

Introduction

2 Species traits are the bridge between evolution and ecology [37, 81]. A trait
is an identifiable property of an organism, such as individual body size, while
4 a species trait is some identifiable property of the entire species, such as the
average body size or geographic range of a species [37]. A class of species
6 traits called functional traits are those traits which clearly describe a species
means of interacting with their environment such as leaf surface area or
8 trophic role [37]. In macroevolutionary studies, analyses are typically focused
on a patterns associated with a single single trait or are instead traitless a
10 analysis of diversity and the diversification process [22, 23, 30, 43, 46, 52, 63,
64, 67]. Macroecological studies are frequently concerned with describing the
12 distribution of species and individuals over space or time, such as shifts in
community composition along some gradient or axis [6–8, 14, 17, 27, 28, 68, 69].
14 My desire with this dissertation is present the types of analyses and results that
are possible through a synthesis of both macroevolution and macroecology;
16 my approach is to develop inference devices (i.e. statistical models) to better
understand the interactions between the effects of multiple species traits, as
18 well as those of a species' temporal and environmental context, on diversity
and differential diversification both in space and time.

1 Emergent patterns, macroevolution, and macroecology

An emergent pattern is one that is not observable or predictable from its individual constituent parts. Emergence is ubiquitous in biological systems: cells form a tissue with a complex function, species extinction requires all individual members to die for possibly unrelated reasons, and a species global geographic range is the product of many individual ranges. The history of a species, or set of species, over time is inherently an emergent pattern as the temporal history of a species is not knowable from an instantaneous sample. Macroevolution and macroecology are the studies of emergent patterns in evolutionary and ecological data, respectively [6, 7, 73, 74]. Traditionally, macroevolution is the study of patterns over time while macroecology is concerned with patterns over space, but I find this division overly reductive.

Both macroevolution and macroecology are disciplines concerned with emergent patterns; they both implicitly and explicitly accept a hierarchical perspective on biology as emergence is not possible without different levels of organization, however they are defined. Even if an analysis is concerned with only a single species, the concept of a species is itself an emergent property or label for a collection of populations and individuals which all share a common evolutionary history. While it may be argued that the species label or identity is a non-biological construct or is simply heuristic for understanding the

complexity of populations and reproductive isolation, we are still concerned
42 with patterns associated with that construct as well as its intrinsic properties
(e.g. extinction, conservation, ecosystem services) [11, 24].

44 Macroevolution is much more than evolution above the species level [16]; this
too is overly reductive and assigns too much meaning to a single level of organi-
46 zation rather than embracing the multitudes of possible levels of organisation.
Instead, I propose defining macroevolution, *qua* field of study, as the study of
48 emergent evolutionary patterns; this means patterns of speciation/extinction
(diversity) as well as trait evolution (disparity), both of which are only observ-
50 able when considering more than one taxon or when considering the temporal
history of one or more taxa. In complement, macroecology is then the study
52 of emergent ecological patterns, which means patterns in spatial distribution
or community composition which are observable only when considering more
54 than one taxon or when considering the temporal history of one or more taxa
[6, 7, 69]. Because taxa inherently respond differently and individually to
56 environmental changes, both biotic and abiotic, macroecological patterns are
those due to the similarity in response across individuals [3].

58 Species selection is enshrined as one of the most important patterns in
macroevolution [24, 44, 51, 65, 73, 74, 79]. Rabosky and McCune [51] portray
60 species selection as resultant phenomenon of the heritability of speciation and
extinction rates, a powerful and useful expansion of which phenomenon fall
62 under this category by divorcing levels of organization from the definition and

thus avoiding the unproductive paleobiological debate surrounding species
 64 selection versus species sorting which has been the cause for a considerable
 amount of confusion and rhetorical fights [34, 44, 78, 79], not the least of
 66 which is the adoption of “sorting” as an important term for understanding
 community assembly [10, 21, 35, 62, 70, 75, 76]. However, I think the definition
 68 presented by Rabosky and McCune [51] misses the mark as an operational
 definition to inspire and guide future study. Species inherit more than just
 70 speciation and extinction rates; they also inherit traits which themselves may
 be linked to differences in speciation or extinction rates due to their effects
 72 on species fitness. Species fitness is a concept that is rarely discussed and
 difficult to define yet is vitally important to understanding species selection
 74 as process [9, 42]. Here I adopt the inclusive definition of fitness presented in
 Cooper [9]: species fitness is, minimally, the expected duration of that species.
 76 Differences in expected species duration that are associated with species traits
 are then the product of (species) selection.

78 A generative definition of species fitness (i.e. relating to speciation rate) is
 more difficult to develop for a variety of reasons, not the least of which being
 80 that the why and how speciation rates can vary both across species and
 time is not well understood [11, 49, 50]. At a minimum, given the earlier
 82 definition of fitness wrt duration, species fitness wrt speciation would require
 the association of differences speciation rate with one or more species traits;
 84 this difference in fitness is then the raw material for selection.

