Chapter 5

Geography, Habitat, and Productivity

The phenomena that affect the diversification of life can be generally classified into physical, or non-biological, and biological factors. The physical phenomena thought to be important in diversification include changes in geography, climate, and available nutrients. Important biological phenomena include evolutionary innovations that open up the possibility of exploiting new resources, specialization on a small sets of resources or environmental conditions, as well as behavioral interactions within species such as mate choice and sexual selection. This chapter will investigate the impact of manipulations to non-biological parameters on diversification in the model. Chapters 6 and 7 will examine the relative importance of biological phenomena in the diversification of life.

In all of the experiments, there is some baseline condition against which the effects of a manipulation are measured. The default values of the parameters were given in Section 3.6. The most common baseline condition, which I call the "vanilla" condition, was one in which there were no barriers to migration and the environment was homogeneous. That is, all patches had the same habitat, or climate, bit pattern (all 0's). The model is initialized with a plant, a herbivore, and a carnivore species. However, the dynamics of the model are generally dominated by the plant organisms. Why is that?

5.1 The Importance of Being Prey

When two species are bound together in an ecological interaction, they act as important determinants of the selective pressures on one another. In other words, they coevolve. When these interactions are antagonistic, as is the case of a predator-prey interaction, coevolutionary arms races ensue. An adaptation in the prey, making it more difficult to capture and consume by the predator, puts strong pressure on the predator species to evolve an effective response to the prey's defense. Conversely, adaptations in the predator that increase its ability to capture prey, put strong pressure on the prey to evolve further defensive mechanisms to avoid capture. And so it goes, each species upping the ante for the other.

Is there ever a winner? In the model, yes. The stability of the food web was shown under ecological conditions, with no mutation and so no evolution. However, in a single patch simulation, once mutation is turned on, the plants soon evolve predation resistance chromosomes that make them immune to predation and the herbivores starve to death. The predators only have a chance when a multi-patch simulation provides a large enough population base for the predators that beneficial mutations to overcome prey defenses become reasonably likely. This is an evolutionary analog to the ecological "rescue effect" where a local extinction can be reversed by re-invasion of the species from a neighboring patch. Due to the *energy-conversion* parameter, prey populations outnumber predator populations by at least 3 to 1. Prey thus have an evolutionary advantage in their likelihood of discovering useful genetic innovations. This contradicts conventional wisdom in ecology which predicts that individual differences, and their evolutionary effects, tend to stabilize predator-prey dynamics (Crawley 1992). In the real world, the hypothesized advantage of a prey species would be complicated by population sizes and generation times. Small animals that reproduce quickly (like insects) would also gain the evolutionary advantage in numbers that plants enjoy in the model. Both short generation times and high mobility have been implicated in diversification (Marzluff & Dial 1991, for example).

5.2 Barriers to Migration and Habitat Heterogeneity

In the literature that emphasizes physical factors in the diversification of life, most authors have focused on the impact of topography and habitat heterogeneity (Cracraft 1985; Vermeij

1987; Valentine & Moores 1972; Benton 1990; Valentine 1980). Topography, or geography, is primarily important because it can spatially isolate subpopulations. The populations might be divided by a mountain range, a valley, a dessert, a river, an ocean or any other feature that makes migration difficult. All of these features have been abstracted into "migratory barriers" for the model. Once populations are separated, they may genetically diverge either due to random genetic drift or differences in the selective pressures of their separate environments. This brings up the issue of habitat heterogeneity. It seems particularly plausible that subpopulations will diverge if they experience different selective pressures in the form of different habitats. Again, this divergence should be particularly swift if the subpopulations are not exchanging genes through migrant organisms.

The implementation of migratory barriers was described in Section 2.2.3. In brief, a barrier value represents the probability that a new organism fails to emigrate from its current location to a neighboring patch. A heterogeneous environment or habitat was modeled by randomly flipping eight bits in each patch, beginning with all 0's. This results in an expected 5.8 bits set to 1 in a patch's habitat pattern and an expected difference of 10.3 bits between any two patches' climates, or habitats (see Appendix B.1 for a derivation of this difference). In all the following experiments a "heterogeneous environment" refers to this condition of flipping 8 bits in each patch's climate bit patterns.

Figure 5-1 shows the effects of migratory barriers on diversity levels for both homogeneous and heterogeneous habitats. While there is a clear increase in diversity with increasing migratory barriers, the introduction of habitat heterogeneity has surprisingly little impact. An analysis of variance across barrier values of $0, 0.5, 0.9, 0.95,$and 0.99, and habitat variation of 0 or 8 bits flipped in each patch, shows that only the migratory barriers act as a significant determinant of biodiversity ($p < 0.001$). Neither habitat variation, nor the interaction of habitat with migratory barriers are statistically significant factors at the $p = 0.05$ level. T-tests show that habitat variation is only a significant factor in diversity levels when the migratory barriers are 0.9.

