Chapter 8

Conclusions

> Whatever topic you select, your project should have three parts: the hypothesis, the part that goes after the hypothesis, and the conclusion (this should be the same as the hypothesis). (Barry 1998)

The preceding chapters have shown how a configuration model can illuminate dynamics that we have never seen before, but suspect must be out there somewhere in the darkness. The results of such models, and this one is certainly no exception, should be treated as guiding hypotheses for future investigation. To accept the results as the truth about biology would require accepting the abstraction of the model as a representation of the essential features of a biological system. Biological systems are too complex, and these models are also probably too complex to allow us any such confidence. Instead, I have presented evidence for why MoD may be a reasonable representation of ecological and evolutionary dynamics. We may thus, with caution, take the results as support for or against the hypotheses for the diversification of life.

8.1 Primary Results

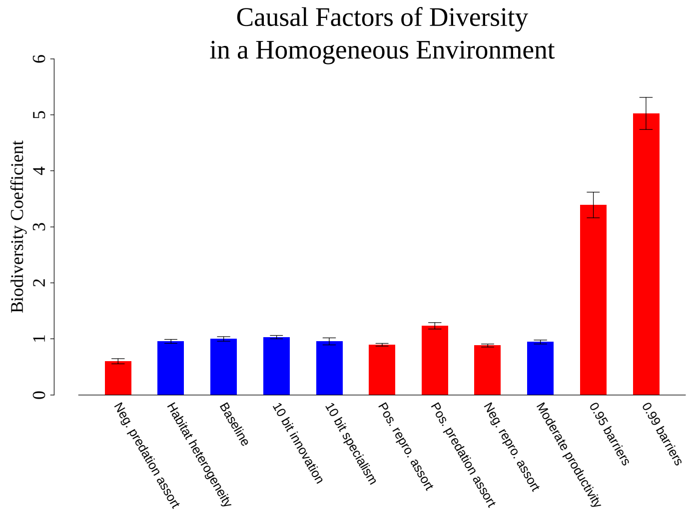
The most important innovation of MoD is its implementation of a species. While neither reproductive barriers (Saruwatari et al. 1994) nor reproductively isolated populations (Todd & Miller 1991) are novel, their combination is. This implementation of the reproductive species concept has allowed us to see that speciation may be far from a rare event. It is possibly occuring all around us every day, given this particular definition and implementation of species. What is rare is the survival and differentiation of those incipient species such that a naturalist might notice them.

There are five general statements that can be made about diversification in MoD. First of all, by far the most important factor that influences diversification is the isolation of populations from one another. In the model, this is represented by geographical isolation. Second, positive assortative mating can dramatically stimulate diversification. Positive assortative mating is similar to geographical isolation in that it also serves to isolate subpopulations. Third, the subdivision of niche space through the evolution of specialization can have significant effects on the processes of diversification. Fourth, evolutionary innovations in resource utilization and predation interactions have no discernible effect except to lower speciation rates. This result poses a challenge to the entire industry of looking for key ecological innovations to explain the diversification of various groups. However, as Cracraft (1990) has pointed out, the connection between ecological pressures and speciation is only indirect and so of questionable importance. Finally, the most direct form of divergent selection in the model is caused by habitat heterogeneity. Yet, this seems to have little effect on diversity. The relative importance of geographic isolation and unimportance of habitat differences directly contradicts evidence from laboratory experiments on flies (Rice & Hostert 1993).

An overview of the importance of the causal factors that have been examined appears in Figures 8-1 and 8-2. Only a representative subset of all the experiments is depicted. The heterogeneous habitat condition with high migratory barriers provides a better gauge of diversity dynamics than the vanilla condition. Diversity levels are too low in the vanilla condition to allow the effect of a manipulation to be detected.

