Ratchet Mechanisms in Macroevolutionary Processes

by

Trevor J. DiMartino

B.S., University of Washington, 2009
M.S., University of Colorado, 2013

A thesis submitted to the
Faculty of the Graduate School of the
University of Colorado in partial fulfillment
of the requirements for the degree of
Masters of Science
Department of Computer Science
2017
This thesis entitled:
Ratchet Mechanisms in Macroevolutionary Processes
written by Trevor J. DiMartino
has been approved for the Department of Computer Science

Prof. Aaron Clauset

Prof. Andrew Martin

Prof. Tom Yeh

Date ________________

The final copy of this thesis has been examined by the signatories, and we find that both the content and the form meet acceptable presentation standards of scholarly work in the above mentioned discipline.
How have we arrived at the diverse set of complex species that we currently find in our world? Using statistical simulations of evolutionary processes, this study investigates how the fundamental minimum sizes of species increase irreversibly over time, and how complexities evolved along the way compound throughout that process. Our results imply that unless a random mutation opens up a new dimension of nichespace for the clade to expand within, the mutation will eventually become extinct due to inherent genetic drift.
Dedication

To Lindsey, Reese, Scott, and Trey—my family throughout this endeavor.

(Sorry, mom.)
Acknowledgements

Over the course of this project I have gotten help from a wonderfully diverse group of people and viewpoints. Whether they were simply asking me about my research or helping me derive efficient algorithms for analysis, every chance I had to talk to about this project helped me in some way; and for that I am very grateful.

More specifically, I’d like to acknowledge Aaron Clauset for taking me on as an advisee and sharing his love of science with me on a regular basis; Lauren Shoemaker for helping me navigate the subtleties of ecology and evolutionary biology; Allison Morgan for helping me use calculus to solve plotting problems; and also the rest of the Clauset Lab for feedback and discussions in group meetings.

Thank you.
# Contents

## Chapter

1. **Welcome**
   - 1.1 Driving Questions ........................................ 2
   - 1.2 Complexity .................................................. 2
     - 1.2.1 Body Mass as Complexity .............................. 3
   - 1.3 Trends in Body Mass Distributions ....................... 4

2. **Generative Statistical Modeling** .................................. 7
   - 2.1 Random Walk .................................................. 8
   - 2.2 The Clauset-Erwin Model .................................... 10
     - 2.2.1 Adding a Lower Limit .................................. 14
     - 2.2.2 Adding Cope’s Rule ..................................... 16
     - 2.2.3 Adding Mass-Dependent Extinction Rates .......... 17

3. **Propagating Ratchets** ........................................... 20
   - 3.1 Identifying Ratchets ....................................... 20
   - 3.2 Modeling Ratchets .......................................... 22
   - 3.3 Getting Ratchets to Stick .................................. 24
     - 3.3.1 Dropping Meteors .................................... 26
     - 3.3.2 Radiative Promotion for Recent Ratchets .......... 28
     - 3.3.3 Early Radiative Ratchets .............................. 29
3.3.4 Discussion .......................................................... 31
3.3.5 Population Genetics ............................................. 31
3.3.6 Genetic Drift vs. Random Mutation ............................. 32
3.4 Conclusions ............................................................ 32

4 Adding Dimensions in Nichespace ................................. 34
4.1 Expanding Nichespace ............................................... 34
   4.1.1 Simulation Modifications .................................... 35
4.2 Simulating MOM Data ............................................... 36
4.3 Letting the Ratchet Click .......................................... 36
4.4 Conclusions ............................................................ 39

5 Conclusions .................................................................. 40
5.1 Future Work ............................................................. 41
   5.1.1 Concrete Continuations ....................................... 41
   5.1.2 Other Facets of Ratchets ...................................... 41

Bibliography .................................................................. 43

Appendix

A Model Subtleties .......................................................... 46
A.1 Seed Mass ................................................................. 46
A.2 Effects of ratchet probability on simulation results ............ 47
A.3 Histogram Normalization ........................................... 47

B Extinction-Centric Model ............................................... 49
B.1 Relaxing Cladogenesis ............................................... 50
B.2 Outcomes ................................................................. 51
| Table | 4.1 Minimum sizes and number of extant species | 35 |
# Figures

## Figure

1.1 4079 extant mammals' masses ............................................. 5

2.1 Three random walks ....................................................... 9

2.2 Three species mass random walks ...................................... 9

2.3 Schematic of cladogenesis ................................................ 11

2.4 Basic diffusion model ..................................................... 13

2.5 Metabolic rates of shrews and mice ................................... 14

2.6 Diffusion model with a lower boundary ................................ 16

2.7 Diffusion model with a lower boundary and growth bias ........... 17

2.8 Diffusion model with a lower boundary, growth bias, and mass-dependent extinction ............................................. 19

3.1 Mass distributions of the entire mammal clade ....................... 21

3.2 Sketch of expected largest seen curves for two clades ............... 24

3.3 Naive ratcheting simulation - largest species seen over time ....... 25

3.4 Ratcheting simulations with meteor drops ............................. 27

3.5 Ratcheting simulations with promotion phase for new ratchets .... 29

3.6 Ratcheting simulations with increased $p_r$ during initial radiation 30

4.1 Ratcheting simulation set up to result in MOM distribution ....... 37

4.2 Ratcheting simulation set free ........................................... 38
A.1 Simulation with different seed masses ........................................... 46
A.2 Examining effects of ratchet probability on extant mass distribution .... 47
A.3 Differences in normalization schemes for histograms .................... 48
Chapter 1

Welcome

Welcome. This thesis is going to explore a niche settled between computer science and evolutionary biology, so before we get too deep, we need to make sure we are on the same page—metaphorically speaking, too. Throughout this document, we will draw motivation and mechanics from evolutionary biology and formalize them in a computer simulation that we will use in numerical experiments.¹

First, this chapter will begin by providing some background so we share a common context as we proceed. Evolution is an undoubtedly complex process, so we will begin by setting the scene of this thesis from an abstract viewpoint—as a study of increasing complexity—and refine it to be more precise: an investigation of the processes behind the long-tailed distribution of extant mammals’ masses.

In Chapter 2 we will formalize our experimental environment: a random walk computer simulation of macroevolutionary processes. We will build our simple diffusion model from the ground up and discuss the origins of the macroecological constraints that we impose.

Chapter 3 will introduce the idea of a ratchet in complexity, and then dive into a collection of numerical experiments to determine the conditions under which we might expect a ratchet step to catch. We will conclude with the identification of an inherent source of competition in the model, and an idea of how to resolve that competition.

Chapter 4 then implements what we discovered in Chapter 3 and discusses some implications

¹ Why not experiment directly? We won’t be around for the next 250 million years to see what happens!
of the results before Chapter 5 wraps everything back up and shares some propositions for future studies.

1.1 Driving Questions

There are a number of big, broad questions that motivate the work performed in this thesis. Obviously, we will not be answering these questions in their entirety—think of them as goals more than objectives—but we will be working to uncover some clues that could work in tandem with other research to form a more complete picture of the processes that shape our world.

Perhaps the broadest question driving this research is “What factors motivate and preserve increasing complexity?” Complexity (which we will discuss more in the following section) is omnipresent, and is undeniably growing through time, but how? Where do new innovations come from? What makes some traits persist, and what selects against others? None of these questions can currently be answered in their entirety, but they are all extant research thrusts to which we hope to contribute. As such, we will return to these questions later (in Chapter 5).

1.2 Complexity

What is complexity? As you might imagine, describing complexity is no simple task. Perhaps the best way to start, as usual, is by breaking the word down into its latin roots, “com” and “plex,” meaning “woven together.” In this way, we can imagine that a study of complexity would be a study of the behaviors and phenomena that emerge as a result of how the components of a system interact.

