

Evolutionary paleoecology and the biology of extinction

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Committee

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Introduction and theoretical framework

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 [13]. 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. These interactions are between the taxon and a factor, which as stated may be either biotic or abiotic. Diversification is the difference between origination and extinction, and is thus the net product of pattern of macroevolution. The study of evolutionary paleoecology is then the link between interactions and macroevolution. Namely, it is the study of the ecological processes that may or may not generate the patterns of macroevolution. As a corollary to Kitchell [13]’s definition, Allmon [2] states that in order to correctly link ecological processes to macroevolution, one must focus on the specific traits and factors that affect the speciation process. Tacitly included in this is the study of the biology of extinction [12].

It is under this framework that I purpose to study

I will be comparing extinction selectivity 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 [18].

anagenesis

taxonomy

Jurassic of Europe Kiessling Aberhaan

John Hunter OHIO STATE -Watson Seminar

Marie Hoerner

Dave Polly Feb 7th -Geo Sci seminar

Paleobiological theory

Extinction, away from mass extinctions, is non-random [8]. Additionally, times of “background extinction” represent the vast majority of geological time compared to periods of “mass extinction.”

Paleobiology is the study of life over time and in particular the processes that generate the observed patterns in diversity and disparity and how these may have changed. Intimately related to this is the concept of macroevolution. Macroevo-*lution*, *sensu stricto*, is the pattern of speciation and extinction dynamics over time [9]. The study of macroevolution, thus,

is the method by which the processes underlying these patterns are delineated. 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 [5].

Macroevolution, *sensu lato*, is both phyletic and anagenetic evolutionary dynamics [7]. Phyletic means speciation/extinction dynamics and anagenetic means within lineage disparity dynamics. This concept has also been termed the tempo and mode of evolution [24]. This broader definition more closely links paleobiology and macroevolution.

In contrast to macroevolution is microevolution [7, 24] which is defined strictly 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 [7] 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.

Of 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 macroevolution *sensu lato* 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 macroevolution *sensu lato* 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 [9] 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.). In paleobiology, emergent traits are frequently defined as those properties not reducible to the organismal level. If a trait is not reducible, it is then considered species, or genus, level traits.

Range size is continually cited as an emergent, species-level trait CITATIONS.

The studies I am and will be undertaking are related to organismal traits such as dietary category and substrate affinity. Each of these traits can be considered to be related to the emergence of range-size. However, the relative importance of these different traits and their interactions in terms of fitness and extinction risk SOMETHING

Cosmopolitan and endemic mammal dynamics of Cenozoic mammals

Questions: Do different continental populations of terrestrial mammals demonstrate different patterns of community similarity and change over the Cenozoic? Are these patterns related to ecological characters, such as dietary category and locomotor category? Are these patterns

related to changes in global temperature?

Hypotheses and Predictions: During the Cenozoic, there is a general global shift from closed, forested habitats to open, savanna habitats. Because of this, it is reasonable to expect a relative decrease in arboreal taxa as well as a relative decrease in terrestrial taxa. Additionally, an increased in the relative endemism of arboreal taxa over time and an decrease in the relative endemism of terrestrial taxa might accompany this. 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.

However, the timing of this shift is different between continents [25, 26], meaning that the patterns reflecting this environmental shift may be globally non-uniform.

Majority of research focused on North America

Europe retains similar balance in trophic categories over at least Neogene

The record of the South American mammalian fauna appears to reflect two distinct biotic provinces between the North and the South of the continent [6, 16, 17, 20]. Because of this, South America is predicted to have a very different record of biogeographic connectedness than either North America or Europe, specifically in terms of patterns of endemism. Specifically, it might be expected that would be a high or progressively increasing degree of endemism along with low connectivity. but increase in land-dwelling herbivores relative to arboreal (at least in the south).

Reasoning:

Proposed research: Using methods first proposed by Sidor et al. [23] and Vilhena et al. [28].

Compare generic results to specific results because that is what Jernvall and Fortelius [10] and Jernvall and Fortelius [11] did and what Tomiya [27] did not.

Fitness and extinction risk related to ecology in Cenozoic mammals

Questions: How do ecological characters, such as dietary category and locomotor category, affect extinction risk in mammals? Does this relationship change over time? Is anyone trait the best predictor of extinction risk, or do multiple traits together or interacting better explain extinction?