The divergence between diversity and speciation rates can be seen in both the manipulations to productivity and specialization. When productivity is boosted to moderate levels, speciation rates dramatically increase but there is no effect on diversity levels. Extinction rates rise in tandem with speciation rates in this case. In contrast, allowing organisms to specialize results in a decrease in speciation rates but an increase in the standing diversity. The ability to specialize lowers extinction rates.

The counter-intuitive results of Chapter 7 show up most clearly in Figure 8-2. Both positive and negative assortative mating based on reproductive characters dramatically suppress speciation rates (and diversity) in a homogeneous environment (top chart). Yet,



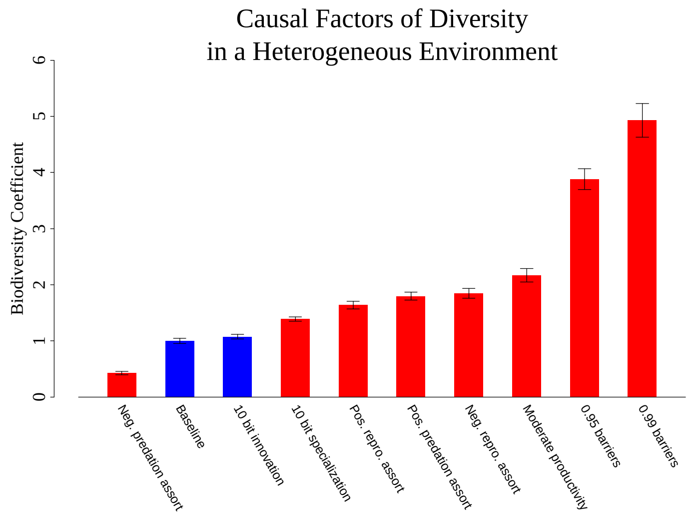
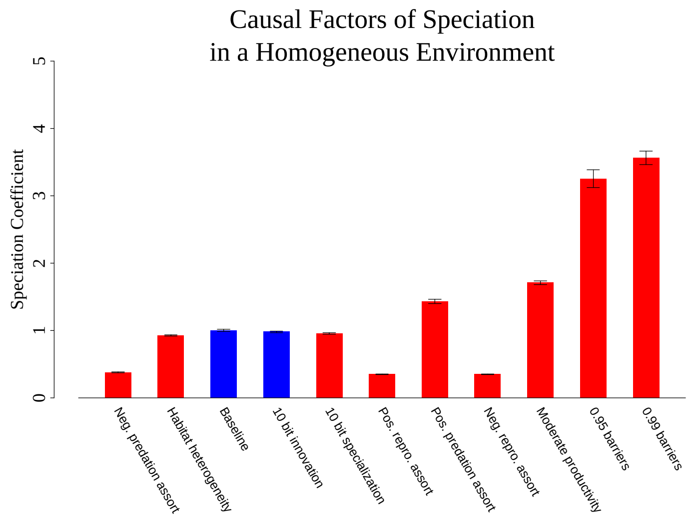


Figure 8-1: A summary of manipulations to species diversity. The top chart shows the manipulations in the context of a homogeneous environment with no migratory barriers. The bottom graph shows the same manipulations in the context of a heterogeneous environment and 0.95 migratory barriers. Each effect has been normalized by its relevant baseline and include standard error bars. In the case of the manipulations to the barriers, the relevant baseline is either the homogenous or heterogeneous habitats with no migratory barriers. The bars indicate the magnitude of an effect relative to the baseline. The blue bars indicate that the manipulation had no statistically significant effect. Red bars indicate a significant effect, with $p < 0.05$.