Often times “complex” and “complicated” are confounded, so first it is important to distinguish them. Something that is complicated would have many different parts, but wouldn’t necessarily be complex. Samuel Arbesman describes this difference in his book Overcomplicated with the following example:

Living creatures are complex, while dead things are complicated. A dead organism is certainly intricate, but there is nothing happening inside it: the networks of
biology—the circulatory system, metabolic networks, the mass of firing neurons, and more—are all quiet. However, a living thing is a riot of motion and interaction, enormously sophisticated, with small changes cascading throughout the organism’s body, generating a whole host of behaviors. [4]

For example, let us consider my dog Reese. As a result of the complex, interwoven workings of the neurons firing in her brain—potentially spurred by subtle visual or auditory cue—she will often erupt into motion, burning the digested calories of her breakfast in her muscles, using her connective tissues to leverage her skeleton into a sprint towards her favorite hole in the fence. Reese’s ability to protect her territory is an example of how an emergent phenomenon from a complex system can allow actions that none of its constituent parts would be able to achieve on their own. Contrast this to when Reese passes (a sad but inevitable fact): she will still be complicated—still have all the parts mentioned above in the same configuration—but her emergent abilities will have been lost; Reese will no longer be a complex organism capable of notifying us when the neighbor’s cat gets home.

1.2.1 Body Mass as Complexity

Arbesman’s remarks on the difference between complicated and complex is actually quite helpful in determining how we can estimate complexity in an organism. Since we can generally assume that something now dead was once living, we can determine how many different components the organism has postmortem and use that as a measure of how complex the organism was when it still possessed life. In fact, the most commonly adopted measure of complexity in organisms today is the amount of variation among their constituent parts [13].

Now we can make it even easier for ourselves if we abstract out one more level, on the assumption that variation among constituent parts in an organism increases as that organism’s mass increases. Under this assumption, we can even estimate complexity measures for species we have only discovered through partial skeletons preserved in geological strata (by employing fossil-to-mass estimation methods, like those used in [22] for example); something that would not be possible through any other means.
Mass has also been shown to correlate with a large number of other characteristics. Habitat preference, diet, range, life span, gestation period, metabolic rate, population size, extinction risk, as well as trophic level and niche position in food webs have all been found to have mass relations [5, 30, 25, 6, 31].

Considering one of the simplest qualities of an organism to measure is its mass; mass estimates are available even for long extinct species; and mass is easily assumed as a measure of complexity (among a large number of other traits), we elect to use mass in this study as our primary characteristic of interest. And, adhering to our assumption stated earlier, we could choose to read “mass” and “complexity” as synonyms throughout this thesis.

1.3 Trends in Body Mass Distributions

So far as we have discussed mass, we have been speaking more specifically about body mass. That is to say, for the purposes of this thesis, mass will denote the average body mass of a given species. For example, we consider the mass of homo sapiens to be 62 kg, the global mean of human masses.

Thinking of homo sapiens in this lens might bring up questions about our mass-as-complexity assumption above, namely: Could we not argue that humans are the most complex organisms alive today? In our case, by choosing to look at average body mass, we are solely commenting on a species’ body plan complexity and not social or intellectual complexities.²

Figure 1.1 depicts the distribution of 4079 mammals’ masses from the late Quaternary (from MOM, [25]); the horizontal axis shows mass, which was broken up into “bins” (on a log scale), and the vertical axis shows the relative probability (also on a log scale) of picking a mass in a given bin. In this way we are looking at a probability distribution, but instead of absolute probabilities—how likely it is that we choose a mammal of mass \( x \)—we are only concerned with relative probabilities—how much more likely we are to choose a mammal of mass \( x \) than one of mass \( y \).

² Hopefully the idea that our bodies are less complex than those of hippopotamuses is a gentle enough blow to our egos that we can proceed under our mass-as-complexity assumption.
We can see immediately that the distribution of extant mammals’ masses does not have the characteristic bell shape of a normal distribution. In fact, the distribution of terrestrial mammals’ masses is heavy-tailed, meaning that it has considerably more large species than would be expected (in a normal distribution). In other words, the mode of the distribution occurs around 40 g, only one order of magnitude away from the minimum (1.8 g) and more than five orders from the maximum ($10^7$ g).

In fact, most distributions of species masses in the higher taxonomic orders exhibit right-skew. Smaller geographical regions produce less skewed distributions; is this because the clade hasn’t fully expanded into its environment, or because the environment imposes a maximum size as well as a minimum size? Basically, right-skewness is expected, but as with everything in biology, there are often exceptions. These exceptions include groups of aquatic birds, bivalves, and primates, along with some lower taxa such as Orders, and in smaller, contained geographic regions such as islands.

---

3 In the field of Materials Science, we see that skew in particle size distributions is correlated strongly with the packing density achievable by those (assumedly) spherical powders; with right skew achieving the greatest density. The same could apply to species—right skew patterns allow for the most dense usage of resources available, and so large groups of species may have evolved for maximum resource utilization.
Now the question arises: What processes and trends inherent in macroevolution combine to generate a right-skewed distribution of masses? Our next chapter will discuss these processes and trends, and use them to build a baseline generative computer model capable of evolving clades with right-skewed mass distributions.
When studying (organic) phenomena, it is natural to develop hypotheses that describe the underlying processes. However, it is often the case that these hypotheses cannot be evaluated directly, which could happen for any number of reasons. For example, in our investigation we are unable to directly measure our hypotheses due to the sheer complexity, and notably non-human time-scale, of macroevolution. Thus the question arises: How can we confirm or deny the validity of our hypotheses if we are incapable of providing adequate control over the environment to test them directly?

Enter scientific computation. By using a computer to run simulations built on our hypotheses, we can check to see whether or not the simulation’s results are indistinguishable from the data we can measure. If the results do end up being indistinguishable from the data, then we can conclude that our set of hypotheses constitutes one possible explanation of the phenomenon, and then continue to test for further dimensions of fit. Along the way, the evidence we collect may help to corroborate our hypothesis (further showing that our guess was a good one), or it may help us see where our model differs from reality—either way, what we learn is valuable information about the model and how it relates to reality.

Note here that we will be modeling effective processes. Obviously there are an astronomical number of steps involved in the emergence of a new species, but here we consider all those steps to be collectively approximated through random draws from empirically measured distributions. This condensation of processes into a single, probabilistic step is critical for creating this model since we
do not know how all the underlying steps intertwine, and even if we did know for certain all the factors that contribute to speciation and how they interact, simulating all of them together would (currently) be prohibitively computationally expensive.

There are many classes of statistical models, but we will focus here on random walks, as they are the most natural choice in modeling evolution.

2.1 Random Walk

Evolution is a natural candidate for random walk modeling. In fact, in 1977 Raup [21] performed a random walk computer simulation of cladogenesis and found that even some large extinction events, previously thought to be the result of massive one-time ecological changes, could emerge from random walks.

Named for the fact that each next step in the model is determined independently by a draw from a distribution, random walk models are characterized by their non-deterministic behavior. This gives random walks an important property: they have neither memory nor intention—the direction and magnitude of every step is taken independently of previous and next steps. Thus location is the only quality of the walker preserved between steps.

Synthesizing the properties of a random walk, we can see that they are an appropriate approximation of stochastic incremental changes. This follows from the fact that a walker’s position after taking a step is more dependent on where it was stepping from than how far it stepped. Take Figure 2.1 for example, where three random walk trajectories are pictured with a dotted line at position 0 for reference. Notice how the trails have a semblance of trajectory despite each step direction and magnitude being chosen uniformly at random on the interval \([-1, 1]\). Also of note: the expectation of the final position of a random walk is equivalent to its current position. This does not mean it is surprising if it does not meeting that expectation (none of the three walks in Figure 2.1 end at 0, though some do cross it again), but merely that if we were to run the same random walk simulation many times and take the average of the walkers’ final positions, the result would be their starting position.
Figure 2.1: A collection of three random walks. Step magnitudes (and directions) were generated by taking a draw from a uniform distribution ranging on the interval $[-1, 1]$. New positions were calculated by addition.

Figure 2.2: A collection of three random walks from a run of the evolution model (see Figures 3.4c and d for other views of the model run). Step magnitudes (and directions) were generated by taking a draw from a slightly biased lognormal distribution (as discussed later), and multiplied to the previous position to determine the new one. As a result, values walk across multiple orders of magnitude—note the log scale on the vertical axes.
Figure 2.2 shows random walks taken from a run of the simulation that we will discuss later, in Section 3.3.1. The paths depict fluctuations in the masses of the chosen species’ ancestors; the ultimate point on the trajectory is the mass of that species upon simulation termination. (Notice how the top and bottom species have the same mass lineage up until the final quarter of the simulation time, when their most recent common ancestor went extinct.) Despite our generating species masses through a multiplicative factor—mass differences are measured in percentages, not absolute values—the walks have the same properties as before, just over a log scale instead of a linear one.

