of the suitability of an environment and the accompanying environmental energy level and acts as a limit on the possible geographic extent of a taxon.

The three principle ways of classifying affixing strategies are pedunculate, reclining, and cementing. During the Permian, pedunculate taxa tend to be associated with shallow on-shore environments while reclining taxa are associated with deep off-shore environments [20]. However, this association is weak as most assemblages are composed of a heterogeneous mix of taxa [20]. Previous analysis of brachiopod durations indicated that affixing strategy is associated with differential longevity [2]. Among endemic taxa, reclining taxa have longer durations than all other affixing strategies. In contrast, among cosmopolitan taxa, pedunculate and cementing taxa had longer durations than all other taxa.

The three principle classifications of substrate affinity are carbonate, clastic, or mixed. These are descriptions of the lithology of the sites at which the taxa are predominately found [7, 32, 55, 70, 71]. The Phanerozoic is characterized by an overall decline in carbonates relative to clastics [32, 70]. Because of this, it is expected that taxa with clastic or mixed affinities will have greater durations than taxa associated with carbonate substrates.

The primary ways of classifying habitat preference are on-shore, off-shore, or mixed. Habitat preference has been the focus of a great deal of research in terms of explaining global diversity dynamics [16, 45, 49, 55, 90]. Importantly, habitat preference is related to sea-level rise and fall and the availability of that habitat with changing environment. On-shore environments have declined in areal extent over the Phanerozoic [75]. Because of this decrease in areal extent, the expectation would be that taxa predominately associated with on-shore habitats would have overall lower durations than taxa associated with off-shore habitats or mixed preference.

An important consideration is that taxonomic survival might not be linked to single environments *per se*, but the variability of environments [33, 40, 62]. This adaptation to variable environments has been found to relate strongly with survival past origination [33]. In this case, it would be expected then that taxa with mixed preferences for both substrate and habitat would have potentially longer durations than taxa with single preferences. This makes logical sense as it would mean that a taxon's potential geographic extent is not expressly limited by either of these two traits and thus decreasing expected extinction rate due to large range size [39, 42, 48, 71, 88].

During the Permian there was a shift from an "ice house" to a "hot house" world [14, 28, 54, 76] which could be expected to have some effect on brachiopod survivorship. Taxa in Australia

are of particular interest because of their proximity to the south pole during the Permian and the repeated glacial activity in the region [14, 28, 54]. According to Olszewski and Erwin [72], sea-level and climate change do not wholly explain the ecological dynamics experienced by brachiopods in the Permian of Texas. The prediction then is that the best model of brachiopod survivorship will have to have some biotic component such as affixing strategy or substrate preference. Climate being a predictor in the best model of survivorship is less clear cut and necessary to determine empirically.

Proposed research: I propose to a survival analysis approach similar to that described above to estimate the differential survivorship of Permian brachiopods. Survival analysis is the analysis of time-till-event data. In a paleontological context this is the time from origination (first appearance date; FAD) till extinction (last appearance date; LAD). I restrict this analysis to Australasia because it represents a relatively continually sampled and well worked area that preserves the majority of the entire Permian [8, 22, 23, 106]. I plan to compare different models of trait based survival in order to best understand which factors are most important. In this analysis, the time-independent covariates are substrate preference, affixing strategy, and habitat preference. Climate will be modeled as either an ancillary Heaviside function or a time-dependent covariate depending on the quality of the Permian isotope record. Additionally, as in the mammalian survivorship analysis described above, the age dependence of brachiopod extinction rates will be estimated using different fundamental hazard models by comparing the fit various probability distributions to survival.

Permian brachiopod occurrence information is available via the PBDB and is primarily based on the work of Clapham [20–24] and Waterhouse [106].

Preliminary results Preliminary analysis of brachiopod survivorship based on substrate affinity and habitat preference. Depositional environment of all occurrences were classified into one of the three substrate affinity categories following Foote [32] while paleoenvironmental setting of all occurrences were classified into one of the three habitat preferences following Kiessling et al. [56]. Both of these traits were assigned using the approach of Simpson and Harnik [94] where trait value is determined as the posterior probability of the occurrence ratio in comparison to the all occurrences during the duration of that taxon. Assignment probability ($P(H_1|E)$) was calculated as

$$P(H_1|E) = \frac{P(E|H_1)P(H_1)}{P(E|H_1)P(H_1) + P(E|H_2)P(H_2)} \quad (1)$$

where $P(H_1)$ and $P(H_2)$ were prior probabilities of assignment while $P(E|H_1)$ and $P(E|H_2)$ were conditional, binomial probabilities.

For substrate affinity $P(H_1) = P(H_2) = 0.5$ and if $P(H_1|E) > \frac{2}{3}$ then the taxon was considered of carbonate affinity while if $P(H_1|E) < \frac{1}{3}$ then the taxon was considered to have a clastic affinity. Otherwise, the taxon was considered to have no or mixed affinity. In the case of habitat affinity, the posterior probability for each habitat (inshore, offshore, none) was calculated with $P(H_1) = \frac{1}{3}$ and $P(H_2) = \frac{2}{3}$ and the preference with maximum of the three posterior probabilities was the assignment.

Preliminary parametric model fitting with both exponential and Weibull hazard functions and either or both trait indicated that the best fit model based on comparison of AICc scores [1, 19, 41] was the model with substrate affinity as the sole predictor and a Weibull hazard function. This model is illustrated below (Fig. 1a). While this model is the preliminarily best model of survivorship, the model with both substrate affinity and habitat preference as additive effects and a Weibull hazard function is almost as good a model of survival ($\Delta\text{AICc} \approx 0.9$). Additionally, as illustrated by the difference between the nonparametric Kaplan-Meier survival curves and the predictions of the parametric model of survival (Fig. 1a) and there is room for improvement in model specification.

