

# Evolutionary paleoecology and the biology of extinction

Peter D. Smits  
psmits@uchicago.edu

Dissertation Proposal Hearing  
November 12, 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 theoretical framework

## 2 Evolutionary paleoecology

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 [29]. Ecological traits and factors are any and all 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 thus the net pattern of macroevolution. The study of evolutionary paleoecology is then the link between interactions and macroevolution. Namely, it is the study of the ecological interactions that may or may not generate the patterns of macroevolution. As a corollary to Kitchell [29]’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 then the study of the biology of extinction and how it relates to ecological properties and interactions [28].

It is under this framework that I purpose to study how ecological traits associated with range size have affected both the availability of biotic interactions and survivorship. I will be comparing survivorship in two very distantly related and biotically very different groups: mammals and brachiopods. Both of these groups are considered to have very good fossil records able to reflect massive long term evolutionary patterns [35].

Importantly, Simpson [48] defined the set of all biotic and abiotic interactions that a lineage may experience as the “adaptive zone.” The also termed this the “environment” which the dynamics of were later expanded upon by Van Valen [53]. This usage of “environment” is frequently misinterpreted thus it is important to note it here. The adaptive zone represents one of the fundamental metaphors in paleobiology [48, 49].

## Paleobiological theory

Extinction, when not during periods of mass extinction, is widely considered non-random with respect to biology [24]. Additionally, times of “background extinction” represent the vast majority of geological time compared to periods of “mass extinction.” The exact definition and distinction between periods of background and mass extinction is based on the relative intensity of extinction at a particular time versus all times prior CITATIONS. Simply put, the major indicator of a mass extinction is an event that is across taxonomic categories and the biotic interactors before and after the event are dramatically different CITATIONS. RAUP BAMBACH SEPKOSKI JABLONSKI KITCHELL ETC

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. Macroevolution, here defined, is the pattern of speciation and extinction over time [25]. The study of macroevolution, thus, is the estimation of the processes underlying these observed patterns. The term origination is frequently used in place of speciation because it is considered impossible to observe speciation in the fossil record and instead we only observe the sudden appearance of a new taxon [13].

Macroevolution, as metaphor, is both phyletic and anagenetic evolutionary dynamics [19]. Phyletic means speciation/extinction dynamics and anagenetic means within lineage disparity dynamics. This concept has also been termed the tempo and mode of evolution [48]. This broader definition more closely links paleobiology and macroevolution. This raises an important question: can we have paleobiology without macroevolution?

In contrast to macroevolution there is microevolution [19, 48] which is strictly defined as change in allele frequency in a population from one generation to the next. A weaker definition is that microevolution is change below the species level [19] though there is no qualifier on what this change is defined as. It is important to note that changes in allele frequency affect phenotype frequency and expression. This definition, by corollary, describes phenotypic change. Just as Simpson [48] described, this link can explain rates of evolution and (most) patterns of disparity without invoking any macroevolutionary phenomenon.

What makes a definition strong or weak? Why would we prefer one over the other? What is the difference between definition, metaphor and metonymy?

Of major concern with the broader definition of macroevolution is that this concept subsumes all aspects of anagenetic change. The difference between microevolution versus macroevolution is unclear. Interestingly, the link between broad sense macroevolution and Simpson's tempo and mode of evolution is that Simpson's statement assigns no hierarchical level to these patterns. The pervasiveness of the use of broad sense macroevolution then is because this usage is metaphoric and explicitly because it is not the actual definition of macroevolution.

Traits are properties that are expressed at some level. Emergent traits are defined as traits that are not reducible to a lower level [25] OTHER CITATIONS. An emergent trait is thus a relative concept which must be defined in relation to a specific organizational level (e.g. species, organism, etc.). An emergent property is effectively a trait that is the product of multiple traits expressed at one or more hierarchical levels in concert and is not reducible to a lower level [25] CITATIONS. It is extremely important to recognize a fundamental hierarchy in biology in order to allow for emergent traits Vrba and Eldredge [57]. In paleobiology, an emergent property is normally one ascribed to the species or genus level as opposed to the organism level [20, 25, 56] LLOYD CITATIONS, and thus the root of the term "species selection" [25]. Range size is considered an emergent property that has continually been demonstrated to play a crucial role in extinction selectivity with species with larger geographic ranges having lower extinction rates than species with smaller geographic ranges [23, 24, 36]. Range size is emergent because no one property of a single organism can explain this trait, instead it is a combination of multiple properties in addition to multiple members of the species which helps to determine global range size CITATIONS.