Speciation rates seem to be more sensitive to the effects of migratory barriers and habitat heterogeneity, as shown in Figure 5-2. For example, speciation rates at 0.5 barriers are significantly higher than speciation rates with no barriers ($p < 0.001$). In an analysis of variance, both migratory barriers ($p < 0.001$) and habitat heterogeneity ($p < 0.05$) were statistically significant, although their interaction was not ($p = 0.058$). However,

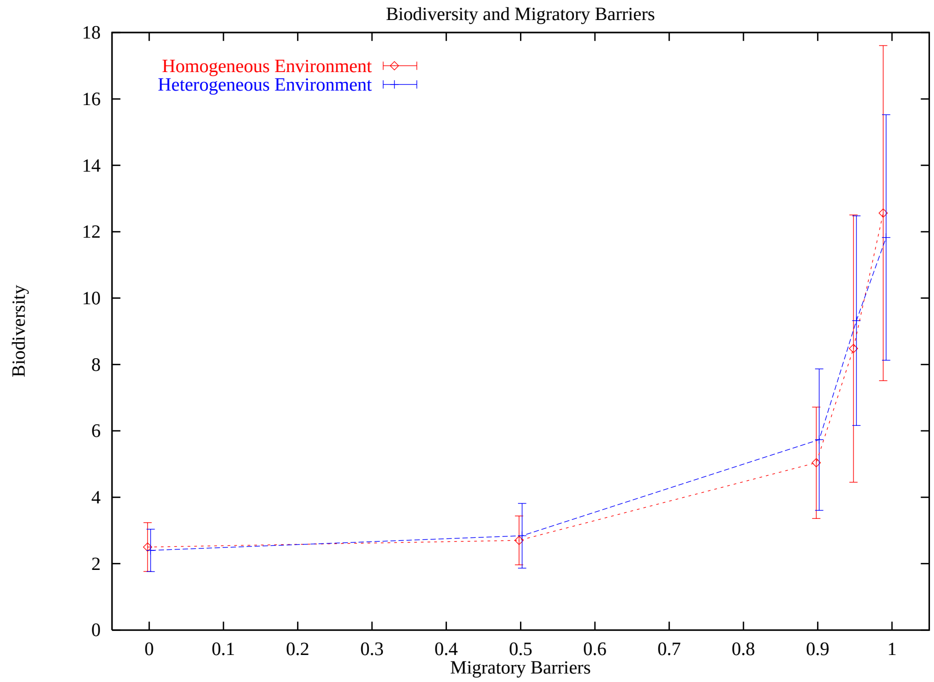

Figure 5-1: The effect of migratory barriers and habitat heterogeneity on biodiversity. The means of 50 runs in each condition are shown along with standard error bars. Migratory barriers have a strong impact on diversity only when those barriers are high. Habitat heterogeneity appears to slightly increase diversity but the effect is not statistically significant.

the apparent crossing of the homogeneous habitat curve and the heterogeneous habitat curve between barriers of 0.95 and 0.99 is significant. At a migratory barrier of 0.95, the heterogeneous habitat incites significantly more speciation events than the homogeneous habitat ($p < 0.001$). Yet, when the migratory barriers are raised to 0.99, the homogeneous habitat leads to a higher speciation rate ($p < 0.001$).

It may appear surprising, particularly to population geneticists, that patches need only be isolated by 0.9 barriers in order to see an effect of habitat heterogeneity. One common result of population genetics is that a very little migration[1] between populations is sufficient to prevent genetic divergence. This is generally measured by the fixation index F which can be interpreted as the chance that two alleles, randomly chosen from a population, are "identical by descent." That is, the two alleles are identical copies of a single allele from an organism that was an ancestor to both of the organisms that were randomly sampled. With 0.9 migratory barriers in the model, we can expect to exchange approximately 5 migrants with a neighboring patch every generation. This means a migration rate of only about

[1] $O(1)$ migrants per generation.

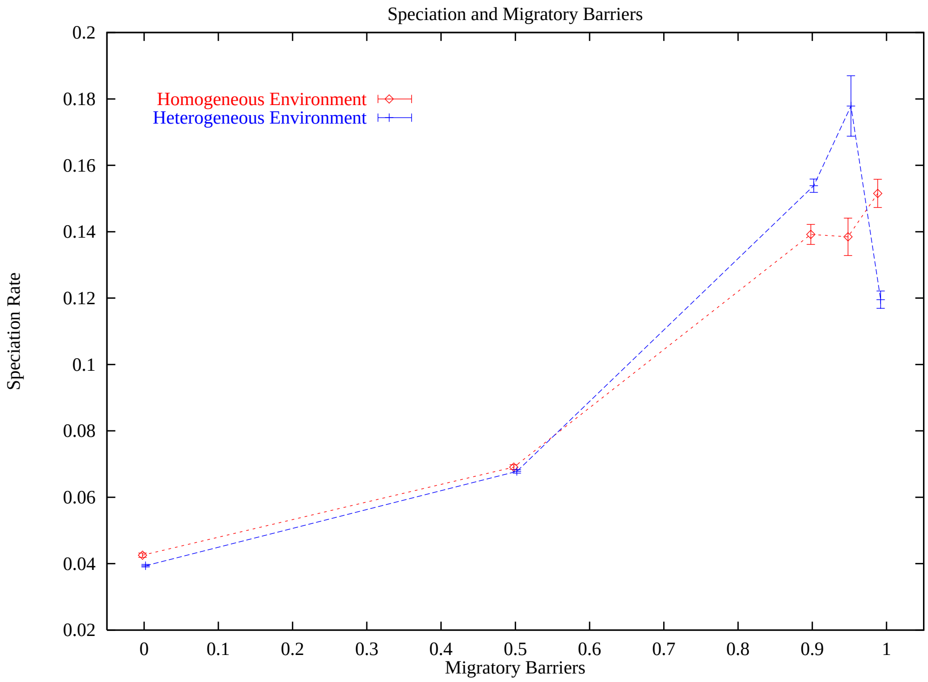

Figure 5-2: The effect of migratory barriers and habitat heterogeneity on speciation rates. Speciation rates also increase with migratory barriers, and even show a response to low (0.5) barriers. Here, habitat heterogeneity has a statistically significant impact on speciation rates.

