Chapter 6

What's in a Niche: Specialization and Innovations

As scientists, and perhaps more generally as humans, we tend to look under the lamp post. We focus on what is easily discernible, and often fail to notice that important questions have been left behind in the dark. Even within our pool of light, we act like crows. We are particularly attracted to the bright shiny objects. In the study of evolution this has meant focusing on the evolutionary innovations in taxa as causes of diversification (Slowinski & Guyer 1993). We are drawn to the drama of our creation from the relatively homogenous primordial soup, as well as the flowering of diversity all around us. What could be more compelling in that story of emergence than the innovations that have repeatedly unlocked the gates to a new Eden.

6.1 Niche Space

In the previous chapters, I have often referred to adaptive space. Adaptive space is imagined to be a many dimensional space which maps an organism's phenotype (one dimension for each relevant phenotypic character) onto a fitness value. The fitness value is an additional dimension and is conceptualized to be the "altitude" of a point in space. Thus the language of fitness "peaks" and "valleys."

Ecologists and evolutionary biologists often work with a related conceptual tool, niche space. This is the space of all possible niches. But first, what do we mean by a niche? Colwell (1992) has reviewed the often subtle controversy between two basic interpretations of the term. Under one interpretation, a niche is an aspect of the environment, an "opportunity for survival and reproduction." Colwell calls this the *environmental niche* concept. In contrast, the *population niche* concept identifies a niche as an aspect of a population in relation to its environment. It is, at heart, just "an ecological description of the phenotype of some particular population or species." It is impossible for a *population niche* to be empty. Under the *population niche* concept species do not adapt to a niche, rather they merely adjust their niche. The distinction hinges in part on whether you want to emphasize the action of the environment on the evolution of species (the *environmental niche* concept) or the action of the species to define and shape its own environment (the *population niche* concept). The work of Valentine and Walker, which models the dynamics of taxa filling and relinquishing discrete locations in niche space, implicitly subscribes to the *environmental niche* concept (Valentine & Walker 1986; Walker 1985).

The metaphors of niche space and adaptive space imply the use of the *environmental niche* concept. One might try to force a *population niche* interpretation upon niche space by characterizing how populations flow across that space. But if there is no representation of differences in the viability or fitness in that space, we are simply talking about character space, with special reference to ecological characters.

For any given ecological model, it may be difficult to describe what the viable locations are in niche space, however, the formalizations of the model will bound that space. For example, in our model, we know that the genomes[1] include 160 bits and so there are 2^{160} potentially different organisms. Due to the generalism chromosome, many of these organisms will be ecologically equivalent, though not evolutionarily equivalent. The same mutation in two ecologically equivalent organisms will not produce the same behavior in the mutant organisms. Only a few of the niches in the model can be determined from a description of the initial state of the model. Given the bit patterns of the habitats in the patches, it is easy to describe viable genotypes for plant organisms. However, since organisms eat each other, the success of most genotypes will depend on the current population of both prey and their predators. Furthermore, the composition of these populations evolves over time and so viable niches will shift over time. A niche is thus a characteristic of the environment only if we avoid a naive interpretation of "environment" which fails to consider

[1] Recall that there is no distinction between genotype and phenotype in the model. The bits of the "genome" alternatively stand for the inheritable characters of an organism's phenotype.

the ecological context of an organism.

If we are careful to avoid the conflation of speciation and the survival of the new isolated gene pools (see Chapters 4 and 5), the concept of niche space is a useful tool for thinking about the factors that determine how many species can coexist in the environment. Two major dynamics stand out from this perspective. If you want to feed more guests, you can either cut the pie into smaller pieces, or you can bake more pies. That is, species may specialize on a small fraction of the niche space. This fine grained division of niche space allows the packing of more species into a fixed amount of the space. More intriguing, however, is the possibility that a species may evolve some innovation that opens up vast new tracts of niche space that were previously uninhabited. The descendants of that species are then free to diversify into all those unfilled niches. Think of plants colonizing land, or the evolution of the hard egg shells that allowed reptiles to sever the bonds to water in their life cycles.

Benton (1990) noted a correlation between diversification and an expansion in the habitats and diets of tetrapods (four legged vertebrates). In addition, Benton cites the increased diversity in comparable groups of tetrapods over the same surface area as evidence for increased specialization.