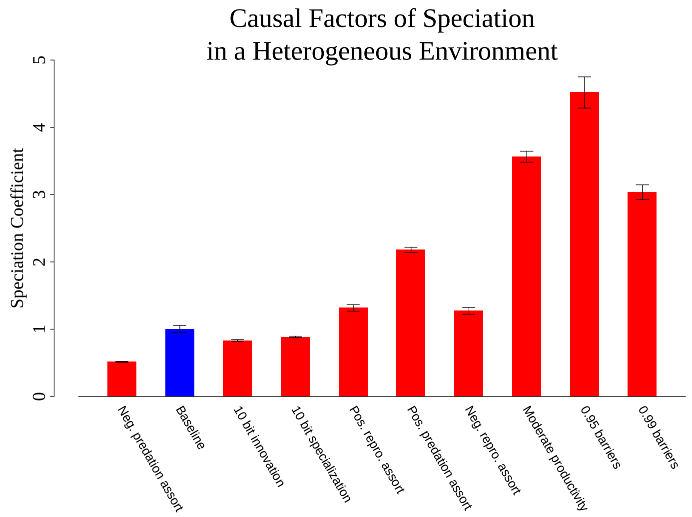


Figure 8-2: A summary of manipulations of speciation rates. The top chart shows the effect in the context of a homogeneous environment with no migratory barriers. The bottom graph shows the same manipulations in the context of a heterogeneous environment and 0.95 migratory barriers. Standard error bars have been added to the means of the effects. Differences between these graphs and those in Figure 8-1 illustrate the fact that diversity is determined by the interaction of both speciation and extinction rates. Each condition has been normalized by its relevant baseline. In the case of the manipulations to the barriers, the relevant baseline is either the homogenous or heterogeneous habitats with no migratory barriers. The blue bars indicate that the manipulation had no statistically significant effect. Red bars indicate a significant effect, with $p < 0.05$.

in a heterogeneous environment with migratory barriers (bottom chart), both forms of assortative mating significantly increase speciation rates (and diversity). This can only be understood through the dynamics of the reproductive graphs. Assortative mating based on the reproductive characters biases the dynamics of the graphs towards the maintenance of large internal nodes. Since only the death of all the organisms of an internal node can cause speciation, these biases tend to reduce speciation. However, in a subdivided population, which nodes are "peripheral" and which are "internal" can sometimes change. This may cause the reproductive graphs in the patches to pull apart from one another. The divergence of the graphs leads to an increase in speciation rates. While this may appear particular to the reproductive graphs used in MoD, the dynamics derive from the way in which relative rarity interacts with assortative mating and so may have broader relevance to other implementations of species and perhaps biology in general.

Fluctuations in an organism's physical environment does not appear to be important as a cause of diversification in and of itself. Amongst the abiotic influences, only geographical isolation showed a major, monotonic effect on diversity. Changes that increase the geographical isolation or fragmentation of populations are expected to stimulate diversification.

The model implies that there is a negative feedback dynamic in diversification that causes diversity levels to be regulated once they reach a sort of diversity carrying capacity. This is not due to a decline in total speciation rates per time step, as diversity rises. On the contrary, speciation rates rise with diversity. However, extinction rates also rise with diversity, and, crucially, they rise faster than the speciation rates. The implication that diversity is similarly regulated in the real world does not answer the question of where we are on that logistic curve. If, as Benton (1995) would have it, global diversity is increasing exponentially, that is still consistent with the early part of a logistic curve. On the other hand, if one hypothesizes that the diversity ceiling will be reached quickly, then the apparent continuous increase in species diversity must be explained by arguments for why the ceiling on diversity might have been raised over time.

It is difficult to raise the ceiling. Let us consider each of the hypotheses for diversification that MoD supports. Arguments for the importance of geographical isolation would have to explain why populations have been increasingly fragmented and isolated over time. Geologically this seems implausible. At the large scale, we know that continents have both fragmented and come back together over time. At a smaller scale, there is no obvious trend. Biologically, one would have to posit less and less dispersal over the history of life. If anything, with the development of multicellular life, the opposite is more likely to be true.

