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Evolutionary Dynamics of Speciation and Extinction

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EVOLUTIONARY DYNAMICS OF SPECIATION AND EXTINCTION

by

DAWN MICHELLE KING

A DISSERTATION

Presented to the Faculty of the Graduate Faculty of the

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ABSTRACT

Presented here is an interdisciplinary study that draws connections between the fields of physics, mathematics, and evolutionary biology. Importantly, as we move through the Anthropocene Epoch, where human-driven climate change threatens biodiversity, understanding how an evolving population responds to extinction stress could be key to saving endangered ecosystems. With a neutral, agent-based model that incorporates the main principles of Darwinian evolution, such as heritability, variability, and competition, the dynamics of speciation and extinction is investigated. The simulated organisms evolve according to the reaction-diffusion rules of the 2D directed percolation universality class. Offspring are generated according to one of three reproduction schemes. Mate choice dictates offspring placement, and it defines a species based on reproductive isolation (known as the biological species concept), while a globally enforced death process ensues within each generation. This system is shown to exhibit nonequilibrium, continuous phase transitions as a function of the individual death probability. The dynamical rules that enable phase transition and clustering behavior to transpire behavior is discussed, and a connection is drawn to another type of phase transition that arises by mate choice alone. Coalescent theory is then used to explore common descent in evolved phylogenetic tree structures at both the individual and cluster level. Finally, an extinction scenario is implemented where, after reaching a steady-state, a large population percentage is killed. Historical contingency is shown to play a major role in recovery from mass extinction at criticality.

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Glossary

Adaptive Radiation — the process of organisms diversifying rapidly, often due to newly opened ecological niche space. For example, the Galápagos Finches have ~fifteen distinct species, each with a unique beak, which feed on different food sources. It is thought that these birds rapidly diversified to feed at different trophic levels.

Allele — different versions of a gene. Diploid organisms have two alleles for a single trait, one from each parent. A simple example is the possible expressions of a gene that is encoded by a recessive or dominant allele that comes from either parent.

Allopatric speciation — a type of speciation event induced when ancestral populations are separated by a geographical barrier, or when an ancestral population is divided into two or more geographical subpopulations.

Analogy — species that have similar morphological characters (traits) that are not derived from common descent (*i.e.*, there is not a common ancestor). An example would be the wings from a bat and a bird. The bat is in the class Mammalia and a bird is in the class Aves. The common ancestor cannot be traced backward in time from a shared-derived trait of a wing, thus the wing evolved independently, and a common ancestor exists deeper in time.

Biramous — refers to a segmented leg of an Arthropod that branch into two.

Cambrian Explosion — refers to the evolution of multi-cellular life ~542 million years ago, where nearly all modern phyla date back to this time. The diversification of metazoan life occurred rapidly relative to the millions of years of subsequent evolution.

Control Parameter — it is an external parameter that is varied. For example, it tunes a system through a phase transition.

Convergent Evolution — when different species share a morphological character but do not share a common ancestor from which the trait evolved. For example the evolution of wings in bats and birds happened independently, for bats and birds do not share common descent.

Disparity — a measure of morphological diversity; having many distinct body plans.

Eutrophication — the enrichment of nutrients in bodies of water, particularly nitrates and phosphates.

Fecundity — the reproductive rate (#offspring/time) of an organism or a population.

Fitness — the number of offspring an organism produces that survives to produce in the next generation.

Fixation — the situation where there is a change in the gene pool from at least two or more alleles to only one allele.

Genotype — the specific DNA sequence of an organism.

Haploid — describes a cell that has a single set of chromosomes. Gametes are haploid.

Homeotic Mutation — a mutation that causes a developmental oddity, such as bodily structures that end up in odd locations.

Homology — characteristics from distinct species that share common descent. For example, all mammals have seven neck vertebrae that trace to a common ancestor.

Kin Selection — an evolutionary process where organisms assist in the survival of other organisms if they are closely related, even at a cost to themselves.

Leaky-replacement Hypothesis — the hypothesis that *Homo Sapiens* were not the only species of the genus *Homo* to migrate out of Africa. New research has shown that *Homo Sapiens* also mated with other groups, such as the Neanderthals, instead of outrightly replacing them.

Macroevolution — evolutionary process that occurs at and above the species level of biological organization. In the past, the term has been used to describe speciation events that were caused by genetic changes.

Microevolution—evolutionary processes that occur below the species level, such as resulting from changes in allele frequencies within a population.

Multi-level Selection I — selection shown between groups, such as species, based on the collective fitness of the individuals within the group.

Multi-level Selection II — selection shown between groups based on fitness of the group, *i.e.*, individual fitness of the group constituents is not considered. An example of a fitter group based on a group property could be group size. Large groups could be considered better 'fit' since they are harder kill, and the entire group is more likely to survive into future generations than a small group.

Ontogeny — is the origination or development of an organism starting from fertilization to maturity. Sometimes the entire lifespan of an organism can be considered.

Order Parameter — An observable quantity that can be used to distinguish between two phases of a system.

Pedogenesis — the process of the formation of soil.

Phenotype — the visible expression of an organism's genotype, such as eye color, height, tail length, etc.

Saltation — a sudden evolutionary change that occurs from one generation to the next.

Sessile — an organism that is attached at its base and does not move for the entirety of its lifespan.

Single-origin Hypothesis — the hypothesis that the first species of the genus *Homo* are descended from Africa, and that every species except for the species *Homo sapiens* were driven to extinction before migrating out of Africa.

Sympatric Speciation — a type of speciation that occurs when subsets of a population that reside in the same geographical area form a reproductive barrier.

Transgression — a geological event where the sea level rises or land sinks into the ocean causing flooding and the coastline to move to higher ground.

Uniramous — refers to a segmented leg (from base to tip) of an Arthropod that does not branch.

1. INTRODUCTION

'The history of an idea is paved by the constraints of language.'

-Leo W. Buss

1.1 BIOLOGICAL BACKGROUND

Biodiversity is a loaded term. There are many viewpoints of the drivers of biodiversity, let alone the patterns that prevail at many different levels of biological organization. Almost all viewpoints have proposed natural selection among individual organisms as the evolutionary driving force. Popular culture has propagated this individualist view of natural selection through abuse of the phrase of 'survival of the fittest,' which has invoked an image of man versus nature, whether it be Bear Grylls, the survivalist, overcoming all odds on the popular T.V. show *Man vs. Wild*, or the competition among industrialists that laissez-faire capitalism has induced—may the best man prevail has been the overarching theme. The 'survival of the fittest' motto has given popular culture an unrealistic glimpse into the underlying process of natural selection and taken away from its true meaning of differential fitness between organisms based on reproductive success. It has led to a misunderstanding that the natural world is something to be dominated rather than something that demands coexistence. Further, it has led to a purely individualistic view of the natural world.

There is a much needed synthesis in recent evolutionary thought — that the process of natural selection can 'act' at many levels of biological organization, and also that natural selection is not the only mechanism driving evolution and the patterns of diversity. The natural, organic world is driven by processes both large and small. All organisms can be defined by their genome and, also, be defined as belonging to a species. Traditionally, the biological species concept grouped organisms based on reproductive isolation (which is still a valid method to define a species), but it is now known, thanks to the pioneering efforts of the many scientists studying genetics since the time of Mendel, that each species will have specific genetic markers. If biodiversity

is a measure of the number of distinct species, at what level does the evolutionary process of speciation proceed? Is it based on individualistic reproductive behavior, or is it based on reproductive isolation due to genetic incompatibilities? Which level is the appropriate level to examine evolutionary process? The answer is that all biological levels of organization can undergo evolutionary processes, and that evolutionary processes are constrained by selective pressures from the environment.

This section is written to give the reader a general overview, and some history, of current controversies over the main evolutionary themes prevalent today. For the reader who wants less background information, sections 1.1.4 and 1.1.5, as well as paragraphs that pertain to specific criticisms of the different evolutionary views, may be skipped without losing key definitions that are used in the model.

1.1.1 Darwinian Evolution. Darwin provided one the first tangible accounts of a mechanism for ‘how’ organisms came to exist, by outlining a process called natural selection based on years of observational study. His revolutionary work, *On the Origin of Species*, outlined three main tenets of natural selection – variation of traits, heritability of traits, and competition for resources in the natural environment – with the key feature of differential fitness based on adaption to the environment. Thus, varieties of organisms (meaning the different assemblages of traits that different organisms possess) that are better ‘fit’ will be more successful in their competition for resources, and as a result, will produce more surviving offspring that pass their heritable traits to future generations. Therefore, it is a selective advantage, in the natural environment, to possess certain traits.

1.1.2 Neutral Evolution. Neutral evolution takes the selective advantage of possessing certain traits out of the evolutionary picture. All of the key features of natural selection can still be present, such as variation of heritable of traits and competition for resources, but there is not a selective advantage to possessing a particular trait, and thus differential fitness is not exhibited among organisms. Rather, a population or a species may evolve via a process called drift. There are two main forms of drift discussed below.

1.1.2.1 Genetic drift. ‘The frequency of a given gene in a population may be modified by a number of conditions including recurrent mutation to and from it, migration, selection of various sorts, far from the very least important, *mere chance variation.*’ (Wright, 1931 p. 155 my italics) The chance variation that Wright was discussing is the evolution of a genetic trait without differential fitness, which is now known as genetic drift. In this view, no single gene, or genotype, is more fit than another, and thus, the probability that a given allele will dominate a population can arise by pure chance. Drift was first modelled by Fisher (1930) and Wright (1931), although they did not specifically call their work ‘genetic drift’. The term genetic drift was coined and popularized by Motoo Kimura (1968, 1983), and it was recently expanded upon by population geneticists through the use of the Wright-Fisher (WF) process¹ (discussed in Chapter 3) in coalescent models (Wakeley, 2009; Hein, 2005).

1.1.2.2 Ecological drift. Ecological drift rocked the ecological community’s world in 2001 with Stephen Hubbell’s book entitled *The Unified Theory of Biodiversity and Biogeography*. Here Hubbell defined ecological drift as a process that occurs at the organismal level: ‘By *neutral* I mean that the theory treats organisms in the community as essentially identical in their per capita probabilities of giving birth, dying, migration, and speciating. This neutrality is defined at the *individual* level, not the species level,’ (p. 6) but it does imply some degree of ecological equivalence among species since a ‘fitter’ species cannot manifest its greater fitness by a higher fecundity among the constituent organisms. Emergent clustering can transpire with this definition of neutrality among organisms, and by chance some clusters will emerge as dominate over the others – despite the complete neutrality between organisms.

¹ Because of the prevalence of the WF process in coalescent theory (which is discussed at length below), I sought for a publication by the two men and found that Wright and Fisher never wrote a paper together. But it does appear that they were intimately familiar and built upon each other’s work. Wright would cite things such as, ‘thus confirming Fisher’s predictions...’ (Wright, 1931), and then Fisher would cite ‘Professor Sewall Wright of Chicago, who had arrived by an independent calculation at the correct result, drew my attention to the discrepancy and has thus led me to a more exact examination of the whole problem.’ (Fisher, 1930 p.87)

While the concept of ecological equivalence was not new in 2001 (Hubbell, 1979; Goldberg & Werner, 1983), Hubbell's work has, importantly, produced much discussion, and some contention, among the ecological community. Chave notes in his review of neutral theory (2004) that 'Hubbell's (2001) book represents an outstanding attempt to promote the neutral theory as an operational theory in community ecology.' This was evidenced by an impressive explosion of papers, where '2 years after the publication of Hubbell ..., ISI's Web of Science reports 178 scientific articles citing this work.' The discussion of neutral theory among ecologists has not waned over the years, with relatively recent articles arguing for (Rosindell *et al.*, 2012) and a vehement attack against (Clark, 2012) neutral theory appearing in the same journal issue. Further, a 2015 Google Scholar search using the key word 'neutral theory' had ~22,000 hits – with adding the word 'ecology' to the search there were ~13,000 hits. Thus, over half of the literature produced pertained to neutral theory's application in ecology.

While much of the criticism against the Unified Theory of Biodiversity has been hyped as an argument based on the unrealistic nature of ecological equivalence, Hubbell never claimed that his theory was explicitly true.

While the assumption of complete neutrality is patently false, few ecologists would deny that real populations and communities are subject not only to physical factors and biotic interactions, but also to demographic stochasticity. To study ecological drift theoretically, it is easier to make the assumption of per capita ecological equivalence – at least to begin with. (Hubbell, 2001 p. 6)

Further, '*... the essential defining characteristic of a neutral theory in ecology is not the simplicity of its ecological interaction rules, but rather the complete identity of the ecological interaction rules affecting all organisms on a per capita basis.*' (Hubbell, 2001 p. 7) These beautiful insights of Hubbell have fostered theoretical discussions of simple population-based models for ecology that still, importantly, allow for complex ecological interactions. So while it is unrealistic to think of species as having the same fecundity (with fecundity defined as the rate of reproduction), or all individuals within a species

being equally fit regardless of the expressed phenotype, individuals within a community can still compete for food, be subjected to random death, and produce mutated offspring as long as every individual in the population is subjected to the same rules. This still acknowledges an extremely complex range of behavior, while making one key assumption – all organisms are created equal.

‘A number of critiques of Hubbell (2001) deal with the difficulties of its mathematical developments and the poor linking with existing mathematical theories developed in population genetics.’ (Chave, 2004 p. 25) This major criticism from ecologists stems from the reductionist approach that Hubbell’s neutral theory inspires, in that some ecologists have issue with the ‘equality among constituents’ premise that neutral theory promotes. Because critics have latched onto the idea that reductionism is an unrealistic assumption for ecological drift, Chave reasons that mathematical development of ecological drift has been stymied, as evidenced by the abundance of mathematical work that has been done on ecological drift’s counterpart — genetic drift. (Chave, 2004) There is, in fact, much mathematical work that has been inspired by genetic drift (Kingman, 1980; Moran 1958, Nordborg, 1997, 2004; Berestycki, 2009), as well as an entire mathematical field, known as Coalescent Theory, inspired by genetic drift models (Hein *et al.*, 2004; Wakeley, 2009).

Of course, if it was up to Clark (2012), none of the above criticisms were relevant because, according to him, neutral theory is fundamentally incoherent. He wrote that ‘[p]roponents of the Unified Neutral Theory of Biodiversity ... describe its history as ‘controversial’. ... The continuing confusion comes from misidentifying what is controversial and the fundamental coherence problem with UNTB.’ This coherence problem is that ‘UNTB has nothing to say about how species differences affect diversity’, in that ‘...neutral models do not assume that species occupy the same niche, have the same fitness or are the same in any sense’, coupled with ‘the fact that there are no ‘neutral forces’...’. The term ‘force’ is not used in the traditional sense—like the magnetic or gravitational force — for it used in a vague, biological sense. For example, selective forces are the drivers of evolutionary processes, such as any mechanism that

allows for a certain species to survive better than another in a particular environment. Therefore, Clark argues that there is not an analogue of a selective force to a 'neutral force', and even though stochastic models can demonstrate evolutionary phenomena such as speciation, they do not demonstrate that neutral forces act in nature. (Clark, 2009) As for the rebuttal, well there isn't one... how do you argue with: 'If the UNTB has become nothing more than an assumption that 'all species have equal probability', then it cannot be theory of biodiversity. This is just a statement of ignorance about which species cannot succeed and why.' (Clark, 2012)

Contrary to the claim above, neutral models can be developed with species occupying the same niche space (Dieckmann & Doebeli, 1999; de Aguiar *et al.*, 2009; Scott *et al.*, 2013) – though, to be fair, one of those models was published after Clark's opinion piece and the others, while still individual-based models, used binary genotypes that defined each individual while demonstrating emergent speciation. Further, if there are 'no neutral forces', then why do physicists still teach Newton's 1st law, the law of inertia, which, with some word play, could be considered a neutral force in relation to the other two force laws. With the law of inertia, no force is needed to keep an object in perpetual motion; only to change motion is the application of a force necessary. Thus, the argument that there are 'no neutral forces' is not a valid argument against the use of a neutral theory in ecology since 'inertial' processes could be operating even without the application of a 'selective force.' Rosindell *et al.* (2012) described much of the contradiction to be a matter of semantics.

The term 'neutral theory' is widely (but regrettably) used in ecology to mean different things, leading to misconceptions that take the debates in a less fruitful direction. For some, the term is used purely interchangeably with 'null model'; to others it refers specifically to the contents of Hubbell's book [*i.e.*, comparisons with species-abundance curves, *etc.*]. We use 'neutral theory' to refer to 'an ensemble of different neutral models by various authors', that retains the spirit of what most think of as neutral theory without having too narrow a scope. If 'neutral theory'

were taken instead to be a direct statement that there really were no ecological differences between organisms, then it would be reduced to a straw man; no person supports such a 'neutral theory'. (Rosindell *et al.*, 2012 Box. 1)

In fact, Hubbell does state in his book that 'I will consider only one class of all possible neutral theories' (p. 7), thus allowing for the many different applications of neutral theory seen today.

'Neutral Theory is about improving understanding by making some simplifying assumptions about complex systems and seeing what can be explained with the resulting models, a procedure [that is] widely accepted in other branches of science that does not require the assumptions to be strictly accurate.' (Rosindell, 2012) While Hubbell defined neutrality as ecological equivalence of all organisms among many species in a community, and Kingman developed a mathematical field of coalescent theory based on genetic drift that is widely accepted by population geneticists, others (Ricklefs, 2012) have looked towards applying neutral theory at higher levels of biological organization. As seen in 'Global Correlations in Tropical Tree Species Richness and Abundance Reject Neutrality', Ricklefs and Renner (2012) rejected neutral theory at a higher than species level of organization by showing that the abundance curves of individuals-per-family and species-per-family (counter to the traditional individual-per-species curves of Hubbell's work), did not fit the predictions of neutral theory. With major scientific journals publishing results such as this, perhaps neutral theory has done its job by acting as an appropriate *null hypothesis* that can be rejected. Yet, Ricklefs's article further highlights (though inadvertently) the idea *that evolution may proceed on very different timescales depending on the level of organization in question*, and this may point to the reason why a neutral theory that was initially designed to act at the individual-per-species level is not applicable when comparing the individual-per-family and the species-per-family level abundance curves.

1.1.3 Singular Evolutionary Viewpoints. The next subsections will give an overview of some key concepts of evolutionary views at different levels of biological organization.

1.1.3.1 Gene's eye view. The gene's eye view is a perspective popularized in the 70's by Richard Dawkins with his book entitled *The Selfish Gene*. Dawkins is not alone in his views, for his noted inspiration for viewing evolution at the lowest level of biological organization came from the work of C.G. Williams² (1966). Dawkins argues that '[t]here are two kinds of unit of natural selection, and there is no dispute between them. The gene is the unit in the sense of the replicator. The organism is the unit in the sense of the vehicle. Both are important.' In Dawkins's view, organisms are simply protective casings for the genes, where genes that express successful phenotypic enclosures continue to thrive and replicate. 'Without the gene's-eye view of life there is no particular reason why an organism should 'care' about its reproductive success and that of its relatives, rather than, for instance, its own longevity.' (Dawkins, 1989)

'Darwin's 'survival of the fittest' is really a special case of a more general law *survival of the stable*', writes Dawkins, where survival of the stable refers to the replicators known commonly as genes. Our bodies (or actually any living organism's body) are 'survival machines' for genes.

Different sorts of survival machine appear very varied on the outside and in their internal organs. An octopus is nothing like a mouse, and both are quite different from an oak tree. Yet in their fundamental chemistry they are rather uniform, and, in particular, the replicators that they bear, the genes, are basically the same kind of molecule in all of us — from bacteria to elephants. We are all survival machines for the same kind of replicator-molecules called DNA — but there are many different ways of making a living in the world, and the replicators have built a vast range of machines to exploit them. A monkey is a machine that preserves genes

² Though Williams work still included a defense of Darwinism, which is a notable difference in perspective from the 'survival of the stable' view of Dawkins.

up trees, a fish is a machine that preserves genes in water; there is even a small worm that preserves genes in German beer mats. DNA works in mysterious ways. (Dawkins, 1976 p. 21)

But then, Dawkins goes on to explain that 'DNA works in mysterious ways' by invoking an imagery of 'passive manipulation by our gene captors' (Lewontin, 1997):

They swarm in huge colonies, safe inside gigantic lumbering robots, sealed off from the outside world communicating with it by torturous indirect routes, manipulating it by remote control. They are in you and me; they created us body and mind; and their preservation is the ultimate rationale for our existence. (Dawkins, 1976 p. 19- 20)

In recent years—the last 600 million of so—the replicators have achieved notable triumphs of survival-machine technology such as the muscle, the heart, and the eye (evolved several times independently). (Dawkins, 1976 p. 24)

It leaps from body to body down the generations, manipulating body after body in its own way for its own ends, abandoning a succession of mortal bodies before they sink into senility and death. (Dawkins, 1976 p. 34)

As opposed to the general view of natural selection's process that holds genes as the unit of inheritance, Dawkins gene's eye focuses on longevity, fidelity, and fecundity as the general evolutionary scheme. By doing this 'Dawkins is clearly envisioning something quite different from the idea of a lineage branching and expanding through time within a space of possibilities. For Dawkins, the point is not to evolve, but to stay the same.' (Bahar, in prep)

1.1.3.2 Individual level. The genetic view of evolution can be traced back to the work of Fisher (1930) with his work, 'The Genetical Theory of Natural Selection'.

However, contrary to Dawkins gene's eye view of the universe, for Fisher, the organism acts as the unit of selection, and the genes act as the unit of inheritance. This view was not the traditional view of Darwin in 1859, for Mendelian inheritance had not yet been rediscovered. Darwin's view of inheritance (which we now know to be fundamentally wrong), called pangenesis, was illustrated as a complicated mechanism that included the life history of the breeding organism (Geison, 1969). Nevertheless, while his mechanism of inheritance was blatantly incorrect, the mechanism of natural selection has prevailed throughout time and it has proven useful for explaining much of the biodiversity patterns seen today.

As Darwin conceived it, natural selection acts primarily at the level of the individual, and it involves the passing of genetic material via sexual or asexual reproduction. Over time populations of organisms diverge in their genetic traits, and, as a result, organisms that are better suited for the natural environment survive to continue to pass on their heritable traits to future generations. Those organisms that cannot adapt do not survive to pass on their traits. This also leads to the view that evolution proceeds in a gradualist manner and that the surviving diversity is the result of a culmination of small, positive, beneficial changes. There are not many people who reject Darwin's notion of individual level selection and adaptation, but there is a history of people rejecting anything other than strict organismal-level adaptationism (Maynard Smith, 1964; Wilson, 2006; Gould, 2002).

1.1.3.3 Group selection. Like neutral theory, the idea of 'group selection' has produced considerable debate. As its name implies, group selection means that natural selection acts at the level of the group, not the individual. While group selection was not completely omitted as a possible evolutionary force during the mid-twentieth century period of evolutionary biology known as the "modern synthesis", it was usually dismissed and treated as rare and unimportant. Many examples can be found of Darwin supporting his ideas of natural selection at the organism level, yet there are also examples of Darwin considering group level selection. In the *Origin*, Darwin, when discussing the problem of insects with sterile castes such as bees and ants, said 'if on the

whole the power of stinging [is found to] be useful to the social community, it will fulfill all the requirements of natural selection, though it may cause the death of some few members.' (Origin, p. 257) The difficulty in explaining such cases 'is lessened, or, as I believe, disappears, when it is remembered that selection may be applied to the family, as well as to the individual.' (Origin, p. 354) Darwin can also be found addressing the evolutionary origins of altruism in groups: 'It must not be forgotten that although a high standard of morality gives but a slight or no advantage to each individual man and his children over the other men of the same tribe, yet that an increase in the number of well-endowed men and an advancement in the standard of morality will certainly give an immense advantage to one tribe over another. A tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to aid one another, and to sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection.' (Descent, p. 157-8)

The evolution of altruistic behavior is a contentious topic among group selection theorists. As noted by Maynard Smith, some scientists such as, '...E.O. Wilson (1975), D.S. Wilson (1975), and M.E. Gilpin (1975) ... either propose[d] a blurring of the distinction between "group" selection and "kin" selection, or suggest[ed] an importance for group selection greater than it has usually been given, or both.' (Maynard-Smith, 1976) Much of the argument, to this decade, still lies within the explanations and disagreements over the evolution of altruistic behavior, and whether kin selection or group selection is the primary motivator of altruism (Nowak *et al.*, 2010). Often articles with vehement, sometimes scientifically unproductive, words are spouted back and forth between the proponents and opponents. (Wilson, 2010 & 2012; Coyne, 2010; Okasha, 2015)

'If groups are the units of selection, then they must have the properties of variation, multiplication, and heredity required if natural selection is to operate on them. In a finite universe, multiplication implies death. Group selection could operate for a short time on differences in group reproduction, without group extinction, but in

the long run evolution by group selection requires group extinction just as evolution by individual selection requires individual death.’ (Maynard-Smith, 1976) In fact, many agree with this statement (Stanley, 1975; Gould, (2002); Wilson, 2006), and that ‘group selection’ of this type could actually be deemed ‘species selection’, or a process outlined by Okasha (2009) as multi-level selection II (MLS2). We will see later that the concept of species selection is extremely important for explaining macroevolutionary patterns in the fossil record of deep time.

Opponents claim that what many call ‘group selection’ can be explained as a form of kin selection (Maynard Smith, 1976), a process by which altruistic traits are preserved within a population because organisms will assist in the survival of other organisms, at a cost to themselves, if they are closely related. Therefore, the survival of the group is maintained by individual behavior, and the individual will expend costly energy (one can think of this as a decrease in individual fitness) on the survival of others in the group if they are closely related. Hamilton called this inclusive fitness, which is quantified using Hamilton’s rule: $rB > C$, where r is the degree of relatedness of the recipient individual, B is the benefit that the recipient receives from the altruistic act, and C is the reproductive cost to the individual performing the act. (Hamilton, 1964) While it is a valid point that individuals are acting as the ‘agents’ of the selection by choosing to help other individuals even at a cost to themselves, it is also valid to note that if a group benefits from individualistic, altruistic behavior (as opposed to another group that has not developed altruistic tendencies), then differential fitness can be shown between groups as a result of different individual behavior within each group. This kind of idea (selection of groups based on the behavior of the individuals within a group) relates to what Okasha (2009) calls multi-level selection I (MLS1).

Dawkins attributes altruism to selection at the gene level. In his 1979 article entitled ‘Twelve Misunderstandings of Kin Selection,’ Dawkins writes that ‘[c]aring for close relatives at the expense of distant relatives is predicted from the fact that close relatives have a high chance of propagating the gene or genes ‘for’ such caring: the gene

cares for copies of itself³.' But can it not be true that, even at the genic level, there must be some sort of group assemblage of DNA in a genotype that causes the simultaneous expression of unique phenotypes? Even Dawkins acknowledges, counter to his previous works, that there is some sort of grouping that occurs at the level of the gene:

Given that life can be viewed as consisting of replicators with their extended phenotypic tools for survival, why in practice have replicators chosen to group themselves together by the hundreds of thousands of cells, and why have they influenced those cells to clone themselves by the millions and billions of organisms? (Dawkins, 1999 p. 251)

Dawkins concludes that, '...it follows that highly complex systems which exist in the world are likely to have hierarchical structure. ... In the present context the hierarchy consists of genes within cells and cells within organisms.' (Dawkins, 1999 p. 251) Dawkins's work is often riddled with analogies that are in direct opposition to the gene's eye view, and thus, perhaps, why he is the recipient of much heated discourse.

While much of the group selection debate still has a focus on groups of organisms (as seen in the kin v. group selection camps), it has been suggested (Gould, 2002) that a more modern synthesis should include groups at all levels of biological organization, and we should look for mechanisms that enable each level of biological organization (from the gene to the cell, from the cell to the individual, or from the individual to the species) to be built upon each other and to interact (Buss, 1996). As mechanisms, natural selection and drift stand as likely candidates... but it is also crucial to remember that the tempo and mode of process at each level will be inherently different.

1.1.4 The Synthesis of Hierarchical Thinking: Multi-level Evolution. Now that some of the singular views of evolution have been outlined, and some of the major players discussed, some of the key insights that have emerged over the last few decades will now be considered.

³ Note the emotional aspect of 'caring' that Dawkins ascribes to the behavior of genes. In fact, his works are riddled with anthropomorphisms when discussing how genes behave, as if genes have emotions.

The idea of the evolutionary process of natural selection acting at multiple levels has emerged as a result of the synthesis of the many views of evolution acting at the different levels of organization. (Buss, 1989; Gould, 2002; Okasha, 2009) Gould (2002) discussed the 'seeds of hierarchy' emerging in the pre-Darwinian school of evolutionary thought, and also that Darwin, while not offering his 'principle of divergence as ... any explicitly developed theory of species selection, for no such formulation existed when he wrote, ... understood the logical requirements of his theory [of divergence] so well that he provided the necessary rationale with the spur of a formally stated alternative.' (p. 241) This formally stated alternative refers to Darwin's discussion of describing evolutionary trends, in that 'only a few vigorous species will produce variants leading to the "recruitment" of new species.' (p. 241) Because only a few species will lead to an evolutionary branching event that is sustained through time, patterns of evolutionary stasis (an important concept discussed at length below) could arise. Though the trend of stasis, as we will see, is a concept tied to a process known as species selection, so while Darwin was correctly describing trends that could arise out of species divergences, explanations of these trends followed with natural selection acting at the organismal level.

'Stephen Jay Gould, in championing the hierarchical view, recognized the units of selection debate as essentially a matter of definition: gene selectionism redefines the 'unit of variation' [or 'unit of inheritance'] as the 'unit of selection.'" (Buss, 1987 p. 177) In the hierarchical view of evolution all 'units' of biological organization can act as 'units of selection', and there is an interplay with both the level above and the level below. The levels of biological organization in order from smallest to largest (or first to the last) go as follows: the replicators (known as genes or DNA) are composed of atoms, cells are composed of DNA, tissues are composed of cells, organs are composed of tissue, organisms are composed of organs, and species are composed of organisms.

The levels of biological organization were also built upon by taxonomists, who added beyond the species level, to include that genera are composed of species, families are composed of genera, orders are composed of families, classes are

composed of orders, phyla of orders, kingdoms of phyla, domains of kingdoms, and, finally, life of domains. The levels above the species level (genus, family, order, phylum, kingdom, domain, and life) are the result of a man-made construction of the taxonomic classification system, rather than a true biological organizational level that can be observed in microevolutionary studies, as they are at, or prior to, the level of species. (Note that there is still disagreement over how to classify species as well.) The distinction between biological organization and taxonomic classification must be made because both concepts are useful to evolutionary theory since the taxonomic classification system can aid in understanding the trends of evolution in deep time.

Biological organization at the microevolutionary scale is also important for the study of evolution during pre-Cambrian and post-Cambrian life (*i.e.*, the formation and study of single-celled organisms and the evolution of multicellularity, respectively), and to the continuing processes of evolution that can be observed today; while taxonomic classification is useful for the macroevolutionary study of the fossil record of deep time – which is also useful to studying the evolution of early life, but in fundamentally different ways. Two important pioneers of the multi-level hierarchical view of evolution discussed below outline this perspective at different levels.

Leo Buss, in his book *The Evolution of Individuality*, elaborates on a theory of metazoan development. The term metazoan means any animal that is multi-cellular and undergoes development from an embryonic stage. Buss examines ontological changes of ancestral organisms, and he holds the view that cellular development of multi-cellular organisms is itself selected for. ‘Nowhere in early ontogeny of early coral or the clams are their differences as adults apparent; the essential process of cleavage, blastulation, and gastrulation [a process of embryonic development that every metazoan today undergoes] mask the diversity of the adult structures into which the embryos ultimately develop.’ Thus, ‘[i]n over a half billion years, metazoan development has followed the same basic formulae. The major innovations of metazoan development were experiments of the Precambrian.’

At the heart of Buss's argument lies a view of nested hierarchies in the rise of multicellularity. He states that there

...is the simple observation that the history of life is a history of the elaboration of new self-replicating entities by the self-replicating entities contained within them (or the incorporation of some self-replicating entities by others). Self-replicating molecules created self-replicating complexes, such complexes created (or become incorporated into) cells, cells obtained organelles, and cellular complexes gave rise to multicellular life. At each transition—each stage in history of the life in which a new self-replicating unit arose—the rules regarding the operation of natural selection changed utterly. (Buss, preface vii)

This theoretical development of early life was also remarked upon in the same fashion by Dawkins (2006), although, with one crucial exception — the replicators drove the process at every step, instead of each step being viewed as participants in a cumulative process that needed different rules regarding the application of natural selection at each level. Thus, scale is important in the hierarchical view of evolution since processes defined in space and time will behave differently depending on the level of organization being viewed (Jablonski, 2007). For example, the spatial and temporal behavior of DNA, microbes, organisms and species vary greatly.

'The Structure of Evolutionary Theory' by Stephen Jay Gould is a 1,400 page treatise that is both a 'celebration of Darwin's exemplary toughness, and ... a call for the reinstatement of causal hierarchy ...'. Gould writes that '[h]ierarchy has resided at the heart of evolutionary theory from the very beginning, despite a temporary eclipse during the rally-round-the-flag period of strict Darwinism at the middle of the 20th century.' (p. 175) Noting that the 'seeds of hierarchy' and the gradually, adaptive organism perspective started with Lamarck in the early 1800s – even though Lamarck's idea of hierarchy poised humans at the highest level on the chain of being and viewed humans as the result of cumulative adaptations from all lower level organisms. To explain the presence of 'primitive organisms' (*e.g.*, organisms at the bottom of the

chain) that appear early in ancient evolutionary history, Lamarck invoked spontaneous generation out of dead 'higher order' individuals.

Lamarck's evolutionary system operates as a grand steady state, even as any bit of protoplasm moves on a historical path up a sequence. The ladder of life really operates as a continuous escalator, with all steps occupied at all moments. The simplest forms continue to arise by spontaneous generation from chemical constituents formed by the breakdown of higher creatures upon their individual deaths. (Gould, 2002 p. 180)

At least, Lamarck utilized the principle of conservation of energy since simpler life forms were generated from dead higher order animals. Luckily, a lot has changed since then.

