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Comparing causal factors in the diversification of species

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What have been the most important factors in the diversification of life? A configuration (individual-based) model (MoD) was constructed to examine the origins and maintenance of species diversity through time. The model represents a species as a connected component in a graph of the potential mating relationships between organisms. This allows us to detect speciation events and track species diversity over time. We may thereby test many "untestable hypotheses" for the causes of diversification. The results suggest that much of the emphasis placed on the evolutionary innovations, in resource utilization and predation interactions, in order to explain the diversification of a group, is flawed at best. Furthermore, habitat heterogeneity had little impact on species diversity. Instead, the model points to the importance of geographical isolation as a primary causal factor for diversification, along with the evolution of specialization and sexual selection, in the form of positive assortative mating. The influence of assortative mating is particularly interesting because it is opaque to the methods of paleobiology.

1 Introduction

Evolutionary biology is characterized by a relatively solid understanding of microevolutionary phenomena, but little understanding of macroevolutionary phenomena. One of the most important open questions of macroevolution is what have been the most important causal factors that have driven the diversification of species.

For clarity of discussion, we will consider a species to be a reproductively isolated gene pool. This is the dominant understanding of species in biology and is due in large part to the work of Ernst Mayr[23, 24, 25]. The question then becomes what factors tend to split gene pools apart and preserve them from extinction?

Most of the hypotheses that attempt to answer this question are both hard to test experimentally, and difficult to resolve in the fossil record. Thus, a model of diversification (MoD) has been developed that instantiates enough of the components of biological life to test and compare hypotheses for the diversification of life within a common framework.

2 Hypotheses

The hypotheses for the diversification of life fall into two broad categories: abiotic and biotic explanations[2].

2.1 Abiotic causes of diversification

Hypotheses for the diversification of species that depend on physical characteristics of the environment inevitably make reference to topology and/or climate. The conventional wisdom in theoretical biology holds that new species arise primarily from allopatric speciation. That is, populations of a species are separated geographically (topologically in the broad sense) and slowly diverge. This genetic divergence can emerge out of random genetic drift or differential selection between the two populations, as long as there are few enough migrants between the populations to avoid genetic homogeneity. Regardless of geographical separation, if two subpopulations experience different climates, or more generally, different selective pressures, it is reasonable to expect them to diverge and perhaps eventually become reproductively incompatible. These are the two basic abiotic hypotheses. Experiments on laboratory organisms show little effect of geographical separation on hybrid fertility between members of the subpopulations. However, such experiments do demonstrate that when allopatry (or any other manipulation that prevents viable hybridization between subpopulations) is paired with divergent selection, reproductive isolation does tend to evolve[29].

Cracraft[5] has proposed that the fact of environmental complexity may not be as important in the evolution of diversity as is change in the environment. He does not require the change to be in any one particular direction, as long as the environment is dynamic. Vermeij[40] also cites changes in climate and topography as being an important engine of speciation. Perhaps these changes have repeatedly isolated and then remixed populations, providing many opportunities for the separation of gene pools. A simpler variation on this idea is Benton's suggestion[2] that perhaps the physical environment has become more complex and fragmented over time. This should tend to fragment the populations and so boost speciation.

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2.2 Biotic causes of diversification

Biotic causes for diversification have been more popular in the literature as compared to abiotic causes. Generally, biologists and paleobiologists have engaged in a search for the evolution of some "key innovation" that catalyzed the diversification of their group of interest[6, 17, 33]. Of course, the set of characters that have been proposed as key innovations has been biased by the set of characters that can be observed in the fossil record or inferred from phylogenies, as well as the measurement of diversity under consideration[16, 18].

Raup[27] observed a decline in the extinction rate of families over time. This should also lead to the observation of increasing diversity over time. Van Valen[39] argues that the observed decreases in extinction rates may be due to the decrease in the overlap between species' niches and so a reduction of extinction through competitive exclusion. Niche overlap can be reduced in two ways. Species may reduce the "size" of their niches through specialization, or they may find and shift to the use of new, unexploited resources. Benton[2] emphasizes both of these factors, specialization and innovation, as the most important causes of diversification. In fact, an innovation that helps to exploit a new set of under-utilized resources might lead to an increase in diversity regardless of any change in extinction rates.

