Conclusion

Macroevolution and macroecology are disciplines devoted to explaining emergent patterns in evolutionary and ecological data. These disciplines are linked through the analysis of the distribution of trait values across time, space, and/or species [16, 28]. Emergent evolutionary and ecological patterns in time can require at least a million of years to observe [25]. Paleontological and phylogenetic data preserve aspects of these large scale temporal patterns. Paleontological data is unique however in being empirical observations of these dynamics while phylogenetic data only preserves the branching history leading to the diversity pattern exhibited by the tips.

In the studies presented as a part of this dissertation, I have emphasized functional traits. These are traits which directly relate to the way in which a taxon interacts with its environment [16]. When these traits are defined for a species, they are called species traits [16]; examples include species geographic range, average body size, trophic level, environmental preference, etc. Functional traits are an excellent window in macroevolution and macroecology because of their obvious selective importance; an organism which cannot interact with its environment is by definition maladapted. Additionally, by focusing on functional traits as well as the inclusion of multiple traits in analysis improves overall process-based inference because the ways in which species interact have been emphasized.

1 Summary

All of the studies conducted here were analyses of fundamentally emergent patterns which are not reducible to the properties of their constituents. In each of these studies, hypotheses and analysis were framed in terms of how a species functional ecology can be associated with or shape these emergent patterns. Because of the complexity of processes which shape these emergent patterns, as well as the vagaries of the fossil record, each of these studies required the development of specific inference devices (e.g. statistical models) which attempt to estimate the actual quantities of interest to that analysis.

The emergent pattern at the heart of both the first and second studies (Chapters **??**, **??**) is species duration. A species endures because of the continued success of individuals of that species but the duration of that species is only knowable by integrating across all individuals. The third study (Chapter **??**) deals with a fundamentally different emergent pattern: the functional composition of a regional species pool. A regional species pool is the set of species present in all communities. While the functional composition of a community depends on the set of interactors at that locality, the functional composition of a regional species pool depends on the possibility of those interactors being present in at least one constituent community.

In Chapter **??** I tested two long standing hypotheses of how species durations are structured: the survival of the unspecialized hypothesis [24], and the

Law of Constant Extinction [26]. I analyzed how the distribution of mammal species durations is affected by differences in multiple species traits, species' phylogenetic relatedness, and species' origination cohort. My results supported the conclusion that generalist mammal species will, on average, have a greater duration than more specialized mammal species. I also found that phylogeny and origination cohort contribute sub-equally to variation in species duration. Finally, I found evidence of species extinction risk increasing with species duration, a result that is counter the Law of Constant Extinction.

Chapter **??** also deals with the survival of the unspecialized hypothesis as well as the Law of Constant Extinction, this time with the global record of post-Cambrian Paleozoic brachiopods. In addition to these hypotheses, I also analyzed the relationship between extinction intensity and the strength of trait selection, namely "do the selective differences between traits increase or decrease with average fitness increases or decreases?" I found a negative correlation between intensity of extinction and the effects of geographic range and environmental preference. As with Chapter **??**, I also found support for greater survival among environmental generalists than specialists. These results supported the conclusion that, at least for Paleozoic brachiopods, as extinction intensity increases, the selective difference of traits increases. In this analysis this means that when average duration decreases (e.g. intensity is high) the effect of genus geographic range increases in magnitude and taxa which favor epicontinental environments are expected to have a greater duration than those which favor open-ocean environments. I also find that

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the change in magnitude of effect is expected to be greater for environmental preference than for geographic range as the overall effect of former have a much greater variance than that of the later.

The final study of this dissertation (Chapter **??**) was an analysis of how the functional composition of the North American mammal regional species pool changed over time and in response to multiple environmental factors. The goals of this analysis were to understand when are different ecotypes enriched or depleted in the regional species pool, and to undestand how changes to environmental context may affect changes to the functional diversity of the regional species pool. By focusing on functional groups instead of taxonomic groups, the results from this study are phrased in terms of species interactions and not differences in clade diversity. My results add considerable nuance to the taxon-focused narrative of North American environmental change. There are many results and conclusions from this analysis, so I focus here on a few key results. I found that mammal diversity is more strongly shaped by changes to origination rate among a few ecotypes rather than being driven by selective extinction one or more ecotypes. I also found that all arboreal ecotypes decline through out the Paleogene and disappear from the species pool by the Neogene. Additionally, I found that most herbivore ecotypes expand their relative contribution to functional diversity over time. Finally, I found that the environmental factors analyzed here structure differences in ecotype origination probability but not survival probability.