As mentioned earlier, Darwin had the 'seeds of hierarchy' embedded within his great work *On the Origin of Species*, with his acknowledgement of natural selection acting on groups, but he did not make a formal statement promoting species selection as the mechanism behind evolutionary trends seen in deep time (Gould, 2002). Species selection works much like the adaptive process of natural selection, except that, unlike the birth and death process at the organismal level, there is diversification into specialized groups and extinction of entire groups. Therefore, speciation replaces birth and extinction replaces death (Stanley, 1975; Gould, 2002). Further, unlike the generational birth and death process⁴ at the individual level, speciation that is considered to have occurred rapidly to paleontologists unfolds over timescales on the order of tens of millions of years (Myr).

We now have a wealth of evidence suggesting that the origin and initial diversification of most invertebrate **phyla** occurred during only a few tens of millions of years. The gradualist model cannot account for such rapid change. Rapid speciation, on the other hand, can easily account for the

⁴ Generations can be anything from a few hours to a couple of decades depending on the organism in question. For example, yeast and bacteria can regenerate in a matter of hours, while humans reproduce anywhere from approximately ten to fifty years.

required rate of diversification. The same argument holds for the adaptive radiation of the placental Mammalia in the early Cenozoic. The major **orders** of mammals arose from primitive ancestors during an interval of the Paleocene and earliest Eocene that could not have greatly exceeded 12 Myr. (Stanley, 1975, p. 647, my underline (for definition) and boldface)

The above words, phyla and orders, are highlighted to point out a major distinction that seems to be lost among camps against species selection - *that paleontologists are describing trends that are observed in the fossil record at higher-order levels of taxonomic classification, that these trends are based on morphological body plans that existed on the order of 500 Myr ago, and that they must explain why some body plans have gone extinct and others have proliferated throughout an entire diversified kingdom.* For example, all metazoans produce offspring by similar patterns of cleavage, blastulation, and gastrulation (Buss, 1987), yet they exhibit considerable diversity in the times between their reproductive cycles and the number of offspring they produce in each cycle.

An important example of a 'paleontological trend' was identified in the 1970s through reinvestigation of the Burgess fauna by Harry Whittington, Derek Briggs, and Conway Morris. This 'drama' of the reinvestigation was told eloquently by Stephen Jay Gould in *Wonderful Life: The Burgess Shale and the Nature of History*. While the creatures of the Burgess Shale do not represent the Cambrian Explosion itself, they do mark 'a time soon afterward, about 530 million years ago' (Gould, 1989 p. 55). Also, they mark the first soft-bodied preservation, thus allowing for direct observation of disparate (see disparity) body plans. Since the discovery of the Burgess Shale, the discovery of soft-bodied preservations has increased significantly all over the world. But, '[as] a primary fascination the Burgess Shale teaches us about an amazing difference between past and present life: with far fewer species—one quarry in British Columbia, no longer than a city block—contains a disparity in anatomical design far exceeding the modern range throughout the world!' (Gould, p. 62) This concept of 'disparity in

anatomical design' is important for Gould's argument against the hypothesis of gradual phyletic change and in favor of a hypothesis of punctuated bursts followed by long periods of stasis (known as punctuated equilibrium) and historically contingent behavior—discussed in detail below.

The Phylum Arthropoda is the most abundant (species-rich) of the entire animal kingdom, with the Trilobites being the only extinct subphylum. Under the umbrella of Arthropods are: arachnids (spiders, mites, scorpions), hexapods (insects), crustaceans (lobsters, shrimp, crabs), and myriapods (millipedes, centipedes). What groups all of these diverse organisms together in a phylum is that they all have the same general body plan of a head, thorax, and abdomen. They further either have uniramous or biramous limbs, and the head always has two appendages pre-mouth and three post-mouth. The profound and eye-opening discovery was that, of the many odd arthropod body plans excavated from the Burgess Shale, only one body plan is still present today. The rest of disparate body plans no longer exist (Gould, 2002). Thus, in over 500 million evolutionary years, the most species-rich phylum, the Arthropods, remaining today has been characterized by ubiquitous structures—a kind of evolutionary stability called stasis. However, the description of why stasis occurs is a complex matter; Gould maintains that stasis requires selection to act at the species level.

Gould is not narrow in his view of species selection. Incorporated into the view that selection may act at the species level is the view that species are also the resultant product of a nested genealogical hierarchy of biological organization. (Vrba & Gould, 1986) (This idea of nested hierarchy can also be seen in Buss's work on the development of multi-cellular life.) Therefore, species selection is not autonomous from the nested hierarchies of the lower level levels of biological organization. Each lower level is built upon itself to create higher levels, yet each higher level pushes back on the lower levels.

...[S]patiotemporal bounds upon organisms arise from epigenetic programs that, together with environmental causes, determine their forms and life spans. (Sexually reproducing organisms are additionally constrained by population structure from above because they must

recognize and mate with another conspecific individual to ensure their genetic survival.) While the sorting of organisms is, to a large extent, conditioned by their own interaction with the environment, the sorting of still lower-level individuals, genes and cells, is almost entirely constrained by whole-organism imperatives (or produces disastrous results at several levels if not so regulated, as in cancer). (Vrba & Gould, 1986 p. 226)

Gould, Eldredge, and Vrba, further make an argument that ‘as a consequence of the laws of hierarchy’, nested hierarchies lead to a gain in autonomy at the species level. ‘...[C]ausality is asymmetrical, with downward flow ineluctable and upward flow possible; lower levels are more strongly impacted and constrained, higher levels more independent. ... [H]ierarchies build and elements become incorporated as functioning parts of a complex system, their lineages evolve from selfish and competitive to mutually interacting entities.’ (Vrba & Gould, 1986 p. 226) There are also phenomena common to all levels of organization. For example: all biological entities (genes, demes, species, etc.) can be considered as the focal unit of selection at each level; all focal units can have aggregate characters at each level or emergent characters between levels; selection causes the differential sorting of entities at each focal level (Vrba & Eldredge, 1984).

Thus, I have briefly outlined two hierarchical perspectives that act at radically different scales of space and time, yet both provide a logical hypothesis of early, ancient life—one focused on the evolutionary study of multi-cellular life through the lens of ontogeny (Leo Buss), and the other through observed patterns and trends in the fossil record, invoking species selection (Stephen Jay Gould).

1.1.5 Phyletic Gradualism v. Punctualism. When studying evolutionary theory, it is important to be aware of the field of study and background of the authors. For instance, the same words can mean different things depending on whether the author comes from a paleontological or microbiology background—such as the word macroevolution, which will be discussed below. This basic matter of semantics seems to

be prevalent in misinterpretations of scientific work that could have otherwise been prevented.

Phyletic gradualism is the view that evolutionary changes occur in successive gradual steps. It describes a mechanism where entire populations of organisms evolve slowly and gradually until speciation has occurred, and to some, it therefore follows that speciation is itself a gradual process. Proponents of the gradualist description maintain that the reason for the lack of gradual pattern in the fossil record is because the fossil record is incomplete. (Gould & Eldredge, 1972; Stanley, 1975) 'Darwin wrote that our imperfect fossil record is like a book preserving just a few pages, of these pages few lines, and these lines few words, and of those words few letters' (Gould, 1989 p. 60), where '[t]he most promising version of the "imperfection theory" holds that the Cambrian explosion only marks the appearance of hard parts in the fossil record.' (p. 59) Therefore, '[M]ulticellular life may have undergone a long history of gradually ascending complexity leaving no record in the rocks because we have found no "Burgess Shale", or soft-bodied fauna, for the Precambrian.' (Gould, 1989 p. 59) This still does not diminish the fact that, since the discovery of Burgess fauna, not many other ancestral body plans have been found.

'In reality, gradual phyletic change is only recognized for a few fossil lineages, and in these it is only of minor morphologic consequence.' Further, 'the gradualist view ... simply recognizes no increase in rate of evolution of splitting.' (Stanley, 1975) Gradualism implies a type of evolutionary process where species linearly morph into other species, or that an ancestral species gradually morphed into two or more species simultaneously, rather than there being a differential rate of species divergence. And further, gradualism implies that these gradual, adaptive changes are directional, in that species are positively selected for as 'survivors' who are best able to procreate in their given environment.

In contrast to gradualism, punctuated equilibrium, proposed by Niles Eldredge and Stephen Jay Gould, emerged in 1970s as an alternative explanation for the

incomplete fossil record. Eldredge and Gould explicitly argued against phyletic gradual change through the lens of the paleontologist. In their work, they argue:

- (1) The expectations of theory color perspective to such a degree that new notions seldom arise from facts collected under the influence of old pictures of the world. New pictures must cast their influence before facts can be seen in a different perspective.
- (2) Paleontology's view of speciation has been dominated by the picture of "phyletic gradualism." It holds that new species arise from slow and steady transformation of entire populations. Under its influence, we seek unbroken fossil series linking two forms by insensible gradation as the only complete mirror of Darwinian processes; we ascribe all breaks to imperfections in the fossil record. (Eldredge & Gould, 1972 p. 84)

Thus, the shadow of gradual, Darwinian organismal level adaption has imprinted the field of Paleontology with the preconceived notion that changes in the fossil record should also be gradual. Therefore, no one was looking to change the existing paradigm.

- (3) The theory of allopatric (or geographic) speciation suggests a different interpretation of paleontological data. If new species arise very rapidly in small, peripherally isolated local populations, then the great expectation of insensibly graded fossil sequences is a chimera. A new species does not evolve in the area of its ancestors; it does not arise from the slow transformation of all its forbears. Many breaks in the fossil record are real.
- (4) The history of life is more adequately represented by a picture of "punctuated equilibria" than by the notion of phyletic gradualism. The history of evolution is not one of stately unfolding, but a story of homeostatic equilibria, disturbed only "rarely" (*i.e.*, rather often in the fullness of time) by rapid and episodic events of speciation. (Eldredge & Gould, 1972 p. 84)

Therefore, the fossil record should be looked at as it is, composed of long periods of stasis with rare, diversifying bursts.

Since 1972, the theory of punctuated equilibrium has been increasingly developed to explain macroevolutionary trends using species as the primary unit of selection. Gould and colleagues ‘...were terribly muddled for several years about the proper way to treat, and even to define, selection at the level of the species—the most important of all theoretical spinoffs from punctuated equilibrium.’ (Gould, 2002 p. 1008) Thus, some important clarifications ensued, which involved modifying the theory to include the hierarchical perspective of evolution. The first important distinction was aimed at better describing the process of species selection, which involved an untwining of Darwinian *sorting* from Darwinian *selection*. This also led to explanations for the reasons why ‘hierarchy is a property of nature, not a conceptual scheme for organization.’ (Vrba & Gould, 1986) According to Vrba and Gould,

...evolutionary change is the product of sorting (differential birth and death among varying organisms within a population). Sorting is the simple description of differential representation; it contains, in itself, no statement about causes. As its core, Darwinism provides a theory for the causes of sorting — natural selection acting upon organisms in the ‘struggle for existence.’ However, other processes (genetic drift, for example) produce sorting as well; thus, the two notions—sorting and selection (a favored theory for the cause of sorting)—are quite distinct and should carefully be separated. (Vrba & Gould, 1986 p. 217)

Lloyd and Gould (1993, 1999) further expanded upon the properties of species-level entities; a species will either possess aggregate characters (based on average inherent properties of its constituent parts) or emergent characters (characters that arise from the organizational structure of its parts). Emergent characters arise between focal levels of the biological hierarchical scale, and thus also have implications for the fitness of focal units that arise due to emergent properties of constituent organisms.

A further salient criticism, addressed in *The Structure of Evolutionary Theory*, involves Gould and Eldredge's original claim that punctuations are described by rapid, episodic bursts of speciation (as seen in point four above). Gould states that '[o]ur critics have strongly argued that such a proposition cannot be justified by our best understanding of evolutionary processes and mechanisms. I believe that our critics have been correct in this argument, and that Eldredge and I made major errors by advocating ... a direct acceleration of evolutionary rate by the processes of speciation.' (p. 796) Even with such pointed criticisms, the theory of punctuated equilibrium has remained robust; with the criticisms came developmental arguments that have continued to push towards a cohesive understanding of the link between hierarchical evolution and punctuation. This is seen in the work of Futuyma (1987), who was initially a stark critic of punctuated equilibrium (Gould, 2002), that provided an account of how punctuation could naturally appear in the fossil record from lower level evolutionary processes.

Other criticisms are completely dismissed by Gould. Daniel Dennett claimed that 'for a while ... [Gould] had presented punctuated equilibrium as a revolutionary 'saltationist' alternative to standard neo-Darwinism.' (Gould, *Structure*, p. 1009⁵, my underline) However, Gould is insistent that he never equated his theory of punctuated equilibria to genomic punctuations:

We started small as a consequence of our ignorance and lack of perspective, not from modesty of basic temperament. As stated before, we simply didn't recognize at first, the interesting implications of punctuated equilibrium for macroevolutionary theory—primarily gained in treating species as Darwinian individuals for the explanation of trends, and in exploring the extent and cause of stasis. With the help of S.M. Stanley and E.S. Vrba and other colleagues, we developed these

⁵ This quote actually comes from a heated discourse between Gould and Daniel Dennett (1997), in which Dennett is adamant that Gould did equate punctuated equilibrium with saltations. There was a further comment included by Robert Wright, who seemed obviously upset about a review Gould did on his work. Gould simply replied to both critics by saying 'I wish you no ill, and I'm sorry if I offended you both by not paying enough attention to your work—the only common theme, in the absence of any intellectual response, in their replies printed above.'

implications over the years, and the theory grew accordingly. But *we never proposed a radical theory for punctuations (ordinary speciation scaled into geological time), and we never linked punctuations to microevolutionary saltations*. (Gould, 2002 p. 1008, my italics, my underline)

Yet, others, such as Jerry Coyne and Brian Charlesworth hold a view antithetical to that of Dennett, and say that there is no real difference between punctuations and stasis at the micro- versus the macroevolutionary scale. They state that: '[o]ur concern as evolutionary geneticists has been with Eldredge and Gould's repeated revisions of the mechanisms proposed for stasis and rapid evolution. Punctuated equilibrium originally attracted great attention because it invoked distinctly non-Darwinian mechanisms for stasis and change. These mechanisms were said to decouple macroevolution from microevolution, ... yet many evolutionists saw no obvious contradiction between punctuated pattern and Darwinian process: Stasis can result from stabilizing selection (for example, long periods of environmental stability); rapid evolution can result from selection-driven responses to sudden environmental change or invasion of new habitats; and the association of morphological change with speciation can result from the fact that both are promoted by adaptation to new environments.' (Coyne & Charlesworth, 1997)

While it is true that some form of punctualism and stasis may act at different biological levels of organization (for example, it is clear that Coyne and Charlesworth are thinking of stabilizing selection at the organismic level), I think the point gets lost by some that 'rapid' to a paleontologist is on order of tens of millions of years, and that scale involves examining morphological patterns of organisms that, at best, can be grouped into orders, but most often, in deep time, can only be assigned to a phylum. Because of these truths of time and scale, Gould and others hypothesized that species selection was the important mechanism driving macroevolutionary trends in the fossil record, and therefore a hierarchical synthesis was in much need.

The theory of punctuations at the genic level was a radical idea proposed by Goldschmidt in the mid 1900's. His saltationist theory saw evolution as proceeding via two distinct *macroevolutionary* mechanisms: the first being 'systemic mutations [which] could be extended over a long period of time, but their phenotypes suddenly appear. ... The second mechanism ... proposed that mutations in developmentally important genes could produce large phenotypic effects.' (Dietrich, 2002) Both mechanisms could lead to speciation, but with the former 'he called these developmental macromutations "hopeful monsters" because they were the embodiment of large phenotypic changes', as observed from his studies on homeotic mutations⁶. 'It is convenient to use [the term] macromutation for any genetic change leading to a striking change in phenotype, even if the change is a point mutation'. (Maynard Smith, 1983) But wait, did I just label Goldschmidt's genic macromutation mechanism for speciation as macroevolution when I previously made an argument for species selection to act as the driver of macroevolutionary trends in the fossil record? Indeed I did. I wanted to emphatically point out that the heated debate between Dennett and Gould, and perhaps much scientific misinterpretation on the subject, stems from two different fields of study staking claim on the same word – macroevolution.

Goldschmidt used the term macroevolution to describe the process by which changes in the genome could lead to speciation and microevolution to describe changes of allele frequencies in a population (such as antibiotic resistance in bacteria); while paleontologists utilize the term macroevolution to describe evolution at large scales, invoking species selection, while microevolution refers to any evolutionary process below the species level. Even though the macroevolutionary study being conducted depends on the research field in question, there is one unifying theme — punctuation and stasis are real phenomena that can transcend the biological and taxonomic levels of organization. For Gould, breaks and stasis in the fossil record are real, and for

⁶ Such as the *Drosophila* mutant *Aristopedia*, for which the bristle-like structures at the tip of the antenna are replaced with legs: hence, the reason for term 'hopeful monsters'.

evolutionary biologists, such as Richard Lenski, stasis and punctuation in microbial populations are also real (Elena *et al.*, 1996; Blount *et al.*, 2008).

Even today the terms tend to be intermingled. Chouard (2010) writes that: ‘the shift [shift as in a call for a synthesis] even promises to bridge microevolution and macroevolution, suggesting how, for example, genetic changes—large and small—might eventually lead to new species.’ A major example cited by Chouard is the work of Richard Lenski and colleagues (Blount *et al.*, 2008), who have been running a long-term evolution experiment involving twelve strains of *E. coli* that has, as of 2015, evolved for over 60,000 generations (Fox & Lenski, 2015). The 2008 article enlightens us on historical contingency (a concept discussed in depth below) at the genomic scale, where, at ~30,000 generations, one of twelve ancestral strains evolved to utilize a different food source — citrate instead of glucose. Thus, at ~30,000 generations a new phenotype had evolved in only one of the twelve populations! The article by Chouard then gets ‘muddy’ when tying early work of Lenski’s group (1996), entitled *Punctuated Evolution Caused by Selection of Rare Beneficial Mutations*, to the 2008 article. The 1996 article reports ‘adaptive jumps in his bacterium’s cell size [that] were reminiscent of the abrupt morphological changes punctuating long periods of stasis in the paleontological record’ (Chouard, 2010), and further that

[t]he debate over punctuated equilibria in evolutionary biology revolves around distinct issues. One issue is whether, and how often, the actual dynamics of evolutionary change are punctuated by alternating periods of rapid change and relative stasis. This is an empirical issue, and the answer may depend on the *coarseness of the time scale* over which observations are made... The other issue concerns the processes responsible for any punctuation that does occur. It has been argued that punctuation involves complex population genetic processes that are believed to play an important role in speciation. ... To the extent that these conditions are fulfilled in nature, then the selective sweep of beneficial alleles through a population *might* explain *some* cases of

punctuated evolution in the fossil record. In any case, our experiment shows that punctuated evolution can occur in bacterial populations as a consequence of the two most elementary population genetic processes: mutation and natural selection. (Elena *et al.*, 1996, my italics)

Supporters of Gould and Eldredge rejected the 1996 claim that a microevolutionary study could demonstrate punctuation and maintained that ‘there was neither speciation nor species selection in Lenski’s studies. But that was years before the ‘new land’ of citrate was discovered’. (Chouard, 2010)

The point is this: punctualism—or long periods of stasis followed by punctuated bursts – can exist at all levels of biological and taxonomic classification. There is evidence of punctuated bursts of phenotypes in bacteria (Elena *et al.*, 1996; Fox & Lenski, 2008), in organisms such as the stickleback (Chouard, 2010), as well as remarkable stasis of morphological characters such as the arthropod body plan that has persisted for over 500 Myr in the fossil record (Gould, 1990). Depending on the level in question, whether it is a genetic mutation that spontaneously causes a rapid burst of speciation or a paleontologist describing patterns in the fossil record, words can mean different things, thus possibly leading to some of the confusion (like the accusations that Gould and Eldredge’s theory of punctuated equilibria was a saltationist theory). Punctualism at the individual level will appear in Chapter Three.

1.1.6 The Hypothesis of Historical Contingency. Previously, I mentioned that the revision of the Burgess fauna was key for the development of the hypothesis of punctuated equilibrium and historical contingency. Originally, Charles Doolittle Walcott discovered the Burgess quarry in 1909, and excavated many specimens in the following two years. He ‘was a fine geologist, but he was an even greater administrator’, who ran the Smithsonian Institute for twenty years (until his passing in 1927). ‘He played a key role in persuading Andrew Carnegie to found the Carnegie Institute in Washington, and worked with Woodrow Wilson to establish the National Research Council. He served as president of the National Academy of Sciences and the American Association for the Advancement of Science’, (Gould, 1989 p. 242) all while suffering tragic losses in his

personal life. Admirably, he continued to publish research even though he seemed to be stretched thin, but he did not, however, aid in the development of the corrected modern understanding of the Burgess fauna — that credit can be given entirely to Whittington, Briggs, and Morris, who worked on Walcott's specimens many decades later (Gould, 1989).

The 1970s reinvestigation of the specimens collected from Walcott's quarry revealed that many of the organisms had been misinterpreted as belonging to already-existing classes of organisms. Further, with a new technique developed by Whittington, he was able to reconstruct a 3D picture of the organisms with the exact location of appendages and specificity of anatomical design. This leads me to the conjecture that if Walcott had never discovered the soft-bodied fauna, and if Whittington had never decided to reinvestigate the Burgess shale and perfect his method, we might never have achieved a new view of the incredible range of diversity and disparity marking the beginnings of early life. If we 'replayed the tape' of this inquiry, would we still be lacking a viable hypotheses to explain evolutionary trends in deep time other than the conjecture that the fossil record is incomplete? The hypothesis of historical contingency plays upon thought experiments such as that — if something were done slightly different in the past, would the present look the same?

The historical contingency hypothesis is a thought experiment that sets the stage of early life to tell a story of decimation and unpredictability. Gould wrote that 'most of us labor under a false impression about the pattern of human evolution. We view our rise as a kind of global process encompassing all members of the human lineage, ...[by which] *Homo sapiens* became the anticipated result of an evolutionary tendency pervading all human populations.' (Gould, 1989 p. 319) There is a preconceived notion that 'intelligence' was bound to happen, that evolution is a sort of destiny. 'The major argument of this book [Gould, *Wonderful Life*] holds that contingency is immeasurably enhanced by the primary insight won from the Burgess Shale — that current patterns were not slowly evolved by continuous proliferation and advance, but by a pronounced decimation (after a rapid initial diversification of anatomical design), probably

accomplished with a strong, perhaps controlling, component of lottery.’ (Gould, 1989, p. 301)

Mass extinction, a topic that will be discussed in more detail in Chapter Four, is an important component of the historical contingency hypothesis.

The main question raised by mass extinction has always been, Is there any pattern to who gets through and who doesn’t—and if so, what causes the pattern? The most exciting prospect of new views on mass extinction [*i.e.*, Alvarez’s theory of extinction triggered by extraterrestrial impact] holds that reasons for differential survival are qualitatively different from the causes of success in normal times—thus imparting a distinctive, and perhaps controlling, signature to diversity and disparity in the history of life. (Gould, 1989 p. 306)

‘Normal times’ refers to stasis (note that stasis does not imply that complicated evolutionary processes are stagnant); non-normal times refers to the Cretaceous extinction due to the meteor impact or to the fact that an estimated 96 percent of the earth’s biodiversity was lost during the late Permian extinction (Raup, 1979). At the time of these mass extinction events, who (had a scientist been there...) could have predicted that mammals would out-survive the dinosaurs or whether the 4 percent that survived the end-Permian extinction did or did not survive purely by chance?

We probably owe our existence to such good fortune. Small animals, for reasons not well understood, seem to have an edge in most mass extinctions, particularly in the Cretaceous event that wiped out the remaining dinosaurs. Mammals may therefore have survived that great dying primarily because they were small, not because they embodied any intrinsic anatomical virtues relative to dinosaurs, now doomed by their size. And mammals were surely not small because they had sensed some future advantage; they had probably remained small for a reason that would be judged negatively in normal times—because dinosaurs dominated environments for large terrestrial vertebrates, and

incumbents have advantages in nature as well as politics. (Gould, 1989 p. 307)

'[N]early all modern phyla made their first appearance [during the Cambrian era], along with an even greater array of anatomical experiments that did not survive very long thereafter. The 500 million subsequent years have produced no new phyla, only twist and turns upon established designs'. (Gould, 1989 p. 64) But this story is only the beginning of multi-cellular life, which 'arose at least 3.5 billion years ago, about as soon as the earth became cool enough for stability of the chief chemical components.' (Gould, 1989 p. 309) The oldest fossils—the prokaryotes—date back to this time. Stromatolites (biofilms or biomats of prokaryotic cells) dominated the fossil record for more than 2 billion years, with the first eukaryotic cell (the cell type that made multi-cellular life possible) entering stage left approximately 1.4 billion years later. Multicellular organisms did not arise until about 570 Myr ago – just before the Cambrian explosion. 'Hence a good deal more than half of life's history is a story of prokaryotic cells alone, and only the last one-sixth of life's time on earth has included multi-cellular animals. Such delays and long lead times strongly suggest contingency and a vast realm of unrealized possibilities.' (Gould, 1989 p. 310) This topic will be discussed again in Chapter Four.

1.2 PHYSICAL BACKGROUND

Key physical concepts that pertain to the work presented in this dissertation will be discussed below.

1.2.1 Phase Transitions. When ice turns to water, when a ferromagnetic material is magnetized, or when a population goes from a state of survival to extinction, a phase transition has occurred. For example, the H₂O transition from solid to liquid can be modelled with the molecular density as a function of temperature or pressure, where the density is considered the order parameter, and the temperature or pressure is the control parameter. For the ordering of magnetic spins, magnetization could act as an order parameter, while the strength of the magnetic field or temperature could act as a

control parameter (as is the case for the Ising model); while a death probability could act as a control parameter for a system whose behavior is characterized by the order parameter of population size. There will exist in all of these examples a value of the control parameter for which the system changes state – this point is known as the transition point. Further, phase transitions can be classified into particular types, and simply knowing the type of phase transition tells much about the dynamics of a system.

1.2.1.1 Classification. Phase transitions are categorized by the specific behaviors of the system. One category provides information about how an entire system behaves when sweeping across the transition region of the control parameter, and the other characterizes the behavior at the transition point. The former of the two categories classifies a system as either an *equilibrium* or *nonequilibrium* phase transition. When a system is in the equilibrium class, the *principle of detailed balance* applies, with a seamless sweep across the transition point from above and below. For example, a material can magnetize, demagnetize, and then magnetize again, and so on. If a system is in the nonequilibrium class, the principle of detailed balance is broken, and once the transition point is crossed, the system will never recover to the previous state, even when the control parameter is returned to a previous value past the transition point. Nonequilibrium transitions can also be called *absorbing* phase transitions when a system falls into an absorbing state from which there is no return. For instance, when a population goes extinct, it will never come back, and thus it falls into an absorbing state.

The second category classifies a system based on its behavior at the transition point. Ehrenfest made the distinction between types of phase transitions based on the behavior of the free energy in a thermodynamic system. A *first order* phase transition was classified by a discontinuity in the first derivative of the order parameter (typically the free energy) as a function of the control parameter, while a *second order* phase transition was classified by a discontinuity in the second derivative of an order parameter. Not all systems that exhibit phase transition behavior can be described by the classical equations of state; rather, many are phenomenological. Therefore, when a system, which is not described by continuous equations, shows a phase transition with a

continuous curve and a large fluctuation at the transition point, it is more appropriate to call this transition a *critical* or *continuous* phase transition. (Yeomans, 1982) The value at which a continuous or critical phase transitions changes state is known as the *critical point*.

Thus, simply identifying a phase transition as nonequilibrium and continuous conveys some important qualities of the system. For one, since it is a nonequilibrium transition, the system will not be able to recover to the previous state once it crosses the transition point, or it could fall into an absorbing state. And two, there will be large fluctuations of the order parameter before it changes state. This dissertation will present a phase transition of this type.

1.2.1.2 Universality. Continuous phase transitions may further be classified by the scaling behavior near the critical point. This scaling behavior is determined by the critical exponents of power law distributions. These exponents, derived from scaling relations, enable systems to be grouped into particular *universality classes*. All systems in a particular universality class will have the same critical exponent values. Models that fall into a particular universality class can describe a wide range of phenomena, such as the spread of forest fire, a contagion, catalysis of a chemical reaction, or patterns of diversity.

1.2.2 Ordinary, Continuous, and Directed Percolation. Canonical models that demonstrate continuous phase transition behavior, and thus universality, include ordinary percolation, with continuous percolation as a derivative of ordinary percolation, and directed percolation.

A well-studied percolation theory example is the forest fire model of ordinary percolation. Consider a two-dimensional square grid where a square can either be occupied or unoccupied with a tree. If one tree is on fire, and fire can spread only if the burning tree has a neighboring square occupied with a tree; otherwise, the fire stops. The question is what proportion of the squares needs to be occupied in order for the fire to spread across the space (*i.e.*, from one end to the opposite end)? If p is the probability a square is occupied, and $(1-p)$ is the probability that it is unoccupied, then

the question becomes at what probability p does a cluster of trees lead to a forest fire that spans the space? This point is known as the critical probability, p_c , for which this system undergoes a continuous phase transition. The remainder of the text will refer to the critical cluster that spans the space for the first time as the *spanning cluster*.

Since a percolating system undergoes a continuous phase transition, it can be classified into a particular universality class. Critical exponents of these systems will scale identically regardless of the microscopic details, but the exact location of the critical point will change. The example described above is a *site percolation* problem on two-dimensional square lattice. Lattice sites need not be square, for they can be in any regular lattice configuration, such as triangular, hexagonal, or diamond, and still scale identically but with different critical points. For example, $p_c = 0.592746$ for a square lattice and $p_c = \frac{1}{2}$ for a triangular lattice, yet both will scale identically. Similarly, two-dimensional *bond percolation* (where bond percolation considers a set of connected nearest neighbor nodes on a regular array) will also scale identically to the site percolation problem but have a critical of $p_c = \frac{1}{2}$ for the square lattice and $p_c = 0.34729$ for the triangular (Stauffer & Aharony, 1996). As long as regular lattice systems have the same number of spatial dimensions, they will scale identically; once the dimension of the space is changed, the scaling exponents will change. (Stauffer & Aharony, 1996; Sahimi, 1994)

Critical scaling arguments for two-dimensional percolation systems are as follows:

$$\begin{aligned}
 P(p) &\sim (p - p_c)^{\beta_p}, \\
 X^A(p) &\sim (p - p_c)^{\beta_p}, \\
 X^B(p) &\sim (p - p_c)^{\beta_B}, \\
 \xi_p &\sim |p - p_c|^{-\nu_p}, \\
 S_p &\sim |p - p_c|^{-\gamma_p},
 \end{aligned}$$

where $P(p)$ is the probability that a given site or bond belongs to the spanning cluster; $X^A(p)$ is the fraction of sites or bonds that belong to the spanning cluster; $X^B(p)$ is the fraction of the sites or bonds that could carry flow (*e.g.*, the movement of a fire), also known as the backbone cluster since some components of the cluster are dead ends; ξ_p is the correlation length, which is the typical radius of a cluster; S_p is the average number of clusters of a certain size. (Sahimi, 1994).

With the exception of solid state physics, many phenomena in the natural world do not occur on a regular grid. Unlike the regular array of trees arranged in an orchard, trees in a forest do not grow in a regular array, and they will each occupy variable amounts of space. Continuous percolation addresses problems such as this. Since trees in a forest will have a variable amount of reach, some trees will be close enough to affect each other if there were a fire and others may not. To model the spread of a forest fire in this case, imagine a set number of nodes randomly dispersed on a two-dimensional continuous space, and that each of these nodes further has a random radius size⁷, r . The disks may overlap up to length r . The question of interest then becomes, instead of the number of neighboring sites, what is the critical density for which a spanning cluster of overlapping disks first emerges? A rigorous mathematical construction of continuum percolation processes is available in Meester & Roy (1996).

Directed percolation (DP), the final canonical percolation example, considers the case where bonds or sites are restricted to move only in a certain direction. Commonly, time is considered as an independent direction that runs perpendicular to a d -dimensional space. For this reason, the terminology $(d + 1)$ dimensional has been adopted when referring to a DP system, with time as the preferred direction of motion. (Hinrichsen *et al.*, 2000; Henkel *et al.*, 2008; Ódor, 2008) For example, imagine water percolating through coffee grounds that can only move in one direction due to the influence of the gravitational field. Therefore, within each time step the water percolating through the ground coffee beans moves downward through the coffee until

⁷ This process is known as the Poisson blob model — the first continuum percolation process to be mathematically addressed (Meester & Roy, 1996).

the water either is blocked or moves through the grounds to make the lifesaving liquid, coffee.

In the simplest case, a DP system can obey the following reaction-diffusion (RD) process, at each time step, for each particle A:

- Birth $A \rightarrow 2A$
- Death $A \rightarrow \emptyset$
- Coalescence $2A \rightarrow A$

DP systems may deviate from this particle RD process in such a way that the number of births may be increased ($A \rightarrow mA$, where $m > 2$) or the number of coalescents may be increased ($nA \rightarrow A$, where $n > 2$) without changing the universality class of the system. The system will no longer belong to the DP universality class if the RD process no longer has the $A \rightarrow \emptyset$ term (Vojta, *personal communication*). Furthermore, according to the DP conjecture, it is expected that a system will belong to the DP universality class if:

1. the model displays a continuous phase transition from a *fluctuating* active phase into a *unique* absorbing state,
2. the transition is characterized by a non-negative one-component order parameter,
3. the dynamic rules are short ranged,
4. the system has no special attributes such as unconventional symmetries, conservation laws, or quenched randomness. (Janssen, 1981; Grassberger, 1982)

DP universality is characterized by four critical exponents. Let $\Delta = |p - p_c|$ be the off-critical measure, ρ the population density, ξ_{\perp} the correlation length, ξ_{\parallel} the correlation time, and P the survival probability, where each of these measures obeys the following scaling relations:

$$\rho \sim \Delta^{\beta},$$

$$\begin{aligned}\xi_{\perp} &\sim \Delta^{-\nu_{\perp}}, \\ \xi_{\parallel} &\sim \Delta^{-\nu_{\parallel}}, \\ P &\sim \Delta^{\beta'}.\end{aligned}$$

The exponents β , β' , ν_{\parallel} , and ν_{\perp} are defined from quantities characterizing the stationary state in the long-time limit. Relations among the critical exponents have been shown to exist. One is due to time reversal symmetry and allows for equating $\beta = \beta'$. The others are due to the Fisher exponent, α , which relates β and ν_{\parallel} ,

$$\alpha = \frac{\beta}{\nu_{\parallel}},$$

and the dynamical exponent, z , which relates ν_{\parallel} and ν_{\perp} ,

$$z = \frac{\nu_{\parallel}}{\nu_{\perp}}.$$

Depending on the dynamical system, sometimes it is easier to calculate the exponents based on the above scaling relations. For instance, the exponent α refers to the time dependence of ρ at criticality, and thus scales with the population density as a function of time:

$$\rho \sim t^{\alpha},$$

while the correlation length grows as:

$$\xi_{\perp} \sim t^{1/z}.$$

The critical dimension for a DP system is $d_c = 4$. For $d > 4$, the mean-field approximation for scaling arguments applies. (Hinrichsen *et al.*, 2000; Henkel *et al.*, 2008) The model discussed below belongs to the (2+1) dimensional DP universality class.

