UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

INCREASE AND MAINTENANCE OF COMMUNITY DIVERSITY BY POSITIVE FREQUENCY-DEPENDENT PREDATION IN THE TIERRA SYSTEM

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

Degree of

DOCTOR OF PHILOSOPHY

By

JIE SHAO
Norman, Oklahoma
2012

INCREASE AND MAINTENANCE OF COMMUNITY DIVERSITY BY POSITIVE FREQUENCY-DEPENDENT PREDATION IN THE TIERRA SYSTEM

A DISSERTATION APPROVED FOR THE
DEPARTMENT OF BIOLOGY

BY

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Acknowledgements

When someone asked me why I came to OU, I always answered with pride: “Because I love Tierra and my advisor is the creator of the Tierra system”. “Self-replicating computer programs (digital creatures) freely evolve inside a computer and spontaneously diversify to various types of forms”, “Just like the creatures living on another planet, digital creatures which evolve in their silicon world experience a completely different environment than the organic life on earth.” … I was fascinated by those descriptions of the digital world in Tierra. To me, it was a research field combining deep scientific inquiry with imagination. Although by the time that I came to OU, my advisor, Dr. Thomas S. Ray, had started a new research direction, he fully respected my interest in Tierra and gave me complete freedom to choose any research topic that I would like to explore for my Ph.D. study. After I decided my research topic, Dr. Ray gave me very detailed guidance on how to design a digital predator, which parts of the programs in Tierra I should modify to implement predation and what kinds of built-in software tools in Tierra I could use to speed up my work. When I encountered difficulties in my research, Dr. Ray was always available to help. I especially appreciated that when my simulation results did not work out well, he always saw clearly where the problems were and guided me to the correct directions. Besides the tremendous help that Dr. Ray gave me when I worked on the simulations, he also spent a substantial amount of time reviewing my dissertation, providing deep-thought and detailed comments, which greatly improved the quality of my dissertation. With Dr. Ray’s help and guidance, my adventure in Tierra was very enjoyable and fruitful. What I learned most from Dr. Ray was the passion for research. I will never forget what he once told me: “I believe that we do our best job when we follow our passion.” I am very grateful for the opportunity that Dr. Ray provided me to do the research work of my dream.

The professors on my thesis committee, Dr. James N. Thompson, Dr. Jeffrey F. Kelly, Dr. Kenneth R. Hobson, Dr. Nikola P. Petrov and Dr. Michael Morrison, were very supportive of my research work. They carefully listened to my research topic and guided me to read the books and papers in the fields of evolution, ecology, genetics and non-linear dynamics. Those readings not only markedly extended my knowledge in those diverse fields but also helped me develop deep thoughts on my research challenges. During each year’s committee meeting, they always provided valuable feedback and suggested new ideas for me to improve my work. Without their generous help, some very nice simulation results would not exist in my dissertation.

The Department of Biology kindly offered me a teaching assistantship, which provided the crucial financial support for my Ph.D. study, as well as a rich teaching experience for my future career. Without this assistantship, my dream of pursuing a Ph.D. degree would not be possible.

My parents, Zuhong Shao and Wenzhen Pu, gave me all the love, support and moral education which helped to shape my personality and ultimately my desire to study at the Ph.D. level. My sister, Ying Shao, was my best friend throughout my life. She fully understood and supported my passion for science and always gave me very good suggestions when I faced difficult personal problems during my Ph.D. study. Finally, my fiancé, Dr. Alex A. Freitas, completely understood that my Ph.D. degree was crucial to my future research career. He came to Norman to visit me several times every year, patiently waiting for me to finish my Ph.D. study. Moreover, he proofread all the chapters in my dissertation and provided me many valuable advices on my Ph.D. research. Alex gave me all his love and always did his best to help me. I feel very lucky that I have met him in my life.

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Abstract

Ecological communities often contain a wide diversity of species but how different species may arise and stably coexist, especially in homogenous spatial environments, is poorly understood. In this dissertation, I use the well-known digital life system, Tierra, to explore the influence of predation on community diversity in a homogenous environment. In order to introduce predation into the Tierra system, I design a digital predator whose survival and reproduction depend on the amount of CPU energy acquired through predation. This energy dependence of predators on their prey robustly generates a “Lotka-Volterra-like” cyclic oscillation in Tierra. This cyclic outcome suggests that the design of digital prey and predators may capture some essential properties of the predation relationship observed in nature.

After predation is built into the Tierra system, I study two predation strategies that predators may use when encountering two or more different types of prey, namely, proportional predation and positive frequency-dependent predation. I block all the mutations in Tierra so that predators and prey interact with each other in an ecological scenario. The simulation results show that a predator population with positive frequency-dependent behavior maintains a stable coexistence of multiple competing prey species, but a predator population with proportional predation behavior fails to do so. Further studies on the underlying mechanisms of the maintenance of prey diversity reveal that by consuming disproportionately more of the common prey type than of the rare one, positive frequency-dependent predation essentially provides a strong negative feedback regulation on prey populations, which tends to equalize the abundances of different prey species and thus results in a stable persistence of prey diversity.

Therefore, in contrast to the previous studies which questioned whether the mechanism of positive frequency-dependent predation functioned at a population level, the simulation results here strongly support that a population of frequency-dependent predators has the potential to maintain the diversity of prey species in nature.

Besides their effects on maintaining prey diversity, the two predation strategies are further examined from the perspective of enhancing the fitness of predators when they feed on two different types of prey. The simulation results show that when the predators with one predation strategy become the dominant type, they change the relative abundance of two prey types in such a way that favors, rather than depresses, the predators with the other predation strategy. This mutual support, rather than exclusion, allows the two predation strategies to be comparably competitive and thus may coexist in the population or either one of them may go extinct.

With the understanding of prey diversity maintained by a population of predators with positive frequency-dependent behavior in the ecological scenarios, I proceed to explore the changes in community diversity influenced by predators during evolution when various types of mutations in Tierra are turned on to allow digital creatures to evolve. The simulation results show that the community with persistent intensive predation robustly exhibits significantly higher diversity than the community without predation. Therefore, positive frequency-dependent predation may also be able to promote and maintain a high level of diversity in an evolving ecological community. In addition, with the presence of predation in the community, the sizes of digital creatures remain relatively constant during evolution, which prevents the loss of complex structures in the genomes of creatures as well as promoting rich interactions among creatures. This suggests that the community of prey and predators may maintain interesting ecological dynamics through longer periods of evolution. Furthermore, as digital creatures constantly adapt to their ever-changing biotic environment, a coevolving pattern between prey and predator populations spontaneously emerges in Tierra: prey mutate their templates to avoid being found by predators and predators evolve their templates to circumvent the escape strategy developed in the newly evolved prey. These reciprocal adaptations may continuously create new niches and thus drive the evolution of prey and predators in the digital community.

Chapter 1: Introduction

In this chapter, I review a few classic papers and recent studies on the increase and maintenance of high species diversity in homogenous environments by predation (in addition to the literature review in this chapter, more literature review on “Lotka-Volterra” cycles, proportional predation, especially positive frequency-dependent predation, are included in chapters 2, 3 and 4 where each of those topics is studied in detail). Then I briefly describe the history of digital life and emphasize its recent applications to explore general principles in evolutionary biology. After that, I introduce the well-known digital life system, Tierra, which I use to investigate how a population of digital predators with positive frequency-dependent behavior may promote and maintain high community diversity during evolution. Finally, I lay out the questions that are examined in this dissertation.

1.1 Effects of Predation on the Increase and Maintenance of Species Diversity in Homogenous Environments

Species diversity is one of the most ubiquitous and spectacular phenomena in nature, but how it may arise, persist and shape the evolutionary process is still far from being fully understood. One of the ecological theories proposes that in a homogenous environment, high species diversity may be achieved by predation. Due to competitive exclusion, many species may be driven to extinction by a few dominant competitors. But this reduction of species diversity can be avoided by the presence of predators. Predators limit the populations of dominant prey species and thus more resources become available to support the survival of other species. This predation mechanism to prevent the loss of prey diversity has been supported by several classic and elegant experimental studies. For example, Paine discovered that without the predatory sea star *Pisaster*, the dominant competitors, mussels and barnacles, began to occupy more and more space and eventually crowded out other invertebrate prey species in the area. The 15 prey species that stably coexisted in the presence of sea stars rapidly decreased to 8 species after the predator was removed (Paine, 1966; Paine, 1974). Morin observed a similar effect of predation on the abundances of different prey species, as he studied a vertebrate predator, newt (*Notophthalmus viridescens*), feeding on 3 species of larval frogs (*Scaphiopus holbrooki*, *Hyla crucifer* and *Bufo terrestris*). In the absence of predation, *Scaphiopus* tadpoles dominated the pond along with some *Bufo*, but *Hyla* population was almost driven to extinction. However, with the introduction of newts which preferentially fed on *Scaphiopus* and *Bufo* tadpoles. *Hyla* population markedly increased and the 3 frog species coexisted in the community with a more even relative abundance (Morin, 1981).

Recently, research has begun to reveal that in addition to maintaining prey diversity in ecological scenarios, predators may also act as a selection force to promote the diversification of prey species. For example, Fine *et al*. found that tree species that lived on nutrient-poor white-sand soils (white-sand soil specialists) were different from those that lived on nutrient-rich lateritic red-clay soils (clay soil specialists). However, this difference was not caused by the soil types, but rather by the herbivores that inhabited the white-sand soils. When the tree seedlings of clay soil specialists were transplanted to white-sand soils, in the absence of herbivores, they actually survived significantly better than the tree seedlings of white-sand soil specialists. However, under the attack of herbivores, white-sand soil specialists outcompeted clay soil specialists. Meanwhile, probably due to resource demands to maintain herbivory defense, white-sand soil specialists could not grow as fast as clay soil specialists on the clay soils. Therefore, herbivores may facilitate habitat specialization, which besides allowing different tree species to coexist, may also promote new tree species to emerge (Fine *et al*., 2004; Marquis, 2004). This predation initiated diversification process in prey was also reported by Eklöv and Svanbäck, as they found that predation risk in different habitats may induce morphological changes in prey fish (Eklöv and Svanbäck, 2006). Nosil and Crespi conducted a field experiment to examine the influence of visual predators on the divergence of *Timema* walking sticks. Their results demonstrated that two ecotypes of walking stick insects differed significantly in their phenotypic traits and this difference was strongly positively correlated with the divergent selection imposed by bird predators (Nosil and Crespi, 2006). In addition to field studies in which the consequence of predators on prey divergence may be examined, well-designed laboratory experiments allow researchers to directly observe the ongoing process of prey diversification under predation. For example, bacterium *Pseudomonas fluorescens*, when incubated in static broth cultures, rapidly evolved phenotypic diversity: from the isogenic population of a single smooth morph (SM) to 3 coexisting morphs (smooth (SM), wrinkly spreader (WS) and fuzzy spreader (FS)), with each occupying a different place in the spatially heterogeneous environment provided by the static cultures (Rainey and Travisano, 1998). By constantly shaking the cultures, Gallet *et al* created a homogeneous environment for *P. fluorescens* and found that the ancestral SM morph did not diversify. However, after the predator *Bdellovibrio* *bacteriovorus* was introduced into the cultures, WS and FS morphs emerged. Those results suggested that in the presence of predation, the phenotypic diversity of *P. fluorescens* could also be achieved in a spatially homogenous environment (Gallet *et al*., 2007). Brockhurst *et al*. conducted a similar experiment but used viral parasites (bacteriophage). Besides demonstrating that the presence of parasites increased the phenotypic diversity of *P. fluorescens* in homogenous environments, they also revealed that predation or parasitism may generate novel ecological opportunities for prey to evolve resistance or escape strategies and thus result in the diversification in prey species (Brockhurst *et al*., 2004).

On the other hand, stable coexistence of multiple prey species, generated and maintained by predation, provides more feeding options for predators. To avoid competing for the same resource, predators may also diversify to different species, with each specializing on a different prey type (Stanley, 1973). Therefore, predation may have the potential to facilitate the increase of diversity in both prey and predator species.

1.2 Studying Evolutionary Challenges by Using Digital Creatures

The earliest study of digital life began around the mid 1980s as researchers tried to invent computer programs that were able to reproduce themselves. Mutations did not occur, thus those self-replicating programs could not evolve (Dewdney, 1984). Thomas Ray was the first to create freely evolving digital life. In his “Tierra” world, digital creatures competed for limiting resources, CPU time and memory space, for their survival and reproduction. The genomes of digital creatures, composed of machine instructions, were continuously modified by random mutations which provided the creatures with the potential to evolve a variety of adaptations to their ever-changing environment, as described in detail in section 1.3 (Ray, 1991). Many design features in Tierra were later adopted by Christoph Adami as he developed digital life in the Avida system. Besides self-replication, the digital creatures in Avida could also receive data input, carry out computations and output results, and earned extra CPU energy to speed up their replication if they evolved pathways to perform correct calculations. Through the evolution of computational ability, complex digital creatures were first observed to emerge from their simple ancestors in Avida (Wilke and Adami, 2002; Adami, 2006). Currently, the evolution of digital life inside a computer has become an alternative but powerful experimental method to explore general principles in evolutionary biology. In addition to strikingly fast generation times of digital creatures (on the order of seconds), the evolutionary experiments in the digital world can be accurately repeated and thoroughly analyzed: almost any variables in the experiments can be manipulated and be precisely measured; moreover, complete genetic information of all digital creatures can be recorded, which allows one to trace back any evolutionary path of interest. Therefore, by examining the evolution of digital creatures, researchers may be able to address some fundamental questions that are difficult or impossible to study with organic life forms (Wilke and Adami, 2002; Adami, 2006; O'Neill, 2003).

Many studies have demonstrated the power of using digital creatures to unravel evolutionary challenges. For example, Lenski *et al.* explored a long-standing question in evolutionary biology — how can complex features in organisms be generated by random mutations and natural selection? Through tracking the evolutionary path from an ancestral digital creature with a complete lack of computational ability to its remote descendant which performed a complex logic function by coordinately executing many machine instructions in its genome, and examining the consequence of every mutation in the intermediate genomes along this pathway, Lenski *et al*. showed that the ancestral creature first, by a relative few mutations, evolved the ability to perform simple functions. Those groups of machine instructions which were responsible for carrying out simple computations served as building blocks, from which the instructions for executing the complex function emerged. They also found that not all the mutations were beneficial but deleterious mutations were often necessary for the appearance of the subsequent beneficial mutations. Furthermore, the ability to perform the complex function could be achieved through many different evolutionary paths, which indicated that the origin of complex features by random mutations and natural selection may occur with a high probability, rather than being a rare event (Lenski *et al.*, 2003). Lenski *et al.* also studied interactions among mutations in the genomes of digital creatures and found that antagonistic epistasis (a deleterious mutation at one site mitigated the deleterious effect of a mutation at another site) was much more significant in genomes with a complex structure than in simple genomes. This epistasis allowed complex genomes to be less influenced by deleterious mutations (Lenski *et al.*, 1999). Ostrowski *et al*. investigated the transition process from generalist to specialist by examining the evolutionary path of digital generalist creatures which were able to perform different logic functions. They found that when the digital creatures evolved the ability to perform one function very efficiently, they often lost the ability to perform other functions, through neutral and deleterious mutations (Ostrowski *et al*., 2007). Due to their simple genomic structures, digital creatures were not able to store resources for subsequent use. This feature was exploited by Kraaijeveld as he investigated the costs of parasite resistance in the absence of resource reallocation. He found that as digital creatures competed for limiting resources for their reproduction, the host genotypes which evolved better resistance to parasites had a slower replication rate than the susceptible host genotypes in the environment lacking parasites. Therefore, resistance to parasites may also be costly when resistance was not resource based (Kraaijeveld, 2007).

Long-term evolutionary patterns, which may be difficult to study with organic life forms due to their long generation times, are frequently explored in the digital world. For example, research on macro-evolution showed that in the evolving digital community, long periods of stasis during which the genomes of digital creatures remained relatively constant, were often interrupted by brief periods of rapid change during which the structures of genomes were dramatically modified, allowing a significant increase in the fitness of digital creatures (Ray, 1991; Ray, 1994; Adami, 1995). This intermittent picture of evolution observed in the digital community was consistent with the pattern that occurred in long-term experiments with *Escherichia coli* (Lenski and Travisano, 1994) and supported the punctuated equilibrium theory (Gould and Eldredge, 1977). Adami *et al*. examined the changes of genomic complexity in digital creatures over more than 10,000 generations and reported that a distinctive increase in complexity occurred, along with a jump in the fitness of digital creatures, during a major evolutionary transition (Adami *et al*., 2000). Yedid and Bell systematically varied one of the crucial parameters of the evolutionary process — mutation rate, to observe its consequence on the digital community. Their results showed that at low mutation rates, as a beneficial mutant emerged, it quickly became a dominant genotype, reaching an abundance of more than 80% and the succeeding dominant genotype was always the direct descendant of the current dominant type. However, at high mutation rates, the dominant genotype typically had an abundance of less than 40% and coexisted with many rare genotypes in the community. The succeeding dominant genotype often originated from a non-dominant type. Those results suggested that classic periodic selection may only apply to the cases of very low mutation rates, thus new theories may need to be developed to explain the evolutionary patterns in a community with high mutation rates (Yedid and Bell, 2001). Wagenaar and Adami investigated the effect of history on adaptations when digital creatures were transferred from one environment to another and found that the digital creatures were able to quickly adapt to the new environment by evolving new computational ability to acquire extra CPU energy. However, their fitness in the new environment was affected by their history of living in the old environment and this historical influence was less significant when the two environments were different than when they were similar to each other (Wagenaar and Adami, 2004).

The mechanisms of increasing and maintaining community diversity during evolution in a spatially homogenous environment have also been investigated by using digital creatures. For example, Cooper and Ofria studied the influence of resource availability on the evolution of diversity in a digital community. They provided nine different computational resources in the environment which rewarded digital creatures with extra CPU energy if they developed the ability to correctly perform the calculations. They found that when those resources were depletable (that is, as more individuals consumed a resource, the resource level would decrease, which reduced the benefit gains to further exploit this resource), high genotypic diversity emerged and persisted in the community and coexisting genotypes often specialized on using different resources. However, as they increased the resource level to be infinite, that is, a resource was always available regardless of the number of creatures that consumed it, the diversity disappeared and the community was dominated by a single genotype. Their results supported the idea that competition for limiting resources may be fundamental to the rise of community diversity (Cooper and Ofria, 2002). This mechanism of density-dependent resource consumption was further examined by Chow *et al*. as they explored the relationship between the rate of resources flowing into the digital community (productivity) and the species richness in the community. They found that species richness achieved its maximum value at an intermediate productivity level, rather than at low and high productivities, which suggested that sufficient but limited resources could facilitate the speciation process among digital creatures (Chow, *et al*., 2004). Zaman *et al*. studied the effects of parasites on host diversity in the evolving digital community and revealed that the host population that coevolved with parasites exhibited a higher diversity than the host population that evolved alone. Moreover, the evolving host-parasite community was more diverse than the host-parasite community lacking continuous new mutations (Zaman *et al*., 2011).

With these successful and convincing studies with digital life, more and more researchers are starting to recognize that these non-carbon based life forms may provide important contributions to our understanding of the evolutionary process in organic life.

1.3 Tierra System

Tierra is a virtual computer which implements Darwinian evolution inside a real computer. It operates on a block of RAM memory, referred to as the "soup", where digital creatures "live" and actively interact with one another. The "genome" of each digital creature consists of a sequence of machine instructions which, when being executed, allow the creature to reproduce itself. The Tierran virtual operating system specifies the mechanisms of the allocation of memory space and CPU time among creatures. Moreover, to achieve the simultaneous survival of many digital creatures in the soup, the operating system emulates a parallel execution of the genomes of different creatures by allowing each creature to execute a small portion of its genome in turn. Old and defective creatures are constantly removed from the soup to provide space for newborn creatures. Furthermore, various types of mutations occur in Tierra to modify the genomes of creatures and thus produce new genotypes. Those mutations may arise as background noise, similar to the effect of cosmic rays, to change the machine instructions of any creatures in the soup, or may occur during the replication process and cause some instructions in the daughter cell to be different from those in its mother cell. With the continuous emergence of new genotypes by mutations and selection favoring the genotypes that successfully acquire resources to replicate themselves in the highly competitive environment, the evolution of a digital ecological community begins in Tierra (Ray, 1991).

Most evolutionary simulations use some pre-defined criteria to evaluate the fitness of each individual in the population. Then based on its fitness value, each individual is assigned to leave a certain number of offspring to the next generation.

However, in nature, there are no explicit criteria; instead, the fitness of an individual is directly measured by its ability to survive, and by the number of offspring it produces. This implicit fitness function is fully achieved in Tierra as creatures compete for limiting resources (CPU time and memory space) for their survival and reproduction. The digital creatures which acquire more resources may leave more descendants in the soup. More importantly, digital creatures are able to enhance their fitness by evolving novel strategies to exploit one another. For example, after the soup was dominated by populations of creatures that were able to reproduce by themselves, digital parasites emerged which relied on some machine instructions in their hosts (normal self-replicating creatures) to complete their reproduction process. This exploitation of the genomes of other creatures allowed parasites to significantly reduce their size and under selection favoring smaller genomes, digital parasites flourished in the soup and caused their host populations to decline (a separate ecological run showed that the digital host and parasite populations essentially exhibited a “Lotka-Volterra” cycle). Surrounded by abundant parasites, some hosts evolved resistance to parasites and became the dominant genotypes in the soup. Later on, the populations of those immune hosts were invaded by a new type of parasite which developed some strategies to circumvent the immunity in the hosts. In addition to the immune hosts, the presence of digital parasites also facilitated evolution of hyper-parasites which, when attacked by parasites, not only prevented parasites from using their genomes but also seized the parasites’ CPU time. This exploitation of other creatures’ CPU time as an additional energy source increased the reproduction rate of hyper-parasites. After parasites, being deprived of CPU time, went extinct, the community of hyper-parasites reached a high level of genetic uniformity which promoted the emergence of social creatures (social hyper-parasites), which invented a strategy to reproduce in groups by cooperating with their neighboring creatures. This community of social hyper-parasites was later invaded by cheaters (hyper-hyper-parasites): a cheater inserted itself between two neighboring social hyper-parasites and stole the hyper-parasite's CPU time when a cooperative reproduction occurred between the two social creatures (Ray, 1991).

This spontaneous emergence of diverse types of digital creatures, with each evolving a novel strategy to exploit its biotic environment, strongly suggests that the Tierra system may have the potential to support an open-ended evolution inside a computer by continuously creating new niches through the active interactions among digital creatures. Furthermore, instead of simulating the life forms on earth, the Tierra system supports the synthesis of digital life forms as they exploit their silicon world. Therefore, digital life may be considered as an independent instance of life which evolves in a completely different environment than the organic life on earth. The comparison between organic life and digital life may provide us a deep understanding of the fundamental characteristics of life.

1.4 Questions Investigated in This Dissertation

In this dissertation, I conduct simulations in the Tierra system to explore the effects of predation on the increase and maintenance of community diversity in a homogenous environment. I attempt to create a predation scenario in Tierra similar to the one in nature: I design a digital predator which is able to capture digital prey and acquire CPU energy from them, and then I evaluate this design by examining whether the dynamics of digital prey and predator populations follow the “Lotka-Volterra” cyclic oscillation, the most fundamental predation relationship observed in nature.

After predation is built into the Tierra system, I study two predation strategies that predators may use when they feed on different types of prey, that is, proportional predation and positive frequency-dependent predation. I first compare the influence of those two predation strategies on the maintenance of prey diversity in an ecological scenario and explore the underlying mechanisms for a predation strategy to support the stable coexistence of multiple competing prey species. Then I examine which of the two predation strategies would provide predators a higher fitness in a dynamic biotic environment in which the relative abundance of different prey types is constantly changing.