Proponents of sexual selection as a diversifying force would have to argue that the ceiling on diversity has been raised through the ever increasing capacity or tendency of organisms to discriminate between their potential mates. This argument might rest on the proposition that, on average and across species, organisms have become more structurally or behaviorally complex. That is a common assumption. However, it has yet to be proven. Certainly there is a higher variance in biological complexity now than there was 3.5 billion years ago. But to be fair, since we are counting species, and we have chosen a species definition based on sexual reproduction, we should restrict our attention to changes in complexity in sexual organisms. Again, we might argue that the variance in complexity has increased, but it is not at all clear that average complexity has increased. Not to mention the average propensity to be choosy about one's mate.

The argument for specialization as the factor that has elevated the diversity ceiling is very similar to the argument for sexual selection. We would have to argue that the capacity to specialize has increased over time. If the simple ability to specialize was a constant source of diversity, then we could not explain any regulation, not to mention the release of regulation, of species diversity. One must posit that the capacity to specialize at a given time led to a diversification which was eventually muted by a rising extinction rate. Then, further capacity to specialize evolved, allowing the packing of even more species into the niche space, and so diversity increased again until it hit a new, higher ceiling. An argument for the increasing capacity to specialize would probably have to be based on arguments of increasing developmental and behavioral complexity. Again, this is a tenuous position.

Finally, let us turn to the favored hypotheses regarding niche space. Perhaps niche space has been repeatedly enlarged by evolutionary innovations. Can niche space be enlarged? Niche space, at least *environmental niche* space, is the space of potential niches. Proponents of evolutionary innovations in the utilization of resources would not argue that the potential niche space was enlarged, just the amount of it that was occupied. An innovation allows organisms to expand into virgin territory. The ceiling effect must come from an additional assumption. We must assume that there are some form of barriers or topology in niche space that prevent species from expanding freely in that space. In other words, some innovations must be less likely than others. This may be a reasonable assumption given the complexities of biological development[1]. The hypothesis, then, is that organisms were constrained to a valley in niche space and that occasionally, an innovation arose allowing the lineages to break free from the valley into the surrounding lands. However, we must hypothesize that the organisms would soon run up against new obstacles in this territory that prevented any further expansion. Until, of course, the next innovation opened the gates to a successive radiation. The challenge comes in relating the filling of adaptive space with the splitting of gene pools. That connection is not at all clear and has been challenged by the model.

The only reason to argue for changes in the ceiling to diversity is the belief that life has butted up against that ceiling at various times in the past. If we narrow our attention to any one clade, or branch of the tree of life, we will often see it diversify up to some point and then, often, decline. However, we often cannot even tell if a specific clade reached a species diversity equilibrium because the fossil record generally does not allow resolution at the species level. The typical compromise is to count families as proxies for species diversity. This adds strong biases to the perception of the underlying diversity (Maley et al. 1997). Furthermore, the model, and its results, are based on species coevolving in an ecosystem. Most taxa that people study are not large enough to encapsulate more than one trophic level of the ecosystems that shaped those species. In summary, the jury is still out on whether diversity regulation has yet to play an important part in the history of life. Until there is better evidence for the regulation of diversity across trophic levels in evolutionary time, we should shave with Occam's razor, and favor the simpler assumption that the world has yet to reach the diversity ceiling.

In other words, MoD argues for a world view in which speciation is generally more likely than extinction. This diversification is presumed to be based on geographical isolation of populations, assortative mating, and specialization. Of course, there may well be other important factors in diversification that were not tested in MoD.

The results imply that when biologists seek an explanation for an adaptive radiation in some key innovation of that taxon, they should try to weigh potential changes in dispersal as well as secondary sexual characteristics equally with, if not more than, apparent ecological innovations. Furthermore, paleobiologists should give greater weight to reproductive

[1]For example, it is probably much less likely that my future children will develop an extra set of arms than they will develop a superior intelligence compared to their father.

characters in their attempts to subdivide fossils into groups of related individuals. Similarly, biologists of living organisms might look more closely at species that display strong sexual selection. What we think is an individual species may well be a complex of cryptic species.