As the fossil record shows, characteristics of species evolve incrementally over time and in undetermined (if slightly biased) directions. That is to say that the characteristics of a given species will not differ greatly from those of its direct ancestor, especially when compared to differences between other lineages. In fact, before genome sequencing was ubiquitous and inexpensive enough to give us more direct insight on genetic lineages, species relationships were determined by comparing differences with others: more similarities denoted closer relationships.

2.2 The Clauset-Erwin Model

Now that we have established that the use of a random walk is appropriate for modeling evolution of a particular species, we need to expand the random walk to simulate the evolution of an entire clade. The first step is to implement the branching process inherent in cladogenesis—depicted schematically in Figure 2.3—to the model. We choose to model speciation events as purely bifurcating processes, resulting in two descendants (both with novel masses), and the extinction of the ancestor species. To keep our simulation simple, one cladogenesis event occurs at every time step of our discrete time model. As a result, our model time has a complicated relationship with real time that is not in the scope of this thesis but which has been investigated (in [22], for example).

Obviously, there are many ways that speciation can occur—take allopatric speciation, peripatric speciation, and sympatric speciation for example—and not all have the signature of spawning
Figure 2.3: A schematic of the process of cladogenesis, where branching speciation events cause one ancestor species to differentiate into a collection of descendants. Circle sizes denote masses. Noted on the figure are examples of the mass of an ancestor, $m_A$, and the mass of the descendant, $m_D$, which are related by multiplicative growth factor, $\lambda$.

Algorithm 1 Unconstrained Diffusion

```
while evolve do
    ancestor ← extant.random()
    loop twice
        spawn descendant
        $\lambda ← \text{log-normal}()$
        descendant.mass ← ancestor.mass $\times \lambda$
        insert descendant into extant
    remove ancestor from extant
    for all species in extant do
        if species.extinct() then
            remove species from extant
```

two new species while one goes extinct. Luckily for us, changing this process in the model has minimal consequences on the effects that we are investigating\[1\].

Here we present our model in the form of an algorithm, seen in Algorithm 1. We will use this algorithmic layout repeatedly to describe the model and the modifications we make to it, so

\[1\] The differences in model output caused as a result of altering the speciation model to allow the ancestor to remain extant after cladogenesis can be absorbed in a re-tuning of the $\beta$ parameter discussed in Section 2.2.3.
let us first walk through the most basic version. We will be running the described process at every cladogenesis step, noted in the algorithm as “while evolve.” In reality, the total number of cladogenesis steps, $t_{\text{max}}$, is decided as a function of two fossil record estimates—mean species lifespan, $\nu = 1.6$ My, and total model time, $\tau = 250$ My since the mammal clade began—and the expected number of species alive at simulation termination, $n$, estimated by extant species count. This results in $t_{\text{max}} = \tau \nu n$.

The first step in the cladogenesis model is to choose the ancestor uniformly at random from our set of extant species. Note: for convenience, variables (ancestor) and collections (extant) in the algorithms are highlighted denoted with blue and orange, respectively. After choosing the progenitor, we spawn two descendant species and assign them masses $m_D = \lambda \ast m_A$, where $\lambda$ is drawn from a balanced log-normal distribution ($\langle \log(\lambda) \rangle = 0$) at random to represent the descent with variability inherent in evolution. The parameters of the log-normal distribution were estimated from the fossil record by Clauset and Erwin in [8] and used here without alteration. After spawning each descendant species, we put both of them in the extant pool, then remove the ancestor since, under the assumptions of our model, it has gone extinct in the process of cladogenesis.

Finally, we enter the extinction step where we determine whether any species have gone extinct due to non-cladogenesis factors. To do so, we iterate through all species and check to see if they have gone extinct. species.extinct() abstracts this process in Algorithm 1 behind the scenes, this decision function simply replies with some probability $p_{\text{ext}} = 1/n$ that the species has gone extinct. (To speed up the process of iterating through thousands of species with every model time step, we use the properties of a geometric distribution to pre-determine how many trials we would have had to perform, without actually performing them. For more information, see Appendix B.)

Considering we perform cladogenesis and extinction with every step, our model approaches an equilibrium species count of $n$ after about $n$ steps. Every speciation step creates two new species (descendants), and causes the ancestor to go extinct; every extinction step will kill off an
expected \( n_s/n \) species \((n_s \text{ tries at } p_{ext} = 1/n)\), where \( n_s \) is the number of species alive at that time. Thus when \( n_s = n \) we will expect one extinction per model step, balancing our net speciation and extinction rates overall and making \( n \) a stable attractor for species count.

Under this simple model, the distribution of species masses diffuses over time to fill the available “space.” We can imagine that species in nature do the same: say a mammal finds its way to an island where there are no other mammals yet, we would expect that, over evolutionary time, our exploratory mammal would give rise to a entire clade of diverse (diffuse) mammals species that find ways to leverage their diversity and take advantage of ecological peculiarities. In this sense, we are abstracting away a number of ecological factors into the random walk processes of our model.

![Figure 2.4: A very basic multiplicative random walk model, averaged over 1000 runs of the simulation. Note how the generated distribution (black diamonds with dashed 95% confidence interval) looks nothing like the MOM terrestrial mammal distribution (green Xs, [25]). Notably missing from the simulation’s results: the lower probability of species at the small and large ends of the distribution.](image)

Looking ahead to Figure 2.4 we quickly see that a simple multiplicative random walk does not model the distribution of extant mammals’ masses very closely. Luckily, we do not expect it to. Without some pressures to shape the distribution, it will diffuse out to the fullest extent it can, reflecting the shape of the log-normal distribution we drew our growth factors from. Thus, to hone
the model we need to distill ecological factors—individuals, populations, location, range, niches, predation, adaptation, and others—into some constraints that will influence the shape of our fully developed diffusion model.

2.2.1 Adding a Lower Limit

Terrestrial mammals exhibit a lower mass limit. While this fact might not be surprising, it is an important one; especially because we need to have a model that adheres to this observed constraint. However, before we implement our minimum size constraint, let us examine why mammals can only be so small.

![Figure 2.5: Pearson's figure showing the steep increase of metabolic rate as species get smaller.](image)

Starting with observations of metabolic rates in shrews, Pearson [20] noted that the curves of metabolic rate vs. mass exhibited a steep curve at smaller species masses. Figure 2.5, showing the metabolic rate vs. mass curves, is from Pearson’s 1948 paper where he argues that the mass floor for mammals is determined by their ability to keep themselves warm. Near 2 g, mammals’ surface-area-to-mass ratio gets so large that, due to heat loss, they have to consume (relatively) massive
amounts of food to satisfy their metabolism and sustain their body temperature. Unsurprisingly, the smallest mammal known to be alive today (Remy’s Pygmy Shrew, 1.8 g) lives in the tropical forests of central Africa; the consistently warm temperatures there are likely what allow Remy’s Pygmy Shrew to survive at such a small mass.

Algorithm 2 Diffusion with Lower Limit

```
while evolve do
    ancestor ← extant.random()
    loop twice
        spawn descendant
        repeat
            λ ← log-normal()
            descendant.mass ← ancestor.mass * λ
            until descendant.mass ≥ m_{min}
            insert descendant into extant
        remove ancestor from extant
    for all species in extant do
        if species.extinct() then
            remove species from extant
```

To add this lower limit to our simulation, we add in a check when drawing the growth factor, λ, from a log-normal distribution. As seen in Algorithm 2, we simply disallow λ values that would cause the new descendant’s mass to drop below the minimum size, m_{min}, and redraw until we find a λ that satisfies our constraint. In a study of diffusion this lower limit would be considered a reflecting boundary, causing species that would have crossed it to “reflect” back into the distribution’s bulk.

The results of adding a minimum size boundary of 1.8 g to the model can be seen in Figure 2.6. Notice the downward bend in the distribution near 10^0 g, our model’s minimum mass, which also has the effect of moving the mode from the minimum to a point just above the minimum. Adding a minimum size boundary does not serve to fully specify our model yet, though; we still need to add constraints for two other empirical trends.
Figure 2.6: The basic cladogenesis diffusion model with an enforced minimum species mass, 1.8 g, averaged over 1000 runs of the simulation. Note how the simulations’ frequency distribution (black diamonds with dashed 95% confidence interval) demonstrates fewer species with masses near the minimum than it did in Figure 2.4.