4

2 Synthesis

These three chapters are united by their analysis of species functional traits. Analysis of species traits is the easiest way to unite macroevolutionary and macroecological inference by using this commonality to develop and test integrated hypotheses [16, 28]. While individual hypotheses may be generated from macroevolution when inferrence based on traits the results are more transferable and can then generate new macroecological hypotheses; the reverse is of course also possible.

The first two studies, when considered together, add a considerable degree of nuance to our understanding of multiple macroevolutionary hypotheses such as the Law of Constant Extinction and the survival of the unspecialized.

First and foremost, the results of neither study support the Law of Constant Extinction [26]. Instead, I found evidence for extinction risk increasing with taxon duration. Instead, these results are consistent with those of a "nearly-neutral" theoretical model of macroevolution [23]. While the dynamics of this model are described as "Red Queen" [23], this is not strictly true as Red Queen dynamics as described by Van Valen [26] require that extinction does not increase with taxon age. Instead, the dynamics of the nearly-neural model are "Red Queen" in the sense that while all species are increase in expected fitness, their relative fitnesses do not change. Interestingly, the decrease absolute in extinction risk towards the Modern [6, 22], which translates to an increase in

expected species duration, may reflect similar dynamics to the nearly-neutral model.

These two studies also provide broad support for the hypothesis of the survival of the unspecialized [24], at least with respect to the covariates included in either model. The survival of the unspecialized appears to be a nearly universal pattern in macroevolution [2, 13, 14, 17, 18, 21, 24]. I did find, however, that for post-Cambrian Paleozoic brachiopods when extinction intensity increases, the relationship with environmental preference and duration changes from pattern where intermediate environmental preference are favored to one where more specialized taxa from one end of the environmental spectrum are favored. This result adds a degree of nuance to the survival of the unspecialized, specifically with regards to when it is expected to "hold." My conclusion is that during periods of low intensity extinction risk or "background extinction" [7, 12], the survival of the unspecialized hypothesis will hold. However, as extinction intensity increases, this hypothesis may not accurately describe differences in extinction risk across taxa. As such, the survival of the unspecialized may serve as an excellent default for studies of trait selection and taxon extinction.

In the third study I analyzed how the functional composition of a regional species pool changes over millions of years (Chapter ??). While this pattern is macroecological, many of the hypotheses and questions encompassed by this study were generated from macroevolutionary analyses. For example, the result from the first study that arboreal taxa have a greater extinction risk than

other mammal locomotor groups did not have an unambiguous explanation for if and how extinction risk could have changed over the Cenozoic: always present but high risk, or higher extinction risk in the Neogene compared to the Paleogene (Chapter **??**). The third study, in its analysis of the relative diversity of mammal ecotypes, was able to more fully resolve the previous results as I found that diversity of arboreal ecotypes declined through the Paleogene, becoming extremely rare or entirely absent from the species pool by the Neogene (Chapter **??**). This result is much more nuanced than the either of two proposed processes (Chapter **??**) and speaks to the improved insights and inferences a unified macroevolutionary and macroecological research program can provide.

The third study also, methodologically, represents the strongest unification of macroevolutionary and macroecological approaches to inference (Chapter **??**). The question at the heart of this study is "when are mammal ecotypes enriched or depleted relative there average diversity" is both macroevolutionary and macroecological, inference needed to represent this. The model at the center of this study was a combination of a birth-death process with a fourth-corner model from ecology. The birth-death process provided a mechanism for changes to species diversity over time while the fourth-corner model recast diversification in terms of the relative contribution of functional groups to the regional species pool. The results of this study could then be phrased in how well adapted the functional groups are to their changing environmental context.

3 Future

There are many possible ways to expand on the analyses presented in this dissertation. There are also many unanswered questions which have been raised by each of these analyses which require future study.

A major limitation the fossil record of North American mammals is poor spatial resolution for the entire Cenozoic, something that restricts macroecological analyses (Chatter ??). While a regional species pool represents the set of all species present in a region, the individual dynamics communities give a much more complete idea of why species pool diversity changes. For example, I've been unable to estimate how changes to functional diversity of local communities scales up to the functional diversity of the regional species pool these communities are drawn from [11]. Given a fossil record with a high resolution spatial record, the types of analyses presented in Chapter ?? could be expanded to incorporate the spatial dynamics of functional diversity. The Bayesian modeling framework used throughout this dissertation makes this imminently possible given the right dataset [1]. The results of such an analysis would shed a lot of light on how the functional diversity of communities can vary spatially and how those communities respond differently to environmental change.