There is another realm of biotic causes of diversification that has only recently received much attention. Since species are determined by reproduction, and reproduction involves a complex constellation of both behaviors and physical traits, its stands to reason that behavioral changes should have had an impact on diversification. Unfortunately, it is all but impossible to recover behavioral innovations from fossil data, except to the extent that the morphology of organisms evolved to support those behaviors. Todd and Miller[38, 37] have shown in simulations that sexual selection can quickly fracture populations into mutually exclusive mating groups. Other models[21, 10] have shown that positive assortative mating can evolve under divergent selection on some other trait even when the populations are mixed (sympatric). All this suggests that positive assortative mating may have played an important role in the diversification of life.

3 Model

We approach model design for theoretical biology through a focus on hypothesis testing. All models are simplifications. The difficulty of modeling lies in the decisions of what to include and what to exclude from the model. We endeavor to include only those dynamics which are necessary to test the hypothesis. More cannot be easily justified. The hypotheses for the diversification of life require an implementation of the following phenomena: organisms, reproduction, heredity, and mutation. This much is necessary to implement microevolution. Furthermore competition is required to model extinction through competitive exclusion. Hypotheses about niches, or at least resource utilization, dictate the inclusion of discriminate predation and the phenomenon of specialization. In addition, geographical barriers, migration, and habitats all feature prominently in hypotheses of diversification. Finally, we are interested in species diversity. Thus, we must have some representation of species as collections of organisms. As we have adopted the reproductive concept of species[23, 24, 25] we are obliged to implement sexual reproduction and reproductive barriers. Furthermore, if one assumes that offspring are generally not reproductively isolated from their parents, then speciation, and indeed extinction, require the phenomena of death. Some parents must die in order to fragment gene pools.

MoD is a configuration[4] model (a.k.a., individual-based or agent based model) at the level of the organism. It bears a strong similarity to Echo[13, 14, 15, 19] as well as a number of other models in Artificial Life[20, 32, 11]. Each organism is described by 4 bit pattern "chromosomes" where each bit represents a heritable character. The first three "ecological" chromosomes structure the predator-prey interactions between the organisms. If the prey template chromosome of one organism matches the bit pattern of the predation resistance chromosome of another organism, the first organism may prey upon the second. This interaction is further modified by the generalism chromosome in the predator. The bits set to 1 in the generalism chromosome flag which loci in the prey template chromosome are ignored when checking the match between predator and prey. The combination of the prey template and generalism chromosomes is called the search template of an organism. An organism with all 1's in its generalism chromosome would be a complete generalist. While an organism with all 0's would be an extreme specialist, only able to digest organisms with one particular predation resistance genotype. The autotrophs (a characteristic encoded by a non-mutating flag in each organism) match their search template against a bit pattern in the environment that represents the characteristics of the habitat in their patch. For the particular details of the predation algorithm as well as the model in general, see [22]. Competitive exclusion arises from the fact that the autotrophs that better match their environment, and the heterotrophs that better match the prey population of their patch will be more likely to gather food and avoid starvation in any give time step than their more poorly adapted competitors.

The fourth and last chromosome is the reproductive chromosome. This encodes all of the characters that influence reproductive isolation between organisms, such as mating time, mating behaviors, reproductive organ morphology, gamete morphology, etc. Reproductive barriers are modeled by the rule that organisms can only mate with each other if their reproductive chromosomes differ in at most 1 locus.

Given this implementation of reproductive barriers, we can unambiguously identify the gene pools or species amongst the organisms. if we consider a graph where each extant reproductive genotype is a node and there is an edge between the genotypes that can mate (within hamming distance 1 of each other), then a gene pool or species is just a connected component in this graph. Over the generations, genes can flow within these connected components but not between them. A speciation event occurs when all of the organisms bearing a particular reproductive genotype die, and thereby disconnect one of the previously connected components[1]. While all of the ecological chromosomes consist of 32 bits, the reproductive chromosome is represented by 64 bits. We doubled its size so as to reduce the chance that two species would coalesce into one[2].