Bambach (1985) has compiled a vast description of the changes in diversity of the classes of marine life.

> [I]ncrease in diversity is achieved only by organisms that develop features that permit them to utilize more ecospace (the multidimensional hypervolume of ecologic resources such as food, mode of life, behavior, physiologic tolerance of ambient conditions, etc.). (Bambach 1985, p.240)

Among the more striking examples of innovations that have allowed the utilization of more ecospace are the evolution of multicellularity, predation, and burrowing behavior to colonize the sediments[2] just below the sea floor.

Ausich and Bottjer (1985) also note a correlation between diversity and "tiering" in their suspension feeding marine communities. Tiering is the vertical range between the deepest burrowers to the highest altitude organisms living in and about the sea floor. Over time this range has extended in both directions. Ausich and Bottjer argue that this is indicative of an

[2]Marine biologists refer to this as an "infaunal" life style.

expansion into new niches as well as more finely subdividing previous niches. However, they explicitly avoid the claim that there is a causal connection between tiering and diversification (Ausich & Bottjer 1985).

These theories depend on the connection between the evolution of ecological traits and the formation of species. Under the reproductive species concept, this implies a connection—perhaps a completely indirect connection—between the genes that code for ecological characters and the genes that code for reproductive characters. If such a connection exists, it is not well understood (Schluter 1996). The assumption is that once the niches have sculpted the ecological characters of population, reproductive isolation from other populations will follow. One might even postulate selection for mutations that prevent an organism from mating with dissimilar organisms. Organisms that try to mix their genes with organisms that lacked their specific ecological adaptations may well produce poorly adapted hybrid offspring. The accumulation of mutations that prevent these hybrid matings is called speciation by reinforcement (Liou & Price 1993). In the following experiments, we will be concerned with the occupation of niches described by the characters that effect resource utilization and predator-prey interactions. The results do not bear on a wider conception of "population" niches that include such characters as reproductive and dispersal behavior or other aspects of an organism's life history.

6.2 Specialization

How has the capacity to specialize, to narrow one's occupation of niche space, affected the evolution of diversity? Specialism may interact with diversification through natural selection against hybrids. If two subpopulations specialize on different resources or habitats, then hybrids from matings between the two subpopulations may be ill fit to survive on either resource (Schluter 1996). This selection against hybrids might isolate the subpopulations enough that genetic drift in the reproductive characters would establish pre-mating barriers and thus cause a speciation event.

In the model, we have a direct handle on specialization through the generalism chromosome of the organisms. By setting portions of this chromosome to 1's, producing wild-card positions in the prey search pattern, and preventing those loci from mutating, we can enforce various degrees of generalism on the organisms. In other words, we can "clamp" a portion of the generalism gene such that it always stays "on." This may be compared to the "vanilla" condition of the model. The change from the restricted condition to the vanilla condition shows how the increased ability to subdivide niche space influences diversification.

The model was run with the upper 10 bits of all the organism's generalism chromosomes fixed to 1's. This prevented specialization in that range of the genome. The results listed in Table 6.2 includes data for runs with no migratory barriers in a homogeneous environment as well as runs with 0.95 migratory barriers and a heterogeneous environment. These results, like all of the results exhibited in this chapter, are the averages of at least 50 runs of the model under each set of parameter values.

Condition	**Species Diversity**	**Speciation Rate**
Restrictions on specialization	2.62	0.04349
Allow specialization	2.50	*0.04254
Restrictions on specialization with 0.95 barriers and hetero-environment	6.70	0.20154
Allow specialization with 0.95 barriers and hetero-environment	***9.32	*0.17786

Table 6.1: The results for allowing specialism to evolve. The * indicates statistical significance at the $p < 0.05$ level. The *** indicates significance at the $p < 0.001$ level. There are significant effects in the heterogeneous environment condition with 0.95 migratory barriers for both an increase in biodiversity ($p < 0.001$) and a decrease in speciation rates ($p < 0.05$). In the vanilla condition, the only significant effect of allowing specialization is a slight reduction in speciation rates ($p < 0.05$).

