

Evolutionary paleoecology and the biology of extinction

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Introduction and Theory

Paleobiology is the study of life over time and the processes that 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 [41]. 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 [54]. 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 [54]’s definition, Allmon [2] 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 [53].

It is under this framework that I propose to study how ecological traits associated with range size have affected both the availability of biotic interactions and differential survival. 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 [66]. 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 ecological traits associated with range size (described below) are fundamentally very different.

Theoretical framework

For the majority of geological time, extinction can be considered non-random with respect to biology [38]. These times of “background extinction” are in comparison to the alternative periods of “mass extinction.” The distinction between background and mass extinction is based on the relative intensity of extinction at a particular time versus times preceding and following. Simply put, the major indicator of a mass extinction is an event that is across higher taxonomic levels and the biotic interactors before and after the event are dramatically different [38, 40, 55, 56].

Survival can be considered the fundamental measure of fitness or evolutionary success because ultimately a successful lineage is not one that speciated greatly but one that never went extinct [22, 70]. Because during periods of background extinction extinction is non-random

with respect to biology [38], it should be possible to estimate how various ecological traits affect relative fitness [53, 54].

Species geographic range size has continually been demonstrated to play a crucial role in extinction selectivity. Species with larger geographic ranges tend to have lower extinction rates than species with smaller geographic ranges [36, 38, 45, 68, 84]. 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. Additionally, the ecological adaptations to variable environments has been shown to be important in predicting species longevity [30, 60]. Here I propose to study the individual and combined effects of organismal traits related to range size on extinction and, by extension, fitness.

Dynamics of community connectedness in Cenozoic mammals

Questions: How does the average set of possible biotic–biotic interactions in mammalian communities 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: In mammals, two important ecological traits in determining range size are dietary category, locomotor category, and body size [50, 62, 63]. Body size is also extremely important in determining range size [24, 92, 93] and is discussed in the next section. Different dietary categories acts as a limit on abundance because of the available environmental energy or resources in a location [16, 23, 48, 88, 99]. Abundance is correlated with occupancy, or the number of unique localities at which a taxon is found [15, 31, 49]. It follows then that limits imposed by environmental energy would then effect 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 [11, 32, 43] 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 [95, 96], 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 [47].

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 [103, 104]. This transition was known to have caused major shifts in the global climatic envelopes and the reorganization of communities along with it [5, 13, 26, 31, 47]. 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 [50]. 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 [3–5, 8, 10, 13, 26, 33, 34, 90, 91]. The long term effects of climate change on North American mammalian diversity dynamics and community connectedness remains unresolved and controversial [5, 10, 13, 26]. 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 less studied compared to North America and research has focused primarily on faunal dynamics in the Neogene [49, 50, 61, 76–78]. One of the major findings is that there was very little shift in relative dietary category abundance [50] while the patterns within herbivores (browse–graze transition) were mostly driven by abundant, cosmopolitan taxa [49]. 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 [50].

The biogeographic patterns of Cenozoic South American mammalian fauna are unstudied in all but qualitative forms. This lack of information is due to historical reasons, with the fossil record of southern continents being in general under studied compared to that of northern continents. Recently, there has been a dramatic increase in the amount of fossil collecting and coverage of most of the Cenozoic [27, 64, 65]. Because of this, it should be possible to analyze quantitatively the biogeographic structure of the South American mammal fossil record. The South American mammalian faunal record reflects two distinct biotic provinces between the North and the South [27, 64, 65, 71]. 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.

Proposed research: Using methods first proposed by Sidor et al. [87] and Vilhena et al. [100],

I propose to construct bipartite biogeographic networks between taxa and localities. Here taxa are defined as species and localities are defined as formations. 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 patters 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 [87]: 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 [82, 83]. The logic of the map equation is that a good map compresses reality into a few simple symbols. This means we want to compress sections of a graph into a single symbol. The fewer symbols needed to accurately depict a graph, the lower the code length. A high code length indicates that the graph is very difficult to compress. In the case of measuring community connectedness, a low code length means lower community connectedness than a high code length [87]. This is effectively a measure of provinciality.

Phylogenetic similarity between localities may play an important role in community structuring [102]. As such, it is necessary to estimate average phylogenetic distance between all localities during a time bin. Two possible approaches for measuring the similarity in taxonomic composition between two localities: a tree distance metric such as the the Robinson-Foulds metric [81] can be used to estimate the distance between two topologies or the two localities can be combined to form one tree and the average pairwise patristic distance [94] is calculated. The average of either of these measures is the average phylogenetic similarity which can then be used in partial correlation tests or modeling questions.

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.

Taxonomic occurrence 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 by John 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, 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. 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 Notoungulates, Marsupials, Carnivores, and Primates.

Ecology, survivorship, and fitness in Cenozoic mammals

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

Background and Predictions: As discussed above, dietary and locomotor categories are strong candidate constituent traits of range size. Additionally, body size is a classically cited constituent trait of range size [23, 24, 92, 93]. 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 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 [16, 23, 23, 63].