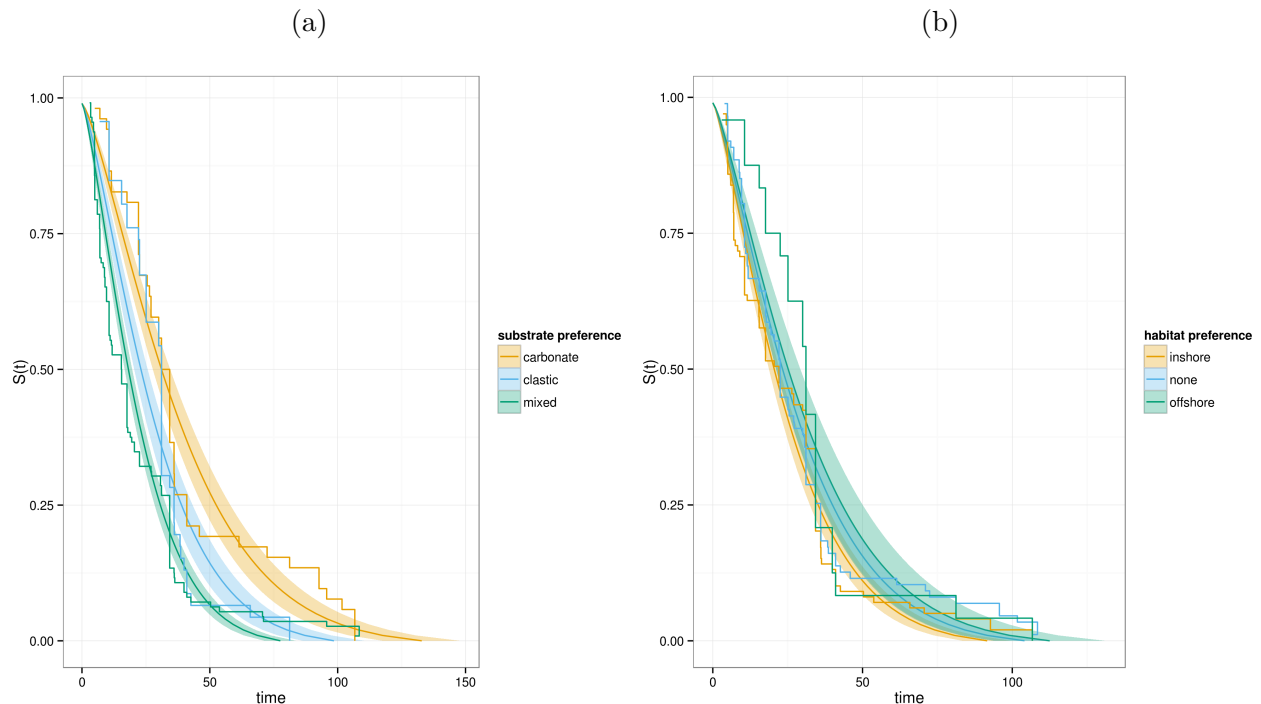


Figure 1: Survivorship curves of Australasian Permian brachiopod genera based on substrate affinity (a) and habitat preference (b). The three stepwise functions are nonparametric Kaplan-Meier survival curves for each of the three substrate affinities. The three smooth lines are the predicted survivorship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

The AICc best survival modeling has substrate affinity as the sole predictor and the response modeled as a Weibull distribution. Importantly, the shape parameter (k) of the Weibull distribution is estimated to be approximately 1.3. Values of k that are greater than 1 means that failure (extinction) rate increases with time, which may mean that an age-independent extinction rate is inappropriate when modeling generic level diversification in brachiopods.

For brachiopods split but substrate affinity (Fig. 1a), survival probability of low duration

(time) values are higher in both carbonate and clastic lowest in taxa with mixed durations. In comparison, the survival probabilities of high duration (time) values is highest in carbonates and very low in both clastic and mixed duration taxa. There is a noticeable deviance between the estimated survival function and the nonparametric curve for taxa with clastic affinities at both the short durations and long durations, underestimating and overestimating respectively. Otherwise, the estimated survival functions are fairly good fits for the data.

For brachiopods split by environmental affinity and survival modeled as a Weibull distribution is not as good a model of survival, with an approximate ΔAICc of 16.8 between this model and the previous model. There is a great degree of deviance between the nonparametric Kaplan-Meier curves and the model predictions. Additionally, this model is not significantly different from the model with only an intercept ($\chi^2 = 1.99$, $df = 2$, $p = 0.37$). This means, preliminarily, that habitat preference alone makes no difference in generic level extinction rate.

Further refinements to these models include modeling survival using other distributions of survival such as a log-normal distribution. Additionally the inclusion of affixing strategy as a predictor will increase the understanding of the biology underlying brachiopod generic survival based on organismal traits.

Ecology, survivorship, and fitness in Cenozoic mammals

Questions: How do ecological traits related to range size affect mammalian taxon duration? Is any single trait the best predictor of mammalian survivorship, or do multiple traits together best model taxon duration? Is climate an important factor in modeling mammalian taxon duration?

Background and Predictions: As discussed above, dietary and locomotor categories are candidate constituent traits of range size. Additionally, body size is a classically cited constituent trait of range size [26, 27, 97, 98]. An organism of a certain body size has an associated energetic cost in order to maintain homeostasis, which in turn necessitates enough of the appropriate supply of prey items. Because of this, it is expected that larger organisms have higher energetic costs and thus a greater range size in order to obtain necessary resources [18, 26, 26, 65].

Mammalian herbivores and carnivores have been found to have a greater diversification rate than omnivores [77]. This analysis was global in scope, and based purely on extant taxa in a comparative phylogenetic context. Diversification rate can increase via either an increase in origination relative to extinction or a decrease in extinction relative to origination. Which of these two processes is occurring is (currently) impossible to determine from a phylogeny of only extant organisms [78] which means that analysis of the fossil record is necessary to estimate which scenario is most likely to have occurred.

Depending on the continent, body size has been demonstrated to be related to extinction rate or not [63, 101]. By expanding to include a third continent, South America, I hope to elucidate how differences in taxonomic diversity at a continental level might affect body size mediated extinction rate. Additionally, I will be modeling body size as a continuous instead of binary variable.

Proposed research: To analyze differential mammalian survival, I propose a survival analysis approach similar to that described above. Dietary category, locomotor category, and body size will be modeled as time-independent covariates of survival because these traits are constant at the species level, especially the first two traits. The climate proxy δO^{18} oxygen curve [109] will be modeled as an ancillary time-dependent covariate. Also, constant versus time varying extinction rate will be estimated using different fundamental hazard models by comparing the fit of survival to various probability distributions.

While many previous analyses of survivorship are done using generic data [39, 63, 101], there are potential biases in accurately modeling specific level processes using generic level data [82, 84, 89, 93, 103]. There are important concerns regarding anagenesis, hierarchical selection, and taxa that did not go extinct in the time frame of interest [82, 84, 93, 103]. Interestingly, the effect of incomplete sampling on estimation of survivorship curves appears rather minimal and uniform [89]. The problems involving taxa that did not go extinct have mostly been dealt with following advances in modeling right-censored and interval data [59].

In order to assess potential specific versus generic effects, I will estimate the difference between specific and generic mammalian survivorship models. Using an approach based on previous work to estimate specific origination and extinction rates from generic level survival curves [31], or a variant thereof, I will measure the deviance between extinction rate estimated from the specific survivorship and the specific level extinction rates estimated from the analysis of the generic survivorship data.

In addition to the above studies of mammalian survivorship, I also propose a simulation study to analyze the effects of varying sampling probability and anagenesis on estimation of models of survivorship using *paleotree* [10]. Phylogenies are frequently simulated as a time-homogeneous birth-death process, with a constant origination and extinction rate. The expected hazard function of survival is exponentially distributed with a time-constant rate parameter (λ). Sampling has been found to have minimal effect on inference of the survival function assuming biases are evenly distributed amongst taxa [89], the effect of (cryptic) anagenesis is unknown.

Taxonomic occurrence and FAD/LAD data will be collected through a combination of the Paleobiology Database (PBDB; <http://fossilworks.org>), Neogene Old World Database (NOW; <http://www.helsinki.fi/science/now/>), and museum collections. North American fossil mammal data is very well represented and vetted in the PBDB because of the extensive work of Alroy [4–6]. European fossil mammal data is also well represented between the PBDB and NOW. South American fossil mammal data is available through the PBDB, but is not particularly well vetted and has poor overall coverage. Because of this, South American

fossil mammal data will be gathered via various museums such as the Field Museum of Natural History and the American Museum of Natural History as well as 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.

Dynamics of community connectedness in Cenozoic mammals

Questions: How does the relationship between endemic and cosmopolitan taxa in average community composition change over time? Is there a single global pattern, or do different continents have different patterns? Do patterns differ between ecological categories? Is global climate change an important predictor of these patterns?

