

## Project summary

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## Introduction

Why certain species go extinct while others do not is one of the most fundamental questions in paleobiology. It is expected that for the majority of geological time, extinction is biologically non-random [64, 85, 87, 95, 96, 104, 105]. Determining which biological factors or traits influence extinction risk and how is vital for understanding the differential diversification of life during the Phanerozoic. Periods of background extinction also represent the majority of geologic time, remain relatively predictable and change slowly, and thus providing a better opportunity to study how traits are related to survival than periods of mass extinction [87, 111]. The Law of Constant Extinction [122] posits that extinction risk of taxa within a given adaptive zone is age independent (memoryless), however the generality of this statement is possibly suspect [77, 78, 109, 114]. By analyzing survival patterns within adaptive zones during periods of background extinction, it should be possible to determine if extinction is best modeled as age independent or dependent.

A simple expectation based on purely stochastic grounds, where extinction is not selective, is that abundant and widespread taxa are less likely to go extinct than rare and restricted taxa [? ]. For example, species with larger geographic ranges tend to have lower extinction rates than species with smaller geographic ranges [84, 87, 90, 104, 113]. However, this common pattern does not explain why certain taxa may be less prone to extinction than others. In the example, how range size is formed varies between clades and thus remains a black box for most taxa [86] and so determining if differential extinction is a purely stochastic process or is actually the product of selection is impossible. Instead, by focusing on traits related to environmental preference, the traits which may underly why a taxon is abundant or widespread, the process of selection underlying differential extinction may be elucidated.

In addition to understanding patterns of survival, how community composition changes over time is extremely important for understanding how trophic structure changes or is maintained over time. Additionally, community connectedness is important for understanding the degree to which global, regional, or local scale processes are important for shaping the environment, or the set of all possible biotic and abiotic interactors. In addition to total community connectedness, the dynamics of connectedness of taxa within various ecological categories are important for understanding whether different adaptive conditions are differently affected by global, regional, or local scale processes. The Law of Constant extinction is theorized to hold during periods of environmental stability and is thus considered extremely difficult/impossible to test [99]. However, if environmental shifts are incorporated into the analysis of survival distributions, it may be possible to actually test the relationship between taxon age and extinction risk in the context of their adaptive zone

and environment. Additionally, this may allow for illumination of what actual processes underly extinction during the majority of geologic time.

It is under this framework that I propose to study how ecological traits associated with environmental preference have affected both differential survival and cosmopolitan-endemism dynamics. I will be studying two distantly related and biotically different groups: Permian brachiopods and Cenozoic mammals. Both of these groups are considered to have very good fossil records able to reflect long term evolutionary patterns [102]. These two time periods were chosen because they represent periods of approximately the same length (47 My and 65 My) and of climatic change, global warming and global cooling respectively. Also, these two groups are a marine and terrestrial system respectively and the traits associated with environmental preference and range size (described below) are fundamentally very different. Both patterns of survival and community connectedness will be measured for both of these groups. The differences between these two groups in terms of life-habit and environmental preference, along with global climatic context, provides a fantastic scenario to understand how long-term, large-scale processes away from mass extinctions proceed.

Mammals are motile organisms which can track their preferred environmental context over time and space. However, if a taxon requires rare or fragile environmental conditions, or is a poor disperser, this would limit the availability of suitable environments or ability to track the preferred environment. Three important traits that describe the relationship between mammals and their environmental context are body size, dietary category, and locomotor category [74, 75, 94, 100, 101, 117, 118]. Each of these traits describe different aspects of a taxon's adaptive zone such as energetic cost, population density, expected home range size, set of potential prey items, and dispersal ability among others.

Environmental availability, along with stability, is crucial for both the establishment and persistence of a species. During the Cenozoic, primarily between the Paleogene–Neogene, there was a shift from a predominately closed environment to a predominately open environment [70, 92, 112]. This environmental shift was differently timed between continents [119, 120]. Because of the differential timing of environmental shift, along with the different biotic context, the survival and community patterns are expected to vary between continents.