0.005 between two neighboring patches and a fixation index of $F \approx 0.09$. See Section B.2.3 for a rough derivation of these values. A fixation index of 0.09 is considered to indicate a moderate level of divergence between populations (Hartl & Clark 1997, p.119) and so is consistent with the observed effects.

The combination of migratory barriers and habitat heterogeneity should have an important interaction. Heterogeneity in the environment means that a species that specializes on one habitat may be a superior competitor in that patch but an inferior competitor in another patch that includes the same community of species. The migratory barriers allow the populations of the superior competitors in a patch to expand without losing too many new members to emigration. So the combination of high migratory barriers and habitat heterogeneity allows a variety of species to specialize on a particular patch and coexist comfortably with other species specializing on different patches. It is interesting that this does not emerge as a dominant effect in the model. Even without habitat heterogeneity, the barriers allow reproductively isolated populations to coexist even though they have essentially the same prey search pattern and so inhabit the same niche. A locally dominant population is buffered from competition with rare migrants because the migrants have difficulty finding mates (Bernstein et al. 1985).

5.3 Flux

Some researchers have argued that it is not the mere presence of topographical or climatic heterogeneity that drives diversification. Rather, it is the *changes* in the topography and climate that have stimulated speciation events (Cracraft 1985; Vermeij 1987). These fluctuations might be random or systematic, and where it is appropriate, I have simulated both types of dynamics.

5.3.1 Change in Migratory Barriers

In the previous experiments, the migratory barriers were static. They stayed at the same value throughout a run. The populations of organisms lived within the subdivided environment and, depending on the intensity or height of the barriers, migrants would occasionally slip out of one subpopulation and into a new one. This is a view of organisms acting on top of the environment. What if the environment acts upon the organisms? Some changes in the physical environment may actively divide a population. A change in course of a stream, a forest fire, a falling tree, or other environmental phenomenon might cut off a group of organisms from the rest of a population. Alternatively, geographical changes might also unite previously isolated populations.

Increasing Barriers

Benton (1990) identifies "increased provinciality" as a potential explanation for increasing diversity over time. Given the results of the previous section, this seems reasonable. Certainly when the model was run under higher migratory barriers the diversity increased. Two questions might be posed. First, does an increase in barriers over time lead to an increase in diversities over time? Second, would increasing barriers result in higher diversities than constant barriers?

To address these questions, I let the migratory barriers increase linearly from an initial value of 0 to a final value of 0.99. Figure 5-3 shows the change in diversity levels over time as the barriers increase. Fifty runs of the model resulted in a mean biodiversity of 8.7 and a mean speciation rate of 0.0853 per time step. These are both significantly higher than the biodiversity (2.7) and speciation rate (0.0691) when the migratory barriers are held constant at 0.5. The question arises, is the significant factor here the change in the migratory barriers, splitting apart populations, or do the high biodiversity and speciation rates derive from the final stages of the runs when the migratory barriers were high? Figure 5-3 essentially mirrors the curve of Figure 5-1 and shows that the high diversity levels is only a product of the last part of the run. It is difficult to say whether this is due to the cleaving of populations by the rising barriers or to migrants leaping those barriers and establishing new colonies in neighboring patches. That is perhaps an arbitrary distinction. However, organismal migration generally occurs on a much faster time scale and frequency than geographical changes to migratory barriers. So it is reasonable to say that the presence of the barriers, not their arrival, is the most important factor in diversification.