Background and Predictions: Community connectedness is the degree to which localities are composed of endemic versus cosmopolitan taxa, and how similar this ratio is between all localities. How community composition changes over time and in relation to organismal traits as well as a changing environment is extremely important for understanding how trophic structure changes or is maintained. Additionally, understanding how unique different communities are is extremely important for understanding the interplay between local, regional, and global level environmental changes and which one can be considered most important.

In mammals, two important ecological traits in determining range size and distribution of taxa are dietary category and locomotor category [53, 64, 65]. Dietary categories are broad trophic categories that subsume more specific classifications. The categories used here are carnivore, herbivore, omnivore, and insectivore. It should be noted that most prior analyses have not included insectivore as a category [53, 77]. Similarly, locomotor categories are combinations of more specific classifications and are here represented as arboreal, ground dwelling, and scansorial/mixed. Both of these traits are constant at the specific level and thus there is no concerns about probability of assignment (see below).

Different dietary categories act as a limit on abundance because of the available environmental energy or resources in a location [18, 26, 51, 92, 104]. Abundance is correlated with occupancy, or the number of unique localities at which a taxon is found [17, 34, 52]. It follows then that limits imposed by environmental energy on abundance would then affect the (possible) range size of a taxon. Locomotor category describes the motility of a taxon and the plausibility of occurrence. Locomotor category also limits the dispersal ability of a taxon. 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 tree cover. Dispersal ability is considered important in determining the extent of a taxon's geographic range [13, 35, 46]

and thus any trait that would limit the ability for an organism to disperse would most likely limit the range size of that organism.

During the Cenozoic there was a global shift from predominately closed, forested habitat to more open, savanna-like habitat. It is expected that there was an increase in relative endemism of arboreal taxa over time and a decrease in relative endemism of terrestrial taxa. The timing of this environmental shift was different between continents [99, 100], so the patterns of community connectedness may not be globally uniform and could reflect regional differences. Shifts in distribution of taxa by locomotor category may not necessarily be accompanied by shifts in distribution related to dietary category, though previous studies are limited and qualitative [50].

A global trend during the Cenozoic was the shift from a “hot house” environment with no polar ice caps to an “ice house” environment with polar ice caps [108, 109]. This transition was known to have caused major shifts in the global climatic envelopes and the reorganization of communities along with it [6, 15, 29, 34, 50]. For mammalian community connectedness there are two possible scenarios. First, it could be possible that while the environment was shifting, lineages may have adapted in place and overall trophic structure and biogeographic structure remained rather constant through time [53]. Alternatively, species may have shifted ranges and thus changed the set of possible interacting taxa which would be associated with changes in trophic structure as well as community connectedness.

The majority of previous research on mammalian faunal dynamics has focused on the North American fossil record and the effects of climate change on diversity and distribution [4–6, 9, 11, 15, 29, 36, 37, 95, 96]. The long term effects of climate change on North American mammalian diversity dynamics and community connectedness remains unresolved and controversial [6, 11, 15, 29]. The basic predictions are that over the Cenozoic there would have been a relative increase in endemism in arboreal taxa versus a relative decrease in endemism in ground dwelling taxa. Because of the vast amount of prior work on North American mammalian faunal dynamics, this forms the basis for the global predictions made above and the North American record becomes the baseline for comparison with other regions.

The European mammalian fossil record is similarly well studied to North America though research has focused primarily on faunal dynamics in the Neogene [52, 53, 63, 79–81]. One of the major findings is that there was very little shift in relative dietary category abundance [53] while the patterns within herbivores (browse–graze transition) were mostly driven by abundant, cosmopolitan taxa [52]. Because of this, the major predictions for the European record is that occupancy will increase for herbivorous taxa, while increasing or remaining constant in carnivores, and remaining relatively constant or random for omnivores. These different predictions for each of the dietary categories is based on the differences in resilience and relationship with primary productivity, with herbivores being more resilient than carnivores and omnivores being random in their resilience [53].

The biogeographic patterns of Cenozoic South American mammalian fauna are comparatively less studied than that of North American and Europe. Instead, cross–continental dynamics

during the Neogene between North and South America are much more studied [69]. The South American mammalian faunal record reflects two distinct biotic provinces between the North and the South [30, 66, 67, 74]. Because of this, the South American record is expected to have a different pattern of community connectedness than either North America or Europe. Also, there is an expected increase in land-dwelling herbivores relative to arboreal related to the aridification of high-latitude South America.

Proposed research: Using methods first proposed by Sidor et al. [91] and Vilhena et al. [105], I propose to construct bipartite biogeographic networks between taxa and localities. Here taxa are defined as species and localities are defined as 2x2 grid cells of an equal-area map projection. Networks will be made for every 2 million year bin of the Cenozoic. This bin width is chosen to have minimum two localities be present in every bin. Additionally, networks will be constructed for each dietary and locomotor category. Previous studies of mammalian occurrence patterns have restricted analysis to major orders, such as Primates and Artiodactyls, in order to account for apparent sampling and taxonomic biases. Here, analysis will be done using all available taxa and with a restricted sample of just major orders in order to observe any differences in community connectedness.

Community connectedness will be measured using four summary statistics [91]: average relative number of endemics, average relative occupancy, biogeographic connectedness, and code length. The average relative number of endemics is defined as $E = \frac{\sum_{i=1}^L \frac{u_i}{n_i}}{L}$ 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. This is a measure of how unique localities are. Average relative occupancy is the number of localities a taxon is, on average, found at. It is defined as $Occ = \frac{\sum_{i=1}^N \frac{l_i}{L}}{N}$ where N is as the number of taxa present in the biogeographic network and l is the number of localities a taxon occurred in. Biogeographic connectedness is a measurement of the shared taxa between localities and is defined as $BC = \frac{O-N}{LN-N}$ 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 all that taxa shared between all localities. Importantly, BC is infinite when there is only one locality.

Code length is a measurement of the compressibility and information flow of a graph and is estimated via the map equation [86, 87]. The logic of the map equation is that a good map compresses reality into a few simple symbols. This means we want to compress each section of a graph into individual single symbol. A network with a low code length can be compressed into more distinct subunits/provinces compared to a network than a large code length. In the case of measuring community connectedness, a low code length means greater provinciality than a high code length [91].

Phylogenetic similarity between localities may play an important role in community structuring [107] such as closely related taxa being “repulsed” due to similarity in niche or “clumped” because of inability to disperse. Average phylogenetic similarity will be estimated between all localities during a time bin. As a preliminary approach, for every pairwise combination of localities an informal phylogeny will be constructed for the pool of all taxa present in both

localities. This informal phylogeny will be based solely on available taxonomic information such as order, family, and genus assignments. The average patristic distance between all taxa will then be estimated. The average of all pairwise comparisons per bin can then be used in partial correlations and modeling questions for understanding what best explain patterns of community connectedness.

The next step is to compare patterns of community connectedness both within and between regions in order to understand if there is a single global trend or if regional processes dominate as well as comparisons of the different dietary and locomotor categories for similarity within and between traits and regions. The approach and methodology to accomplish this analysis is currently under development.

The data necessary to complete the empirical aspects of this study will be the same as for the above analysis of mammalian survival.