Dietary categories are coarse groupings of similar dietary ecologies: carnivores, herbivores, omnivores, and insectivores. Each of these categories is composed of taxa with a variety of ecologies. For example, herbivores include both browsers and grazers which are known to have had different diversification dynamics during the Cenozoic [91]. Dietary categories are roughly linked with position in trophic hierarchy, with decreasing stability away from the “base.” Stability here meaning trophic “distance” from primary productivity, with herbivores having greater stability than carnivores because of the increased likelihood of prey item occurrence. Additionally, with increased likelihood of prey item occurrence, abundance can increase [72, 74, 91, 115, 124] which can effect both survival and increase occupancy [71, 82, 93, 94].

Locomotor categories describe the motility of a taxon, the plausibility of occurrence, and dispersal ability. 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. Locomotor categories are similar to dietary categories in that they represent coarse groupings of taxa with similar life habits. Here, the categories are arboreal, ground dwelling, and scansorial. Similar to dietary category, this trait is considered constant at the specific level. Dispersal ability is important

for determining the extent of a taxon’s geographic range [69, 83, 89] and affects both the taxon’s extinction risk and regional community evenness. With the transition from primarily closed to open environments, there is an expected shift in stability associated with arboreal and ground dwelling taxa.

An organisms body size, here defined as (estimated) mass, has an associated energetic cost in order to maintain homeostasis which in turn necessitates a supply of prey items. Many life history traits are associated with body size: reproductive rate, metabolic rate, home range size, among others [72, 74, 106, 117]. While studies of body size dynamics are very common [67, 73, 75, 95, 97], the interactions or processes that are correlated with body size might better explain the observed diversity pattern more than body size itself. By combining analysis of body size and both dietary and locomotor categories, it should be possible to better understand what processes underly the patterns of survival and community connectedness.

Because dietary category describes, roughly, the trophic position of a taxon and its related stability, it is predicted that more stable categories will have longer durations than less stable categories. Stability here being “distance” from primary productivity, thus it is expected that herbivores will have greater duration than carnivores. Omnivorous taxa are expected to have average taxon durations compared to the other two categories. If dietary category is not found to be important for modeling survival it may mean that trophic category is not a major factor for determining species level survival and that other factors, such as body size, may dominate.

Mammalian herbivores and carnivores have been found to have a greater diversification rate than omnivores [107] which may indicate that these traits are better for survival. However diversification can be caused either by an increase in origination relative to extinction or a decrease in extinction relative to origination. Which scenario occurred, however, is (currently) impossible to determine from a phylogeny of only extant organisms [108] which means that analysis of the fossil record is required. If survival is found to be similar between all dietary categories, this may mean that the differential diversification patterns observed by Price et al. [107] are due to differences in speciation and not extinction.

It is expected that arboreal taxa during the Paleogene will have a greater expected duration than Neogene taxa while the opposite will be true for ground dwelling taxa. In comparison, taxon duration of scansorial taxa is expected to remain relatively similar between the two time periods because it represents a mixed environmental preference that may be viable in either closed or open environments. If locomotor category is not included in the best model of survival this may mean that it is either a poor descriptor of dispersal ability, which may or may not affect mammalian survival. It may also be the case that other factors, measured or unmeasured, may be of greater importance in determining differential survival. The difficulty of a Paleogene–Neogene comparison, which is potentially undermined by heterogeneous preservation, will be explored in simulation.

Body size can possibly scale up to affect species level patterns because, for example, as body size increases, home range size increases [74]. If individual home range size scales up to reflect minimum total species geographic range, we would expect that taxa with larger body sizes would have lower extinction rates than species with smaller body sizes. This expectation, however, may not be right. As body size increases, reproductive rate decreases [95], populations get smaller [125], and generations get longer [103] all of which can increase extinction risk, as has been observed

[76, 97]. However, the relationship between body size and extinction rate at the generic level has been found to vary between continents [97, 121]. By expanding to include a third continent, South America, and analyzing specific level data I hope to elucidate how differences in taxonomic diversity at a continental level might affect body size mediated extinction rate. If body size is found to be unimportant for modeling survival, as in the generic level analysis of Tomiya [121], this means that other biotic or abiotic factors may dominate. This may also mean that individual level home range size does not scale to increased species level range size, and there is therefore no correlated decrease in extinction rate. If increase in body size increases extinction risk, this may be due to traits correlated with body size and not necessarily body size itself [95].

The interaction of body size, locomotor category, and dietary category is also extremely important. For example, a small bodied arboreal taxon of any trophic category during the heavily forested and warm time of the Paleogene would be expected at once to have both a small body size determined range, a large potential geographic range determined by locomotion, as well as an increased availability of resources. Together this would mean that relative survival would be expected to be less than, greater than, and greater than average respectively. Determining which factors dominate during the Paleogene, as well as other parts of the Cenozoic, must be done empirically.