2.2.2 Adding Cope’s Rule

Looking at evolutionary trends in fossil records, Cope [9] recognized a tendency for animal groups to evolve towards larger sizes. While Cope did not attribute the cause of the bias appropriately, his observation has been re-confirmed multiple times, resulting in two new explanations for its occurrence. Some popular reasons for Cope’s Rule include the short-term advantages of being larger than ancestors, ability to escape predation, or access to larger foraging areas, but Stanley [28] argues that Cope’s Rule is not due to intrinsic advantages of larger size, rather it is more accurately described as a result of species originating from a small size rather than evolving towards a large one. (We may not fully accept Stanley’s argument due to the fact that in our fully specified model, the mass of the seed species has no effect on the final distribution. See Appendix A for more information.)

Alroy in 1998 [3] used paired fossil data to quantify Cope’s rule, and noted an average trend of descendants being 9.1% larger than their direct ancestors. However, in our model we choose to
use Clauset and Erwin’s piecewise estimate from 2008: \( \langle \log(\lambda) \rangle = 0.04 \pm 0.01 \), with an increasing bias for species smaller than 32 g [8].

Figure 2.7: The basic cladogenesis diffusion model with an enforced minimum species mass and a bias towards larger descendants, averaged over 1000 runs of the simulation. Note how the addition of Cope’s Rule pushes more species (black diamonds with dashed 95% confidence interval) away from the minimum size boundary (causing the frequency seen at the mode to drop) and greatly increases the number of extremely large species.

Figure 2.7 shows how our simulation outcomes change as a result of biasing the log-normal distribution we draw our growth factor from. As expected, a positive bias caused many of the species to grow to massive sizes, greatly overestimating the number of species larger than elephants (> \( 10^7 \) g). It becomes obvious here that larger species must experience different extinction pressures that keep their prevalence suppressed, so let us incorporate a mass-dependence term to our extinction probability.

2.2.3 Adding Mass-Dependent Extinction Rates

As species increase in size, they are more prone to extinction [16, 6, 27, 29]. This could be due to smaller population sizes for large species, or the amount of specialization required to be so large, both of which would make it difficult to adapt in the face of (rapid) environmental changes.
Note that adding this constraint brings us to the complete Clauset-Erwin model, as described in \[8\] and in Algorithm 3 below.

We include this dependence as an allometric relationship of the form \( \log p_{\text{ext}} = \rho \log m + \log \beta \), with \( \beta \) being our baseline extinction rate \((1/n)\) and \( \rho \) describing the effects of mass dependence. Considering the sparsity of data on speciation and extinction rates in the fossil record \([18, 12]\), \( \rho \) is the only parameter that we cannot estimate empirically, so we will use Clauset and Erwin’s \( \rho = 0.025 \), found by tuning \( \rho \) to get the best fit between the model’s output and extant mammal mass distribution. This change to the model is noted by the abstraction in Algorithm 3 through the dependence of \( \text{species.extinct()} \) on \( \text{species.mass} \). Note that this constraint addition causes an overall increase in the model’s extinction rate, bringing the equilibrium number of species below \( n \).

**Algorithm 3** Diffusion with Lower Limit and Growth Bias

```plaintext
while evolve do
    ancestor ← extant.random()
    loop twice
        spawn descendant
        repeat
            \( \lambda ← \text{biased-log-normal()} \)
            descendant.mass ← ancestor.mass \( \times \lambda \)
            until descendant.mass \( \geq m_{\text{min}} \)
        insert descendant into extant
        remove ancestor from extant
    for all species in extant do
        if species.extinct(species.mass) then
            remove species from extant
```

Relaxing the extinction probability’s dependence on mass could be seen as decreasing selective pressures against being large. As such, one way we could think of \( \rho \) is as a variable that combines many ecological factors that contribute to selective pressures. For example, \( \rho \) would be smaller before the Cretaceous/Paleogene boundary when the atmosphere was richer and global temperatures were warmer, resulting in the observed prevalence of larger species.

Finally, Figure 2.8 shows the results of the full Clauset-Erwin model as compared with the MOM terrestrial mammals. Overall, the model reproduced all features of the MOM distribution—
Figure 2.8: The basic cladogenesis diffusion model with an enforced minimum species mass, a bias towards larger descendants, and a higher probability of extinction for larger species; averaged over 1000 runs of the simulation. Note how the generated frequency distribution (black diamond with dashed 95% confidence intervals) now matches many of the trends in the MOM terrestrial mammal data (green Xs, [25]).

Visual discrepancies in the lower mass regime are partially artifacts of the normalization process used to create the histograms; see Appendix A for a visual comparison of normalization processes.

Now that we have a suitable baseline model to work with, let us expand on it by adding in the ability for species to evolve new minimum sizes.
Chapter 3

Propagating Ratchets

As the complexity of a species follows its random walk, there comes a possibility that an evolved characteristic provides some implicit advantage. Along with that advantage, let us also say that the increase in complexity has made it impossible to be smaller than a certain size—that the advantage has raised the floor for how small any descendants could be. For convenience, we will name occurrences of these innovative (effectively) irreversible increases in complexity ratchets.

There are many examples of ratchets in evolution. For example, when eukaryotes emerged from prokaryotes the range of abilities of the organisms increased but at the cost of having a larger minimum size—each eukaryote has to be at least large enough to fit a nucleus and mitochondria, features their ancestral prokaryotes did not possess. For another example, we can fast forward roughly two billion years from the first of the eukaryotes to the emergence of mammals, whose minimum size is determined by a complicated combination of evolved traits that resulted in endothermy.

3.1 Identifying Ratchets

Ratchets, and their resulting mass floors, are quite difficult to identify. For example, let us examine a sub-clade of mammals: the canines. What is the minimum size of a canine? We could look for the smallest adult canine known to exist—as a result of our artificial selection, this figure is currently just under 700 g (about 1.5 lbs) [26]—but how do we know that it is the smallest dog that could exist? Short answer: We do not (but it is probably a good estimate). Currently, determining
the minimum size of a clade requires that the clade be large enough to have fully expanded to its viable size boundary, giving us empirical data to draw from like we did in determining the minimum size for terrestrial mammals by taking the smallest known mammal, Remy’s Pygmy Shrew at 1.8 g, as our minimum terrestrial mammal size.

![Mass distributions of terrestrial mammals and fully aquatic mammals (cetaceans). Data from MOM dataset, [25].](image)

One ratchet we can determine is the increase in the mass floor as terrestrial mammals moved into the ocean and became the cetaceans (whales, dolphins, and porpoises) we know today. We can see the effects of that ratchet in Figure 3.1 where the aquatic mammals (blue circles) have no species with masses less than $10^4$ kg. So what is the minimum size of a cetacean?

Using metabolic/thermodynamic arguments, based on Pearson’s [20] study of metabolic rates in shrews, Donhower and Blumer [11] leveraged available river dolphin data to determine that the smallest viable size of a cetacean neonate is 6.8 kg. Years later, from a first-principles mathematical approach, Ahlborn calculated the minimum size for aquatic mammals to be 8.6 kg [1, 2]. Considering the similarity of these two estimates, and the fact that the rest the data we used to estimate model parameters is from empirical measurements, we will deem 7 kg as the minimum size for cetaceans.
Algorithm 4 Adding an Inheritable, Ratcheting Minimum Size

\begin{algorithm}
\begin{algorithmic}
\While{evolve}
    \State ancestor $\leftarrow$ extant.random()
    \Loop twice
        \State spawn descendant
        \Repeat
            \State $\lambda \leftarrow$ biased-log-normal()
            \State descendant.mass $\leftarrow$ ancestor.mass $\times$ $\lambda$
        \Until{descendant.mass $\geq$ ancestor.min}
        \If{ratchet()}
            \State descendant.min $\leftarrow$ descendant.mass
        \Else
            \State descendant.min $\leftarrow$ ancestor.min
        \EndIf
        \State insert descendant into extant
    \EndLoop
    \State remove ancestor from extant
    \For{all species in extant}
        \If{species.extinct(mass)}
            \State remove species from extant
        \EndIf
    \EndFor
\EndWhile
\end{algorithmic}
\end{algorithm}

Clauset [7] has already employed our estimate of a cetacean mass floor by updating only the minimum size parameter of the simulation described in Section 2.2.3 to create a version that simulates aquatic mammals. Remarkably, the results of the cetacean model revealed that by changing only the minimum size, and leaving all other parameters as estimated for terrestrial mammals, species as large as blue whales became likely! In other words, raising the hard minimum size boundary increases the pressure towards higher masses pushing the maximum likely mass deeper into the passive pressures of mass-dependent extinction.