Preliminary results Preliminary results of the community connectedness patterns of both North America and Europe based on PBDB data are presented here (Fig. 2). Both regions have qualitatively very different patterns of community connectedness, primarily in the early Cenozoic. However, almost all four of the network statistics are extremely volatile over the Cenozoic, especially for the European record. However, there some interesting qualitative patterns as illustrated by the generalized additive model smooths.

While average relative occupancy remains relatively stationary for North America, there is a qualitative decrease in average relative occupancy in Europe until approximately the start of the Neogene (approximately 23 My). Average relative occupancy is a measure of how cosmopolitan any individual taxon is and the qualitative decrease in average relative occupancy in Europe over the entire Cenozoic indicates that the average taxon is becoming generally less cosmopolitan over time. In contrast, average relative occupancy in North America is qualitatively stationary over the entire Cenozoic and almost always lower than that observed for the European record. This means that, on average, North American taxa are present in very few localities at any given point in time.

Biogeographic connectedness is a measure of shared taxa between all localities, and higher values mean that more shared taxa then when there are lower values. Biogeographic connectedness of North American mammalian communities qualitatively decreases over the early Cenozoic until approximately the start of the Neogene. In Europe there is a qualitative rise in biogeographic connectedness in the first few million years of the Cenozoic, but afterwards remains relatively stationary. This may indicate that the average proportion of shared taxa remained qualitatively stationary. In comparison, North American 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 average relative number of endemic taxa. North America, in contrast, has a qualitatively constant average relative number of endemics over the Cenozoic with a slight decrease in the Neogene. As discussed above, average

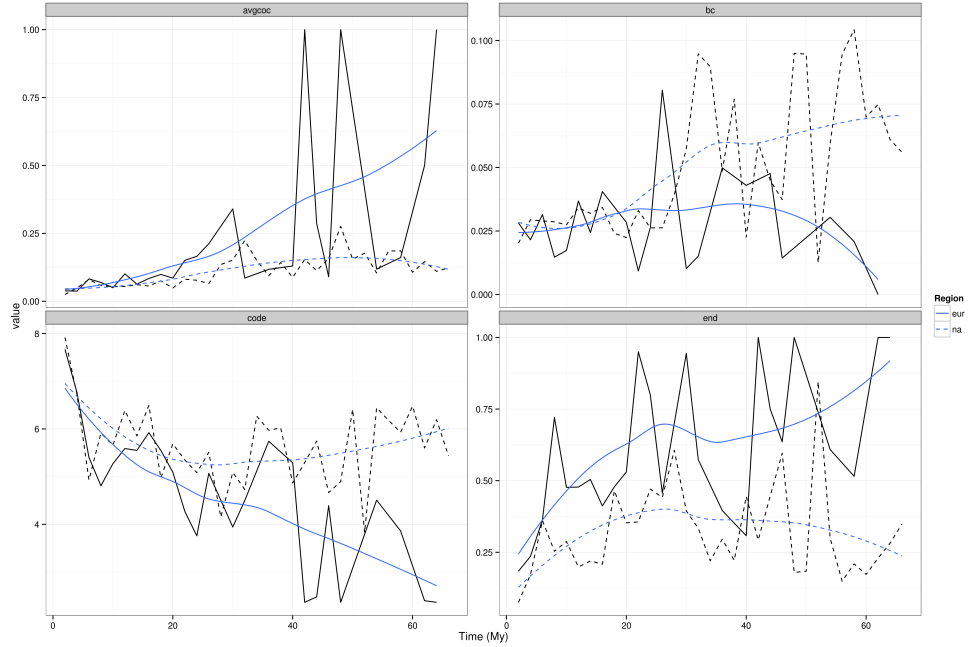


Figure 2: Biogeographic network summary statistics for mammalian communities in North America (dashed line) and Europe (solid line). The summary statistics are, clockwise from top left: average relative occupancy (avgcoc), biogeographic connectedness (bc), average relative number of endemics (end), code length (code). Blue lines are generalized additive model smooths and are presented to illustrate the over all pattern of the two regions.

relative number of endemics is a measure of relative uniqueness of localities. Qualitatively, North America retained approximately the same amount of site uniqueness through out the Cenozoic. In comparison, the pattern of the European record shows a qualitatively nonmonotonic decrease in locality uniqueness because of the decrease in average relative number of endemics.

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. Code length acts as a measure of general provinciality, with a high code length indicating little provincially between localities. Initial interpretation of these results indicates that North America maintains a stationary degree of provinciality while Europe has a qualitatively decreasing degree of provinciality.

Summary of proposed research

One of the most important questions in (paleo)biology is why do certain species go extinct while others do not? Elucidating what interactions, or traits governing interactions, are

important when estimating survival is then extremely important and a fundamental concern of evolutionary paleoecology. While the species level property of range size is continually found to be an extremely vital for both origination and extinction [33, 39, 43, 48, 88], which of the candidate constituent lower level traits are necessary to “form” range size remains more nebulous and is frequently framed as which traits in addition to range size [33, 38, 71]. If the favored models of survival include the additive or interactive effects of multiple organismal traits this is possibly the signature of emergence, particularly in the case of interaction. Related to this is the general question of how climate change impacts diversity dynamics [6, 11, 29, 72]. Here I analyze different adaptive zones of two biologically different clades in order to understand patterns of survival and expectations of whether global, regional, or local process should dominate. By comparing the patterns of survival in brachiopods and mammals it should be possible to determine when different variables matter to survival and when they do not and potentially how they matter.

Timeline

430 Spring/Summer 2014

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

Fall 2014/Winter 2015

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

436 Spring/Summer 2015

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

Fall 2015/Winter 2016

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

444 Spring/Summer 2016

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

Fall 2016/Winter 2017

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

450 Spring/Summer 2017

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

References

- [1] H. Akaike. A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, 19(6):716–723, 1974.
- [2] R. R. Alexander. Generic longevity of articulate brachiopods in relation to the mode of stabilization on the substrate. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 21: 209–226, 1977.
- [3] W. D. Allmon. Taxic evolutionary paleoecology and the ecological context of macroevolutionary change. *Evolutionary Ecology*, 8(2):95–112, Mar. 1994. ISSN 0269-7653. doi: 10.1007/BF01238244.
- [4] J. Alroy. Constant extinction, constrained diversification, and uncoordinated stasis in North American mammals. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 127: 285–311, 1996.
- [5] J. Alroy. Cope’s rule and the dynamics of body mass evolution in North American fossil mammals. *Science*, 280:731–734, 1998. doi: 10.1126/science.280.5364.731.
- [6] J. Alroy, P. L. Koch, and J. C. Zachos. Global climate change and North American mammalian evolution. *Paleobiology*, 26(1981):259–288, 2000.
- [7] B. M. Anderson, D. Pisani, A. I. Miller, and K. J. Peterson. The environmental affinities of marine higher taxa and possible biases in their first appearances in the fossil record. *Geology*, 39(10):971–974, Sept. 2011. ISSN 0091-7613. doi: 10.1130/G32413.1. URL <http://geology.gsapubs.org/cgi/doi/10.1130/G32413.1>.
- [8] N. W. Archbold and G. R. Shi. Permian brachiopod faunas of Western Australia: Gondwanan-Asian relationships and Permian climate. *Journal of Southeast Asian Earth Sciences*, 11(3):207–215, 1995.
- [9] C. Badgley and J. A. Finarelli. Diversity dynamics of mammals in relation to tectonic and climatic history: comparison of three Neogene records from North America. *Paleobiology*, 39(3):373–399, Apr. 2013. ISSN 0094-8373. doi: 10.1666/12024.
- [10] D. W. Bapst. paleotree: an R package for paleontological and phylogenetic analyses of evolution. *Methods in Ecology and Evolution*, 3:803–807, 2012. doi: 10.1111/j.2041-210X.2012.00223.x. URL [http://doi.wiley.com/10.1111/j.2041-210X.2012.00223.x](http://doi.wiley.com/10.1111/j.2041-210X.2012.00223.xpapers2://publication/doi/10.1111/j.2041-210X.2012.00223.x).
- [11] A. D. Barnosky. Distinguishing the effects of the Red Queen Court Jester on Micene Mammal Evolution in the Northern Rocky Mountains. *Journal of Vertebrate Paleontology*, 21(1):172–185, 2001.
- [12] T. K. Baumiller. Survivorship analysis of Paleozoic Crinoidea: effect of filter morphology on evolutionary rates. *Paleobiology*, 19(3):304–321, 1993.