Here I am studying the individual and combined effect of organismal traits related to emergent range size on extinction and, by extension, fitness.

## Cosmopolitan and endemic mammal dynamics of Cenozoic mammals

*Questions:* How do patterns of community connectedness change over time, specifically in Cenozoic terrestrial mammals? Do these patterns differ between continents? Are these patterns related to ecological traits, such as dietary category and locomotor category? Are these patterns related to changes in global temperature?

*Background and Predictions:* During the Cenozoic, there was a global shift from predominately closed, forested habitats to more open, savanna habitats. This pattern leads to the expectation that there would be a relative decrease in arboreal taxa as well as a relative decrease in terrestrial taxa. Additionally, an increase in the relative endemism of arboreal taxa over time and a decrease in the relative endemism of terrestrial taxa might have accompanied this. The timing of this shift was different between continents [50, 51], meaning that the patterns reflecting this environmental shift may be globally non-uniform and any progressive changes in community structures would reflect regional scale changes instead of any global trend.

However, this expected shift in distribution of taxa according to locomotor category is not necessarily accompanied by broad shifts in distribution of (coarse) dietary categories. The majority of previous research on mammalian faunal dynamics has focused on the North American fossil record [3, 4, 6, 7, 9, 11, 14, 21, 22, 48, 49]. The major focuses have been on the effect of climate change on diversity and distributions between different higher taxonomic levels. The long term effects of climate change on North American mammalian diversity dynamics and community connectedness and similarly remains unresolved and controversial [6, 9, 11, 14]. The basic predictions that can be made are coherent with the general predictions made above. Namely, that over the Cenozoic there would be a relative increase in endemism in arboreal taxa versus a relative decrease in ground dwelling endemism. Because of the vast amount of prior work on North American mammalian faunal dynamics, this forms the basis for the global predictions made above. The North American record then inadvertently becomes the baseline comparison for regional differences.

In comparison to North America, the European mammalian fossil is less studied. Importantly, a great deal of work has focused on faunal dynamics in the Neogene [26, 27, 31, 42–44]. One of the major findings is that, during the Neogene, there was very little shift in relative trophic level abundance [27] while the patterns in dietary shifts were mostly driven by abundance and cosmopolitan herbivores [26]. Because of this, the major predictions for the European record is that occupancy will increase for herbivorous taxa, while increasing or remaining identical in carnivores, and remaining relatively constant for omnivores. These are the expectations

for at least the Neogene.

The record of the South American mammalian fauna appears to reflect two distinct biotic provinces between the North and the South [15, 33, 34, 39]. Because of this, I predict the South American record to have a very different pattern of biogeographic connectedness than either North America or Europe, specifically in terms of endemism. Namely, the expectation would be a high or progressively increasing degree of endemism along with low connectivity. Also, an increase in land-dwelling herbivores relative to arboreal (at least in the south) would be expected.

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 [58, 59]. NEED SOME LITERATURE ON RANGE SIZE SHIFTS AND CLIMATE SEE MACRO NOTES. This transition is predicted to cause major shifts in biomes, causing reorganization of communities CITATIONS. For global mammalian community connectedness and trophic structure, it is predicted that while the environment might be shifting, lineages may adapt in place and overall structure will remain rather constant through time [27].