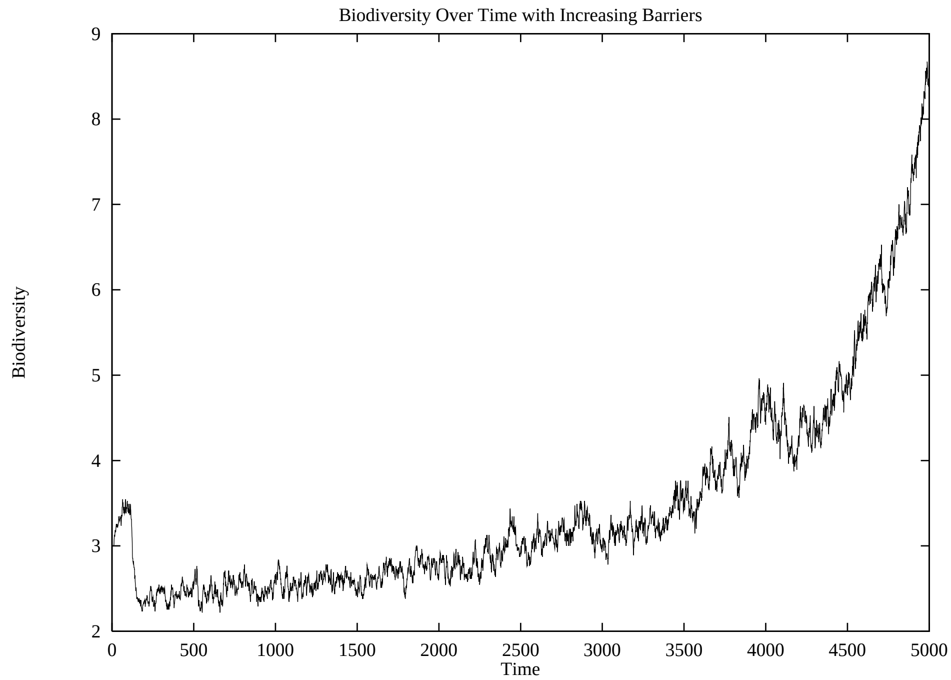

Figure 5-3: The effects of increasing barriers over time on species diversity in a heterogeneous environment.

Figure 5-3 actually shows data averaged over 55 runs with a heterogeneous habitat. This resulted in 8.48 species which was not significantly different from the homogeneous habitat condition with 8.7 species. Speciation rates in the homogeneous (0.0853) and heterogeneous (0.0841) environments were also not significantly different.

Random Fluctuations

Cracraft (1985, p.799) suggests that the important factor in diversification is change in the environment. Unlike the previous experiment, the directionality of that change is unimportant to Cracraft. The environment need not become more fragmented over time, it need only change over time. Perhaps the frequent isolation and then reuniting of populations has a sort of "churning" effect that stirs up diversification. Topographical flux was implemented by allowing the migratory barrier in each patch to individually, randomly change its value by 0.05, either increasing or decreasing by that amount, every time step. In other words, the barrier values of the patches took random walks with 0.05-sized steps. The barriers were not allowed to go below 0 or above 1.

The random walks of the barriers in the patches should average out to a barrier value of 0.5. Thus the constant barrier of 0.5 is the appropriate baseline against which to compare the effect of changing barriers. The introduction of randomly fluctuating migratory barriers generates significantly greater biodiversity (mean = 3.06, $p < 0.05$) than constant barriers of 0.5 which resulted in an average of only 2.7 species after 5000 time steps. Similarly, randomly fluctuating barriers stimulated a significantly higher speciation rate of 0.0782 as compared to a speciation rate of 0.0691 for 0.5 barriers ($p < 0.001$).

Oscillating Barriers

The previous experiment assumed that the migratory barriers in the patches changed independently. This need not be the case. If organisms of a species were constrained to cool climates then long term changes in temperature might alternately confine them to high altitudes when the climate warmed, and release them into the valleys when the climate cooled. The barriers in a region might change in concert. To simulate this, I set the migratory barriers to follow a sine wave with a period of 500 time steps, a minimum of 0 and a maximum of 1, as shown in Figure 5-4.

The resulting biodiversity of 2.74 species was not significantly different from the diversity under 0.5 barriers. However, the speciation rate was (mean = 0.0865, $p < 0.001$). The lack of a significant effect in diversity levels may be due to the fact that all the migratory barriers of the patches were lower than 0.5 for the last 250 time steps of a run. This contrasts with the randomly fluctuating barriers in which at least a few of the 16 patches probably have

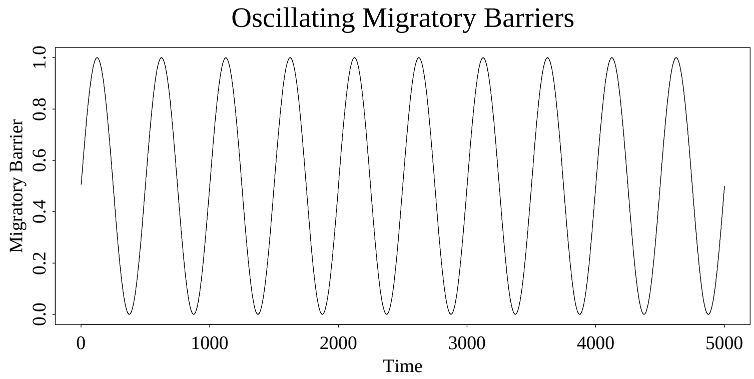

Figure 5-4: The sine wave function for oscillating barriers.

high migratory barriers at any given time.

5.3.2 Habitat Heterogeneity in Time

Cracraft's (1985) emphasis on change was not only directed towards topographical change and migratory barriers. He assumed that most species would be well adapted to their environments and so it would require environmental change, including changes in habitat, to disrupt ecological communities. This disruption might well drive some species extinct but it also might provide new opportunities for other species to diversify.

Random Habitat Fluctuations

I simulated change in habitats by changing the climate bit patterns in the patches over time. All the patches began with the same habitat bit pattern. However, within a patch, and for every time step, there was a $32/5000 = 0.0064$ probability that one bit in that patch's climate pattern would flip. This leads to an expected 32 bit flips in a patch over the entire run of the model. Each patch changed independently of the others. The expected number of bits that differ between any two patches, as a function of time, is plotted in Figure 5-5. This averages out to a 12 bit divergence between patches.