With the understanding of prey diversity maintained by frequency-dependent predators in the ecological scenarios, I proceed to explore a more challenging but more intriguing question: whether those predators could also generate high and stable community diversity during an evolutionary process. I design the rules to allow predators to track the new prey types which continuously emerge during evolution, and thus to execute positive frequency-dependent predation based on their most recent predation history. Then, I compare diversity in the community with intensive predation with that in the community lacking predation. Furthermore, by examining changes in the genomes of evolving creatures, I study the coevolutionary dynamics between predator and prey populations in Tierra.

Chapter 2: Introducing Predation into the Tierra System

In the original Tierra implementation, two forms of predation emerged through evolution: parasites and hyper-parasites. Digital parasites evolved to exploit the genome codes of other creatures and thus relied on those creatures for reproduction. A “Lotka-Volterra-like” cycle existed between those parasites and their hosts (Ray, 1991). Digital hyper-parasites were able to reproduce themselves and steal additional CPU energy from parasites to enhance their reproduction rate (Ray, 1991). Because the survival of hyper-parasites did not depend on the existence of parasites, a “Lotka-Volterra” predation relationship was not present between the hyper-parasite and parasite populations. Rather, hyper-parasites tended to drive parasites to extinction. In this chapter, I attempt to create a predation scenario more similar to the one in nature, that is, predators acquire energy from their prey and the predator and prey populations exhibit the “Lotka-Volterra” cycle. I design a digital predator which is able to capture multiple prey individuals in its local area and obtain a small amount of energy from each prey. Then I evaluate this design by exploring whether or not the “Lotka-Volterra” cyclic dynamics exist between the digital predator and prey populations in Tierra.

2.1 Digital Predator and Prey

In Tierra, each digital creature is a self-replicating computer program whose execution requires CPU time. Therefore, the survival and reproduction of a digital creature depend on the amount of CPU time that the creature possesses, similar to the energy requirement for the survival and reproduction of an organic creature in nature.

2.1.1 Ancestral Creature in the Original Tierra System

The ancestral creature was an 80 instruction-long, self-replicating algorithm. It was composed of three basic functional blocks: self-examination, replication loop and copy procedure, as shown in Figure 2.1. The ancestral creature first examined itself to find its beginning and ending locations in the memory space. Then it calculated its size by subtracting the addresses of those two locations and allocated a block of memory of this size for its daughter. After that, the copy procedure was called to copy the entire genome into the daughter cell, one instruction at a time. Following the completion of genome replication, the daughter cell was released as a mature individual by the DIVIDE instruction. After the first daughter was produced, the size of the ancestral creature had already been recorded, so the procedure of self-examination was not necessary when initiating the production of the second daughter. The ancestral creature directly proceeded to allocate memory space for the second daughter cell and then the copy procedure was followed by cell division, in an endless loop (Ray, 1991).

Due to the exact numeric addresses used in the traditional Von-Neumann machine language, programs were extremely vulnerable to mutation, that is, any mutation events were almost certain to completely break down the programs. In order to develop evolvable programs, Tierran language used a novel address technique, called “address by templates”. This technique was inspired by molecular interactions in the biological system, for example, in order for molecule A to find and bind to molecule B, some conformations on the surface of molecule A needed to be complementary to those on molecule B. Similarly, Tierran language implemented 6 pairs of complementary templates to mark and locate sites in the ancestral creature. For example, the creature began with the template 1111 and the complementary template 0000 was used to find the beginning address; the beginning of the copy procedure was marked with the template 1100 and the complementary template 0011 was used to call the copy procedure, and so on. When a template mutated, it was likely to match another template in the creature, rather than to cause the death of the program. Therefore, programs with "address by templates" were able to survive under mutations and thus had potential to evolve (Ray, 1991).

2.1.2 Digital Predator

The digital predator is 100 instructions long and shares the same basic structures of self-examination, reproduction loop and copy procedure as the ancestral creature in the original Tierra system. However, the predator has an additional predation loop inserted before reproduction, as shown in Figure 2.2. When the predator executes this predation loop, it starts to search for prey from its two ends (beginning and ending locations) bi-directionally, as shown in Figure 2.3. If a template in a prey is complementary to the predation template in the predator and that prey has not been eaten by other predators yet, then the predator eats that prey. This causes a certain percent of the prey's CPU time to be transferred to the predator, and the prey's CPU time is reduced to a small amount. Then the predator continues searching for more prey until either it has eaten the maximum number of prey allowed in one predation loop or it has reached the boundary of its local area, as illustrated in Figure 2.3.

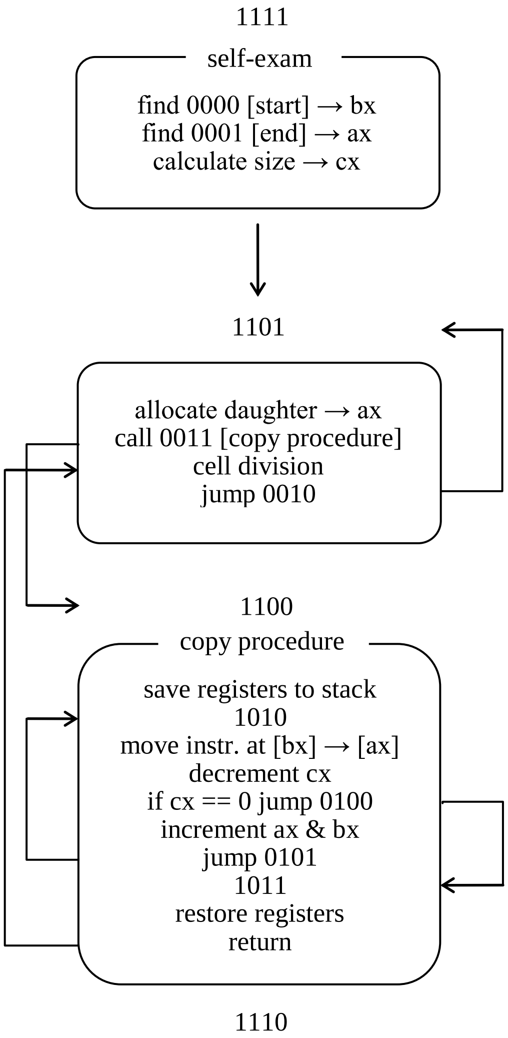


Figure 2.1: Algorithmic flow chart for the ancestral creature in the original Tierra system: ax, bx, and cx are CPU registers and arrows outside of the boxes indicate jumps in the flow of the execution of the program. The creature begins with the template 1111 and the complementary template 0000 is used to find the beginning location of the creature which is then stored into bx. Similarly, the ending location is found and stored into ax. The size of the creature is calculated and stored into cx. Then the creature allocates a block of memory of this size for its daughter and the beginning location of the daughter cell is stored into ax. After that, the copy procedure is called by matching the two complementary templates 0011 and 1100. The values in the 3 registers, ax, bx, and cx, are saved to the stack before the execution of the copy loop. Then the genome of the mother cell (starting from the address saved in bx, with the size saved in cx) is copied to the daughter cell (starting from the address saved in ax, with the same length as its mother), one instruction at a time. When the duplication completes, the copy loop is exited by matching the templates 0100 and 1011. The original values of ax, bx, and cx are restored from the stack and the program proceeds to release the mature daughter through cell division. After the reproduction of its first daughter, the creature continues producing more daughters through the loop of memory allocation, copy procedure and cell division.

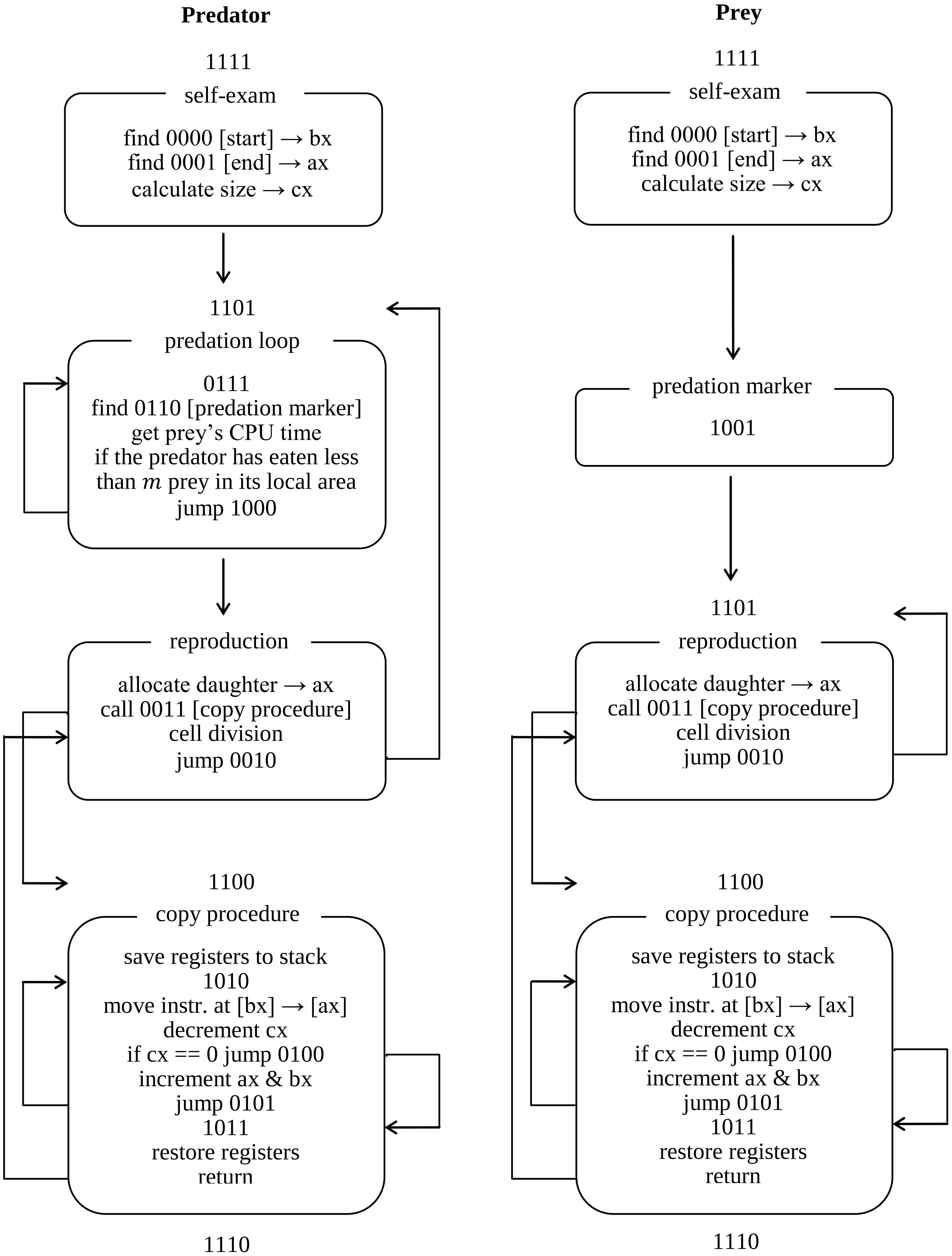


Figure 2.2: Algorithmic flow chart for the predator and prey in the Tierra system. The predation template in the predator (0110) is complementary to the template in the prey (1001), which allows the predator to catch the prey and acquire CPU time from it. In each predation loop, the predator is allowed to eat at most *m* prey in its local area. If either the predator has eaten *m* prey or the predator has reached the boundary of its local area before it captures *m* prey, the predation loop is exited and the program proceeds to reproduction.

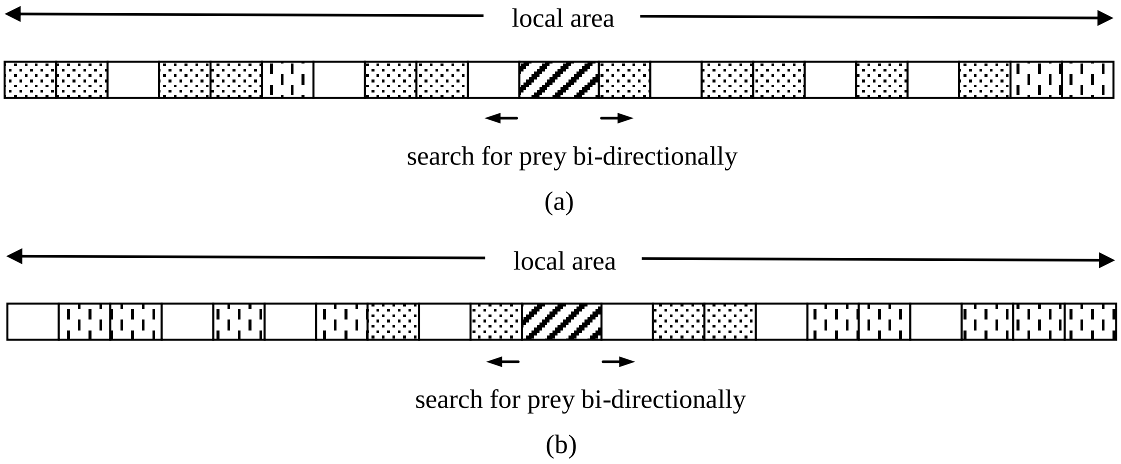


Figure 2.3: Illustration of the function of the predation loop in a predator. The predator detects its prey by searching for the template in the prey's genome, which is complementary to the predation template in itself. ▨ represents the predator; ░ represents the prey that is available to the predator (the prey can be detected by the predator and has not been eaten by other predators); ┆ represents the prey which can be detected by the predator but has already been eaten by other predators; □ represents the prey which cannot be detected by the predator. Starting from its two ends, the beginning and ending locations, the predator searches for prey bi-directionally in its local area. The local area demonstrated in this figure is about 10 creatures long on either side of the predator. In one predation loop, the predator is allowed to eat at most m prey. This figure shows the case of $m = 6$. (a) The number of available prey in the predator's local area is greater than (or equal to) 6. The predator captures 6 prey individuals and then exits the predation loop. (b) The number of available prey in the predator's local area is less than 6. The predator catches 4 prey individuals but is not able to find more prey before reaching the boundary of its local area. It then exits the predation loop with 4 captured prey individuals.

After the predator exits the predation loop, it finds a space for its daughter and enters the copy procedure for replication. Following the release of its mature daughter, the predator enters the predation loop again to accumulate more energy for future reproduction. This loop of predation and then reproduction repeats until death.

The commented Tierran assembler source code for the digital predator is presented in Appendix A.

2.1.3 Digital Prey

The digital prey is the same as the ancestral creature in the original Tierra system except for an additional template before the reproduction loop, as shown in Figure 2.2. This template is complementary to the predation template in the predator and thus by template matching, the predator is able to find its prey.

The commented Tierran assembler source code for the digital prey is presented in Appendix B.

2.1.4 CPU Energy for Digital Prey and Predators

The Tierra system assigns a standard amount of CPU time to each prey to support the survival and reproduction of the prey throughout its lifetime. However, a predator obtains reasonable CPU energy from the system only at the very beginning of its lifetime, that is, the amount of CPU time provided by the system is only sufficient for the predator to execute the predation loop to try to capture its first prey. After that, the predator receives only a very small amount of CPU time from the system (about 5% of the CPU time that a prey obtains from the system). If the predator fails to catch prey, it has almost no CPU time to execute more instructions. Therefore, the survival and reproduction of a predator almost completely depend on the CPU energy that it acquires from its captured prey.

2.2 “Lotka-Volterra-like” Cycle between Digital Predator and Prey Populations

2.2.1 Predator-prey Cycle in Nature and the “Lotka-Volterra” Model

Predator and prey populations in nature often exhibit closely synchronized cycles and long-term observations have confirmed that those population cycles continue more or less unchanged over many generations. For example, the populations of Canadian lynx and its principal prey, the snowshoe hare, showed very regular fluctuations of large magnitude. Over the observation period of 206 years, the cycles of those two species stably persisted and each cycle, on average, lasted about 9.6 years. The cycles were also highly synchronized with peaks in hare abundance one or two years ahead of the peaks in lynx abundance. This synchrony of the two species occurred over distances of more than 1000 km across Canada (Elton and Nicholson, 1942). Such cyclic behaviors of populations also occur between hosts and their pathogens. As the host population becomes abundant and crowded, the chances for pathogens to contact a new host significantly increase. Therefore, disease spreads rapidly among host individuals and causes the host population to decline to low levels. The low density of the host population breaks the chain of contagion, which results in the re-establishment of the host population. This pattern of host-pathogen interactions was clearly demonstrated by the synchronized population cycles of forest tent caterpillars and nuclear polyhedrosis viruses, the pathogen that caused high mortality of tent caterpillars at high population densities (Myers, 2000).

In the natural environment, besides predation, other factors such as weather conditions, habitat suitability and population dispersal may also affect population cycles. To further investigate the impact of predator-prey interactions on the oscillation of populations, researchers have tried to establish those cycles in laboratory settings. For example, Gause introduced *Paramecium* as the prey and *Didinium* as the predator into a nutritive medium in a test tube and after providing some hiding places for prey to escape, he achieved recurring oscillations in the predator and prey populations (Gause, 1934; Gause *et al.*, 1936). Huffaker used two different mite species with one feeding on the other to establish experimental populations. As he increased the spatial complexity of the environment and introduced barriers to retard predator dispersal so that prey could escape predation and re-establish themselves in a remote habitat before predators arrived, he obtained coexisting cyclic fluctuations of predator and prey populations (Huffaker, 1958). Those laboratory experiments confirm that the synchronized population cycles of predators and their prey could result from the predation-escape interactions between them.

During the 1920s, Alfred J. Lotka and Vito Volterra developed the first mathematical model of predator-prey interactions to explain the cyclic dynamics of populations. The “Lotka-Volterra” model used differential equations to describe the factors that caused the changes in population sizes. The prey population declined due to predation and the larger the prey and/or the predator population, the higher the rate of encounter between predator and prey. Therefore, in the “Lotka-Volterra” model, the rate of prey removal by predators was directly proportional to the product of the population sizes of predators and prey. On the other hand, predation provided energy for predators to survive and reproduce thus, in the “Lotka-Volterra” model, the birth rate of predators depended on the number of captured prey. According to the “Lotka-

Volterra" model, the change in the abundance of predator and prey populations followed a continuous closed cycle, one-quarter cycle out of phase, with the prey population increasing and decreasing ahead of the predator population (Lotka, 1925; Volterra, 1926).

In conclusion, both laboratory experiments and mathematical models reveal that the highly synchronized cyclic oscillations of predator and prey populations observed in the natural environments could be explained by the dynamic interactions between predators and their prey. As predators acquire energy from their prey through predation, and the escaped prey restore the prey population, the cycles form: an abundant prey population provides more food for predators and thus is followed by a rise in the predator population. But as the number of predators increases, the growing predation pressure depresses the prey population. When fewer prey individuals are available, the predator population decreases which reduces the predation pressure. With fewer predators around, the remaining prey survive better and thus the prey population begins to increase again.

2.2.2 "Lotka-Volterra-like" Cycle in Tierra

To evaluate the predation relationship built in Tierra, I compare the dynamics between digital predator and prey populations with those in nature and investigate whether or not the fundamental pattern of the "Lotka-Volterra" cycle exists in Tierra.

Methods

The dynamics of the digital predator and prey populations are examined in ecological simulations, in which Tierra is run without mutation. Two types of prey, which differ only in their genome lengths, are used to interact with the predator. Type-

A prey is 86 instructions long and type-B prey is 96 instructions long. Each prey type contains a template complementary to the predation template in the predator, so the predator is able to detect both of them. I seed the soup (a block of RAM memory) with 300 predator individuals evenly distributed among 3000 individuals of type-A prey. Each predator is allowed to search for prey in its local area, about 10 creatures long on either side of the predator. In each predation loop, a predator can eat at most m (m = 6) prey individuals and it receives 15% of the CPU time from each prey. The amount of CPU time remaining in the captured prey is reduced to 15% of its original value. In a simulation run, I use the number of instructions that have been executed to measure the passage of time. The runs in this experiment last until 1000 million instructions have been executed, and I record the population sizes of predators and type-A prey during the runs. Then I use exactly the same parameter settings, except replacing type-A prey with 3000 individuals of type-B prey, to explore the relationship between the predator and type-B prey populations.

Results

In Tierra, each digital prey receives a certain amount of CPU time from the system, but a digital predator, similar to its counterpart in nature, acquires energy only through predation. When a digital predator searches for multiple prey in its neighboring area and obtains a small amount of CPU time from each prey, the “Lotka-Volterra-like” cycle forms between the predator and prey populations (Shao and Ray, 2010).

As shown in Figure 2.4(a), after the transient initial stage, the type-A prey population rapidly reaches a constant level of about 2400 individuals and stably coexists with the predator population of about 900 individuals.

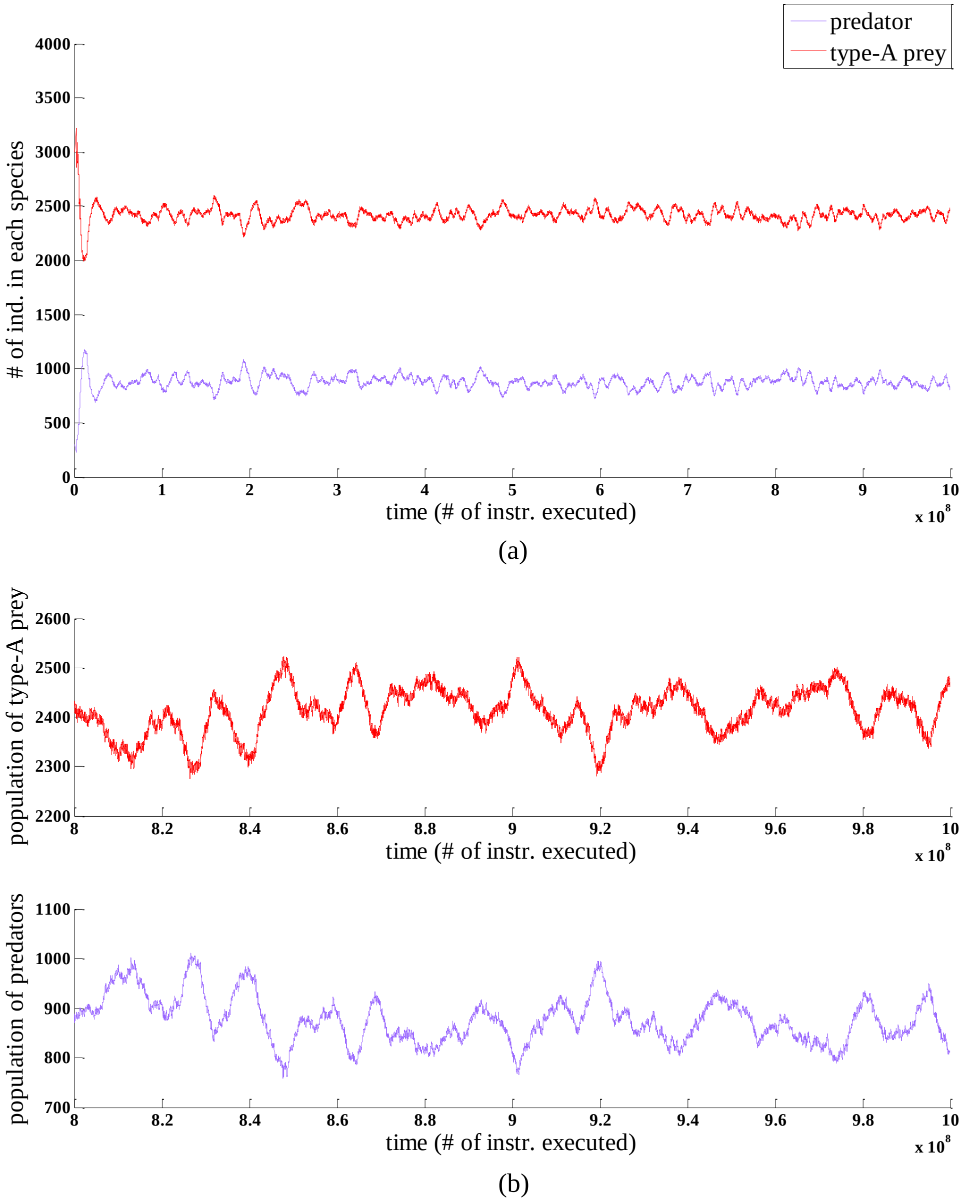


Figure 2.4: Coexistence of the predator and type-A prey populations in Tierra. (a) The predator and type-A prey populations stably coexist in the Tierra system. (b) "Lotka-Volterra-like" cycle between the predator population and the type-A prey population at the steady state from 800 to 1000 million instructions executed in the Tierra system.