Specialism seems to have a particularly strong effect on diversity levels when the population is subdivided by barriers to migration and the patches have different habitats. Diversity is boosted despite the slight drop in speciation rates. This means that extinction rates dropped even further than speciation rates. A decline in extinction rates is consistent with the common ecological dynamic of species avoiding competition by specializing on relatively unexploited resources. Though it should also be noted that specialization can also make a species more vulnerable to extinction due to changes in the available resources.

6.3 Evolutionary Innovations in Niche Occupancy

A similar experiment may be performed to examine the effect of allowing the organisms to explore previously restricted areas of adaptive space. By preventing mutations in the middle 10 bits of the prey template and generalism chromosomes, we prevent organisms from being able to exploit any resources in that area of adaptive space. Similarly, by preventing mutations in the predation resistance chromosome, we prevent organisms from escaping predation in that area of adaptive space. In combination, these restrictions prevent the exploitation of novel resources as well as the escape from predation pressures. Note that in a heterogeneous habitat, some of the bits of the habitat bit patterns will be set to 1 in this restricted area. This means that while the clamps are on, plants will not be able to exploit the full range of resources in their environment. The innovations that effect resource utilization and predation interactions are only a subset of the evolutionary innovations that may affect diversification. The results from Chapter 5 imply that innovations that affect dispersal should have important consequences on the diversification of a species. However, here I am seeking to test the hypothesis that expansions in niche space occupancy, the exploitation of previously unutilized resources and the avoidance of predation, increases diversification.

Once again, I compared the results of evolution under these restrictions against the baseline conditions with no restrictions on adaptive space. Table 6.3 shows the data for runs under a homogeneous environment with no migratory barriers as well as runs under a heterogeneous environment with 0.95 migratory barriers.

Condition	**Species Diversity**	**Speciation Rate**
Restrictions on innovation	2.42	0.04348
Allow innovation	2.50	0.04254
Restrictions on innovation with 0.95 barriers and hetero-environment	8.67	0.21515
Allow innovation with 0.95 barriers and hetero-environment	9.32	***0.17786

Table 6.2: The results for allowing evolutionary innovations in predation interactions and resource utilization. *** indicates a significant difference from the baseline with $p < 0.001$. The only effect occurs under a heterogeneous environment with 0.95 migratory barriers. In this case, evolution in the expanded adaptive space results in a suppression of speciation.

The only observed effect appears when migratory barriers are high and there is habitat heterogeneity. In this case, releasing restrictions on innovations significantly reduces speciation rates. The change in species diversity levels is not significant. It seems that allowing the exploration of untrammeled niche space does not stimulate diversification, but may even suppresses it.

6.4 Extreme Restrictions on Niche Space

The preceding results are based on restricting 10 out of 32 bits in each of the ecological chromosomes. Perhaps the loss of 10 bits just is not particularly restrictive to the evolution of the ecosystems. We are dealing with only an average of 9.32 species in the most diverse case. Perhaps the set of 2^{22} possible genotypes for each ecological chromosome is large enough that the restrictions on innovations in predation interactions never really impact the evolution of the species. Would we see an effect if niche space were to be drastically reduced? A pair of experiments were run under a heterogeneous environment with 0.95 migratory barriers. However, this time, 28 of the 32 bits in the ecological chromosomes were fixed. In the case of the specialization experiment, 28 bits of the generalism chromosome were fixed as 1's. In the case of the predation innovation experiment, 28 bits of the predation resistance chromosome, the prey template chromosome, and the generalism chromosome were fixed as 0's. Thus, each restricted chromosome could only take on a possible 16 different states.

Condition	**Species Diversity**	**Speciation Rate**
Extreme restrictions on specialization with 0.95 barriers and hetero-environment	6.92	0.20096
Allow specialization with 0.95 barriers and hetero-environment	***9.32	*0.17786
Condition	**Species Diversity**	**Speciation Rate**
Extreme restrictions on innovation with 0.95 barriers and hetero-environment	8.08	0.212644
Allow innovation with 0.95 barriers and hetero-environment	9.32	***0.17786

Table 6.3: The results for extreme restrictions on niche space. The data come from running the model with 0.95 barriers to migration and a heterogeneous environment. *** indicates a significant difference from the baseline with $p < 0.001$ and * indicates $p < 0.05$.