*Proposed research:* Using methods first proposed by Sidor et al. [47] and Vilhena et al. [55], I propose to construct bipartite biogeographic networks between taxa and localities. A link between a taxon and a locality is formed when that is present at that locality. Because the network is bipartite, by definition there are no links between a taxon and another taxon or a locality and another locality. Here taxa are defined as species and localities are defined as formations. Biogeographic networks will be constructed for every 2 million year bin of the Cenozoic. This bin width is chosen to have minimum 2 formations to be present in the same bin, even though it has been found that at least the North American fossil record is resolvable at the 1 My level [3–5]. Additionally, while the European fossil record may be resolvable at comparable levels to the North American record [26, 27] OTHER CITATIONS, it is expected that the South American fossil record may not be accurately resolvable at the 1 My level.

Additionally, networks will be constructed for each dietary category and each locomotor category. These ecology specific networks will also be made for every 2 million year bin of the Cenozoic.

Network complexity and connectedness is measured using the four summary statistics previously used [47].

In order to compare whether patterns observed on different continents are similar or different, as well as compare patterns between

## Fitness and extinction risk related to ecology in Cenozoic mammals

*Questions:* How do ecological characters, such as dietary category and locomotor category, affect survivorship in mammals? Is the hazard (instantaneous extinction rate) in adaptive zones constant with respect to taxon age, or does instantaneous extinction rate change with taxon age? Is any single trait the best predictor of survivorship, or do multiple traits together predict survivorship better?

*Background and Predictions:* Survival can be considered the ultimate measure of fitness or evolution success [12, 38] because ultimately a long-term successful lineage is not one that speciated greatly but one that never went extinct [38]. During periods of background extinction we expect that extinction events are non-random with respect to biology [24]. Survival is effectively the opposite of extinction, thus during periods of background extinction we should be able to effectively measure the relative fitness of various ecologies or adaptive zones [28, 29, 48, 53].

In mammals, three of the arguably most important ecological traits are dietary category, locomotor category, and body size CITATIONS. Additionally, each of these traits are important in determining the emergent species level property of range size.

Survivorship is a statement of a sample of organisms and is a summary over all of them. This approach to studying extinction and selection has a long history in paleobiology [10, 16, 28, 30, 48, 54] RAUP CITATIONS SEE CARL'S CHAPTER. This is not the same as temporal extinction rate [17, 18] ALROY CITATIONS. The hazard/extinction rate from a survivorship curve is a statement of the rate at which organisms go extinction following origination. Temporal extinction rates are statements of how extinction intensity has varied across lineages over time. Hazard rates are potentially more comparable to the diversification rates estimated via phylogenetic comparative methods CITATIONS, however hazard rates are an estimate of extinction rate which is considered difficult if not impossible to estimate in this fashion [41].

As discussed above, as the Cenozoic progressed on all Continents there was a shift from closed habitat to more open habitat. In the intermediate, one would expect some degree of patchiness in the landscape. Expectedly, there would be a increase followed by a decrease in both speciation rate and extinction rate, with the peak being during the intermediate period.

According to Price et al. [40], herbivores and carnivores should have a greater diversification rate than omnivores. This analysis was global in scope, and purely extant taxa in a comparative phylogenetic context. Importantly, diversification rate is the difference between origination and extinction rate. 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 impossible to determine from a phylogeny of only extant organisms [41] which means that only via the analysis of the mammalian fossil record is it possible to

estimate which process is more likely.

Depending on the continent, body size has been demonstrated to play either some or no roll in extinction selectivity during the Neogene [31, 32, 52]. 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 risk. Additionally, I will be using alternative methods to better understand the dynamics governing trait based extinction probability.

ADD IN MODELS. NEED TO READ MORE SURVIVAL BOOK.

Given [26], it might be expected that the pattern for all mammals will be most similar to the pattern from (common) herbivores. However, I am unsure if this is a reasonable prediction.

While many analyses of extinction risk and survivorship are done using generic level data [23, 31, 52], there is a known biasing effect in survivorship analysis of paleontological data where the hazard function describing the survivorship curve is biased away from uniformity [45, 46] which can cause potentially false results in relation to the Van Valen's Law of Constant Extinction [53]. There are also important concerns regarding anagenetic lineages, extant taxa or taxa that did not go extinct in the time frame of interest [45, 54] PROBABLY MORE. Interestingly, the effect of incomplete sampling on estimation of survivorship curves appears rather minimal and uniform [46]. However, the problems involving extant taxa and taxa that did not go extinct have mostly been dealt with following advances of how to describe right-censored survivorship data and estimate the likelihood of various parametric models of hazard and survivorship CITATION TEXTBOOK. Hierarchical models of survivorship CARL'S CHAPTER.