- [13] A. Birand, A. Vose, and S. Gavrillets. Patterns of species ranges, speciation, and extinction. *The American naturalist*, 179(1):1–21, Jan. 2012. ISSN 1537-5323. doi: 10.1086/663202. URL <http://www.ncbi.nlm.nih.gov/pubmed/22173457>.
- [14] L. P. Birgenheier, T. D. Frank, C. R. Fielding, and M. C. Rygel. Coupled carbon isotopic and sedimentological records from the Permian system of eastern Australia reveal the response of atmospheric carbon dioxide to glacial growth and decay during the late Palaeozoic Ice Age. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 286(3-4): 178–193, 2010. URL <http://dx.doi.org/10.1016/j.palaeo.2010.01.008papers2://publication/doi/10.1016/j.palaeo.2010.01.008>.
- [15] J. L. Blois and E. A. Hadly. Mammalian Response to Cenozoic Climatic Change. *Annual Review of Earth and Planetary Sciences*, 37(1):181–208, May 2009. ISSN 0084-6597. doi: 10.1146/annurev.earth.031208.100055.
- [16] D. J. Bottjer and D. Jablonski. Paleoenvironmental patterns in the evolution of Post-Paleozoic benthic marine invertebrates. *Palaios*, 3(6):540–560, 1988.
- [17] J. H. Brown. On the Relationship between Abundance and Distribution of Species. *The American Naturalist*, 124(2):255, Aug. 1984. ISSN 0003-0147. doi: 10.1086/284267. URL <http://www.journals.uchicago.edu/doi/abs/10.1086/284267>.
- [18] J. H. Brown and B. A. Maurer. Evolution of species assemblages: effects of energetic constraints and species dynamics on the diversification of the North American aidauna. *The American Naturalist*, 130(1):1–17, 1987.
- [19] K. P. Burnham and D. R. Anderson. *Model selection and multi-model inference: a practical information-theoretic approach*. Springer, New York, 2nd edition, 2002.
- [20] M. E. Clapham and D. J. Bottjer. Permian marine paleoecology and its implications for large-scale decoupling of brachiopod and bivalve abundance and diversity during the Lopingian (Late Permian). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 249 (3-4):283–301, June 2007. ISSN 00310182. doi: 10.1016/j.palaeo.2007.02.003. URL <http://linkinghub.elsevier.com/retrieve/pii/S0031018207000600>.
- [21] M. E. Clapham and D. J. Bottjer. Prolonged Permian Triassic ecological crisis recorded by molluscan dominance in Late Permian offshore assemblages. *Proceedings of the National Academy of Sciences of the United States of America*, 104(32):12971–5, Aug. 2007. ISSN 0027-8424. doi: 10.1073/pnas.0705280104. URL <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=1941817&tool=pmcentrez&rendertype=abstract>.
- [22] M. E. Clapham and N. P. James. Paleocology Of Early-Middle Permian Marine Communities In Eastern Australia: Response To Global Climate Change In the Aftermath Of the Late Paleozoic Ice Age. *Palaios*, 23(11):738–750, Nov. 2008. ISSN 0883-1351. doi: 10.2110/palo.2008.p08-022r. URL <http://palaaios.sepmonline.org/cgi/doi/10.2110/palo.2008.p08-022r>.

- [23] M. E. Clapham and N. P. James. Regional-scale marine faunal change in Eastern Australia during Permian climate fluctuations and its relationship to local community restructuring. *Palaios*, 27:627–635, Oct. 2012. ISSN 0883-1351. doi: 10.2110/palo.2012.p12-003r. URL <http://palaios.sepmonline.org/cgi/doi/10.2110/palo.2012.p12-003r>.
- [24] M. E. Clapham, D. J. Bottjer, C. M. Powers, N. Bonuso, M. L. Fraiser, P. J. Marengo, S. Q. Dornbos, and S. B. Pruss. Assessing the Ecological Dominance of Phanerozoic Marine Invertebrates. *Palaios*, 21(5):431–441, Oct. 2006. ISSN 0883-1351. doi: 10.2110/palo.2005.P05-017R. URL <http://palaios.sepmonline.org/cgi/doi/10.2110/palo.2005.P05-017R>.
- [25] W. S. Cooper. Expected time to extinction and the concept of fundamental fitness. *Journal of Theoretical Biology*, 107:603–629, 1984.
- [26] J. Damuth. Home range, home range overlap, and species energy use among herbivorous mammals. *Biological Journal of the Linnean Society*, 15:185–193, 1979.
- [27] J. Damuth. Population density and body size in mammals. *Nature*, 290:699–700, 1981. URL <http://www.jstor.org/stable/10.2307/2461771><http://www.nature.com/nature/journal/v290/n5808/abs/290699a0.html>.
- [28] C. R. Fielding, K. L. Bann, J. A. Maceachern, S. C. Tye, and B. G. Jones. Cyclic-ity in the nearshore marine to coastal, Lower Permian, Pebbly Beach Formation, southern Sydney Basin, Australia: a record of relative sea-level fluctuations at the close of the Late Palaeozoic Gondwanan ice age. *Sedimentology*, 53(2):435–463, 2006. URL <http://doi.wiley.com/10.1111/j.1365-3091.2006.00770.x>
[/publication/doi/10.1111/j.1365-3091.2006.00770.x](http://publication/doi/10.1111/j.1365-3091.2006.00770.x).
- [29] B. Figueirido, C. M. Janis, J. A. Pérez-Claros, M. De Renzi, and P. Palmqvist. Cenozoic climate change influences mammalian evolutionary dynamics. *Proceedings of the National Academy of Sciences*, 109(3):722–727, Jan. 2012. ISSN 1091-6490. doi: 10.1073/pnas.1110246108.
- [30] J. J. Flynn and A. R. Wyss. Recent advances in South American mammalian paleontology. *Trends in ecology & evolution*, 13(11):449–54, Nov. 1998. ISSN 0169-5347. URL <http://www.ncbi.nlm.nih.gov/pubmed/21238387>.
- [31] M. Foote. Survivorship analysis of Cambrian and Ordovician Trilobites. *Paleobiology*, 14(3):258–271, 1988.
- [32] M. Foote. Substrate affinity and diversity dynamics of Paleozoic marine animals. *Paleobiology*, 32(3):345–366, Sept. 2006. ISSN 0094-8373. doi: 10.1666/05062.1. URL <http://www.bioone.org/doi/abs/10.1666/05062.1>.
- [33] M. Foote and A. I. Miller. Determinants of early survival in marine animal genera.