Extinction is a property of, or a phenomenon affecting, species as it requires the
86 death of all organisms within a species which do not have to all occur for the
same reason [65]. Extinction is a fundamentally emergent phenomenon that is
88 the ultimate manifestation of selection; it is also central to macroevolutionary
studies and the definition of (species) fitness used here [9]. Extinction is
90 featured centrally in one of the few “laws” in macroevolution and paleobiology:
the Law of Constant Extinction [33, 77]. This law states that a species risk of
92 going extinct is independent of that species age [33, 77], a conclusion reached
via analysis of patterns of (higher) taxon survival patterns. The Red Queen
94 hypothesis was proposed as a process that would result in the observation
underlying the Law of Constant Extinction [77], though it has obviously
96 grown to have a life of its own [33].

The functional composition of a community or species pool is a property of
98 that unit; observing a single species at a locality does not reveal the functional
composition of the community in which it interacts. The composition of a
100 community or species pool in terms of functional groups is a community
ecology exercise. Comparing the distribution of functional groups across
102 communities or species pools is where community ecology and macroecology
intersect [7, 37, 69]. In paleobiology, a successful means of classifying marine
104 invertebrate functional groups has been a three dimensional classification
scheme called an “ecocube” which uses consistently identifiable functional
106 traits to label both possible and observed functional groups [2, 8]. It is this
strategy that inspires the third study presented in this dissertation.

108 2 Structured data and modelling emergent patterns

110 An inference device is a theoretical tool for improving our knowledge by
processing new information and observations [26, 36]; this device has initial
112 conditions describing what we know (e.g. nothing), mechanisms for updating
this knowledge to reflect new information, and can then produce an updated
114 “picture” that better represents our current knowledge as well as the uncertainty
surrounding this knowledge. Each inference device has a specific and narrow
116 purpose and functionality [36]; unless the mechanisms are similar, a device for
processing the rate of imperfections in the manufacturing of widgets cannot
118 process the queuing times of callers to a help line.

We can think of the well known battery of statistical tests [71] as re-usable
120 inference devices with very narrow utility; these are unmodifiable tools for
handling very specific questions and data. All (Bayesian statistical) models
122 act as inference devices because they fulfill the requirements described above:
initial conditions, updating mechanism, and output as updated knowledge
124 along with the uncertainty surrounding that knowledge [26, 36]. By developing
a new model for each new question there is a precision of translation; the
126 model actually reflects the questions at hand, something that is preferable
to forcing questions and data to fit into pre-made inference devices (e.g.
128 models, tests) that do not update knowledge in a means relevant to the actual

question(s) of interest.

130 Structure occurs naturally in the collection of data. For example, imagine a
drug trial that takes place across multiple hospitals. It is possible to consider
132 the results from all hospitals in aggregate by ignoring the hospital labels;
alternatively, these results can be considered individually by hospital. In a
134 biological example, imagine the study of individuals within a single species
that are collected from multiple locations. For many reasons, we might expect
136 that individuals from the same location are more similar to each other than
to individuals from other locations. The goal in the analysis of structured
138 data through hierarchical or multi-level models is to leverage this structure
into the analysis in order to improve estimation by having groupings share
140 information about associated parameter estimates [19, 36].

Two of the most important analytical approaches at the core of macroevolu-
142 tionary study are the birth-death process for diversification in both discrete
and continuous time [38–41, 53, 55, 72], and the random walk heuristic for
144 (continuous) trait evolution [4, 15, 20, 22, 23, 54, 56–58, 61]. All three of
the studies covered by this dissertation make use of some variant to the
146 birth-death process. The first two studies are analyses of extinction, which is
a pure-death processes. The third study utilizes a discrete-time birth-death
148 process to model species presence in a species pool.

Similar analytical cores are harder to identify for macroecology as a whole,
150 so instead I will focus on species distribution models (SDMs) as a powerful

framework for understanding the distribution of species, both do to envi-
ronmental factors [13] and species traits [62]. SDMs are a class of models
which attempt to operationalize the multitude of processes which result in the
distribution of one or more species in both space and/or time. In effect, SDMs
are a means of operationalizing the concept of a species’ “realized niche” in
order to understand the limits on a species distribution [13]. Typically, SDMs
are used to analyze the relationship between species presence at a locality
and the environmental factors which characterize that locality. From this
analysis, the possible distribution of a species in space can be then estimated
and compared to the observed distribution of that species [1, 13, 45]. The
maximum entropy theory of community assembly, and its related model, view
community assembly as an ecological sorting process where traits mediate the
effects of environmental filters [62, 80]; also called “community assembly via
trait selection” (CATS regression). By analyzing the composition of species at
localities based on their traits, the strength and relative importance of which
traits most strongly structure community composition can be elucidated.

Both of these approaches to analyzing species distributions can be united
in a single fourth-corner model [5, 80]. The fourth-corner problem is an
old problem in community ecology originating in the multivariate analysis
literature: assuming species distribution is the result of functional traits
interacting with environmental factors, how do we estimate which interactions
are important and their relative strengths [12, 29]? By phrasing the fourth-
corner problem as a model based framework, results are much more easily

174 interpretable and actually provide estimates of the effects of species traits
and environmental factors instead of the simple significance provided from
176 the older Monte Carlo based methodology [5, 25, 47, 48].