1.3 DISSERTATION SUMMARY

The dissertation presented here examines a neutral model of evolutionary dynamics on a phenotype space. The chapter highlights are outlined below.

1.3.1 Chapter Two. This chapter examines the phase transition and clustering behavior of a neutral evolution model. The model is characterized as belonging to the *directed percolation universality class*, and ideas from ordinary and continuous percolation are used to examine how directed percolation clusters fill a continuous phenotype space. Some important distinctions are made between mating schemes, and an investigation of the underlying dynamics of the system is presented.

1.3.2 Chapter Three. In this chapter, concepts from *coalescent theory* are used to investigate phylogenetic tree structures. The times to most recent common ancestor (TMRCA) are calculated, and the distributions of the TMRCA, at and near the critical point, are examined, at both the individual and cluster level. There is also remarkably different behavior depending on the reproduction scheme examined.

1.3.3 Chapter Four. The final analytic chapter investigates simulated mass extinctions. After the system has reached equilibrium, a large, randomly selected percentage of individuals are removed. The surviving simulations and populations are examined for historically contingent behavior at and near the critical point.

1.3.4 Chapter Five. Here, possible future research directions are discussed. Each the chapters presented in this dissertation will be expanded upon. Included is a small discussion about the up-and-coming dynamical population experiments that will use the microbial yeast populations, *S. cerevisiae*.

2. PHASE TRANSITIONS IN A NEUTRAL EVOLUTION MODEL

2.1 INTRODUCTION

Understanding the evolutionary process of speciation is a key topic in evolutionary theory – in particular, which mechanisms yield observed patterns of biological *disparity* (assortment of population morphology or body plans) and *diversity* (number of distinct species or groupings of biological taxa in a population) – where the latter is the focus of much agent-based work (de Aguiar *et al.*, 2009; Baptestini *et al.*, 2012; Martins *et al.*, 2013). It is thought that if the underlying mechanisms of pattern and community formation can be understood, then, by observation of how populations fill their niches, the processes (or mechanisms) by which species evolved can be inferred (Chave *et al.*, 2002). Clustering patterns have been demonstrated in agent-based models with distinctly different dynamical rules (see Fuentes, 2003; Houchmandzadeh, 2002; Houchmandzadeh and Vallade, 2003; Meyer *et al.*, 1996; Young *et al.*, 2001; Chave *et al.*, 2002; Pie and Weitz, 2005; de Aguiar *et al.*, 2009). For example, Young *et al.* (2001) utilized a diffusion equation to govern population dynamics, while de Aguiar *et al.* (2009) implemented an assortative mating scheme that allowed independent organisms to pick mates based on spatial proximity and genetic distance. Even though the above-cited models utilized different dynamical processes, they all demonstrated that an essential ‘ingredient’ for the development of clustering patterns was a spatial asymmetry between the birth and death process. Births must disperse locally, while death is a global affair.

Allopatric speciation (speciation induced by geographical isolation) is thought to be most the common mechanism driving speciation, while sympatric speciation (speciation that occurs within the same niche space) is thought to be a less common mechanism. Yet, the importance of speciation in sympatry can be argued to be significant for evolutionary processes, especially for adaptive radiation. Adaptive radiation in sympatry has been observed, for example, in East African cichlid fishes, the

Hawaiian Silverswords (Schluter, 2000), and the *Anolis* lizards of the Caribbean (Knox *et al.*, 2001). While experimental observation shows that sympatric speciation can be significant to natural processes, computational models can address the important mechanisms which drive this form of speciation. For instance, Kondrashov *et al.* (1999) showed the possibility of sympatric speciation with the addition of sexual selection and a fitness component via different implementations of trait choice between the sexes. Dieckmann and Doebeli (1999) demonstrated with a genetic assortative mating model that competition for similar resources 'can initiate sympatric speciation even if mating depends on an ecologically neutral marker trait.'

Similarly, the neutral model designed by de Aguiar *et al.* (2009) utilized a hermaphroditic population evolved in sympatry (*i.e.*, modelled without geographic barriers) that combined both genetic and spatial dynamics to compare simulated spatial patterns (or clustering of individuals in genetic space) to patterns observed in nature. The model predicted a constant speciation rate over long periods of time; after an initial transient period of rapid growth dominated by mutation and recombination, the number of species reached a steady state. Their observations were compared to the mammalian fossil record of the Meade basin in Kansas, with the striking conclusion that speciation events in the basin occurred without geographical barriers. Since their model is inherently sympatric, they cited these results as proof that these observed speciation events were not caused by glaciation, because the simulated clustering patterns, modeled without geographic barriers, mimicked patterns found in the mammalian fossil record. This model is inherently in the class of equilibrium models since populations were held constant throughout the entire simulation, and thus no form of extinction due to outside sources was possible. However, since life is inherently a nonequilibrium process (no species may ever come back from extinction), models such as this are of questionable realism. Furthermore, until agent-based models are able to show hierarchical relations in evolutionary processes, relating a microevolutionary simulation to processes on the macroevolutionary scale such as those revealed by the fossil record

(Jablonski, 2007), comparison of the fossil record to an actual biological processes will remain speculative at best.

Chave *et al.* (2002) incorporated the possibility of nonequilibrium dynamics in their spatially explicit model of sessile organisms, with the aim of understanding mechanisms that underlie community formation. They compared the patterns that emerged when offspring were dispersed locally versus globally, and when the underlying dynamics were governed by neutral conditions versus models where birth and death rates were asymmetric (*e.g.*, deaths were not immediately replaced by births). They found that the main mechanism governing biodiversity was offspring dispersion, rather than the presence or absence of neutral conditions. This recalls the results of Meyer *et al.* (1996), Young *et al.* (2001), and Pie & Weitz (2005), which showed that the local dispersion of births and the globally distributed deaths were the key 'ingredients' for emergent clustering. All of the models discussed above (with exception of the null model created by Pie & Weitz), while demonstrating the underlying mechanism of cluster pattern formation, make no explicit mention of belonging to a class of biologically null models eventhough they implement neutral conditions. The appearance of clustering, regardless of whether selection is present or not, shows that the emergent property of cluster formation is due wholly to an underlying dynamical process, and thus cluster formation may be subject to universal laws. Further, while key dynamical processes underlying cluster formation are exposed by the body of literature reviewed above, no examination of population disparity ensued, thus leaving an important aspect of biological pattern formation by the wayside. This fact is paramount to the Burgess Shale re-investigation, where high morphological disparity and low species diversity prevails (Gould, 1989).

The previous work of Dees and Bahar (2010) using an agent-based model of evolutionary dynamics similar to the work presented below, but on a rugged fitness landscape, exhibited a mutability-driven phase transition. The control parameter, mutability (μ), characterized how phenotypically different offspring could be from their parent organisms, which reproduced via an assortative mating scheme. It was then

shown by Scott *et al.* (2013) that this phase transition behavior transpired even with implementation of a *neutral* fitness landscape, and not only for the assortative mating reproduction scheme, but also for a bacteria-like fission scheme. Continuous, absorbing phase transition behavior was shown for both reproduction schemes and for two order parameters, the population size and the number of clusters (considered analogous to species). Selective forces did not determine emergent properties of the system, since there was a mutability-driven, continuous phase transition despite the underlying neutral fitness landscape. Random mating was also investigated in the neutral version of the model, but no evidence of a critical phase transition behavior was observed in this case (a similar result that showed a lack of ‘evolutionary branching’ with random mating was presented by Dieckmann *et al.* (1999)). Most recently, it was shown that this continuous phase transition (at least for bacterial fission scheme) belonged to the directed percolation universality class (Scott, 2014), thus classifying and demonstrating universality in a model of evolutionary dynamics.

Previous null models that have explicitly examined speciation branching patterns characterize branching events via stochastic Markovian simulations (Raup & Gould, 1974; Slowinski & Guyer, 1989; Pie & Weitz, 2005). While these models do explicitly demonstrate that ‘patterns of diversity might be due to chance alone and thus not require specific explanations’ (Slowinski & Guyer, 1989), they do not incorporate or classify speciation due to the dynamics of agent-based interactions between individuals. Thus, an agent-based null model for this phenomenon has yet to be presented with an explicit purpose of classifying the underlying mechanisms of sympatric speciation or adaptive radiation. Adaptive radiation is the biological process by which species diversify rapidly usually due to newly opened ecological niches. Such models could predict the branching radiations of the Cambrian Explosion or the recovery patterns following a mass extinction event. The null condition for adaptive radiation is nonadaptive radiation, and thus the appropriate null hypothesis does not consider the environment as a factor when determining a phylogenetic radiation (Schluter, 2001). This model

could be used for the development of an agent-based null model for adaptive radiation by considering no environmental influence on the simulated reproducing organisms.

In this chapter, Agent-based dynamics and phase transition behavior are investigated. The model is neutral, in the sense for which Hubbell (2001) used the term, in that no single organism has a selective advantage over another. The neutral condition utilized in this model is the appropriate condition to consider this model as a null model for adaptive radiation since phenotypic differentiation is not driven by environmental influence. Using this null model, I investigate the relationship between morphological and lineage diversity. Understanding the relation between these two types of diversity is of great importance to evolutionary theory since paleontologists must rely on morphological character alone to trace ancestry in the fossil record of deep time (Pie and Weitz, 2005). This long-standing problem of taxonomic classification was first modelled by Raup and Gould (1974), who utilized branching random walks to investigate lineages. They showed that morphological ‘outliers’ could occur within a species of known lineage, thus identifying a potential problem with characterizing species based on morphology alone in a computational model.

The agent-based model used here incorporates the fundamental characteristics of Darwinian evolution (heritability, variation and competition), but on a neutral fitness landscape. The model can be characterized by a branching random walk, a mathematical process that directly maps onto a reaction-diffusion (RD) process in physics. The RD process $A \rightarrow 2A$, $A+A \rightarrow A$, and $A \rightarrow \emptyset$, undergoes a continuous phase transition belonging to the directed percolation universality class (Henkel *et al.*, 2008; Hinrichsen *et al.*, 2000; Ódor, 2008). Here, I specifically investigate the DP phase transition behavior as a function of a control parameter, called the individual death probability, δ and the emergent properties of cluster formation that occur when individual agents reproduce, mutate, and die on generational timescales that could not be typically observed in human lifetimes. In fact, it will be shown that *two* types of phase transitions occur in this model, and that one of the phase transition types allows for the investigation of disparity patterns. Further, the results will show that neutral

evolution is a suitable null condition for phenotypic speciation and, thus, for adaptive radiation.

2.2 THE MODEL

All simulations were run on a two-dimensional, continuous phenotype space, with a landscape size of 45x45 units. Thus, the x- and the y-axes define arbitrary traits of arbitrary organisms on a square unit space. Simulations were started with an initial population of 300 individuals. Original MATLAB code was used for all simulations and analysis.

2.2.1 Birth Process. To incorporate neutral conditions, every organism reproduces and generates two offspring, in each generation, based on the specific reproduction rules outlined below.

2.2.1.1 Reproduction schemes. There were three reproduction schemes represented in this model. Assortative mating was based on the idea that organisms chose mates that are most similar to themselves (Kondrashov & Shpak, 1998; de Cara *et al.*, 2008). In this scheme, organisms picked their nearest neighbor as their mate. Random mating acts as the control case, and all organisms chose their mates at random. Asexual fission could represent any asexually reproducing organism such as bacteria, yeast, fungi, or algae⁸. For this, each organism simply splits in two, which is represented as a branching process.

2.2.1.2 Offspring dispersion. After the chosen reproduction scheme was implemented, each organism gave birth to two offspring (hence neutral fitness). For the assortative and random mating schemes, a box defined by the mutability, μ , was defined for each reproducing pair of parents. See the schematic of Figure 2.1 for an illustration. For asexual fission, each organism had a reproductive box that surrounded it with sides of length 2μ . After the reproductive area was determined, the two offspring of each parent were randomly placed in the box. The parents were then removed.

⁸ There are microbial species of sexually reproducing variants, as well.

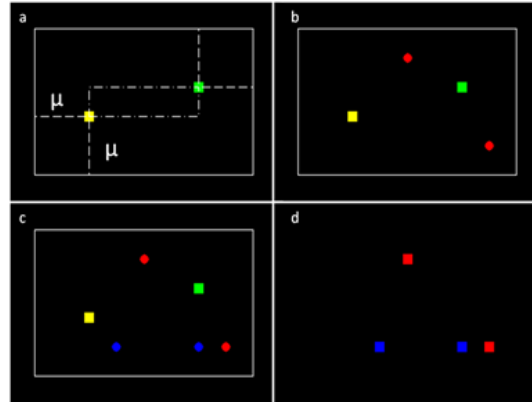


Figure 2.1. Schematic Diagram for Assortative Mating — Steps a-d can be read from left to right. Parents are labeled as squares and offspring as circles. (a) A reference organism (yellow) selects its nearest neighbor (green) as a mate. Offspring are distributed in an area defined by the locations of the two parent organisms, extended by the mutability μ . (b) Yellow's offspring organisms are generated (red circles). (c) Green's offspring are generated (blue circles). Note that this example assumes that the yellow parent organism is also the nearest neighbor of the green organism; this will not always be the case, and thus mating pairs will not necessarily be 'monogamous'. (d) After every parent has mated (each acting once as the reference organism), all parents are removed, leaving their offspring to act as parents for the next generation

2.2.2 Death Processes. All offspring were then subjected to a series of death processes. They proceeded in the order given. The first, dubbed the competition limit, κ dictated that when any two offspring were generated within a distance of 0.25 units, one was randomly removed. To represent other random vagaries of fate, each individual was assigned a random number from a uniform distribution between 0 and 1. If an organism fell below the *individual death probability*, δ , it was removed. This individual death probability also acted as the control parameter for the system. Lastly, in boundary death, if an organism fell outside the boundary of the landscape, it was removed. Boundary death can be thought of as preventing 'runaway' — a concept well known by sexual selection experts that explains ornamental traits of organisms, such as the peacock tail, as growing forever and becoming even more elaborate if the environment did not constrain it from growing out of control (Fisher, 1930).

2.2.3 Clustering. In accordance with the “biological species concept”, clusters were determined by mating pairs. The clustering algorithm is represented schematically in Figure 2.2 for the assortative mating scheme. A group of three organisms – a reference organism, its mate, and its second nearest neighbor – formed a “cluster seed”, and then an iterative process determined whether organisms within one cluster

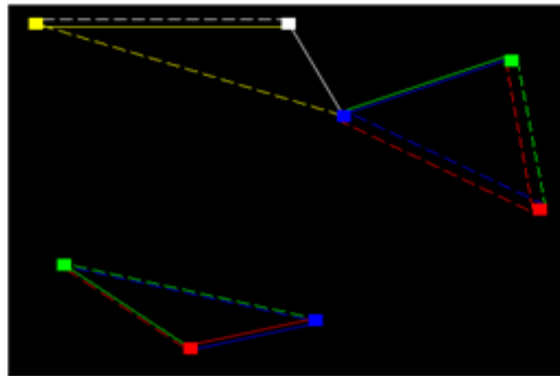


Figure 2.2. Schematic Representation of the Formation of Clusters — This algorithm is used for both the assortative mating and the fission model. The nearest organism to a reference organism is its mate (solid lines). The second nearest organism to the reference organism is its “alternate” mate (dashed lines). Lines are colored to indicate the mate and alternate mate of the correspondingly colored reference organism; for example, the white organism’s mate is the blue organism, and its alternate is the yellow organism.

seed belonged to another. If so, then this other cluster seed was incorporated into the growing cluster. This process generated a closed group of mating organisms that can be representative of a species. The same algorithm is also used to identify clusters in the bacterial fission case. However, in this case, the nearest neighbors and second nearest neighbors represent the most phenotypically similar and second-most phenotypically similar organisms, respectively. For the random mating scheme, both mates and

alternate mates were chosen at random, and the clustering algorithm was applied to these mates as in the assortative case.

2.3 ANALYTIC METHODS

2.3.1 Continuum Percolation. The organisms exist, choose mates, and cluster on a continuous space. The organisms in a cluster can be represented as disks with radius κ , and these disks may overlap up to the radial distance (see Fig. 2.3 for schematic representation). In the case of overlapping percolating disks, the percolation threshold

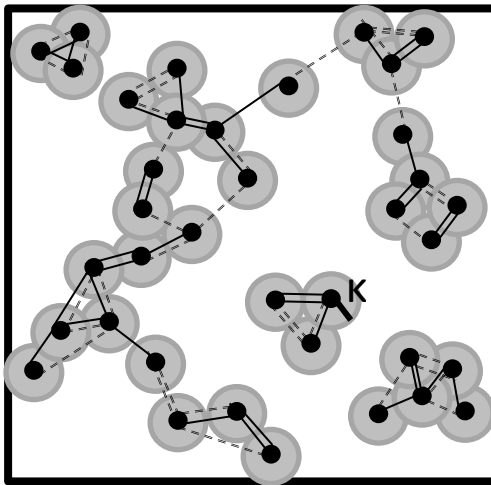


Figure 2.3. Schematic Representation of Clusters Formed by Mate Choice and by Percolating Disks — Dots represent mating organisms. Mates (solid lines) and alternate mates (dashed lines) are included in the definition of species. $\kappa = 0.25$ for all simulations, and represents the radii of the disks. There are four clusters of bonded mates and seven disk clusters. Note how the largest cluster of bonded mates spans the space from end to end, while the disks do not form a continuous overlapping chain.

is considered to occur at the point for which there is a continuous chain of overlapping disks that span the space from end to end. In general, for models of this type, the fraction of the landscape filled is $\phi = pf_1$, where p , the *percolation probability*, and f_1 , the *filling factor*, are dependent on the model and dimension of the space (Sahimi,

1994). It was found that for the 2D continuum model with overlapping disks, $\phi = 1 - e^{-\eta}$, where $\eta = \rho a$ is the *filling factor*, ρ is the population density, and a is the disk area. Critical percolation values are calculated to be $\eta_c \cong 1.12$ and $\phi_c \cong 0.67$ (Mertens & Moore, 2012). Note that the use of the continuum percolation equations is an ‘after the fact’ measurement; this is not demonstrating an actual percolation process.

2.3.2 Nearest Neighbor Index, R. The Clark and Evans (1954) nearest neighbor index, R , measured the spatial distribution within a population. The measure characterizes the spatial departure of nearest-neighbor distances from a randomly distributed population. The random distribution is defined by the random placement of N points on a space. The average nearest neighbor distance in a randomly distributed population was calculated to be

$$r_E = 1 / (2\sqrt{\rho}),$$

where ρ is the population density. The ratio

$$R = r_A / r_E,$$

where r_A is the actual measurement of average nearest neighbor distance of the population being sampled, quantifies a population’s departure from a random distribution. Thus, when $R < 1$, the population is distributed in a more clumped, aggregated manner, and when $R > 1$, the population is more uniformly dispersed across the space. At $R = 1$, the spatial distribution of the population is said to be random. For the maximum packing of a space (with a population arranged in a hexagonal lattice structure) this measure approaches a limit of $R = 2.1491$. (Clark and Evans, 1954)

2.4 RESULTS

Figures 2.4 and 2.5 are visual representations, at different parameter values, of population snapshots at the 2000th generation for the reproduction schemes of assortative mating and asexual fission. In each snapshot, five example clusters are highlighted in yellow, white, purple, blue, and red, while the green dots represent the remaining population. Note the qualitative change in the clustering patterns of the population: for some values of μ and δ , the populations are aggregated, for other values the individuals appear more uniformly distributed, while for others an example cluster can either span the space or fill most of the entire morphospace.

Continuous, nonequilibrium phase transitions for the order parameters of population size and cluster number are shown as a function of the individual death probability, δ , in Figure 2.6. Panels 2.6a and b represent the assortative mating scheme, while 2.6c and d represent the asexual fission scheme. For both reproduction schemes, three values of the maximum mutation size are represented: $\mu = 0.30, 0.60, \text{ and } 0.90$. The insets in the figures show the standard deviation of the population size and cluster number, with largest fluctuations occurring at the critical point of each of the transitions. For assortative mating at $\mu = 0.30, 0.60, \text{ and } 0.90$, the critical point, δ_c , was estimated to be 0.23, 0.38, and 0.43, respectively, while for asexual fission, it was estimated to be $\delta_c = 0.26, 0.40, \text{ and } 0.44$, respectively. Further, there is a trend of increasing system robustness as μ increases, with up to 43% (assortative) and 44% (bacterial) death probability before extinction at $\mu = 0.90$. Example clusters are also represented in Figures 2.4 and 2.5 at the critical point for each μ and δ , as well as for values above δ_c for each μ represented. Note that, for some values of μ and δ , the populations are dispersed in an aggregated manner, while for other values of μ and δ , the population is more uniformly dispersed, with example clusters that can either span the space from end to end or fill the entire phenotype space. There was distinctly different behavior from the random mating scheme as shown by the non-critical phase transition behavior shown in Figure 2.7, since there was not a large fluctuation of population as the system changed state from extinction to survival. The population curves also did not

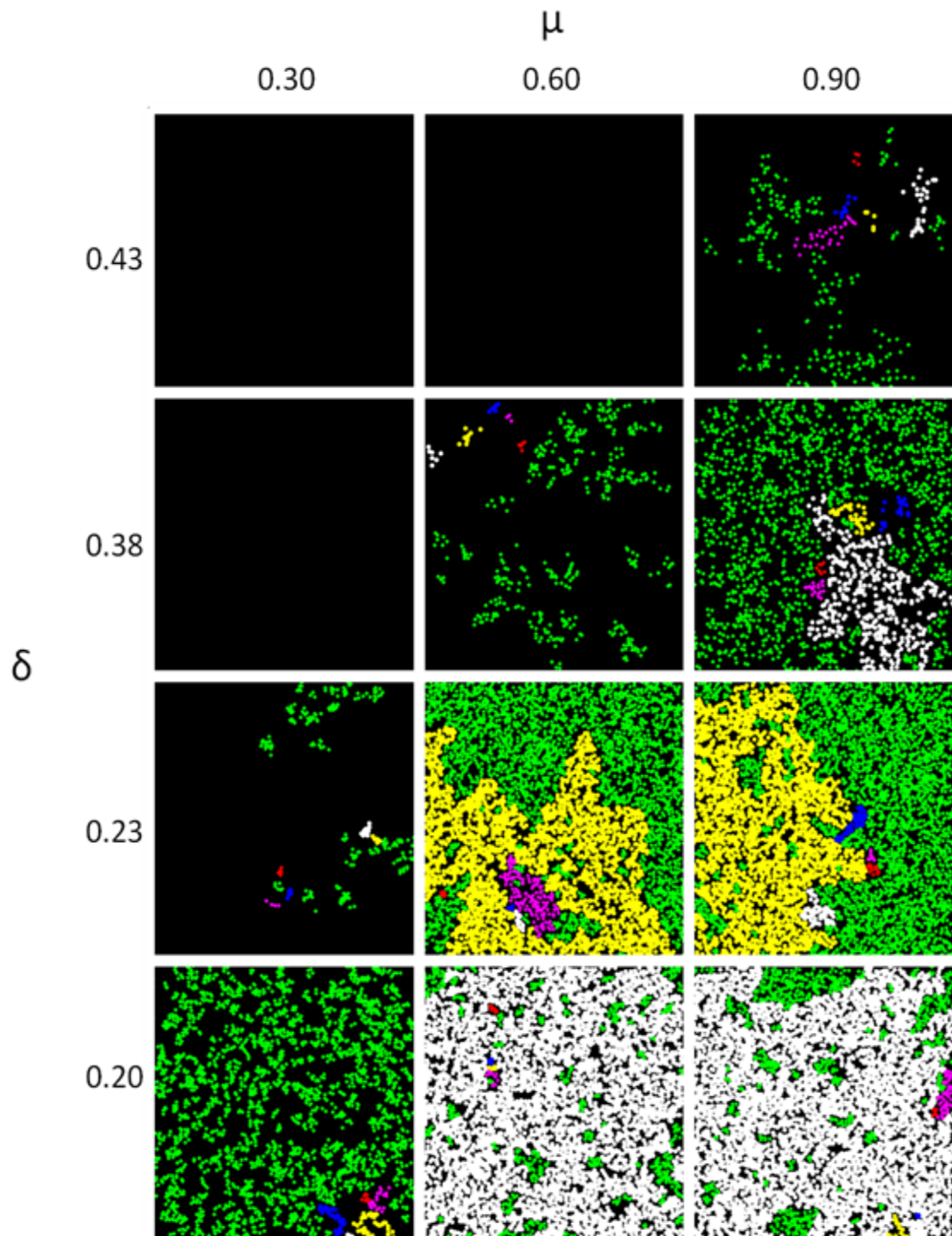


Figure 2.4. Clustering for Assortative Mating on a 45 x 45 Landscape at 2000 Generations — Individuals are represented by dots, with example clusters highlighted in red, white, yellow, purple and blue. Critical parameter values of $\delta_c = 0.23, 0.38,$ and 0.43 for $\mu = 0.30, 0.60,$ and 0.90 are shown respectively. $\delta = 0.20$ exists within the survival regime for each value of μ .

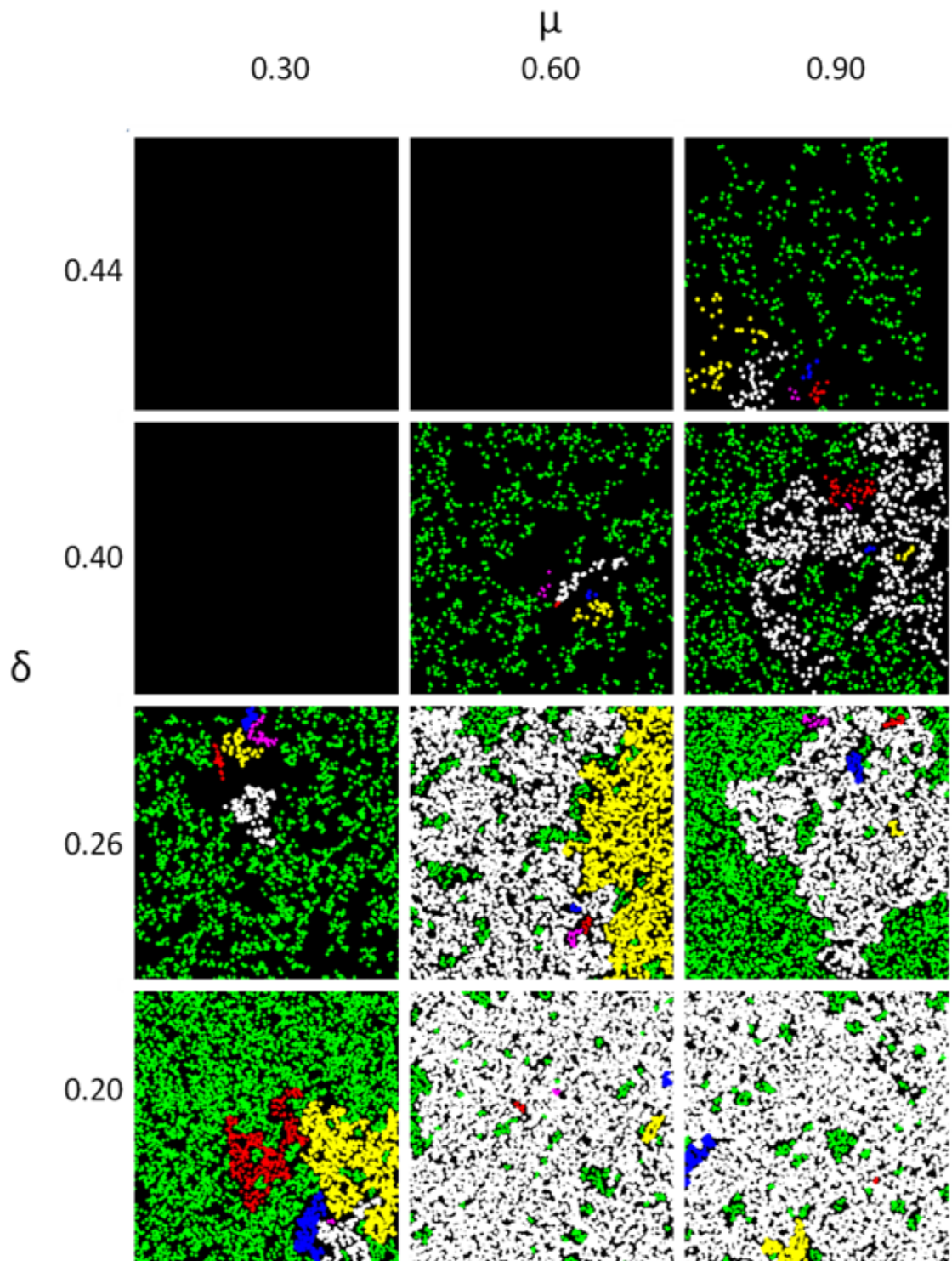


Figure 2.5. Clustering for Asexual Fission on a 45 x 45 Landscape at 2000 Generations — Individuals are represented by dots, with example clusters highlighted in red, white, yellow, purple, and blue. Critical parameter values of $\delta_c = 0.26, 0.40, 0.44$, for $\mu = 0.30, 0.60, 0.90$, are shown respectively. $\delta = 0.20$ exists within the survival regime for each value of μ .

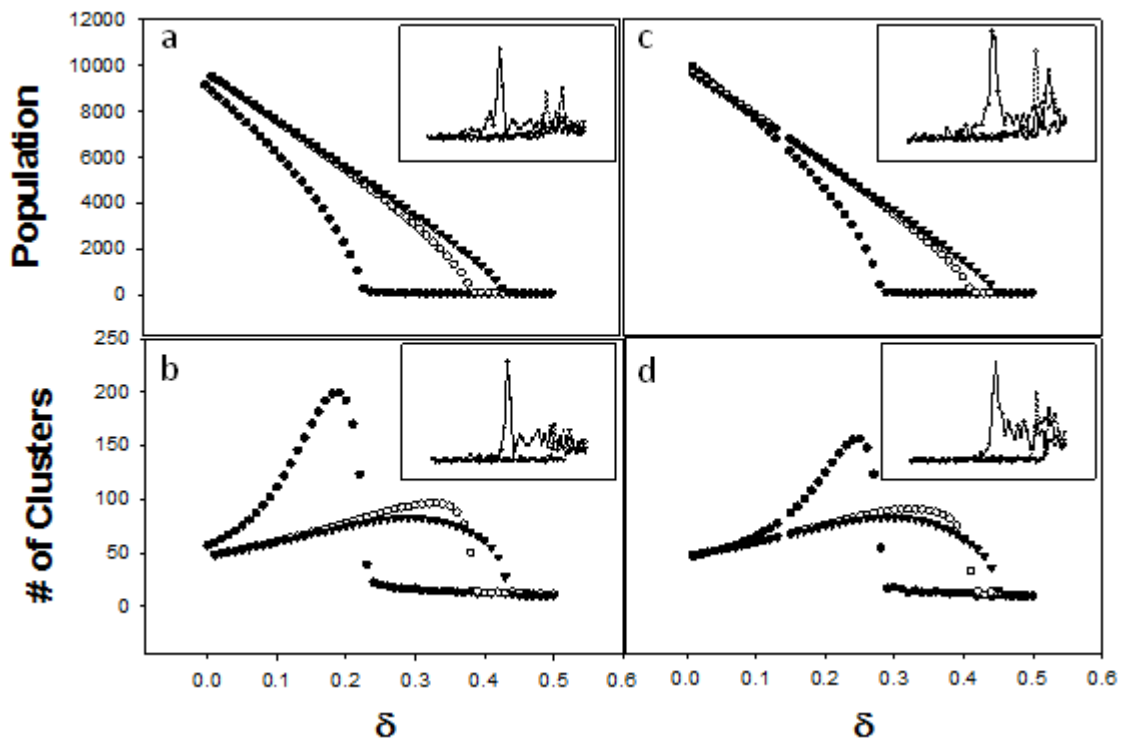


Figure 2.6. Phase Transition Behavior — Population size and number of clusters for assortative mating scheme (a&b) and asexual fission (c&d) are shown. Solid circles represent $\mu = 0.30$, hollow circles $\mu = 0.60$, and triangles $\mu = 0.90$. Insets show sharp increase of the standard deviation, averaged over five simulations, indicating the critical point of the phase transition. X-axis insets are scaled with represented δ . Y-axis insets are scaled from (a) 0-100, (b) 0-60, (c) 0-60, and (d) 0-60.

exhibit a sharp change as well. Rather, the curves qualitatively appear to exponentially decrease for $\mu = 0.60$ (black circles), 0.90 (hollow circles), 1.50 (black triangles), 2.00 (hollow triangles), and 5.00 (black squares); in contrast, for $\mu = 10.00$ (hollow squares), 15.00 (crosses), and 20.00 (stars), the populations appear to linearly decreased as a function of δ . Further, there was only one giant-component cluster of mates, thus no emergent clustering was observed (data not shown). Figure 2.8 shows the nearest neighbor index, R , as a function of δ , for the assortative mating scheme (a), asexual fission (b), and random mating (c). Panels 2.8a and 2.8b show data for $\mu = 0.30$ (filled circles), 0.60 (open circles), and 0.90 (triangles), while for panel 2.8c, $\mu = 1.50$ (filled circles), 2.00 (open circles), 3.00 (filled triangles), 4.00 (open triangles), 5.00 (filled

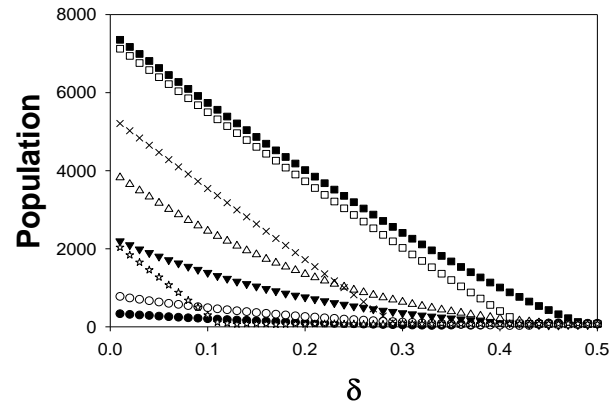


Figure 2.7. Population Size for the Random Mating Scheme — The various shapes represents different μ values (described in text).

squares), 10.00 (open squares), and 12.00 (diamonds) are shown. Note that R acts as an order parameter of the system undergoing a nonequilibrium, continuous phase transition, as seen by the higher standard deviation at the critical point (similar to what was seen with the behavior of the population size from the assortative mating and asexual fission reproduction schemes). The critical points shown in 2.8a and 2.8b have the same values as for the population size and cluster number of the corresponding mating schemes. In all panels, the horizontal, dashed line marks the R -distribution transition from $R < 1$, where individuals are dispersed in a clumped, aggregated manner, to $R > 1$, where individuals are dispersed more uniformly. Along the dashed line, where $R = 1$, the individuals fall into random distribution pattern. All mating schemes exhibit such an “ R transition”, but with some notable differences. Both asexual fission and the assortative mating scheme show the R transition occurring slightly above the critical point, while the random mating scheme shows an R transition possible for $2.00 < \mu < 10.00$. Below $\mu = 2.00$, all populations aggregate ($R < 1$), and above $\mu = 10.00$, the population is uniformly dispersed ($R > 1$). Figure 2.9 represents a parameter space plot of μ versus δ for the assortative mating scheme. The solid circles represent the critical point (marked by the highest standard deviation) of the continuous phase transition, while the hollow circles represent the R transition at the value that $R = 1$. Figure 2.10a

shows the filling factor η and 2.10b, the fraction of the landscape filled, ϕ , as a function of the fitness, f . The horizontal line indicates the first point for which a spanning percolation cluster could appear, showing that a spanning continuum percolation cluster can only appear for $f > 2$.