To see if habitat change, and not just habitat heterogeneity, stimulates diversification, we can compare the randomly fluctuation habitat to the "heterogeneous environment." Recall that in the heterogeneous environment the habitat bit patterns in the patches were static though different from each other by an average of 10.3 bits. So we should expect a slightly higher average heterogeneity from the randomly fluctuating habitats. The ran-

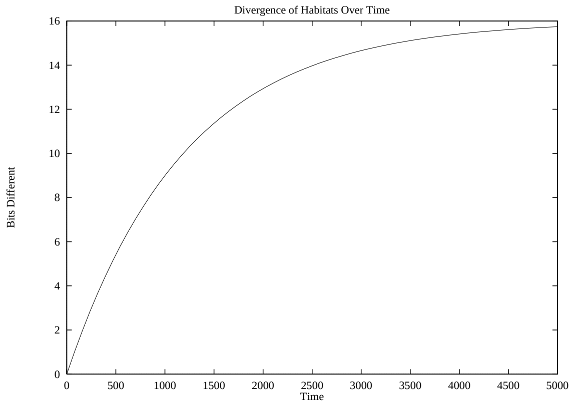

Figure 5-5: The expected number of bits that differ between patches as a function of time, when habitats are fluctuating randomly. This has an asymptote at 16 and a mean value of 12 for the first 5000 time steps.

domly fluctuating habitats result in an average of 2.57 species which is not significantly different from the 2.4 species produced by the static heterogeneous environment. The speciation rates in the two conditions (0.03978 and 0.03939 respectively) are also statistically indistinguishable.

Seasonal Fluctuations

Changes in the climate can play out in both changes to an organism's habitat as well as changes in the productivity of the autotrophs or plants. Productivity in an ecosystem is the rate of energy flow into the autotrophs (Rosensweig 1995). In the model productivity directly corresponds to the *energy-input* parameter. That is, the number of energy units a plant may absorb in a time step if it is perfectly adapted to its habitat. I investigated the effects of fluctuating productivity levels by altering the *energy-input* parameter over time. Specifically, the *energy-input* followed a sine wave with a minimum of 0.2 (a minimum of 0 would have been cataclysmic) and a maximum of 1.8, so as to maintain an average equal to the *energy-input* of the baseline runs. I examined sine waves with a period of 4 time steps, to simulate a sort of seasonal scale of change in productivity. I also examined sine waves with a period of 500 time steps to simulate global warming and cooling dynamics. I will refer to this longer time scale fluctuation as the "ice age" condition. There were no migratory barriers in these runs and the habitats were kept homogeneous. The "vanilla" parameter settings act as the comparison or baseline condition.

Under the seasonal fluctuations in productivity, only 2.3 species survived. This is not significantly different from the biodiversity in the vanilla runs of the model. The diversity dropped further to 2.23 under the ice age conditions. This is significantly lower than the vanilla biodiversity ($p < 0.05$). The speciation rates for both the seasonal fluctuations (0.0381) and the ice age fluctuations (0.0281) are significantly lower than the speciation rates in the vanilla condition ($p < 0.001$). When productivity is low, survival becomes more difficult for the organisms. This probably drives some species extinct, while high productivity periods are not able to compensate with raised raised diversity levels.

Both the seasonal and the ice age fluctuations in productivity were also run with 0.95 migratory barriers and environmental heterogeneity. Perhaps the diversity levels are just too low in the vanilla conditions to see any effects of oscillating productivity. Under these higher diversification settings of the parameters, seasonal fluctuations to productivity have no significant effects on either diversity or speciation rates. The ice age condition also has no effect on diversity, but it has a significantly lower speciation rate (0.0865) than the comparison condition (0.1779) with 0.95 barriers, habitat heterogeneity, and a constant *energy-input* of 1.

5.4 Productivity

The effects of productivity on diversity is a hot topic in Ecology today (Rosensweig 1995; Tilman 1987; Goldberg & Miller 1990). In real ecosystems productivity is often manipulated by altering nutrient levels, rainfall, or sunlight. The basic question has been the relationship between productivity and diversity. However, experiments to investigate that relationship have been hobbled by practical constraints that dictate the manipulation of only small spatial scales over short periods of time. Rosenzweig (1995, p.347) writes:

> [T]he experimental results now available cast little or no light on patterns at larger scales of time and space. None of these experimental results take evolution into account.

The previous investigations into the effects of fluctuating productivity were a little hasty. The more fundamental question is, how are diversity and speciation affected by productivity? This can be tested by running the model under constant *energy-input* levels and measuring the results.

The model was run with *energy-input* values of 1, 3, and 9[2]. A plant may reproduce once for every 3 energy units it accumulates. This means that a plant could reproduce more than once in a time step when the *energy-input* is 9. All three of the *energy-input* levels were run under both homogeneous environments with no migratory barriers as well as heterogeneous environments with 0.95 barriers. The 0.95 barrier value was chosen so as to maximize animal species diversity. While total diversity might have been maximized under 0.99 barriers, such high barriers cause the animal populations to crash. Since productivity in the plants may well have an effect on diversity through the herbivores, 0.95 migratory barriers seemed a more appropriate choice.