3.2 Modeling Ratchets

How do we modify our model so that it can produce a mass distribution like we see with all mammals, including cetaceans? We need to add in an inheritable trait that will track the progression of our mass floor: $m_{\text{min}}$. Algorithm 4 shows how we updated our simulation. Notice how the minimum size of a species is now a trait of each species (\texttt{species.min}), and how on the occurrence of a ratchet—determined by \texttt{ratchet()}—we update the descendant’s minimum to be its mass.

The fact that we choose the minimum mass of a newly evolved species to be equivalent
to its current mass follows the logical upper bound of the problem: a species of mass $m$ must have a minimum mass $m_{\text{min}}$ such that $m_{\text{min}} \leq m$. We can also identify a lower bound to our new species’ minimum size in the ancestor’s $m_{\text{min}}$, giving us a viable range of minimum sizes from $m_{\text{min,A}} \leq m_{\text{min,D}} \leq m_D$, where the $A$ and $D$ subscripts denote ancestor and descendant, respectively. We opt to take the maximum of this range because the mass of the first species in the clade does not affect the qualities of the resulting equilibrium distribution. Thus, by the assumption that the $m_{\text{min}}$ of concern would have evolved regardless, we can choose to take the maximum for convenience. (Also, the differences induced in the model by choosing an $m_{\text{min,D}}$ other than than $m_D$ are not significant enough to change the qualitative behavior of the model and therefore do not warrant deviating from convenience.)

Another large change to the model is the addition of the \texttt{ratchet()} decision function, seen in Algorithm 4. This function performs a simple probabilistic decision: with some probability, $p_r$, the function will return \texttt{true}. In short, we are implementing ratchets under the assumption that the chance a ratchet occurs is independent from all other factors, and constant for all species.

Now we encounter a difficult question: How often do ratchets occur? Answers to this question could span many orders of magnitude, from “every time a new feature evolves,” $p_r = 1$, to “only when factors are \textit{just right},” which could make $p_r < 10^{-6}$, less than one in a million. In fact, owing to the difficulty of determining different mass floors, making an estimation of ratchet prevalence from (sparse) fossil records is currently nigh impossible. Thus we will investigate different ratchet probabilities in the following sections, where appropriate, and the probabilities will generally be in the range $10^{-6} < p_r < 10^{-3}$, because higher probabilities can cause the model to “run away” and evolve species of inconceivable masses. Unless otherwise specified, we will use $p_r = 1/20000$ to get a good balance between ratchet prevalence without overloading the model. Note that despite not being able to estimate $p_r$, we still find value in experimenting with the model as a means of building intuition, which we do through the careful numerical experiments that follow.
Figure 3.2: A sketch of how we would expect largest-species-seen-to-date curves to look, for two groups. The first group (blue, solid) is the seed of the experiment. As it expands to equilibrium, a descendant species evolves a ratchet characteristic and starts a second group (orange, dashed) with a higher minimum mass. As the second group continues through cladogenesis, its maximum size grows beyond what could be achieved by the seed group.

3.3 Getting Ratchets to Stick

Now that we have updated the model to include ratchets, we need to perform some experiments to see whether or not we can (qualitatively) reproduce what we see in extant mammals today. That is to say, we would like to see something akin to Figure 3.2, where a descendant species evolves a ratchet characteristic that causes its descendants (dashed orange) to eventually grow to larger masses than would have been achieved by the ancestors without that characteristic (solid blue). Or, more concretely, we can imagine that the solid blue line represents the terrestrial mammals, and the dashed orange line represents the cetaceans, qualitatively speaking.

Our first step is to run the naïve ratcheting simulation we described in Algorithm 4 and see how it behaves. Figure 3.3 shows the results of one run of the simulation, with $p_r = 1/20000$. Over arbitrary model time $t$ (one step is one cladogenesis event; $x$ axis), the plot shows the largest species seen up to $t$, grouped by minimum sizes. The thicker blue line represents the group with a minimum size of 1.8 g—the “seed group;” species that have not evolved a ratchet trait—and the
Figure 3.3: Results from a run of the naïve simulation, depicting the largest species seen up to time $t$ grouped by their minimum size traits. The thicker blue line represents the group which has a minimum mass of 1.8 g—species that have not evolved a ratchet trait. The thinner lines all depict the largest species seen for other groups. The last point of a line marks the time when the final species with that $m_{\text{min}}$ emerged.

The thinner lines represent other groups. Note that the most massive species is likely not extant at end of simulation—the last point of a line simply denotes when the last species of group $G$ with $m_{\text{min},G}$ was seen to speciate.

Examining the thinner lines, we can see at which sizes ratchets originated (their minimum masses), how large a species of that lineage was able to grow, and how quickly the minimum mass trait went extinct. Note that we cannot infer how many species from a group are extant at any given time from Figure 3.3; in fact, were we to examine every group’s maximum species population at any given time we would find the seed group in first place with 4555 species, and the second most populous group only accounting for at most 35 species alive at one time.

Considering the fact that we choose a species uniformly at random during the cladogenesis step of our model, it makes sense that these ratcheted groups could die off quickly; every time we choose a species to continue its lineage, we choose a non-seed group species less than 0.8% ($35/4590$) of the time, at best. Perhaps the newly ratcheted species need a more level playing field to radiate.
To give the newly ratcheted species this fighting chance to thrive, we will perform experiments to perturb the balance of species and see if there are any conditions under which we see what we have predicted in Figure 3.2. After all, it is entirely possible that certain perturbation events need to occur for new ratchets to find their ecological foothold and radiate—many argue that the extinction of the dinosaurs at the Cretaceous/Paleogene (K/Pg) boundary is what opened up the space for the radiation of mammals [24].

3.3.1 Dropping Meteors

Our first method of perturbing the system involves a massive extinction event, ostensibly caused by a meteor. However, more generally, we can imagine this perturbation to be a global change—whether it is due to a shift in climate, massive volcanic eruption, runaway greenhouse effect, or the impact of an enormous rock.

We simulate the impact of a meteor by choosing a timestep halfway through the simulation when the event will occur. When that timestep occurs in the simulation, we iterate over all species that are extant and kill them off with some probability of extinction by meteor, $p_{ebm}$. Figure 3.4a shows the effect of dropping a meteor halfway through a run of the na"ıve simulation—killing off species with a $p_{ebm} = 0.5$ and making 2256 of 4501 go extinct—through the largest-species-seen lens. Referring back to Figure 3.3 we can see that there is no real appreciable difference between the two.

Examining Figure 3.4b—a view of the number of species extant at model time $t$ grouped by minimum sizes—we can verify that a mass-extinction event took place. (Note: the impact of the meteor on the seed group, thick blue line, is underrepresented in the figure due to the numerical integration used to generate the plot.) Figure 3.4b also graphically demonstrates what we discussed about the na"ıve model above: populations of ratcheted groups make up less than 2% of the entire pool of extant species at any given time.

Due to $p_{ebm}$ being independent and identical for all species in the last experiment, we made little to no impact on the relative populations between the seed and ratcheted groups. Thus, to
Figure 3.4: Results from two runs of the naïve simulation with a mass extinction event halfway through model time. During the simulation shown in a) and b), a meteor killed off 2256 of 4501 species at a \( p_{ebm} = 0.5 \); a different simulation with a biased meteor, killing 4368 of 4501 species with \( p_{ebm,seed} = 0.9995 \) and \( p_{ebm,ratchet} = 0.0005 \), is shown in c) and d). a) and c) depict the largest species seen up to time \( t \); b) and d) show how many of each subgroup are extant at time \( t \)—grouped by their minimum size traits. The thicker blue line represents the group which has a minimum mass of 1.8 g—species that have not evolved a ratchet trait. The thinner lines all depict the largest species seen for other groups.

more closely model an event akin to the dinosauriaphylic extinction at the K/Pg boundary, we will add a bias to the meteor so that it prefers to kill off seed group species.