As discussed above, as the Cenozoic progressed there was a global shift from closed to open habitat. In the intermediate, one would expect some degree of environmental patchiness. It follows that there would have been an increase followed by a decrease in both speciation and extinction, with the peak being during the intermediate period.

Mammalian herbivores and carnivores have been found to a greater diversification rate than omnivores [74]. 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 [75] 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 [61, 97]. 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 investigate the effect of ecological traits and climate change on survivorship, I plan to compare different models of trait based survival in order to best understand which factors are most important.

Survivorship 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). Dietary category, locomotor category, and body size will be modeled as time-independent covariates of survival. The climate proxy δO^{18} oxygen curve [104] will be modeled as an ancillary time-dependent covariate. Also, constant versus accelerating, decelerating, or time variant extinction rate will be estimated using different fundamental hazard models by comparing the fit of survival to various probability distributions.

While many analyses of survivorship are done using generic data [36, 61, 97], there are potential biases in accurately modeling specific level process from generic level data [79, 80, 85, 89, 98]. There are important concerns regarding anagenesis, hierarchical selection, and extant taxa or taxa that did not go extinct in the time frame of interest [79, 80, 89, 98]. Interestingly, the effect of incomplete sampling on estimation of survivorship curves appears rather minimal and uniform [85]. The problems involving extant taxa and taxa that did not go extinct have mostly been dealt with following advances in modeling right-censored data [57].

In order to asses potential specific versus generic effects I will estimate the difference between specific and generic survivorship models. Using an approach based on previous work to estimate specific origination and extinction from generic level survival curves [28], or a variant there of, 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 study of mammalian survivorship, I also propose a simulation study to analyze effect of varying sampling probability and/or anagenesis rate on estimating various models of survivorship using *paleotree* [9]. Principally, I am interested in the effect of these paleontological realities on estimation of survival and in particular departures from an exponential hazard function.

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

Permian brachiopods, extinction and environmental preference

Questions: In Permian brachiopods in Australasia, do traits directly related to environmental selection relate to differential survivorship? 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 involved in determining possible range size are affixing strategy, substrate preference, and habitat preference. While larval biology is considered extremely important in determining range size in marine invertebrates [43, 44], this does not preserve in brachiopods and thus cannot be used to model survivorship [44]. 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 [43, 44].

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 [1, 58, 59]. 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. The availability of appropriate habitats then 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 [17]. However, this association is weak as most assemblages are composed of a heterogeneous mix of taxa [17]. Previous analysis of brachiopod durations indicated that affixing strategy is associated with differential longevity [1]. 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 [6, 29, 52, 67, 68]. The Phanerozoic is characterized by an overall decline in carbonates relative to clastics [29, 67]. 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 [14, 42, 46, 52, 86]. On-shore environments, and in particular epicontinental seas, have declined in areal extent over the Pharenozoic [72]. 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 [30, 37, 60]. This adaptation to variable environments has been found to relate strongly with survival past inception [30]. In this case, it would be expected then that taxa with mixed preferences for both substrate and habitat would have potentially longer 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.

During the Permian there was a shift from an “ice house” to a “hot house” world [12, 25, 51, 73] 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 [12, 25, 51]. According to Olszewski and Erwin [69], 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 an approach similar to that described above to estimate the differential survivorship of Permian brachiopods. I restrict this analysis to Australiasia because it represents a relatively continually sampled and well worked area that preserves the majority of the entire Permian [7, 19, 20, 101]. In this analysis, the time-independent covariates are substrate preference, affixing strategy, and habitat preference. Climate will be modeled as either an ancillary heavyside 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 [17–21] and Waterhouse [101].

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 [30, 36, 39, 45, 84], 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 [30, 35, 68].
Related to this is the general question of how climate change impacts diversity dynamics
[5, 10, 26, 69]. Here I compare the impact of various constituent traits of range size on both
community connectedness and survival. The former is a discussion of the range and limitations
of possible biotic–biotic interactors and the later is a discussion of what ecological traits,
either alone or in concert, best model time from origination till extinction. By comparing two
distantly related clades, mammals and brachiopods, the hope is to determine how necessary
discussion of “emergent” properties is and how ecological traits may interact to increase the
survival of a taxon.

Timeline

314 Spring/Summer 2014

- Evolution Meeting: preliminary brachiopod survival results

316 • South American fossil mammal data from Field Museum of Natural History collections

Fall 2014/Winter 2015

318 • GSA: survivorship simulation for anagenesis and sampling

- Doctoral Dissertation Improvement Grant

320 Spring/Summer 2015

- Evolution Meeting: mammalian survivorship analysis for North America and Europe

322 • South American fossil mammal data from American Museum of Natural History collections

324 • write and submit survivorship simulation paper

Fall 2015/Winter 2016

326 • SVP or GSA: mammalian biogeographic connectedness

- write and submit mammal connectedness paper

328 Spring/Summer 2016

- Evolution Meeting: brachiopod survival analysis results

330 • write and submit brachiopod survival paper

Fall 2016/Winter 2017

332 • SVP or GSA: mammalian survivorship analysis

- write and submit mammal survival paper

334 Spring/Summer 2017

- Evolution Meeting

336 • write and submit review/philosophy paper

- **Defend**

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