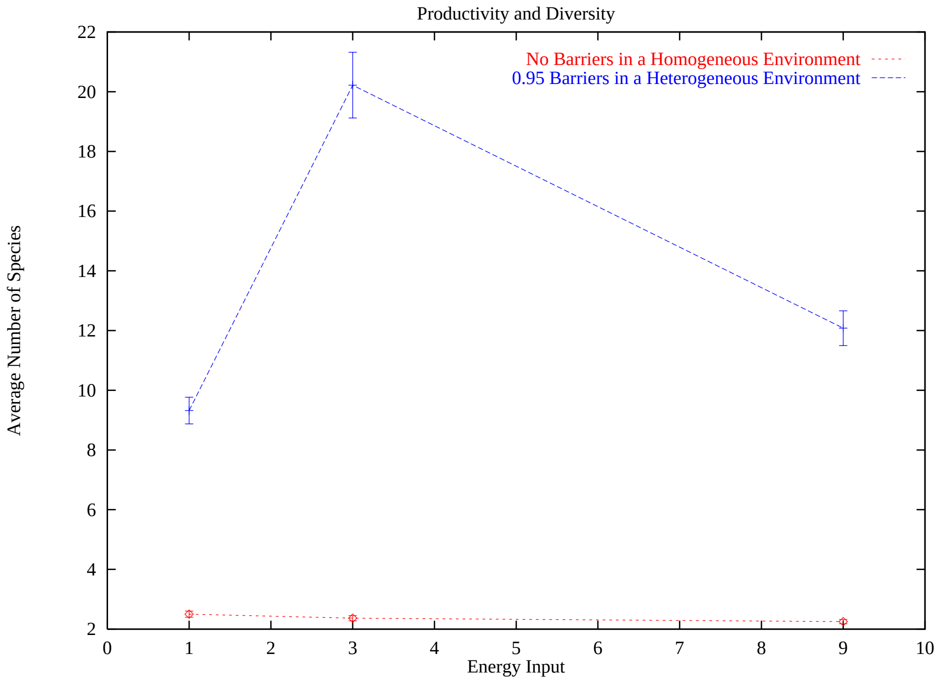

Figure 5-6: The effects of productivity on diversity. The lower curve shows the effects, or the lack of effects, of productivity in a homogeneous environment with no migratory barriers. The upper curve shows that diversity has a non-linear relationship to productivity in a heterogeneous environment with 0.95 migratory barriers. The means are surrounded by standard error bars derived from 50 runs of the model for each parameter setting.

The results for species diversity levels and speciation rates are shown in Figures 5-6 and 5-7, respectively. In a homogeneous environment with no migratory barriers there is no significant difference in diversity levels between the higher productivity conditions and

[2]I chose an exponentially increasing series of parameter settings to maximize the likelihood of finding an effect. Before the experiment, we don't know if the important dynamics only show up at a particular scale in the parameter. The factor of 3 derives from the *energy-conversion* parameter which sets the generation time to 3 time steps.

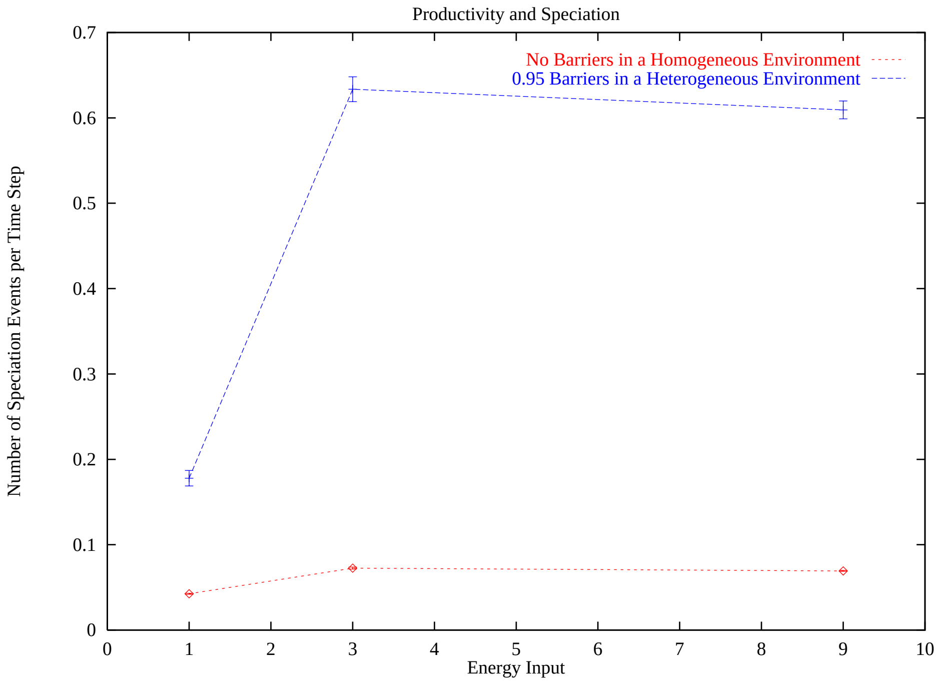

Figure 5-7: The effects of productivity on speciation rates. As before, the upper curve represents the dynamics of a heterogeneous environment with 0.95 migratory barriers. The lower curve has no migratory barriers and a homogeneous environment. The means are surrounded by standard error bars derived from 50 runs of the model for each parameter setting. In all cases, the elevated productivity levels lead to speciation rates significantly greater than the baseline ($energy\text{-}input = 1$). However, for both curves, there is no significant difference between speciation rates with energy inputs of 3 and 9.

the "vanilla" condition ($energy\text{-}input = 1$). However, the lower curve in Figure 5-7 shows that raising productivity did significantly increase speciation rates ($p < 0.001$), though only slightly. When the context is changed to include 0.95 barriers and habitat heterogeneity, the increased speciation rates bear fruit in significantly higher biodiversity levels for the raised productivity conditions ($p < 0.001$).