To analyze differential mammalian survival, I propose a survival analysis approach similar to that described above for Permian brachiopods. Mammalian occurrence data will be collected primarily through a combination of the PBDB, Neogene Old World Database (NOW; <http://www.helsinki.fi/science/now/>) and museum collections. North American fossil mammal data are well represented in the PBDB because of the extensive work of Alroy [65–67]. European fossil mammal data is also well represented between the PBDB and NOW. South American fossil mammal data is available through the PBDB, but has poor overall coverage. Because of this, South American fossil mammal data will be gathered via various museums such as the Field Museum of Natural History and the American Museum of Natural History as well as published occurrence compilations. With the South American taxa, taxonomy and sampling may not be as well resolved as for North and South America and it may be necessary to restrict analysis to the most taxonomically resolved and sampled groups such as Notoungulata, Marsupials, Carnivora, and Primates.

As described above, duration will be measured as the difference between the observed FAD and LAD of every taxon. Taxa which originated prior to the Cenozoic and all taxa that are either extant or went extinct within 2 My of the present will be censored. This threshold is to limit the effect of the improved record of the Recent.

Dietary category, locomotor category, and body size will be considered constant throughout the duration of a taxon and will be modeled as time-independent covariates of survival. While body size is actually a distribution of values, it is quite common to use a single estimate of mean body size as an aggregate trait in studies of clade-wise dynamics [88]. While all three of these traits may have evolved over a taxon’s duration, this will not be considered as part of this study.

While many analyses of survivorship are done using generic data [78, 80, 84, 97, 121], there are potential biases in accurately modeling a specific level process using generic level data [109, 110, 114, 116, 123]. In order to assess some of the differences between generic and specific level survival, I will estimate specific and generic level survival models. Using an approach similar to previous work on estimating specific level origination and extinction rates from generic level survival curves [79], I

will measure the deviance between extinction rate directly estimated from the specific survivorship and the specific level extinction rates estimated from the generic level survival data. In addition to empirical comparison between generic and specific level survival, simulations of diversification with varying levels of cryptic speciation (anagenesis). This may also act as a proxy for generic level diversification because a lineage having a long duration because it is not correctly broken up can be considered analogous to a genus persisting because it continues to speciate.

In order to account for environmental shifts, two different time-dependent covariates will be used.  $\delta O^{18}$  isotope information for the whole Cenozoic [126] will be used as a global climate proxy. Additionally, the Paleogene–Neogene divide, which may reflect global environmental shift, will be modeled as a time-dependent step-function.

## Preliminary results and proposed work

### Intellectual merit

### Broader impacts

## References Cited

- [64] Richard R Alexander. Generic longevity of articulate brachiopods in relation to the mode of stabilization on the substrate. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 21:209–226, 1977.
- [65] John Alroy. Constant extinction, constrained diversification, and uncoordinated stasis in North American mammals. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 127:285–311, 1996.
- [66] John 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.
- [67] John Alroy, Paul L Koch, and James C Zachos. Global climate change and North American mammalian evolution. *Paleobiology*, 26(1981):259–288, 2000.
- [69] Aysegul Birand, Aaron Vose, and Sergey Gavrilets. Patterns of species ranges, speciation, and extinction. *The American naturalist*, 179(1):1–21, January 2012. ISSN 1537-5323. doi: 10.1086/663202. URL <http://www.ncbi.nlm.nih.gov/pubmed/22173457>.
- [70] Jessica L Blois and Elizabeth 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.
- [71] James H. Brown. On the Relationship between Abundance and Distribution of Species. *The American Naturalist*, 124(2):255, August 1984. ISSN 0003-0147. doi: 10.1086/284267. URL <http://www.journals.uchicago.edu/doi/abs/10.1086/284267>.