Hypotheses and Predictions:

During periods of background extinction we expect that extinction events are non-random with respect to biology [8]. Additionally, survival can be considered the ultimate measure of

fitness or evolution success [4, 19] because ultimately a long-term successful lineage is not one that speciated greatly but one that never went extinct [19].

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.

While diet and locomotor categories are known to evolve in context amongst terrestrial mammals, they are not the same trait and thus it is very possible that there is not necessarily any direct causal connection between the evolution of these traits. However, it may be quite possible that there is a correlation between them. This is similar, also, with correlations between either of these traits and body size.

Difference between survivorship/hazard rate and (bin) rate

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. [21], herbivores and carnivores should have a greater diversification rate than omnivores. This analysis was global in scope, and purely extant taxa in a phylogenetic comparative method context. If this is still the case for the survival analysis, that will be very interesting.

Depending on the continent, body size has been demonstrated to play either some or no roll in extinction selectivity during the Neogene [14, 15, 27]. By expanding to include a third continent, South America, I hope to elucidate how differences in constituent taxa 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.

Given [10], 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.

Compare generic results to specific results because that is what Jernvall and Fortelius [10] and Jernvall and Fortelius [11] did and what Tomiya [27] did not.

Biasing effect of using generic data [22]

Reasoning:

Proposed research:

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?

Hypotheses and Predictions: progressive loss of epicontinental seas: decrease in fitness (for proportion) of that trait

shift relative proportion of pedunculate/reclining/cementing taxa: almost random [3] in terms of any “trend.”

substrate preference: NEED TO CHECK LITERATURE

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.

climate: shift from icehouse communities to greenhouse communities. NEED TO CHECK WITH CLAPHAM TO QUANTIFY THAT IDEA

Reasoning:

Proposed research:

Importance

Timeline

Spring/Summer 2014

- Evolution Meeting: brachiopods
- cosmo prov
- survivor

Fall 2014/Winter 2015

- GSA: simulation
- cosmo prov
- survivor
- mammal risk

Spring/Summer 2015

- Evolution Meeting: mammals
- survivor
- mammal risk
- review 1

Fall 2015/Winter 2016

- SVP or GSA
- mammal risk
- review 1
- review 2

Spring/Summer 2016

- Evolution Meeting
- review 1
- review 2

Fall 2016/Winter 2017

- SVP or GSA
- review 2

Spring/Summer 2017

- Evolution Meeting
- **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] 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>.
- [4] W. S. Cooper. Expected time to extinction and the concept of fundamental fitness. *Journal of Theoretical Biology*, 107:603–629, 1984.
- [5] J. A. Coyne and H. A. Orr. *Speciation*. Sinauer Associates, Sunderland, MA, 2004.
- [6] 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>.
- [7] M. Foote and A. I. Miller. *Principles of Paleontology*. Freeman, New York, third edition, 2007.
- [8] D. Jablonski. Background and mass extinctions: the alternation of macroevolutionary regimes. *Science*, 231(4734):129–133, 1986.
- [9] 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>.
- [10] 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.
- [11] 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.
- [12] 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>.

- [13] J. A. Kitchell. Evolutionary paleoecology: recent contributions to evolutionary theory. *Paleobiology*, 11(1):91–104, 1985.
- [14] 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.
- [15] 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.
- [16] B. J. Macfadden. Origin and evolution of the grazing guild in New World terrestrial mammals. *Trends in ecology & evolution*, 12(5):182–187, 1997.
- [17] 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>.
- [18] G. A. Mark and K. W. Flessa. A test for evolutionary equilibria: Phanerozoic brachiopods and Cenozoic mammals. *Paleobiology*, 3(1):17–22, 1977.
- [19] 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>.
- [20] B. Patterson and R. Pascual. The fossil mammal fauna of South America. *The Quarterly review of biology*, 43(4):409–451, 1968.
- [21] 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>.
- [22] 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>.
- [23] 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.
- [24] G. G. Simpson. *Tempo and Mode in Evolution*. Columbia University Press, New York, 1944.
- [25] 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>.

[26] 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>.

[27] 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>.

[28] 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.