Table 6.4 shows the results for the extreme restrictions on niche space. The extreme restrictions have the same effects as the mild restrictions. Restrictions on specialism reduces diversity but increases speciation rates. While, restrictions on innovations in the predation interactions has no significant effect on diversity levels yet significantly boosts speciation rates.

6.5 The Cost of Generalism

It is time to revisit an early assumption. Perhaps the reason restrictions on innovations in niche space have so little, or even a negative, impact on diversification is that there is no advantage to specialization in the model. This seems counterintuitive, and indeed, for most of the history of ecology we have assumed that generalists must be worse at exploiting resources as compared to a specialist. Yet, this assumption is controversial.

> Although intuitively appealing, this concept of a reduction in efficiency with niche width has proved notoriously difficult to confirm empirically. Indeed, where a general trade-off between diet breadth and efficiency has been investigated, experimental confirmation has been relatively unusual. (Dall & Cuthill 1997)

The debate has shifted to searching for trade-offs between specialism and generalism that have gone unnoticed in these efficiency studies. Dall and Cuthill (1997) argue that generalists should not be able to track all of the relevant ecological variables of their different habitats as well as a specialist that remains within its specialty. In addition to the efficiency of resource utilization, other important ecological pressures include the avoidance of predators, the location and courtship of mates, and direct competition with other organisms in the environment.

Before we add an artificial trade-off to the model, we should be clear about what it would tell us. Up until now the results argue that with no trade-off between generalism and other beneficial traits, the capacity to expand into unexplored niche space does not stimulate diversification. If the addition of a trade-off changes this, such that innovations do have a significant impact on diversity, we can only argue for their importance predicated on an assumption that has resisted empirical confirmation. While innovation of ecological characters may seem like an intriguing, and even compelling factor in the evolution of diversity, it rests on a rather shaky limb that the empiricists have been busily sawing.

Selection for specialization of a preference for a resource does not require increased efficiency in one habitat at the expense of another. It only requires that some traits vary in their effects across habitats (Fry 1996). For example, the proboscis of a mosquito may be a good instrument for extracting blood from many kinds of animals. However, if it is particularly effective for extracting blood from a human, then that species of mosquito will be selected for specialization on human hosts. Dall and Cuthill's (1997) discussion of the costs of generalism caution us that we need not be simplistic in the design of a trade-off between generalism and specialism. The costs of generalism may play out in increased susceptibility to predation, the consumption of suboptimal prey, and reproduction, in addition to the more traditional view of a loss of efficiency in resource utilization.

The choice of implementation for a trade-off between generalism and some other benefit is, as usual, somewhat arbitrary. Furthermore, the simplicity of the model imposes its own set of constraints. Four possible elaborations of the model suggest themselves. First, we might make it more difficult for generalists to find a mate. Second, we might make it easier for predators to locate generalists. Third, we might raise the threshold of "meals" required for a generalist to reproduce. This would effectively lower the efficiency with which a generalist transforms prey matter into generalist matter. And finally, we might make it more difficult for generalists to gather resources.

The first suggestion, that generalists have a harder time finding a mate, lacks a biological motivation and seems exceptionally arbitrary. The second suggestion, that generalists are exposed to predation is at least biologically motivated. A generalist would have to defend against predators in all of the habitats in which it thrives. It is probably difficult to evolve cryptic coloration or chemical defenses that work well across a heterogeneous environment. However, since most of the diversification in the model happens at the autotroph level, and herbivores do not generally thrive, it is unclear that predation represents a strong enough selective pressure to have much of an effect. The third suggestion is to raise the *energy-conversion* parameter for generalists from 3 to some higher number. While this need not be an integer, by allowing reproduction with probability proportional to any fractional part, this seems like an awfully crude hammer with which to hit the generalists. In comparison, the fourth suggestion seems better in that it also changes resource utilization efficiency, but in a more flexible and subtle manner.