- [72] James H Brown and Brian A Maurer. Evolution of species assemblages: effects of energetic constraints and species dynamics on the diversification of the North American avifauna. *The American Naturalist*, 130(1):1–17, 1987.
- [73] Aaron Clausen and Douglas H Erwin. The evolution and distribution of species body size. *Science*, 321:399–401, 2008.
- [74] J Damuth. Home range, home range overlap, and species energy use among herbivorous mammals. *Biological Journal of the Linnean Society*, 15:185–193, 1979.
- [75] J Damuth. Population density and body size in mammals. *Nature*, 290:699–700, 1981. URL <http://www.jstor.org/stable/10.2307/2461771>  
<http://www.nature.com/nature/journal/v290/n5808/abs/290699a0.html>.
- [76] Ana D Davidson, Alison G Boyer, Hwahwan Kim, Sandra Pompa-Mansilla, Marcus J Hamilton, Daniel P Costa, Gerardo Ceballos, and James H Brown. Drivers and hotspots of extinction risk in marine mammals. *Proceedings of the National Academy of Sciences*, 109(9):3395–400, February 2012. ISSN 1091-6490. doi: 10.1073/pnas.1121469109. URL <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3295301&tool=pmcentrez&rendertype>
- [77] John M. Drake. Tail probabilities of extinction time in a large number of experimental populations. *Ecology*, page 140206083444001, February 2014. ISSN 0012-9658. doi: 10.1890/13-1107.1. URL <http://www.esajournals.org/doi/abs/10.1890/13-1107.1>.
- [78] Seth Finnegan, Jonathan L. Payne, and Steve C. Wang. The Red Queen revisited: reevaluating the age selectivity of Phanerozoic marine genus extinctions. *Paleobiology*, 34(3):318–341, September 2008. ISSN 0094-8373. doi: 10.1666/07008.1. URL <http://www.bioone.org/doi/abs/10.1666/07008.1>.
- [79] Michael Foote. Survivorship analysis of Cambrian and Ordovician Trilobites. *Paleobiology*, 14(3):258–271, 1988.
- [80] Michael Foote. Substrate affinity and diversity dynamics of Paleozoic marine animals. *Paleobiology*, 32(3):345–366, September 2006. ISSN 0094-8373. doi: 10.1666/05062.1. URL <http://www.bioone.org/doi/abs/10.1666/05062.1>.
- [82] Mikael Fortelius, Jussi Eronen, Jukka Jernvall, Liping Liu, Diana Pushkina, Juhani Rinne, Alexey Tesakov, Inesa Vislobokova, Zhaoqun Zhang, and Liping Zhou. Fossil mammals resolve regional patterns of Eurasian climate change over 20 million years. *Evolutionary Ecology Research*, 4:1005–1016, 2002.
- [83] Kevin J Gaston. Geographic range limits: achieving synthesis. *Proceedings. Biological sciences / The Royal Society*, 276(1661):1395–406, April 2009. ISSN 0962-8452. doi: 10.1098/rspb.2008.1480. URL <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=2677218&tool=pmcentrez&rendertype>
- [84] 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), October 2013. ISSN 0962-8452. doi: 10.1098/rspb.2012.1902. URL <http://rspb.royalsocietypublishing.org/cgi/doi/10.1098/rspb.2012.1902>.