Paleobiology, 39(2):171–192, Mar. 2013. ISSN 0094-8373. doi: 10.1666/12028. URL <http://www.bioone.org/doi/abs/10.1666/12028>.

- [34] M. Fortelius, J. Eronen, J. Jernvall, L. Liu, D. Pushkina, J. Rinne, A. Tesakov, I. Vislobokova, Z. Zhang, and L. Zhou. Fossil mammals resolve regional patterns of Eurasian climate change over 20 million years. *Evolutionary Ecology Research*, 4: 1005–1016, 2002.
- [35] K. J. Gaston. Geographic range limits: achieving synthesis. *Proceedings. Biological sciences / The Royal Society*, 276(1661):1395–406, Apr. 2009. ISSN 0962-8452. doi: 10.1098/rspb.2008.1480. URL <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=2677218&tool=pmcentrez&rendertype=abstract>.
- [36] G. Gunnell, M. Morgan, M. C. Mass, and P. D. Gingerich. Comparative paleoecology of Paleogene and Neogene mammalian faunas: trophic structure and composition. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 115:265–286, 1995. URL <http://www.sciencedirect.com/science/article/pii/0031018294001150>.
- [37] E. A. Hadly and B. A. Maurer. Spatial and temporal patterns of species diversity in montane mammal communities of western North America. *Evolutionary Ecology Research*, 3:477–486, 2001.
- [38] P. G. Harnik. Direct and indirect effects of biological factors on extinction risk in fossil bivalves. *Proceedings of the National Academy of Sciences of the United States of America*, 108(33):13594–9, Aug. 2011. ISSN 1091-6490. doi: 10.1073/pnas.1100572108. URL <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3158225&tool=pmcentrez&rendertype=abstract>.
- [39] P. G. Harnik, C. Simpson, and J. L. Payne. Long-term differences in extinction risk among the seven forms of rarity. *Proceedings of the Royal Society B: Biological Sciences*, (October), Oct. 2013. ISSN 0962-8452. doi: 10.1098/rspb.2012.1902. URL <http://rspb.royalsocietypublishing.org/cgi/doi/10.1098/rspb.2012.1902>.
- [40] N. A. Heim and S. E. Peters. Regional environmental breadth predicts geographic range and longevity in fossil marine genera. *PloS one*, 6(5):e18946, Jan. 2011. ISSN 1932-6203. doi: 10.1371/journal.pone.0018946. URL <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3087726&tool=pmcentrez&rendertype=abstract>.
- [41] C. M. Hurvich and C.-L. Tsai. Regression and time series model selection in small samples. *Biometrika*, 76(2):297–307, 1989. URL <http://biomet.oxfordjournals.org/content/76/2/297.shortpapers2://publication/uuid/FC795396-A722-468D-AF8E-4E1F7C97998C>.
- [42] D. Jablonski. Background and mass extinctions: the alternation of macroevolutionary regimes. *Science*, 231(4734):129–133, 1986.
- [43] D. Jablonski. Heritability at the species level: analysis of geographic ranges of cretaceous

mollusks. *Science*, 238(4825):360–363, Oct. 1987. ISSN 0036-8075. doi: 10.1126/science.238.4825.360. URL <http://www.ncbi.nlm.nih.gov/pubmed/17837117>.

[44] D. Jablonski. Species Selection: Theory and Data. *Annual Review of Ecology, Evolution, and Systematics*, 39(1):501–524, Dec. 2008. ISSN 1543-592X. doi: 10.1146/annurev.ecolsys.39.110707.173510. URL <http://www.annualreviews.org/doi/abs/10.1146/annurev.ecolsys.39.110707.173510>.

[45] D. Jablonski and D. J. Bottjer. Environmental patterns in the origins of higher taxa: the post-paleozoic fossil record. *Science (New York, N.Y.)*, 252(5014):1831–3, June 1991. ISSN 0036-8075. doi: 10.1126/science.252.5014.1831. URL <http://www.ncbi.nlm.nih.gov/pubmed/17753259>.

[46] D. Jablonski and G. Hunt. Larval ecology, geographic range, and species survivorship in Cretaceous mollusks: organismic versus species-level explanations. *The American naturalist*, 168(4):556–64, Oct. 2006. ISSN 1537-5323. doi: 10.1086/507994. URL <http://www.ncbi.nlm.nih.gov/pubmed/17004227>.

[47] D. Jablonski and R. a. Lutz. Larval Ecology of Marine Benthic Invertebrates: Paleobiological Implications. *Biological Reviews*, 58(1):21–89, Feb. 1983. ISSN 1464-7931. doi: 10.1111/j.1469-185X.1983.tb00380.x. URL <http://doi.wiley.com/10.1111/j.1469-185X.1983.tb00380.x>.

[48] D. Jablonski and K. Roy. Geographical range and speciation in fossil and living molluscs. *Proceedings. Biological sciences / The Royal Society*, 270(1513):401–6, Feb. 2003. ISSN 0962-8452. doi: 10.1098/rspb.2002.2243. URL <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=1691247&tool=pmcentrez&rendertype=abstract>.

[49] D. Jablonski, J. J. Sepkoski, D. J. Bottjer, and P. M. Sheehan. Onshore-offshore patterns in the evolution of Phanerozoic shelf communities. *Science*, 222(4628):1123–1125, 1983.

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

[51] C. M. Janis, J. Damuth, and J. M. Theodor. Miocene ungulates and terrestrial primary productivity: where have all the browsers gone? *Proceedings of the National Academy of Sciences*, 97(14):7899–904, July 2000. ISSN 0027-8424. URL <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=16642&tool=pmcentrez&rendertype=abstract>.

[52] J. Jernvall and M. Fortelius. Common mammals drive the evolutionary increase of hypsodonty in the Neogene. *Nature*, 417(6888):538–40, May 2002. ISSN 0028-0836. doi: 10.1038/417538a.

[53] J. Jernvall and M. Fortelius. Maintenance of trophic structure in fossil mammal communities: site occupancy and taxon resilience. *American Naturalist*, 164(5):614–624, Nov. 2004. ISSN 1537-5323. doi: 10.1086/424967.