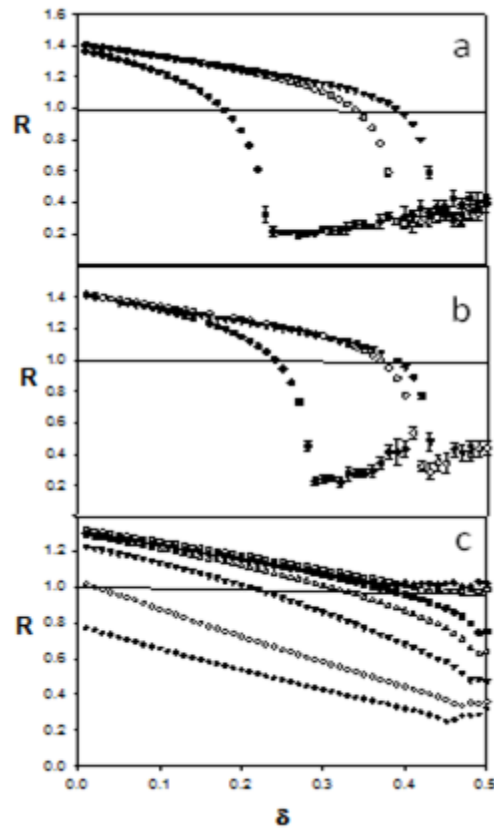


Figure 2.8. R Transition Curves — Averages are over five simulations. Assortative mating (a) and bacterial fission (b) show continuous phase transitions. The random mating case (c) shows no phase transition behavior. The black horizontal lines indicate the point where $R = 1$.

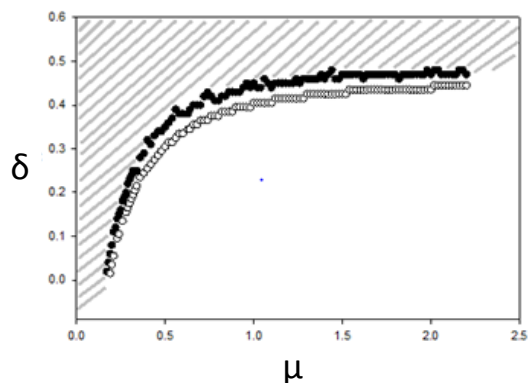


Figure 2.9. Parameter Space Plot for Assortative Mating — Shaded area represents the extinction regime. Solid dots indicate the critical points of the continuous phase transition. Hollow dots show where $R = 1$, thus showing that the populations always change their distribution structure within the active phase of the phase transition.

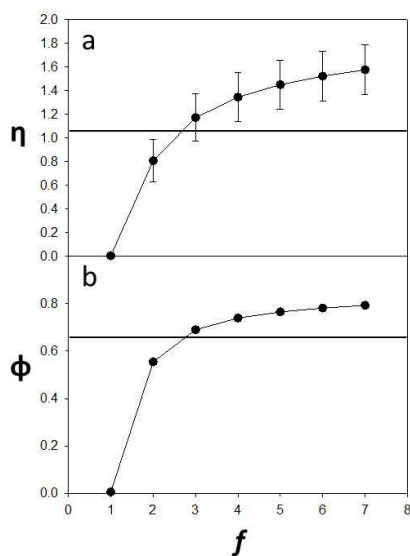


Figure 2.10 The Filling Factor and the Fraction of the Landscape Filled — Panel a shows the filling factor, and panel b shows the fraction of the landscape filled. Horizontal lines represent the percolation threshold at critical parameter values of $\eta_c \approx 1.12$ and $\phi_c \approx 0.67$. Plot (a) was averaged over 20 simulations that were run for 250 generations.

2.5 DISCUSSION

In a family of agent-based evolutionary models, the existence of nonequilibrium, continuous phase transitions, for both fluctuating fitness landscapes and neutral conditions, as a function of mutability has previously been demonstrated (Dees and Bahar, 2010; Scott *et al.*, 2013; Scott, 2014). In this dissertation, a version of this model is presented that incorporates not only neutral fitness conditions but also an individual death probability that was uniform for all organisms at every generation. The existence of nonequilibrium, continuous phase transitions as this individual death probability was varied was shown (Figure 2.6). The nonequilibrium phase transitions in this system are a result of a generational reaction-diffusion (RD) process of the form $A \rightarrow 2A$, $2A \rightarrow A$, and $A \rightarrow \emptyset$ that define the system as belonging to the directed percolation (DP) universality class.

The previous work of Dees & Bahar (2010), Scott *et al.* (2013), and Scott (2014) modelled the mutability-driven phase transitions with a *time-dependent* death probability, δ^T , defined such that individuals had up to a seventy percent chance of being killed in any given generation (*i.e.*, the percentage of deaths varied from generation to generation). Here, an individual death probability, δ , was used rather than δ^T , so that in each generation every individual had the *same probability* of being killed. This modification allowed for a more stringent matching to the definition of neutral fitness outlined by Hubbell (2001).

It was determined by Scott (2014), with the time-dependent death process and for asexual fission, that this model belongs to the directed percolation (DP) universality class. Any model that is in agreement with the DP conjecture, and undergoes the RD process of $A \rightarrow 2A$, $2A \rightarrow A$, and $A \rightarrow \emptyset$ is said to belong to the directed percolation universality class (Henkel *et al.*, 2008; Hinrichsen *et al.*, 2000; Ódor, 2008). Therefore, since the continuous phase transitions shown in the present paper follow the same RD process, and are consistent with the four properties of the DP conjecture outlined by Henkel *et al.* (2008), it can be concluded that the phase transitions as function of δ , shown in Figure 2.6, also belongs to the DP universality class. In the case of random

mating, however, the dynamical rules of dispersion are no longer short-ranged (conjecture #3 is broken); hence, the non-critical phase transition behavior that does not belong to the DP universality class (Figure 2.7). Since clustering behavior did not occur for the random mating case as well, this result is also consistent with the body of literature above that shows that, in order for emergent clustering to appear, the dynamics must be governed by a local dispersion process and global death (*e.g.*, Young *et al.*, 2001).

A second type of phase transition is present in this system. As discussed in the Introduction, ordinary percolation transpires in systems without time acting as an independent dimension from space. When organisms choose mates, mate choice represents bonds between organisms, and thus clusters of bonded mates represent a problem of a different flavor – bond percolation on a continuous space. (Note that the DP clusters are time-dependent genealogical clusters between parents and offspring.) Figures 2.4 and 2.5 provide visual confirmation that there are indeed bonded clusters of mates that can span the space from end to end for certain values of δ ; at other values of δ , clusters of mates are small and cannot span the space, or the clusters of mates have completely filled the space. Therefore, at some point, this system should exhibit critical behavior of cluster size between mating organisms.

Since organisms cannot get within $\kappa = 0.25$ units of each other, they can be defined as circles with radius $r = \kappa$. With this definition, clusters of organisms could be defined as overlapping disks. Therefore, utilizing aspects continuum percolation (described above) allowed for investigation of how the organisms were filling the landscape. Figure 2.10 shows, by utilizing the known percolation threshold for this system, that it is not possible for a spanning cluster of disks to span the space with a fitness of $f = 2$. In order for a spanning disk cluster to occur, the fitness must be increased. For the reaction-diffusion process utilized in this system the birth process was confined to $f = 2$ offspring ($A \rightarrow 2A$). Recall that it was indicated that increasing f to 3 and beyond changes the number of diffusing organisms from $A \rightarrow (m+1)A$, but it does not change the universality class from DP (Vojta, *personal communication*). However,

clearly, increasing the number of births changes how the directed percolation clusters fill the morphospace. Therefore, for the most basic RD process of DP, where $A \rightarrow 2A$, organisms sparsely fill the morphospace in such a way that it is not possible for a cluster of disks to span the space, while it is possible for a bonded parent-offspring cluster or a bonded cluster of mates to spread across the space.

To be clear in distinguishing the two types of percolation problems at hand, it is important to emphasize that the filling factor is a space-filling measure of continuum percolation. In contrast, the DP clusters are represented *in time* as bonds between parent and offspring, whereas, mates define bonded percolation clusters in the two-dimensional plane. Much as DP clusters do not saturate the landscape, clusters that are formed by bonded mates could also contain many clusters of organisms defined by disks. Thus, many disk clusters could be contained in a cluster of bonded mates (see schematic illustration in Figure 2.3), since it is not possible for a spanning disk cluster to occur at $f = 2$, yet as evidenced by Figures 2.4 and 2.5, clusters of bonded mates do span the entire landscape.

The Clark and Evans (1954) nearest neighbor index, R , characterizes the dispersal patterns of populations based on a nearest neighbor measure. When $R < 1$, the populations are distributed in an aggregated manner; when $R = 1$, they are distributed as if the points were placed randomly on the space; when $R > 1$, the organisms are said to be uniformly distributed within the space. In this sense, the measure is strictly used to identify the patterns of the already dispersed organisms, and it does not specifically characterize dispersion due to the underlying reaction-diffusion process. In other words, it describes the average structure of the population at a moment in time, rather than the directed percolation of the population across multiple generations. Furthermore, the index R does not distinguish whether a clumped, aggregated population distribution is composed of many small clusters or one giant cluster. For this reason, it is not a good measure of morphological disparity. Although the emergent properties of clustering are determined by the type of reproduction which the system undergoes, the population distribution as measured by R yields a transition from $R < 1$ to $R > 1$ regardless of the

reproduction scheme, though it should be noted there are some significant differences in the behavior of R between the reproduction schemes (Figure 2.8).

The R transition is shown to occur in the active phase of the continuous phase transition (Figs. 2.8a, b, 2.9), but also only for a select range of μ in the random mating case (Fig. 2.8c). The R measure directly shows, by observation of how populations fill the morphospace, that the process by which a species evolves *cannot be determined by community pattern alone*. In other words, the clumping or grouping of morphological characters by nearest-neighbor distance provides little, if any, information about how a population evolved. This is highlighted by the fact that the assortative mating and bacteria-like fission reproduction schemes exhibited many clusters, while the random mating scheme only had one giant cluster on order of the population size, yet all reproduction schemes exhibited an R transition, at least for some parameter values (Figure 2.8). Thus, the spatially asymmetric birth and death placements, generated via the RD process (with the underlying reproduction schemes acting as the driver of birth placements) allow for emergent clustering, but do not completely determine organismal dispersal patterns on the landscape. Rather, the interplay of the mutability and the individual death probability (*i.e.*, the location in parameter space as demonstrated in Figure 2.9 for assortative mating) determine population dispersal pattern, while the mating scheme determines the number of clusters.

The properties of the DP phase transitions, the ordinary bond percolation properties of clusters of mating groups and the corresponding continuum percolation problem, as well as the R transition in the overall dispersion of the organisms regardless of mating scheme, all demonstrate the inability of the organisms to completely saturate the morphospace. This is because, for DP reaction-diffusion dynamics, dispersion is restricted to $f = 2$, and f needs to be greater than 2 for a space-filling continuum disk cluster to occur. However, it is possible for a cluster of bonded mates to span the space. This is consistent with the observation that the maximum R value obtained in the simulations for $f = 2$ was 1.42, while a value of $R = 2.1491$ is needed for a maximally filled space (Clark and Evans, 1954). In essence, since bonded percolation clusters of

mates do span the entire phenotype space, but there is not a continuum percolation cluster of disks, then a cluster of bonded mates that does span the space could contain many disk clusters (Fig. 2.3); in other words, in this model, species could have a range of distributed, and even discontinuous, phenotypic characters.

The sparse filling of phenotype space is consistent with the potential pitfalls presented by Raup and Gould (1974) and Pie and Weitz (2005) for classifying lineages based on morphological character alone. This is because, as outlined above, a species (bonded cluster of mates) could have many distinct groups of clusters that fill different regions of the morphospace, and therefore may display a range of phenotypic characters. Further, as evidenced from soft-bodied creatures of the Burgess Shale, it is possible to have high disparity and low diversity, thus indicating that many body plans may exist within groups (Gould, 1989). This is a significant problem for paleontologists because much of the existing data contained in the fossil record of deep time results from classification via morphological characters, as discussed above. The potential of the present model lies in its ability to track lineages as well as morphological patterns, and to quantitatively characterize the relationship between the two. In the future, continuum percolation may be used to develop a within-cluster diversity measure that could be used to address the relationship between lineage and morphological diversity (diversity vs. disparity) in generational time. Yet, a number of steps must be taken in order for models of this type to become practically useful to the paleontological community. These steps will include development of analytical techniques to investigate existing branching patterns, comparison of null models with ones that incorporate selection, simulations of adaptive radiation of both lineages and morphologies during recovery from mass extinction, and the identification of hierarchical relations between levels of clustering.

3. MULTI-LEVEL ANALYSIS OF PHYLOGENETIC TREE STRUCTURES

3.1 INTRODUCTION

Here, common descent is investigated by exploring phylogenetic tree structures. Embedded in the simulation RD dynamics is the coalescing of two organisms – when one organism is within 0.25 units of another, then one is randomly removed. These coalescent events of individual organisms should not be confused with the coalescent process that will be discussed hereafter. It is an unfortunate terminological side effect that cannot be helped, and since an entire mathematical field of study cannot be renamed, nor can the events of the directed percolation RD process be renamed. For the remainder of this dissertation, a coalescent event will be considered to occur when two or more individuals (or clusters) find a common ancestor. Thus, coalescence is the merging of genealogical branches backwards in time.

3.1.1 Phylogenetic Trees. A phylogenetic tree, sometimes called a genealogy or phylogeny, describes relationships in time between living things. A tree can describe relationships at all levels of biological organization, such as a family tree of individuals or the ancestral relationships and divergences of species. It can also show hierarchical relationships. For example, the class Mammalia branches into 19 orders (carnivore, primate, cetacean, *etc.*); these nineteen orders further branch into families, the families into genera, and the genera into species, *etc.*

There are a variety of methods to reconstruct phylogenetic trees, but all entail finding common descent. For example, models demonstrate that gene trees can be used to reconstruct species phylogenies (Madison, 1997), or that structured mating populations (*i.e.*, not random mating) can demonstrate common descent of all living humans (Chang, 1999; Rohde *et al.*, 2004). Paleogeneticists have uncovered the relationships between our ancient ancestors and us, notably by countering the 'recent single-origin' with the 'leaky replacement' hypothesis (Kolbert, 2014). Basically, the recent single-origin hypothesis (also known as the 'out-of-Africa hypothesis) claims that

the first descendants of the genus *Homo* were discovered in Africa, and these descendants date back to a few million years ago. Of the 22 known species of our genus, only one species survived and migrated out of Africa: *Homo sapiens*. The counter to the single-origin hypothesis is not arguing that the genus *Homo* originated out of Africa, but that *homo sapiens* were not the only genus to migrate out of Africa. Recent paleogenetic studies have shown that not all humans have descent out of Africa. Humans mated with the Neanderthals before the latter were driven to extinction, and all non-Africans share 4-6% of Neanderthal DNA, while at the same time some humans do not have any trace genetics tied to Africa (Green *et al.*, 2010). At nearly the same time, another article in *Nature* tied a different extinct genus of hominids to all descendants of the New Guinean people; therefore showing that not all hominids went extinct before migrating out of Africa (Reich *et al.*, 2010). My own DNA test from ancestry.com showed that I had no trace genetic material from regions of Africa. I am strictly of European descent; thus, according to my own genome, I have trace amounts of Neanderthal, and no descent out of Africa. So while it may be true that the first humans may have originated from Africa, new evidence showing that common descent of *all* humans alive today do *not* genetically trace to Africa. Thus, the tree of human ancestry is being revealed as a branched and tangled web of descent.

Paleogeneticists are limited to studying recent fossils because DNA deteriorates in time, though this in no way diminishes the importance of genomic sequencing from the recent fossil record and comparing the fossil genomes to extant species. In deep time, when there is not a genetic record that can be traced, paleontologists must classify organisms based on morphological characters alone. Paleontological methods must determine whether morphological similarities are analogies or homologies.

The first kind of similarity, called homology, is the proper guide to descent. I have the same number of neck vertebrae as a giraffe, a mole, and a bat, not (obviously) because we all use our heads in the same way, but because seven is the ancestral number in mammals, and has been retained by descent in nearly all modern groups (sloths and their relatives

excepted). The second kind of similarity, called analogy, is the most treacherous obstacle to the search for genealogy. The wings of birds, bats, and pterosaurs share basic aerodynamic features, but each evolved independently, for no common ancestor of any pair had wings. Distinguishing homology from analogy is the basic activity of geological inference. ... Bats are mammals, not birds. (Gould, 1989 p. 213)

This basic distinction between homology and analogy is important to understanding the fossil record of deep time. The fact that most mammals have seven vertebrae that can lead to an eventual common ancestor shows that the ancestral number of seven, whether selected for or not, has been a stable evolutionary development that has not changed in hundreds of millions of years. This concept is called 'evolutionary stasis', as in the popular catch phrase coined by Stephen Jay Gould — 'Stasis is Data.' Stasis is a concept that is tied to the theory of punctuated equilibrium discussed above. However, organisms such as the bat and bird share wings as a common trait, but since bats and birds are not ancestrally related, the trait 'wings' does not provide an example of evolutionary stasis. Rather, wings in this case are an example of an analogy, and is representative of a concept called convergent evolution.

Genealogical trees have a mathematical formulation deriving from graph theory. Trees that show common descent from a single ancestor are called 'rooted' trees, while 'unrooted' trees, sometimes called forests, do not have common descent. For example, common descent can be found between mammals characterized by the homologous character of seven neck vertebrae (rooted tree), while the analogous character of wings from a bat, bird, and pterosaur does not have common descent (unrooted tree). Graphs that are defined by a set, $G = (V,E)$, where V are the vertices (or nodes) and E are the edges, where no more than two edges connect to a node, are termed simple, acyclic graphs. (Diestel, 2012) Organisms that asexually reproduce would create these types of trees, while organisms that mate would not, because a parental organism could be related to more than two offspring organisms.

3.1.2 Coalescent Theory. The British mathematician Sir John Charles Frank Kingman was knighted by Queen Elizabeth II five years after he developed an entirely new mathematical field — coalescent theory. This new field was designed for use by population geneticists, and it describes an ancestral process that seeks to find a common ancestor of a sample population (Wakeley, 2009). Kingman’s seminal proofs (1980 a&b) described a Markovian mathematical process known as the n -coalescent, which traced the common ancestor from the most recent generation of n -haploid genotypes from a large population. His proof of the n -coalescent defines ‘the ancestral limit process for a broad class of population models that includes the Wright-Fisher model and the Moran model.’ (Wakeley, 2009)

The n -coalescent is a backwards-in-time process that requires no previous knowledge of the lineage in question, and it has been shown to have a dual relation with the Wright-Fisher (WF) diffusion (Berestycki, 2009). ‘Intuitively, the Wright-Fisher diffusion describes the evolution of a subpopulation forward in time, while Kingman’s coalescent describes the evolution of ancestral lineages backward in time, so this relation is akin to a change in the direction in time.’ (Berestycki, 2009) Wright-Fisher diffusion is used in both the WF and Moran models. Kingman’s n -coalescent and details of these models will be discussed in the sections below.

3.1.2.1 Wright-Fisher and Moran models. Two models have been extensively used by population geneticists: the WF model and the Moran model. The difference between the two models is that the Moran model allows for overlapping generations and, as it turns out, that makes the difference between the models significant because ‘many results can be derived exactly under the Moran model that are available only approximately under the WF model...’ (Wakeley, 2009 p. 57), such as the dual relation that relates the forward- and backward-in-time processes for the WF diffusion utilizing the Moran model. Both models are, importantly, representations of genetic drift, and thus they are neutral evolution models that date back to 1930 (for Fisher), 1931 (for Wright), and 1958 (for Moran).

Critical assumptions must be made in order to class models into what are known as Cannings models (Cannings, 1974, 1975), which converge to Kingman's coalescent in the ancestral limit process regardless of changes 'to the microscopic details of the underlying probability model', such as allowing generations to overlap (Berestycki, 2009 p. 43). The assumptions are:

- (1) Population of constant size, and individuals typically have few offspring.
- (2) Population is well-mixed (or mean field): everybody is liable to interact with anybody.
- (3) No selection acts on the population.

(Berestycki, 2009 p. 39)

The forward-in-time WF and Moran models utilize a Markov process, which is a stochastic process whose transition rules depend on the current state of the system, and thus each step is independent from past and future events.

For the WF model, consider a sample of N haploid individuals with subpopulations marked by either allele A or a . Consider a grid that has width N and length t , where initially each node on the line at $t=0$ is assigned an allele a or A . At $t+1$, each of the new N alleles (on line $t+1$) are found by copying the allele of a randomly chosen individual from the previous generation. This allows for the population size to stay constant, but also it lets some alleles die out and others to come from a common parent. The generations do not overlap, so for each time step, the process is independent. (Wakeley, 2009; Hein *et al.*, 2010)

Population geneticists often want to know when fixation of a given allele in a population of genes has occurred. For the WF model described above, let i be the number of a 's, and k be the number of A 's, such that $i + k = N$. At $t = 0$, the current frequency of the a 's in the population is given by $p = i/N$, while the current frequency of the A 's is $1-p$ (or k/N). Since evolution of allele frequency is dictated by a stochastic process forward in time, there are a number of different genealogical outcomes that could happen with a population of size N . Therefore, the outcome of several

independent trials is given by a binomial distribution, where the transition probability that a given gene, a , with i copies is found with j copies in the next generation is:

$$P_{ij} = \binom{N}{j} p^j (1-p)^{N-j} \quad 0 \leq j \leq N.$$

The expectation value and variance of a binomial distribution are well known. Thus, if S_t represents the count of allele a at time t , then $E[S_t] = Np$ and $Var[S_t] = Np(1-p)$. Therefore, it is expected that at $t = 1$ the frequency of allele a will remain about the same, but in reality, since the WF model evolves by a Markov process with the transition probabilities given above, the frequency of a could drift to become any number from 0 to N .

Similarly, for the Moran model, a population starts with a given number of alleles a and A , but in this case, generations overlap, and at each generation two individuals are chosen at random, with probability $1/N$, to replicate. One allele of the two genes replicate and the other gene dies off. The gene that replicated replaces the gene that died off and also persists into the next generation. All other individuals survive into the next generation. (Wakeley, 2009; Hein *et al.*, 2010) If i is the number of alleles a at $t=0$, then there are three possibilities for the frequency of a to change in time: the number of a 's can increase by 1, the number of a 's can decrease by 1, or the number of a 's can stay the same. The transition probability for this Markov chain, where $p = i/N$, for this case is:

$$P_{ij} = \begin{cases} p(1-p) & \text{if } j = i + 1, \\ p(1-p) & \text{if } j = i - 1, \\ p^2 + (1-p)^2 & \text{if } j = i. \end{cases}$$

Even with overlapping generations, the expected change in allele frequency per generation is equal to the current generation, thus giving the same expectation value and variance as the WF model, *i.e.*, $E[S_t] = Np$ and $Var[S_t] = Np(1-p)$.

A final calculation that is often examined is the heterozygosity of a population forward in time. Heterozygosity, in this sense, is ‘the probability that two randomly sampled gene copies [in a population] are different.’ (Wakeley, 2009 p. 56) For the WF model, the expectation is derived, after t generations, to be:

$$E[H_t] = H_0 \left(1 - \frac{1}{N}\right)^t \approx H_0 e^{-t/N},$$

where $H_0 = 2p_0(1 - p_0)$ (note that p_0 is the initial frequency of one allele) is the initial binomial chance that the two different alleles are chosen in one draw. ‘The decrease in the heterozygosity is a common measure of genetic drift, and we say that the drift occurs in the Wright-Fisher model at a rate $1/N$ per generation.’ (Wakeley, 2009 p. 56) The distinguishing factor between the WF model and the Moran model is that rate of genetic drift increases in the Moran model, as seen through the derived expectation value from the Moran model:

$$E[H_t] = H_0 \left(1 - \frac{2}{N^2}\right)^t \approx H_0 e^{-2t/N^2}.$$

With an equivalent definition of generation between the WF and Moran models, it can be shown that ‘rate of genetic drift is twice as fast in the Moran model as it is in Wright-Fisher model.’ (Wakeley, 2009 p. 58) For the Moran model, let time be rescaled to the mean lifetime of the individual, $\tau = t/N$. The expectation value then becomes:

$$E[H_\tau] \approx H_0 e^{-2\tau/N},$$

which, rescaled, shows that genetic drift increases by a rate of $2/N$, and thus happens twice as fast when compared to the WF model.

This is interesting from a biological standpoint because it means that differences in breeding structure can lead to differences in the time scale

of change in the population even though the way in which it changes (*e.g.*, exponential decay [shown above]) may be the same for different kinds of populations. (Wakeley, 2009 p. 58)

Derivations of the equations in this section can be found in Wakeley (2009).

3.1.2.2 Times to most recent common ancestor. While the original interpretation of neutral, allelic survival in these models was the result of forward-in-time evolutionary processes (Fisher, 1930; Wright, 1931; Moran, 1958), Kingman successfully showed that the WF process could be modelled utilizing the coalescent as the backward-in-time process (Wakeley, 2009). The coalescent process is also a Markov process where each offspring chooses its parent with some probability; when multiple offspring choose the same parent, a coalescent event has occurred. The ultimate result is a branching tree that maps the genealogy back to a common ancestor. Interestingly, population geneticists, such as Nordberg (2004), consider forward-in-time, genetic modelling as the ‘classical approach’, where ‘the coalescent process [viewed as] ... genetic drift viewed backwards in time’ is computationally efficient and, because of Kingman’s proofs, is known to be realistic (Wakeley, 2009 p. 69).

The ‘robustness of the coalescent’ is seen when the haploid or diploid WF model, the Moran model, or any Markovian population model that follows the 3 basic assumptions outlined above ‘tend to give similar genealogies for large N ’. In these types of models the rate of convergence towards a final coalescent event will scale linearly with respect to the times to the most recent common ancestor (TMRCA of the entire population (Nordborg, 2004). (Note this was shown above with the forward-in-time heterozygosity calculations.) Further, many discrete time population models can utilize the coalescent process; thus, it is not limited to simple WF populations, for it can be used in concert with mutation, selection, mating, and re-combinatory processes (to name a few) (Hein *et al.*, 2010).

Kingman’s n -coalescent seeks to find, from a total of N genes in the present generation, the most recent common ancestor (MRCA) of a sample of n genes, where $n \leq N$. The coalescent time, T_n , is the time it takes to reach a common ancestor of n

randomly sampled genes. Suppose we take a sample of $n = 2$ genes from the population of size N , then the probability that these two genes choose the same parent is $p = 1/N$, and the probability that the two genes have different ancestors is then $1 - p$. The probability that the two genes find a common ancestor in t generations follows a geometric distribution:

$$P(T_2 = t) = \frac{1}{N} \left(1 - \frac{1}{N}\right)^{t-1},$$

and therefore, the mean value of T_2 is known to have an expectation value of $E[T_2] = 1/p = N$ with a variance of $Var[T_2] = (1 - p)/p^2 = N^2(1 - 1/N)$. This result was then generalized by Hein *et al.* (2010) to include the transition probabilities of coalescent times, T_n , for all $n \leq k$, where $k \ll N$ and N is sufficiently large :

$$P(T_n = t) = \binom{n}{2} \frac{1}{N} \left\{1 - \binom{n}{2} \frac{1}{N}\right\}^{t-1}.$$

Kingman showed that in the limit of $N \rightarrow \infty$ as $n \rightarrow N$, the coalescent times T_n are exponentially distributed for a Wright-Fisher (WF) population when time is scaled appropriately; meaning time is normalized, and rescaled from the time measured in generations to $\tau = t/N$. Because the coalescent times are exponentially distributed, and each coalescent time is independent the expectation value and variance are known: $E[T_n] = \frac{2}{n(n-1)}$, $Var[T_n] = \left(\frac{2}{n(n-1)}\right)^2$. For the Moran model, the solutions are exact (*i.e.*, there is no need to take the limit to infinity). (Wakeley, 2009)

Another common calculation of the coalescent examines the branch lengths of the ancestral trees. It does this by keeping a record of the waiting times, T_i^w , between coalescent events on the journey to find the common ancestor (schematically represented in Figure 3.1.). Let T_{entire} be the total time it takes to reach the common ancestor of an entire population of size N (also referred to as the height of the tree, h). It obeys the summation: $\sum_i T_i^w = T_{entire}$, where T_N^w is the time to the first merging

event, T_{N-1}^w is the time to the second event, T_{N-2}^w to the third, and so on. The waiting time, T_i^w , differs from the T_n calculation of common descent of n -individuals described above because, for WF type models, T_i^w is the time in history where exactly i lineages exist, whereas T_n is the time it takes for n samples to converge. After much mathematical manipulation (and much hair pulling), the expectation value of the T_{entire} (with normalized time) is shown to be

$$E[T_{entire}] = \sum_{i=2}^{2N-2} \tau_i \approx 2\left(1 - \frac{1}{N}\right),$$

with a variance of

$$Var[T_{entire}] = 8 \sum_{i=2}^N \frac{1}{i^2} - 4\left(1 - \frac{1}{N}\right)^2.$$

Thus, the time-scaled result indicates that as $N \rightarrow \infty$, $T_{entire} \rightarrow 2$, while if $N = 2$, $T_{entire} \rightarrow 1$, which indicates that when a population of sample size N is at the final

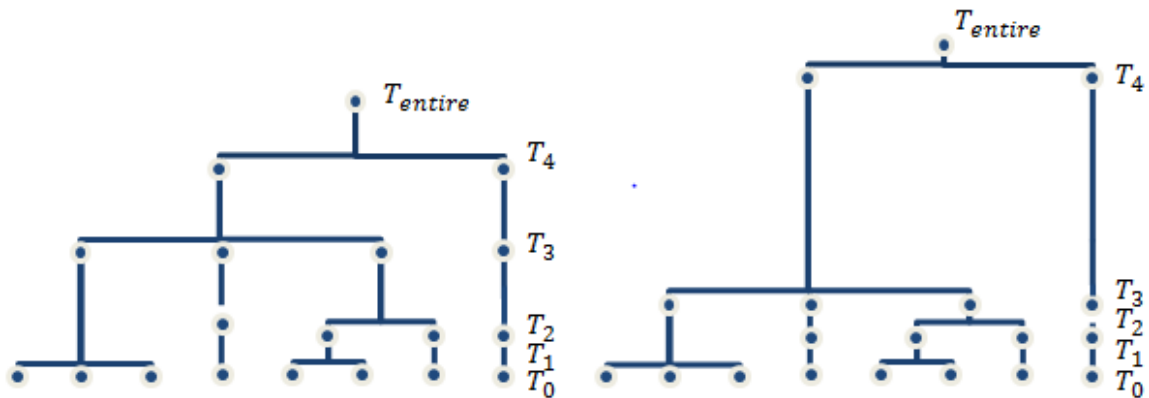


Figure 3.1. Example Tree Structures for the Calculation of T_{entire} – T_i 's are the waiting times between coalescent events (also known as branch lengths). This instance allows for multiple coalescent events in a single time step. The right tree is schematic of a deep branch would look like between T_3 and T_4 . T_{entire} is also known as the tree height, h .

time, T_2^w , the expected value at convergence is 1. This means that ‘... the expected time of which there are only two branches is greater than half the total expected tree height’ with a finite population size N (Nordborg, 2004 p. 608). Therefore, ‘trees tend to be dominated by deep branches when there are few ancestors left’ (Nordberg, 2004 p. 608).

3.1.2.3 Other coalescent models. There are many unexplored aspects of the dynamics and mathematics from coalescent theory, as much focus has gone into examining the behavior of WF type models that follow the three assumptions outlined above. Tavaré *et al.* (1997) were possibly the first to examine the coalescent without constant population size, finding that, in the limit of large population size, the rate for which a population of size n scales nonlinearly (instead of linearly as with the case of constant population size). The structured coalescent includes population substructures that cannot exchange genetic materials, but allows for some limiting migration between substructures. Thus, structured coalescent models can incorporate migration and allopatric speciation. Wright (1931) was the first to consider this case with what is known as the ‘island model’ (Wakeley, 2009). More recently, Rohde *et al.* (2004) calculated the T_{entire} of all living humans using a model that incorporated migration, as well as mating. Models have also been developed to incorporate recombination, horizontal gene transfer, and mutation into the coalescent process (Wakeley, 2009; Hein, 2010).