Consider penalizing a generalist by reducing the chance of consuming a prey organism in proportion to the number of generalism bits that were used to match the prey's predation resistance chromosome. Under this suggestion, a generalist would suffer no penalty if its prey template chromosome exactly matched the prey's predation resistance chromosome. This meets Fry's (1996) criterium that a trait should vary in its effect across habitats or resources. More interestingly, it spans all of the three genetic effects on generalism that Thompson (1994) describes. Recall that a gene that allows the utilization of a new resource may have one of three effects. It can act independently of genes for utilizing other resources. In the model, the addition of a wild-card bit to an organism's generalism chromosome allows the utilization of new resources without affecting its utilization of other resources. A gene may also positively contribute to the effects of other genes for resource use. This is a generalization of the previous effect. In the model, a single bit mutation may allow the utilization of one or many new resources depending on the nature of the resources. For example, if two species of prey both tend to have 1's in a particular locus of their predation resistance chromosomes, then a mutation to a 1 in a predator's prey template gene would facilitate the exploitation of both of those species. Finally, a gene can interfere with the effects of other genes for resource utilization. Flipping a bit in the prey template chromosome, depending on the resources available in the environment, may reduce the predator's ability to utilize some resources at the exchange of facilitating the use of others.

A trade-off was introduced between generalism and the efficiency of capturing and utilizing food sources. Recall, from Equation 2.2, that the probability that a predator consumes a prey organism is a function of the match between the predator's search pattern and the prey's predation resistance characters. A trade-off was implemented by penalizing the match of a generalist predator to its prey by half a bit for every wild-card position in the predator's search pattern that was used. A wild-card position was considered useful if that loci would not have matched the prey in the absence of the wild-card bit. For example, consider a single locus in the ecological chromosomes. If a predator had a 1 in that position of its generalism chromosome (a wild-card) and a 0 in that position of its prey template chromosome, then if it tried to capture a prey organism with a 1 in that position of its predator resistance chromosome, the predator would only score 0.5 for the match at that position. However if the predator had a 1 in both its generalism and its prey template chromosome, then it would have scored a full 1 bit match at that position. So a generalist only suffers a disadvantage when its generalism is relevant to its survival. This is a fairly weak form of a trade off. A generalist can be just as good as a specialist at utilizing a resource if they have identical prey template chromosomes. However, now a generalist cannot be as effective as two different specialists. The generalist will suffer a penalty when trying to exploit any resource that does not exactly match its prey template.

Condition	Species Diversity	Speciation Rate
Restrictions on specialization with 0.95 barriers and hetero-environment	5.58	0.08158
Allow specialization with 0.95 barriers and hetero-environment	***9.32	***0.17786
Condition	**Species Diversity**	**Speciation Rate**
Restrictions on innovation with 0.95 barriers and hetero-environment	10.48	0.25312
Allow innovation with 0.95 barriers and hetero-environment	9.32	***0.17786

Table 6.4: The results for extreme restrictions on adaptive space with a trade-off between generalism and prey capture. The data come from running the model with 0.95 barriers to migration and a heterogeneous environment. *** indicates a significant difference from the baseline with $p < 0.001$.

Once again, the same comparison was made to the results of the model with no restrictions on specialism or innovation. However, this time, in an attempt to up the ante so as to find *any* effect, 28 loci of the 32 bit chromosomes were restricted. The organisms could only freely evolve in 4 of the 32 bits in their ecological chromosomes. However, there is a difference this time when specialism is restricted. Previously, when 10 bits of the generalism chromosome were clamped at 1, mutations in the predation resistance chromosomes at those 10 loci had no effect. Now, given the trade-off between generalism and specialism, the states of those bits in both the predation resistance and the prey template chromosomes matter. To maximize the chance of finding an effect, the model was run with 0.95 migratory barriers as well as a heterogeneous habitat. The results are given in Table 6.5. The combination of trade-offs and these extreme restrictions on specialization dramatically reduces diversification in the model. Or, vice versa, allowing specialization increased both biodiversity and speciation rates. Yet again, the opening of adaptive space for evolutionary innovations in resource utilization and predation interactions only reduces speciation rates and has no effect on diversity levels. In summary, the addition of a trade-off between generalism and prey capture, along with extreme restrictions on adaptive space do not produce any qualitatively different results from the mild restrictions on adaptive space examined in Sections 6.2 and 6.3.

6.6 Heterotroph Diversities

Restrictions to adaptive space can have an interesting effect on the coevolution of predators and prey. When there are no restrictions on adaptive space, very high barriers (e.g., 0.99) lead to the extinction of the animals. It seems that the small population of animals in a patch is not adequate to the task of tracking the evolution of plants as they change their predation resistance chromosomes. When the barriers are lower, the animals have a combined population size large enough that mutations will arise to counter the plant's adaptations in the evolutionary arms races.