The organisms are distributed on a 4 by 4 grid of patches, with each patch able to hold 2048 organisms. All ecological interactions occur between organisms within the same patch. Every organism is given a chance to eat in each time step of the model. If an organism fails to find a prey organism in its patch, it dies of starvation. If an organism survives for three consecutive turns, consuming three prey organisms, it is given the chance to find a mate in its patch and reproduce. The chromosomes of the offspring are constructed through two-point crossover of the parental chromosomes in conjunction with a Poisson mutation rate of on average 1 bit flip for every 10 new genomes. The only migration between patches happens when a new organism was born. New organisms take a random walk of 0-2 steps to locate their new patch. This random walk is modified by a "migratory barrier" parameter associated with each patch representing geographical obstacles to migration. The migratory barrier of a patch is a real number between 0 and 1 which encodes the probability that an organism will be prevented from entering the patch on a step of its random walk. If the new organism tries to settle in a patch that is already full[3] it has a 50% chance of displacing (and killing) one of the resident organisms of its type (autotroph or heterotroph).

4 Testing the model

The model was subjected to four tests in order to determine if its ecological and evolutionary dynamics were notably unrealistic as compared with accepted theory. We tested to see if the model demonstrated predator-prey population oscillations, trophic cascades, competitive exclusion, and adaptation.

Stable predator-prey oscillations do not appear at all three trophic levels unless the implementation of predation is stochastic and there is some representation of competitive interference between predators. This may be modeled as a spatial distribution within a patch such that not all predators may pursue a particular prey organism. We chose to implement this restriction by the following equation.

$$Pr[\text{predation}] = ce^{-dn-m} \tag{1}$$

where c is the *prey-location* parameter, d is the *predation-distribution* parameter, n is the number of times that the prey organism has escaped predation this time step (simulating competitive interference of the predators), and m is the number of bits that mismatch between the predator's search template and the prey's predation resistance characters. When the *predation-distribution* is 0, there is effectively no spatial structure. With this elaboration, predator-prey oscillations are stable at all trophic levels over a wide range of parameter settings.

The model also exhibits a trophic cascade[3]. Trophic cascades are observed in the population levels of a species when its predator and then its predator's predator are introduced to the ecosystem. In the absence of predation, a species should expand until its population reaches the carrying capacity of its environment. When a predator is introduced to the ecosystem, the prey species population generally declines to a level below the carrying capacity of the environment. Finally, when the predator's predator is added to the ecosystem, the predator's population is reduced, thus allowing some recovery in population levels of the initial prey species. This cascade effect is readily observable in MoD.

Competitive exclusion also occurs in the model. The model was seeded with two plant species, one slightly better adapted to the habitat (at 1 locus). The model was tested with the inferior competitor's search template matching the habitat bit pattern at 1, 8, 16, 24, 28 and 31 loci. In each case, the superior competitor's search template matched the habitat in one additional locus. The model was seeded with equal population sizes of each species. A competitive exclusion event was recorded if one species expanded to 90% of the total population in less than 2000 time steps. The model was run 100 times for each of the 6 competitions. In all cases, the superior competitor excluded the inferior one.

The previous experiments were carried out in the absence of evolution. The mutation rate was set to 0. In order to test that simple adaptation occurs in Mod, the model was initialized with an autotroph that matched its habitat in 24 out of 32 loci. This is the expected proportion of matches if both the prey template and the generalism loci were evolving randomly. Adaptation should appear as a increase in the degree of match between the plant and its environment above the level for random mutation. The model was run 32 times for mutation rates of $0.02, 0.11, 0.155, 0.2, 1.1$ and 2 bits flipped on average per genome. In all cases the plants evolved adaptations to their environment as determined by a one-tailed t-test relative to neutral evolution ($p < 0.001$).

5 Experiments and results

MoD was used to test ten different hypotheses for the diversification of life. In all cases, the model was initialized

[1]There are several strange consequences of this implementation of reproductive barriers. The mating relationship is non-transitive. Thus, while two organisms may be members of the same species, they may not be able to produce fertile offspring. However, if two organisms can produce fertile offspring, they must be members of the same species. In addition, a speciation event, the severing of a connected component of the reproductive graph through the removal of a node, may often lead to the creation of more than one daughter species. In other words, speciation events are not necessarily just bifurcations.