*Proposed research:* Simulation study to analyze effect of varying sampling probability and/or anagenesis rate on estimating various models of survivorship using `paleotree` [8]. Principally, I am interested in the effect of these paleontological realities on estimation of the hazard function of the survivorship data and in particular departures from a constant, or exponential, hazard function. Alternatives are, for example, models of accelerating or decelerating extinction rate. I intend to revise the previously analyzed effect of sampling on estimation survivorship in this new context [46].

Do not use generic data? Or figure out a correction factor? Do both generic and specific level analysis and then use [16] to get deviance/concordance and see what potential biasing effect might be occurring?

## Extinction risk related to traits affecting habitat selection in Permian brachiopods

*Questions:* How do traits directly related habitat selection and range size relate to extinction risk? Are certain traits more explanatory of extinction risk than others? Does changing environmental and substrate availability affect trait-based extinction risk?

*Background and Predictions:* Affixing strat: pedicle, reclining, cementing. Pedicles are associated with shallow, on-shore environments while reclining on associated with deep, off-shore environments. Note, global Permian pattern is rather heterogeneous in terms of relative abundance between the three affixing strategies CLAPHAM. According to Alexander [1], endemic unattached/reclining taxa have longer durations than all other affixing strategies of other endemic taxa. on the other hand, cosmopolitan pedunculate and cementing taxa have longer durations than unattached/reclining taxa. in terms of regional scales, it will be necessary to correct for relative abundance to actually measure survivability/fitness.

Substrate: carbonate, clastic, mixed. Overall decline in carbonates relative to clastics, decreased fitness for carbonate lovers relative to clastic lovers. Best to be mixed? Brachiopods are mixed slash switchers CARL AND MELANIE'S UNPUBLISHED WORK.

Habitat: on-shore vs off-shore / epicontinental vs oceanic. How possible is this? Very difficult to resolve accurately. Progressive loss of epicontinental seas during the Pharenozoic which would predict over all lower fitness in taxa which occur solely in epicontinental environments. On-shore off-shore dynamics of Sepkoski and Raup.

During the Permian there was a shift from an "ice house" world to a "hot house world" CITATIONS which could be expected to have some major effects on brachiopod survivorship. In particular, taxa in modern Australia would be of particular interest because of the proximity of Australia to the south pole during the Permian and the repeated glacial activity in the region CITATIONS. According to Olszewski and Erwin [37], 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. If climate or environmental information, such as habitat preference, is a predictor in the best model of survivorship is less clear cut and necessary to determine empirically.

*Proposed research:*



# Timeline

- 248 Spring/Summer 2014
- Evolution Meeting: brachiopods
- 250 Fall 2014/Winter 2015
- GSA: simulation
- 252 Spring/Summer 2015
- Evolution Meeting: mammals
- 254 Fall 2015/Winter 2016
- SVP or GSA
- 256 Spring/Summer 2016
- Evolution Meeting
- 258 Fall 2016/Winter 2017
- SVP or GSA
- 260 Spring/Summer 2017
- Evolution Meeting
- 262 • **Defend**

## References

- [1] 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.
- [2] 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.
- [3] J. Alroy. Constant extinction, constrained diversification, and uncoordinated stasis in North American mammals. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 127: 285–311, 1996.
- [4] 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.
- [5] J. Alroy. New methods for quantifying macroevolutionary patterns and processes. *Paleobiology*, 26(4):707–733, 2000.
- [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] 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.
- [8] 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>.
- [9] 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.
- [10] T. K. Baumiller. Survivorship analysis of Paleozoic Crinoidea: effect of filter morphology on evolutionary rates. *Paleobiology*, 19(3):304–321, 1993.
- [11] 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.
- [12] W. S. Cooper. Expected time to extinction and the concept of fundamental fitness. *Journal of Theoretical Biology*, 107:603–629, 1984.
- [13] J. A. Coyne and H. A. Orr. *Speciation*. Sinauer Associates, Sunderland, MA, 2004.