The effect of selection on simple WF type models has been studied (Brunet *et al.*, 2006, 2007), as well as selection models that have incorporated the structured coalescent (geological isolation with migration) with and without recombination (for instance, see Kaplan *et al.*, 1988, 1991; Hudson & Kaplan, 1988; Hey, 1991, Nordborg, 1997). Others, discussed below, have specifically investigated universal properties of the simple WF type models, such as neutral coalescent models versus ones that incorporate selection (Brunet & Derrida, 2011, 2012; Brunet *et al.*, 2006, 2008).

3.1.3 Universal Ratios. A tantalizing idea that has emerged maintains that a distinct ratios calculated from the n -coalescent (Brunet *et al.*, 2006, 2007, 2008; Brunet

& Derrida, 2011, 2012). At the mean field level, Brunet *et al.* (2008) state that two universality classes arise with respect to tree structures. These are Kingman's trees for neutral evolution, which are characterized by the ratios:

$$\langle T_3 \rangle / \langle T_2 \rangle = 4/3, \langle T_4 \rangle / \langle T_2 \rangle = 3/2, \langle T_2^2 \rangle / \langle T_2 \rangle^2 = 2, \text{ and } \langle T_3^2 \rangle / \langle T_2 \rangle^2 = 26/9,$$

and Bolthausen-Sznitman's trees for the case with selection:

$$\langle T_3 \rangle / \langle T_2 \rangle = 5/4, \langle T_4 \rangle / \langle T_2 \rangle = 25/18, \langle T_2^2 \rangle / \langle T_2 \rangle^2 = 2, \text{ and } \langle T_3^2 \rangle / \langle T_2 \rangle^2 = 11/4.$$

All neutral and selection models that follow a WF process should fall into one of these two classes. The model discussed here does not fall into one of these classes due to violation of assumption 1 (must have constant population size). Nevertheless, by calculating these ratios, I provide some of the first results of the ratios corresponding to the DP universality class. Scott (2014) showed that the universal ratios from the TMRCAs of the clusters formed with the asexual reproduction scheme varied with respect to the control parameter, μ , and that, as μ_c was approached, the ratios fell within the expected range for Kingman trees. Why this is the case is still unexplained since this model violates assumption 1.

3.2 THE MODEL

All simulations presented in this section were run identically to the simulations of Chapter Two, with some crucial exceptions. In order to always guarantee that all organisms in a given generation will have a common ancestor, a rooted tree is necessary, and thus the initial population size was started with either one (for bacterial fission) or two (for assortative and random mating) organisms. If simulations had started with an initial population of 300 individuals – as they did in Chapter Two – there would

be no guarantee that organisms would find common descent. Since this chapter is dedicated to analyzing the evolved tree structures at the organismal and cluster level, alleviating this possible caveat simply allowed for better analysis of the evolved tree structures.

Another important clarification is also needed about the system behavior. Regardless of the mating scheme, the overall behavior was identical to the results of Chapter Two. This means that, even though the populations only started with one or two individuals, phase transition behavior was still observed, and the values of δ_c were identical to those obtained previously for bacterial fission and assortative mating. The results for random mating were also equivalent to previous simulations. The main difference, for all reproduction schemes, was the time it took for the population to reach its steady state since populations started with few individuals.

The number of simulations analyzed for each reproduction type varied. (The number of simulations used in the distribution plots will be discussed below.) The reason is two-fold: random mating, which exhibits non-critical transition behavior, does not require an abundant amount of simulations to average over in order to obtain robust results, while assortative mating needed many simulations to be able to examine scale-free behavior at criticality.

In contrast to the phase transition curves shown in Chapter Two, this chapter only evaluated surviving simulations. Thus, even though many simulations were performed at δ_c , many of these went extinct and are therefore not included here. The motivation to evaluate only surviving runs was to, simply, examine genealogical behavior over a uniform number of surviving generations. All simulations for assortative mating and asexual fission were performed at $\mu = 0.30$, while random mating was performed at $\mu = 2.00$.

Finally, the number of generations run between the mating schemes and asexual reproduction was different. Assortative and random mating simulations were run for 2000 generations, while bacterial fission simulations were run for 10,000 generations.

The reason for this discrepancy in generations will be discussed after the results are presented.

3.2.1 Multi-level, Forward-in-Time Dynamics. The evolutionary dynamics of populations may be different depending on the genealogical level observed. The levels in question here are those of the organism and the species (clusters in this model). It is interesting to note that, while this dissertation focuses on phenotype evolution, and has thus characterized individuals by morphological traits, each phenotype has an underlying genotype, and evolution will proceed in an entirely different manner at the level of the gene. Factors such as ontogeny and replication rate of DNA changes the timescale for which phenomena can be observed. Further, in microbial evolution, factors such as horizontal gene transfer and recombination must be considered, and it has been proposed that the genealogy of microbes – instead of a tree-like structure – would look more like an evolving web or network (Madison, 1997; Rosenberg & Nordborg, 2002; Swithers, *et al.*, 2009). But for now, and sake of sanity, two levels of evolution will be focused on: the individual defined by phenotype and the cluster defined by mating behavior.

At the organismal level, populations evolved via the RD dynamics described in Chapter Two, which proceeded as follows. At each generation, each individual produced two offspring, regardless of the reproduction scheme, and then the organisms were exposed to various death processes... and the cycle was repeated. Therefore, each organism's lineage, at each generational step, could propagate forward with zero, one, or two branches. How the offspring dispersed was the key difference between the reproduction schemes. Offspring organisms choose local mates with the assortative mating scheme, so offspring dispersed near their parents; when organisms chose mates at random, the offspring dispersal was no longer constrained to be near the parent organisms. Dispersion was also local for the bacterial fission scheme since the reproductive area around each parent was defined by μ , and thus only a local fission reproduction area was allotted for each organism. Figure 3.2a schematically represents individual level reproduction. The forward-in-time dynamics at the cluster level is solely

dependent on ‘who mates with whom’, thus the forward propagation of a cluster’s lineage depended on the organisms mating behavior. In any given generation, a cluster could branch into new clusters, or merge with other clusters, or it could simultaneously branch into new clusters and merge with another cluster. This is illustrated in the simple schematic shown in Figure 3.2b.

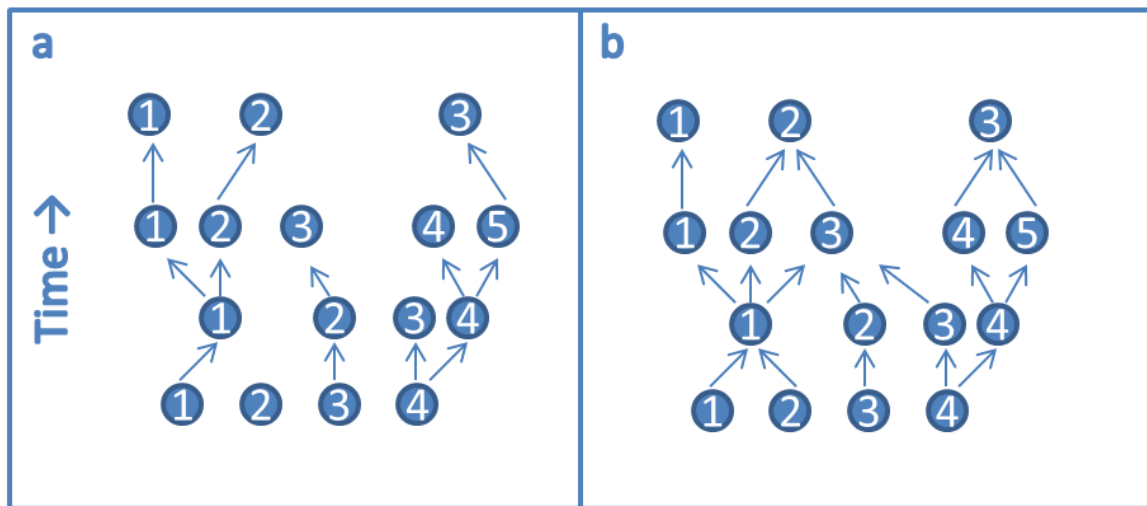


Figure 3.2. Schematic Representations of Forward-in-time Dynamics. Subplot (a) shows individual level RD dynamics where lineages can propagate forward with zero, one, or two offspring. No lineages can merge in this case. For subpanel (b), consider each number as representative of a cluster that contains many organisms within it. Clusters can fragment into a variable number of clusters, or they can merge with other clusters.

3.2.2 Analytic Methods. The next subsections outline the different backward-in-time dynamics depending on the level of biological organization analyzed, as well as the backward-in-time analysis that was utilized.

3.2.2.1 Multi-level, backward-in-time dynamics. At the organismal level, tracing a lineage backwards in time is different depending on the reproduction scheme. This is because for both assortative and random mating there are two parents for each individual to trace, while for bacterial fission there is only one. This means that each

asexual organism will independently, backwardly trace to one parent until it finds a common ancestor with another organism, while each sexually reproducing organism will branch backwards to two parents until there is a common parent between two organisms. Further, sexually reproducing parents can mate with more than one organism in each generation; therefore a common parent may be shared by more than two offspring. At most, only two offspring can coalesce in one generation for the case of asexual fission.

Tracing clusters backwards will be similar to the forward-in-time process described above. Clusters may merge together, indicating a coalescent process, but they may also branch or fragment. Depending on the forward-in-time reproductive behavior of the organisms, these numbers of mergers and backwards branching events will also vary within each generation.

3.2.2.2 Times to most recent common ancestor. For each mating scheme, the times to the most recent common ancestor of n individuals (denoted T_n^i) were calculated with $n = 2, 3$ or 4 . Similarly, the times were calculated for n -clusters (denoted T_n^c) with bacterial fission and assortative mating. Random mating only had one cluster throughout time (as discussed in Chapter Two), so there was no need for cluster-level calculations. T_n^i and T_n^c were calculated at and slightly above δ_c for the assortative mating and asexual fission schemes, with μ held at 0.30. T_n^i was shown at various values of δ , at $\mu = 2.00$, for the random mating scheme.

For assortative and random mating, organisms and clusters were traced backwards-in-time from the 2000th generation, while bacterial fission was traced back from 10,000th.

3.3 RESULTS

Phase transitions for $T_n^i = T_2^i, T_3^i,$ and T_4^i (from top to bottom), where $n = 2, 3,$ or 4 individuals that were traced to the most recent common ancestor (MRCA) are represented in Figure 3.3 for random (left column) and assortative (right column) mating. The averages are representative of 10 simulations. In each simulation, for each

δ , 1,000 randomly chosen samples were averaged from the present generation of $n = 2, 3,$ or 4 individuals who were tracked from the present generation (2000th) to the MRCA. The behaviors between the two mating schemes shown in Figure 3.3 are distinctly different. For assortative mating, as δ approaches δ_c , the times to reach the MRCA increase sharply, while for the random mating scheme, as δ increases, the times to reach the MRCA curve decreases smoothly. There is a high variance at the critical point for the assortative mating scheme, and the critical point, $\delta_c = 0.23$, is identical to the results presented in Chapter Two.

Figure 3.4 shows histograms of $T_2, T_3,$ and T_4 at $\delta = 0.15, 0.30,$ and 0.45 for the

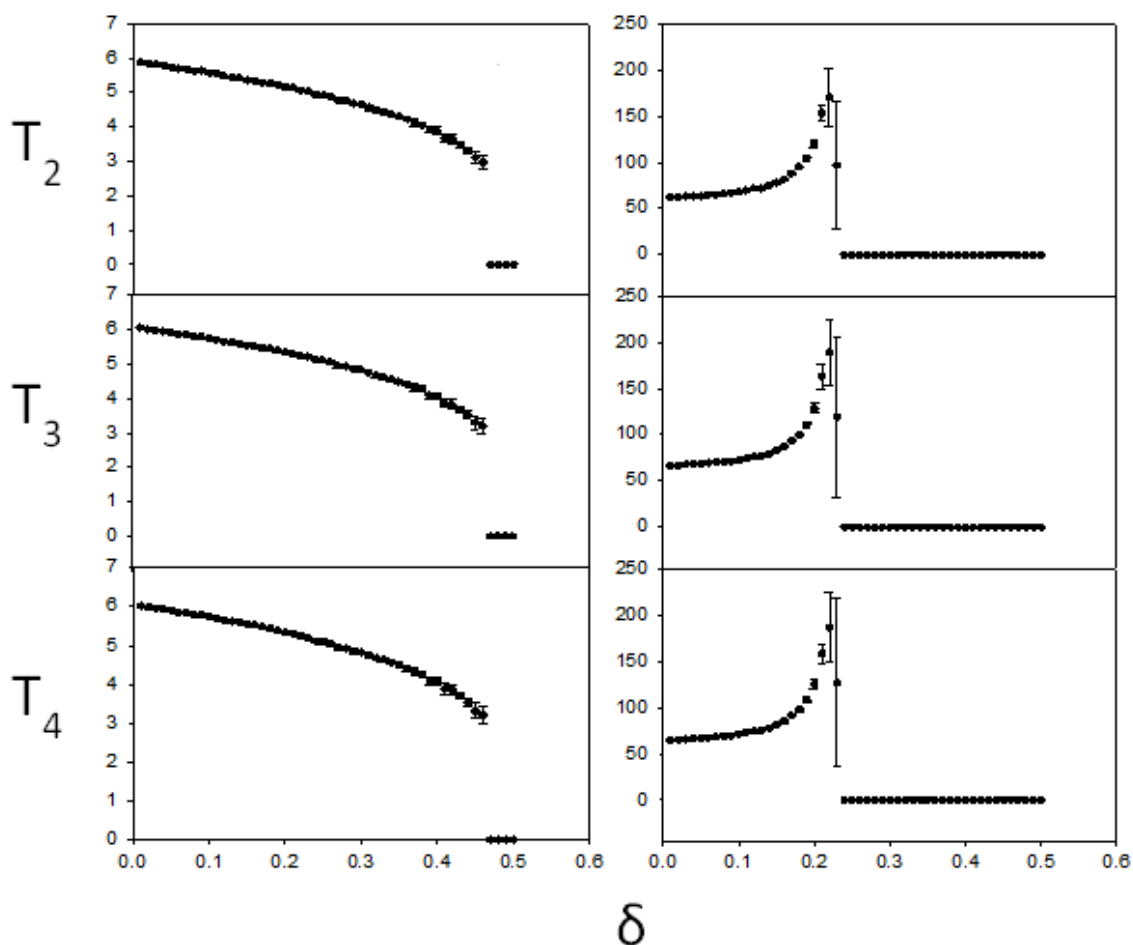


Figure 3.3. Phase Transition Curves of $T_2, T_3,$ and T_4 —The calculated times to most recent common ancestor of $n = 2, 3,$ and 4 individuals (denoted $T_2, T_3,$ and T_4) for the random (left column) and the assortative (right column) mating schemes.

random mating scheme. Each distribution plot shows all possible values of T_n over 200 simulations, and shows that populations reached a common ancestor within at most 7 generations. Distinctly different from the random mating scheme, Figure 3.5 shows the distribution of all possible combinations of $n = 2$ individuals (left column) and clusters (right column) for the assortative mating scheme. Shown here, from top to bottom, are histograms at the critical point ($\delta_c = 0.23$) and slightly beyond ($\delta = 0.22, \delta = 0.21$). At criticality, the distribution follows power-law-like behavior; while beyond criticality, the distributions start to become more Gaussian-like. Depending on the value of δ , the number of simulations represented in Figure 3.5 varied: at δ_c , all possible combinations

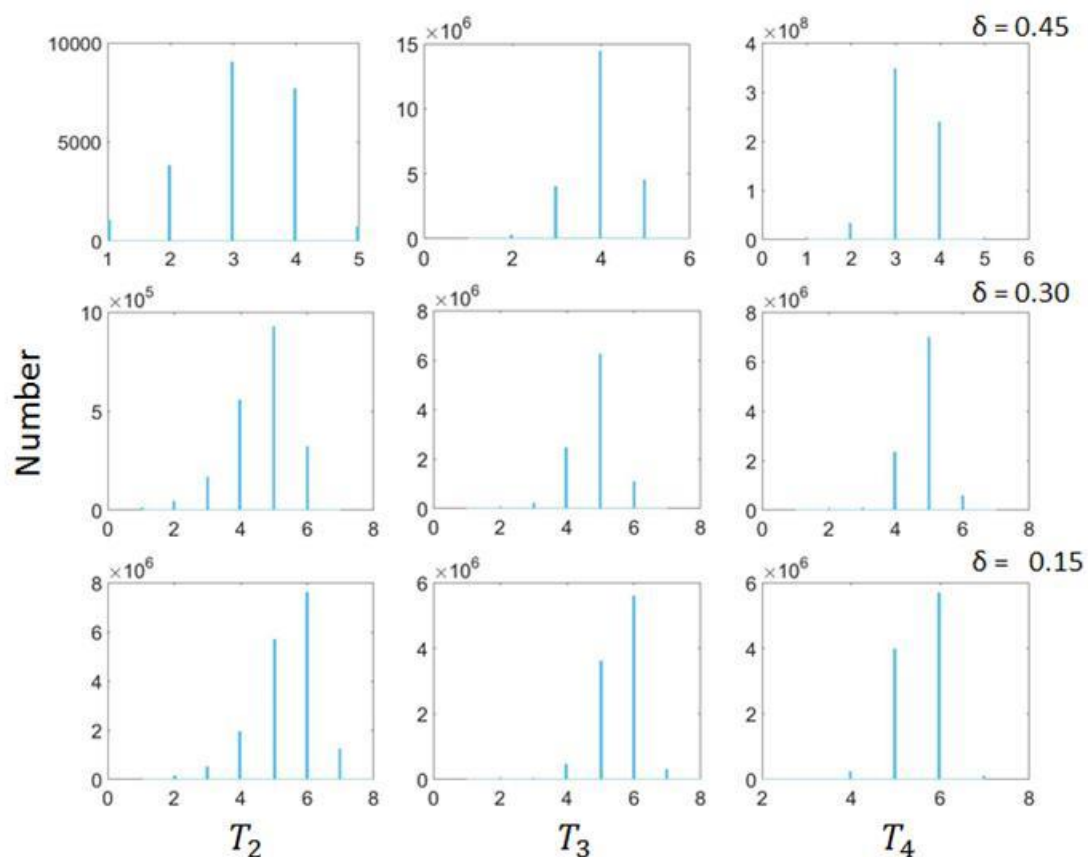


Figure 3.4. Histograms of T_2 , T_3 , and T_4 for random mating — The times to most recent common ancestor for all possible combinations of $n = 2, 3$, and 4 individuals (denoted T_2 , T_3 , and T_4) at $\delta = 0.45, 0.30, 0.15$ (top to bottom).

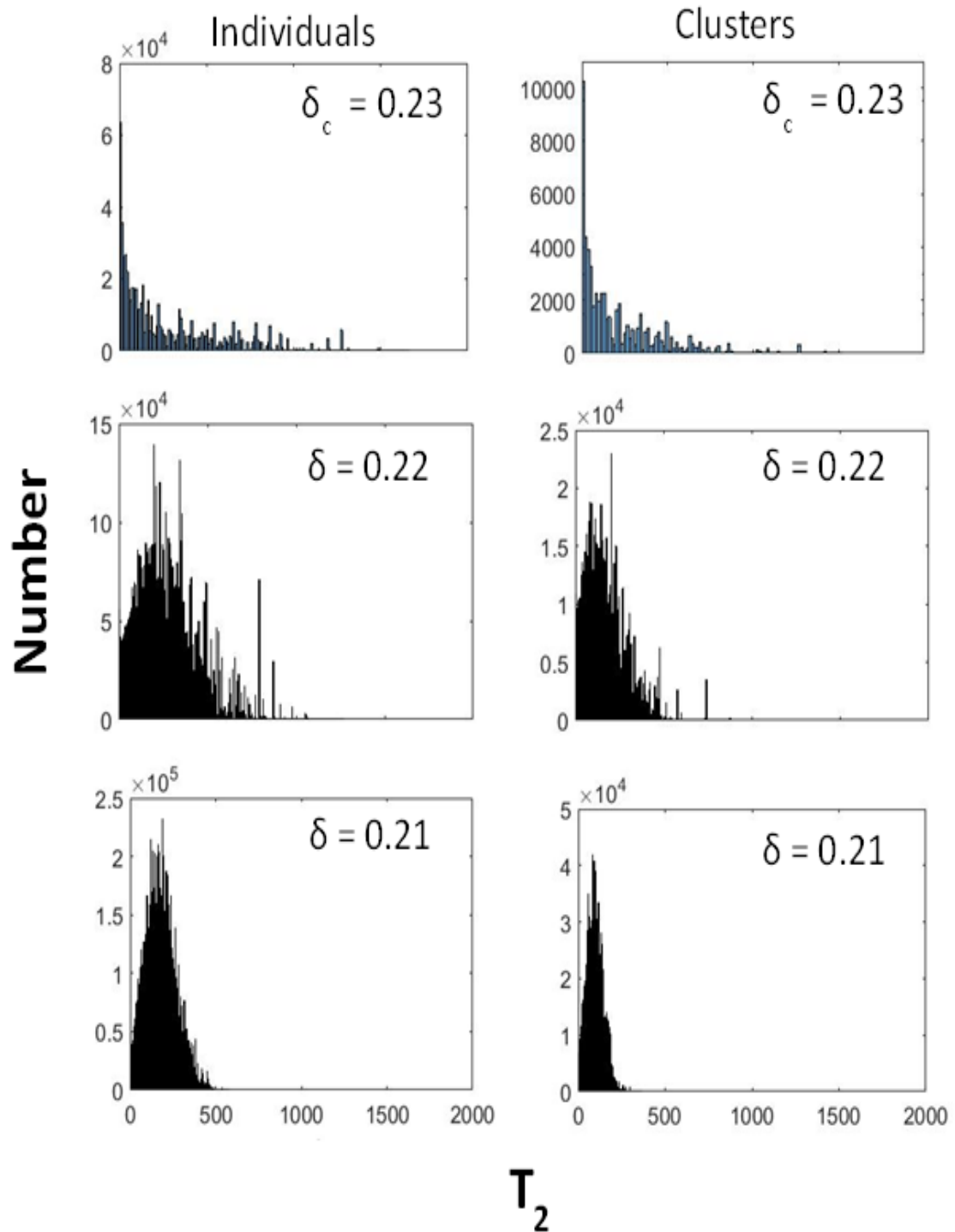


Figure 3.5. Individual and Cluster Level Histograms of T_2 : Assortative Mating — Left column shows results at the individual level, and the right column shows results at the cluster level. Histograms of the times to the most recent common ancestor of $n = 2$ individuals or clusters. Distributions show the transition from δ_c to slightly above criticality from top to bottom.

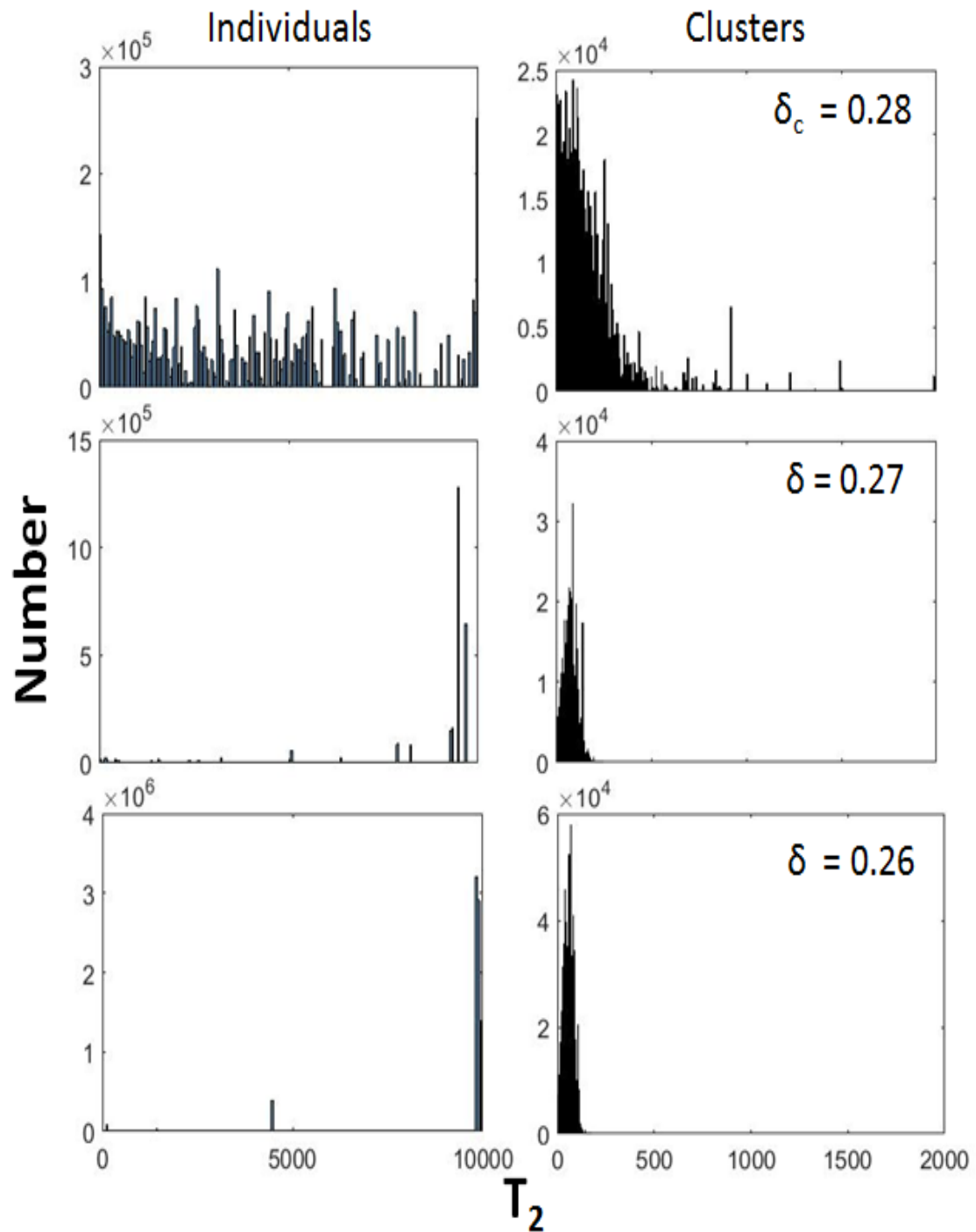


Figure 3.6. Individual and Cluster Level Histograms of T_2 : Asexual Fission — All possible combinations of two individuals (left column) or two clusters (right column) tracing to the MRCA starting from the present generation ($10,000^{\text{th}}$) for the asexual fission scheme. Top plots show distribution at the critical point ($\delta_c = 0.28$), with values just above criticality shown below ($\delta = 0.27$ in middle, $\delta = 0.26$ on bottom).

of two individuals were evaluated from 200 simulations; at $\delta = 0.22$, the combinations were taken over 50 simulations; at $\delta = 0.21$, 25 simulations were used.

Figure 3.6 shows T_2 for the asexual fission scheme for both the individual and cluster level at criticality ($\delta_c = 0.28$) and slightly above ($\delta = 0.27$, $\delta = 0.26$). When simulations were run for 2000 generations, populations almost always traced back to the 2000th generation (data not shown); therefore, the simulation time was increased to 10,000 generations. Figure 3.6 shows that, even with increasing the run time to 10,000 generations, the organisms will still trace back to the root of the tree, meaning that it often took the entire 10,000 generations to find the MRCA. There are 200 simulations represented at δ_c , but only 2 simulations are represented at $\delta = 0.27$ and $\delta = 0.26$ because the calculations became too computationally expensive. Interestingly, the cluster level distributions are similar to those shown in Figure 3.5. Distributions are shown with 145 simulations at δ_c , with 11 at $\delta = 0.27$, and 17 at $\delta = 0.26$.

Table 3.1 shows the calculated universal ratios for $n = 2, 3$, and 4 individuals at $\delta = 0.15, 0.30$, and 0.45 for the random mating scheme and at $\delta = 0.21, 0.22$, and 0.23 for

Table 3.1. Universal Ratios — Universal ratios for phylogenetic trees calculated from $n = 2, 3$, or 4 individuals from the random (top) and assortative (bottom) mating schemes at various δ . Averages were calculated over 200 simulations, where each of the 200 simulations were averaged over all possible combinations for $n = 2$ and 50,000 randomly chosen individuals for $n = 3$ and 4.

Random Mating	$\frac{\langle T_3 \rangle}{\langle T_2 \rangle}$	$\frac{\langle T_4 \rangle}{\langle T_2 \rangle}$	$\frac{\langle T_2^2 \rangle}{\langle T_2 \rangle^2}$	$\frac{\langle T_3^2 \rangle}{\langle T_2 \rangle^2}$
$\delta = 0.15$	1.0345±0.0007	1.0340±0.0010	1.0318±0.0006	1.0846±0.0016
$\delta = 0.30$	1.0392±0.0009	1.0381±0.0020	1.0424±0.0015	1.0994±0.002
$\delta = 0.45$	1.0694±0.1180	1.0749±0.1960	1.0800±0.0083	1.1842±0.0208
Assortative Mating				
$\delta = 0.21$	1.0626±0.2109	1.0467±0.2088	1.2673±0.0692	1.3122±0.5554
$\delta = 0.22$	1.0421±0.1078	1.0505±0.1215	1.3719±0.1147	1.3228±0.2834
$\delta = 0.23$	1.2428±0.1824	1.3736±0.2488	1.7004±0.3355	2.0888±0.6604
Kingman Trees				
	1.3333	1.5000	2	2.8888

the assortative mating scheme. The universal ratios change according to their location in parameter space for each mating scheme. The values reported for the random mating scheme are also generally lower than the reported values for the assortative mating scheme. The ratios for both the random mating scheme at $\delta = 0.45$ and the assortative mating scheme at $\delta = 0.23$ show a higher standard deviation; however, the standard deviation is more prominent for the assortative mating scheme (note that those are the transition points for both mating schemes, but only assortative mating has been shown to exhibit continuous phase transition behavior). For values of δ in the survival regime, the both the ratios and the standard deviation decrease in value.

In Figure 3.7, the T_{entire} that assortatively mated, starting from the 2000th generation, is shown for each simulation (left column) and as function of the population size (right column). The left column, moving from top to bottom, shows a distinct change in the distribution of the times to find common descent from the entire population of individuals among all 200 simulations. Note the significant change in scale moving out of the critical regime. The right column indicates that, at δ_c , there is no correlation between the population size and the T_{entire} , for at lower population sizes (~ 50 individuals) the number of generations varies from 25 to 1600 generations. However, as δ decreases into the survival regime (above criticality), there is a general trend towards a decrease in the time it takes to reach the common ancestor, and this trend is correlated with an increasing population size. Similarly, Figure 3.8 shows the T_{entire} of all clusters generated, from the assortative mating scheme, at the 2000th generation as a function of the cluster number (right column) and for each simulation (left column). Moving from δ_c to above (top to bottom), the behavior of the cluster level curves is similar to the behavior of individual level. Figures 3.9-3.11 are example tree structures (from the assortative mating scheme) that trace backwards to the MRCA of the entire population, moving from above criticality (Fig. 3.9) to at criticality (Fig. 3.11). The general trend of an increasing time to common descent as the population size decreases is qualitatively represented in these snapshots as $\delta \rightarrow \delta_c$. Further, the critical

tree structures exhibit deep branches that appear as punctuated bursts from the common ancestor.

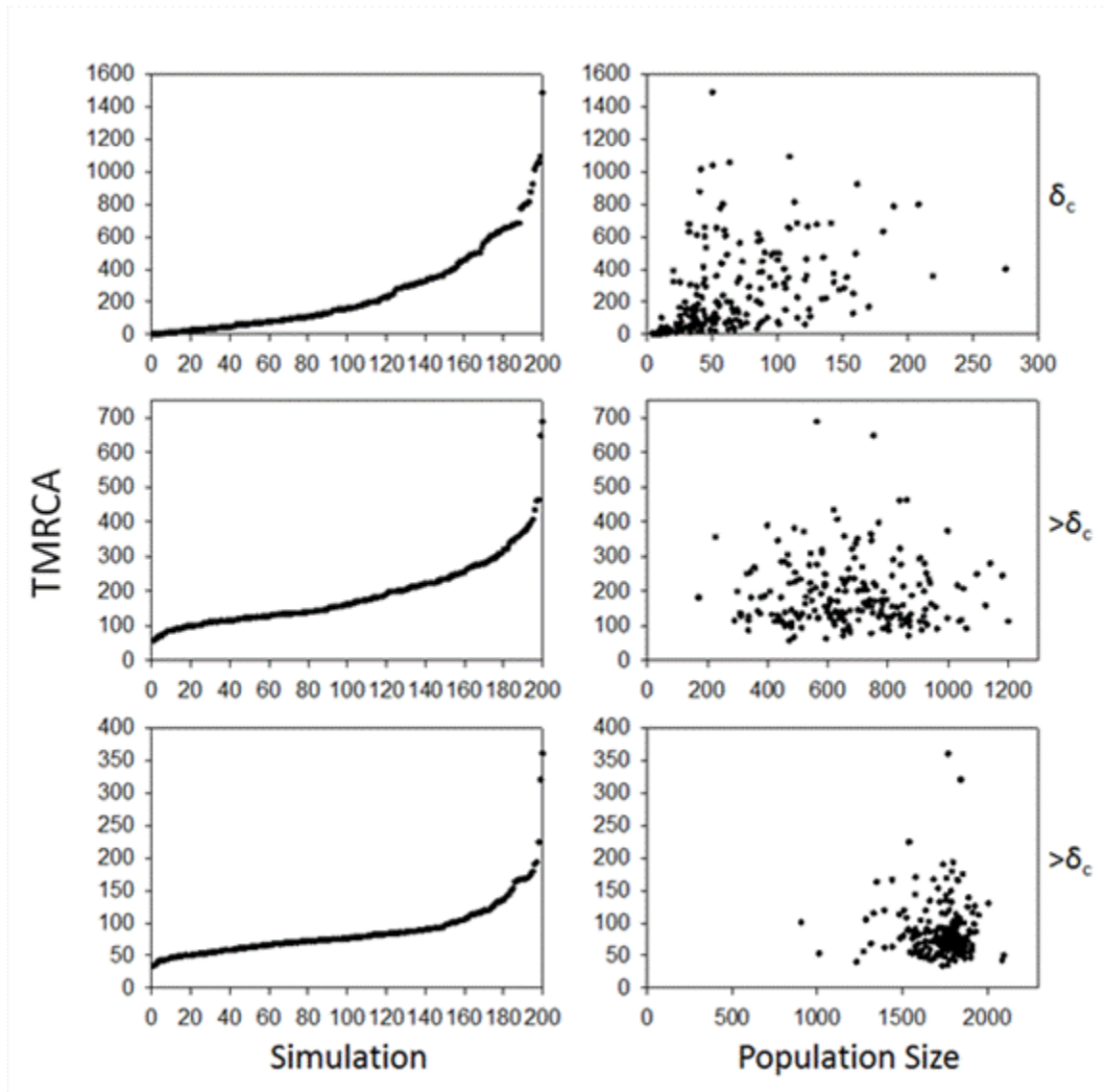


Figure 3.7. Individual Level: T_{entire} — The times to most common ancestor (TMRCA) traced from the entire population at generation 2000 from the assortative mating scheme. Left column indicates the TMRCA of each simulation (sorted in ascending order), while the right column indicates the TMRCA from each of the 200 simulations as a function of the population size at the 2000th generation. $\delta_c = 0.23$ (top); $\delta = 0.22$ (middle); $\delta = 0.21$ (bottom).