Figure 3.4d shows the effect of an extremely biased meteor impact (\( p_{ebm,seed} = 0.9995 \), \( p_{ebm,ratchet} = 0.0005 \)) on the number of extant species by group. The meteor killed off 4368 of 4501 species alive at the time of impact. Of the 131 species that survived the extinction event, 1 was from the seed group (0.0076%), 106 (80.92%) were from a group with \( m_{min} = 6.2 \) g, and 24 (18.32%) were from a group with \( m_{min} = 38.9 \) g. (Both species born during the same time step as the meteor fell were part of the \( m_{min} = 6.2 \) g group and survived the impact.)

In Figure 3.4c, we can see a hint of the leap-frogging behavior we hypothesized in the largest-seen view (where the thin purple, \( m_{min} = 6.2 \) g, and yellow, \( m_{min} = 38.9 \) g, lines cross the thicker
blue one), but upon comparing it to Figure 3.4d it becomes obvious that the behavior is a byproduct of the near-extinction of the seed group. Thus we have determined that the behavior we expect can happen as the result of a (heavily) biased mass-extinction event that tips the balance of $m_{\text{min}}$ frequency out of the seed group’s favor. However, this result does not satisfy the conditions under which we see cetaceans emerge—the terrestrial mammals have not gone extinct to make way for the water-dwellers—so we will continue to search for a more general condition.

### 3.3.2 Radiative Promotion for Recent Ratchets

The second way we will perturb the equilibrium is to give recently ratcheted species a short phase of preferential radiation. We implement this in the model by choosing only to speciate from groups that have experienced a ratchet within the last $t_r$ model steps. Figure 3.5 shows some results from two simulations with different $t_r$ values. Plots a) and b) in Figure 3.5 are from a run with $t_r = 100$, and plots c) and d) had $t_r = 500$.

The first item of note in Figures 3.5a and c is the longer time that we see ratcheted groups survive. Instead of the short-lived ratchet groups we saw in our naïve and meteor models (Figures 3.3 and 3.4), we now have many groups surviving until the present day. In fact, in the simulation with $t_r = 100$, 20 groups remained extant at model termination. It is apparent that giving recently ratcheted groups a more populous base (and therefore a greater chance of getting chosen for cladogenesis after the promotion phase) significantly increases their longevity.

Looking at Figure 3.5d, we can easily see the radiative spikes due to the promotion phase, extending up to a population of 500, then following a trajectory akin to a random walk. Figure 3.5b has a similar pattern, which is harder to distinguish due to the radiative phase in that run of the simulation only bolstering group populations to 100 before returning to choosing ancestors uniformly at random from the extant pool. Despite the more interesting behavior of these simulations, large promotional phases are not ecologically justifiable without unrealistic assumptions about the way speciation events over short periods of time are distributed across a diverse ecosystem.

Together, Figures 3.5b and d serve to show how the seed group manages to push other,
ratcheted $m_{\text{min}}$ traits out of the pool of extant species. Even with a significant population boost (at one point in Figure 3.5, a group (thin light blue line) has a population greater than 1000; over 50% of the seed group’s), the competition for getting chosen as a progenitor eventually causes the ratcheted groups to go extinct. Knowing this, let us continue down this road of inquiry and speciate new ratchets early in the simulation ($t < n$) to give them even more balanced populations.

3.3.3 Early Radiative Ratchets

In our final perturbation experiment, we will increase the ratchet probability during the initial radiation phase and see how the populations settle over time. That is to say, we will increase $p_r$ until the model has spawned $n$ species, then relax back to the default $p_r = 1/20000 = 0.0005$. 

Figure 3.5: Results from two runs of the naïve simulation with a promotional cladogenesis phase for recent ratchets. During the simulation shown in a) and b), new ratchets were given 100 model steps during which they were the only group to speciate; a different simulation in which new ratchet were given a 500 step promotion phase is shown in c) and d). a) and c) depict the largest species seen up to time $t$; b) and d) show how many of each subgroup are extant at time $t$—grouped by their minimum size traits. The thicker blue line represents the group which has a minimum mass of 1.8 g—species that have not evolved a ratchet trait. The thinner lines all depict the largest species seen for other groups.
Figure 3.6: Results from two runs of the na"ıve simulation, with $p_r = 1/20000$ except during the initial radiation phase (until 5000 species have spawned). The simulation shown in a) and b) had $p_r = 0.25$ during initial radiation; a different model, shown in c) and d), had $p_r = 0.5$ for the same time span. a) and c) depict the largest species seen up to time $t$; b) and d) show how many of each subgroup are extant at time $t$—grouped by their minimum size traits. The thicker blue line represents the group which has a minimum mass of 1.8 g—species that have not evolved a ratchet trait. The thinner lines all depict the largest species seen for other groups.

Seeing as how the initial $n$ time steps is where the seed group gains its numerical advantage over the pool of extant species, we would expect that having more ratchets during that early phase could balance the relative prevalence of different $m_{\text{min}}$ values.

Figure 3.6 shows the results of two simulations with increased ratchet probabilities during the initial radiation phase ($t < n$). In Figures 3.6a and b we set $p_r = 0.25$ during the radiation, compared to $p_r = 0.5$ in Figures 3.6c and d. We can immediately see the severely increased density of ratcheted species during the radiation phase in the largest seen plots, Figures 3.6a and c, and the effect that density has on the number of species in a group in Figures 3.6b and d.

Interestingly, the simulation run with $p_r = 0.5$ during radiation is the first simulation we have seen in which the seed group does not survive. Without doubt, this result is due to the seed group not having sufficient time to become an overwhelming majority of the extant species—the
first species to spawn from cladogenesis experienced a ratchet, giving the seed group only a 50% chance of survival by step 2. Compound that with a continued $p_r = 0.5$ and we can see that if the only remaining seed group is chosen as an ancestor, it is expected that one of its two descendants will experience a ratchet, reducing the seed group’s prevalence even further.

3.3.4 Discussion

Combined, the above experiments highlight a prevalent theme—the groups seem to be competing for slots in the pool of extant species, occupancy of which correlates strongly with a group’s longevity. We can see this competition prevalently in Figures 3.5b and d (where the population of the seed group declines noticeably with every promotional phase), as well as in Figures 3.6d (where another group takes an early advantage and causes the seed group to go extinct).

Where does this competition come from? We have not included any ostentatious competition in the model, so it must be an emergent behavior stemming from a choice we made in the design of our simulation. To understand more, we turn to a method of modeling evolution on a smaller scale: population genetics.

3.3.5 Population Genetics

Having a species’ minimum size as an inheritable trait—selected for inheritance from a pool of ancestors uniformly at random—results in competition between sub-populations for dominance of the pool. Diving into population genetics literature, we can see that this is exactly how we would expect the prevalence of alleles (variations on a gene) to act in a population. [14]

Note that our model is not the same as ones used in population genetics because we are not concerned with mating (as that happens on the population level and, by definition, not between species). In fact, comparing basic population genetics models with ours, we notice that only the method used to choose an allele ($m_{\text{min}}$) to inherit is the same: uniformly at random from the entire population. That similarity alone is enough to cause the behavior we see: due to choosing inheritance uniformly at random, the probability of a particular trait to saturate a pool becomes
equal to the frequency of that allele at a given time. In this way, the survival probability of beneficial mutations is (approximately) independent of population size, and depends only on the relative prevalence of the mutation in the population [14].

3.3.6 Genetic Drift vs. Random Mutation

*Genetic Drift* is the random walk of the prevalence of an allele, which can result in the vanishing of alleles—and therefore reduction in the diversity of the population—throughout generations. This plays counter to random mutations (descent with variability), which provide new alleles and increase diversity. [14]

In our model, random mutations come from the ratcheting step: evolved $m_{\text{min}}$ values create new “alleles” in the pool with probability $p_r$. Genetic drift then occurs due to the process by which we are choosing ancestors in the cladogenesis step, pushing many of the mutated $m_{\text{min}}$ alleles to extinction.

Instead of neutral theory, discuss in terms of random walks: drift, extinction, fixation. This interplay between genetic drift and random mutation is the heart of Neutral Theory in Population Genetics, which states that most genetic substitutions are due to genetic drift pushing other alleles out of the population, not due to the pressures of natural selection. This is seen as not being at odds with Darwin—the implication of Neutral Theory is simply that most substitutions have no influence on fitness.