[2]The coalescence of species in the history of life is thought to have been a rare event, but little data exists which bears upon this issue.

[3]Plants are not allowed to fill more than half of a patch (1024 organisms) so that they cannot compete with the animals for space.

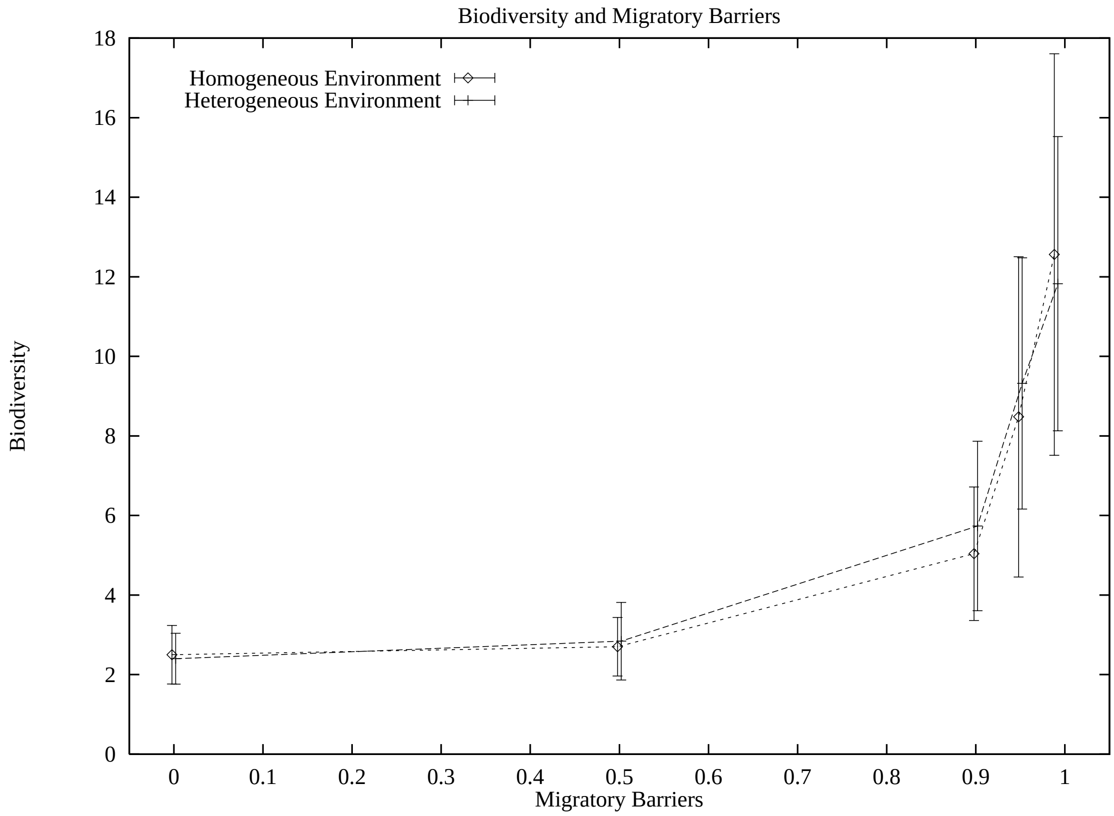

Figure 1: The effect of migratory barriers and habitat heterogeneity on biodiversity. The means of 50 runs in each condition are shown along with standard error bars. Migratory barriers have a strong impact on diversity only when those barriers are high. Habitat heterogeneity appears to slightly increase diversity but the effect is not statistically significant.

with three genetically homogeneous species (plant, herbivore, and carnivore) and then run for 5000 time steps. The number of surviving species was recorded at the end of that time. The model was run 50 times under each parameter setting. In most cases, the baseline for comparison was the result of running the model with no migratory barriers and the same habitat pattern in every patch (a homogeneous environment). Averaged over 50 runs, the baseline condition results in only 2.5 surviving species. Furthermore, most experiments were also run under "heterogeneous environmental conditions." This meant 0.95 migratory barriers and the random flipping of 8 bits in each habitat pattern (resulting in an expected average of 10.3 bits different between any two patches). Under the heterogeneous environmental conditions, an average of 9.32 species are observed after 5000 time steps.