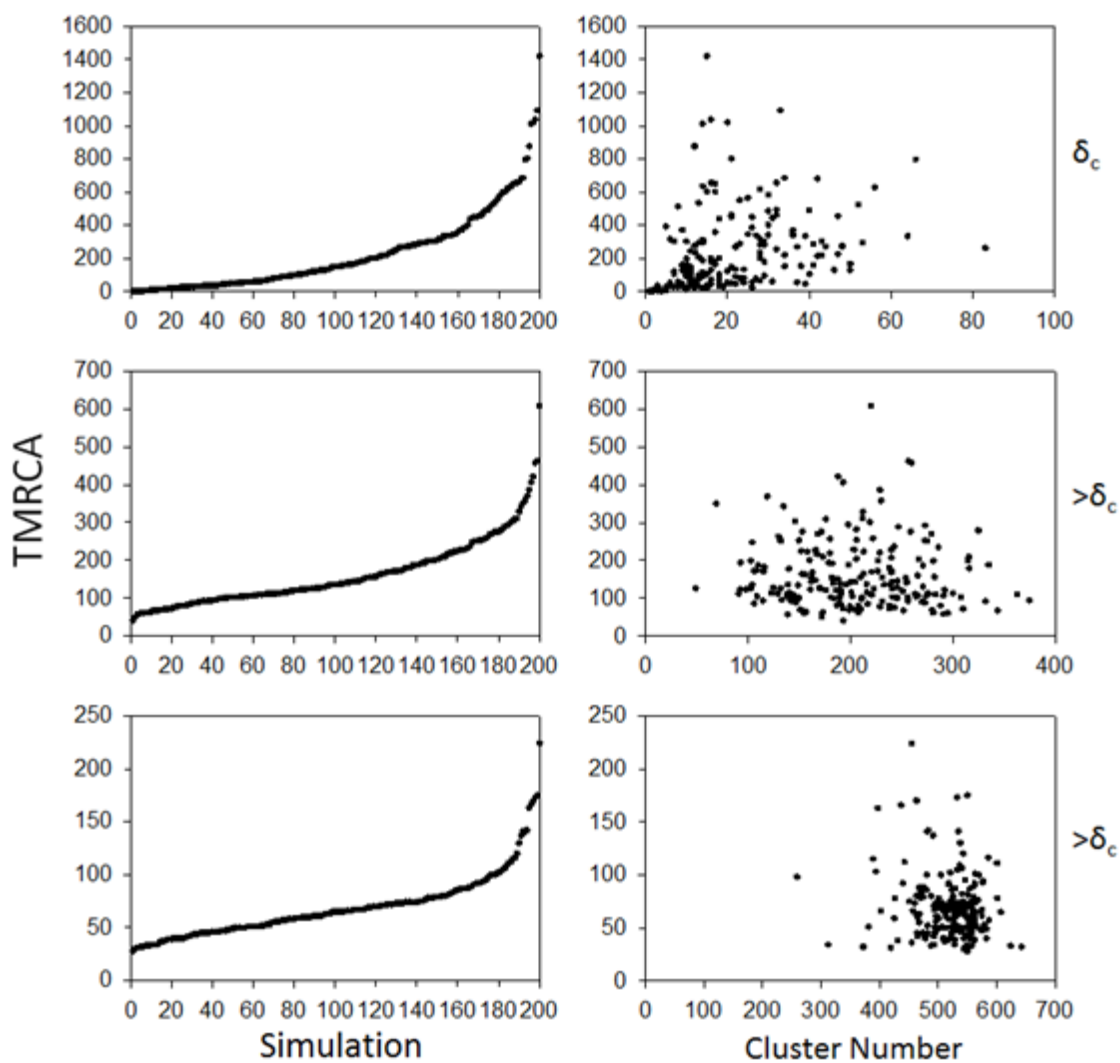


Figure 3.8. Cluster Level: T_{entire} — The times to most common ancestor (TMRCA) traced from all clusters at generation 2000 from the assortative mating scheme. Left column indicates the TMRCA of each simulation (sorted in ascending order), while the right column indicates the TMRCA from each of the 200 simulations as a function of the number of clusters at the 2000th generation. $\delta_c = 0.23$ (top); $\delta = 0.22$ (middle); $\delta = 0.21$ (bottom).

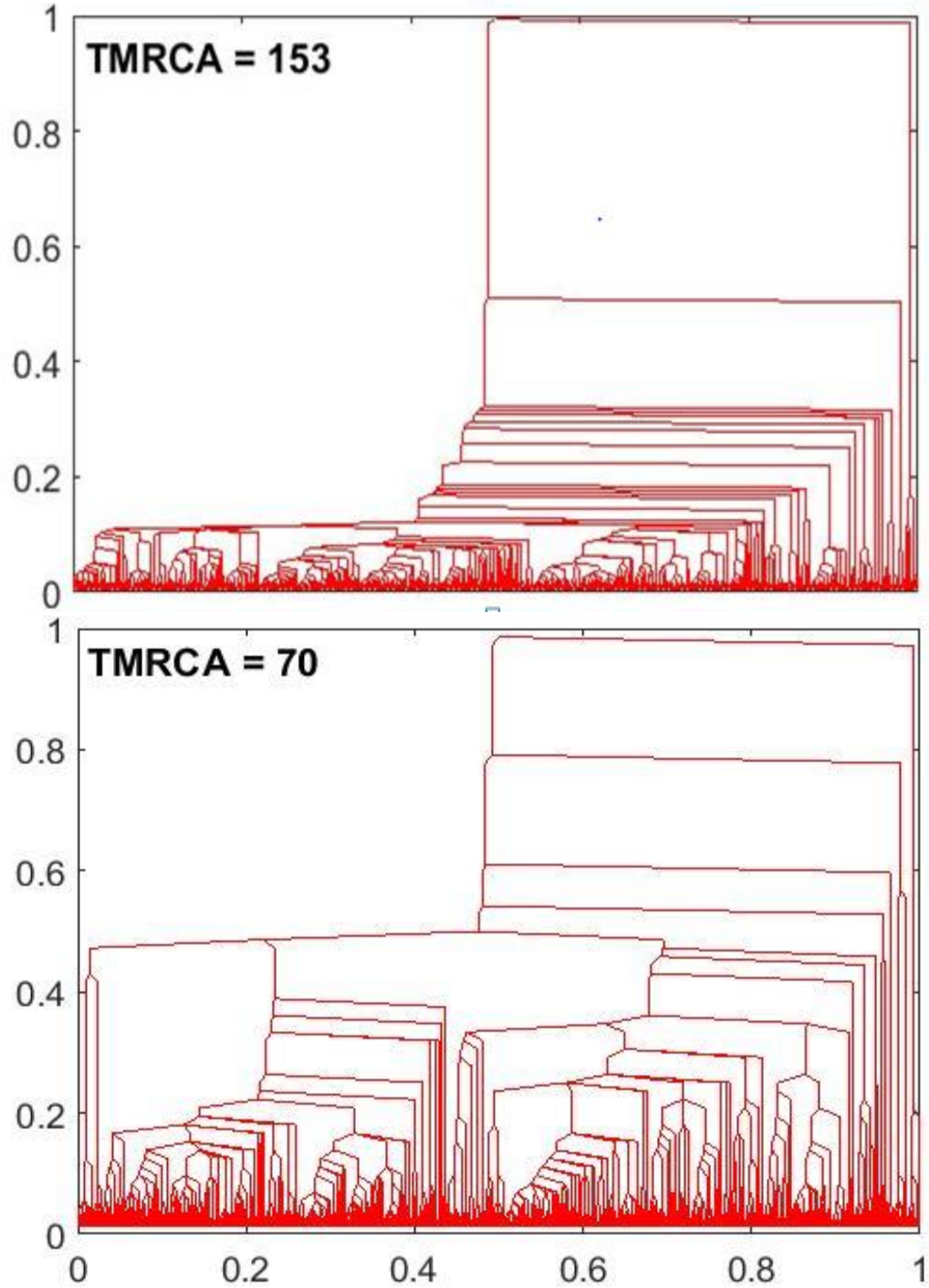


Figure 3.9. Example Phylogenies at $\delta = 0.21$ — Normalized tree structures of T_{entire} of the entire population (above criticality). TMRCA indicates the actual number of generations it took to find common descent.

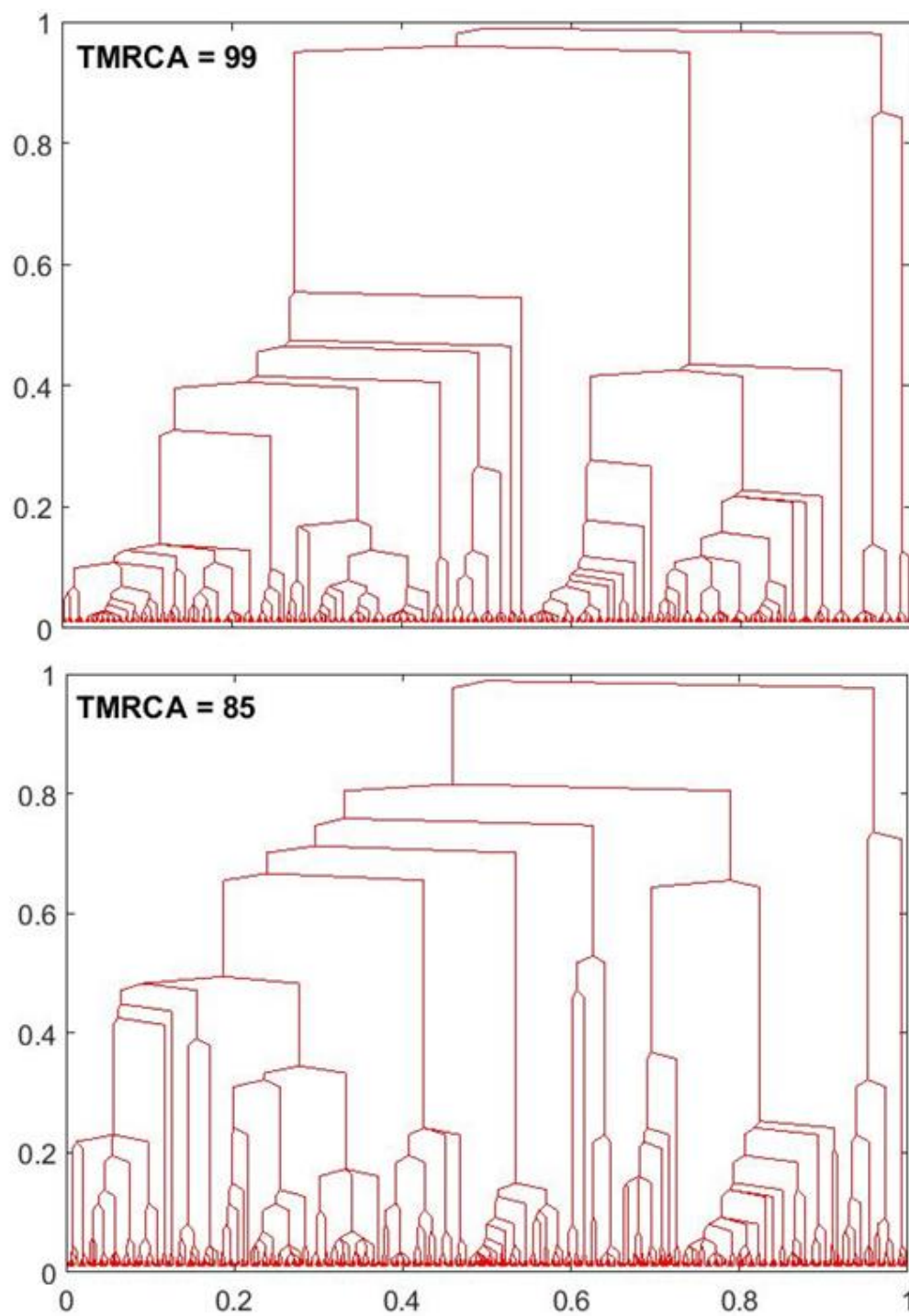


Figure 3.10. Example Phylogenies at $\delta = 0.22$ — Normalized tree structures of T_{entire} of the entire population (above criticality). TMRCA indicates the actual number of generations it took to find common descent.

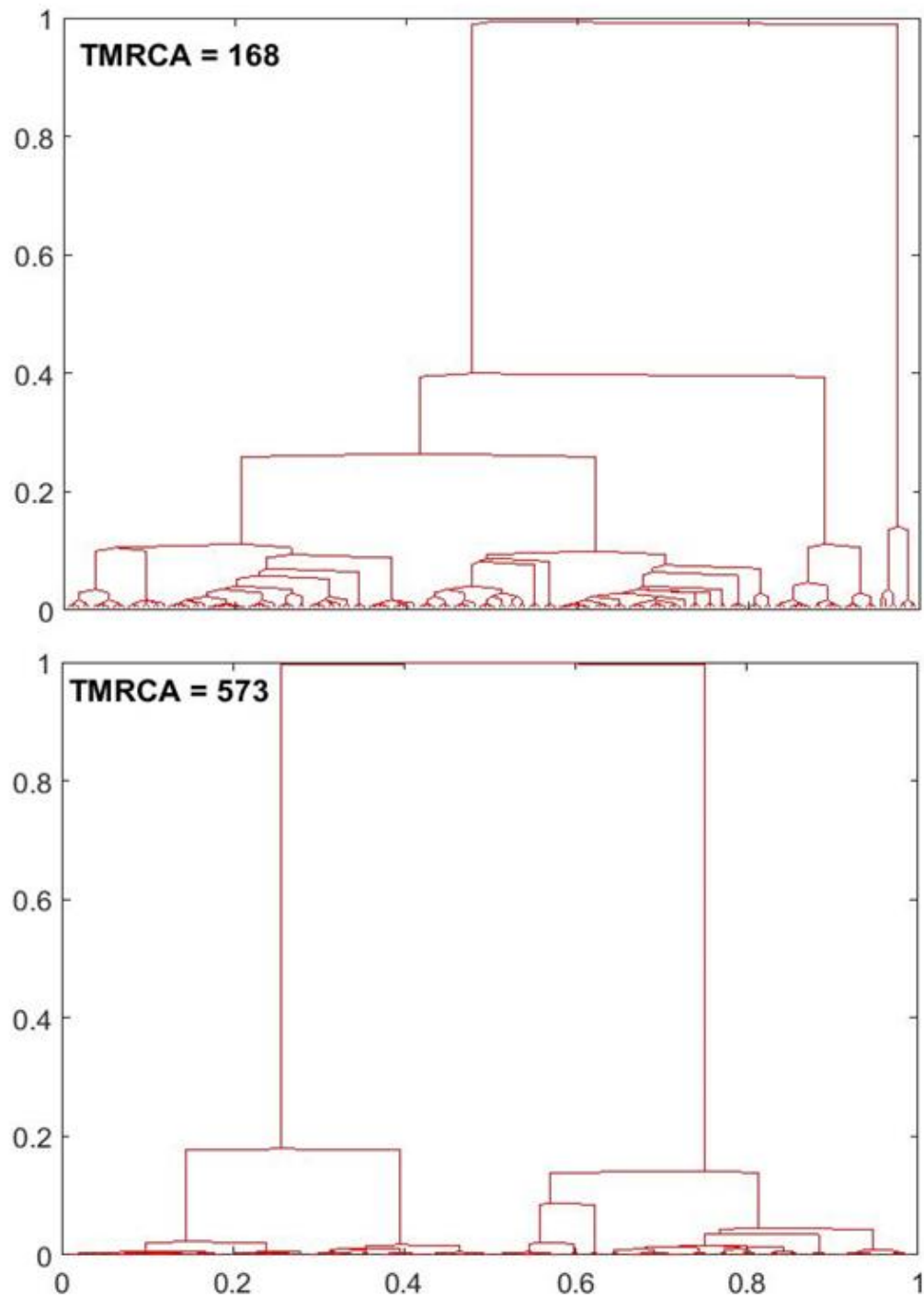


Figure 3.11. Example Phylogenies at $\delta_c = 0.23$ — Normalized tree structures of T_{entire} of the entire population (at criticality). TMRCA indicates the actual number of generations it took to find common descent.

3.4 DISCUSSION

Phase transitions abound! Figure 3.3 demonstrates that the TMRCA of $n = 2, 3,$ and 4 individuals also can act as an order parameter for the system. Note that the results shown in Figure 3.3 are averaged only over surviving simulations. Thus, the higher standard deviation observed for the assortative mating scheme indicates a higher variability within the surviving phylogenetic tree structures. It is clear that the assortative mating scheme (right column) reveals a continuous phase transition with an extremely high standard deviation at the critical point, but it is unknown whether this behavior will still exist as $n \rightarrow N$.

The random mating scheme (left panel), which exhibits noncritical transition behavior (shown in Fig. 2.7), shows a discontinuous jump at $\delta = 0.46$ (with a small standard deviation) in the times to find a common ancestor. The discontinuous jump of the order parameter for the random mating scheme could indicate a first order transition; however, it should be noted that if $T_n^{i'}$ s were calculated starting from a different generation, the critical point might change. For example, at $\delta = 0.45$, calculations were made starting at the 2000th generation. If calculations of T_n^i were made starting at the 3000th generation, then perhaps the populations would not have survived that long, and thus the transition would occur at a lower δ .

Asexual fission will, most likely, show similar phase transition behavior to the assortative mating scheme; however, calculating this became too computationally expensive due to the extra time that is needed to find a common ancestor. This does introduce a notable difference between the sexual and asexual reproduction schemes, namely that *mating significantly increases the rate at which common ancestors can be identified*. This is most likely due the fact that for asexual fission each offspring will only trace back to one parent, while each offspring from mating populations trace back to two parents; thus, significantly increasing the probability that two offspring find common descent with each time step taken. If there was a dual process for the RD dynamics of the DP universality class in the same sense that the Markov process for the forward-in-time WF diffusion is dual to the backwards-in-time Kingman's n -coalescent,

then perhaps it would be possible to form an idea of how much time is needed to find the MRCA for the bacterial populations (For example, the WF populations discussed in Section 3.1.2.1 derived the expectation value of the coalescent times of $n = 2$ organisms to be $(E[T_2] \approx N)$ to be on order of the population size).

Not only does *local mating* give rise to emergent clustering as discussed in Chapter Two, it also affects the evolved phylogenetic tree structure by *increasing the time it takes for a mating population to reach a common ancestor*. As discussed previously, when organisms mate, each offspring organism will have two parents; therefore, all offspring organisms will trace backwards in time to two parents. Consider this thought experiment: let two individuals start two independent seeds at the present generation to trace backwards in time. Each of the two seeds containing one individual is more likely to increase in size, geometrically, by 2^t for every t generations for the random mating scheme rather than the assortative scheme. If $t = 6$ (as can be the case for random mating), a seed for each individual could contain 64 individuals by the time $t = 6$; whereas, if $t = 50$ (a possible case for the assortative mating scheme), 1.1258999×10^{15} individuals would be in each seed, which is an unrealistic population size according to the maximum population sizes shown in Figure 2.6. Therefore, there must be some feature of the assortative mating scheme that is preventing each seed from getting extremely large and also preventing them from coalescing earlier. The answer lies in the local mating behavior of the assortative mating scheme because even though each offspring will have two parents to trace back in time, the lineages of parents that mate locally are more likely to merge within each seed rather than between seeds (this is schematically represented in Figure 3.12).

Figure 3.4 shows the distribution of T_2 , T_3 , and T_4 of all possible combinations $n = 2, 3$, and 4 individuals at $\delta = 0.15, 0.30$, and 0.45 for the random mating scheme. The histograms appear Gaussian-like, with the most recent common ancestor identified relatively rapidly (within 7 generations), as expected from the results shown in Figure 3.3. Figures 3.5 and 3.6 show the T_2 distribution of all possible combinations of $n = 2$ organisms (left columns) and clusters (right columns) at and slightly above δ_c .

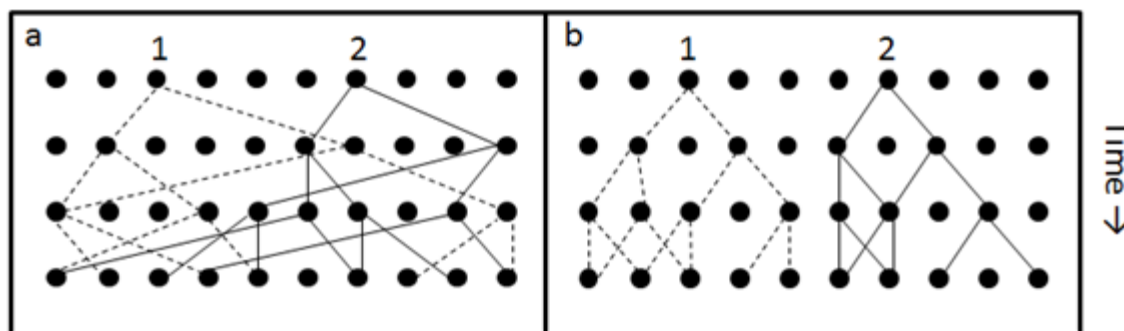


Figure 3.12 Schematic Representation of Tracing Two Seeds Forward in Time — Two individuals start two independent seeds from the present generation for the random (a) and the assortative (b) mating schemes. Dashed lines represent all ancestry from organism seed one, and solid lines represent all ancestry from organism seed two. Starting from the current generation ($t=1$), each organism traces to its parents, and then, at $t=2$, those parent organisms trace to their parents. At $t=3$, offspring organisms coalesce to the same parent, but all of the coalescing events are contained in the same initial seed. At $t=4$, organisms coalesce between seeds 1 and 2 in panel a (random mating), but continues to only coalesce within their seed in b (assortative mating).

Assortative mating (Fig. 3.5) shows power law-like behavior at δ_c for both the individual and cluster level; above δ_c the distributions become more Gaussian-like. Similarly, Figure 3.6 demonstrates, for the asexual reproduction scheme, that at the cluster level there is also power law-like behavior, but at the individual level this behavior has yet to be confirmed. Determining whether or not there could be power law behavior was too computationally expensive for the scope of this dissertation—with most organisms needing the entire 10,000 generations to trace their lineages back to a common ancestor.

The histograms generated from the assortative mating and the asexual reproduction schemes are markedly different than the random mating histograms, and they are yet another prime example of what is expected of continuous phase transition behavior. The fact that the random mating histograms did not exhibit power law-like behavior at $\delta = 0.45$, further lends evidence that the phase transition shown in Figure 3.3 (left panel) is, indeed, not a critical one.

Previously, similar power law behavior was shown with respect to the system lifetimes, abundance curves (Scott *et al.*, 2013), and the genealogical lifetimes (Scott, 2014) from the asexual model on a neutral landscape. The novelty shown here is the power law structure of the phylogenetic trees themselves at the critical point, and that there is wide divergence in behavior across mating schemes. Furthermore, while clustering behavior has been shown to be an emergent property of the evolving DP system, the resulting species trees also show power law-like behavior at criticality, which may have implications for multi-level selection theory.

Kingman showed that the average time to most recent common ancestor of the entire population scaled with the population size N . In fact, linear scaling with respect to T_{entire} of many different types of WF and Moran models has been shown to occur (Wakeley, 2009), while nonlinear scaling has been demonstrated with the relaxation of the constant population size assumption (Tavaré *et al.*, 1997). The result shown in Figure 3.7 (left column) is consistent with the results presented by Tavaré *et al.*, in that there is indeed nonlinear scaling with regard to the TMRCA of the entire population. While the curves exhibit slight qualitative differences depending on the value of δ , utilizing the nonlinear regression tool from SigmaPlot software, the three curves best fit a cubic function ($R^2 \sim 0.97$ at $\delta = 0.23$, $R^2 \sim 0.93$ at $\delta = 0.21, 0.22$).

Figures 3.9-3.11 are examples of phylogenetic tree structures above and at criticality (top to bottom, respectively). By qualitative inspection, the branch lengths become deeper and the TMRCA of the entire population increases as $\delta \rightarrow \delta_c$. It was mentioned in Section 3.1.2.1 that for WF type models, ‘the dependence of deep branches becomes increasingly apparent as n increases’ and only a few ancestors are left (Nordborg, 2004 p. 608). (Note that in this quote, Nordborg’s n is referring to the population size N .) The result presented here is counter to that statement because above the critical point the branches are shallow, yet the population sizes are inherently larger, whereas, at the critical point, the population sizes are smaller, but have deeper branches. The distinguishing characteristic of this model is that population sizes are not held constant (as opposed to WF type models), and populations may go extinct.

Therefore, the deep branches may be dictated by the critical behavior of the DP phase transition, and further the tree structures exhibit *punctuated bursts* from the common ancestor.

The universal ratios shown in Table 3.1 are novel, in that they differ from the universal ratios expected for neutral Kingman trees. This result is not surprising because the population size fluctuates, thus this model broke one of the key assumptions required of systems with ratios associated with neutral Kingman trees. Further, the table indicates that the ratios change depending on the value of δ ; thus, in the critical regime the ratios display a high variance that wanes as the system moves further into the survival regime.

Finally, these results confirm that speciation can occur in this model. Recall that because of the forward-in-time clustering dynamics, where clusters could either merge or fragment, it was left up to speculation whether distinct species lineages were possible since distinct reproductively isolated groups should not be able to mate in a future generation. Figure 3.5 confirms that tracing all possible combinations of $n = 2$ cluster lineages (right column) leads to as similar distribution of all possible individual lineages (left column). Further, the calculations of T_{entire} (Fig. 3.7) for individual organisms and for the number of clusters (Fig. 3.8) showed nearly identical in behavior, with the only difference being that the cluster level took less time to find a common descent than the individual level. Because the cluster and individual scale identically, the qualitative appearance of the tree structures at the cluster level should also resemble those shown at individual level in Figure 3.9-3.11, therefore the phylogenetic tree structures should show distinct species lineages traced backwards in time. Future work will address the problem of demonstrating the existence of distinct species lineages.

4. THE SIMULATED 'REPLAYING OF LIFE'S TAPE' — THE STORY OF HISTORICAL CONTINGENCY AND MASS EXTINCTION

4.1 INTRODUCTION

4.1.1 Wait... You Mean the Earth is NOT ~10,000 Years Old? Contrary to the extreme, religious fundamentalist belief, the Earth is approximately four and half billion years old — with the first found evidence of life dating to ~3.5 billion years ago. The 10,000 year mark is approximately when humans began to develop agricultural techniques, which enabled our species to move away from a hunter/gatherer nomadic society to a more sedentary one. This ability to produce larger quantities of food propelled a burst in the human population, which has brought us to the astonishing numbers of ~7,265,000,000 people (according to the US Census Bureau's website <http://www.census.gov/popclock/>). However impressive and simultaneously destructive we have been at rapidly dominating the Earth, humans are still representative of a 'geological wink' when it comes to the totality of life on Earth.

Our rapid domination has not come without consequence. A new 'debate has shone a spotlight on the typically unnoticed process by which geologists carve up Earth's 4.5 billion years of history.' (Monastersky, 2015) This debate is the proposition of a new geological division called the Anthropocene Epoch that was coined by Paul Crutzen, 'a Dutch chemist who shared a Nobel Prize for discovering the effects of ozone-depleting compounds.' (Kolbert, 2014) 'More importantly, it was coined at a time of dawning realization that human activity was indeed changing the Earth on a scale comparable with some of the major events of the ancient past. Some of these changes are now seen as permanent, even on a geological time-scale.' (Crutzen *et al.*, 2010) 'Through mining activities alone, humans move more sediment than all the world's rivers combined. *Homo sapiens* ha[ve] also warmed the planet, raised sea levels, eroded the ozone layer and acidified the oceans.' (Monastersky, 2015) Humans have also dropped atomic bombs.

The unprecedented debate concerns when to define the beginning of the new epoch. Should it immediately follow the Holocene, impede into the Holocene boundary, or act as a finer-tooth division of the Holocene Epoch by deeming it an age of the Holocene rather than a separate epoch? (Geological divisions are discussed in detail below.) Proponents argue strongly that it be defined as an epoch.

Procedures developed during the late 1960s by the International Commission on Stratigraphy require that the lower boundary of each stratigraphic unit is defined by a Global Stratotype Section and Point (a GSSP or 'golden spike'). If this procedure was to be followed for the Anthropocene, possible markers include anthropogenic deposits and landforms, novel minerals, nondegradable plastic debris, subsurface changes, or bomb-test radioisotopes, with the latter having the advantage that they are a global signal. (Corlett, 2015)

Scientists are preparing to make the case before the International Commission in 2016 for the new division (Kolbert, 2014; Monastersky, 2015). Eerily and yet justified at the same time, if this division comes to fruition, *Homo sapiens* will be naming the current global extinction crisis, as it is in process, after themselves.

This Chapter is about extinction. In order to understand the current global crisis, and to motivate the computational studies of mass extinctions discussed below, various components of Earth's history must be understood. For this, I will outline the geological and fossil record of deep time. I will then discuss mass extinction in the context of the 'big five,' since the big five mass extinctions are identified by evidence found in the geological and fossil record. Lastly, I will revisit historical contingency.

4.1.1.1 The geological record. The geological record is an important component That is used by paleontologists and evolutionary biologists alike in study of life history, especially in deep time. 'Evolutionary changes since the origin of life have been accompanied by extensive changes in environmental conditions, some caused by purely physical and chemical processes and others by interactions of organisms with the atmosphere, oceans, and crustal materials.' (Erwin & Valentine, 2013 p. 3) Here, I will

outline some major geological features that are used in aid to evolutionary theory, and then, in the sections below, tie these features to important life history events as evidenced by the appearance and decimation of preserved life forms.

“The present is the key to the past” is a popular catch-phrase that originates from uniformitarian Charles Lyell in his work *Principles of Geology*. Uniformitarianism is a fundamental concept in most sciences, especially in physics, that is simply ‘the uncontroversial assumption that scientific laws are invariant in space and time.’ (Erwin & Valentine, 2013 p. 10) Lyell proposed a concept, called substantive uniformitarianism, which assumes ‘the rates and processes of geological change have been invariant through time.’ (p. 10) In contrast to the uniformitarian view, the majority of geologists today ‘recognize that the rates of geological process have varied considerably through the history of Earth and that many processes have operated in the past that may not be readily studied today’, yet some uniformitarian themes are still debated regarding ‘the nature of geochemical evidence, the processes involved in the construction of Ediacaran and Cambrian assemblages, and the processes of change in developmental evolution in early metazoans’. (Erwin & Valentine, 2013 p. 10) The uniformitarian perspective creates an ideological division. One view supports geological certainty and maintains that by studying the present we can understand the past, and therefore predict the future. The other view conveys a message of uncertainty; the world today is the result of billions of years of historically contingent evolutionary steps, and the past looked much different than the present, thus the present is *not* the key to the past. There is, of course, a pluralistic approach that attempts to incorporate aspects of both uniformitarian and nonuniformitarian views, depending on the study and question at hand. This leads to the question, what aspects of evolution can be predicted, if any? If much of life’s history was unpredictable, what does that say for our future? Can we control any aspect of our ultimate fate or the fate other species?

Regardless of the uniformitarian view, major divisions of geological history are marked by major climatic shifts (such as glaciations), tectonic plate movement and volcanic activity, and by the prevalence of organisms in certain regions. Thus, divisions

of geologic time are demarcated by global stratigraphic correlations among sedimentary rocks or the emergence or disappearance of preserved biota. (Erwin & Valentine, 2013) The largest unit of geological time, the eon, has four divisions — three of which belong to the Precambrian period. (Allison *et al.*, 2010) (Recall that the Cambrian division has traditionally been hallmarked as the beginning of multicellular life.) The Hadean⁹, Archean, and Proterozoic Eons represent most of Earth's history — some 4 billion years (Bys) of the 4.6 Bys since Earth's origin (Campbell, 2005) — while the current geological eon, the Phanerozoic Eon, represents approximately the last 550 Myr. There is no evidence of life during the Hadean Eon, which was originally named after the Greek God of the underworld, Hades, due to the theorized volatile, volcanic 'hell on Earth' that was proposed to exist at this time — though recent work argues against this metaphor due to new evidence of zircon crystals found in Australia which paint a picture of a rather placid earth, 'with both oceans and lands.' (Chang, 2008)

Eons are further divided into eras, except for the Hadean Eon, which stands alone. The Archean Eon is subdivided, in increasing order of time to the present, into the Eoarchean, Paleoarchean, Mesoarchean, and Neoarchean Eras, while the Proterozoic Eon contains the Paleoproterozoic, Mesoproterozoic, and Neoproterozoic Eras. The eras of the Proterozoic Eon can also be divided into periods, but here, only the Cryogenian and Ediacaran Period of the mid to late Neoproterozoic Era are distinguished (Cohen *et al.*, 2013). The current geological eon, the Phanerozoic, contains the Paleozoic, Mesozoic, and Cenozoic Eras. Each era is divided into periods, each period is then divided into epochs, and each of these epochs can further be divided into ages (Campbell & Reece, 2005; Allison *et al.*, 2010). Since the Paleozoic Era represents the beginning of multi-cellular life with the celebrated Cambrian Explosion, the further fine-tooth geological divisions of this era into periods and ages are typically distinguished by the appearance and disappearance of various animal biota, while the geological

⁹ The Hadean Eon was not recognized in Campbell & Reece (2005), though it is not clear whether this is due a recent establishment of this geological period or if it was deemed not important for a Biology textbook since they document the earliest known fossils of prokaryotic cells to appear in the Archean Eon.

divisions of the epoch level and above, and the Precambrian times, are distinguished by global correlations of sedimentary materials.