Preservation of the fossil record is a pervasive issue in paleontology [3–5, 8, 15, 27]. The first two studies gloss over issues of preservation by either ignoring

it (Chapter **??**) or including a sampling proxy as a covariate (Chapter **??**); these decisions were partially due to limitations of the models underlying both those studies. In contrast, in Chapter **??** I directly modeled the preservation process and allowed preservation probability to vary with time and allowed species body size to potentially affect differences in preservation probability across taxa. However, I ignored the possible differences in preservation over time due to species functional group or changes to environmental context. I chose to limit the possible covariates which could affect of preservation because this type of analysis was beyond the scope of Chapter **??**.

All of three of these studies could be improved by incorporating more information about fossil preservation such as how functional groups and environmental context can shape differences in preservation probability. For example, when studying marine invertebrates covariates such as sea-level or shell composition (e.g. aragonitic vs calcitic) are all potentially very important for better understanding the differential preservation of species [9, 10, 19, 20]. Given a more representative model of preservation, even more complete and accurate macroevolutionary and macroecological inferences can be made.

4 Final thoughts

The three studies presented in this dissertation are all representative of my rhetoric championing integrated macroevolutionary and macroecological study

(Chapter **??**). Each study emphasizes the importance of framing hypotheses in terms of ecological interactions in order to make strong inferences. By using an extremely flexible and expressive modeling strategy, I have been able to translate precise scientific questions into statistical models. The scope of inferences that can be made for each study are clear and conditioned on the explicit modeling assumptions made for each analysis. My hope is that this approach to using paleontological data for answering questions about the processes underlying emergent patterns in evolutionary and ecological data fosters a stronger relationship between the disciplines of macroevolution and macroecology as well as paleontologists and neontologists.

References

[1] Sudipto Banerjee, Bradley P Carlin, and Alan E Gelfand. *Hierarchical modeling and analysis for spatial data*. Chapman and Hall/CRC, 2004.

[2] Tomasz K Baumiller. Survivorship analysis of Paleozoic Crinoidea: effect of filter morphology on evolutionary rates. *Paleobiology*, 19(3):304–321, 1993.

[3] M Foote and J J Sepkoski. Absolute measures of the completeness of the fossil record. *Nature*, 398(6726):415–7, apr 1999. ISSN 0028-0836. doi: 10.1038/18872. URL http://www.ncbi.nlm.nih.gov/pubmed/11536900.

[4] Michael Foote. Estimating taxonomic durations and preservation probability. *Paleobiology*, 23(3):278–300, 1997. URL http://www.psjournals.org/paleoonline/?request=get-abstract&issn=0094-8373&vol

[5] Michael Foote. Inferring temporal patterns of preservation, origination, and extinction from taxonomic survivorship analysis. *Paleobiology*, 27(4):602–630, dec 2001. ISSN 0094-8373. doi: 10.1666/0094-8373(2001)027¡0602:ITPOPO¿2.0.CO;2. URL http://www.bioone.org/doi/abs/10.1666/0094-8373%282001%29027%3C0602%3AITPOPO%3

[6] Michael Foote. Origination and extinction through the Phanerozoic: a new approach. *Journal of Geology*, 111:125–148, 2003.

11

[7] Michael Foote and Arnold I Miller. *Principles of Paleontology*. Freeman, New York, third edition, 2007.

[8] Michael Foote and DM Raup. Fossil preservation and the stratigraphic ranges of taxa. *Paleobiology*, 22(2):121–140, 1996. URL http://www.psjournals.org/paleoonline/?request=get-abstract&issn=0094-8373&vol

[9] Michael Foote, James S Crampton, Alan G Beu, and Campbell S Nelson. Aragonite bias, and lack of bias, in the fossil record: lithological, environmental, and ecological controls. *Paleobiology*, 41(2):245–265, 2015. doi: 10.1017/pab.2014.16.

[10] Bjarte Hannisdal and Shanan E Peters. Phanerozoic Earth system evolution and marine biodiversity. *Science*, 334:1121–1124, nov 2011. ISSN 1095-9203. doi: 10.1126/science.1210695. URL http://www.ncbi.nlm.nih.gov/pubmed/22116884.

[11] Susan Harrison and Howard Cornell. Toward a better understanding of the regional causes of local community richness. *Ecology Letters*, 11: 969–979, 2008. doi: 10.1111/j.1461-0248.2008.01210.x.

[12] David Jablonski. Background and mass extincitons: the alternation of macroevolutionary regimes. *Science*, 231(4734):129–133, 1986.