- [85] Paul G Harnik. Direct and indirect effects of biological factors on extinction risk in fossil bivalves. *Proceedings of the National Academy of Sciences of the United States of America*, 108(33):13594–9, August 2011. ISSN 1091-6490. doi: 10.1073/pnas.1100572108. URL <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3158225&tool=pmcentrez&rendertype=full>
- [86] D Jablonski. Heritability at the species level: analysis of geographic ranges of cretaceous mollusks. *Science*, 238(4825):360–363, October 1987. ISSN 0036-8075. doi: 10.1126/science.238.4825.360. URL <http://www.ncbi.nlm.nih.gov/pubmed/17837117>.
- [87] David Jablonski. Background and mass extinctions: the alternation of macroevolutionary regimes. *Science*, 231(4734):129–133, 1986.
- [88] David Jablonski. Species Selection: Theory and Data. *Annual Review of Ecology, Evolution, and Systematics*, 39(1):501–524, December 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>.
- [89] David Jablonski and Gene Hunt. Larval ecology, geographic range, and species survivorship in Cretaceous mollusks: organismic versus species-level explanations. *The American naturalist*, 168(4):556–64, October 2006. ISSN 1537-5323. doi: 10.1086/507994. URL <http://www.ncbi.nlm.nih.gov/pubmed/17004227>.
- [90] David Jablonski and Kaustuv Roy. Geographical range and speciation in fossil and living molluscs. *Proceedings. Biological sciences / The Royal Society*, 270(1513):401–6, February 2003. ISSN 0962-8452. doi: 10.1098/rspb.2002.2243. URL <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=1691247&tool=pmcentrez&rendertype=full>
- [91] C M Janis, J Damuth, and J M Theodor. Miocene ungulates and terrestrial primary productivity: where have all the browsers gone? *Proceedings of the National Academy of Sciences*, 97(14):7899–904, July 2000. ISSN 0027-8424. URL <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=16642&tool=pmcentrez&rendertype=full>
- [92] Christine M Janis. Tertiary mammal evolution in the context of changing climates, vegetation, and tectonic events. *Annual Review of Ecology and Systematics*, 24:467–500, 1993.
- [93] Jukka Jernvall and Mikael 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.
- [94] Jukka Jernvall and Mikael Fortelius. Maintenance of trophic structure in fossil mammal communities: site occupancy and taxon resilience. *American Naturalist*, 164(5):614–624, November 2004. ISSN 1537-5323. doi: 10.1086/424967.
- [95] C N Johnson. Determinants of loss of mammal species during the Late Quaternary ‘megafauna’ extinctions: life history and ecology, but not body size. *Proceedings of the Royal Society B: Biological Sciences*, 269:2221–2227, 2002. doi: 10.1098/rspb.2002.2130.
- [96] Jennifer A Kitchell, David L Clark, and Andrew M Gombos. Biological selectivity of extinction: a link between background and mass extinction. *Palaios*, 1(5):504–511, 1986.



- [97] L H Liow, Mikael 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](http://papers2://publication/uuid/5A93DDA3-204F-4D9C-AFAC-A15722A18C61).
- [99] Lee Hsiang Liow, Leigh Van Valen, and Nils Chr Stenseth. Red Queen: from populations to taxa and communities. *Trends in ecology & evolution*, 26(7):349–58, July 2011. ISSN 0169-5347. doi: 10.1016/j.tree.2011.03.016. URL <http://www.ncbi.nlm.nih.gov/pubmed/21511358>.
- [100] S Kathleen Lyons. A quantitative model for assessing community dynamics of pleistocene mammals. *The American naturalist*, 165(6):E168–85, June 2005. ISSN 1537-5323. doi: 10.1086/429699. URL <http://www.ncbi.nlm.nih.gov/pubmed/15937741>.
- [101] S Kathleen Lyons, Peter J Wagner, and Katherine Dzikiewicz. Ecological correlates of range shifts of Late Pleistocene mammals. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 365(1558):3681–93, November 2010. ISSN 1471-2970. doi: 10.1098/rstb.2010.0263. URL <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=2981999&tool=pmcentrez&rendertype=full>.
- [102] Graham A Mark and Karl W Flessa. A test for evolutionary equilibria: Phanerozoic brachiopods and Cenozoic mammals. *Paleobiology*, 3(1):17–22, 1977.
- [103] A P Martin and S R Palumbi. Body size, metabolic rate, generation time, and the molecular clock. *Proceedings of the National Academy of Sciences*, 90(9):4087–91, May 1993. ISSN 0027-8424. URL <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=46451&tool=pmcentrez&rendertype=full>.
- [104] Sabine Nürnberg and Martin Aberhan. Habitat breadth and geographic range predict diversity dynamics in marine Mesozoic bivalves. *Paleobiology*, 39(3):360–372, April 2013. ISSN 0094-8373. doi: 10.1666/12047. URL <http://www.bioone.org/doi/abs/10.1666/12047>.
- [105] Jonathan L Payne and Seth Finnegan. The effect of geographic range on extinction risk during background and mass extinction. *Proceedings of the National Academy of Sciences of the United States of America*, 104(25):10506–11, June 2007. ISSN 0027-8424. doi: 10.1073/pnas.0701257104. URL <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=1890565&tool=pmcentrez&rendertype=full>.
- [106] Robert Henry Peters. *The ecological implications of body size*. Cambridge University Press, Cambridge, 1983.
- [107] Samantha A Price, Samantha S B Hopkins, Kathleen K Smith, and V Louise 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>.
- [108] Daniel 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>.
- [109] David M Raup. Taxonomic survivorship curves and Van Valen’s Law. *Paleobiol-*