Productivity seems to have an effect on speciation, but not on diversity levels unless the environment includes heterogeneous habitats and migratory barriers. It is particularly interesting to note that the diversity curve in this case supports Rosenzweig's (1995, pp.345–372) hypothesis that there is a unimodal or "humped" relationship between productivity and diversity at a regional spatial scale.

Rosenzweig (1995) reviews 9 hypotheses for the unimodal relationship between productivity and diversity. Most of these can be rejected as explanations for the results because they depend on factors that do not vary across the experimental conditions in the model.

For example, the amount of area in high and low productivity experiments was held constant, so one cannot argue that low diversity at high productivity is an artefact of the rarity of highly productive areas. Nor can one explain the decrease in diversity due to productivity homogenizing the environment (Tilman 1987). There is no such relationship between productivity and habitat heterogeneity in the model. The model is run over evolutionary time scales, so we can dismiss arguments that are based upon short term ecological disruption. A hypothesized relationship between productivity and disturbance is irrelevant here because disturbance is not modeled. Finally, competition between taxa is also irrelevant because each trophic level begins diversifying from a single species and so is filled by a single taxon. The only remaining explanations are based on arguments that competition must be more intense at intermediate levels of productivity than at either extreme. Yet, the *energy-input* settings of 3 and 9 result in almost identical total population numbers of $20,735$ and $20,725$, respectively. This suggests that the effect is not simply due to competition for space.

The explanation for the unimodal relationship between productivity and diversity rests on the phenomenon of migration in the model. There are two countervailing forces in the model. First off, an increase in productivity, which increases the number of new organisms generated per time step, raises the amount of genetic upheaval. Mutations are tabulated at the point of reproduction[3]. Also, crossover between the parental chromosomes introduces new combinations of genes to the population. Because of the finite carrying capacity of the patches, these new organisms are replacing their parent's generation at a faster rate under high productivity levels. So an increase in productivity should stimulate genetic change and thus diversity. However, an increase in productivity also leads to more migration between patches. As we know from the experiments in Sections 5.2 and 5.3.1, the prevalence of migration between patches has a dramatically negative affect on diversity. To see that productivity affects the amount of migration between patches, first consider the vanilla condition of the model. One third of the organisms, on average, will reproduce in a given time step, because they can collect a maximum of 1 energy unit per time step, and the *energy-conversion* parameter specifies that it requires 3 energy units to reproduce. In the worst case, from the perspective of the migrants, the population is at carrying capacity and only half of the new organisms will survive, replacing other organisms in the patch. So, at

[3]We may assume that mutations actually accumulate in the germ line of an individual throughout its life span. However, these need only be tabulated when one of the mutant germ cells forms a new organism.

the least, 1/6 of the population in the next time step will be composed of new organisms[4]. If we raise the productivity by increasing the *energy-input* to 3, then roughly all of the plants will reproduce in a time step and half of the next generation will be composed of new organisms. With an *energy-input* of 9, the parental population will be swamped with approximately three times their number in new organisms. At some point, the boost to diversity given by the genetic turnover in the populations will be offset by the homogenizing effect of migration between patches. Extreme productivity does not homogenize the habitat as proposed by Tilman (1987). Rather, the subpopulations across the environment become homogenized through migration. This is why we only see the unimodal relationship between productivity and diversity under high migratory barriers.

5.5 Conclusions

Despite claims of the importance of a dynamic environment, barriers to migration overshadows all other factors. The relative effects of all the manipulations can be seen in Figure 5-8. Each of the effects has been normalized against its baseline. The red bars indicate manipulations that result in significantly different diversities or speciation rates relative to the baseline.

The central message in the results is that barriers to migration have dramatic effects on both speciation rates and diversity levels. The results provide little support for the importance of habitat heterogeneity. Speciation rates are much more sensitive to manipulations than diversity levels. In many cases an increase in speciation rates did not lead to a significant change in diversity. This emphasizes again the common conflation of speciation with the success of the new species. Species diversity levels must be a function of both speciation rates and factors that help to maintain those new species.

The comparison of the bar charts in Figure 5-8 is particularly illuminating. The productivity experiments with *energy-input* of 3 and 9 in a homogeneous environment with no migratory barriers results in high speciation rates but has no effect on diversity levels. The increase in speciation rates is probably due in part to larger population sizes under the

[4]In the 0.95 migratory barrier condition that was explored here, most of the new organisms in the next generation are not migrants, due to the high probability that the barriers will prevent them from leaving. Yet, the number of migrants will always be a fixed proportion of the new organisms (in this case approximately 4.9% as derived in Appendix B.2.3). As the proportion of new organisms in a patch increases, so does the proportion of migrants.

high productivity condition. When *energy-input* is 3 and 9, the average total population at the end of 5000 time steps was $20,735$ and $20,725$ respectively. Both of these are significantly higher than the average of $17,507$ organisms produced by the vanilla conditions of the model ($p < 0.01$). The same effect of population size on speciation rates can be seen at the opposite end of the spectrum. When the *energy-input* oscillates over a long period in the "ice age" condition, the average final population size is $13,372$ which is significantly below the vanilla condition ($p < 0.01$), and the speciation rate is also significantly lower. However, this explanation for differences in speciation rates only works for the experiments that manipulated the *energy-input* parameter. The oscillating barrier condition maintained significantly fewer organisms than the constant 0.5 barrier condition ($p < 0.05$), yet it supported a significantly higher speciation rate.