As I examine the population dynamics at the steady state between 800 and 1000 million instructions executed, as shown in Figure 2.4(b), a coupled cyclic oscillation between the predator and prey populations appears. But unlike "a quarter cycle out of phase" in the traditional Lotka-Volterra cycle, the phase shift between the predator and prey populations in Figure 2.4(b) seems to be “a half cycle out of phase”, namely, as the predator population reaches the maximum, the prey population reaches the minimum, and vice versa. This phase shift may result from the “birth causes death” setup in the Tierra system: all digital creatures live in the same finite memory space and when this memory space is full, one or several old creatures are killed in order to provide enough room for a new-born creature. As a result, when one population grows with many new-born individuals, it occupies more and more memory space and thus forces the other population to shrink. However, despite the difference in the phase shift, the underlying mechanism that drives the cyclic oscillation of the prey and predator populations in Tierra is the same as that in the Lotka-Volterra cycle. As shown in Figure 2.5, which is a copy of Figure 2.4(b) with 4 vertical dividing lines, as the prey population increases in region A, predators acquire more CPU energy from their prey through predation. As a result, the predator population ceases declining and starts to increase in region B. The growth of the predator population prevents the expansion of the prey population and causes it to decrease. As the available prey individuals drop in region B, the CPU energy transferred from the prey population to the predator population reduces which hinders the further growth of the predator population and causes it to decrease in region C. Therefore, the coupled cyclic dynamics between the digital predator and prey populations result from the energy dependence of predators on their prey, the very critical component which supports the Lotka-Volterra cycle in nature. Due to this fundamental similarity in producing population cycles, the dynamic oscillations of prey and predators in Tierra are called a “Lotka-Volterra-like” cycle.

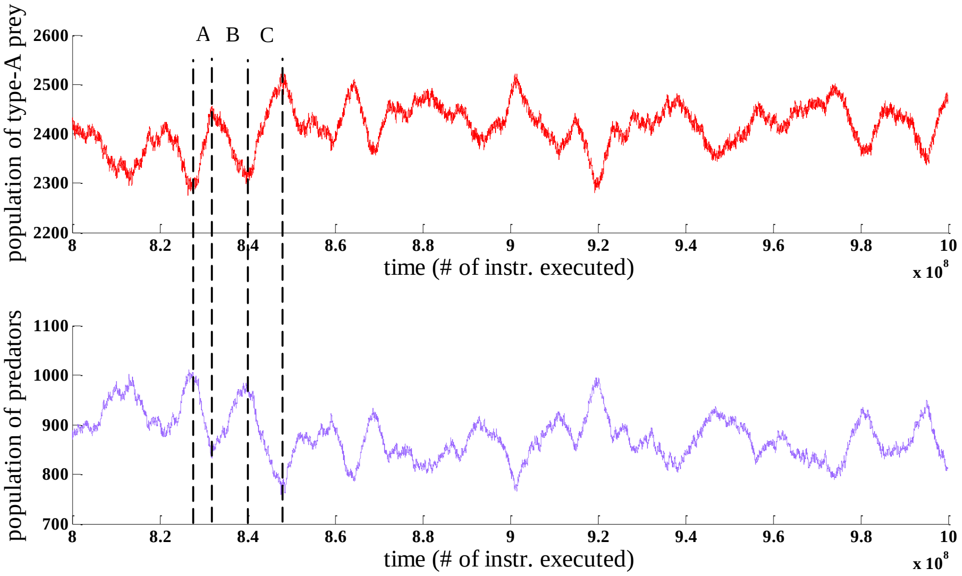


Figure 2.5: Coupled cyclic dynamics between the digital predator and prey populations. A copy of Figure 2.4(b) with 4 vertical dividing lines demonstrates that the coupled cyclic dynamics between the digital predator and prey populations result from the energy dependence of predators on their prey.

A very similar dynamic pattern appears when predators forage on type-B prey. As shown in Figure 2.6(a), the type-B prey population of about 2200 individuals steadily coexists with the predator population of about 850 individuals. This coexistence is achieved through the establishment of the "Lotka-Volterra-like" cycle between the predator and type-B prey populations, as shown in Figure 2.6(b).

2.2.3 Fluctuations due to Randomness in the Tierra System

To verify that the dynamic pattern between the predator and prey populations results from predation, rather than from random fluctuations in the Tierra system, I investigate the changes in population sizes caused by randomness in the system and compare those changes with the population dynamics shown in Figure 2.4.

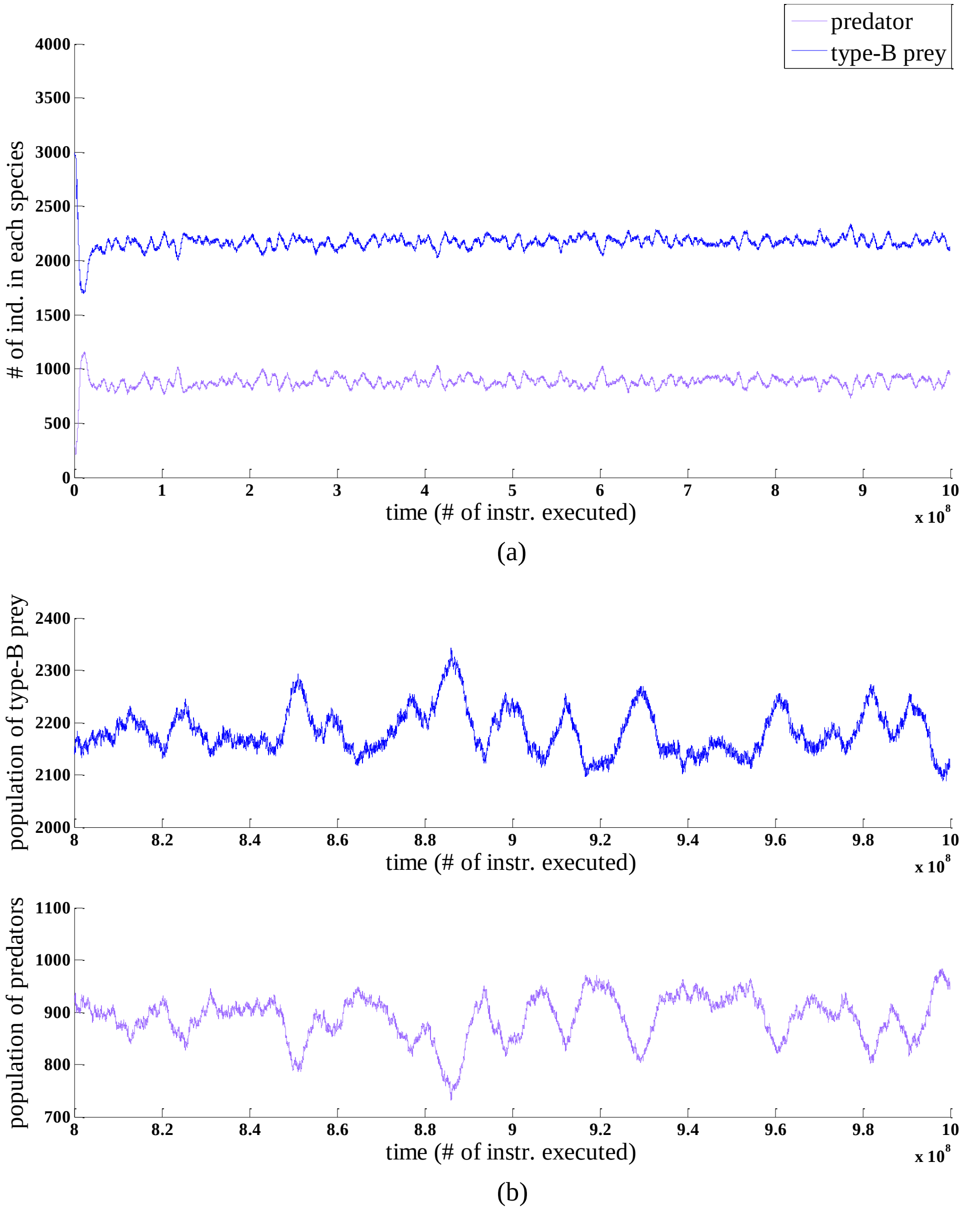


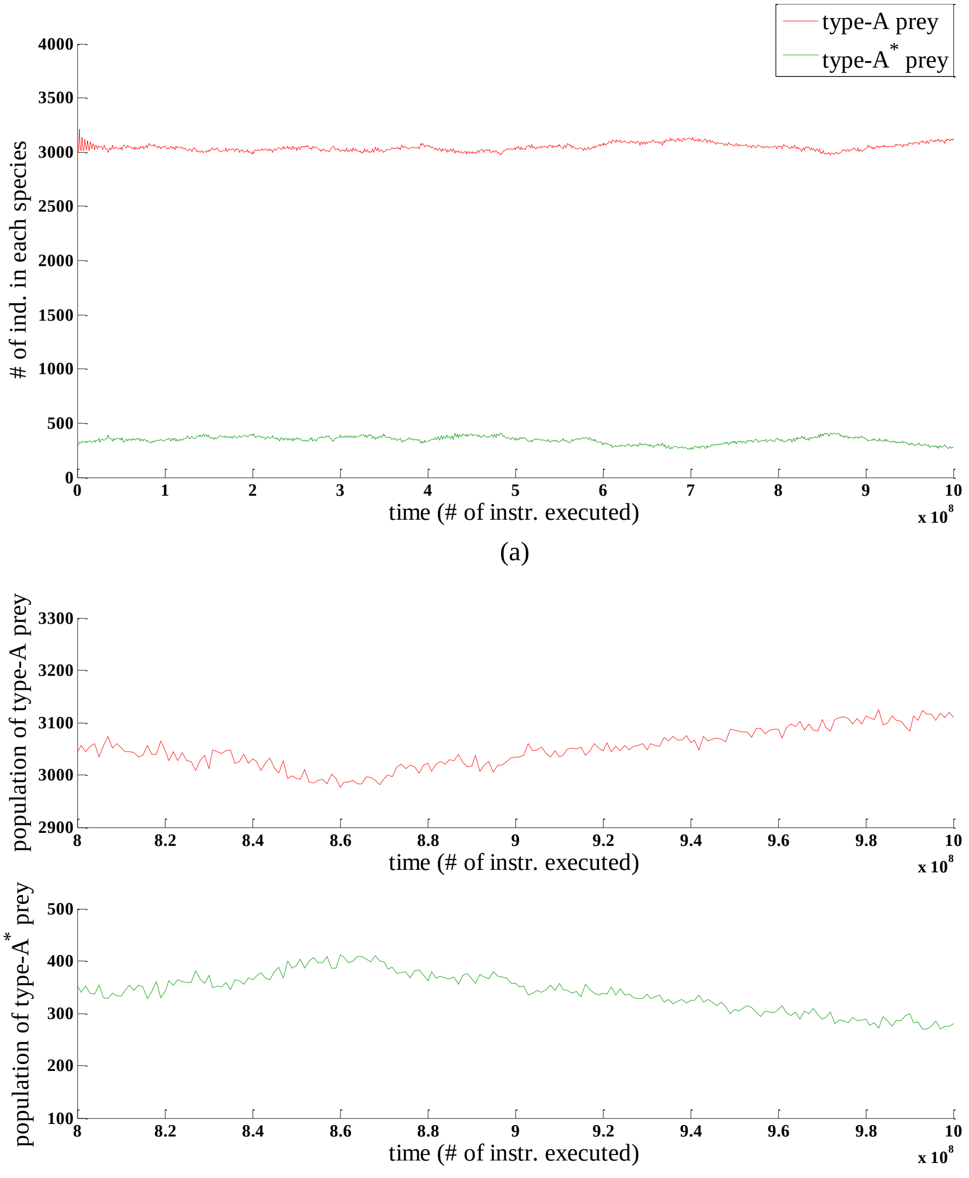
Figure 2.6: Coexistence of the predator and type-B prey populations in Tierra. (a) The predator and type-B prey populations stably coexist in the Tierra system. (b) "Lotka-Volterra-like" cycle between the predator population and the type-B prey population at the steady state from 800 to 1000 million instructions executed in the Tierra system.

Methods

I design two variants of the type-A prey, that is, type-A^* prey and type-A^{**} prey. Each of the variants is developed by changing the locations of non-functional, dummy instructions in the genome of type-A prey. Therefore the two variants have the same function and share the same genome length as the type-A prey. Because each prey receives, on the average, the same amount of CPU time from the system, the prey types with the same genome length theoretically have the same reproduction rate and thus their population sizes should be maintained at a constant level. The fluctuations in the population sizes of type-A prey and its variant (type-A^* or type-A^{**} prey), therefore, reflect randomness in the system. I seed the soup with 300 individuals of type-A^* prey evenly distributed among 3000 individuals of type-A prey and run the simulation until 1000 million instructions have been executed to observe the population dynamics between type-A prey and type-A^* prey. Then I replace type-A^* prey with 300 individuals of type-A^{**} prey to explore the variations of the population sizes of type-A prey and type-A^{**} prey.

Results

In contrast to those shown in Figure 2.4, the population dynamics caused by random fluctuations in the system present a completely different pattern. As shown in Figure 2.7(a), the type-A prey and type-A^* prey populations slowly drift over 1000 million instructions executed. Similarly, in Figure 2.8(a), the type-A prey and type-A^{**} prey populations also change slowly with type-A^{**} prey drifting to extinction. The population dynamics from 800 to 1000 million instructions executed, as shown in both Figure 2.7(b) and Figure 2.8(b), exhibit a slow drift of the type-A prey and its variant populations without visible cycling.

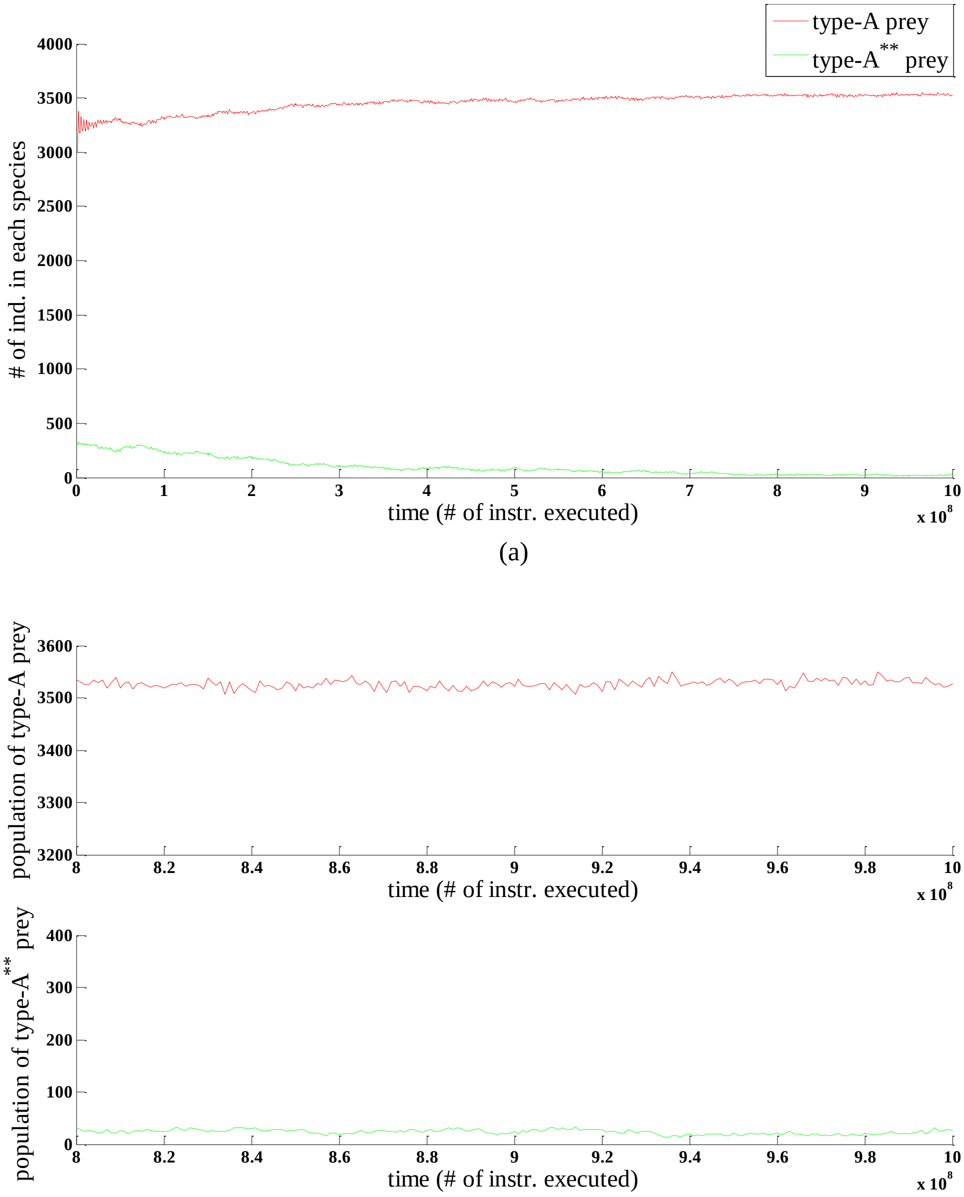


(a)

(b)

Figure 2.7: Population drift due to randomness in the Tierra system. (a) The type-A prey and type-A* prey populations slowly drift due to randomness in the Tierra system. (b) The type-A prey and type-A* prey populations slowly drift without visible cycling from 800 to 1000 million instructions executed in the Tierra system.

Those dynamic patterns shown in Figure 2.7 and 2.8 confirm that the coupled cyclic oscillations between the predator and prey populations in Figure 2.4 are not the results of random fluctuations in the Tierra system, but rather result from the energy transfer from prey to predators through predation.



(a)

(b)

Figure 2.8: Population drift due to randomness in the Tierra system. (a) The type-A prey and type-A** prey populations slowly drift due to randomness in the Tierra system, and type-A** prey drift to extinction. (b) The type-A prey and type-A** prey populations slowly drift without visible cycling from 800 to 1000 million instructions executed in the Tierra system.

2.2.4 Robustness to the Variations of Parameter Settings

The synchronized cyclic patterns of predator and prey populations depend on conditions that support the persistence of both populations. If predators could not acquire enough energy from the prey population, the predator population would go extinct. On the other hand, if, under high predation pressure, prey fail to find refuges to escape predation, predators would eat the prey population to extinction and then become extinct themselves. Here, I vary the amount of energy transferred from a captured prey individual to its predator and the amount of energy that remains in a captured prey to explore the conditions that maintain the coexistence of the predator and prey populations in Tierra.

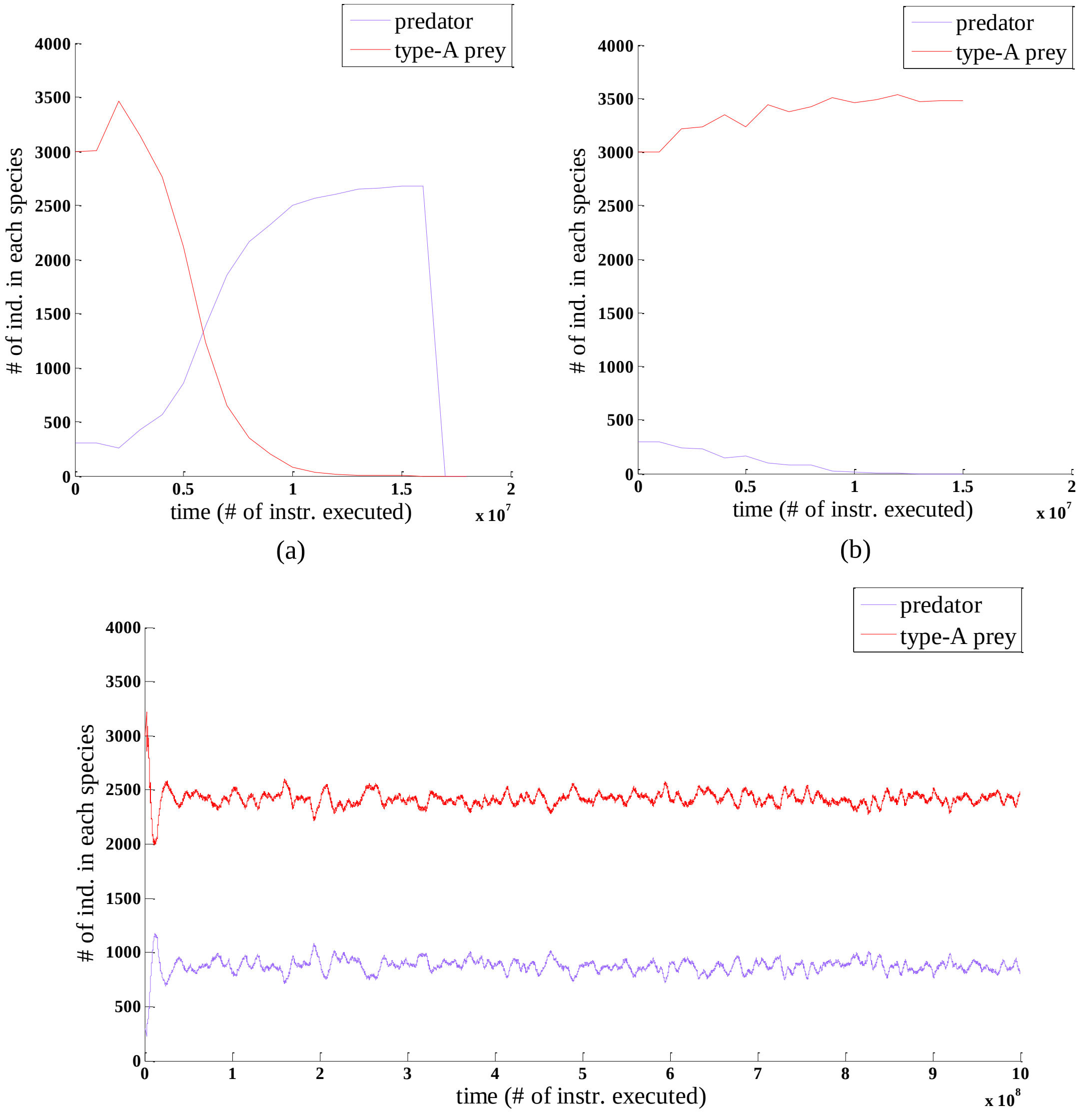
Methods

I seed the soup with 300 predator individuals evenly distributed among 3000 individuals of type-A prey. Each predator searches for prey in its local area (about 10 creatures long on either side of the predator) and it is allowed to eat at most m (m = 6) prey individuals in each predation loop. The allocation of the amount of CPU time between a predator and its prey has three different combinations as follows: the predator receives 15% of the CPU time from its prey and the prey's CPU time is reduced to 0; the predator receives 10% of the CPU time from its prey and the prey's CPU time is reduced to 15% of its original value; the predator receives 15% of the CPU time from its prey and the prey's CPU time is reduced to 15% of its original value. The simulation runs last until either the prey or the predator population goes extinct but if both populations persist, the runs last until 1000 million instructions have been executed. I record the population sizes of predators and type-A prey during the runs.