8.2 Related Results

In the course of the experiments some of the complexity of predator-prey interactions has emerged. An initial, naive implementation of predation failed because rare prey were too easy to find by common predators. Three trophic levels were only stabilized when interference competition between predators was introduced.

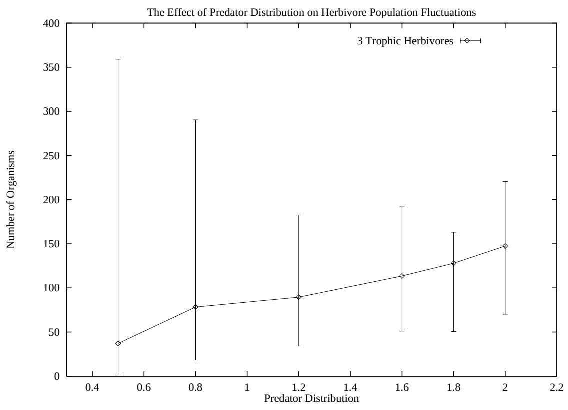


Figure 8-3: The average herbivore population sizes as a function of the *predation-distribution* parameter. The error bars indicate the average maximum and average minimum population sizes for 50 runs. As *predation-distribution* increases, adding more competitive interference between the herbivores, the oscillations in the herbivore population diminish and the average population size rises.

Chapter 3 illuminated some counter-intuitive dynamics in predator-prey interactions. When parameters of MoD were changed so as to make life "harder" for predators, the predator population, averaged over time, increased. This occured when the prey were more protected from predation by raising the *predation-distribution* parameter, lowering the probability of finding prey with the *prey-location* parameter, or restricting the patrolling of the predators with the *search-radius* parameter. All of these effects dampen the oscillations between the predator and prey populations and so stabilize both populations. The net result is an average boost to predator population size, as indicated by Figure 8-3.

Similarly, Chapter 6 illuminated a further complexity in the coevolution of predators and their prey. In general, MoD showed that the prey have an advantage in the evolutionary arms race. With a larger population, the prey have more opportunities for evolving novel forms of resistance to predation. Yet, when we restrict adaptive space, when we constrain the number of possible prey innovations, in some cases this allows the predators to keep up in the race. This implies that evolutionary models of predation are critically affected by the number of dimensions in the adaptive space.

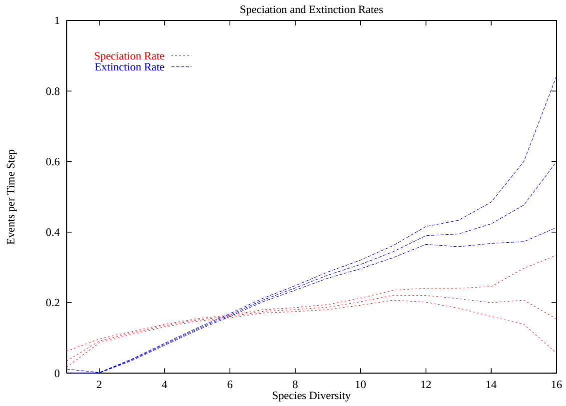


Figure 8-4: The interaction of speciation and extinction rates as functions of diversity. The means for both rates are surrounded by curves representing the 95% confidence intervals. In contrast to the theory of island biogeography, origination rates, i.e., speciation rates, do not decline with rising diversity.

Chapter 4 investigated the species-area curve from island biogeography in an evolutionary context. Rather than introducing new species through immigration from a mainland population, new species were generated by the model through speciation events within the ecosystem. This results in speciation rates that increase, roughly linearly, with diversity as shown in Figure 8-4. The only reason this does not lead to "run-away" diversification is that extinction rates also rise with diversity. Extinction rates rise faster than speciation rates. Where these two lines cross, the ecosystem settles down into a stable equilibrium diversity level. The scaling of diversity with area in MoD showed a far more realistic species-area curve than previous attempts (Jones et al. 1997). The difference probably derives from the fact that Jones et al. substituted genotypic diversity for species diversity. The more realistic species-area curve in MoD inspired the prediction that any ecological model that uses a reproductive graph definition of species will produce realistic species-area curves.