The first two experiments examined the effect of geographical isolation on diversity and the interaction of geographical isolation with habitat heterogeneity. The model was run under $0, 0.5, 0.9, 0.95$ and 0.99 migratory barriers. The third experiment examined the effects of habitat heterogeneity by flipping 8 bits in every patch before running the model. The results of these experiements can be seen in Fig. 1. The following experiments on abiotic factors tested Cracraft's[5] and Vermeij's[40] theories that change in the abiotic environment has been an important cause of diversification. In the fourth experiment, the habitat bit patterns of the patches were independently modified by flipping a bit, selected randomly, once very 156 times steps in each patch. This meant that by the end of 5000 time steps, the habitat in each patch would have changed 32 times. The fifth experiment varied the migratory barriers of all the patches over time so that they followed a sine wave with a period of 500 time steps, a maximum value of 1.0 and a minimum value of 0. In this way the subpopulations were repeatedly isolated and mixed. The sixth experiment involved allowing the migratory barriers of the patches to individually and independently follow a random walk between 0 and 1 with increasing or decreasing steps of 0.05 every time step.

The seventh experiment examined the effect of allowing evolutionary innovations with the potential for species to capitalize on unexploited resources in their environment. A restricted innovation condition was modeled by preventing mutations in 10 loci of the generalism chromosome (set to 0), 10 loci of the prey template chromosome (set to 0), and 10 loci of the predation resistance chromosome (set to 0). This was then compared to evolution when mutations, and thus adaptations, were allowed in all 32 loci of those chromosomes. Similarly, the eighth experiment examined the effects of the evolution of specialism by fixing 10 bits of the generalism chromosome (set to 1). In this restricted specialism condition, all organisms were forced to be generalists in those 10 loci. This was compared to the case where species could evolve specialism in all 32 loci of their generalism chromosome. Finally, the ninth and tenth experiments examined the effects of assortative mating on diversifica-

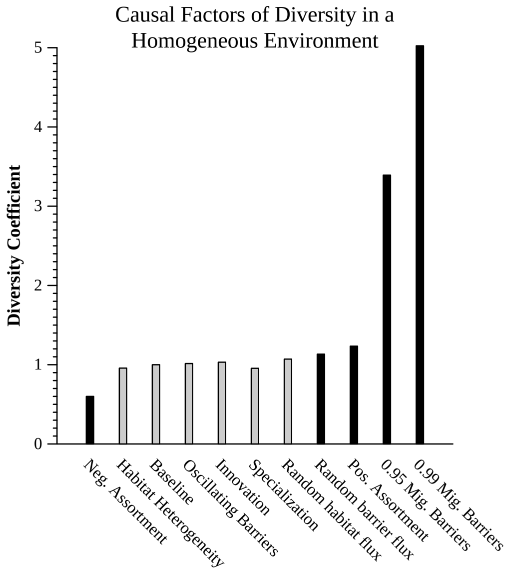

Figure 2: A summary of manipulations to species diversity. The chart shows the manipulations in the context of a homogeneous environment with no migratory barriers. Each effect has been normalized by its relevant baseline. The bars indicate the magnitude of an effect relative to the baseline. The light grey bars indicate that the manipulation had no statistically significant effect. Black bars indicate a significant effect, with p ¡ 0:05.

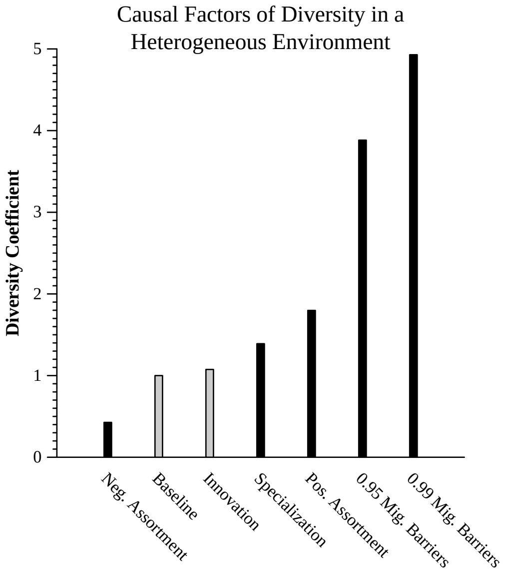

Figure 3: A summary of manipulations to species diversity in the context of a heterogeneous environment and 0:95 migratory barriers. Here the baseline is a heterogeneous environment with 0:95 barriers. In the case of the manipulations to the barriers, the relevant baseline is a heterogeneous habitat with no migratory barriers. Again black indicates a statistically significant effect with p ¡ 0:05.