Results

In Tierra, digital predator and prey individuals live in the same memory space (soup). When a simulation run starts, the population size of prey is 10 times larger than that of predators. Surrounded by abundant prey resources, the predator population rapidly increases which causes the prey population to decline. If a prey's CPU time is reduced to 0 when caught by a predator, this prey would lose all the energy to execute its genome and thus fail to reproduce offspring. In the setup of Tierra simulations, there are no refuges for prey to hide. Thus, as predators occupy more and more space in the soup, they are able to find and eat every single prey. After predators consume the last prey individual in the soup, the predator population itself becomes extinct as well, as shown in Figure 2.9(a). Therefore, in the scenario that the CPU time of a captured prey is reduced to 0, the predator population would drive the prey population to go extinct and thus the "Lotka-Volterra" cycle is not possible.

As discussed in 2.2.1, when refuges are available, predators are unable to completely eliminate the prey population and those prey individuals surviving in the refuges re-establish the prey population after the predation pressure declines. In the absence of refuges in Tierra, I mimic this "refuges effect" by preserving a small amount of CPU time in captured prey individuals. That is, a predator does not completely remove all the CPU time of its prey, but rather reduces its prey's CPU time to a low value, such as 15% of the prey's original CPU time. As shown in Figure 2.9(b) and (c), with the restoration resulting from the small amount of CPU time maintained in the captured prey individuals, the prey population persists under predation.



(a)

(b)

(c)

Figure 2.9: Coexistence of predator and prey populations depends on the amount of CPU energy in each population. (a) When a predator receives 15% of the CPU time from its prey and the prey’s CPU time is reduced to 0, the prey population goes extinct, followed by extinction of the predators. (b) When a predator receives 10% of the CPU time from its prey and the prey’s CPU time is reduced to 15% of its original value, the predator population goes extinct. (c) When a predator receives 15% of the CPU time from its prey and the prey’s CPU time is reduced to 15% of its original value, the predator and prey populations stably coexist in the Tierra system.

As shown in Figure 2.9(b), when a predator receives 10% of the CPU time from each of its prey, the predator population goes extinct after 15 million instructions have been executed. However, when the amount of CPU time that a predator acquires from its prey increases to 15%, as shown in Figure 2.9(c), the predator and prey populations stably coexist over 1000 million instructions executed. Therefore, sufficient energy transfer from prey to predators is required for the persistence of the predator population.

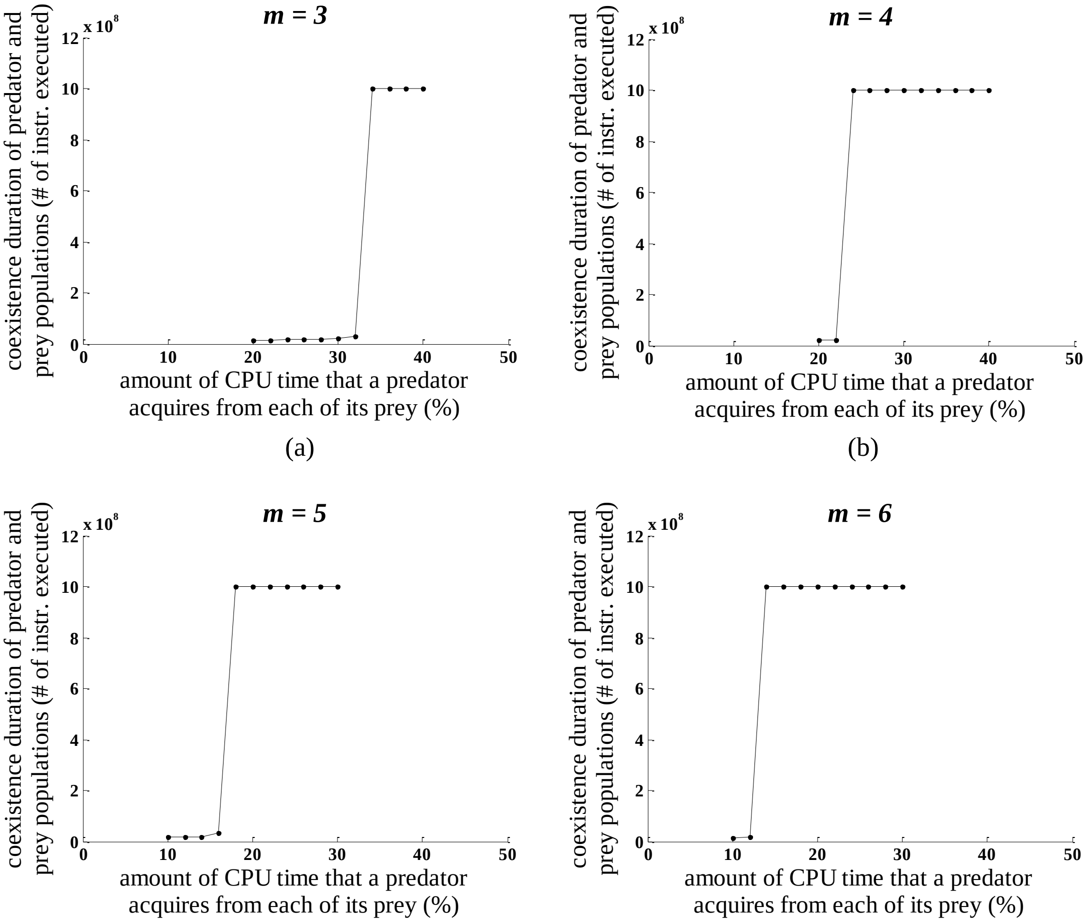
The amount of CPU time remaining in captured prey individuals affects the persistence of the prey population. The amount of CPU time that predators acquire through predation (the number of prey caught and the amount of CPU time received from each captured prey) influences the maintenance of the predator population. Here, I investigate the effects of those three parameters on the robustness of the "Lotka-Volterra-like" cycle between the predator and prey populations.

Methods

I seed the soup with 300 predator individuals evenly distributed among 3000 individuals of type-A prey and each predator searches for prey in its local area (about 10 creatures long on either side of the predator). I vary the number of prey individuals that a predator is allowed to eat in each predation loop in the range of 3 to 6 (m = 3, 4, 5, 6) and for each value of m, I systematically increase the amount of CPU time transferred from a captured prey to its predator. When a predator is allowed to eat at most 3 or 4 prey individuals in one predation loop, the amount of CPU time that the predator acquires from its prey increases from 20% to 40% in 2% increments and the amount of CPU time of a captured prey is reduced to 30% of its original value; when a predator is allowed to eat at most 5 or 6 prey individuals in one predation loop, the amount of CPU time that the predator acquires from its prey increases from 10% to 30% in 2% increments and the amount of CPU time of a captured prey is reduced to 15% of its original value. The simulation runs last until either the prey or the predator population disappears but if both populations persist, the runs last until 1000 million instructions have been executed. I record the duration (the number of instructions executed) that the predator and prey populations coexist.

Results

When a predator eats at most 3 or 4 prey individuals in each predation loop (m = 3 or 4), the prey population, with 30% of the CPU time remaining in the captured prey, persists regardless the changes in the amount of CPU time that the predator population receives. On the other hand, as shown in Figure 2.10(a) and (b), the predator population could not avoid extinction until it acquires enough energy through predation. For example, when m = 3, the predator population persists only after at least 34% of the CPU time from each captured prey is delivered to its predator; when m = 4, at least 24% of the CPU time from captured prey needs to be transferred to predators for the persistence of the predator population. The “Lotka-Volterra-like” cycle robustly appears when the predator and prey populations stably coexist in the soup. As m increases from 3 to 4, the range of the amount of CPU time required for supporting the predator population extends from [34%, 40%] to [24%, 40%]. Therefore when predators are allowed to consume more prey individuals, the “Lotka-Volterra-like” cycle exists over a larger parameter space.

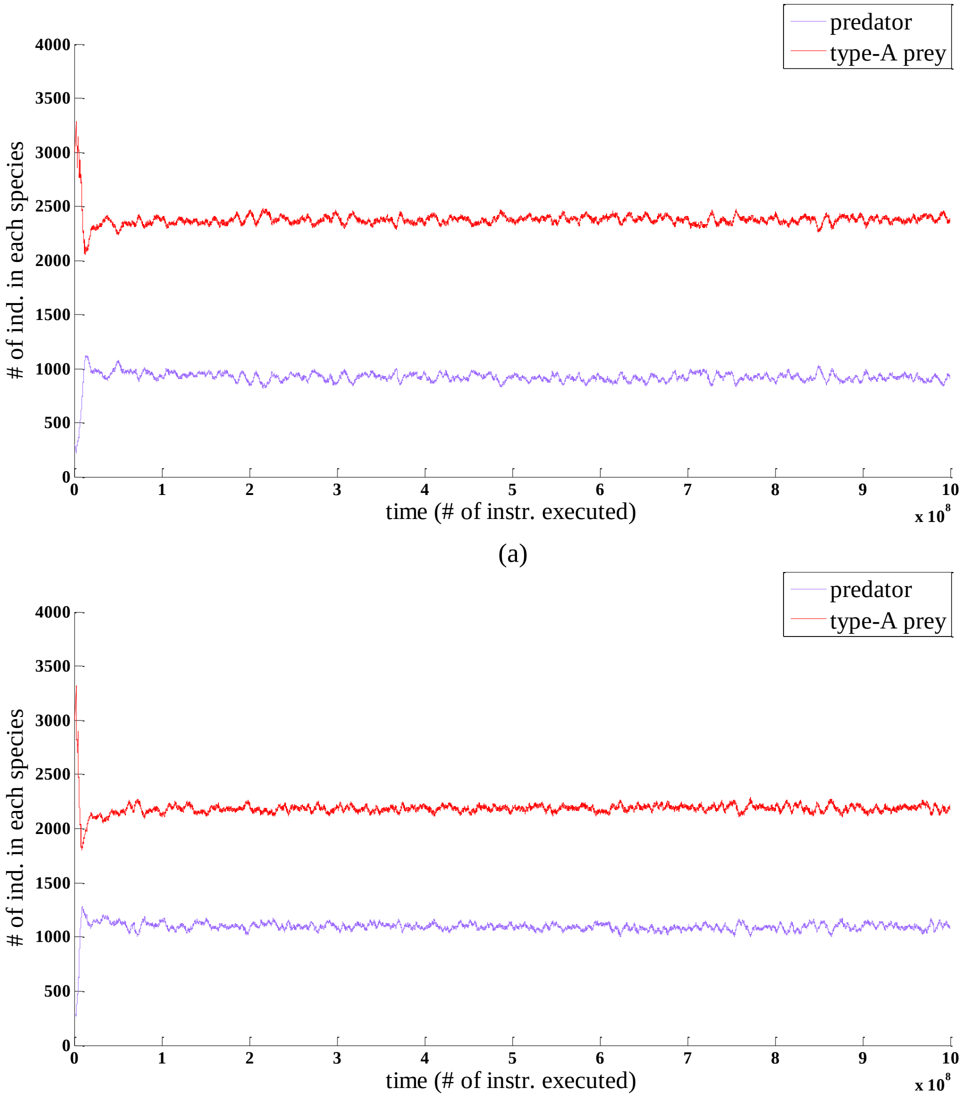


(a) (b) (c) (d)

Figure 2.10: Robustness of the “Lotka-Volterra-like” cycle between the predator and type-A prey populations in the Tierra system. (a) With m = 3, the “Lotka-Volterra-like” cycle appears when the amount of CPU time that a predator acquires from its prey is equal to or greater than 34%. (b) With m = 4, the “Lotka-Volterra-like” cycle appears when the amount of CPU time that a predator acquires from its prey is equal to or greater than 24%. (c) With m = 5, the “Lotka-Volterra-like” cycle appears when the amount of CPU time that a predator acquires from its prey is equal to or greater than 18%. (d) With m = 6, the “Lotka-Volterra-like” cycle appears when the amount of CPU time that a predator acquires from its prey is equal to or greater than 14%.

A very similar pattern appears, as shown in Figure 2.10(c) and (d), when a predator eats at most 5 or 6 prey individuals in each predation loop (m = 5 or 6). The prey population persists with 15% of the CPU time remaining in the captured prey. The predator population persists when sufficient energy is obtained through predation. As m

increases from 5 to 6, the “Lotka-Volterra-like” cycle occurs over a broader range of the amount of CPU time acquired by predators, from [18%, 30%] to [14%, 30%].



(a)

(b)

Figure 2.11: As predators acquire more CPU energy through predation, the size of the predator population increases. (a) Coexistence of the predator and type-A prey populations in the Tierra system when *m* = 4, a predator receives 24% of the CPU time from its prey and the amount of CPU time of a captured prey is reduced to 30% of its original value. (b) Coexistence of the predator and type-A prey populations in the Tierra system when *m* = 4, a predator receives 28% of the CPU time from its prey and the amount of CPU time of a captured prey is reduced to 30% of its original value.

In the parameter ranges where the “Lotka-Volterra-like” cycle between the predator and prey populations occurs, such as the amount of CPU time that predators receive is [34%, 40%] when $m = 3$, [24%, 40%] when $m = 4$, [18%, 30%] when $m = 5$ and [14%, 30%] when $m = 6$, the population size of predators increases with the amount of energy transferred from prey to predators. As illustrated in Figure 2.11(a) and (b), in the case of $m = 4$, as the amount of CPU time that a predator acquires from each of its prey increases from 24% to 28%, the predator population at the steady state increases from about 920 individuals to about 1080 individuals.

2.3 Conclusion

In nature, when a prey is caught by a predator, only a small amount of energy is transferred to the predator. A predator has to catch multiple prey in order to acquire sufficient energy. Similar to its counterpart in nature, a predator in Tierra catches multiple prey in its local area and obtains a small amount of energy from each prey. The simulation results show that the “Lotka-Volterra-like” cycle robustly appears in Tierra over a wide range of parameter settings. This suggests that the design of digital prey and predators may capture some essential properties of predation which allow the creatures in Tierra to follow the same fundamental relationship between predator and prey populations observed in nature and thus may be suitable to study predator-prey population dynamics.

Chapter 3: Exploring Effects of Two Predation Strategies on Prey and Predator Populations in an Ecological Scenario

In contrast to chapter 2 in which the dynamic relationship between one digital predator species and one digital prey species is examined, in this chapter, I attempt to use the Tierra system to investigate more complicated ecological challenges, the interactions between one predator species and two or more prey species. I compare two predation strategies, that is, proportional predation and positive frequency-dependent predation, to explore their effects on maintaining prey species diversity in an ecological scenario when all mutations are blocked. Then I study the underlying mechanisms for a predation strategy to support the stable coexistence of multiple prey species. Furthermore, I examine those two predation strategies from the perspective of enhancing the reproductive success of predators in a dynamic biotic environment in which prey populations are continuously changing.

3.1 Proportional Predation and Positive Frequency-dependent Predation

3.1.1 Proportional Predation

Proportional predation, namely frequency-independent predation, means that when provided with two or more types of prey, predators feed on different prey in proportion to their relative abundances in environment. This predation strategy has been documented in various predatory species. For example, in a study of food habits of longnose dace, *Rhinichthys cataractae*, a fish feeding primarily on insects at the bottom of streams, Gerald collected samples of longnose dace from the Yellowstone River and the benthic organisms in the same area where fish lived. Through carefully analyzing the food contents in fish's digestive tract and examining the abundances of various insects in the samples of benthic organisms, he found that the frequency occurrence of inactive and/or inconspicuous insects, such as Tendipedidae and Plecoptera, in fishes' digestive tracts was approximately the same as that in the benthic samples. This result suggested that longnose dace may consume the partially hidden insects in proportion to their abundances in the river bed (Gerald, 1966). Several laboratory experiments were also conducted to explore proportional predation under more controlled settings. For example, when studying the selective feeding behavior of the starfish *Pisaster*, Landenberger placed two types of prey which were equally favored by starfish, spiny whelks and turban snails, in the tanks and recorded the number of each prey type consumed by starfish over a 3-week period. As he gradually increased the percentage of whelks in the initial prey population (composed of whelks and snails) from 20%, 33%, 67% to 80%, he found that the percentage of whelks in starfish's diet was 21%, 37%, 64.6 and 87.7%, respectively. These experimental data indicated that starfish may exhibit proportional predation behavior when feeding on equally preferred prey alternatives (Landenberger 1968). The predatory behavior of ladybird beetles *Coccinella* on two aphid species, *Acyrthosiphon pisum* and *Aphis fabae*, also exhibited the characteristics of proportional predation: each ladybird larva had been fed a pure diet of one of the aphid species before it was placed on a bean plant with both prey types. However, the feeding preference of ladybird larvae was not modified by previously consumed prey type and the percentage of *Acyrthosiphon pisum* eaten by ladybird larvae increased linearly with the percentage of *Acyrthosiphon pisum* in the mixtures of the two prey species. Thus, ladybird larvae fed on the two aphid species in direct proportion to their relative abundances (Murdoch and Marks, 1973). Proportional prey consumption was also reported when juvenile flounders *Platichthys flesus L.* fed on two of their common prey species, active swimming amphipod *Bathyporeia* and sedentary bivalve *Macoma*, as the relative abundances of the two prey species varied in a series of aquarium experiments (Mattila and Bonsdorff, 1998). A recent study on the interactions between two prey species, pea aphids (*Acyrthosiphon pisum*) and potato leafhoppers (*Empoasca fabae*), which shared a common predator nabid (*Nabis* spp.) revealed that as the ratio of aphids-to-leafhoppers on an alfalfa plant changed, nabids attacked the two prey species in proportion to their availabilities (Östman and Ives, 2003).

Those field studies and laboratory experiments demonstrate that proportional predation may be widely used by various types of predators, especially when predators have an equal or weak preference between two prey alternatives and their feeding preference does not alter as the relative abundances of different prey types fluctuate.

3.1.2 Positive Frequency-dependent Predation

Positive frequency-dependent predation means that the predation risk of a prey individual increases with the relative frequency of that prey type in the environment. That is, a predator consumes disproportionately more of the common prey type than of the rare one (Allen, 1988). Positive frequency-dependent predation occurs when predators show an equal or weak preference between two equally abundant prey types, however, in contrast to proportional predation, predators' feeding preference changes in response to prey abundances, namely, predators strongly favor the common prey type and ignore the rare one (Murdoch, 1969).

The studies on positive frequency-dependent predation originated from the inquiry on the persistence of balanced color polymorphism in a population. Poulton (1884) hypothesized that the brown-green dimorphism in the larvae of geometrid moths (*Cyclophora* spp.) could result from predation if predators tended to consume the more abundant morph over the rare one. Tinbergen (1960) proposed that as predators encountered prey, they may acquire ‘search images’ which enhanced their ability to rapidly distinguish cryptic prey from the background. Due to the higher encounter rate with the prey individuals of the common type, predators would quickly form a ‘search image’ of this prey type which was then followed by heavy exploitation of the prey from the common type. Clarke (1969) suggested that the formation of ‘search images’ could be the proximate cause of positive frequency-dependent predation and the consequent maintenance of polymorphism in a population (Allen, 1988). When Murdoch studied the predatory behavior of sea-shore snails feeding on barnacles and mussels, he found that snails showed a weak preference between the two prey species when they were equally abundant. However, this feeding preference was changed dramatically by previous experience on prey consumption: snails strongly favored barnacles if they had consumed barnacles before they were given equal numbers of the two prey species; similarly, mussels were disproportionately overeaten if snails had previous feeding experience on mussels. Those results suggested that positive frequency-dependent predation may also apply to different prey species which shared a common predator (Murdoch, 1969). Murdoch *et al*. further investigated the switching behavior of predators by laboratory experiments on guppies (*Poecilia reticulatus*) feeding on *Drosophila* and tubificid worms. The two prey species distributed at different places in the aquarium tank: *Drosophila* stayed on the water surface while tubificid worms located at the bottom of the tank. As the availabilities of the two prey varied, the guppies moved to and spent more time in the area where the prey increased in abundance, relative to the other alternative prey. This caused frequency-dependent mortality as the guppies disproportionately attacked the more abundant prey species (Murdoch *et al*, 1975). Murdoch's work extended the potential of positive frequency-dependent predation from maintaining the genetic diversity within the same species to maintaining the species diversity within ecological communities.

As a proposed mechanism for maintaining genetic polymorphisms and species diversity in nature, positive frequency-dependent predation has been intensively investigated (Allen 1988; Punzalan *et al*., 2005). A variety of theoretical models were developed to study the frequency-dependent behavior of predators. For example, Elton and Greenwood (1970) designed a mathematical equation to describe the sigmoid relationship between the frequency of a prey type in predator's diet and the availability of this prey type in the environment. Manly's switching model (1973) focused on relative prey risk as a function of relative prey density. Combining the features of the Elton-Greenwood and Manly models, Gendron proposed a more general model which, similar to the two earlier models, fit well with the empirical data on frequency-dependent predation but also provided a better insight into the underlying mechanisms of this predation behavior (Gendron, 1987). Hubbard *et al*. explained frequency-dependent behavior of predators from the perspective of optimal foraging. They examined two mathematical models of optimal diet which predators would take in order to maximize their inclusive fitness and found that the predictions deduced from the models were consistent with the experimental results on frequency-dependent selection. Therefore, they suggested that frequency-dependent predation and optimal foraging may represent different aspects of the same process (Hubbard *et al*., 1982). Besides theoretical analysis, many field studies and laboratory experiments were conducted to show evidence of search image formation and the resulting frequency-dependent behavior in both invertebrate and vertebrate predators. For example, Allen and Clarke used two approaches to investigate the predation behavior of wild birds, such as blackbirds, house sparrows and so on, when presented with green and brown artificial prey. In the first approach, the number of prey with one color was 9 times more than that with the other color and birds were observed to take disproportionately more of the prey with the common color. In the second approach, birds had been familiarized with prey of one color before they were provided with prey of both colors in equal proportions. This time, birds took more of the prey with the familiar color. Therefore, both approaches demonstrated that birds seemed to exhibit frequency-dependent behavior (Allen and Clarke, 1968). Rausher observed that when ovipositing female butterflies *Battus philenor* searched for host plants in their natural habitats, some of them focused on narrow-leaved host plants while others concentrated on broad-leaved ones. This leaf shape preference appeared to be a learned behavior, rather than genetically fixed response, because females were able to modify their preference based on the leaf shapes that they had previously exploited. Rausher's study indicated that females may form a search image of the leaf shape which may continuously be reinforced as females successively visited the same type of host plants. The females with the strong search image of a leaf shape discovered the corresponding host plants more rapidly and thus exploited those host plants in greater proportion than their abundance in the habitat (Rausher, 1978). Pietrewicz and Kamil studied search image formation in blue jays *Cyanocitta cristata* as those birds detected the image of cryptic moths on slides. By providing the birds a 16-slide series with 8 slides containing the image of a moth (positive slides) and 8 background slides with no moth (negative slides), they found that if all positive slides contained the image of the same type of moths, the percentage of correct detection increased dramatically after the birds had been exposed to 3 or 4 positive slides; however, if the images of two moth types with 4 slides each intermixed to form the 8 positive slides, the percentage of correct detection remained relatively low over the entire test series. Those experimental data, which demonstrated that the predator's ability to detect a particular type of cryptic prey could be significantly improved through the recent successive detection of that prey type, provided the first direct evidence of search image formation (Pietrewicz and Kamil, 1979). Jackson and Li examined the predatory behavior of araneophagic jumping spiders *Portia labiata* and discovered that those spiders tended more often to eat the same type of prey that they had consumed previously, which indicated that *P. labiata* may adopt the search images of their prey. In contrast to the traditional opinion that several repeated encounters with the same type of prey may be necessary for predators to form a search image, *P. labiata* acquired strong search images of their favorite prey types, such as web-building spiders, after a single encounter. Forming a specific search image for one type of spider enhanced *P. labiata*'s success rate to capture that prey type but decreased their ability to detect other types of spiders (Jackson and Li, 2004). Olendorf *et al* studied positive frequency-dependent predation from the perspective of prey, when exploring color polymorphism in male guppies (*Poecilia reticulatus*). In contrast to the experiments conducted by Murdoch *et al*. (Murdoch *et al*., 1975), Olendorf *et al* used guppies as prey, rather than predators. They manipulated the frequencies of male guppies with different color patterns in native streams and estimated their survival rates through a standard mark-release-recapture protocol. Because the short-term mortality of male guppies was mainly caused by their predators in the river, the experimental results, which showed that the males of the rare phenotype had a significantly higher recapture rate than those of the common phenotype, suggested that the rare type had a larger survival advantage under predation (Olendorf *et al*, 2006).

