

Evolutionary paleoecology and the biology of extinction

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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 [10]. 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. Allmon [2] amends Kitchell’s definition by stating 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 [9].

It is under this framework that I purpose to study

16 Paleobiological theory

Extinction, away from mass extinctions, is non-random JABLOSNKI REFERENCE

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. Macroevolution, *sensu stricto*, is the pattern of speciation and extinction dynamics over time [6]. 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 [4].

Macroevolution, *sensu lato*, is both phyletic and anagenetic evolutionary dynamics [5]. Phyletic means speciation/extinction dynamics and anagenetic means within lineage disparity dynamics. This concept has also been termed the tempo and mode of evolution [14]. This broader definition more closely links paleobiology and macroevolution.

In contrast to macroevolution is microevolution [5, 14] 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 [5] 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 [6]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: transition from forested, closed environments to open plains. differential timing on continents.

Over Cenozoic, with the changes in habitat availability there would be a relative decrease in arboreal taxa and a relative increase in terrestrial taxa. Increase in avg cooc and decrease endemism in terrestrial fauna.

north america

europa retains similar balance in trophic categories over at least Neogene

south america has very distinct provincialism, potentially causing strange effects in endemism. high endemism, low connectivity. but increase in land-dwelling herbivores relative to arboreal (at least in the south).

68 Compare generic results to specific results because that is what Jernvall and Fortelius [7] and
Jernvall and Fortelius [8] did and what Tomiya [15] did not.

70 *Reasoning:*

Proposed research:

72 **Fitness and extinction risk related to ecology in Ceno- zoic mammals**

74 *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
76 the best predictor of extinction risk, or do multiple traits together or interacting better
explain extinction?

78 *Hypotheses and Predictions:*

As the Cenozoic progressed, on all Continents there was a shift from closed habitat to
80 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
82 rate and extinction rate, with the peak being during the intermediate period.

What characters: diet, locomotion, body size

84 According to Price et al. [13], herbivores and carnivores should have a greater diversification
rate than omnivores. This analysis was global in scope, and purely extant taxa in a phyloge-
86 netic comparative method context. If this is still the case for the survival analysis, that will
be very interesting.

88 While diet and locomotor categories are known to evolve in context amongst terrestrial
mammals, they are not the same trait.

90 Depending on the continent, body size has been demonstrated to play either some or no roll
in extinction selectivity during the Neogene [11, 12, 15]. However, their analysis (capture-
92 mark-recapture) did not treat body size as a continuous variable. This is something I can do
in survival analysis.

94 Given [7], 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.

96 Compare generic results to specific results because that is what Jernvall and Fortelius [7] and
Jernvall and Fortelius [8] did and what Tomiya [15] did not.

98 *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:

FOURTH UNKNOWN CHAPTER

Questions:

Hypotheses and Predictions:

Reasoning:

Proposed research:

Importance

Timeline

- 126 Spring/Summer 2014
- cosmo prov
- 128 • survivor
- Fall 2014/Winter 2015
- 130 • cosmo prov
- survivor
- 132 • mammal risk
- Spring/Summer 2015
- 134 • survivor
- mammal risk
- 136 • review 1
- Fall 2015/Winter 2016
- 138 • mammal risk
- review 1
- 140 • review 2
- Spring/Summer 2016
- 142 • review 1
- review 2
- 144 Fall 2016/Winter 2017
- review 2
- 146 Spring/Summer 2017
- **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] J. A. Coyne and H. A. Orr. *Speciation*. Sinauer Associates, Sunderland, MA, 2004.
- [5] M. Foote and A. I. Miller. *Principles of Paleontology*. Freeman, New York, third edition, 2007.
- [6] 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>.
- [7] 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.
- [8] 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.
- [9] 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>.
- [10] J. A. Kitchell. Evolutionary paleoecology: recent contributions to evolutionary theory. *Paleobiology*, 11(1):91–104, 1985.
- [11] 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.
- [12] 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.

[13] 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>.

[14] G. G. Simpson. *Tempo and Mode in Evolution*. Columbia University Press, New York,
1944.

[15] 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>.