The average biodiversity with no restrictions on adaptive space and 0.99 barriers is 11.83. All of those species are plants. The average biodiversity with the same barriers but mild restrictions on adaptive space (preventing mutations in 10 loci of the predation resistance, prey template, and generalism genes) leads to the evolution of a whopping 37.51 extant species. Needless to say, these two conditions are significantly different ($p < 0.001$). Yet if we look at this condition more closely we see that only 10.63 out of 37.51 species are plants[3]. There is no significant difference between the number of plants in the two different conditions. It is the remaining average of 26.88 animals that makes all the difference. The animals thrive under mild restrictions in adaptive space. This effect makes it appear that an expansion of adaptive space dramatically lowers species diversity. In contrast, the animals do not die out when migratory barriers are set to 0.95. And so the comparison between the conditions with and without restrictions on adaptive space, under 0.95 migratory barriers, is a better indicator of the general dynamics of the ecosystem.

6.7 Conclusions

Figure 6-1 summarizes the results from all the experiments on specialization and evolutionary innovations in resource utilization and predation interactions. The first thing to notice is that there were no parameter settings under which the availability of additional niche space significantly increased diversification. In fact, allowing the populations to ex-

[3]On a few occasions the model recorded more extinctions than speciations amongst the animals. However, the total number of speciations minus the extinctions matched the final biodiversity. Clearly something went wrong in the labeling of the species. This is a bug, also known as a "feature" in computer science, in the algorithm for tracking the trophic level of the species. It is a bug in the algorithms that record the data, not in the algorithms that produce the data. I have excluded these cases from my analyses of animal diversities. Yet, the results that distinguish plants from animals should be treated with caution.