The Cryogenian Period of the mid-Neoproterozoic Era, as its name implies, suffered two major climatic events: the Sturtian (717-665 Myr ago) and Marinoan (645-635 Myr ago) glaciations.

Geologists have long puzzled over these deposits because many glacial tillites ... are immediately overlain by extremely unusual rocks known as cap carbonates [which reflect warm conditions].... These layers of limestone or dolostone (a calcium magnesium carbonate) range from a few meters to more than 30 meters thick, are thinly laminated, can be found around entire basins, and may even globally correlate. Distinctive cap carbonates are associated with both the Sturtian and Marinoan-age glacial deposits. (Erwin & Valentine, 2013 p. 33-34)

There are three prevailing hypotheses for the causes of these glaciations, but the most notable according to Erwin and Valentine, is known as the Snowball Earth hypothesis. This hypothesis states that 'an extreme drawdown of carbon dioxide cooled Earth and plunged it into a positive ice-albedo feedback loop where continental ice sheets eventually extended equatorward of 35°, rapidly causing glaciers to spread through tropical regions.' As indicated by climate models, 'the latitude of 35° appears to be the climatic tipping point' for rapid cooling. (Erwin & Valentine, 2013 p. 36)

The ending of the Marinoan glaciation marked the beginning of the Ediacaran Period of the late Neoproterozoic Era. A short-lived, regional glacial cycle occurred during the Ediacaran, called the Gaskiers glaciation (583-584 Myr). There is no evidence of further glaciations extending into the Cambrian Period, though there is an abundant, globally correlated inorganic Carbon-13 isotope record that shows a dramatic upswing following the Gaskiers glaciation followed by a rapid downswing around 570 Myr ago—just prior to the Phanerozoic Era. The beginning of the Cambrian Period is followed by another upswing, followed by intermittent up and downswings throughout the rest of the Cambrian. Other inorganic isotopes sensitive to oxygen levels are also evaluated by

geochemists, such as sulfur, molybdenum, and iron (Erwin & Valentine, 2013). 'The data from these elements independently confirm, at least in broad outline, the oxygenation of the oceans during the Ediacaran.' (p. 47) Debates over hypotheses that seek to explain the extent to which animal biota played a role in increasing oxygenation are still a current, sometimes controversial, topic depending on which camp, if any, of uniformitarianism is describing the events. But, as if the odd coincidence of carbonates and glacial debris were not enough, 'cap carbonates, particularly those atop the Marinoan glacial deposits, include such puzzling features as abundant sea floor cements, microbial structures with long vertical tubes, and unusual isotopic compositions.' (Erwin & Valentine, 2013 p. 34) Others have proposed that the cap carbonates played a crucial role in laying the precursory groundwork for biomineralization that led towards the Cambrian Explosion. These carbonates, found on mountainous terrain in Scotland and the Grand Canyon (in the US), are known as the 'great unconformity' (Peters & Gaines, 2012).

As briefly touched upon above, radiometric dating is an important tool to glean insight into the environmental context of the past. Organic dating techniques, i.e., for dating fossils, are limited by the fact that living organisms only accumulate carbon while alive. The relative age of a fossil can be dated using the carbon-14 isotope, which has a half-life of 5,730 years and decays to nitrogen-14, and thus only allows dating of an organism aged 75,000 years or less — basically, a geological wink of an eye. Past this time fossils are often dated by their relative position between radioactive sediments, such as fossils sandwiched between layers of volcanic ash, or by the magnetic record (Campbell & Reece, 2005). The Earth's magnetic polarity has episodically changed over the past 600 million years, and has, therefore, also aided in the construction of global correlations among sedimentary rock (Erwin & Valentine, 2013 p. 27). 'The development of this high-resolution geological timescale and the correlation of geologic sections from every continent through biostratigraphy, chemostratigraphy, and magnetostratigraphy have been essential to any detailed understanding of rates of geological and evolutionary change.' (Erwin & Valentine, 2013 p. 28) Most importantly, it adds an

environmental context to the evolution of early life, and thus we can begin to examine 'how closely various evolutionary events correlate with changes in the physical environment that may have been causally related.' (p. 28)

The complete, up-to-date, International Chronostratigraphic Chart of geological divisions published by the International Commission on Stratigraphy can be found on the web at: http://www.stratigraphy.org/ICSchart/Cohen2013_Episodes.pdf.

4.1.1.2 The fossil record timeline. The earliest known microbial fossils date back 3.5 Bys in the Archean Eon. These cells were prokaryotic, meaning that there were no membrane-enclosed nuclei or organelles. The next evolutionary step, the development of eukaryotic cells (cells with a membrane-enclosed nucleus and organelles), occurred nearly 1.2 Bys later in the early Proterozoic Eon. The endosymbiotic theory hypothesizes two possible mechanisms for the development of the eukaryotic cell, both of which involve the acquisition of mitochondria, which was initially a stand-alone prokaryotic cell, by phagocytosis. The still unresolved controversy is a "which came first, the chicken or the egg", argument about whether the cell that engulfed the mitochondria already had a membrane-enclosed nucleus, or whether the membrane-enclosed nucleus was a developmental step that followed the engulfment of the mitochondrial cell (Martin & Mentel, 2010).

The next notable changes in the fossil record came during the mid-Neoproterozoic Era (or the late-Proterozoic Eon), ~1.4 billion years later, which was the beginning of the Cryogenian Period. At this point, some 600 Myr ago, diversified groups of algae and soft-bodied invertebrates appeared (Campbell, 2004). This raised the question as to whether or not 'the Snowball Earth and its aftereffects were related to metazoan diversification.' (Erwin & Valentine, 2013 p. 38)

All major eukaryotic clades, including a variety of multicellular algae and nonalgal unicellular eukaryotes, survived the Sturtian and Marinoan glaciations. Evidence that animals had evolved prior to the Marinoan glaciation is indicated by pre-Marinoan sponge body fossils ... and sponge

biomarkers that put boundary conditions on the extent of this glaciation.

(p. 38)

Therefore, there must have been sufficient refuge for life to carry on since there was a dampening of photosynthetic activity due to a nearly global covering of sea ice. Perhaps, an evolutionary bottleneck of cellular life occurred as a result.

As the glacial phase ended, surviving lineages would have faced an unforgiving environment, including rapidly increasing temperature and changes in ocean chemistry. One imagines that surviving multicellular lineages would be confined to small, isolated refugia where the environmental conditions would have been less harsh. When normal conditions returned, surviving lineages could diversify, as in many post-mass extinction recoveries.

Following the Sturtian glaciation, the fossil record of Death Valley reveals little loss of biodiversity, as opposed to the Marinoan event that resulted in a significant change in composition. 'Prior to the Marinoan glaciation, acritarchs exhibited low diversity and extremely long species durations. In the aftermath of the glaciation, an entirely new suite of acritarchs appeared, the Doushantuo-Pertataka microbiota...'. (Erwin & Valentine, 2013 p. 38) Acritarchs are microscopic, typically eukaryotic, organic fossils that belong to an unknown taxonomic group (Buick, 2010).

The end of Marinoan glaciation marks the end of the Cryogenian Period and the beginning of the Ediacaran Period. Remarkable discoveries have been made since the discovery of the Burgess Shale fauna in Canada. 'Today the Ediacaran fauna of soft-bodied impressions is known from diverse assemblages of fossils far beyond Newfoundland, Namibia, and Australia and now include more than thirty localities of five continents...' (Erwin & Valentin, 2013 p. 108). Of the major events of the Ediacaran, the post-glacial cap carbonate layer, known as the Great Unconformity discussed above (Peters & Gaines, 2012), set the stage for the evolution of biomineralization ~ 620 Myr ago. The timeline hereafter goes as follows: the first known animal embryo (600 Myr), followed by the Gaskiers glaciation (580 Myr), then the oldest evidence for macroscopic

biota (578 Myr), animal burrows (555 Myr), and the oldest calcified animals (549 Myr) (Knoll *et al.*, 2004). 'Although many display apparent bilateral symmetry, none show evidence of appendages or sensory features, and with two possible exceptions, none display signs of feeding or even digestive systems.' (Erwin & Valentine, p. 112) This is an important distinction because the soft-bodied organisms of the Burgess Shale do have specialized appendages, mechanisms for feeding, and digestive organs. 'Such a lack of anatomical characters has led to persistent controversy about what kinds of organisms these fossils represent.' (Erwin & Valentine, p. 112-113)

This brings us to about 542 Myr ago when there was a sudden increase in animal phyla, marking the beginning of the Phanerozoic Eon, the Paleozoic Era, and the celebrated Cambrian Period (Campbell & Reece, 2005; Allison *et al.*, 2010; Erwin & Valentine, 2013; Knoll *et al.*, 2004). The Cambrian Period marks the beginning of multicellular life (affectionately known as the Cambrian explosion), and nearly all animal phyla date back to this time (Gould, 1989); although, as Erwin and Valentine explain, the recent discoveries 'of soft-bodied fossils in a sequence of rocks older than the Cambrian, [during] the Ediacaran Period, showed that macroscopic life was not strictly limited to the Phanerozoic [Eon] as had been widely believed.' (Erwin & Valentine, p. 14) But '[u]nlike the Ediacaran fossils, whose internal architectures and phylogenetic relationships remain largely unknown, the Cambrian fossils are mostly stem groups of well-known Phanerozoic clades.' (p. 147) Recently, due to new globally correlated discoveries of Cambrian Fauna, the Cambrian Stratigraphic Subcommittee of the International Commission on Stratigraphy introduced a fourth division into the Cambrian Period — for which most previous work only recognized three epochal divisions: the early, mid, and late Cambrian (Erwin & Valentine, 2013).

Some pivotal points in early life history leading up to the beginning of metazoan fauna have been discussed. The early history has depended on millions of years of organismal evolution and has also been interrupted by environmental perturbations. From the endosymbiotic hypothesis to the widespread glaciations that bottlenecked microbial life, the theme of contingency is already present. The remaining divisions of

the fossil record up to the present time will now be discussed in the context of mass extinctions, since the record of animal life is riddled with many such occurrences. I leave this section with a few questions in mind. Why did it take billions of years for multi-cellular life to evolve? And, if all life were obliterated to the extent that only single-celled organisms survived, would life re-evolve to present picture? Are we, conscious, thinking, speaking, writing beings, really the result of historical accidents?

4.1.2 Mass Extinctions. As noted above, the first record of extinction bottlenecked microbial life during the Cryogenian Period, but also set the geological stage for cellular diversification during the Ediacaran Period. Many events during the Ediacaran led to the explosive diversification of early animals, yet much of this diversification had been lost before the start of the Paleozoic Era. Since many of the Ediacaran discoveries were relatively recent, progress towards hypotheses of how life evolved during this time is still underway (Erwin & Valentine, 2013). The Cambrian Period represents a time in evolution that is separated into four distinct stages based on the appearance of new organisms. This time period, interestingly, had a relatively low diversity of species but high morphological disparity among its constituents (Gould, 1989; Erwin & Valentine, 2013). Many of the disparate body plans, which are thought to represent distinct phyla, did not survive into the Ordovician Period. There is no indication of why one body plan was better fit than another, since the most geographically widespread morphologies (which is a typical indicator of robustness) did not survive, while other less common organisms did (Gould, 1989). Furthermore, the end-Cambrian extinction is considered to be one of the ‘lesser events with a high proportion of survivors, which qualify as minor mass extinctions but still mark notable perturbations of the biosphere.’ (Hallam, 2004 p. 31)

Animal evolution is riddled with stories of decimation and diversification. Some events are small and localized, and others occur on a global scale. ‘Determining whether a given extinction was catastrophic or merely gradual is not a straightforward matter...because of the limitations imposed by the stratigraphic record.’ (Hallam, 2004 p. 32) One such limitation, known as the ‘Signor-Lipps effect’, makes the simple

observation that neither the first nor the last organism will appear in the fossil record, thus making it hard to distinguish the exact first appearance or disappearance of a clade.

Those events that can, after rigorous analysis, be genuinely classed as catastrophic in a geological sense are unlikely to ever be pinned down in time more precisely than to a few tens of thousands of years, although exceptionally this limit may be reduced to a few thousand years. This conclusion is based on the study of particular examples in which ingenious juggling of inferred sedimentation rates in a given region is combined with the most refined radiometric dating that is possible. Extinction scenarios that involve events as geologically instantaneous as a few months to a few years are consequently not amenable to rigorous testing from the stratigraphic record. (Hallam, 2004 p. 38)

For instance, it was discovered that the 'great-appendaged' arthropod, *Anomalocaris*, previously thought to have been extinct since the middle Cambrian, had a living relative ~100 million years later in the lower Devonian (Kühl *et al.*, 2009). 'The overall consequence for the study of mass extinctions is that traditional taxonomic methods have probably overestimated the extent of the extinction', which further '... means that whereas the 'big five' mass extinctions still stand out significantly from background extinctions, some of the lesser events that have been claimed are open to question.' (Hallam, 2004 p. 38)

While the geological timing of extinction is open to errors of tens of thousands of years, there is consensus and considerable evidence that the 'big five' mass extinctions were real and catastrophic for large percentages of living organisms. Key extinction events and their speculated causes are listed in Table 4.1, and they appear in order from oldest to the present: the End-Ordovician (~86% species loss), the Late Devonian (~75% species loss), the End-Permian (~96% species loss), the End-Triassic (~80% species loss), and the End-Cretaceous events (~76% species loss) (Barnosky *et al.*, 2011). Furthermore, scientists are now speculating the 'big six' extinctions, by including the extinction event

that is currently underway due to human activities — and also, notably, the first species-driven extinction in life’s history (Kolbert, 2014; Barnosky *et al.*, 2011).

Definitions of what qualifies as a mass extinction have been vague in their expression, mostly due the multitude of challenges that paleontologists are faced with, such as the resolution of the geological timescale. ‘A mass extinction is any substantial increase in the amount of extinction (*i.e.*, lineage termination) suffered by more than one geographically wide-spread higher taxon during a relatively short interval of geologic time, resulting in an at least temporary decline in their standing diversity.’

Table 4.1 The ‘Big Five’ Mass Extinctions and Their Possible Causes. Reprinted by permission from Macmillan Publishers Ltd: [Nature] (Barnosky *et al.*), copyright (2011). My underline.

Event	Proposed causes
The Ordovician event ended ~443 Myr ago; within 3.3 to 1.9 Myr 57% of genera were lost, an estimated 86% of species.	Onset of alternating glacial and interglacial episodes; repeated marine transgressions and regressions. Uplift and weathering of the Appalachians affecting atmospheric and ocean chemistry. Sequestration of CO ₂ .
The Devonian event ended ~359 Myr ago; within 29 to 2 Myr 35% of genera were lost, an estimated 75% of species.	Global cooling (followed by global warming), possibly tied to the diversification of land plants, with associated weathering, <u>pedogenesis</u> , and the drawdown of global CO ₂ . Evidence for widespread deep-water anoxia and the spread of anoxic waters by <u>transgressions</u> . Timing and importance of bolide impacts still debated.

Table 4.1 The 'Big Five' Mass Extinctions and Their Possible Causes (cont.)

<p>The Permian event ended ~251 Myr ago; within 2.8 Myr to 160 Kyr 56% of genera were lost, an estimated 96% of species.</p>	<p>Siberian volcanism. Global warming. Spread of deep marine anoxic waters. Elevated H₂S and CO₂ concentrations in both marine and terrestrial realms. Ocean acidification. Evidence for a bolide impact still debated.</p>
<p>The Triassic event ended ~200 Myr ago; within 8.3 Myr to 600 Kyr 47% of genera were lost, an estimated 80% of species.</p>	<p>Activity in the Central Atlantic Magmatic Province (CAMP) thought to have elevated atmospheric CO₂ levels, which increased global temperatures and led to a calcification crisis in the world's oceans.</p>
<p>The Cretaceous event ended ~65 Myr ago; within 2.5 Myr to less than a year 40% of genera were lost, an estimated 76% of species.</p>	<p>A bolide impact in the Yucatán is thought to have led to a global cataclysm and caused rapid cooling. Preceding the impact, biota may have been declining owing to a variety of causes: Deccan volcanism contemporaneous with global warming; tectonic uplift altering biogeography and accelerating erosion, potentially contributing to ocean <u>eutrophication</u> and anoxic episodes. CO₂ spike just before extinction, drop during extinction.</p>
<p>Myr, million years. Kyr, thousand years.</p>	

(Sepkoski, 1986) A little more concise, but yet equally vague, definition was given by Hallam and Wignall (1997) who state that ‘a mass extinction is an extinction of a significant proportion of the world’s biota in a geologically insignificant period of time.’ While ‘geologically insignificant time period’ is still up for speculation, this definition does explicitly state one major criterion: that in order for an extinction event to be considered a ‘mass extinction’ it has to be global. In a study that examined the environmental effects from large-body, extraterrestrial impacts, Raup (1992) determined that in order to create a mass extinction that is global on scale, at least half of the world’s environment needed to be affected¹⁰. More recently, Barnosky *et al.* (2011) stated that ‘mass extinctions, in the conservative paleontological sense, is when extinction rates accelerate relative to origination such that over 75% of species disappear within a geologically short interval—typically less than 2 million years, in some cases much less.’ (p. 52)

There is, however, an important caveat to stating that ‘over 75% species’ disappeared in a mass extinction, namely that, at best, paleontologists can only estimate species losses since the resolution of the fossil record is at ‘higher order’ taxa (*e.g.* genera and above). An important measure, called *reverse rarefaction*, was developed by David Raup in 1979, which in turn, gave the estimate of the 96% species loss during the Permian extinction shown in Table 2. Reverse rarefaction can be best understood with the ‘Field of Bullets’ thought experiment outlined by Raup (1992b):

Imagine in a world in which each species has ten individual organisms, each genus ten species, each family ten genera, and so on up to a single phylum containing ten classes. The arithmetic works out to precisely one million individuals. Now suppose that individuals are killed at random, without reference to membership in species or higher groups. ... [Now

¹⁰ Interestingly, Raup was investigating what size a meteor would need to be to cause such a devastating environmental effect. His result coincided with Alvarez’s hypothesis for the late Cretaceous extinction, though it seemed as if he initially intended to try to falsify the hypothesis with a comment such as: ‘The arguments above are not compelling, but they do suggest that the hypothesis—that impact is the principle cause of 60% of all extinctions—is not as ridiculous as it first seemed.’ (Raup, 1992 p.85)

imagine] all individuals exist in a field of flying of flying bullets, and death or survival is solely a matter of chance. ... If 75 percent of the individuals ... are killed, what are the extinction percentages for the taxonomic groups? Starting from the top the kill rate for phyla must be zero because there is only one phylum and it losses three-quarters of its members. Each of the 10 classes has 100,000 individuals, so we can ask, what is the probability of losing all 100,000 of its members if the overall death is 75 percent? ... As we move down the taxonomic hierarchy, extinction of groups by chance alone becomes more and more likely. At the bottom, the probability that all ten individuals in any one species will be killed in a Field of Bullets is about one in twenty. (p. 71-72)

The take away message is that the extinction rate will increase down the taxonomic ladder (or decrease up the ladder). Thus, a 75% extinction of individuals should result in about a 5.6% extinction of species. The reverse rarefaction method, as it name implies, takes the reverse approach by examining the known genera or families that have went extinct and estimating the number of species lost based on this random death approach.

It should not be lost that the reverse rarefaction, while providing feasible rationale for the estimation of species loss, has made critical assumptions that are not realistic of what really determines species demise, for the actual culling of different species will be different for each group. Nevertheless, Raup's work does give a good estimate to the upper bound on species extinction, and the rationale that there will be more species lost than there are genera lost is sound. Further, since the number of genera extinct can be an observable quantity, it holds that the 'big five' stand out by the genera loss alone, even if the species loss is over-estimated.

Aside from determining what may have caused a mass extinction, determining which biotic characteristics could have led to a particular species's demise is also an issue. There are two leading discussions: one argument is for selectivity (used here in the sense of susceptibility to extinction by some cause), while the other argues for random chance. Taxonomic selectivity, the extinction of entire lines of genera, family, or

orders, has been shown to be a ‘real phenomena,’ where entire lines of descent have undergone extinction (as seen with the dinosaurs or trilobites). The explanations for why one taxa is more fit than another is often reduced to metrics of body-size, which in reality, is only making a correlation between a trait and extinction, and not giving a definitive cause. The truth is it is hard to distinguish between selectivity and chance (Raup, 1992). The selectionism perspective would try to correlate a trait, such as the mammal body size in the Pleistocene¹¹ or the massive reptiles in the Cretaceous extinction, to the extinction event itself (LaBarbera, 1986). There is little doubt that some sort-of selection of body-size has been prominent in some extinction events, but it cannot be overlooked that not all of the animals that went extinct during an event, such as the Cretaceous extinction, were large, nor could the bolide impact have been predicted. *‘The problem is that organisms have a virtually unlimited number of characteristics that could be important: anatomical, behavioral, physiological, geographic, ecological, and even genealogical.’* (Raup, 1992b p. 96) As Raup put it, ‘is it bad luck or bad genes?’ Most likely, there is some combination of both.

4.2 METHODS

Simulations for this chapter followed the methodology discussed in Chapter Two. Extinction experiments were tested on the assortative mating and asexual reproduction schemes — random mating will not be represented here. The parameter μ was held constant at 0.30.

4.2.1 Simulated Mass Extinction. Simulations were run at and above the critical point for the assortative mating (at $\delta_c = 0.23$, $\delta = 0.22$, and $\delta = 0.21$) and asexual reproduction (at $\delta_c = 0.28$, $\delta = 0.27$, and $\delta = 0.26$) schemes. For each value of δ and each reproduction scheme, 200 simulations were run for 2000 generations. At generation 2001, a random percentage of organisms were chosen to die, and then the simulation ran for another 2000 generations, giving a total run time of 4000

¹¹ The Pleistocene extinction affected the large mammoths, mastodons, giant ground sloths, and sabertooth cats. This event is correlated to last glacial cycle that ended ~12,000 thousand years ago, (which is also about the time humans started to spread into new geological regions. (Raup, 1992)

generations. This random percentage of individuals removed is called the mass death percentage, δ_m , and it was varied from 0.01 to 1.00 in increments of 0.01.

4.2.2 The Test for Contingency. To examine historically contingent behavior in mass extinctions further, 10 trials were conducted under identical conditions. For these experiments, the same 200 simulations were subjected to statistically identical extinction events ten times at generation 2001. For example, this means that for, trial 1, each of the 200 simulations at $\delta_c = 0.23$ underwent a mass extinction at some δ_m at the 2001th generation. Then, the same 200 simulations were then reloaded and subjected to an extinction event again at the 2001th generation at the same δ_m for trial 2. Trial 3 then loaded the same 200 simulations, subjected them to a mass extinction event again at generation 2001 at the same δ_m , and so on, until ten trials had been reached. (Note that subjecting a population to a mass extinction several times at the same δ_m does not mean that the same organisms were removed in each extinction event, only that the same percentages of randomly chosen individuals were removed.) These experiments were run at $\delta_m = 0.50, 0.55, 0.65, 0.75, 0.85, 0.95,$ and 0.99 . These results are presented after the results from the first 200 simulations discussed in Section 4.2.1 above.

4.3 RESULTS

At their respective critical points, Figure 4.1 represents the number of simulations that went extinct as a function of δ_m for the asexual (panel a) and the number of simulations (out of 200) that went extinct before the 4000th generation stayed around ~ 100 until a 50% mass death percentage was reached. At this point, the number of extinctions began to exponentially increase. The number of simulations that went extinct was considerably lower for the asexual scheme, with ~ 25 simulations dying up to a mass death of about 75%. After about a 75% mass death, the number of assortative mating (panel b) reproduction schemes. For the assortative mating scheme, simulations that went extinct increased rapidly. The average population size pre- and post-extinction as a function of δ_m is examined for the asexual (Figure 4.2a) and assortative mating (Figure 4.2b) reproduction schemes. The asexual reproduction

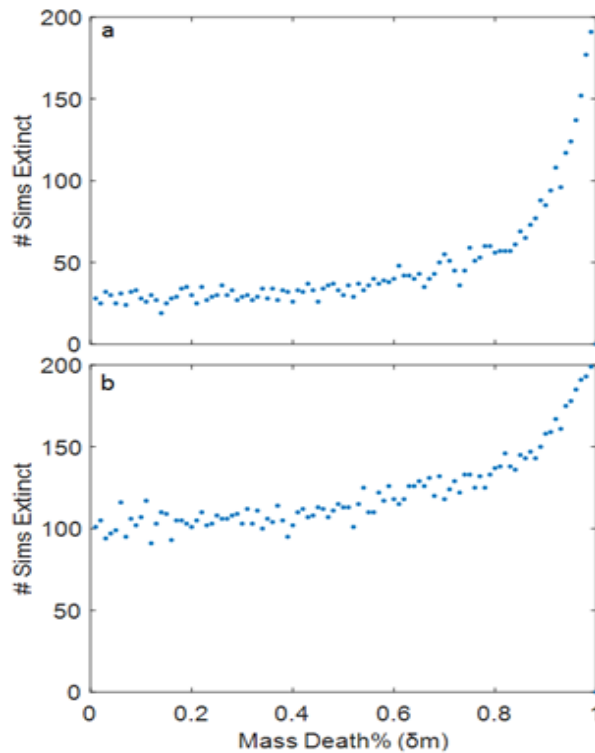


Figure 4.1. The Number of Simulated Extinctions: Assortative and Asexual — The number of simulations that went extinct (out of 200 total simulation) for the asexual fission (a) and assortative mating (b) schemes at the critical point as a function of δ_m .

scheme showed higher post-extinction population sizes, up to about a δ_m of 95%. In contrast, for the assortative mating scheme, the average population sizes pre- and post-extinction exhibit similar fluctuations until $\sim 50\%$ mass death had been imposed. At $\sim 50\%$ mass death the population sizes post-extinction did not recover to pre-extinction levels. The average population size was calculated over surviving simulations. Figure 4.3 shows the average population size as a function of time (in units of generations) at various δ_m above the critical point for the assortative mating scheme. Populations were averaged over 200 simulations at each generation (no simulations went extinct). Moving from the top left ($\delta_m = 0.50$) to the bottom right ($\delta_m = 0.95$), Figure 4.3 shows that the rate of population recovery decreases as δ_m increases, but *the populations always*

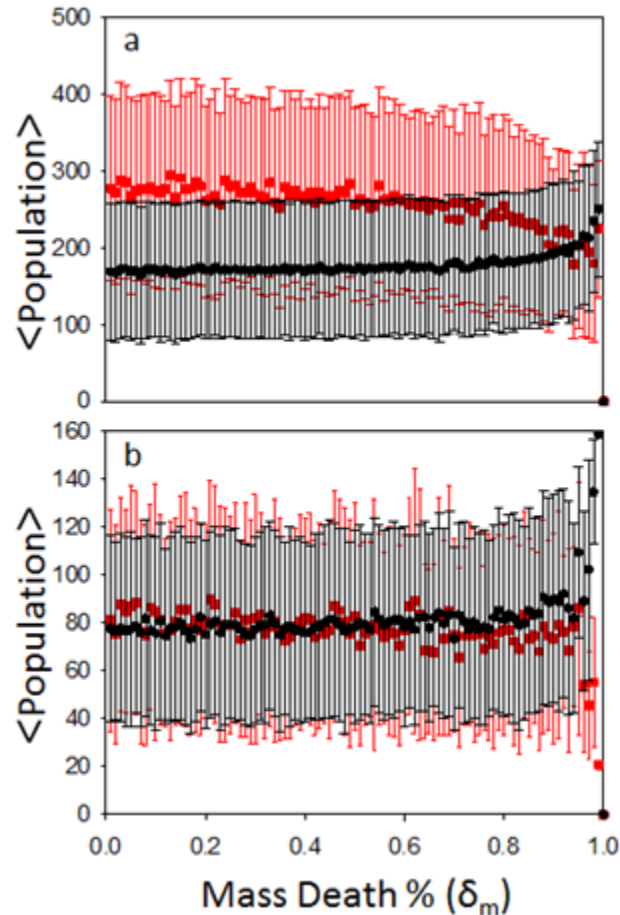


Figure 4.2 Average Population Size Pre- and Post- Extinction: Assortative and Asexual — Pre- (black circles) and post- (red squares) extinction as a function of δ_m for the asexual fission (a) and assortative mating (b) schemes at the critical point.

recover. The gray-scale vertical lines that surround the solid horizontal dots represent the standard deviation in population size (the fuzziness and vertical grayscale bars is an unfortunate side effect of the statistical software). Note that standard deviation in the population size significantly decreases post extinction. Figure 4.4 shows the behavior at the critical point, from the assortative mating scheme, of the average population size as a function of the generation for various δ_m . The population behavior becomes erratic at criticality, in contrast to above criticality, shown in Figure 4.3, with the error bars now showing large fluctuations of the population size. Furthermore, the populations do not recover to pre-extinction values following the simulated extinction. Populations were

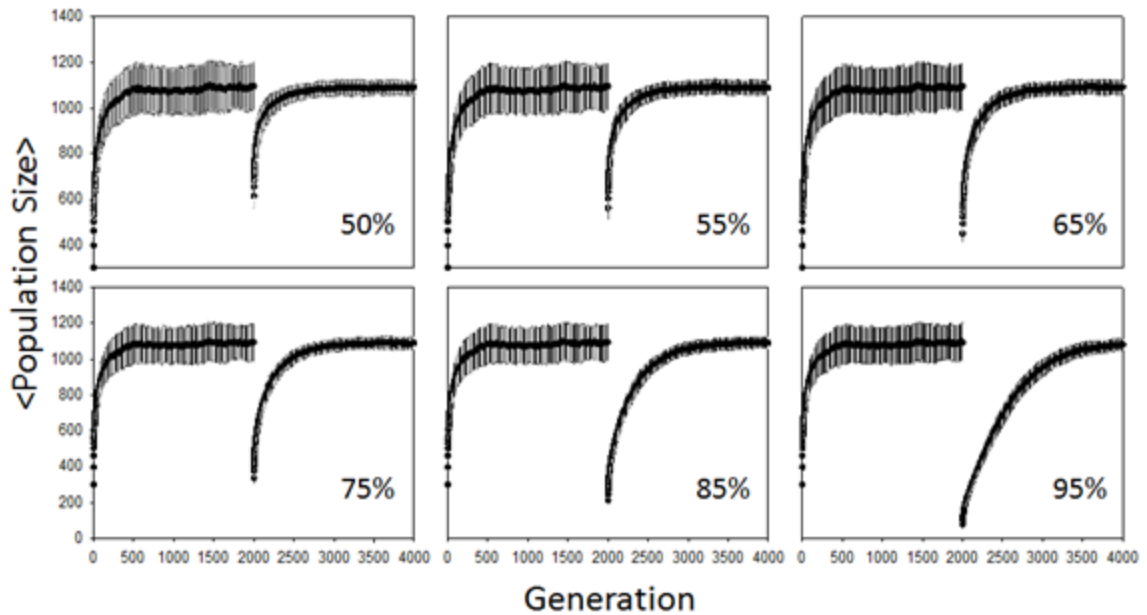


Figure 4.3. Average Population v. Generation at $\delta = 0.22$: Assortative — The average population versus generation at $\delta = 0.22$ (above critical point) for the assortative mating scheme, where at generation 2001 populations were subjected to mass extinction at $\delta_m = 0.50, 0.55, 0.65, 0.75, 0.85, 0.95$. The gray-scale vertical lines represent the standard deviation in population size.

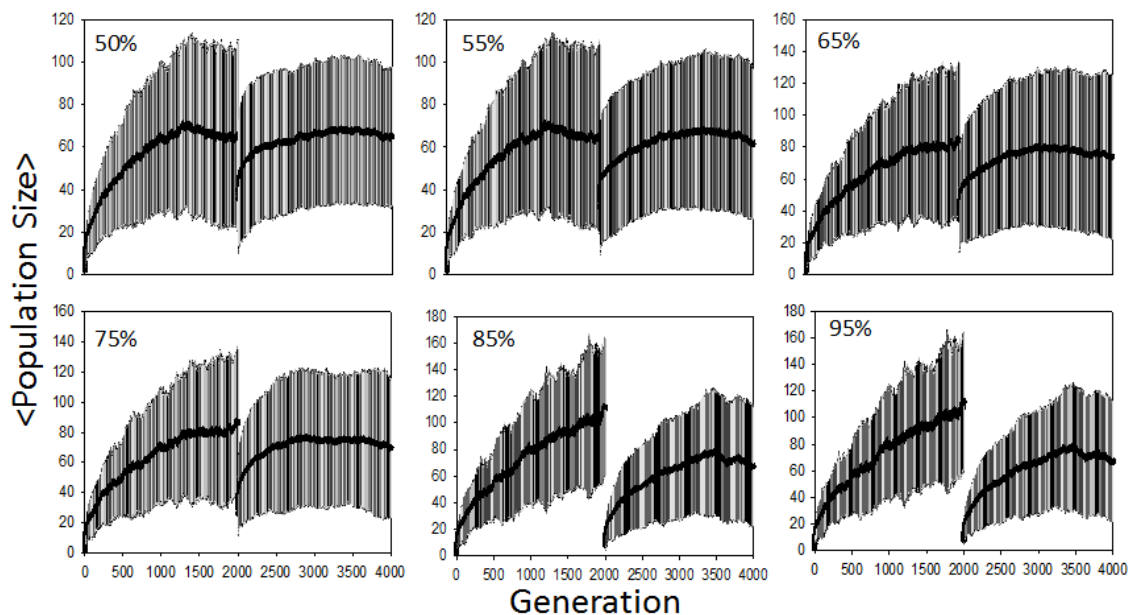


Figure 4.4. Average Population v. Generation at $\delta_c = 0.23$: Assortative — The average population versus generation at $\delta_c = 0.23$ (at critical point) for the assortative mating scheme, where at generation 2001 populations were subjected to mass extinction at $\delta_m = 0.50, 0.55, 0.65, 0.75, 0.85, 0.95$. The gray-scale vertical lines represent the standard deviation in population size.