Despite the strong circumstantial evidence to support search image formation in predators as they foraged for cryptic prey, Gendron and Staddon proposed an alternative hypothesis, namely search rate hypothesis, to elucidate the relationship between prey crypticity and predators' search speed to detect prey. They developed a theoretical model based on the observations that birds spent more time scrutinizing potential prey when the prey became more cryptic (more closely matched the background). Gendron and Staddon reasoned that a high search speed would increase the frequency of prey encounters while a low search speed would improve the detection probability of an encountered prey. Thus, an optimal search rate would exist to balance the encounter rate and the detection probability in order to achieve the maximum rate of prey capture. This optimal search rate would drop as prey became more cryptic (Gendron and Staddon, 1983). The predictions of this theoretical model were supported by the laboratory simulations in which humans acting as model predators searched for a target character (the ‘prey’) embedded in the background characters on a computer screen (Gendron and Staddon, 1984). According to the search rate hypothesis, after several successive encounters with a cryptic prey type, predators learned to decrease their search speed which led to an increase in the detection probability of that prey. Thus, the improvement of predators’ ability to detect a previously encountered prey type could result from a reduction in search rate, rather than the adoption of a search image of the prey. Moreover, the two prey types used in Pietrewicz and Kamil’s experiments were not equally cryptic (Pietrewicz and Kamil, 1979), so when presented with mixed prey, predators may spend more time searching for the more cryptic prey of the two types which could lower their search efficiency. Aiming to distinguish the search image hypothesis and the search rate hypothesis, Plaisted and Mackintosh conducted experiments similar to Pietrewicz and Kamil’s but presented the predators, the pigeon *Columba livia*, with equally cryptic artificial prey. Their results showed the same patterns as those in Pietrewicz and Kamil’s studies. In addition, as Plaisted and Mackintosh manipulated the frequencies of two equally cryptic prey, they found that the prey type with a higher frequency was better detected than that with a lower frequency. Because the search rate hypothesis predicted that the two prey types with equal crypticity would have an equal detection probability regardless of their abundances while the search image hypothesis predicted that the detection probability would increase with prey abundance, these experimental results supported the search image hypothesis and refuted the search rate hypothesis (Plaisted and Mackintosh, 1995). Further experiments revealed that as the interval between the successive encounters of artificial prey decreased, the detection performance of predators improved remarkably. Those results emphasized that a ‘search image’ was a short-term, temporary process (Plaisted, 1997). Dukas and his colleagues investigated the underlying neuropsychological mechanisms for search image formation. Studies on neurobiology revealed that the brain could efficiently process only a limited amount of information at one time therefore when handling difficult tasks, focusing attention on one task, rather than dividing attention to several tasks, often resulted in a better behavioral performance on the attended task. Inspired by those findings, Dukas and Ellner developed a theoretical model which predicted that when foraging for cryptic prey, in order to maximize energy intake, predators should devote all of their attention to search for a single type and ignore alternatives and should always switch to the most abundant prey type (Dukas and Ellner, 1993). Their model was supported by laboratory experiments which demonstrated a cost of dividing attention: when foraging for digital images of cryptic prey on a computer screen, blue jays (*Cyanocitta cristata*) showed a 25% lower detection rate if they searched for two distinct target types simultaneously than if they focused attention on a single target (Dukas and Kamil, 2001). Dukas further proposed that constrained by limited attention, when searching for highly cryptic prey, predators had to selectively attend one specific prey type at a time to increase the probability of detection. Therefore forming a search image of the focused prey type and continuously searching for this type until its abundance significantly dropped seemed to be an optimal foraging strategy that predators would develop (Dukas, 2002).

Positive frequency-dependent predation had the potential to stabilize prey populations because predators tended to switch to and feed on the most abundant prey type, which resulted in relatively even population sizes of different prey species. In the case of two competing prey species which shared a common predator species, the two prey might be able to coexist indefinitely under predation (Murdoch, 1969). This logical deduction of maintaining prey species diversity by positive frequency-dependent predation was examined thoroughly by various theoretical models. For example, the mathematical model developed by Oaten and Murdoch suggested that consuming disproportionately the more abundant prey type was a necessary condition for predators to stabilize prey populations (Oaten and Murdoch, 1975). Analysis of the dynamics of a system composed of two prey and one predator species revealed that when predators fed more heavily on the more abundant prey species, the system had stable coexisting equilibrium states for those three species populations over a wide range of parameter space (Tansky, 1978; Teramoto *et al*, 1979). As the system was extended to one predator species with *n* competing prey species, predators with positive frequency-dependent behavior still produced stability in the system through relaxing the competitive exclusion among prey species (Comins and Hassell, 1976).

Although the elegant and concise mathematical analysis provided strong support for the stable coexistence of multiple prey species or balanced prey polymorphisms maintained by a predator species with switching behavior, not many empirical studies have been performed to directly evaluate it. Some laboratory experiments, which used only a few or just one predator in each trial, demonstrated the stabilizing effect of positive frequency-dependent predation on prey populations. For example, to explore the maintenance of prey polymorphism, Bond and Kamil created a virtual moth population with 3 different morphs on a computer screen and presented it to 6 blue jays, *Cyanocitta cristata*, birds which were known to exhibit positive frequency-dependent behavior when detecting digital cryptic moths. The detected moths were considered ‘killed’ and removed from the population and the relative abundance of the surviving prey, which reflected the predation pressure on different morphs, was preserved when the population was regenerated in the next generation. The experimental results showed that despite variations in the relative proportion of different morphs in the initial population, the 3 moth types stably coexisted over 50 generations. Therefore, the stable prey polymorphism could be maintained by positive frequency-dependent predation (Bond and Kamil, 1998).

Based on the assumption that a population would have an equivalent behavior to a few individuals, the experimental results obtained by using only a few predator individuals were generally extrapolated to predation at the population level, namely a population of frequency-dependent predators in a natural environment would also be able to maintain prey diversity. However, this conclusion was seriously questioned by further empirical and theoretical examinations with a predator population. For example, Cornell and Pimentel investigated the interactions between a predator population, the parasitoid wasp *Nasonia vitripennis*, and its 3 fly host populations *P. sericata*, *P. regina* and *M. domestica* in a laboratory ecosystem. Parasitoid wasps strongly preferred the host type that they had consumed previously and they concentrated their attacks on the most abundant host. When the 3 host species competed against one another in the absence of predators, the strongest competitor *P. sericata* eliminated the other 2 species in about 5 weeks. However, when parasitoid wasps were introduced to attack the pupae of the 3 host species for 48 hours, the persistence of *P. regina* and *M. domestica* was elongated to 7 weeks. Probably due to the relatively short predation period, the stable coexistence of the 3 host species was not achieved in their experiments (Cornell and Pimentel, 1978). Ishii and Shimada established two-host-one-parasitoid populations with two competing beetles, *C. chinensis* and *C. maculates* as the hosts and the pteromalid wasp *A. calandrae* as their common parasitoid. Females of the parasitoid wasps acquired olfactory search images during oviposition and thus developed their feeding preference for the current abundant host species. Two types of beans, azuki beans and black-eye beans, were used as food resources for host larvae, and female parasitoids searched for and attacked the larvae and pupae of both host species inside the beans. However, azuki beans provided a much better refuge for host larvae than black-eye beans: the parasitism rate inside azuki beans was 0-30% while that inside black-eye beans was nearly 100%. In the absence of parasitoids, *C. chinensis* was competitively excluded in about 20 weeks. In contrast, under positive frequency-dependent predation from parasitoids, the coexistence duration of two host species was remarkably prolonged to 118 weeks at the intermediate ratios of the two resource beans. Ishii and Shimada's experiments demonstrated that a population of frequency-dependent predators could significantly enhance the coexistence of two competing prey species (Ishii and Shimada, 2012). However, their experimental results were strongly influenced by the ratio of azuki and black-eye beans. For example, the persistence of two host species could not be elongated under predation at low and high ratios of two bean types (Ishii and Shimada 2010; Ishii and Shimada, 2012). Therefore, protective refuges may play a crucial role in the long-term coexistence of two prey species, which may obscure the effects of positive frequency-dependent predation on prey diversity in their experiments. Merilaita developed an individual-based computational model and explicitly described the increase of attack probability with previous feeding experience as the strength of positive frequency-dependent predation (ΔP). $\Delta P = 0$ indicated that the previously consumed prey type had no influence on a predator's current feeding preference and thus represented proportional predation behavior; $\Delta P > 0$ suggested that a predator favored the familiar prey type and the larger the ΔP, the stronger the frequency-dependent behavior. Thus by varying ΔP, the effect of positive frequency-dependent predation on the maintenance of prey diversity could be directly observed. Her simulation results showed that the coexistence time of two prey phenotypes, although increased with ΔP, dramatically decreased as the number of predator individuals increased (Merilaita, 2006).

I establish a predator population and their prey populations in Tierra. Each digital predator follows the same rules used in Merilaita's paper to capture prey in its local area. By systematically adjusting the strength of positive frequency-dependent predation ΔP, I attempt to explore the permanent coexistence of multiple prey species maintained by a population of frequency-dependent predators.

3.2 Effect of Two Predation Strategies on the Maintenance of Prey Species Diversity

The simulation results in chapter 2 show that the "Lotka-Volterra-like" cycle robustly appears between predator and prey populations in Tierra and predators can detect and acquire energy from either type-A prey or type-B prey for survival and reproduction (Figure 2.4 and Figure 2.6). Here, I present both type-A and type-B prey to predators and apply a set of simple rules to specify the behavior of predators as they encounter different prey types in their neighboring area. Depending on the parameter value in the rules, digital predators may either use a constant probability to catch prey regardless of prey types or adjust their capture rates based on the local abundance of different prey types. Then I verify that those two predation strategies applied in Tierra are essentially the same as proportional predation and positive frequency-dependent predation exhibited by real predators in laboratory experiments (Murdoch and Marks, 1973; Mattila and Bonsdorff, 1998; Lawton *et al*., 1974; Murdoch *et al*., 1975). By comparing the two predation strategies used by digital predators, I investigate the conditions and mechanisms under which the presence of a predator population supports the coexistence of two different types of prey. Those conditions for the maintenance of prey diversity are further examined as I increase the number of prey species from two to three.

3.2.1 Predation Behavior of Predators at a Population Level

Methods

A digital predator searches for prey in its local area by matching its predation template with the complementary template in prey. Then the predator captures its prey and acquires energy from it with a certain probability. This capture probability varies based on the type of prey that the predator encounters and is specified by the following rules:

(1) Initially, each predator is assigned an equal probability to capture type-A and type-B prey when encountered, that is, $P_A = P_B = 0.5$

(2) If the predator captures a type-A prey, its probability to capture type-A prey is increased by ΔP and to capture type-B prey is decreased by ΔP, that is,

$$P_A = P_A + \Delta P \qquad\qquad P_B = P_B - \Delta P$$

(3) If, instead, the predator captures a type-B prey, its probability to capture type-A prey is decreased by ΔP and to capture type-B prey is increased by ΔP, that is,

$$P_A = P_A - \Delta P \qquad\qquad P_B = P_B + \Delta P$$

(4) All capture probabilities are bounded by P_{min} and P_{max} , that is,

$$0 \leq P_{min} \leq P_A, P_B \leq P_{max} \leq 1$$

The default values of the minimal and maximal capture probabilities are $P_{min} = 0$ and $P_{max} = 1$, if not otherwise mentioned.

In the above set of rules, if $\Delta P = 0$, the capture probabilities for two different prey types remain equal, that is $P_A = P_B = 0.5$. This is the scenario of proportional predation in which the predator always uses the same probability to capture prey regardless of their abundance. On the other hand, if $\Delta P > 0$, the predator has a higher probability to capture the type of prey which is more frequently encountered. This behavior of disproportionately consuming the common prey type represents positive frequency-dependent predation.

In a laboratory experiment, a predator's predation behavior is revealed by computing the percentage of one type of prey in the predator's diet as the percentage of that prey type in the environment increases from 0 to 100%. In simulation runs, the behavior of a predator population in which each predator obeys the above predation rules is examined through the following setup: I run 9 separate simulations and in each simulation, I seed the soup with 3000 prey individuals and 300 predator individuals. In each predation loop, a predator is allowed to eat at most *m* (*m* = 4) prey and acquires 35% of the CPU time from each prey and the CPU time of a captured prey is reduced to 40% of its original value. The only difference among the 9 simulations is the relative proportion of two prey types, that is, the percentage of type-A prey in the 3000 prey individuals increases from 10% to 90% in 10% increments. Ideally, I should calculate the percentage of type-A prey in the predators' diet while the ratio of type-A prey in the environment remains constant. However, in the simulations, as the predators start to consume different prey types, the relative proportion of two prey types changes. I allow the predators to explore the prey populations sufficiently but not to appreciably modify the ratio between type-A and type-B populations. Typically, when the percentage of type-A prey differs from its initial value by 5%, I calculate the percentage of type-A prey in the predators' diet. For example, one of the simulations starts with 600 individuals of type-A prey evenly distributed among 2400 individuals of type-B prey, that is, the percentage of type-A in the 3000 prey individuals is 20%. When type-A prey increase to 25%, I calculate the percentage of type-A prey in the predators' diet (the number of type-A prey that have been eaten is divided by the total number of prey that have been eaten by the predator population).

I set ΔP to two different values: $\Delta P = 0$ to allow each predator to capture prey with a constant rate and $\Delta P = 0.1$ to allow each predator to adjust its capture rates for different prey types. For each value of ΔP, I perform the 9 simulation runs described above and observe the behavior of the predator population as the percentage of type-A prey in prey populations increases.

Results

When $\Delta P = 0$, each digital predator applies the same probability ($P_A = P_B = 0.5$) to capture type-A and type-B prey regardless of their local abundance. As shown in Figure 3.1(a), the percentage of type-A prey in the predators' diet is almost completely proportional to the percentage of type-A prey in the environment. Therefore, as each individual predator shows no preference for one prey type over the other, the predator population exhibits proportional predation behavior on the prey populations.

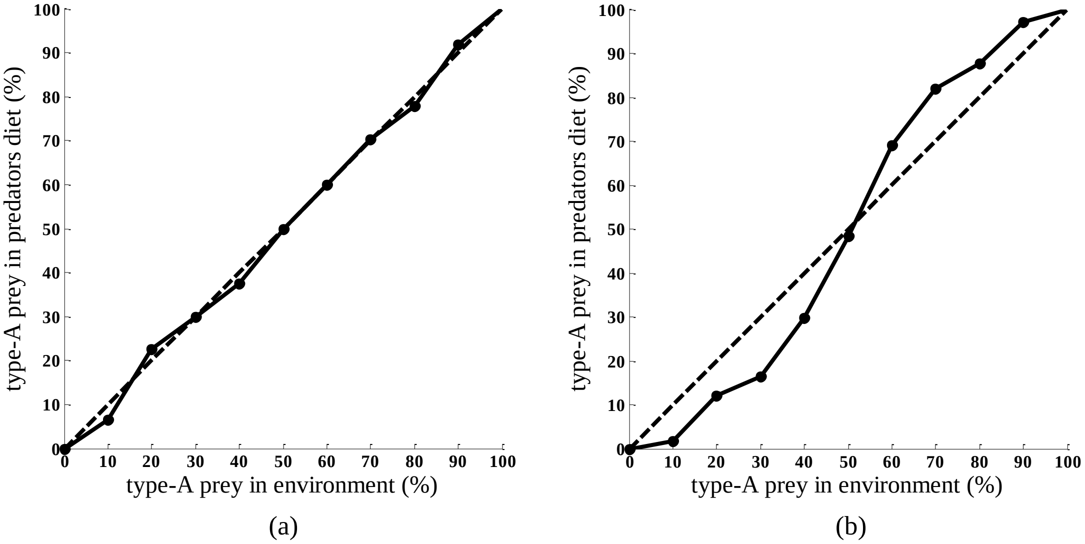


Figure 3.1: Predation behavior of a predator population in Tierra changes with ΔP. (a) A predator population in the Tierra system exhibits proportional predation behavior when $\Delta P = 0$. (b) A predator population in the Tierra system exhibits positive frequency-dependent behavior when $\Delta P = 0.1$. The dashed line indicates the hypothetical situation in which the relative frequency of a prey type in the environment does not affect the predators' feeding preference.

When $\Delta P = 0.1$, each digital predator has a higher probability to capture a previously encountered prey type, as specified by the rules in the "Methods" section. As shown in Figure 3.1(b), when the percentage of type-A prey in the environment is less than 50%, the predator population disproportionately eats less type-A prey and when type-A prey become the abundant prey type (>50%), the predator population disproportionately consumes more type-A prey. The switch of the preferable prey type occurs exactly when type-A prey change from a rare type to a common one (50%). Therefore, although each digital predator exhibits prey preference based on the prey types actually encountered, which may not agree with the relative frequency of prey types at a global scale, the predator population executes almost perfect positive frequency-dependent predation on the prey populations (Shao and Ray, 2010).

3.2.2 Maintenance of the Coexistence of Two Prey Types

Methods

The maintenance of prey diversity by predators is explored by comparing the results of three simulations. In the control run (without predation), I seed the soup with a type-A population of 1500 individuals and a type-B population of 1500 individuals and observe the dynamics of those two prey populations in the absence of predators. The simulation run stops when one of the prey types becomes extinct. In the two experimental runs (with predation), I introduce a predator population of 300 individuals into the same kind of initial prey populations used in the control run, containing two types of prey. The only difference between the two experimental runs is the predation strategy used by each predator after it encounters a prey in its neighboring area (about 10 creatures long on either side of the predator). In the first experimental run, I set $\Delta P = 0$ so that the predator eats the prey with a constant rate of 0.5 regardless of the prey type. However, in the second experimental run, I set $\Delta P = 0.1$ so that the predator is biased to consume the more abundant prey type. For each experimental run, in each predation loop, a predator is allowed to eat at most m (m = 4) prey and acquires 35% of the CPU time from each prey. The CPU time of a captured prey is reduced to 40% of its original value. The simulation run stops when one of the prey populations goes extinct but if both prey populations persist, the run lasts until 1800 million instructions have been executed. I record the population sizes of the predator and two prey species during the runs.

Results

Many field and laboratory experiments demonstrated that in the absence of predators, two prey species which shared the same limiting resources could not coexist indefinitely. The more competitive prey species would gradually occupy more and more resources and drive the less competitive prey species to go extinct (Gause, 1934; MacArthur, 1958; Hardin, 1960). This competitive exclusion is also observed in Tierra when type-A prey compete with type-B prey in the environment with limiting CPU time and memory space. Because a type-A prey (86 instructions long) is shorter than a type-B prey (96 instructions long), when both prey types receive, on the average, the same amount of CPU time from the system, type-A prey reproduce more offspring than type-B prey do. Therefore, although the two types of prey start with the same population size of 1500 individuals, the more rapid replicating type-A prey gradually crowd out type-B prey and drive them to go extinct after 120 million instructions have been executed, as shown in Figure 3.2(a).

When a predator population of 300 individuals which exhibits proportional predation is introduced into the soup, the two prey types are consumed by predators with a constant probability and thus the number of captured individuals of a prey type is proportional to the population size of that prey type. As a result, when the population of type-A prey becomes larger than that of type-B prey, predators start to consume more type-A than type-B prey individuals. This slows down the process by which type-A prey crowd out type-B prey from the soup.

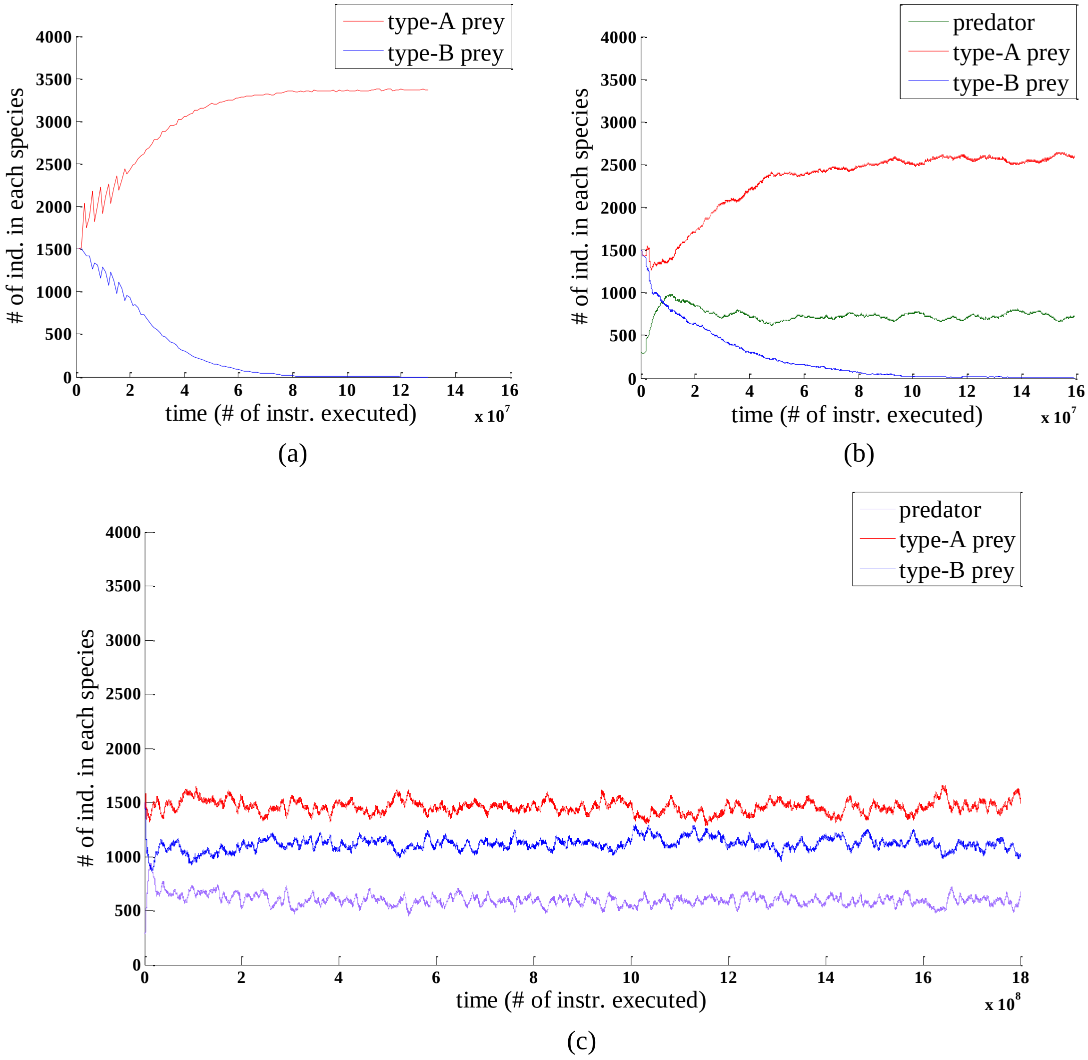


Figure 3.2: Coexistence of two prey species is maintained by a predator population with positive frequency-dependent behavior. (a) Competitive exclusion between two types of prey; type-B prey go extinct. (b) Under proportional predation from a predator population, type-A and type-B prey coexist for a longer period of time. But this coexistence of the two prey types is not stable and type-B prey eventually go extinct. (c) Under positive frequency-dependent predation from a predator population, type-A and type-B prey stably coexist.