- ogy, 1(1):82–96, January 1975. ISSN 0036-8075. doi: 10.1126/science.49.1254.50. URL <http://www.ncbi.nlm.nih.gov/pubmed/17777225>.
- [110] David M Raup. A kill curve for Phanerozoic marine species. *Paleobiology*, 17(1):37–48, 1991.
- [ ] David M Raup. *Extinction: Bad Genes or Bad Luck?* Norton, New York, 1991.
- [111] David M Raup and George E Boyajian. Patterns of generic extinction in the fossil record. *Paleobiology*, 14(2):109–125, 1988.
- [112] Kenneth D Rose. *The beginning of the age of mammals*. Johns Hopkins University Press, Baltimore, Md, 2006.
- [113] Kaustuv Roy, Gene Hunt, David Jablonski, Andrew Z Krug, and James W Valentine. A macroevolutionary perspective on species range limits. *Proceedings. Biological sciences / The Royal Society*, 276(1661):1485–93, April 2009. ISSN 0962-8452. doi: 10.1098/rspb.2008.1232. URL <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=2677224&tool=pmcentrez&rendertype>
- [114] J John Sepkoski. Stratigraphic biases in the analysis of taxonomic survivorship. *Paleobiology*, 1(4):343–355, 1975.
- [115] Marina Silva, James H. Brown, and John a. Downing. Differences in Population Density and Energy Use between Birds and Mammals: A Macroecological Perspective. *The Journal of Animal Ecology*, 66(3):327, May 1997. ISSN 00218790. doi: 10.2307/5979. URL <http://www.jstor.org/stable/5979?origin=crossref>.
- [116] Carl Simpson. *Levels of selection and large-scale morphological trends*. PhD thesis, University of Chicago, 2006.
- [117] F A Smith, J Brown, J Haskell, and S Lyons. Similarity of mammalian body size across the taxonomic hierarchy and across space and .... *The American Naturalist*, 2004. URL <http://www.journals.uchicago.edu/doi/abs/10.1086/382898> papers2://publication/uuid/D5606802-FD91-49EB-BE2F-E2D314A5E71D.
- [118] F. A. Smith, S. K. Lyons, S.K. Morgan Ernest, and J. H. Brown. Macroecology: more than the division of food and space among species on continents. *Progress in Physical Geography*, 32(2):115–138, April 2008. ISSN 0309-1333. doi: 10.1177/0309133308094425. URL <http://ppg.sagepub.com/cgi/doi/10.1177/0309133308094425>.
- [119] Caroline 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, August 2005. ISSN 0027-8424. doi: 10.1073/pnas.0505700102. URL <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=1189350&tool=pmcentrez&rendertype>
- [120] Caroline A E Strömberg, Regan E Dunn, Richard H Madden, Matthew J Kohn, and Alfredo A Carlini. Decoupling the spread of grasslands from the evolution of grazer-type herbivores in South America. *Nature communications*, 4:1478, January 2013. ISSN 2041-1723. doi: 10.1038/ncomms2508. URL <http://www.ncbi.nlm.nih.gov/pubmed/23403579>.

- [121] Susumu Tomiya. Body Size and Extinction Risk in Terrestrial Mammals Above the Species Level. *The American Naturalist*, pages E000–E000, September 2013. ISSN 00030147. doi: 10.1086/673489. URL <http://www.jstor.org/stable/info/10.1086/673489>.
- [122] Leigh Van Valen. A new evolutionary law. *Evolutionary Theory*, 1:1–30, 1973. URL <http://ci.nii.ac.jp/naid/10011264287/>.
- [123] Leigh Van Valen. Taxonomic survivorship curves. *Evolutionary Theory*, 4:129–142, 1979.
- [124] Leigh Van Valen. Three paradigms of evolution. *Evolutionary Theory*, 9:1–17, 1989.
- [125] Ethan P White, S K Morgan Ernest, Andrew J Kerkhoff, and Brian J Enquist. Relationships between body size and abundance in ecology. *TRENDS in Ecology and Evolution*, 22(6):323–30, June 2007. ISSN 0169-5347. doi: 10.1016/j.tree.2007.03.007. URL <http://www.ncbi.nlm.nih.gov/pubmed/17399851>.
- [126] James C Zachos, Gerald R Dickens, and Richard E Zeebe. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature*, 451(7176):279–283, January 2008. ISSN 1476-4687. doi: 10.1038/nature06588.