The experiments on the relationship between productivity and diversity provided another example of a typical ecological experiment transplanted into an evolutionary context. Experiments that have studied the effects of productivity on diversity levels last at most a few years (Tilman 1987; Goldberg & Miller 1990). Thus, any rise in diversity levels must come from immigrants entering the area of study. In contrast, MoD looks at the evolution new species in response to changes in productivity levels. The results match the ecological observations of a unimodal relationship between diversity and productivity. However, the explanation for this dynamic in the model is unlike any of the hypotheses reviewed by Rosenzweig (1995). Increases in productivity boost reproduction rates. This produces two countervailing forces for diversity. On the one hand, larger populations and faster turnover accelerates diversification through greater genetic change in the populations. On the other hand, the production of more individuals increases the number of migrants between populations. This combines with greater turnover in the populations to produce higher proportions of migrant genes entering populations. The barriers between populations are thus effectively lowered and the populations are less likely to diverge.

Finally, the results of Chapter 7 show that the effects of assortative mating on diversity are subtle. Speciation may be stimulated or suppressed depending on whether organisms are choosing mates based on characters that are independently involved in reproductive isolation or predation interactions. Furthermore, the effects may change depending on the sizes of the population. When a population is fragmented, the sampling error between the subpopulations means that a phenotype that is rare in the consolidated population may enjoy the benefits (or penalties) of being common in an occasional subpopulation. Assortative mating is a particularly simple form of sexual selection. Biologists only just begun to explore the complexities of sex.

8.3 Caveats

Biology has largely been a science of specifics. In an attempt to explore generalized dynamics, the model was constructed at a high level of abstraction. The reality of the situation is that there are probably many species and ecosystems that differ from the assumptions of MoD in crucial ways. So, we must first predicate the model, and all of its results, on the set of assumptions upon which it was built. Furthermore, MoD represents only one implementation, or instantiation of those assumptions. As a computational model, it is vulnerable to details of its construction that may significantly impact the results, unbeknownst to its creators. Thus, any attempt to replicate the assumptions, structure, or results of the model would be a valuable contribution.

MoD itself suffers from a number of weaknesses in its representation of the requirements for testing theories of diversity. We have been strict in our focus on species, and not morphological diversity. The complexity of the modeled ecosystems has been severely constrained. There are no parasites or decomposers in the model. The set of resources and the complexity of the underlying physical environment is minimal, practically vestigial. There are no nutrient cycling dynamics. Nor are there any representations of body size or mass of the organisms. Besides complexity issues, the spatial and temporal scales of MoD are not what one would hope. The results bear on diversification over thousands of generations within an isolated region containing only tens of thousands of individuals. Species diversity levels in MoD are nowhere near the magnitudes observed on Earth. In a time scale of millions of years, an extremely rare but dramatic innovation might indeed change the course of natural history. Though, probably not in this model, given its rather simplistic representation of ecology.

Finally, it is not clear that the different hypotheses for diversification have really received a fair hearing. How should we compare the degree of assortative mating with the degree of geographical isolation, or the degree of constraints on niche space? I have attempted to compare representative conditions for each manipulation, but computational constraints have precluded against a thorough exploration of parameter space[2]. In particular, divergent selection may not have been very strong in MoD. An organism perfectly adapted to the habitat in one patch and entering another patch in a heterogeneous environment could expect to find an average of 10.3 bits differences in the new habitat. However, that organism was likely to have wild-cards in its generalism loci for some of those bit positions. So we may be underestimating the impact of real habitat heterogeneity. Still, the competitive exclusion results of Section 3.3 did show that a single bit difference in a plant can make all the difference to that species' survival. So habitat heterogeneity was certainly not a trivial factor in the adaptation of species. But adaptation is a different issue from diversification.