The third study in this dissertation makes extensive use of this framework
178 by casting the fourth-corner problem into an additional dimension: time.
By combining the fourth-corner framework outlined above [5, 80] with the
180 birth-death process used for modeling diversification into a single unified
model of species occurrence through time as a function of both species traits
182 and changing environmental context I've developed a powerful analytical
bridge between macroecology and macroevolution.

184 I emphasize model-based approaches to analysis as well as question or study
specific models because a common language is necessary for clear, coher-
186 ent, and translatable results that actually relate to the question(s) at hand.
Some of the greatest limits to paleobiological, macroevolutionary, and macroe-
188 cological study are a lack of strong, mechanistic predictive theories that
can be expressed mathematically. Some of the greatest strides in advancing
190 discussions of macroevolutionary and macroecological theory disputes have
come from translating verbal theory into mathematical and statistical models
192 [15, 22, 23, 39, 55, 62]. The reality of how complex biological process is rarely
integrated into paleobiological analyses of macroevolutionary and macroe-
194 cological patterns. A move to a model-forward approach to paleobiology,
heavily steeped in evolutionary and ecological theory, would be beneficial for

196 advancement of theories in macroevolution and macroecology.

Paleobiologists historically believe that neontologists ignore their approaches
198 and insights into macroevolution and macroecology study and theory [59,
60], but without a concerted effort to engage within the same theoretical
200 framework and language when developing scientific questions and the related
analytical tools (i.e. statistical models) then this worry and resentment is
202 all but preordained. Because the systems paleobiologists study are unknown
to, have no direct impact on, or are contextualized wrt the systems studied
204 by neontologists, a push towards unification and synthesis most likely has
to begin with the paleobiological community; luckily, it appears that the
206 neontological community is receptive paleobiological insight [18]. The simplest
and fastest way to begin not just a dialogue but a unification is by translating
208 verbal macroevolutionary and macroecological theories from paleobiology into
statistical models that are readable by all researchers, both paleontological
210 and neontological.

3 Study summaries

212 Each of the three studies that make up this dissertation involve developing
a hierarchical model to describe structured data with the goal of making
214 macroevolutionary and/or macroecological inference. The first two studies
are decidedly macroevolutionary in bent as they are analyses of trait-based

216 extinction patterns in mammals and brachiopods, respectively. The third
study is an analysis of mammal species pool temporal dynamics and is of a
218 strong macroecological bent, though makes use of a macroevolutionary model
of diversification in order to describe species turnover.

220 The first study presented is an analysis of North American mammal species
durations and trait-based extinction risk. This analysis is principally concerned
222 with the long standing hypothesis of the “survival of the unspecialized” which
states that average or generalist species are expected to have a greater duration
224 than specialists or other extreme forms [31, 32, 66]. Species duration is an
alternative measure of species extinction risk as species with a shorter duration
226 are of a greater extinction risk than species with a long duration. In this
study, differences in species extinction risk based on multiple functional traits
228 are estimated while also taking into account time of species origination as
well as its relative phylogenetic position. Finally, the possibility of species age
230 affecting extinction risk is also considered because while the Law of Constant
Extinction is extremely hard to “test” it has never definitively been proven
232 [33, 77].

The second study presented is also an analysis of species durations, but this
234 time focuses on all post-Cambrian Paleozoic brachiopod genera. The question
at the center of this study is “what happens to the effects of functional
236 traits on survival when average survival increases or decreases?” Unlike the
previously described study, which focused on the average effects of functional

238 traits on survival, this study requires estimates of how the effects of functional
traits vary through time. The key parameters are those of the correlation
240 matrix of the effects of these traits on duration and the average duration of
species originating at the same time. This study also has results relevant to
242 the “survival of the unspecialized” wrt the effect of environmental preference
on survival, and the Law of Constant Extinction by allowing survival to be a
244 functional of species duration.

As mentioned above, the third study presented is decidedly more macroeco-
246 logical in focus as it is an analysis of how a regional species pool changes
over time due to species turnover and a changing environmental context. The
248 fundamental question is “when are certain ecotypes enriched or depleted wrt
their diversity history?” To that end, I analyze the set of North American
250 mammals for the Cenozoic and the changing functional composition of that
species pool from nearly the beginning of the Cenozoic to almost the very
252 recent (64-2 million years ago). In this analysis, functional composition of
the species pool is described as the relative diversity of 18 different mammal
254 ecotypes which are defined for every species as its dietary and locomotor
combination. The occurrence of an ecotype, both in terms of origination and
256 survival, is modeled as a function of that species environmental context as
described by the dominate plant groups in North America as well as global
258 temperature estimates.

All three of these analyses feature a hierarchical Bayesian model developed

260 explicitly for each study in order to clearly attempt to answer the questions at
hand. Each of these studies exemplifies my earlier rhetoric of how to build and
262 advance macroevolutionary and macroecological study and theory through the
explicit phrasing of scientific questions, precision of translation from question
264 to analysis, and the mobilization of domain specific knowledge to cast results
both in terms of the system specific insights as well as the theoretical insights.

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