## Biographical sketch

Peter D. Smits

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## Professional preparation

University of Washington	Biology (Ecology and Evolution)	B.S. 2010
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University of Chicago	Evolutionary Biology	Ph.D. 2017 (expected)

## Appointments

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July 2010–August 2010, Lab Assistant, Vertebrate Paleontology, Burke Museum of Natural History, University of Washington.

July 2009–August 2009, REU Intern, Mammalogy, American Museum of Natural History.

September 2006–September 2008, Lab and Field Assistant, Mammalogy, Burke Museum of Natural History and Culture, University of Washington.

## Products

### Related publications

- .

### Unrelated publications

- .
- .
- .

## Synergistic activities

Reviewer for *Systematic Biology*, *PLOS One*.

Member of student mental health panel GSMAB, University of Chicago, 2014–present.

Volunteer instructor for peer led programming class, University of Chicago, 2012–2013.

Volunteer expert at “Dino-Day” at the Burke Museum of Natural History and Culture, 2010.

Volunteer expert at “Meet the Mammals” at the Burke Museum of Natural History and Culture, 2007, 2008, 2009.

## **Collaborators and other affiliations**

### **Collaborators and co-editors**

Philip D. Clausen (University of Newcastle), Liliana M. Davalos (Stony Brook University), Alistair R. Evans (Monash University), Richard H. Madden (University of Chicago), Matthew R. McCurry (Monash University), Colin R. McHenry (Monash University), Christopher C. Oldfield (University of Newcastle), P. David Polly (University of Indiana–Bloomington), Michelle R. Quayle (Monash University), Richard H. Ree (Field Museum of Natural History), Heather S. Richards (University of Newcastle), Nancy B. Simmons (American Museum of Natural History), Christopher W. Wamsley (Monash University), Omar M. Warsi (Stony Brook University), Stephen Wroe (University of New England), Paul M. Velazco (American Museum of Natural History).

### **Graduate advisors and postdoctoral sponsors**

Kenneth D. Angielczyk (Field Museum of Natural History), Michael J. Foote (University of Chicago).

## **Facilities, equipment, & other resources**

### **Major equipment**

Calipers, both small (12”) and large (24”), are available through the Committee on Evolutionary Biology.

### **Laboratory**

NA

### **Clinical**

NA

### **Animal**

NA

### **Computer**

All data collected from both databases and personal measurements will be stored on a personal computer owned by the Co-PI as well as in both cloud storage and external hard drives. Computer expertise is available at the University of Chicago and the Co-PI has access to large-scale computer clusters via the University of Chicago. All analysis software is free and open-source and is installed on the Co-PI's personal computer and can be installed on all additionally necessary computing clusters.

### **Office**

The PI has dedicated office space at the Field Museum of Natural History. The Co-PI has dedicated office space provided by both the Committee on Evolutionary Biology and the Department of Geophysical Sciences.

### **Other**

NA

## Data management plan

The major data and analytical products of the proposed project are 1) anatomical measurements of specimens from museum collections, 2) organized and updated ecological information, and 3) statistical analysis code. All information gathered will be stored indefinitely on both the PI's and Co-PI's personal computers. Additionally, they will be archived on an external hard drive indefinitely in case of the loss of either personal computer.

All anatomical measurements and ecological information used in the proposed study will be provided as supplementary material for all papers produced from this research. These data will also be archived using the data storage service Dryad (<http://datadryad.org>). Finally, all measurements and ecological information will be available through the Co-PI's personal website (<http://home.uchicago.edu/psmits/home.html>).

Museums and other institutions where specimens will be measured will be named in all subsequent presentations and papers. These institutions will also be provided with all measurements made to housed specimens, as well as reprints of all related papers.

Anatomical measures, body mass estimates, and updated ecological information will be sent to the Paleobiology Database (<http://paleobiodb.org>) which is the largest repository of paleontological taxonomic, occurrence, and ecological information.

All code used in the proposed analyses will be archived using Dryad, along with the relevant data as discussed above. Code will also be made available through the Co-PI's GitHub page (<http://github.com/psmits>), a free code sharing and archiving service, as well as through the Co-PI's website (<http://home.uchicago.edu/psmits/home.html>).

The Co-PI will present the results of the proposed research at conferences and publish said results in peer-reviewed journals in the fields of evolution, paleontology, evolutionary ecology, and global conservation.