[2]I should note that I have reported all of my investigations of parameter space. There is often the worry in such models with huge numbers of parameters, that the model is over-fit to the desired results. Has the experimenter explored a lot of parameter space and chosen one of a very few parameter settings that produce the desired results? In this case, no. Section 3.2 presented a fair amount of parameter space. For each parameter there was a reasonable portion under which the model behaved well. I chose one point in that space and pushed on, without further tuning.

8.4 Future Work

There are three distinct forms of future work that might result from this initial exploration. First off, there are many remaining questions that might be addressed through elaborations of this and other models. Secondly, as was mentioned above, MoD should be validated through alternative implementations. And finally, the results have provided hypotheses to be tested in the lab and field.

8.4.1 Further Explorations

As was mentioned above, it would be nice to explore the dynamics of the model over a wider spatial scale. It would also be interesting to look at population size effects. We know these are important because of the fact that 0.99 migratory barriers lead to the extinction of the animals. Unfortunately, the problem with expanding the populations within a patch is that the time required to compute intra-patch interactions grows quadratically ($O(n^2)$), whereas expanding the number of patches only increases processing time linearly ($O(n)$). Modifying the mating algorithm to only search a fixed number of locations in the organism array of a patch would change intra-patch computation to $O(n)$ processing time, but might also dramatically affect the growth of rare species, perhaps realistically (Bernstein et al. 1985). Still, this could be avoided with a better data structure for organizing the organisms within a patch, such as a hash table based on the reproductive chromosomes. Related to both the population sizes and the number of patches is the desire to run the model for more time steps. However, the model did appear to settle down to a diversity equilibrium fairly rapidly. So running the model for longer would only be justified under elaborations where rare events (like significant innovations) might change the diversity dynamics.

The environment might be made richer by introducing multiple habitat patterns representing different resources that might support autotrophs. This would allow the autotrophs to specialize within a patch. An elaboration of the complexity of the environment might mesh well with alterations that would provide for evolutionary innovations that would truly open up unoccupied niche space. If there were multiple resources in the environment, then a lineage could escape competition by evolving the use of an unexploited resource. Space within a patch might also be subdivided into separate compartments which could serve as differentiated resources themselves.

We might allow evolutionary innovations in the characters that have a direct impact on the creation and maintenance of isolated gene pools. Organisms could include a gene for dispersal tendencies. We then might examine the effects of reduction in dispersal tendencies upon the diversification of that lineage. Similarly, organisms could be given characters for mate preferences, rather than enforcing a particular kind of assortative mating on all organisms. We then might look at how geographical fragmentation interacts with the evolution of mating preferences and how, together, these factors affect diversification.

The coevolutionary dynamics of MoD have not yet been studied. It would be interesting to know if an enforced speciation event in a prey species would tend to result in a later speciation event in its predators. We could ask the opposite question. How does a speciation event in a predator species affect the diversification of its prey?

Further work might be carried out on different model platforms. The reproductive graph implementation of species could be easily ported to ECHO. We might then re-examine the species-area curve in ECHO to see how the curve changes when we abandon genotypic diversity as the measurement of species. The same could be done in most other artificial life models by adding reproductive chromosomes to the organisms.

Finally, a full analysis of the reproductive graphs in MoD proved intractable. Appendix A lays out some of the open problems in the analysis of reproductive graphs. The results of this, and similar, models depends crucially on the implementation of a species. Section 4.5 made a start at examining the effect of modifying the restrictions on mating between organisms. There remains a host of questions to be answered. How does the number of loci in the reproductive chromosomes (or dimensions of the hypercube that constrains the reproductive graphs) interact with diversification dynamics as well as reproductive barriers. Would an expansion to more than just two possible alleles at a locus change the dynamics qualitatively? How do these manipulations interact with the segregation of the total population into semi-isolated subpopulations? A better approach to these problems might be to construct a model whose analysis would be more tractable. This would mean avoiding such complications as examining 8 potential mates in assortative mating. It would probably be better to either implement a model where all potential mates are examined, or perhaps use some probabilistic function with “nice” analytical behavior.