- [54] A. T. Jones, T. D. Frank, and C. R. Fielding. Cold climate in the eastern Australian mid to late Permian may reflect cold upwelling waters. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 237(2-4):370–377, 2006. URL <http://linkinghub.elsevier.com/retrieve/pii/S0031018205007327papers2://publication/doi/10.1016/j.palaeo.2005.12.009>.
- [55] W. Kiessling and M. Aberhan. Environmental determinants of marine benthic biodiversity dynamics through Triassic–Jurassic time. *Paleobiology*, 33(3):414–434, 2007.
- [56] W. Kiessling, M. Aberhan, B. Brenneis, and P. J. Wagner. Extinction trajectories of benthic organisms across the Triassic–Jurassic boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 244(1-4):201–222, Feb. 2007. ISSN 00310182. doi: 10.1016/j.palaeo.2006.06.029. URL <http://linkinghub.elsevier.com/retrieve/pii/S0031018206004494>.
- [57] J. Kitchell. Biological selectivity of extinction. In E. G. Kaufman and O. H. Walliser, editors, *Extinction Events in Earth History*, pages 31–43. Springer-Verlag, Berlin, 1990. URL <http://link.springer.com/chapter/10.1007/BFb0011132>.
- [58] J. A. Kitchell. Evolutionary paleoecology: recent contributions to evolutionary theory. *Paleobiology*, 11(1):91–104, 1985.
- [59] D. G. Kleinbaum and M. Klein. *Survival analysis: a self-learning text*. Springer, New York, NY, 2 edition, 2005.
- [60] M. LaBarbera. Brachiopod orientation to water movement: functional morphology. *Lethaia*, 11(1):67–79, Jan. 1978. ISSN 0024-1164. doi: 10.1111/j.1502-3931.1978.tb01219.x. URL <http://doi.wiley.com/10.1111/j.1502-3931.1978.tb01219.x>.
- [61] M. LaBarbera. Water flow patterns in and around three species of articulate brachiopods. *Journal of Experimental Marine Biology and Ecology*, 55:185–206, 1981.
- [62] L. H. Liow. Does versatility as measured by geographic range, bathymetric range and morphological variability contribute to taxon longevity? *Global Ecology and Biogeography*, 16(1):117–128, 2007. URL <http://doi.wiley.com/10.1111/j.1466-8238.2006.00269.xpapers2://publication/doi/10.1111/j.1466-8238.2006.00269.x>.
- [63] L. H. Liow, M. Fortelius, E. Bingham, K. Lintulaakso, H. Mannila, L. Flynn, and N. C. Stenseth. Higher origination and extinction rates in larger mammals. *Proceedings of the National Academy of Sciences*, 105(16):6097, 2008. URL <papers2://publication/uuid/5A93DDA3-204F-4D9C-AFAC-A15722A18C61>.
- [64] S. K. Lyons. A quantitative model for assessing community dynamics of pleistocene mammals. *The American naturalist*, 165(6):E168–85, June 2005. ISSN 1537-5323. doi: 10.1086/429699. URL <http://www.ncbi.nlm.nih.gov/pubmed/15937741>.
- [65] S. K. Lyons, P. J. Wagner, and K. Dzikiewicz. Ecological correlates of range shifts of Late Pleistocene mammals. *Philosophical transactions of the Royal Society of London*.

Series B, Biological sciences, 365(1558):3681–93, Nov. 2010. ISSN 1471-2970. doi: 10.1098/rstb.2010.0263. URL <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=2981999&tool=pmcentrez&rendertype=abstract>.

[66] B. J. Macfadden. Origin and evolution of the grazing guild in New World terrestrial mammals. *Trends in ecology & evolution*, 12(5):182–187, 1997.

[67] B. J. Macfadden. Extinct mammalian biodiversity of the ancient New World tropics. *Trends in ecology & evolution*, 21(3):157–65, Mar. 2006. ISSN 0169-5347. doi: 10.1016/j.tree.2005.12.003. URL <http://www.ncbi.nlm.nih.gov/pubmed/16701492>.

[68] G. A. Mark and K. W. Flessa. A test for evolutionary equilibria: Phanerozoic brachiopods and Cenozoic mammals. *Paleobiology*, 3(1):17–22, 1977.

[69] L. G. Marshall, S. D. Webb, J. J. Sepkoski, and D. M. Raup. Mammalian evolution and the Great American interchange. *Science*, 215(4538):1351–1357, 1982.

[70] A. I. Miller and S. R. Connolly. Substrate affinities of higher taxa and the Ordovician Radiation. *Paleobiology*, 27(4):768–778, Dec. 2001. ISSN 0094-8373. doi: 10.1666/0094-8373(2001)027<0768:SAOHTA>2.0.CO;2. URL <http://www.bioone.org/doi/abs/10.1666/0094-8373%282001%29027%3C0768%3ASAHTA%3E2.0.CO%3B2>.

[71] S. Nürnberg and M. Aberhan. Habitat breadth and geographic range predict diversity dynamics in marine Mesozoic bivalves. *Paleobiology*, 39(3):360–372, Apr. 2013. ISSN 0094-8373. doi: 10.1666/12047. URL <http://www.bioone.org/doi/abs/10.1666/12047>.

[72] T. Olszewski and D. Erwin. Dynamic response of Permian brachiopod communities to long-term environmental change. *Nature*, 428(April):2–5, 2004. doi: 10.1038/nature02471.1. URL <http://www.nature.com/nature/journal/v428/n6984/abs/nature02464.html>.

[73] M. E. Palmer and M. W. Feldman. Survivability is more fundamental than evolvability. *PloS one*, 7(6):e38025, Jan. 2012. ISSN 1932-6203. doi: 10.1371/journal.pone.0038025. URL <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3377627&tool=pmcentrez&rendertype=abstract>.

[74] B. Patterson and R. Pascual. The fossil mammal fauna of South America. *The Quarterly review of biology*, 43(4):409–451, 1968.

[75] S. E. Peters. Environmental determinants of extinction selectivity in the fossil record. *Nature*, 454(7204):626–9, July 2008. ISSN 1476-4687. doi: 10.1038/nature07032. URL <http://www.ncbi.nlm.nih.gov/pubmed/18552839>.

[76] M. G. Powell. Latitudinal diversity gradients for brachiopod genera during late Palaeozoic time: links between climate, biogeography and evolutionary rates. *Global Ecology and Biogeography*, 16(4):519–528, July 2007. ISSN 1466-822X. doi: 10.1111/j.1466-8238.2007.00300.x. URL <http://doi.wiley.com/10.1111/j.1466-8238.2007.00300.x>.

- [77] S. A. Price, S. S. B. Hopkins, K. K. Smith, and V. L. Roth. Tempo of trophic evolution and its impact on mammalian diversification. *Proceedings of the National Academy of Sciences of the United States of America*, 109(18):7008–12, May 2012. ISSN 1091-6490. doi: 10.1073/pnas.1117133109. URL <http://www.ncbi.nlm.nih.gov/pubmed/22509033>.
- [78] D. L. Rabosky. Extinction rates should not be estimated from molecular phylogenies. *Evolution*, 64(6):1816–24, June 2010. ISSN 1558-5646. doi: 10.1111/j.1558-5646.2009.00926.x. URL <http://www.ncbi.nlm.nih.gov/pubmed/20030708>.
- [79] P. Raia, P. Piras, and T. Kotsakis. Turnover pulse or Red Queen? Evidence from the large mammal communities during the Plio-Pleistocene of Italy. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 221(3-4):293–312, June 2005. ISSN 00310182. doi: 10.1016/j.palaeo.2005.02.014. URL <http://linkinghub.elsevier.com/retrieve/pii/S0031018205001033>.
- [80] P. Raia, C. Meloro, A. Loy, and C. Barbera. Species occupancy and its course in the past: macroecological patterns in extinct communities. *Evolutionary Ecology Research*, 8:181–194, 2006.
- [81] P. Raia, F. Carotenuto, J. T. Eronen, and M. Fortelius. Longer in the tooth, shorter in the record? The evolutionary correlates of hypsodonty in Neogene ruminants. *Proceedings. Biological sciences / The Royal Society*, 278(1724):3474–81, Dec. 2011. ISSN 1471-2954. doi: 10.1098/rspb.2011.0273. URL <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3189366&tool=pmcentrez&rendertype=abstract>.
- [82] D. M. Raup. Taxonomic survivorship curves and Van Valen’s Law. *Paleobiology*, 1(1):82–96, Jan. 1975. ISSN 0036-8075. doi: 10.1126/science.49.1254.50. URL <http://www.ncbi.nlm.nih.gov/pubmed/17777225>.
- [83] D. M. Raup. Cohort Analysis of generic survivorship. *Paleobiology*, 4(1):1–15, 1978.
- [84] D. M. Raup. A kill curve for Phanerozoic marine species. *Paleobiology*, 17(1):37–48, 1991.
- [85] D. M. Raup and G. E. Boyajian. Patterns of generic extinction in the fossil record. *Paleobiology*, 14(2):109–125, 1988.
- [86] M. Rosvall and C. T. Bergstrom. Maps of random walks on complex networks reveal community structure. *Proceedings of the National Academy of Sciences*, 105(4):1118–23, Jan. 2008. ISSN 1091-6490. doi: 10.1073/pnas.0706851105. URL <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=2234100&tool=pmcentrez&rendertype=abstract>.
- [87] M. Rosvall, D. Axelsson, and C. T. Bergstrom. The map equation. *The European Physical Journal Special Topics*, 178(1):13–23, Apr. 2010. ISSN 1951-6355. doi:

10.1140/epjst/e2010-01179-1. URL <http://www.springerlink.com/index/10.1140/epjst/e2010-01179-1>.

- [88] K. Roy, G. Hunt, D. Jablonski, A. Z. Krug, and J. W. Valentine. A macroevolutionary perspective on species range limits. *Proceedings. Biological sciences / The Royal Society*, 276(1661):1485–93, Apr. 2009. ISSN 0962-8452. doi: 10.1098/rspb.2008.1232. URL <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=2677224&tool=pmcentrez&rendertype=abstract>.
- [89] J. J. Sepkoski. Stratigraphic biases in the analysis of taxonomic survivorship. *Paleobiology*, 1(4):343–355, 1975.
- [90] J. J. Sepkoski. A model of onshore-offshore change in faunal diversity. *Paleobiology*, 17(1):58–77, 1991.
- [91] C. A. Sidor, D. A. Vilhena, K. D. Angielczyk, A. K. Huttenlocker, S. J. Nesbitt, B. R. Peacock, J. S. Steyer, R. M. H. Smith, and L. A. Tsuji. Provincialization of terrestrial faunas following the end-Permian mass extinction. *Proceedings of the National Academy of Sciences*, 110(20):8129–33, May 2013. ISSN 1091-6490. doi: 10.1073/pnas.1302323110.
- [92] M. Silva, J. H. Brown, and J. a. Downing. Differences in Population Density and Energy Use between Birds and Mammals: A Macroecological Perspective. *The Journal of Animal Ecology*, 66(3):327, May 1997. ISSN 00218790. doi: 10.2307/5979. URL <http://www.jstor.org/stable/5979?origin=crossref>.
- [93] C. Simpson. *Levels of selection and large-scale morphological trends*. PhD thesis, University of Chicago, 2006.
- [94] C. Simpson and P. G. Harnik. Assessing the role of abundance in marine bivalve extinction over the post-Paleozoic. *Paleobiology*, 35(4):631–647, Dec. 2009. ISSN 0094-8373. doi: 10.1666/0094-8373-35.4.631. URL <http://www.bioone.org/doi/abs/10.1666/0094-8373-35.4.631>.
- [95] G. G. Simpson. *Tempo and Mode in Evolution*. Columbia University Press, New York, 1944.
- [96] G. G. Simpson. *The Major Features of Evolution*. Columbia University Press, New York, 1953.
- [97] F. A. Smith, J. Brown, J. Haskell, and S. Lyons. Similarity of mammalian body size across the taxonomic hierarchy and across space and *The American Naturalist*, 2004. URL <http://www.journals.uchicago.edu/doi/abs/10.1086/382898papers2://publication/uuid/D5606802-FD91-49EB-BE2F-E2D314A5E71D>.
- [98] F. A. Smith, S. K. Lyons, S. Morgan Ernest, and J. H. Brown. Macroecology: more than the division of food and space among species on continents. *Progress in Physical*

Geography, 32(2):115–138, Apr. 2008. ISSN 0309-1333. doi: 10.1177/0309133308094425.
URL <http://ppg.sagepub.com/cgi/doi/10.1177/0309133308094425>.

- [99] C. A. E. Strömberg. Decoupled taxonomic radiation and ecological expansion of open-habitat grasses in the Cenozoic of North America. *Proceedings of the National Academy of Sciences of the United States of America*, 102(34):11980–4, Aug. 2005. ISSN 0027-8424. doi: 10.1073/pnas.0505700102. URL <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=1189350&tool=pmcentrez&rendertype=abstract>.
- [100] C. A. E. Strömberg, R. E. Dunn, R. H. Madden, M. J. Kohn, and A. A. Carlini. Decoupling the spread of grasslands from the evolution of grazer-type herbivores in South America. *Nature communications*, 4:1478, Jan. 2013. ISSN 2041-1723. doi: 10.1038/ncomms2508. URL <http://www.ncbi.nlm.nih.gov/pubmed/23403579>.
- [101] S. Tomiya. Body Size and Extinction Risk in Terrestrial Mammals Above the Species Level. *The American Naturalist*, pages E000–E000, Sept. 2013. ISSN 00030147. doi: 10.1086/673489. URL <http://www.jstor.org/stable/info/10.1086/673489>.
- [102] L. Van Valen. A new evolutionary law. *Evolutionary Theory*, 1:1–30, 1973. URL <http://ci.nii.ac.jp/naid/10011264287/>.
- [103] L. Van Valen. Taxonomic survivorship curves. *Evolutionary Theory*, 4:129–142, 1979.
- [104] L. Van Valen. Three paradigms of evolution. *Evolutionary Theory*, 9:1–17, 1989.
- [105] D. A. Vilhena, E. B. Harris, C. T. Bergstrom, M. E. Maliska, P. D. Ward, C. A. Sidor, C. A. E. Strömberg, and G. P. Wilson. Bivalve network reveals latitudinal selectivity gradient at the end-Cretaceous mass extinction. *Scientific reports*, 3:1790, May 2013. ISSN 2045-2322. doi: 10.1038/srep01790.
- [106] J. B. Waterhouse. Late Palaeozoic Mollusca and correlations from the south-east Bowen Basin, east Australia. *Palaeontographica Abteilung A*, 198:129–233, 1987.
- [107] C. O. Webb, D. D. Ackerly, M. a. McPeck, and M. J. Donoghue. Phylogenies and Community Ecology. *Annual Review of Ecology and Systematics*, 33(1):475–505, Nov. 2002. ISSN 0066-4162. doi: 10.1146/annurev.ecolsys.33.010802.150448. URL <http://arjournals.annualreviews.org/doi/abs/10.1146%2Fannurev.ecolsys.33.010802.150448>.
- [108] J. C. Zachos, M. Pagani, L. Sloan, E. Thomas, and K. Billups. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science*, 292:686–693, 2001. doi: 10.1126/science.1059412. URL <http://www.sciencemag.org/content/292/5517/686.short>.
- [109] J. C. Zachos, G. R. Dickens, and R. E. Zeebe. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature*, 451(7176):279–283, Jan. 2008. ISSN 1476-4687. doi: 10.1038/nature06588.