The similarity between our naïve simulation and population genetics brings up a critical concern: Neutral Theory violates our assumption that ratcheting provides an increase in fitness.

3.4 Conclusions

Given that our simulation is experiencing dynamics similar to those of population genetics—namely evolution consistent with Neutral Theory—we can conclude that the naïve model we explored in this chapter has a flaw that keeps it from performing as we hypothesized. Implicit competition in the selection of a progenitor during cladogenesis keeps the species in our model from finding a
stable equilibrium with multiple groups living in harmony.

This insight helps us tremendously—in order to see the behavior we hypothesized, we must prevent the implicit competition between groups.
Chapter 4

Adding Dimensions in Nichespace

When ratcheting traits are treated as alleles in a population, they are reduced to just that: alleles in a population. However, ratchets are more than that—they provide an advantage to species which evolve them. Also—as shown in the previous chapter—when a species experiences a ratchet, it must gain access to a new space where it can diversify without competing with other lineages.

If we reimagine our simulation as starting off with one dimension in niche space, with capacity for \( n \) species, along which a group can optimize or adapt, it becomes obvious how we can expand our model to mitigate competition between groups—we can add a new dimension of niche space. In this chapter, we examine how to define that expansion of niche space in the model and then show that our updated model is capable of producing the desired behavior, as discussed in Chapter 3.2.

4.1 Expanding Nichespace

The first question that comes about when adding a dimension to our niche space is “How many species can it hold?” To answer that question, we need to look at how the sizes of taxonomic groups scale with their minimum masses. Our available data include three mammal-related groups—Mammalia [8], Cetacea [7], and Equidae [22]—that have been used in previous studies with the diffusion model as described in Section 2.2.3. These three groups, along with their associated \( m_{\text{min}} \)s and extant species counts are tabulated in Table 4.1.

Canonically, allometric scaling relationships are calculated by fitting a line such that \( y = kx^a \), or in log form, \( \log y = a \log x + \log k \). In our case, we found the coefficients \( a = -0.6 \) and \( \log k = 3.8 \).
Table 4.1: Minimum sizes and number of extant species for three (sub)groups. These data were used to find an allometric scaling relationship between $m_{\text{min}}$ and $n$.

<table>
<thead>
<tr>
<th>Group</th>
<th>$m_{\text{min}}$</th>
<th>$n$ extant</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mammalia</td>
<td>1.8</td>
<td>4002</td>
</tr>
<tr>
<td>Cetacea</td>
<td>7000</td>
<td>77</td>
</tr>
<tr>
<td>Equidae</td>
<td>20000</td>
<td>7</td>
</tr>
</tbody>
</table>

In $\log n = a \log m_{\text{min}} + \log k$ through a fit of Table 4.1's data in log/log space. While this relationship underestimates the capacity of cetacea—at $m_{\text{min}} = 7000$ g, $n = 35$ instead of 77—it gives us a good way to abstract the relationship beyond the single outcome of evolution we observe in the world today. In the future, larger datasets will help to better estimate this allometric relationship, and its variation, on a broader scale (e.g. by including more than mammals).

One way to think of the new dimension’s capacity is as a measure of the sustainable diversity at a particular complexity. That is to say, smaller (less complex) species are capable of greater adaptation while larger (more complex) species are so specialized that they have fewer ways in which they can continue to optimize and adapt. [28].

A second way to view the capacity of a niche space dimension comes from Morse, et al. [19], building on Hutchinson and MacArthur [15]: The world is more spacious for small animals by the claim that vegetation is fractal in nature. [16] Or, in other words: larger species require more space and therefore fewer locations are suitable for them to inhabit.

Looking beyond cetaceans and equines, we find that our allometric relationship predicts that at a minimum mass of about 2 million g, the niche space dimension capacity becomes 1. However, we disallow dimensions of capacity less than 10 in our model to allow enough space for species to diffuse.

### 4.1.1 Simulation Modifications

To represent the opening of new niche space dimensions in our simulation, we added a new extant pool (scaled in capacity by our allometric relationship above) for each ratchet occurrence then seeded that pool with the newly ratcheted species. In subsequent cladogenesis steps, we choose
ancestors from each pool independently to prevent competition by random choice. We cannot, however, choose from every pool at every step without consequences for the smaller dimensions.

Nichespace dimensions with smaller capacities need to be scaled appropriately in terms of model time. In section 2.2 we determined the number of model steps to simulate ($t_{\text{max}}$) based on the “real” time we would like the model to run ($\tau = 250$ My), the mean species lifetime ($\nu = 1.6$ My), and the number of species expected to be alive at any given time ($n$): $t_{\text{max}} = \tau \nu n$. Thus, ratcheted ($n_{\text{niche}} < n_0$) dimensions require fewer model steps to cover the same amount of “real” time. To account for this, we only choose to speciate from smaller niche dimensions every $n_0/n_{\text{niche}}$ steps, where $n_0$ is the number of species in the seed group at equilibrium and $n_{\text{niche}}$ is the smaller niche space dimension’s capacity.

As a result of altering the speciation rate, our uniform extinction rate ($\beta$ from Section 2.2.3) can remain constant throughout the simulation, and in terms of the size of the original niche space dimension: $\beta = 1/n_0$.

4.2 Simulating MOM Data

In a contrived run of the expanding niche space model, we specified particular conditions upon which a single new dimension can arise ($t > t_{\text{max}}/2$ and $6800 < m_D < 7200$) to represent the appearance of cetaceans. Running this contrived model delivers the results seen in Figure 4.1. We would expect this simulation to result in an extant set of species that very closely resembles the MOM dataset, and by removing the competition between lineages implicit in the selection of ancestors, we arrive at generated distributions that match our empirical ones!

4.3 Letting the Ratchet Click

If we remove our contrived cetacean constraints on the expansion of niche space and run the model with our default ratchet probability, $p_r = 1/200000$, we can see three differences over the baseline model (Figure 4.2): an increased maximum likely mass (where the black diamonds cross the $x$ axis), the easing of the slope between 10 and 10000 g, and a broadening of the confidence
Figure 4.1: a) shows the distributions of the two niches over the MOM data for reference. b) shows the largest species seen (thicker line), as well as the largest species alive at a given time (thinner line) for both the seed group (green) and the ratcheted group (blue). c) shows the number of species alive throughout the model for both seed group (green) and ratcheted group (blue).
Figure 4.2: This figure shows the mean distribution of extant masses (with 95% confidence interval) at simulation termination, for two different models run 500 times each. The upper plot shows the baseline (Clauset-Erwin) model (as described in Section 2.2.3), and the lower plot shows the unconstrained expanding niche space model. Both figures have probability mass plotted for exaggeration of the differences between them.
interval (black dashed line).

All of the differences between the plots in Figure 4.2 are anticipated results of evolving multiple mass floors: the increase in maximum likely mass was shown by Clauset [7]; the gentler slope between 10 and 10000 g is explained by the presence of multiple minimum sizes both providing pressures towards an increase in mass, and preventing smaller masses from appearing; and the broadening of the confidence interval represents the effects of having different dimensions, each with unique minimum sizes and capacities, in every run of the model.

From these plots we can also estimate the maximum expected mass of a species. For the Clauset-Erwin model, this maximum occurs around $10^7$ g—the estimated mass of the extinct Imperial Mammoth. For Clauset in [7], the maximum for cetaceans was found to be nearly $7 \times 10^8$ g, almost four times the size of a blue whale. In our expanding niche space model, this estimate (by the edge of the 95% confidence interval) extends out to nearly $10^{10}$ g, which is mind-bogglingly massive.

4.4 Conclusions

In this chapter, we succeeded in simulating the behavior observed in the evolution of cetaceans from mammals through the removal of implicit competition between groups. This had the effect of removing genetic drift from our model, allowing the random mutations—ratcheted minimum masses—to persist.
Chapter 5

Conclusions

At the end of [17], Loreto et al. conclude that an important aspect of any novelty-generating statistical model is the ability to enlarge the space of possibilities. In our model of species complexity, we generate novelties through random mutation in the absence of genetic drift.