[13] Lee Hsiang Liow. A test of Simpson's "rule of the survival of the relatively unspecialized" using fossil crinoids. *The American Naturalist*,

164(4):431–43, oct 2004. ISSN 1537-5323. doi: 10.1086/423673. URL
http://www.ncbi.nlm.nih.gov/pubmed/15459876.

[14] Lee Hsiang Liow. Does versatility as measured by geographic range, bathymetric range and morphological variability contribute to taxon longevity? *Global Ecology and Biogeography*, 16(1):117–128, 2007. URL http://doi.wiley.com/10.1111/j.1466-8238.2006.00269.x papers2://publication/doi/10.1111/j.1466-8238.2006.00269.x.

[15] G T Lloyd, J R Young, and A B Smith. Taxonomic Structure of the Fossil Record is Shaped by Sampling Bias. *Systematic Biology*, 61(1):80–89, 2011. URL http://sysbio.oxfordjournals.org/cgi/doi/10.1093/sysbio/syr076 papers2://publication/doi/10.1093/sysbio/syr076.

[16] Brian J McGill, Brian J Enquist, Evan Weiher, and Mark Westoby. Rebuilding community ecology from functional traits. *TRENDS in Ecology and Evolution*, 21(4):178–185, 2006. doi: 10.1016/j.tree.2006.02.002.

[17] Sabine Nürnberg and Martin 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.

[18] Sabine Nürnberg and Martin Aberhan. Interdependence of specialization and biodiversity in Phanerozoic marine invertebrates. *Nature Communi-*

266 *cations*, 6:6602, jan 2015. ISSN 2041-1723. doi: 10.1038/ncomms7602. URL http://www.ncbi.nlm.nih.gov/pubmed/25779979.

268 [19] Shanan E Peters and Michael Foote. Determinants of extinction in the fossil record. *Nature*, 416(6879):420–4,
270 mar 2002. ISSN 0028-0836. doi: 10.1038/416420a. URL http://www.ncbi.nlm.nih.gov/pubmed/11919629.

272 [20] Shanan E Peters and Noel A Heim. The geological completeness of paleontological sampling in North America. *Paleobiology*, 36(1):61–79,
274 2010.

[21] Pasquale Raia, Francesco Carotenuto, A Mondanaro, S Castiglione,
276 F Passaro, F Saggese, M Melchionna, C Seiro, L Alessio, D Silvestro, and M Fortelius. Progress to extinction: increased special-
278 isation causes the demise of animal clades. *Scientific Reports*, 6: 30965, 2016. ISSN 2045-2322. doi: 10.1038/srep30965. URL
280 http://www.nature.com/articles/srep30965.

[22] David M Raup and J John Sepkoski. Mass Extinctions in the Marine
282 Fossil Record. *Science*, 215(4539):1501–1503, 1982.

[23] James Rosindell, Luke J Harmon, and Rampal S Etienne. Unifying ecol-
284 ogy and macroevolution with individual-based theory. *Ecology Letters*, 18(5):472–482, may 2015. ISSN 1461-0248. doi: 10.1111/ele.12430. URL
286 http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=4403962&tool=pmcentr

[24] George Gaylord Simpson. *Tempo and Mode in Evolution.* Columbia University Press, New York, 1944.

[25] J C Uyeda, T F Hansen, S J Arnold, and J Pienaar. The million-year wait for macroevolutionary bursts. *Proceedings of the National Academy of Sciences*, 108(38):15908–15913, 2011. URL `http://www.pnas.org/content/108/38/15908.short` `papers2://publication/doi/10.1073/pnas.1014503108/-/DCSupplemental/pnas.201014`

[26] Leigh Van Valen. A new evolutionary law. *Evolutionary Theory*, 1:1–30, 1973. URL `http://ci.nii.ac.jp/naid/10011264287/`.

[27] Steve C Wang and Charles R Marshall. Estimating times of extinction in the fossil record. *Biology Letters*, 12(4):20150989, 2016. ISSN 1744-9561. doi: 10.1098/rsbl.2015.0989. URL `http://rsbl.royalsocietypublishing.org/lookup/doi/10.1098/rsbl.2015.0989`.

[28] Marjorie G Weber, Catherine E Wagner, Rebecca J Best, Luke J Harmon, and Blake Matthews. Evolution in a Community Context: On Integrating Ecological Interactions and Macroevolution. *Trends in Ecology & Evolution*, xx:1–14, 2017. ISSN 0169-5347. doi: 10.1016/j.tree.2017.01.003. URL `http://dx.doi.org/10.1016/j.tree.2017.01.003`.