tion. Both positive and negative assortative mating were examined. Assortative mating was modeled by allowing an organism to consider up to 8 potential mates in its patch. Each of these potential mates were still required to differ from the organism in no more than one locus of their reproductive chromosome. In addition to this, the organism compared its predation resistance chromosome characters—a proxy for observable phenotypic characters—to those of its mates and either selected the most similar (positive assortment) or most dissimilar (negative assortment) of the candidates for mating. The results off all these experiments are summarized in Fig. 2 and Fig. 3.

6 Discussion

The first surprise was that the increased capacity for innovations in resource utilization had no significant effect on diversification. This was the dynamic that Benton[2] thought best explained the increasing diversification of life. The same experiment was run with as many as 28 of the 32 loci fixed, restricting adaptive space dramatically. Yet, even this extreme restriction does not significantly lower diversity levels. Perhaps, in the context of no migratory barriers and environmental heterogeneity, diversity is so low in any case that evolving with just 4 bits in the ecological chromosomes is still not particularly restrictive. However, even in the context of 0.95 migratory barriers and a heterogeneous environment, which results in an average of 9.32 species when there are no restrictions on innovation, these extreme restrictions have no statistically significant effect at the $p = 0.05$ level (diversity = 8.08). This results suggests that we should question one of the basic assumptions of the key innovation perspective. Why should expansion in adaptive space stimulate diversification? There is no direct relationship between adaptive space (a theoretical construct in any case) and speciation. Speciation depends on reproductive barriers. We should certainly expect that key innovations that modify characters involved in reproduction, and perhaps even geographical isolation, should have a strong impact on diversification. But it is much more of a stretch to think that the availability of new resources in and of themselves should stimulate diversification.

This is probably a good time to visit some of the caveats of the model. First of all, the model is extremely simple and abstract. At the base of the food web there is only one resource, energy. The physical environment is not rich by any stretch of the imagination. The biotic environment is only rich to the extent that the organisms diversify. Second, the spatial, population, and temporal scales are far below the scales at which most Paleobiologists work. With only 16 patches, a maximum of 32K organisms, and 5000 time steps (roughly 2000 generations) the model represents evolution and ecosystems on a regional and millenial scale at best. Perhaps at geological scales, there are key innovations that spark adaptive radiations in clades due to some novel way of utilizing resources. Third, it should be noted that we have said nothing about morphological diversity. We have strictly considered only the reproductive concept of species. In the absence of a better understanding of the genetic basis of speciation, all of the diversity dynamics of the model have taken place on a binary hypercube (the space of possible reproductive genotypes in the model).

These caveats may also help to explain the difference between Rice and Hostert's[29] findings that habitat heterogeneity had a strong effect on reproductive isolation and the model's result that habitat heterogeneity had little effect on diversification. MoD's representation of a habitat is, again, extremely simplified. It only directly affects the autotrophs. Yet, if one looks closely at Rice and Hostert's review, we see that divergent selection was only effective at producing reproductive isolation when the subpopulations were physically isolated, the hybrids were removed, or the divergent selection was particularly intense (e.g., 95% of the organisms were killed each generation). In the later case, reproductive isolation arises because the reproductive characters "hitchhike" along with the characters that are being intensely selected. Selection is too intense and quick for recombination to allow the reproductive traits to evolve independently of the selected traits. Simple disruptive selection on an arbitrary character does not tend to produce reproductive isolation[29]. Most of the experimental cases where divergent selection leads to reproductive isolation are not represented in the experiments on habitat heterogeneity in MoD. The one exception is the case of divergent selection in allopatry (physical isolation). In MoD there was one case, when the migratory barriers where 0.9, that habitat heterogeneity had a significant effect on diversity levels ($p < 0.05$).