- [14] 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.
- [15] 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>.
- [16] M. Foote. Survivorship analysis of Cambrian and Ordovician Trilobites. *Paleobiology*, 14(3):258–271, 1988.
- [17] M. Foote. Origination and extinction components of taxonomic diversity: general problems. *Paleobiology*, 26(sp4):74–102, Dec. 2000. ISSN 0094-8373. doi: 10.1666/0094-8373(2000)26[74:OAEcot]2.0.CO;2. URL <http://www.bioone.org/doi/abs/10.1666/0094-8373%282000%2926%5B74%3A0AECOT%5D2.0.CO%3B2>.
- [18] M. Foote. Origination and extinction components of taxonomic diversity: Paleozoic and post-Paleozoic dynamics. *Paleobiology*, 26(4):578–605, Dec. 2000. ISSN 0094-8373. doi: 10.1666/0094-8373(2000)026[0578:OAEcot]2.0.CO;2. URL <http://www.bioone.org/doi/abs/10.1666/0094-8373%282000%29026%3C0578%3A0AECOT%3E2.0.CO%3B2>.
- [19] M. Foote and A. I. Miller. *Principles of Paleontology*. Freeman, New York, third edition, 2007.
- [20] T. A. Grantham. Hierarchical approaches to macroevolution: recent work on species selection and the effect hypothesis. *Annual Review of Ecology and Systematics*, 26:301–321, 1995.
- [21] 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>.
- [22] 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.
- [23] 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>.
- [24] D. Jablonski. Background and mass extinctions: the alternation of macroevolutionary regimes. *Science*, 231(4734):129–133, 1986.
- [25] 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>.

- [26] 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.

- [27] 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.

- [28] 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>.

- [29] J. A. Kitchell. Evolutionary paleoecology: recent contributions to evolutionary theory. *Paleobiology*, 11(1):91–104, 1985.

- [30] J. A. Kitchell. The temporal distribution of evolutionary and migrational events in pelagic systems: episodic or continuous. *Paleoceanography*, 2(5):473–487, 1987.

- [31] 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>.

- [32] L. H. Liow, M. Fortelius, K. Lintulaakso, H. Mannila, and N. C. Stenseth. Lower Extinction Risk in SleeporHide Mammals. *The American Naturalist*, 173(2):264–272, 2009. URL <papers2://publication/doi/10.1086/595756>.

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

- [34] 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>.

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

- [36] 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>.

- [37] 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>.

- [38] 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>.
- [39] B. Patterson and R. Pascual. The fossil mammal fauna of South America. *The Quarterly review of biology*, 43(4):409–451, 1968.
- [40] 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>.
- [41] 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>.
- [42] 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>.
- [43] 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.
- [44] 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>.
- [45] 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>.
- [46] J. J. Sepkoski. Stratigraphic biases in the analysis of taxonomic survivorship. *Paleobiology*, 1(4):343–355, 1975.
- [47] 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.
- [48] G. G. Simpson. *Tempo and Mode in Evolution*. Columbia University Press, New York, 1944.

- [49] G. G. Simpson. *The Major Features of Evolution*. Columbia University Press, New York, 1953.
- [50] 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>.
- [51] 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>.
- [52] 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>.
- [53] L. Van Valen. A new evolutionary law. *Evolutionary Theory*, 1:1–30, 1973. URL <http://ci.nii.ac.jp/naid/10011264287/>.
- [54] L. Van Valen. Taxonomic survivorship curves. *Evolutionary Theory*, 4:129–142, 1979.
- [55] D. a. Villhena, 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.
- [56] E. S. Vrba. Macroevolutionary trends: new perspectives on the roles of adaptation and incidental effect. *Science*, 221(4608):387–389, 1983.
- [57] E. S. Vrba and N. Eldredge. Individuals, hierarchies and processes: towards a more complete evolutionary theory. *Paleobiology*, 10(2):146–171, 1984.
- [58] 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>.
- [59] 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.