8.4.2 Alternative Implementations

One of the most powerful theoretical validations of the model's results would be the creation of an alternative model that matched the requirements from Section 2.1 and still produced the same qualitative results. If, instead, that alternative model should produce qualitatively different results, we would have a basis upon which to seek the explanation for that difference. Chapter 2 describes the details of my implementation in sufficient detail that this specific model should be replicable. We might then begin altering the two models, the replicate and the alternative model, bringing them closer together until the crucial detail is found that changes the dynamics of the model.

This suggests a further approach to understanding the fundamental issues. Starting from a model, such as this one, we might systematically remove pieces, bit by bit, until the dynamics qualitatively change. Such an investigation by amputation should also help to identify the necessary pieces of a model of diversification.

Finally, there may well be a distribution model that could be constructed to test these same hypotheses. The discovery of such a model would be an important advance because it may provide us with further analytical tools for understanding and generalizing the dynamics.

8.4.3 Experimental Tests

Support or, more importantly, criticism of the model's results might be gained through traditional observational techniques in paleobiology and systematics. Has the evolution of leking behavior, where a female chooses a mate from a crowd (lek) of males on display, been associated with shifts of diversification rates in phylogenetic trees? More indirectly, have the elaboration of secondary sexual characteristics been associated with shifts in diversification?

One of the fundamental predictions of MoD is that proto-species are being formed at a relatively high frequency. Subpopulations are probably being reproductively isolated and then going extinct before they are able to evolve differentiating characters for us to notice. To test this, ideally, we would like to understand the reproductive system of a species so well that we could construct a reproductive graph of the individuals in a population. Perhaps from a DNA sample or similar non-lethal assay of a pair of individuals, we could predict the probability of their successfully mating and producing viable offspring. If we knew this, then we could sample a population, construct a graph of who can mate with whom, and then detect if there are reproductively isolated gene pools within that population. This sounds a bit far fetched now, but with the level of genetic detail we have on a number of model systems, such as yeast (*Saccharomyces cerevisiae*) or perhaps even fruit flies (*Drosophila*), such a level of understanding might not be too far distant in the future. It might be possible today in some plants where we can examine the so called self incompatibility loci. These are the genes that determine which pollen can fertilize which ova.

Finally, more ambitious experiments that closely mimic the manipulations of the model might be carried out in a laboratory setting. Section 7.5.1 suggested an experiment on fruit flies. Yeast is probably a better model organism for most of these experiments because it has a much faster generation time than fruit flies. Although, it lacks the behavior complexity necessary for some sexual selection experiments. It seems strange that most speciation experiments have been carried out on flies (Rice & Hostert 1993), though it may be an indication of the level of our knowledge of mating compatibility in yeasts. They now seem relatively simple. Still, an automated system could be set up to deliver migrant spores between populations and different populations might be exposed to different selection pressures through toxins, temperatures, and nutrient sources. Mutagens might be used to boost the exploration of adaptive space while viruses might stand in for predators, if natural predators are inconvenient. Analogs of most of the experiments from Chapter 5 should be implementable. Productivity is easily manipulated through the input of nutrients to the cultures. An important benefit of working with yeast is that we should be able to ascertain the genetic basis for any reproductive barriers that evolve between populations.

8.5 Valediction

I hope that, by now, the value of computation models in theoretical biology is obvious. We have been able to throw out some hypotheses, such as the importance of flux in the environment, and emphasize others that have suffered from a paucity of attention, such as sexual selection. Computational models give us another looking glass through which to see nature and also reflect upon some of the biases in our other tools. Yet, this new looking glass is certainly no less distorted than the others. It is merely distorted in different ways. The models, and their abstractions, provide a method for searching for the systematic and fundamental in biology. Is there anything there to be discovered? Will biology always remain the study of the particular? That is the question.