Looking back on our broad questions from Chapter 1, we can now say that (under the assumptions upon which we built this model) increasing complexity occurs as a result of random mutations and is preserved when a complex collection of those mutations (an evolutionary innovation) allows access to a new dimension of niche space—just as mammals’ endothermy allows them to survive in more variable environments, or how the emergence of eyes gave organisms an inherent advantage. Conversely, if an innovation does not promote the lineage to an uncontested dimension, then one of two things can happen: the innovating lineage may push its ancestors to extinction, or it may go extinct itself.

So now we can refine our idea of a ratchet in evolution. A ratchet is not simply any irreversible innovation, but rather one that provides enough of an advantage to elevate the lineage into an uncontested space.

---

1 Loreto et al.’s model is based on Pólya’s urn—a rich-get-richer statistical model of randomly selecting colored balls from an urn and replacing them along with additional balls depending on what was chosen—which has similar (and more general) mechanics to our radiation promotion model (Section 3.3.2), if our model did not include extinction.
5.1 Future Work

This work is rife with opportunities for continuation, from concrete research tasks to applications in other fields. Here we present some ideas of how we would choose to continue this line of research.

5.1.1 Concrete Continuations

Considering the growing popularity and interest in minimum sizes, it would be of value to the evolutionary biology facet of this study to tabulate more data for the allometric relationship discussed in Section 4.1 to further support the relationship itself, and to provide an estimate of the variability in niche space dimension capacity.

Another continuation of this research could be found in applying it to other, non mammal, Classes. If this model is generalizable to wildly different varieties of organisms (such as insects, reptiles, or amoeba), it would have major implications in our understanding of macroevolution. A barrier to completing such research would be the massive amount of data—concerning both extant and extinct species—required to fit the model with non-mammal parameters.

5.1.2 Other Facets of Ratchets

Here we have shown how the ratcheting of complexity influences body mass in biological species, but what other evolving entities exhibit ratchets? There are a number of ways this research on complexity could be broadened—all we need is data.

One area we could explore would be the ecosystem of software and technology. Ratchets in this domain could include such innovations as the wheel or the Internet—each opening up an entirely new dimension along which optimization can occur. For a study of technology, patent records, Github repository data, and other data sources could be compiled for model parameter estimation.

Another area of interest would be the social ecosystem. Social communities or cities are
built very in a similar fashion to complex organisms, with differentiation of expertise coordinating to grow to sizes unachievable without innovations such as agriculture or language. Businesses and companies also have many qualities that could be used to measure complexity (number of employees or reported revenue, for example) and can even be grouped by field of expertise (such as financial, service, or engineering) for comparison.

Regardless of the complex system being studied, the process of adapting our statistical model would be similar. After deciding on a metric that correlates with complexity, we can compile a dataset, examine the distribution of complexity measures, then work to tune parameters of the model to fit the distribution. What could come out of such a study would be technological or social corollaries to biologically observed phenomena—\textit{i.e.} Cope's Rule and mass-dependent extinction—resulting in quantifiable interdisciplinary comparisons of evolution across all aspects of our complicated existence.
Bibliography


Appendix  A

Model Subtleties

A.1 Seed Mass

You can seed the baseline model, as described in 2.2.3 with any mass and get the same final distribution. Figure A.1 shows this graphically.

Figure A.1: Four plots showing the baseline model (see Section 2.2.3) output for four different initially masses: 2, 7000, 20000, and 1000000 g. Each initial mass was run through the model 100 times; plotted is the mean (black diamonds) and 95% confidence interval (dashed black lines) of those runs over the MOM terrestrial data (green Xs).
A.2 Effects of ratchet probability on simulation results

Increasing the ratchet probability of the na"ïve model causes the distribution to spread out even further, increasing the mode and the maximum. Figure A.2 depicts this effect through four different ratchet probabilities. The model was run 100 times at each probability; shown are the means and the 95% confidence intervals for those 100 runs.

![Figure A.2: Four plots showing the na"ïve ratcheting model (see Section 2.2.3) output for four different ratchet probabilities: 1/200000, 1/20000, 1/200, and 1/200. Each plot represents the the mean (black diamonds) and 95% confidence interval (dashed black lines) for 100 runs of the model, shown over the MOM terrestrial data (green Xs) for reference.](image)

A.3 Histogram Normalization

To keep the figures in the document consistent, we used probability density histograms for most plots. To illustrate the visual differences between two ways of normalizing histograms, we
included Figure A.3 below.

Figure A.3: The top plot shows a probability density histogram, the bottom shows a probability mass histogram. Note how different shapes and qualities of the histograms change as function of the normalization scheme.
Appendix B

Extinction-Centric Model

There is another way that we conceived of to remove the inherent competition in species choice, which contained an opportunity to relax the model of cladogenesis we used to be more general. By refactoring the model (from speciation at every iteration) to be based on extinction events, we programmed an “extinction-centric” version of the model.

The move from an iteration- to event-based method of modeling brings along some challenges for performing efficiently. Instead of choosing directly from a collection of species we know to be extant at the time of cladogenesis, we will be waiting until a species goes extinct before executing the speciation step. This means that, to have our simulation terminate in a reasonable time we need to be able to tell when the next species will be going extinct, and “fast-forward” the model to that time.

To pre-determine a species’ extinction date efficiently, we used a geometric distribution (the discrete trial analog to an exponential distribution) to model the number of trials we would have needed to perform (at \( p_{ext} \)) to get our first success—where “success” here denotes extinction. This condenses thousands of random draws into one, making our model more performant. We implemented the geometric distribution computationally by taking a uniform-at-random draw from \([0, 1]\)—standard call to most any random function—as the result of draw from the cumulative distribution function (CDF) of an exponential distribution, and calculated which input value to the CDF would have given us our randomly drawn outcome. Mathematically, we solve for \( x \) in \( \text{random()} = 1 - \exp(-\lambda x) \), where \( \lambda = 1/p_{ext} \)—resulting in \( x = \log\text{random()}/\log(1 - p_{ext}) \). If we
are working with discrete time steps, we then take the floor of $x$ to map it from the continuous exponential distribution to the discrete event geometric distribution; otherwise we can scale the resultant $x$ by a factor of millions of years to get a “real time” extinction pre-determination. (Note that we incorporated the discrete-time method of extinction determination into the Clauset-Erwin model as well; see Section 2.2)

Now that we know when a species will go extinct as soon as it spawns, we need to choose appropriate data structures to keep track of what events (extinction or speciation) are coming up next. We opted to use a binary heap to keep our extinction events ordered ($O(\log n)$ for insertion and for popping largest, due to contents being sorted by key); a hash map for quick, random-access bookkeeping of which species are extant (expected and amortized $O(1)$ insert, expected $O(1)$ remove); and a vector for keeping record of every species seen (amortized $O(1)$ insertion at end). This collection of data structures allows for very rapid and simple determination of the next upcoming event.

Right away we run into an issue with the model that we did not have to account for previously: reaching our equilibrium species count, $n$. In our speciation-centric model we iterate with every speciation event such that the extinction pressure stays constant, causing the species count to reach $n$ and enter equilibrium after $t = n$ steps. However, in our extinction-centric model we link speciation events to extinction events and iterate on extinction, meaning that we will not have radiation in the model during the first $n$ steps. As such, $n$ is no longer a stable attractor for species count; rather species count will perform a random walk. To address this, we have to make speciation events more common ($p_{\text{spec}} > 0.5$) while $t < n$, and then let the probability of speciation to dwindle to the equilibrium probability of $p_s = 0.5$ once $t > n$.

B.1 Relaxing Cladogenesis

To relax our model of cladogenesis, which we naïvely chose to result in the emergence of two new species and extinction of the progenitor, we can assume that speciation events—like extinction events—are distributed throughout time like a Poisson process. As such, we can give a
“speciation rate” as input, and draw speciation event timing from an exponential distribution as well, disassociating speciation from extinction and adding a new type of event to our model.

Making both speciation and extinction events independent in time relaxes our model of cladogenesis by allowing outcomes such as anagenesis (one new species upon extinction, as a result of accumulated changes) and the continuation of the progenitor species after speciation. The drawback here—and ultimately the reason this line of inquiry was closed—is the addition of a difficult-to-estimate parameter to the model: speciation rate.

B.2 Outcomes

It was abandoned due to time constraints and due to the increased parameter space (by introducing a speciation rate) that made fitting the model extremely difficult. In the end, the extinction-centric model is still beholden to competition through selection due to the limited capacity of the extant pool.