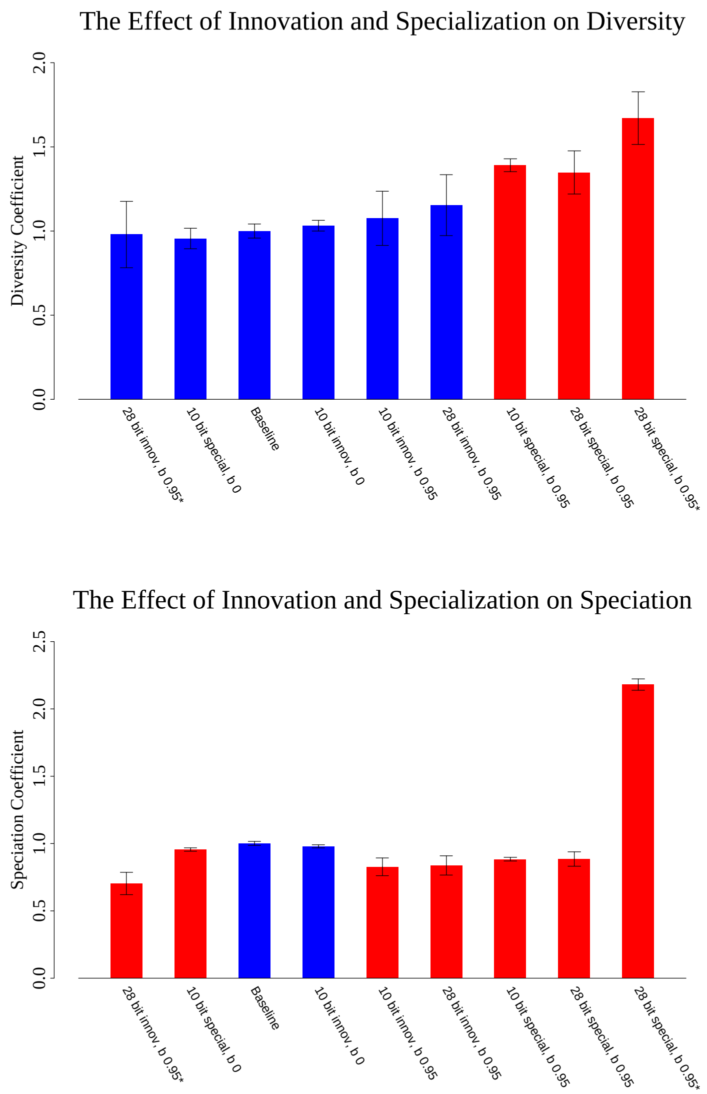

Figure 6-1: A summary of the effects of innovation and specialization on species diversity (top) and speciation rates (bottom). Each effect has been normalized by its relevant baseline. The bars indicate the magnitude of an effect relative to the baseline. The blue bars indicate that the manipulation had no statistically significant effect. Red bars indicate a significant effect, with $p < 0.05$. The conditions have been labeled by the number of bits that were fixed or clamped, out of a total of 32. Abbreviations include "b" for migratory barrier, "innov" for innovation and "special" for specialism. The * marks the runs in which there was a trade-off between generalism and prey capture.

plore new niche space often significantly reduced speciation rates. In contrast, even mild restrictions on specialism had a significant effect on diversification. Specialism seems to facilitate the maintenance of diversity. McPeek (1996) argues that a trade-off between generalism and specialism is necessary to force species to segregate in niche space and thus diversify. The dynamics of the model make this position untenable. Increased capacity for specialism generally lead to an increase in biodiversity. However, the results suggest a restriction of the assertion to speciation rates, not diversity. The increased capacity for specialization generally lowered speciation rates while maintaining greater diversity. The only observed example of an increase in speciation rates was in the runs with a trade-off between generalism and specialism.

The fact that innovations in resource utilization and predation interactions do not seem to increase diversification may be due in part to the simplicity of the model. Heard and Hauser (1995) hypothesize three basic mechanisms by which an innovation might increase speciation. (1) It may allow a lineage to escape competition. (2) It may increase individual fitness. This in turn should increase the population sizes in species with that innovation and so reduce the probability of extinction. One might also add that increased population sizes may provide more opportunities for speciation through mutation and emigration. (3) An innovation may allow more specialization. While innovations in the model can easily boost fitness or increase opportunities for specialization, escaping competition is more difficult. Though it is technically true that a mutation in a prey template chromosome or a generalism chromosome could open up resources that were previously unused, the reality of the matter is that such a mutation would probably just give a lineage an advantage over its competitors. In almost all cases, such a mutation would merely help the lineage exploit a resource that was already under moderate use. Even a slight match of a plant to its habitat gives it a chance of survival. This means that there is probably never a patch completely devoid of plants. So the only reasonable case of an unexploited resource is a plant species that has no predators. In this case, that plant species would likely drive its competitors, who suffer predation, to extinction, and thereby drive the predators extinct as well. An innovation that truly provides new resources in the model is probably rare.

The space limitations in a patch, along with the *energy-conversion* parameter restrict the number of viable trophic levels in the model. This may prevent the kinds of shifts in ecosystem organization that Bambach (1985) identifies as important correlates of increasing diversity in marine life. The model may not allow for that kind of complexity.

Both specialism and innovation have been investigated in the context of predation and resource consumption. While this is fairly reasonable for specialism, evolutionary innovation certainly extends far beyond such a restrictive domain. If it is true that innovations in predator-prey relationships have little impact on diversification, innovations may have dramatic impacts on diversification by way of other aspects of an organism's life history. In fact, the model clearly predicts that an "innovation" that reduces migration between populations of a species should significantly contribute to the future diversification of that species. Cracraft (1990) argues against the idea that an ecological innovation that opens up new adaptive space or facilitates specialism has been a causal factor in the diversification of life. He suggests that for an innovation to stimulate speciation, it must directly impact the processes of speciation through an increase in population isolation, mutation rates, or the fixation of mutations in populations. Most proposed "key innovations" fail to satisfy these conditions (Cracraft 1990). Hunter (1998) adds that there is little evidence for selection directly on characters responsible for speciation. The results of the model seem to support Cracraft's position on innovations, but contradict his dismissal of specialism as an important factor in diversification.

In order to reject Cracraft's position, future work might focus on models in which an evolutionary innovation might allow a lineage to escape competition. Alternatively, the evolution of characters that affect speciation and extinction rates might be examined to test their relative importance against the more typical key innovations of ecological characters.

Another important avenue of research would be to study the evolution of characters that allow reproductive specialization (Hunter 1998). Reproductive specialization might be implemented through characters for mate compatibility or mate preference. The next chapter will examine the effects of enforcing various mate preferences on the populations of organisms.