Let it not be said that niche space has no influence over diversity. Under conditions of habitat heterogeneity and 0.95 migratory barriers, specialization does have a significant impact on diversity. When species are allowed to evolve specialism at all loci of their generalism chromosome, the diversity jumped from 6.7 to 9.32. However, specialization only became important in the presence of migratory barriers and divergent selection. The introduction of heterogeneous habitats with migratory barriers effectively creates more (geographically protected) niches upon which species might specialize.

MoD exhibits a striking influence of geographical barriers on diversification. Simply increasing the migratory barriers to high levels led to a dramatic increase in the number of species. This matches the dominant theory of speciation. Most speciation is allopatric, where populations are physically separated and slowly diverge to the point of reproductive isolation. Note that Fig. 1 shows that the relationship between migratory barriers and diversity is non-linear. This is why the experiment with randomly fluctuating barriers produces significantly more species than its baseline where the all the migratory barriers were held constant at 0.5.

Of particular theoretical interest is the effects of positive assortment. Such behavioral characteristics are difficult to recover from fossil data and so have gone largely untested as factors in speciation. Positive assortative mating significantly increases diversity in MoD under both homogeneous environmental conditions with no migratory barriers, and under heterogeneous environments with 0.95 barriers. Positive assortment acts as a proxy for geographical separation. The populations tend to fracture into the clusters of similar phenotypes (whatever characteristics organisms are using to select their mates) with little mating between these subpopulations. The subpopulations may then diverge to the point of reproductive isolation.

7 Conclusions

The results of the model must be predicated on acceptance of the simplifications in the abstractions and their implementations in the simulations. The results only speak to diversity as identified by isolated gene pools. But as such, MoD suggests that geographical isolation has been of central importance to the diversification of life. Secondarily, positive assortment and specialization may have played important parts in the drama. In addition, the results help to focus our thinking about key innovations. There is no particular reason to think that an innovation related to resource utilization should spark diversification. Rather, innovations that affect reproduction or migration should take primacy in our theories for the causes of an adaptive radiation. These predictions should be tested with laboratory experiments[28, 9, 7], perhaps with *Drosophila* or *Saccharomyces*, as well as comparative phylogenetics[26, 31, 30, 34, 35].

The study of complex systems thrives on the application of knowledge in one field to provide insights and techniques for the study of another. The processes of evolution have been imported into computer science in the form of evolutionary algorithms (EAs). But before we try to extend these results to evolutionary algorithms, we should pause and consider the basis of the analogy and the disanalogy between biological and artificial evolution. Most of the work in EAs has been focused on finding a good or even optimal "solution" to a particular problem. This contrasts with biology and models of biology like MoD in which the only "problem" is to survive and reproduce. In other words, the fitness function in MoD and in biology is endogenous. Secondly, most EAs, with a few exceptions[12, 36], lack coevolutionary dynamics and so have a static fitness function. Finally, to the extent that artificial evolutionary systems have been used to examine diversity, they have tended to focus on genotype diversity[8, 1, 32, 15, 19] rather than species diversity.

In most formulations of EAs, diversity is of interest as a mechanism for searching solution space to find many good solutions, not just the best. This is essentially a genotype diversity issue. However, one of the main lessons of genetic algorithms (GAs) for machine learning is that populations can often search solution spaces more efficiently than individuals. Species diversity may thus form the basis for efficient search of solution space. Deb and Goldberg have already applied positive assortative mating to GAs in order to locate all the local maxima in the fitness landscape. They had particular success when they combined positive assortative mating with "fitness sharing" which negatively related a solution's fitness to the population density of its local in solution space. The addition of fitness sharing effectively imposes a sort of niche space on the solution space by locally limiting the reproductive resources in solution space. Our specialization results would suggest that reducing the distance across which fitness must be shared should boost the absolute number of "species" in the GA. However, it is unclear whether packing more "species" next to each other would improve the GA's ability to locate the fitness optima. Adding geographical separations between subpopulations in GA's is a well known technique for helping to prevent premature convergence. MoD was primarily developed as a tool for theoretical biology, to investigate macroevolutionary dynamics. Much work remains for the future to translate those insights about biology to other fields.

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