As shown in Figure 3.2(b), the decline of the type-B prey population is slower than that in the control run, especially after the number of type-B prey has been significantly reduced. However, type-A prey and type-B prey do not coexist in the soup for a very long time. The type-B prey population keeps declining and eventually goes extinct after 160 million instructions have been executed. Therefore, although proportional predation can prolong the coexistence of the two prey types to some extent, it fails to maintain the stable coexistence of prey species.

However, when a predator population of 300 individuals which exhibits positive frequency-dependent behavior is introduced into the soup, the dynamics of the prey populations change dramatically. As shown in Figure 3.2(c), after the transient initial stage, the predator population reaches a steady level of about 600 individuals and the two prey populations stably coexist with approximately 1500 individuals of type-A and 1100 individuals of type-B. This stable coexistence of the two prey populations is maintained over the entire simulation run of 1800 million instructions executed (Shao and Ray, 2010). Therefore, in contrast to proportional predation, positive frequency-dependent predation is able to maintain the diversity of prey species.

3.2.3 Robustness to the Variations of Parameter Settings

Methods

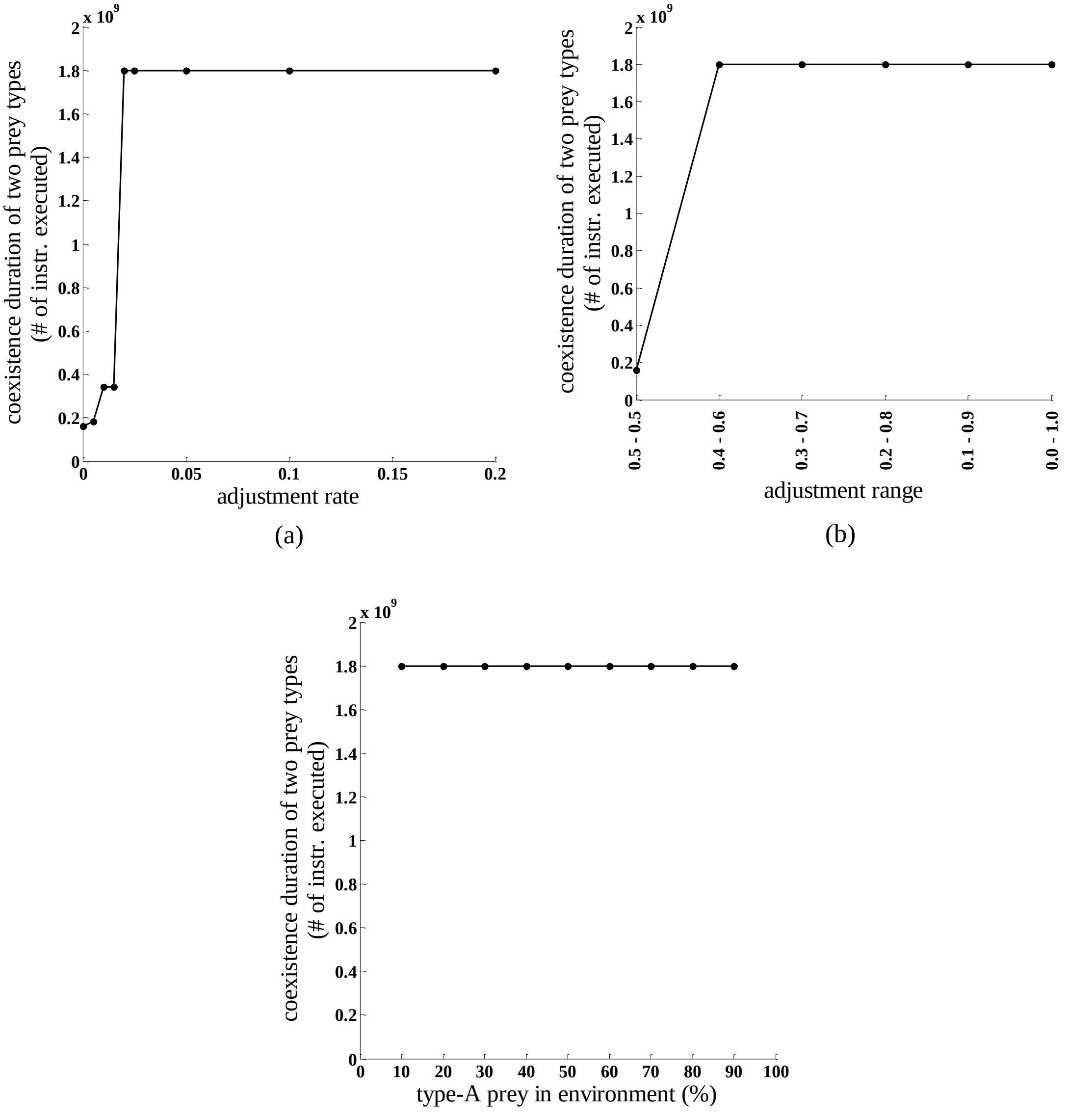
To explore the robustness of positive frequency-dependent predation in maintaining the coexistence of type-A and type-B populations, I systematically vary the two parameters which affect the predation behavior of a predator, the adjustment rate ΔP and the adjustment range $P_{min} - P_{max}$, and the initial relative proportion of two prey types, respectively. The default setting of those three parameters is that $\Delta P = 0.1$, $P_{min} - P_{max} = 0 - 1$ and the percentage of type-A prey in the 3000 prey individuals is 50% (1500 individuals of each prey type) and when one parameter varies, the other two remain unchanged. I set $\Delta P = 0, 0.005, 0.01, 0.015, 0.02, 0.025, 0.05, 0.1$ and 0.2, respectively, to examine the effect of ΔP on the maintenance of prey diversity. Then I set ΔP back to 0.1 and gradually shrink the adjustment range, $P_{min} - P_{max} = 0 -$

$1, 0.1 - 0.9, 0.2 - 0.8, 0.3 - 0.7, 0.4 - 0.6, 0.5 - 0.5$. Finally, after setting $P_{min} - P_{max}$ back to $0 - 1$, I vary the percentage of type-A prey among the 3000 prey individuals from 10% to 90% in 10% increments. For each parameter setting, in each predation loop, a predator is allowed to eat at most m (m = 4) prey and acquires 35% of the CPU time from each prey. The CPU time of a captured prey is reduced to 40% of its original value. I record the duration (the number of instructions that have been executed) that the two prey types coexist.

Results

The adjustment rate ΔP directly affects the strength of positive frequency-dependent predation. $\Delta P = 0$ is the scenario of proportional predation in which a predator always uses the same probability, $P_A = P_B = 0.5$, to eat type-A and type-B prey. As ΔP increases, a predator can more effectively adjust its probability of capturing different types of prey based on the abundance of prey types in its local area. As shown in Figure 3.3(a), when $\Delta P \geq 0.02$, the predator population has sufficient frequency-dependent behavior to maintain the coexistence of the two prey populations over the entire simulation run of 1800 million instructions executed.

The adjustment range $P_{min} - P_{max}$ specifies the lower and upper boundaries of the capture probability, which indirectly limits a predator's ability to prefer the more abundant prey type. For example, when $P_{min} - P_{max} = 0.5 - 0.5$, a predator's probabilities to consume different prey types are fixed at $P_A = P_B = 0.5$ (equivalent to the scenario of proportional predation), that is, a predator fails to adjust its capture probabilities based on local prey abundance even if $\Delta P = 0.1$.



(a)

(b)

(c)

Figure 3.3: Robustness of positive frequency-dependent predation in maintaining the coexistence of two prey types. (a) When the adjustment range is $0 - 1$ and the percentage of type-A prey in the environment is 50%, type-A and type-B prey populations stably coexist when $\Delta P \geq 0.02$. (b) When $\Delta P = 0.1$ and the percentage of type-A prey in the environment is 50%, type-A and type-B prey populations stably coexist under all the adjustment ranges except for $0.5 - 0.5$. (c) When $\Delta P = 0.1$ and the adjustment range is $0 - 1$, type-A and type-B prey populations stably coexist at 9 different initial ratios of the two prey populations.

However, this limitation is gradually relaxed as the adjustment range extends towards $P_{min} - P_{max} = 0 - 1$. As shown in Figure 3.3 (b), except for $P_{min} - P_{max} =$

$0.5 - 0.5$, which eliminates the effect of positive frequency-dependent predation, the two prey populations coexist under all other adjustment ranges over the simulation run of 1800 million instructions executed.

By disproportionately consuming the more abundant prey type, positive frequency-dependent predation can maintain the coexistence of two prey types even when the initial sizes of the two prey populations vary dramatically. As shown in Figure 3.3(c), when the percentage of type-A prey in the 3000 prey individuals increases from 10% (300 individuals of type-A prey and 2700 individuals of type-B prey) to 90% (2700 individuals of type-A prey and 300 individuals of type-B prey), the two prey types coexist under each of the 9 initial ratios of the two prey populations over the simulation run of 1800 million instructions executed.

The stable persistence of two prey populations in Tierra under a variety of parameter settings suggests that positive frequency-dependent predation may robustly support the coexistence of two prey species (Shao and Ray, 2010).

3.2.4 Mechanisms of Maintaining Prey Species Diversity by Positive Frequency-dependent Predation

Methods

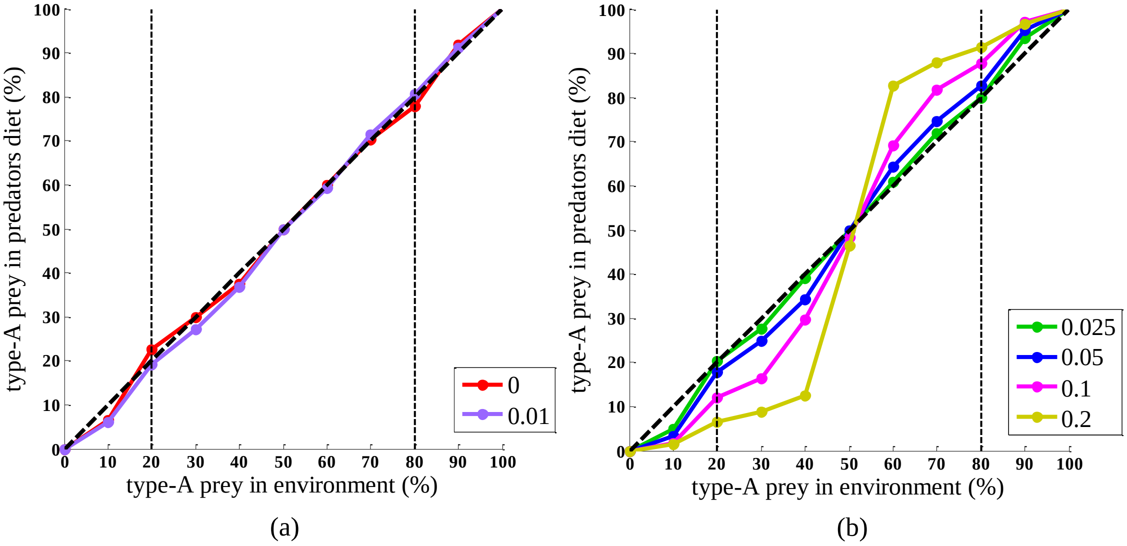
The simulation results in 3.2.1, 3.2.2 and 3.2.3 show that a predator population which exhibits proportional predation fails to maintain the coexistence of two prey types, however, a predator population which performs positive frequency-dependent predation can robustly support prey diversity. The only difference between the two predation strategies is the value of ΔP, that is, $\Delta P = 0$ corresponds to proportional predation and $\Delta P > 0$ corresponds to positive frequency-dependent predation.

Therefore, by systematically varying ΔP, I attempt to explore the mechanisms inherent in the two predation strategies which influence the maintenance of the diversity of prey species.

I set ΔP to 6 different values, that is, $\Delta P = 0, 0.01, 0.025, 0.05, 0.1$ and 0.2, to gradually increase the strength of positive frequency-dependent predation. To observe the influence of ΔP on the switching behavior of a predator population as the abundance of type-A prey increases, for each ΔP value, I perform the 9 separate simulation runs which are described in detail in the Methods section in 3.2.1. Briefly speaking, in each simulation run, I seed the soup with 3000 prey individuals and 300 predator individuals. In each predation loop, a predator is allowed to eat at most *m* (*m* = 4) prey and acquires 35% of the CPU time from each prey and the CPU time of a captured prey is reduced to 40% of its original value. The 9 simulation runs differ only in the relative proportion of two prey types in the initial prey populations, that is, the percentage of type-A prey among the 3000 prey individuals varies from 10% to 90% in 10% increments. In each simulation, when the percentage of type-A prey differs from its initial value by 5%, I calculate the percentage of type-A prey in the predators' diet.

As shown in Figure 3.1(b), the predator population switches its feeding preference when type-A prey change from a rare type to a common one. I study the mechanisms for maintaining the diversity of prey species when type-A prey is a rare type and a common type, respectively. In the scenario that type-A is a rare type, I set the percentage of type-A prey in the 3000 prey individuals to 20%, that is, 600 type-A prey individuals evenly distributed among 2400 type-B prey individuals. On the other hand, in the scenario that type-A is a common type, I set the percentage of type-A prey to 80%, that is, 600 type-B prey individuals evenly distributed among 2400 type-A prey individuals. Except for the difference in the relative proportion of type-A prey in the initial prey populations, the two scenarios share the same parameter settings as follows: for each scenario, I perform 6 separate simulation runs. In each simulation, the soup is seeded with 3000 prey individuals and 300 predator individuals. In each predation loop, a predator is allowed to eat at most m (m = 4) prey and acquires 35% of the CPU time from each prey and the CPU time of a captured prey is reduced to 40% of its original value. The 6 simulation runs differ only in the strength of positive frequency-dependent predation, that is, $\Delta P = 0, 0.01, 0.025, 0.05, 0.1 \text{ and } 0.2,$ respectively. Each run lasts either until one of the prey types becomes extinct or, if both prey types persist, until 2000 million instructions have been executed. I record the relative proportion of type-A prey in the prey populations (R_A), that is, the population size of type-A prey is divided by the summation of the population sizes of type-A and type-B prey, during a simulation run.

Besides observing the effect of ΔP on the coexistence of two prey species over an entire simulation run, I also examine the changes of the type-A prey population during the initial stage of a simulation run (from 0 to 100 million instructions executed). Furthermore, I calculate the average and standard deviation of the relative proportion of type-A prey in the prey populations (R_A) during the period of 1500 to 2000 million instructions executed, to explore how the steady state of the type-A prey population is influenced by the strength of positive frequency-dependent predation.



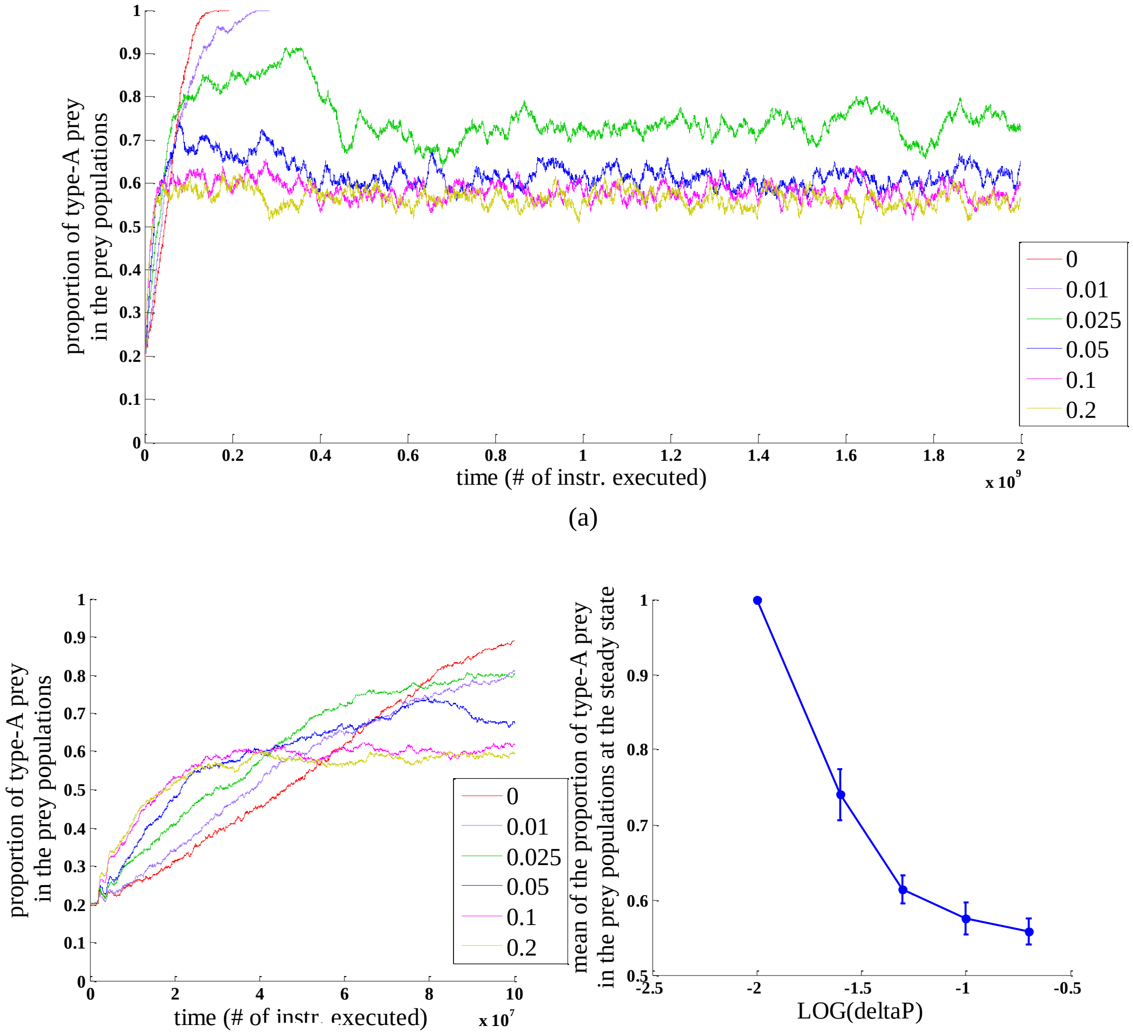
(a) (b)

Figure 3.4: Positive frequency-dependent behavior becomes more distinctive as ΔP increases. (a) A predator population in the Tierra system exhibits proportional predation when $\Delta P = 0$ and extremely weak positive frequency-dependent predation when $\Delta P = 0.01$. (b) A predator population in the Tierra system exhibits increasingly stronger positive frequency-dependent behavior with the increase of ΔP ($\Delta P = 0.025, 0.05, 0.1$ and 0.2). The diagonal dashed line indicates the hypothetical situation in which the relative frequency of a prey type in the environment does not affect the predators' feeding preference. The two vertical dashed lines mark the relative abundance of type-A prey in environment at 20% and 80%, respectively.

Results

As shown in Figure 3.4(a), when $\Delta P = 0$, the predator population executes proportional predation, namely, the number of type-A prey individuals eaten by the predators is proportional to the abundance of type-A prey in the environment. For example, as illustrated by the two vertical dashed lines, when the percentage of type-A prey in the environment is 20% and 80%, the percentage of type-A prey in the predators' diet is also about 20% and 80%, respectively. The behavior of the predator population with extremely weak positive frequency-dependent predation, such as $\Delta P = 0.01$, does not differ significantly from proportional predation. However, as ΔP gradually increases, the predator population exhibits stronger and stronger positive frequency-dependent behavior. As shown in Figure 3.4(b), when less than 50% of the prey populations are composed of type-A prey, predators consume disproportionately less type-A prey and the larger the ΔP, the less the type-A prey individuals are found in the predators' diet. For example, when the percentage of type-A prey in the environment is 20%, as $\Delta P = 0.025, 0.05, 0.1$ and 0.2, the percentage of type-A prey in the predators' diet is 20.2%, 17.8%, 12%, 6.5%, respectively. On the other hand, when type-A prey become the abundant type (>50%), predators disproportionately consume more of them and the larger the ΔP, the more the type-A prey individuals are eaten by the predators. For example, when the percentage of type-A prey in the environment is 80%, as $\Delta P = 0.025, 0.05, 0.1$ and 0.2, the percentage of type-A prey in the predators' diet is 79.9%, 82.7%, 87.6%, 91.5%, respectively.

Based on the calculation of the relative proportion of type-A prey in the prey populations (R_A) defined in the Methods section, $R_A = 1$ indicates the extinction of the type-B prey population, and on the other hand, $R_A = 0.5$ suggests that type-A and type-B prey are equally abundant. In the scenario that type-A is a rare type, R_A starts at 0.2 and quickly rises for all 6 values of ΔP, as shown in Figure 3.5(a). For proportional predation ($\Delta P = 0$) and extremely weak positive frequency-dependent predation ($\Delta P = 0.01$), R_A increases to 1 which suggests that the type-B prey population eventually goes extinct and thus the two prey types fail to coexist (Figure 3.5(a)). When $\Delta P = 0.025$, R_A increases to 0.9 then decreases and after that, it fluctuates between 0.7 and 0.8 with a large amplitude (Figure 3.5(a)). Therefore, at this ΔP value, type-A prey are significantly more abundant than type-B prey.



(a)

(b)

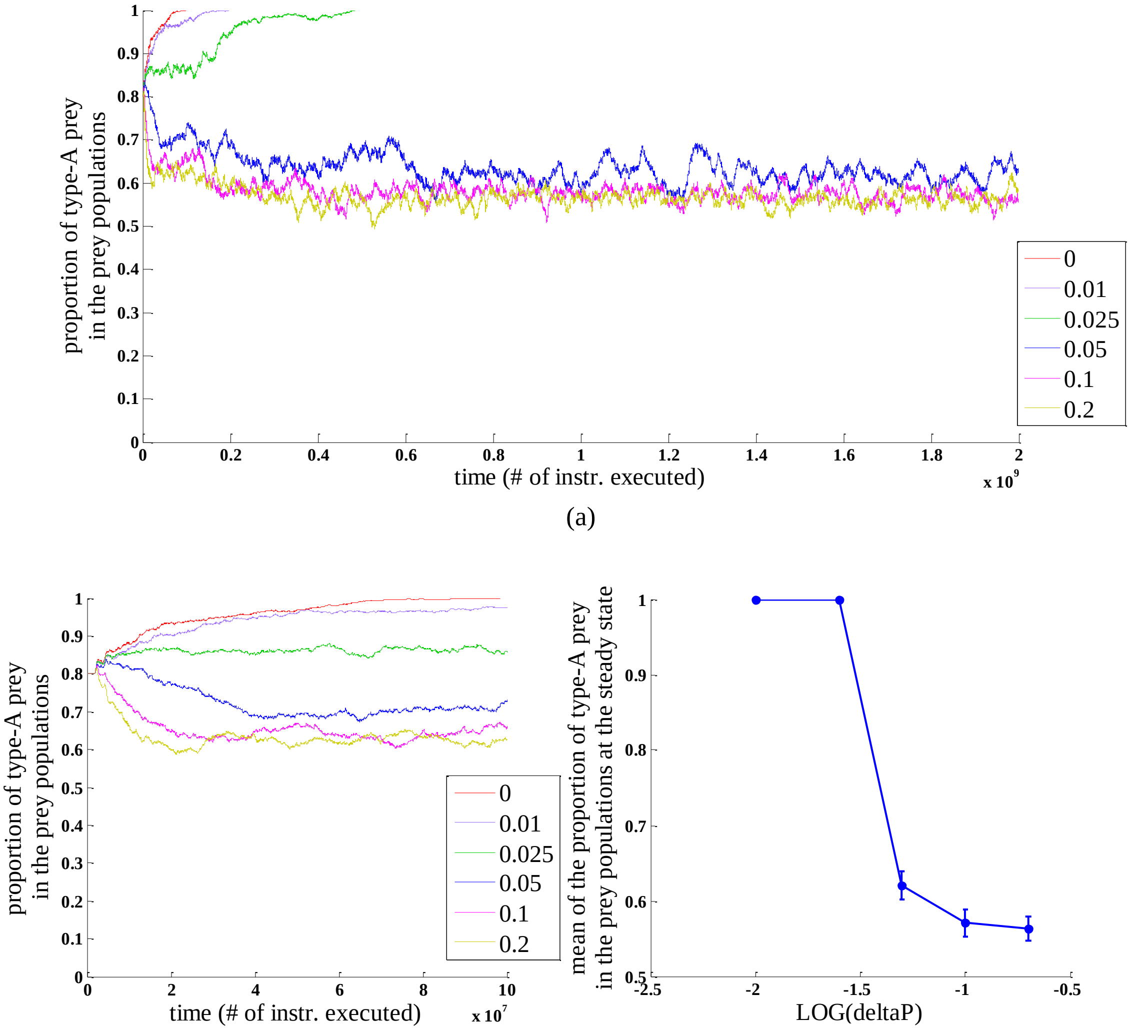
(c)

Figure 3.5: When type-A is a rare type in the initial prey populations, the stable coexistence of two prey types is achieved by the strong negative feedback regulation present in positive frequency-dependent predation. (a) Proportion of type-A prey in the prey populations (R_A) in 6 simulations with each corresponding to a different ΔP value. When $\Delta P = 0 \text{ and } 0.01$, R_A increases to 1, which indicates the extinction of the type-B prey population. When $\Delta P = 0.025, 0.05, 0.1 \text{ and } 0.2$, R_A is smaller than 1 over the entire simulation run, which suggests the coexistence of type-A and type-B prey populations. (b) Proportion of type-A prey in the prey populations (R_A) during the initial stage of the simulation runs (0–100 million instructions executed). When R_A is less than 0.5 (0–50 million instructions executed), the larger the ΔP, the more rapid the growth of the type-A prey population. When R_A is greater than 0.5 (50–100 million instructions executed), the larger the ΔP, the slower the increase of the type-A prey population. (c) As ΔP increases, the average of R_A at the steady state (1500–2000 million instructions executed) approaches 0.5 with decreasing fluctuation (error bars represent the standard deviation). This suggests that a more stable coexistence of the two prey types is attained by a stronger negative feedback regulation on prey populations.