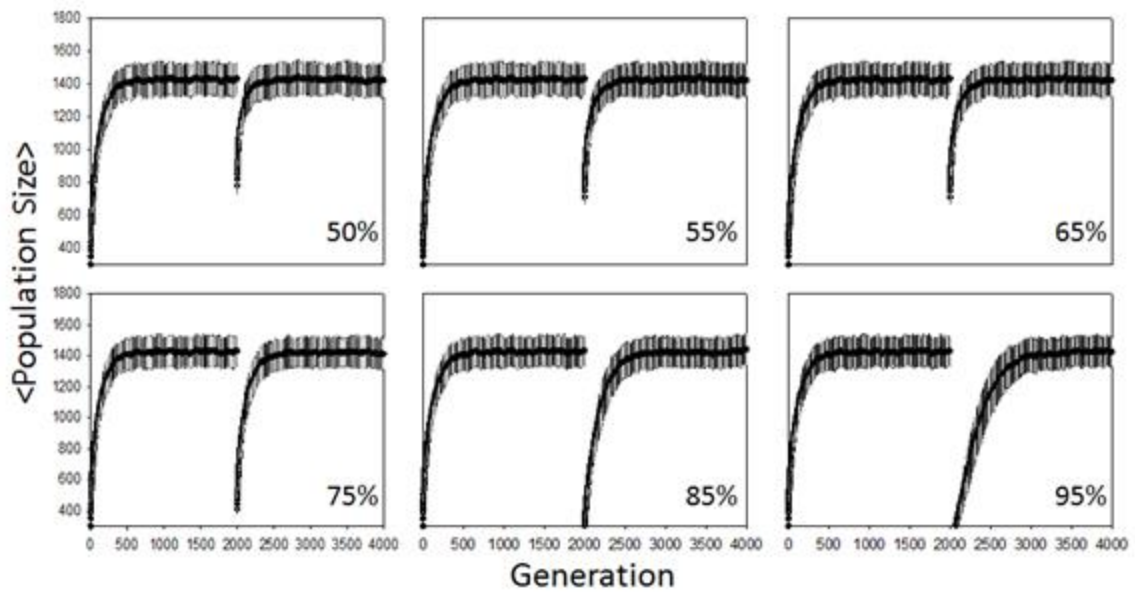


Figure 4.5. Average Population v. Generation at $\delta = 0.27$: Asexual — The average population size versus generation at $\delta = 0.27$ (above the critical point) for the asexual reproduction scheme, where at generation 2001 populations were subjected to mass extinction at $\delta_m = 0.50, 0.55, 0.65, 0.75, 0.85, 0.95$. The gray-scale vertical lines represent the standard deviation in population size.

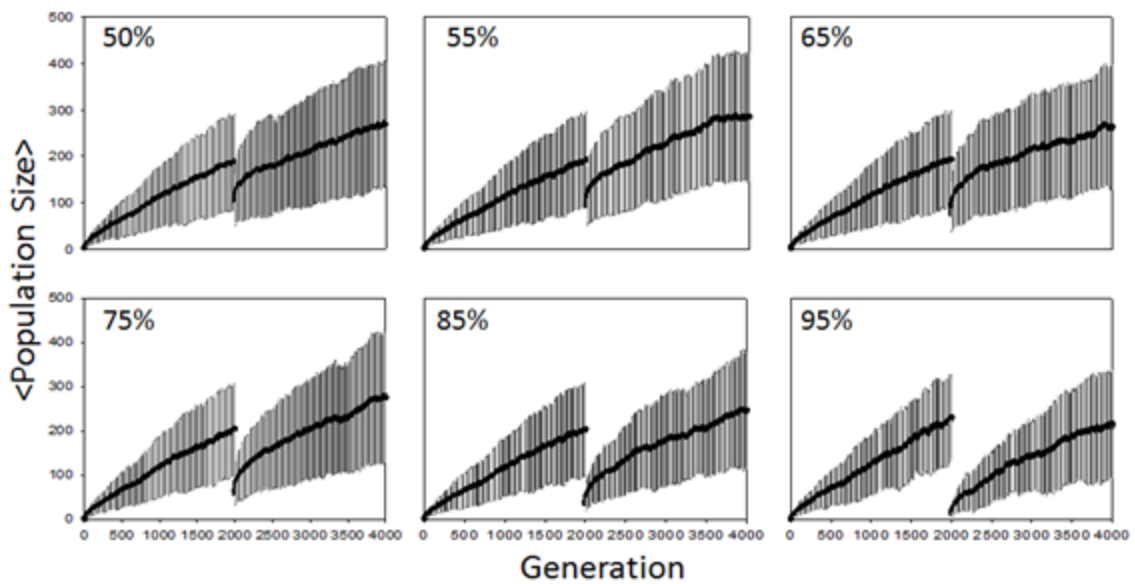


Figure 4.6. Average Population v. Generation at $\delta_c = 0.28$: Asexual — The average population versus generation at $\delta_c = 0.28$ (at critical point) for the asexual reproduction scheme, where at generation 2001 populations were subjected to mass extinction at $\delta_m = 0.50, 0.55, 0.65, 0.75, 0.85, 0.95$. The gray-scale vertical lines represent the standard deviation in population size.

averaged over the surviving simulations at each generation. Figure 4.5 and 4.6 show the population size from the asexual reproduction scheme as a function of the generation above and at the critical point, respectively. In contrast to Figure 4.3, the standard deviation, in Figure 4.5, shows the population size for the asexual populations above criticality does not decrease significantly in the post-extinction regime. At criticality, in Figure 4.6, the populations are still growing, and have thus not reached its steady-state before the extinction event.

The average population size, over ten trials at $\delta_m = 0.50$, pre- and post-extinction, for each of the 200 simulations is represented in Figure 4.7a. Averages were calculated over surviving simulations. There is high variability in the population size for the pre- and post-extinction regimes, with some populations recovering, on average, to populations sizes greater than the pre-extinction regime, and others recovering to levels below the pre-extinction regime. Figure 4.7 (b) and (c) show example simulations, where (b) shows 10 trials of a simulation where the population recovers to a level below pre-extinction population size, and (c) shows 10 trials of a simulation that exceeds its pre-extinction population size after recovery. (Note that there are no error bars for the pre-extinction population sizes because the *same* data set was used for each of the 10 trials.) Figure 4.8 shows $\delta_m = 0.50$ slightly above the critical point ($\delta = 0.22$) for the assortative mating scheme. Panel (a) demonstrates that out of the ten trials, for each of the 200 simulations, all simulations succeeded in recovering following the mass extinction event, as opposed to Figure 4.7a, which shows that 23 simulations failed to recover in each of their ten trials. Figures 4.8b and c further reveal that, while populations recover to their initial size, the mean population size exhibits less fluctuation than before the extinction event. Results for $\delta_m = 0.95$ are shown in Figure 4.9 for the assortative mating scheme, at and above criticality. Panel 4.9a ($\delta_c = 0.23$) shows that many simulations fail to recover from extinction at the critical point, while just above criticality (Figure 4.9b), all simulations survive. Furthermore, Figure 4.9b shows that there is less fluctuation of the population size over ten trials for each of the 200 simulations above criticality; panel 4.9d reflects this point as well.

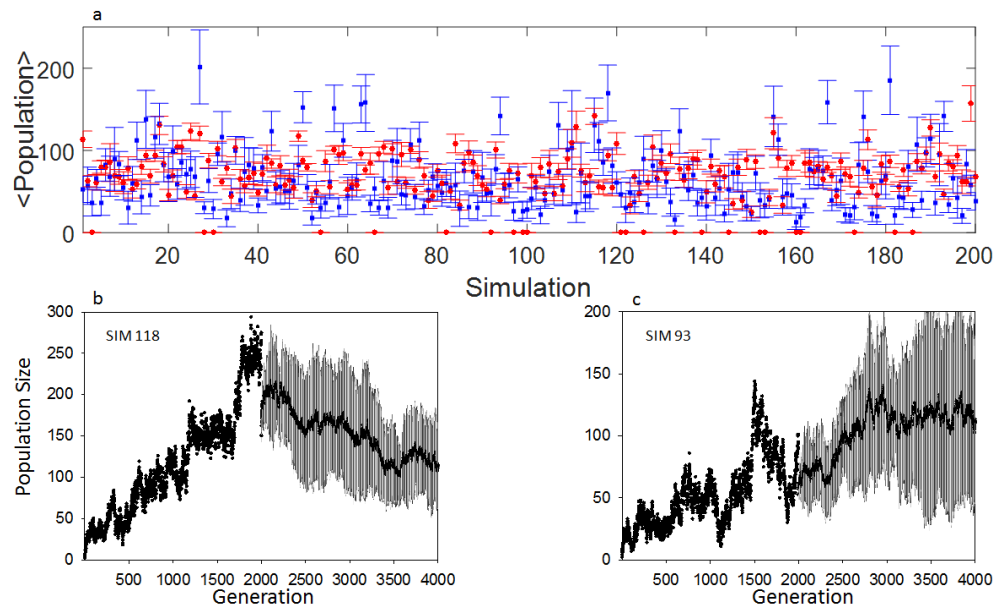


Figure 4.7. Ten Trials at δ_c with 50% Mass Death: Assortative Mating — Panel (a) represents average population size of the last 500 generations pre- (blue circles) and post- (red circles) extinction. Panels (b) and (c) represent selected simulations (118 and 93, respectively) Error bars show the standard deviation of the population size of ten mass extinction simulations, each starting with the same initial conditions.

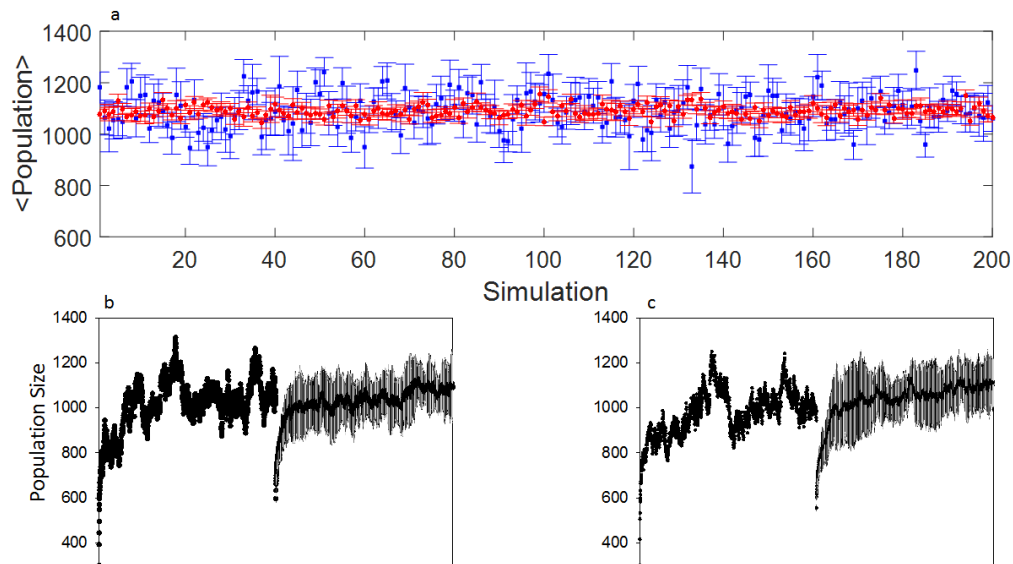


Figure 4.8. Ten Trials at $\delta = 0.22$ with 50% Mass Death: Assortative Mating — Panel (a) represents average population size of the last 500 generations pre- (blue circles) and post- (red circles) extinction. Panels (b) and (c) are selected simulations (simulation 9 and 134, respectively). Error bars show the standard deviation of the population size of ten mass extinction simulations, each starting with the same initial conditions.

Figure 4.10 represents the behavior of the asexual populations, at criticality, when subjected to ten trials with $\delta_m = 0.50$. Panel 30a shows that significantly fewer simulations resulted in complete extinction than in the assortative case; here, 5 went extinct, in contrast to the 23 simulations in the assortative case. Furthermore, on average, the populations recovered to pre-extinction population sizes. Figure 4.11 shows that the asexual population always recovers above criticality at $\delta_m = 0.50$, and Figure 4.12 represents the behavior above and at criticality at $\delta_m = 0.95$. Similarly, the number of simulations that went extinct was considerably less than the assortative mating case shown in Figure 4.9.

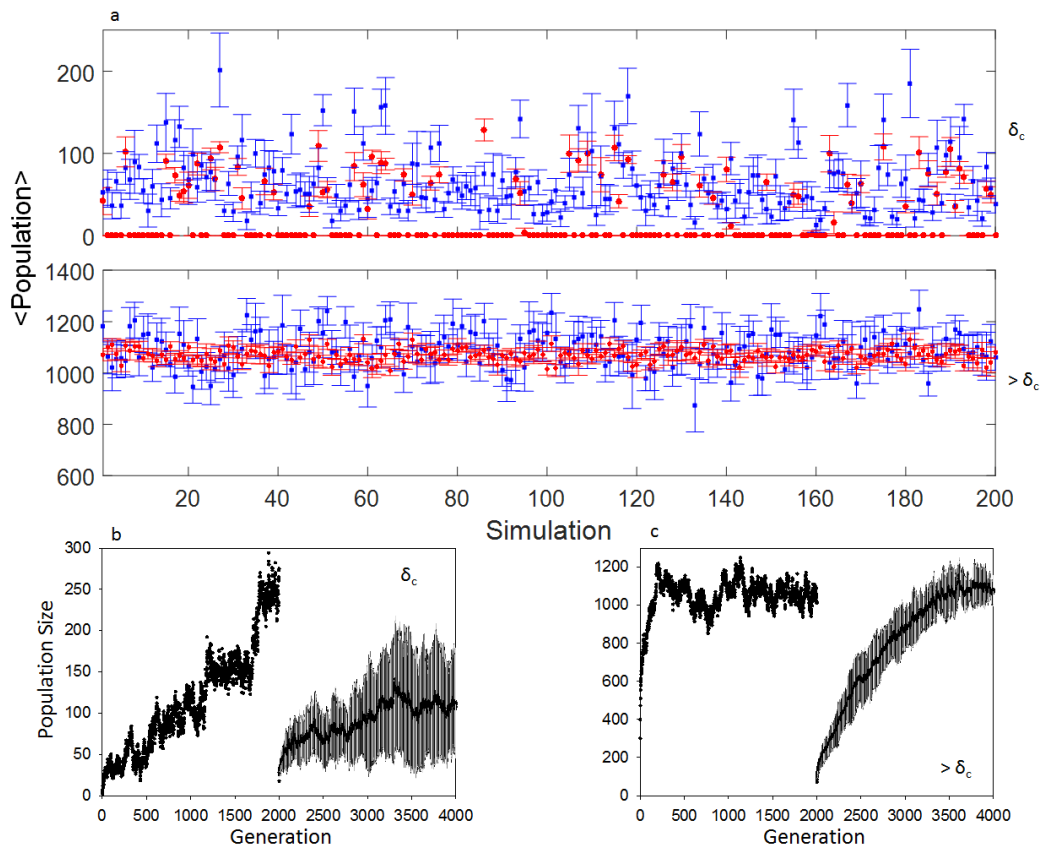


Figure 4.9. Ten Trials at δ_c and $\delta = 0.22$ with 95% Mass Death: Assortative Mating — Average population sizes pre- (blue circles) and post-extinction (red circles) at $\delta_c = 0.23$ (panel a, top) and $\delta = 0.22$ (panel a, bottom). Both panels b and c show population recovery from simulation 27.

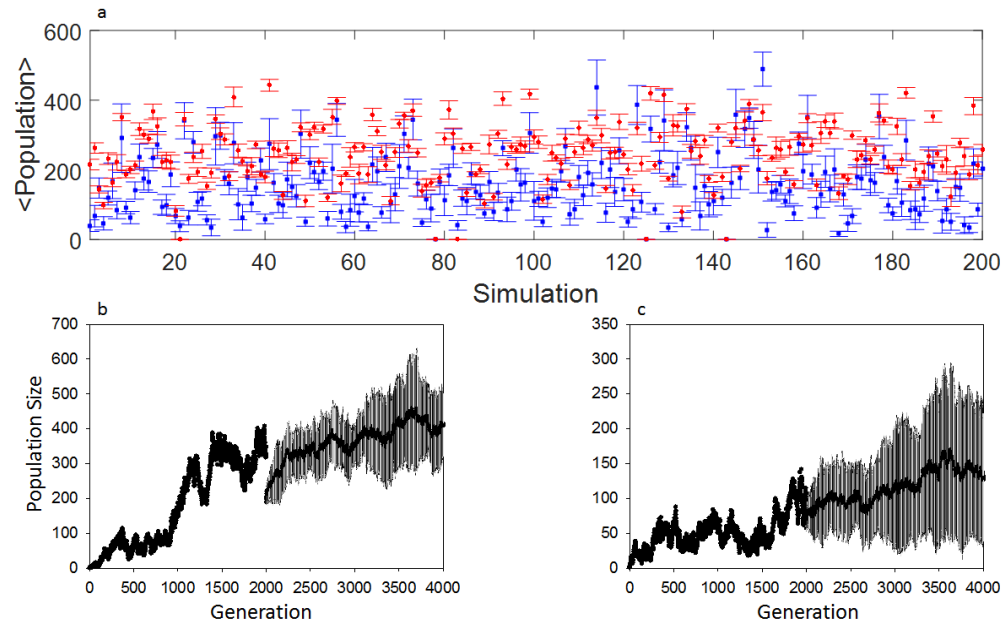


Figure 4.10. Ten Trials at $\delta_c = 0.28$ with 50% Mass Death: Asexual Fission — Panel a represents average population size of the last 500 generations pre- (blue circles) and post- (red circles) extinction. Panels b and c represent chosen simulations 126 and 116, respectively. Error bars show the standard deviation in population size over ten mass extinction simulations.

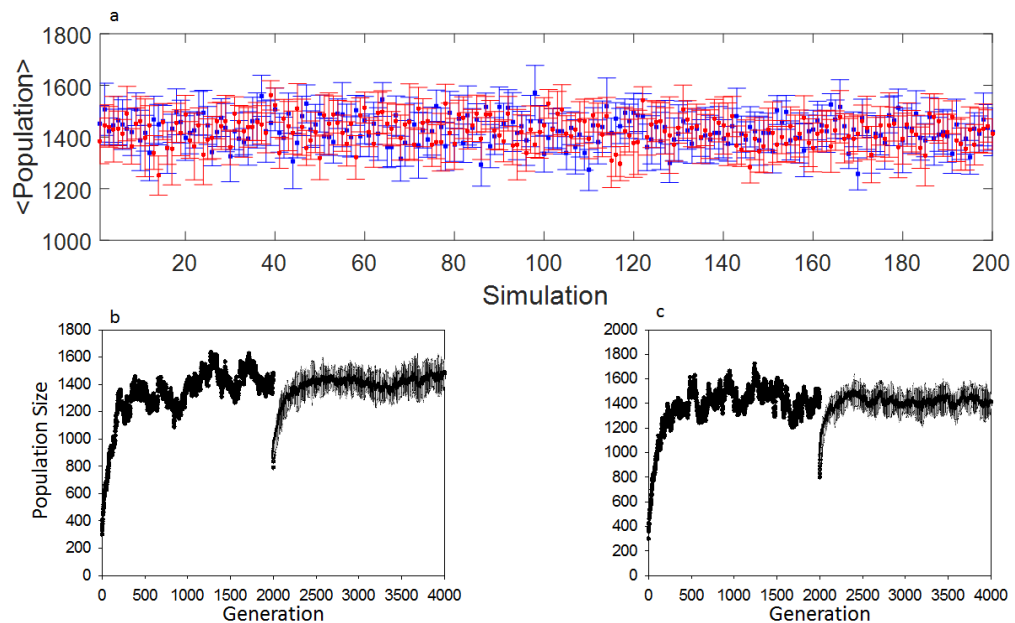


Figure 4.11. Ten Trials at $\delta = 0.27$ with 50% Mass Death: Asexual Fission — Panel a represents average population size of the last 500 generations pre- (blue circles) and post- (red circles) extinction over ten trials. Panels (b) and (c) represent selected simulations 7 and 20, respectively. Error bars show the standard deviation in population size of ten mass extinction simulations.

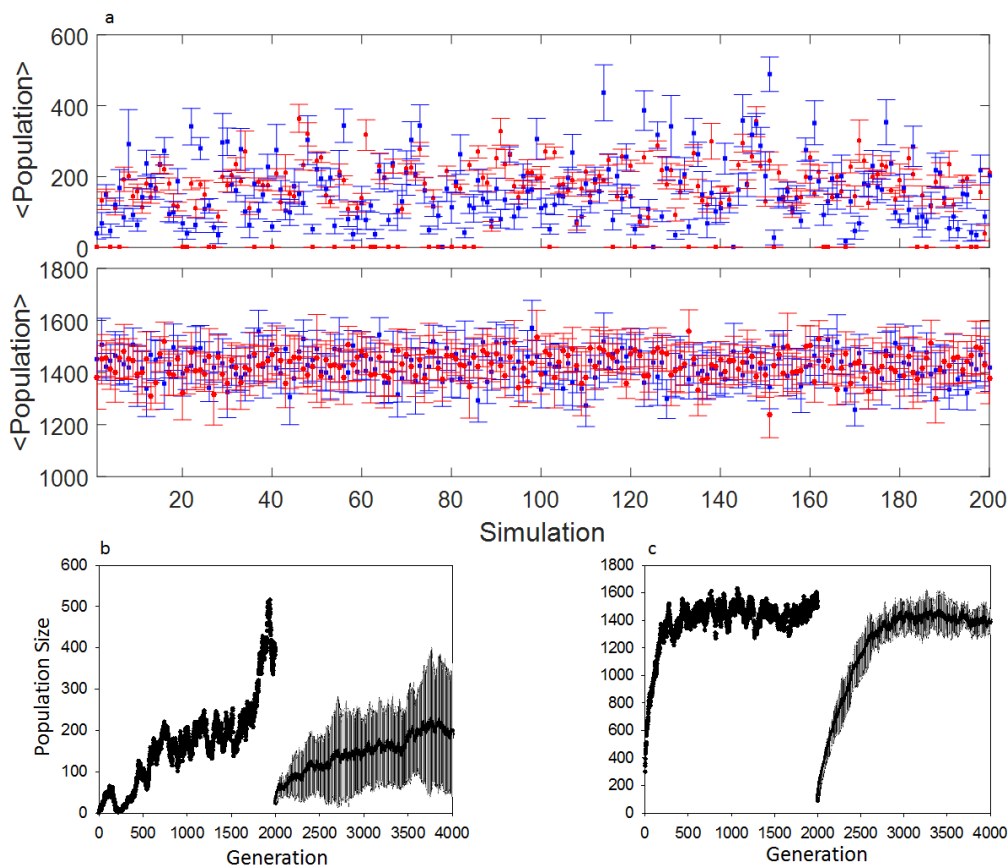


Figure 4.12. Ten Trials At and Above δ_c with 95% Mass Death: Assortative Mating — Results for $\delta_m = 0.95$ for the asexual reproduction scheme at $\delta_c = 0.28$ (panel a, top) and $\delta_c = 0.27$ (panel a, bottom). Blue circles indicate pre-extinction, while red circles indicate post-extinction. Panel b shows population recovery from simulation 27 at $\delta_c = 0.28$, while panel c shows population recovery above at $\delta_c = 0.27$, again from the corresponding simulation 27.

4.4 DISCUSSION

The dynamics of population collapse and recovery following simulated mass extinction has been investigated and will be discussed here. One of the key evolutionary themes discussed above, the role of historical contingency in recovery from mass extinction, has been demonstrated in several ways. The first is with the phase transition behavior itself. It was expected that some degree of contingency existed at the critical point, for we already knew that at criticality some simulations died off and some

survived — this is the hallmark of the nonequilibrium, continuous phase transition. Thus, the simulations presented in this section were hand-picked to simply address what could happen to surviving simulations at criticality.

The remnants of the contingent phase transition behavior following the simulated mass extinction can be seen in Figure 4.1. Of the 200 surviving assortative mating simulations, even with just a slight population perturbation of 1% (up to higher population perturbation of ~50%) death, about half of the populations went extinct for the assortative mating scheme. Therefore, due to historical contingency at the critical point, a certain number of simulations seem to already have a predisposition to go extinct. As δ_m increased above 50%, the percentage of extinctions began to increase exponentially, so even though there was already contingent behavior, at some point (~50% mass death) it became even harder for populations to survive. Above criticality ($\delta = 0.21, 0.22$), simulations survived at a mass extinction of up to a 99% mass death, except for one simulation that died at 99% mass death percentage at $\delta = 0.22$.

The asexual fission model, which also demonstrated contingent behavior at criticality, presented a situation where populations are more robust against extinction than the assortative mating population. Figure 4.1 shows that only ~20 simulations became extinct for each δ_m up to about a mass death of 75%. Even at a mass death of 92%, 100 simulations survived, which was the number of simulations that survived, at best, for the assortative populations. The theme of asexual populations being more robust against mass extinctions than the sexual populations is consistent with all of the data presented above.

The average population size pre- and post-extinction as a function of δ_m is shown for both the sexual and asexual models at δ_c in Figure 4.2. For the assortative mating scheme, at 50% mass death, the populations tend to not recover to the pre-extinction population size, whereas, for the asexual population, failure to recover to pre-extinction population sizes occurs only for $\delta_m > 0.95$. The population behavior is examined further, as δ_m is increased, as a function of time (in units of generation) in Figures 4.3-4.6. At the assortative mating critical point (Fig. 4.4), populations are shown to not recover to pre-

extinction populations sizes, and the lack of recovery to the original population state becomes more pronounced the higher the decimation. In contrast, for the asexual model (Fig. 4.6), populations can recover to the pre-extinction population size up to about 95% decimation. However, it should be noted that asexual populations had been subjected to mass extinction events prior to the system reaching its steady state (*i.e.*, the population size was still increasing at generation 2000), whereas the assortatively mating populations had reached a steady state by generation 2000 (meaning that populations were fluctuating in size but not increasing in overall size). This could account for some of the discrepancy in behavior shown in Figure 4.2 between the reproduction schemes. Since the asexual populations were still growing when they experienced a mass extinction, the average population size grows larger in the post-extinction regime than its pre-extinction size. The only result of implementing the mass extinction event too early was to increase the time needed for the system to reach the steady state during the recovery phase. Extinction experiments with mass extinction events applied to the the asexual populations, at criticality and in their steady state, need to be performed in order to compare the asexual case to the assortative mating scheme. However, these observations do not invalidate the observation of the overall robustness of asexual populations shown in Figure 4.1.

There is a stark difference in the behavior above the critical point (Figure 4.3 and 4.5), with all populations surviving and shown to recover to the original pre-extinction population state. As expected, there was a slower recovery rate as δ_m increased for both reproduction schemes; however, only for the assortative mating case do the populations exhibit markedly decreased fluctuations following the mass extinction event (Figure 4.3). It seems as if perturbing the system has a stabilizing effect for mating populations, but not for the asexual populations. Further investigation into why this is the case is needed. One possible explanation could have to do with the size of the population pre-extinction, since the asexual, pre-extinction population sizes are generally larger (and still increasing in size at generation 2000) than the average assortatively mating population size.

To investigate historically contingent behavior further, each of the 200 simulations were subjected to mass extinction events 10 times at various values of δ_m at and above the critical point. $\delta_m = 0.50$ is shown in Figures 4.7 (assortative) and 4.10 (asexual), at the critical point, for simulations averaged over surviving trials. Panels 4.7a and 4.10a show that at the critical point the average population size over ten different trials fluctuates wildly; in contrast, Figures 4.8 and 4.11, which shows the respective mating schemes at $\delta_m = 0.50$, above the critical point, show less population variation. This general difference in behavior between critical and non-critical populations is also shown in the case of $\delta_m = 0.95$ in Figures 4.9 and 4.12.

Additionally, at criticality (Figures 4.7 and 4.10) there is no clear predictor for why certain simulations survive and others do not. Sometimes all ten simulations survive, sometimes none of the ten simulations survive, and sometimes any number between 1 and 9 survive. Assortative mating did have significantly more simulations that went completely extinction than the asexual case. A typical indicator of survivability is the population size, yet Figure 4.7b and c shows that simulation 118 had a higher than simulation 93 (Fig. 4.7c) population size at generation 2000 (pre-extinction), but that the post-extinction population does not recovery to the pre-extinction population sizes; whereas, simulation 93 (Fig. 4.7c) shows a lower population size at extinction than shown in Figure 4.7b, yet the average population size of these ten simulations are shown to recover to a higher pre-extinction population size. This behavior is even more pronounced when the mass death percentage is increased (Figures 4.9 and 4.12).

In summary, the results presented above show that the behavior at the critical point is highly contingent, and there are, as of yet, no reliable predictors of population recovery, other than the system actually moving out of the critical regime. Furthermore, asexual populations are shown to more be resistant to mass extinction than their sexual counterparts. Interestingly, above criticality, the population fluctuations become less pronounced for the assortative mating scheme, indicating that perturbations could have a stabilizing effect on populations, but there was no evidence for population stabilization following mass extinction events for asexual populations. An interesting

question is whether this stabilizing effect of perturbation can be detected in the phylogenetic trees structures, and whether or not these perturbations can lead to patterns of evolutionary stasis?

5. FUTURE RESEARCH DIRECTIONS

Honerkamp-Smith *et al.* (2008) demonstrated that the lipid bilayer of cell membranes exhibit a phase transition between a “liquid ordered” and “liquid disordered” state as function of temperature. This phase transition was shown to belong to the 2-D Ising universality class by measuring quantities such as the correlation length, ξ_{\perp} , using fluorescence microscopy and applying those measurements to their respective scaling relations (Honerkamp-Smith *et al.*, 2008). Yet, no real biological system has been shown to undergo a phase transition of the directed percolation universality class. Indeed, the only experimental system thus far that has been shown to undergo a DP phase transition is the liquid crystal system studied by Takeuchi *et al.* (2009). In the immediate future, I am designing experimental studies to investigate the scaling behavior of an experimental population of the yeast *S. cerevisiae*. The aim will be to identify the universality class of the phase transition experienced by yeast populations under temperature stress in collaboration with molecular biologist, Wendy Olivas. These studies will form the first part of my postdoctoral research.

Once a phase transition has been identified and classified, or at least the critical points identified, experiments evaluating the dynamics of population recovery and collapse in the yeast system could be investigated as well. It would be interesting to see if the observed population fluctuations following an experimental population shock would exhibit the same kind of behavior observed in our model (*i.e.*, does a perturbation induce an experimentally stable system?).

Recent work from Dai *et al.* (2012) demonstrated critical behavior in an experimental population of yeast. Notably, Dai *et al.* showed that yeast populations could be modelled by the nonlinear Allee effect equations, and he experimentally verified a fold-bifurcation (where the stable and unstable point collide) in the cell density as a function of the dilution factor. ‘Bifurcations [are] the analog to phase transitions under continuous, dynamical systems’, since ‘mathematically, a bifurcation

implies the emergence (and disappearance) of new solutions.’ (Solé, 2011 p. 38) Phase transition behavior may also exist at the fold-bifurcation point, but determining this would require examining for fluctuations in the population size at the critical point, rather than showing the phenomenon of ‘critical slowing’ down behavior found near bifurcations in nonlinear-continuous equations. If true, this implies a bridge between phase transition theory and unstable bifurcations found in nonlinear models.

Another important extension of the studies described above involves computational analysis of the phylogenetic trees structures following the simulated mass extinction. This analysis is in process and will be included in the manuscript that is being prepared for publication from the work described above in Chapter Three and Four. Specifically, I am investigating whether the branching behavior (as shown with T_2) still exhibits power law-like behavior during recovery from mass extinction. It is possible that the population perturbation may disrupt or destroy this behavior. Creating histograms much like those shown in Figures 3.5 and 3.6 will give some indication of whether similar tree structures re-evolve. Also, comparisons of the branch lengths post-extinction to those pre-extinction, as well as calculating the T_{entire} from the post-extinction populations (note the pre-extinction T_{entire} was shown in Figures 3.7 and 3.8) might give key insights into what a mass extinction can do to population structure in time. For instance, a scenario in which more than 2000 generations are needed for an entire population trace to a common ancestor is quite different than one in which far fewer generations are required. The latter case would imply that many lineages survived the extinction, while with the former case, only one lineage survived and diversified. Development of techniques such as these could aid in comparing simulation results to patterns found in the fossil record.

There are several extensions that can be applied to the extinction experiments in the computational model:

1. The duration of the population perturbation can be increased by a certain number of generations and that number of generations can be varied.
2. The population shocks can be repeated after a certain number of generations.

3. Extinctions can be performed on variable fitness landscape.
4. Each individual could be assigned a different mutability.

For both points (1) and (2), it would be most interesting to see how the system behaves in the survival regime (above critical point). We can ask how long stable populations can sustain themselves before extinction. Or, for points (3) and (4), we could ask if there are organisms that when assigned a particular mutability value seem to survive better than another, and whether variable fitness has an effect on survivability.

In all versions of the computational model used here, each organism disperses its offspring based on the mutation parameter μ . Allowing variable mutabilities (or organisms with different dispersion capabilities) could hold some interesting dynamics on population recovery. I showed above in Chapter Two that, as μ increased, the populations were more robust against extinction. Preliminary experiments of Dees and Bahar (2010) suggested that when mutabilities competed on a rugged-fitness landscape that the individuals with intermediate values of μ generally won. Thus, do certain mutabilities recover from extinction better than others when in competition with each other on neutral landscape? It is known that phase transition behavior exists on the rugged landscape version of this model (Dees & Bahar, 2010). Utilizing a rugged landscape incorporates variable fitness into the model, thus this model utilizes a process that is more representative of natural selection. Further, how would a rugged fitness landscape affect the survivability of organisms that are defined by different μ ? Does introducing a rugged-fitness landscape change the outcome for the survivors?

All of these possibilities would yield rich extinction dynamics that have yet to be explored in an agent-based, evolutionary model of the DP universality class.

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VITA

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