The benefits of isolating subpopulations have long been known in the field of evolutionary algorithms (Tanese 1989; Belding 1995; East & Rowe 1996; Cohoon et al. 1987). When these algorithms are used to try to find optimal solutions to various test problems, a "distributed" algorithm, with individuals segregated into subpopulations along with occasional migration between populations, they tend to out perform algorithms with fully mixed populations. The distributed algorithms typically attain higher maximal fitness values (Tanese 1989; Belding 1995; East & Rowe 1996), as well as maintain greater genotypic diversity (East & Rowe 1996).

The importance of geographical isolation of populations reinforces Orr's (1995) result that populations will quickly diverge and form new species if they are separated. It also supports the dominant allopatric theories of speciation, but without any reference to differences in the selective pressures on the different populations. The central role of migratory barriers in speciation and diversity is not a new discovery. It is thought to be the main explanation for the estimated 800–900 different species of fruit fly amongst the Hawaiian islands (Andersson 1994, p. 209). However, the relative importance of migratory barriers, to the exclusion of all other factors tested thus far, is a startling result of the model. Still, we have not yet begun to dig into the heart of the matter. It is oft said that the most important aspect of an organism's environment is other organisms. It is now time to turn to the relative importance of biotic factors that may influence diversification.

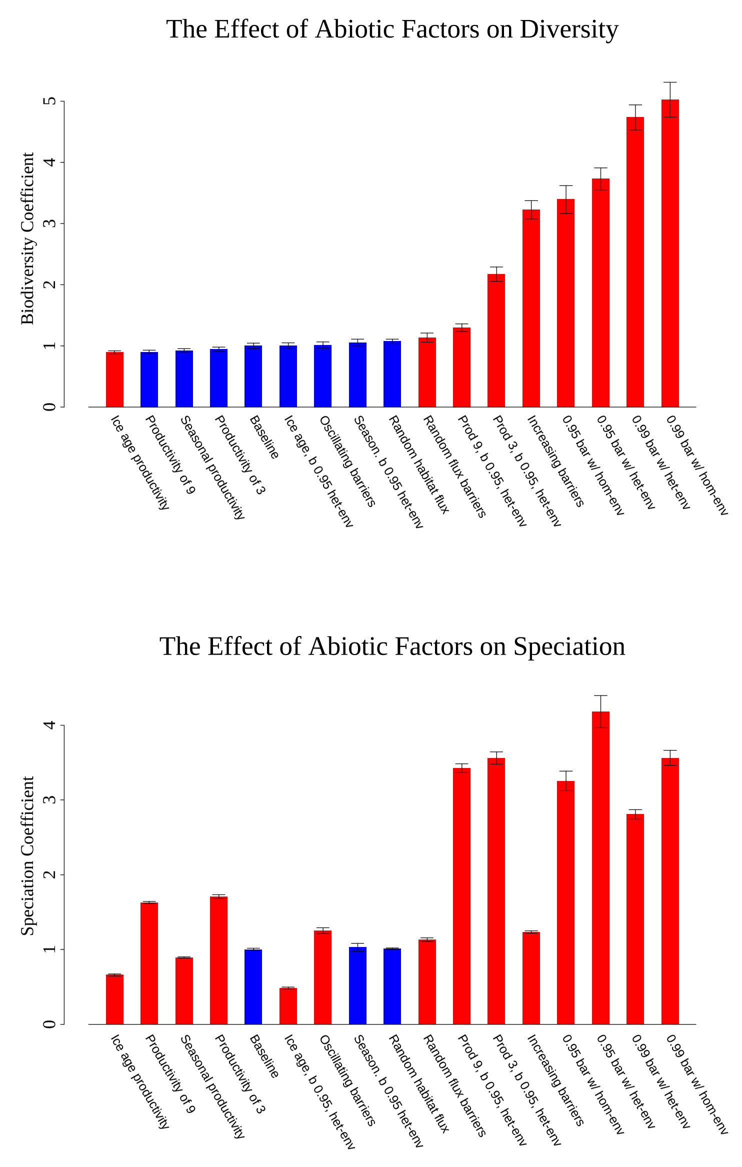

Figure 5-8: A summary of the non-biological effects on species diversity (top) and speciation rates (bottom). Each effect has been normalized by its relevant baseline. The bars indicate the magnitude of an effect relative to the baseline. The blue bars indicate that the manipulation had no statistically significant effect. Red bars indicate a significant effect, with $p < 0.05$. Abbreviations include “b” and “bar” for migratory barrier, “het-env” for heterogeneous environment, “hom-env” for homogeneous environment, “season” for seasonal, and “prod” for productivity.