Although the two prey types coexist, due to the small population size of type-B prey, this coexistence may not be very stable. With the further increase of ΔP ($\Delta P = 0.05, 0.1 \text{ and } 0.2$), R_A falls into the range of 0.5 to 0.7 which suggests that the abundances of type-A and type-B prey become similar to each other (Figure 3.5(a)). The type-B prey population, although still smaller than the type-A prey population, has reached a sufficient size to prevent itself from extinction caused by the competitive exclusion from type-A prey and/or randomness in the Tierra system. Hence, the two prey types achieve a stable coexistence under strong positive frequency-dependent predation.

When type-A is a rare prey type (<50%) in the environment, as shown in Figure 3.4, the larger the ΔP, the less the number of type-A prey individuals eaten by predators. As a result, the type-A prey population has a better opportunity to grow. This growth pattern of the type-A prey population is clearly demonstrated in Figure 3.5(b) in the period of 0–50 million instructions executed: type-A prey, composed of 20% of the initial prey populations, increase over time and the larger the ΔP, the quicker the rise of the type-A prey population. On the other hand, when type-A is a common prey type (>50%), as shown in Figure 3.4, the larger the ΔP, the more the type-A prey individuals are found in the predators' diet. Thus the growth of the type-A prey population is more severely depressed. This change in the type-A prey population is shown in Figure 3.5(b) in the period of 50–100 million instructions executed: when the proportion of type-A prey becomes greater than 0.5, the larger the ΔP, the slower the growth of the type-A prey population. In conclusion, when type-A is a rare prey type, by disproportionately consuming less type-A prey, a predator population with positive frequency-dependent behavior facilitates the rapid increase of the type-A population; while when type-A prey are abundant, by disproportionately consuming more type-A prey, the predator population quickly depresses the type-A population. Therefore, positive frequency-dependent predation provides a strong negative feedback regulation on the prey populations. Due to the lack of this regulation, a predator population with proportional predation or weak positive frequency-dependent predation ($\Delta P = 0 \text{ and } 0.01$) could not effectively prevent the growth of the type-A prey population when type-A prey are prevailing, and thus type-B prey are eventually excluded from the soup. Figure 3.5(c) shows that, at the steady state, with the increase of ΔP, R_A becomes closer to 0.5 with smaller fluctuations, namely, type-A and type-B prey have a more similar abundance. This suggests that the strong negative feedback regulation tends to equalize the population sizes of different prey types, which results in a stable persistence of two prey types. Therefore, the strong negative feedback regulation present in positive frequency-dependent predation may be the critical condition to maintain the coexistence of prey species.

This mechanism that prey species diversity is maintained by strong negative feedback regulation is further examined in the scenario that type-A is a common prey type. As shown in Figure 3.6(a), R_A starts at 0.8 and quickly increases to 1, which indicates the extinction of type-B prey, under proportional predation ($\Delta P = 0$). A predator population with weak positive frequency-dependent predation ($\Delta P = 0.01 \text{ and } 0.025$) allows the type-B prey population to survive in the soup for a longer time but cannot prevent it from going extinct.



(a)

(b)

(c)

Figure 3.6: When type-A is a common type in the initial prey populations, the stable coexistence of two prey types is achieved by the strong negative feedback regulation present in positive frequency-dependent predation. (a) Proportion of type-A prey in the prey populations (R_A) in 6 simulations with each corresponding to a different ΔP value. When $\Delta P = 0, 0.01$ and 0.025, R_A increases to 1, which indicates the extinction of the type-B prey population. When $\Delta P = 0.05, 0.1$ and 0.2, R_A is smaller than 1 over the entire simulation run, which suggests the coexistence of type-A and type-B prey populations. (b) Proportion of type-A prey in the prey populations during the initial stage of the simulation runs (0–100 million instructions executed). The larger the ΔP, the slower the increase of the type-A prey population ($\Delta P = 0, 0.01$ and 0.025) or the quicker the decrease of the type-A prey population ($\Delta P = 0.05, 0.1,$ and 0.2). (c) As ΔP increases, the average of R_A at the steady state (1500–2000 million instructions executed) approaches 0.5 with decreasing fluctuation (error bars represent the standard deviation). This suggests that a more stable coexistence of the two prey types is attained by a stronger negative feedback regulation on prey populations.

However, under strong positive frequency-dependent predation ($\Delta P = 0.05, 0.1 \text{ and } 0.2$), R_A falls into the range of 0.5–0.7 which suggests the continuous coexistence of type-A and type-B prey. Because type-A prey are much more abundant than type-B prey in the initial prey populations, predators impose a stronger depression on type-A prey by consuming more of them in positive frequency-dependent predation than in proportional predation. This depression on the type-A prey population is clearly shown during the initial stage of simulation runs (0–100 million instructions executed) in Figure 3.6(b). Compared to proportional predation ($\Delta P = 0$), weak positive frequency-dependent predation (such as $\Delta P = 0.01$, especially $\Delta P = 0.025$) considerably slows down the increase of the type-A prey population. Moreover, strong positive frequency-dependent predation ($\Delta P = 0.05, 0.1 \text{ and } 0.2$) results in a substantial decrease in the type-A prey population and the larger the ΔP, the more rapid and more significant the decline of the type-A population. Similar to Figure 3.5(c), Figure 3.6(c) shows that at the steady state, R_A approaches 0.5 with the increase of ΔP. Therefore, the stronger negative feedback regulation in positive frequency-dependent predation produces more even population sizes of type-A and type-B prey and thus more stable persistence of prey diversity.

3.2.5 Maintenance of the Coexistence of Three Prey Types by Positive Frequency-dependent Predation

Methods

To further examine the role of positive frequency-dependent predation in maintaining prey diversity, I study a scenario in which the initial prey populations are composed of more than two prey types. Besides type-A and type-B prey, I add one more species, type-C prey with a length of 90 instructions. Except for the length difference, the three prey types share the same structure and function and a predator is able to detect each of them by matching its predation template with the complementary template in prey. When a predator encounters a prey in its local area, the rules of capture probability, which are directly extended from the case of two prey types, are as follows:

(1) Initially, each predator is assigned an equal probability to capture type-A, type-B and type-C prey when encountered, that is: $P_A = P_B = P_C = 0.5$

(2) If the predator captures a type-A prey, its probability to capture type-A prey is increased by ΔP and to capture type-B and type-C prey is decreased by ΔP, that is:

$$P_A = P_A + \Delta P \qquad P_B = P_B - \Delta P \qquad P_C = P_C - \Delta P$$

(3) If the predator captures a type-B prey, its probability to capture type-A and type-C prey is decreased by ΔP and to capture type-B prey is increased by ΔP, that is:

$$P_A = P_A - \Delta P \qquad P_B = P_B + \Delta P \qquad P_C = P_C - \Delta P$$

(4) If the predator captures a type-C prey, its probability to capture type-A and type-B prey is decreased by ΔP and to capture type-C prey is increased by ΔP, that is:

$$P_A = P_A - \Delta P \qquad P_B = P_B - \Delta P \qquad P_C = P_C + \Delta P$$

(5) All capture probabilities are bounded by P_{min} and P_{max}, that is:

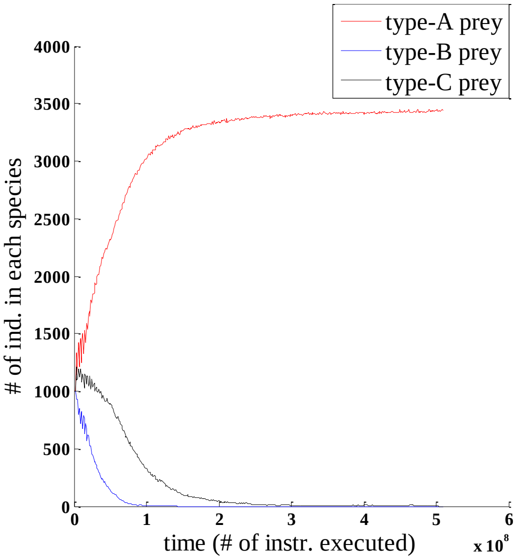
$$0 \leq P_{min} \leq P_A, P_B, P_C \leq P_{max} \leq 1$$

The default values of the minimal and maximal capture probabilities are $P_{min} = 0$ and $P_{max} = 1$, if not otherwise mentioned.

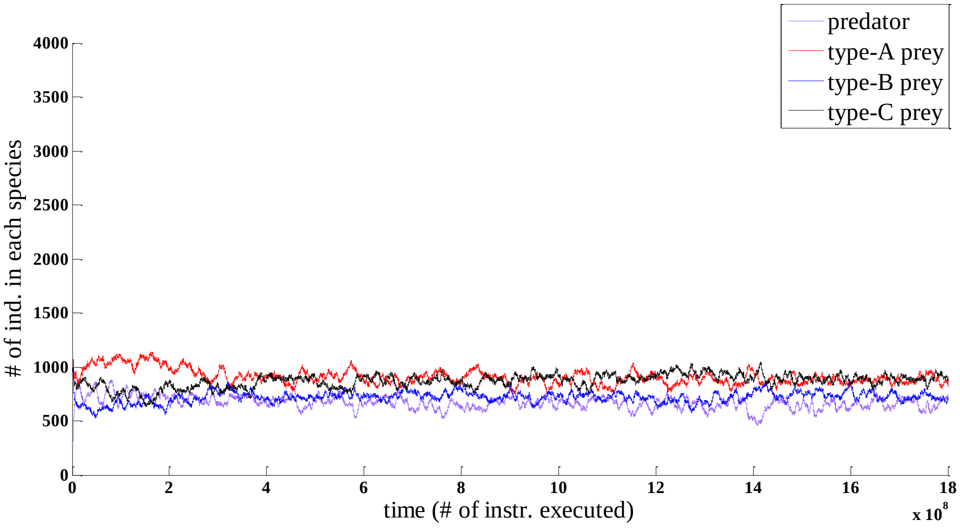
I perform two simulation runs to compare the dynamics of prey populations in the absence of predators with those in the presence of predators. In the control run (without predation), the soup is seeded with 3000 prey individuals with 1000 individuals of each prey type. The simulation run stops when only one prey population remains and the population size of each prey type is recorded during the run. In the experimental run (with predation), I introduce 300 predator individuals into the initial prey populations used in the control run. Each predator searches for prey in its local area and executes positive frequency-dependent predation ($\Delta P = 0.1$) based on local prey abundance. In each predation loop, a predator is allowed to eat at most m (m = 4) prey and acquires 35% of the CPU time from each prey. The CPU time of a captured prey is reduced to 40% of its original value. The simulation run lasts until 1800 million instructions have been executed and I record the population sizes of the predator and three prey species during the run.

Results

The three prey types differ in their genome lengths, type-A prey being 86 instructions long, type-B prey being 96 instructions long and type-C prey being 90 instructions long. In the absence of predators, the three prey types compete with one another and the creatures with a shorter genome length reproduce faster than those with a longer genome length, as each creature receives approximately the same amount of CPU time from the system. As shown in Figure 3.7(a), when the simulation run starts with 1000 individuals of each prey type, due to competitive exclusion, type-B prey go extinct after 144 million instructions have been executed and then type-C prey are crowded out by type-A prey after 504 million instructions have been executed and the type-A prey population occupies the entire soup.



(a)



(b)

Figure 3.7: Coexistence of three prey species is maintained by a predator population with positive frequency-dependent behavior. (a) Competitive exclusion among three types of prey; type-B prey and then type-C prey go extinct. (b) Type-A, type-B, and type-C prey stably coexist under the predation from a frequency-dependent predator population.

However, when a predator population of 300 individuals with positive frequency-dependent behavior is introduced into the three prey populations of 1000 individuals of each type, as shown in Figure 3.7 (b), all three prey types stably coexist over the entire simulation run of 1800 million instructions executed. This result further supports the idea that positive frequency-dependent predation is able to maintain the diversity of prey species (Shao and Ray, 2010).

3.2.6 Discussion

In a natural environment, it is likely to be a full predator population, rather than a few predator individuals, that regulate prey populations. Therefore, after laboratory experiments have successfully demonstrated that the stable coexistence of multiple prey phenotypes could be maintained by one or a few predators with positive frequency-dependent behavior, it is crucial to further investigate whether the prey diversity could be achieved by a population of such predators. Merilaita developed an individual-based computational model in which the strength of positive frequency-dependent predation could be gradually adjusted. Her simulation results showed that although one or two predator individuals could maintain the diversity of prey species, which was consistent with the laboratory experimental results, five or ten predator individuals failed to do so. Because the duration that two prey species coexisted decreased dramatically as the number of predator individuals increased, it was concluded that positive frequency-dependent predation may not be a sufficient mechanism to maintain species diversity in nature (Merilaita, 2006).

However, the setup of the simulations in Merilaita's study may not agree with the natural behavior of a predator population. In the laboratory experiments with one or two predator individuals, each predator was able to explore the entire populations of two prey types and switched to the common type based on the global abundance of different types. Merilaita also allowed each predator to obtain prey from the entire prey populations regardless of the number of predator individuals. It was found that a single predator individual maintained prey species diversity longer than ten predator individuals. This result was rationalized as follows: “when there were ten predators, the behavior of each individual predator was formed by only one tenth of the information about prey type frequencies in relation to the total number of consumed prey, compared to the one-predator case.” (Merilaita, 2006) That is, based on the prey types that a predator had consumed, this predator attempted to acquire the information about the relative abundance of two prey types and adjusted its predation behavior to prefer the common prey type. Clearly, the predator obtained more accurate information on the global abundance of prey types if it consumed more prey individuals. When the same total number of prey individuals was consumed in both cases, the predator in the one-predator case consumed 10 times more prey individuals than each predator in the ten-predator case did. Therefore, in contrast to the predator in the one-predator case, each predator in the ten-predator case lacked the global information on prey type frequencies and thus it failed to constantly consume the abundant prey type. As a result, a population of ten predators could not maintain prey diversity as efficiently and accurately as a single predator individual. However, in a natural environment, a predator individual can neither access the entire prey populations nor acquire complete information about them. Rather, each predator searches for prey only in its local area and switches to the common type based on the local prey abundance which may not be consistent with the frequencies of the prey types at the global scale. This feature of local predation is elegantly executed in the Tierra system where a predator searches for prey in the range of 10 creatures on either side. The simulation results show that when each predator in Tierra, similar to its organic counterpart in nature, implements positive frequency-dependent predation based on the prey type actually encountered and does not have any information about the entire prey populations, a population of 600 predator individuals maintains the coexistence of two prey types. This emergent global pattern of species coexistence from the local interactions between prey and predators is robust to the variations of the parameters that affect either the predation behavior of predators or the initial relative proportion of the two prey types in the environment. Further studies on the underlying mechanisms of the maintenance of prey diversity reveal that predators with positive frequency-dependent behavior support a quick increase of the prey population of a rare type, by disproportionately consuming fewer individuals of that type, and meanwhile depress the prey population of a common type, by disproportionately eating more individuals of that type. This strong negative feedback regulation tends to equalize the abundance of different prey types and thus facilitates the stable persistence of the diversity of prey species. Moreover, as I increase the number of prey types from two to three, the predator population also successfully maintains the coexistence of three prey species. Therefore, those simulation results strongly suggest that positive frequency-dependent predation may be a reasonable mechanism to maintain species diversity in nature.

On the other hand, digital creatures in Tierra compete for limiting CPU time and memory space. As a result, in the absence of predation, the stable coexistence of multiple digital species may not be easy to attain. For example, if two digital species differ in their genome lengths, the one with a shorter genome length reproduces faster and thus crowds out the one with a longer genome length, as shown in Figure 3.2(a). If, instead, the two digital species share the same genome length, theoretically they should reach a stable coexistence, but due to the accumulation of randomness in the system, the populations of those two species slowly drift and sometimes one of them drifts to extinction, as shown in Figure 2.8. However, after predation is introduced into the Tierra system, predators, by consuming more prey individuals of the abundant types, provide a negative feedback regulation on prey populations. The weak negative feedback regulation in proportional predation elongates the coexistence time, although fails to maintain a stable persistence, of different prey species; while the strong negative feedback regulation in positive frequency-dependent predation successfully stabilizes and maintains the diversity of prey species. Therefore, introducing some strong negative feedback mechanisms into the system may be one of the approaches to achieve species diversity in Tierra.

3.3 Effect of Two Predation Strategies on the Fitness of Predators

In a natural environment, the predators with a successful predation strategy are able to capture more prey individuals and thus acquire more energy for reproduction. Those predators leave more offspring which may inherit the same predation strategy from their parents. Therefore, over generations, the individuals with the successful strategy would gradually spread in the predator population, crowding out those with less successful predation strategies.

In section 3.2, I investigate the effect of proportional predation and positive frequency-dependent predation on the maintenance of prey species diversity. In this section, I attempt to study those two predation strategies from the perspective of predators, that is, which strategy would provide predators with higher fitness and whether or not the individuals with the better predation strategy would over time, spread through the entire predator population and drive those with the less competitive predation strategy to extinction.

Assume that there are two types of prey, type-A and type-B, in the environment. A predator with proportional predation always uses the same fixed probability, $P_A = P_B = 0.5$, to capture different types of prey. However, a predator with positive frequency-dependent predation adjusts its capture probabilities based on the abundance of two prey types. Compared to proportional predation, positive frequency-dependent predation seems a more adaptive predation strategy: it is equivalent to proportional predation when the availability of two prey types is similar, but as the abundance of one prey type rises, by increasing the predators' ability to capture the more available prey type, it enables predators to consume more prey individuals than proportional predation does. As a result, positive frequency-dependent predation appears a better strategy and the predators with this strategy should be more competitive, driving those with proportional predation to go extinct.

However, the simulation results in section 3.2.4 suggest that despite the relative proportion of two prey types in the initial prey populations, a predator population with strong positive frequency-dependent predation tends to equalize the abundance of two prey types (R_A approaches 0.5) and thus creates a better circumstance for the survival of predators with proportional predation (proportional predation is comparable to positive frequency-dependent predation only when the two prey types have a similar abundance). On the other hand, a predator population with proportional predation results in type-A prey being much more abundant than type-B prey (the type-B prey population eventually goes extinct), a favorable environment for the predators with positive frequency-dependent predation (when one prey type is significantly more abundant than the other, positive frequency-dependent predation is better than proportional predation). Therefore, when the predators with one predation strategy dominate the predator population in Tierra, they change the relative abundance of two prey types in such a way that favors, rather than depresses, the predators with the other predation strategy. As a result, the competition of two predation strategies may be more complicated than the above simple deduction that positive frequency-dependent predation is definitely a better strategy than proportional predation.

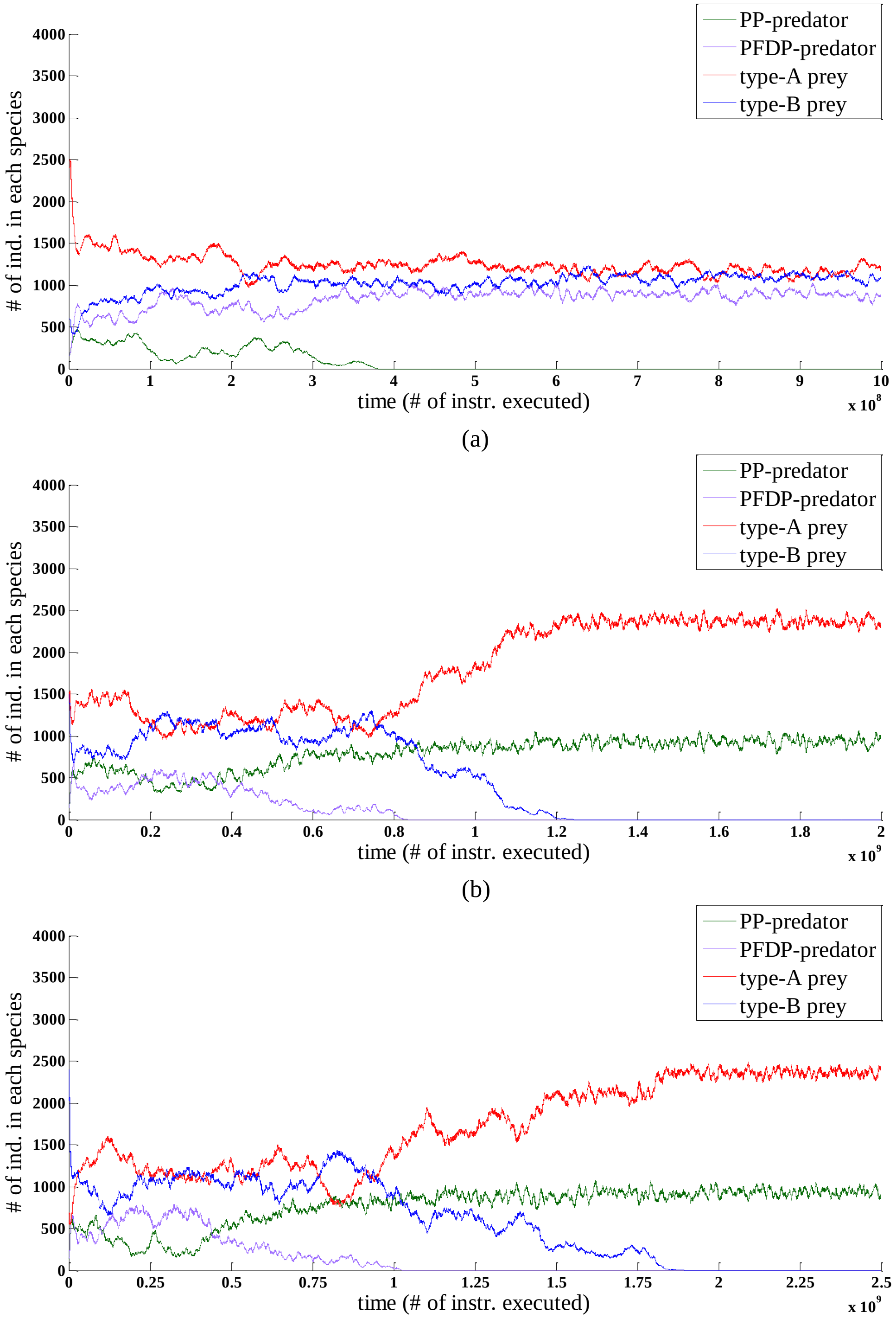
Methods

As shown in Figure 3.4, when $\Delta P = 0.1$ or 0.2, the predator population exhibits distinctive frequency-dependent behavior. Therefore, I use positive frequency-dependent predation with $\Delta P = 0.1$ and 0.2 to compete against proportional predation. In each competition scenario of the two predation strategies, the soup is seeded with 300 predator individuals evenly distributed among 3000 prey individuals. The predator population is composed of the predators using proportional predation (denoted as PP-predators) and the predators using positive frequency-dependent predation (denoted as PFDP-predators) with 150 individuals of each type. However, the relative abundance of two prey types in the initial prey population varies in 3 ways: two prey types are equally abundant with 1500 individuals of each type; type-A prey are significantly more abundant than type-B prey (2400 individuals of type-A prey and 600 individuals of type-B prey); type-B prey are significantly more abundant than type-A prey (2400 individuals of type-B prey and 600 individuals of type-A prey). Therefore, in each competition scenario of the two predation strategies, I perform 3 separate simulation runs, with each corresponding to one of the compositions of the initial prey population. In each simulation run, predators search for prey in their neighboring areas (about 10 creatures long on either side of the predator). After a predator encounters a prey, if it is a PP-predator, it captures the prey with a constant rate of 0.5 regardless of the prey types; but if it is a PFDP-predator, it exhibits prey preference, namely, it has a higher probability to consume the more abundant prey type. In each predation loop, a predator is allowed to eat at most m (m = 4) prey and acquires 35% of the CPU time from each prey. The CPU time of a captured prey is reduced to 30% of its original value. Depending on when a predator type and/or a prey type may go extinct, the length of a simulation run varies between 1000 to 4000 million instructions executed. I record the population sizes of predator and prey species during the runs.

Results

As shown in Figure 3.5(a) and Figure 3.6(a), a population of PFDP-predators with $\Delta P = 0.1$ and 0.2 maintains a very stable coexistence of two prey types by equalizing their abundances (R_A approaches 0.5). In an environment with an equal abundance of different prey types, PP-predators are equivalent to PFDP-predators and thus the two types of predators may coexist or either one of them could go extinct. The competition of PP-predators and PFDP-predators with $\Delta P = 0.1$ under different compositions of the initial prey population is shown in Figure 3.8(a), (b) and (c). At the beginning of each simulation run, type-A prey are significantly more abundant than type-B prey for about 200 million instructions executed, which results in an increase of the PFDP-predator population. Those PFDP-predators then quickly reduce the abundance difference between type-A and type-B prey, providing a better surviving environment for PP-predators. For example, the two prey types achieve an approximately equal abundance during the period of 200-400 million instructions executed in Figure 3.8(b) and (c). As a result, PFDP-predators do not always win the competition, but rather either type of predators could go extinct. In Figure 3.8(a), PP-predators approach extinction around 381 million instructions executed and then PFDP-predators maintain the coexistence of two prey types with a similar abundance. However, in Figure 3.8(b), PFDP-predators become extinct around 836 million instructions executed and then the population of PP-predators fails to maintain the coexistence of two prey types, resulting in the extinction of type-B prey around 1244 million instructions executed. The same dynamic pattern of predator and prey populations reappears in Figure 3.8(c), with the extinction of PFDP-predators around 1026 million instructions executed, followed by the disappearance of type-B prey around 1897 million instructions executed.

The simulation results of the competition of PP-predators and PFDP-predators with $\Delta P = 0.2$ further confirm that the increase of the PFDP-predator population, caused by the unequal abundance of type-A and type-B prey at the beginning of a simulation run, quickly diminishes the abundance difference between the two prey types and thus creates an environment where PP-predators and PFDP-predators are equally competitive.

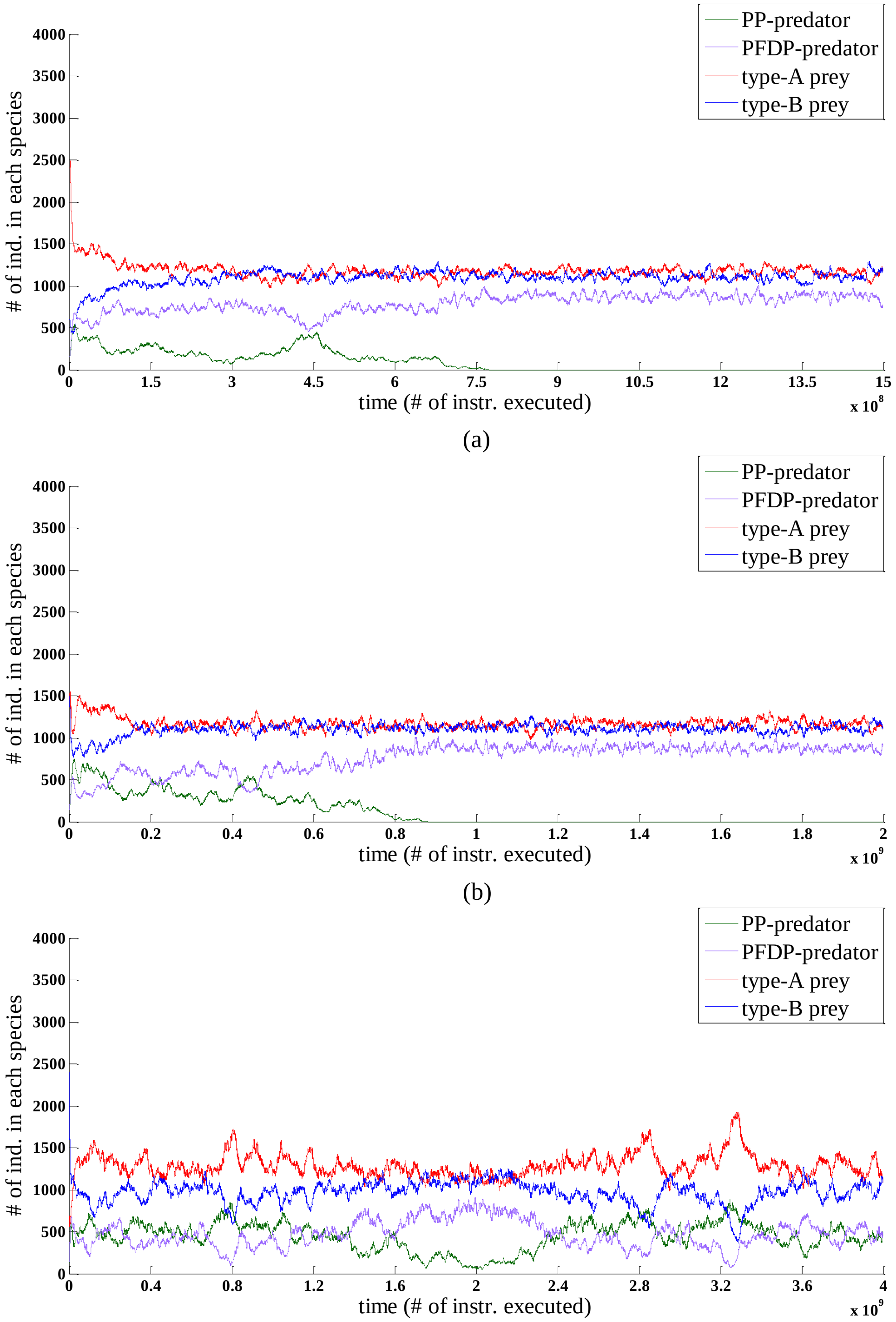


(a)

(b)

(c)

Figure 3.8: Competition between PP-predators and PFDP-predators with $\Delta P = 0.1$. The initial predator population is composed of 150 individuals of each type. The initial prey population has 3 different compositions (a) type-A prey = 2400 individuals and type-B prey = 600 individuals (b) type-A prey = type-B prey = 1500 individuals (c) type-A prey = 600 individuals and type-B prey = 2400 individuals. The simulation run lasts until 1000, 2000, and 2500 million instructions have been executed in (a), (b), and (c), respectively.



(a)

(b)

(c)

Figure 3.9: Competition between PP-predators and PFDP-predators with $\Delta P = 0.2$. The initial predator population is composed of 150 individuals of each type. The initial prey population has 3 different compositions (a) type-A prey = 2400 individuals and type-B prey = 600 individuals (b) type-A prey = type-B prey = 1500 individuals (c) type-A prey = 600 individuals and type-B prey = 2400 individuals. The simulation run lasts until 1500, 2000, and 4000 million instructions have been executed in (a), (b), and (c), respectively.

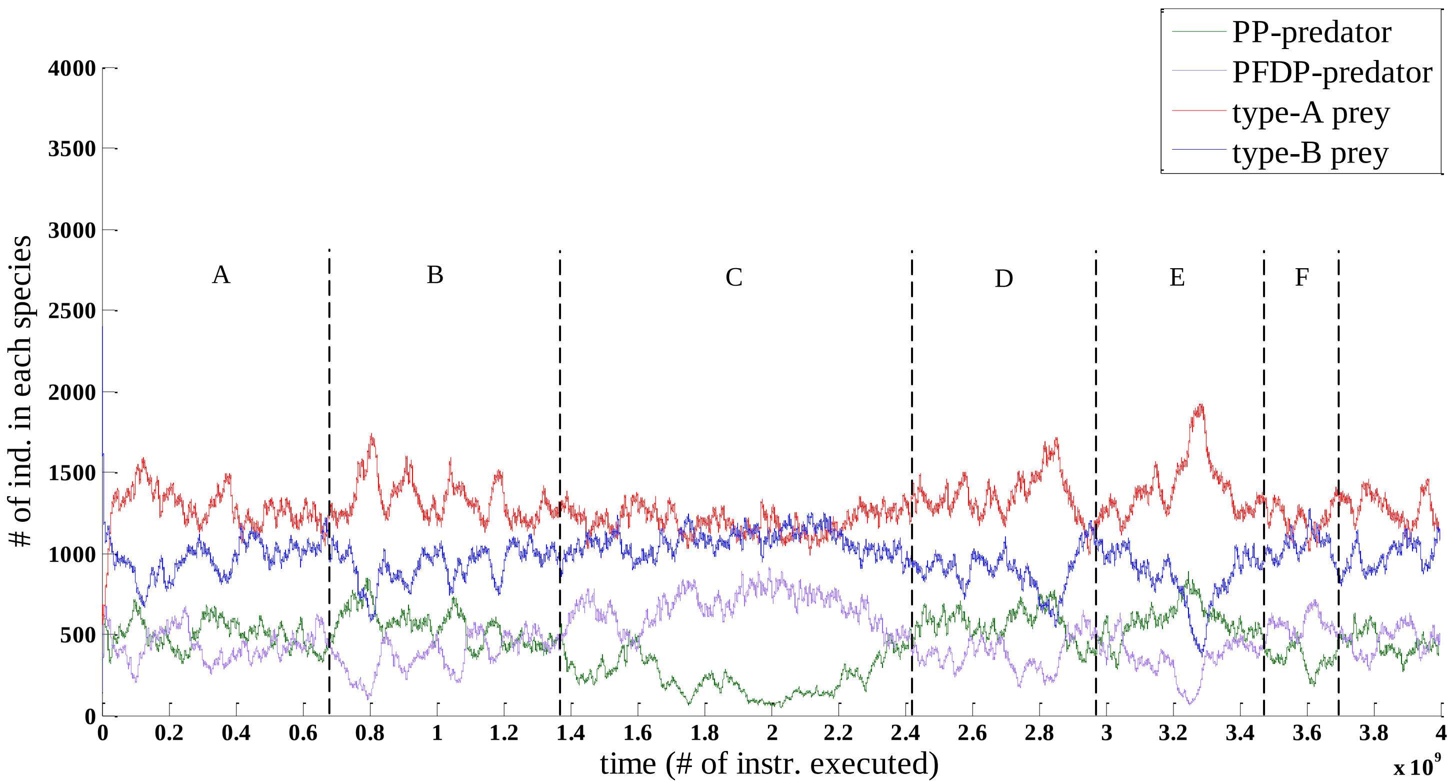


Figure 3.10: Coexistence of PP-predators and PFDP-predators with $\Delta P = 0.2$. The initial predator population is composed of 150 individuals of each predator type. The initial prey population is composed of 600 individuals of type-A prey and 2400 individuals of type-B prey. PP-predators and PFDP-predators achieve an unstable coexistence over the entire simulation run of 4000 million instructions executed. When PP-predators become the dominant type in the predator population, type-A prey are significantly more abundant than type-B prey (region B) which results in an increase of PFDP-predators. When PFDP-predators become the dominant type in the predator population, type-A and type-B prey reach an equal abundance (region C) which prevents PP-predators from going extinct and even provides an opportunity for PP-predators to increase (the second half of region C).

As shown in Figure 3.9(a) and (b), the nearly equal abundance of two prey types achieved by the PFDP-predator population (after about 300 million instructions executed in Figure 3.9(a) and after about 200 million instructions executed in Figure 3.9(b)) leads to an intensive competition between PP-predators and PFDP-predators: the population of PP-predators does not consistently decline, but rather it fluctuates and even increases to a level comparable to or greater than the population of PFDP predators during the period of 400-500 million instructions executed in Figure 3.9(a) and (b). The eventual extinction of the PP-predator population may result from randomness in the Tierra system. After PP-predators are crowded out, the population of PFDP-predators maintains a very stable coexistence of the two prey types with an equal abundance. In Figure 3.9(c), PP-predators and PFDP-predators coexist over the entire simulation run of 4000 million instructions executed, although due to the large fluctuation in the population sizes, this coexistence of the two predator types may be unstable. A close examination of Figure 3.9(c) is demonstrated in Figure 3.10, which is a copy of Figure 3.9(c) with 6 vertical dividing lines. As shown in Figure 3.10, the changes of the relative abundance of type-A and type-B prey concur perfectly with the dominant predator type in the predator population. For example, after the initial stage of the simulation run in region A, PP-predators become the dominant type in region B which results in type-A prey being significantly more abundant than type-B prey, a favorable environment for PFDP-predators. As a result, the population of PFDP-predators increases. Towards the end of region B, the proportion of PFDP-predators in the predator population becomes greater than 50%, which causes type-A and type-B prey to approach a similar abundance, an environment in which PP-predators and

PFDP-predators are approximately equally competitive. Due to randomness in the system, PFDP-predators win the competition and become the dominant predator type in region C. The large number of PFDP-predators further reduces the abundance difference between the two prey types. In the middle of region C, type-A and type-B prey reach an equal abundance, which prevents PP-predators from going extinct and even provides an opportunity for the population of PP-predators to increase. PP-predators eventually become the dominant predator type in region D which, similar to the pattern in region B, causes a considerable increase of the type-A prey population. The huge abundance difference between the two prey types results in an increase in the PFDP-predator population at the end of region D, which then, by equalizing the abundance of the two prey types, creates an environment in which the two types of predators are comparably competitive. Due to randomness in the system, PP-predators win the competition and thus become the dominant predator type in region E. The patterns of population dynamics in region E repeat those in region D, except that at the end of region E, PFDP-predators win the competition and become the dominant predator type in region F. The dominance of PFDP-predators leads to a similar abundance of the two prey types in region F, which provides a chance for the population of PP-predators to increase again. The dynamic patterns of predator and prey populations in Figure 3.10 clearly demonstrate that the dominant predator type, by executing its predation strategy, modifies the relative abundance of the two prey types to create a favorable environment for the other predator type. This mutual support, rather than exclusion, between the two predator competitors may be the mechanism for the coexistence of the two predator types.

In a natural ecological community, species in the same trophic level often experience a much more severe competition than those in different trophic levels (Hardin, 1960). Interestingly, this competition pattern spontaneously emerges in the digital community, composed of two prey and two predator species. As mentioned in chapter 2 (section 2.2.2), all digital creatures in Tierra live in the same finite memory space. In a community with one prey and one predator species, as the population of one species increases, the population of the other species decreases, therefore, a mirror image of the two species is exhibited in Figure 2.4. While, in a community with four species, theoretically, several possible combinations of the abundance of each species exist to fully fill up the memory space. However, as shown in Figure 3.10, only one combination actually occurs over the entire simulation run of 4000 million instructions executed: two pairs of mirror images with one pair between two predator types and the other pair between two prey types. That is, an increase in the population of one predator type causes a decline in the population of the other predator type, but has no significant influence on the populations of two prey types. Similarly, an increase in the population of one prey type severely decreases the population of the other prey type, but has little effect on the populations of two predator types. This similarity between trophic level competition in the digital community and that in the natural community suggests that the competition dynamics among species may follow some very general principles that are independent of any physical life forms.

Discussion

In Tierra, each digital creature receives a certain amount of CPU time from the system to execute and replicate its genome and occupies a block of memory with the size of its genome length. The CPU energy and memory space provided by the Tierra simulator create a relatively static physical environment for digital creatures. With the introduction of predation into the Tierra system, digital predators mainly acquire the CPU time from their prey and thus the availability of digital prey forms a dynamic biotic environment for predators. When two types of prey and two types of predators are present, with each predator type executing a different prey capture strategy, the fitness of each predator type changes with the composition of the prey population which itself is consistently modified by predators through predation. For example, PP-predators tend to increase the abundance difference between two prey types, which enhances the fitness of PFDP-predators. Meanwhile, PFDP-predators tend to equalize the abundance of two prey types, which promotes the fitness of PP-predators and allows the two types of predators to be comparably competitive. As a result, either type of predators could win the competition. Moreover, the two types of predators could also achieve an unstable coexistence during which the dominant predator type, by regulating the relative abundance of two prey types, supports the population growth of the other predator type. Therefore, which predation strategy (PP or PFDP) would provide predators a higher fitness depends on the biotic environment where predators live, and in this biotic environment, the composition of the prey population continuously changes and exhibits different patterns under different predation pressure.

3.4 Conclusion

In this chapter, I explore two predation strategies in an ecological scenario in which all the mutations in Tierra are blocked. The simulation results show that a predator population using a proportional predation strategy fails to maintain prey species diversity. However, a predator population with positive frequency-dependent behavior maintains a stable coexistence of multiple prey species. Further investigations reveal that positive frequency-dependent predation provides a negative feedback regulation on prey populations which tends to equalize the abundance of different prey species and thus results in a stable persistence of prey diversity. On the other hand, when predators consume different types of prey, they actively modify the composition of the prey population. More specifically, as predators execute different predation strategies, the relative abundance of different prey types converges to different patterns. As a result, the competition outcome of PP-predators and PFDP-predators depends on their current biotic environment.

In the next chapter, I will turn on various types of mutations in the Tierra system and study the influence of positive frequency-dependent predation on the increase and maintenance of community diversity in an evolutionary scenario. Furthermore, the evolution of digital creatures, during which new types of prey and predators continuously emerge through mutations, generates a much more complicated biotic environment than the one in the ecological scenario without mutations. I will explore the adaptation of prey and predators to their local, ever-changing ecological communities as the evolutionary processes occur in Tierra.

Chapter 4: Exploring Effects of Positive Frequency-dependent Predation on the Increase and Maintenance of Genetic Diversity in an Evolving Ecological Community and the Coevolution between Prey and Predator Populations

Simulation results in chapter 3 suggest that in an ecological scenario, a predator population with positive frequency-dependent behavior maintains a stable coexistence of multiple competing prey species. In this chapter, by introducing mutations into the Tierra system, I attempt to explore whether those predators could generate high and stable diversity in an evolving ecological community. I redesign the rules that predators follow to capture prey in their local areas in order to adapt to the evolutionary situation in which new types of prey and predators continuously emerge. Then, I compare the diversity present in the populations, measured by the Shannon-Wiener index, before and after predators with positive frequency-dependent behavior are introduced into the community. Furthermore, by examining the changes in the genomes of predators and prey, especially the changes in the predation templates in predators and their complementary templates in prey, I study the coevolution between predator and prey populations during an evolutionary process in Tierra.

4.1 Effects of Positive Frequency-dependent Predation on the Increase and Maintenance of Diversity in an Evolving Ecological Community

Besides as a mechanism to maintain stable prey polymorphisms within populations and prey species diversity within communities in an ecological scenario, positive frequency-dependent predation was also predicted to have the potential to promote genetic diversity and species diversity during evolution, by increasing the richness and the abundance evenness of genotypes in a population and species in a community (Clarke, 1979; Murdoch, 1969; Allen, 1988). This prediction has been investigated by several theoretical models. For example, by using an extension of classical Lotka-Volterra predator-prey models, Doebeli and Dieckmann studied evolutionary branching of prey and predator populations and found that positive frequency-dependent predation, which depressed the common prey phenotypes and thus allowed the rare ones to survive, could easily cause evolutionary branching in prey. However, after a prey phenotype had split into two distinct types, the branching of their predators depended on some specific conditions: the predators may not experience branching, being a generalist feeding on both new prey types, or may split into two predator types, with each specializing on one prey type (Doebeli and Dieckmann, 2000). Furthermore, Doebeli and Ispolatov proposed that positive frequency-dependent predation may need to be considerably strong in order to generate diversity in an isolated phenotype. However, when many different phenotypes in high-dimensional spaces actively interacted with one another, like those in the living organisms, large amounts of diversity could be easily achieved and maintained by positive frequency-dependent predation (Doebeli and Ispolatov, 2010). In addition to the elegant and concise mathematical analysis, the increase of diversity in a community by frequency-dependent predators is also studied through field observations and laboratory experiments as follows. After examining the number of tree species and the density of each species in tropical forest habitats, Janzen suggested that herbivores that preferentially consumed the seedlings growing near their parent trees may lead to the extraordinary diversity of tree species (Janzen, 1970; Huntly, 1991). By comparing the diversity of seeds and seedlings in 200 sites in a tropical forest, Harms *et. al* also concluded that the high diversity of plant species at least partially resulted from the continuing disproportionate predation on the abundant types of seeds and seedlings (Harms *et. al*., 2000). Bond and Kamil reported the first controlled experiment on the evolution of prey phenotypic diversity under positive frequency-dependent predation. They used 4 blue jays (*Cyanocitta cristata*), which were known to exhibit positive frequency-dependent behavior, to hunt for digital moths on a computer screen and allowed the moth population of 200 individuals to evolve via a genetic algorithm in which the moths escaping predation had a much higher chance to reproduce than those detected by the jays. They found that over 100 successive generations, the moth population which was preyed upon by the jays showed significantly greater phenotypic variance than that evolved without predation (Bond and Kamil, 2002; Bond, 2007).

In my work, a predator population of 300 individuals, rather than just a few predator individuals, is introduced into the initial prey community and both predators and prey are allowed to continuously evolve. I attempt to explore the maintenance of predation in the community during evolution and the changes of community diversity by the populations of frequency-dependent predators.

4.2 Execution of Positive Frequency-dependent Predation in Evolving Predator and Prey Populations

When various types of random mutations are introduced into the Tierra system, the genomes of digital creatures are modified and thus new types of prey and predators continuously emerge. Therefore, unlike the ecological scenario in chapter 3 in which the prey types are known and the number of prey types is fixed, in the evolutionary scenario the prey types that a predator can detect in its local area vary over time.

To keep track of the changes in local prey types and their abundances, each predator individual saves the M most common, recently captured prey types, which are constantly updated as prey evolve. This allows a predator individual to execute positive frequency-dependent predation based on its most recent predation history in an evolving local environment. The detailed algorithm is as follows:

(1) Each predator individual keeps a record of the M most common prey types that it has captured previously.

(2) When a predator individual catches a type-i prey individual, this type is compared with the recorded prey types.

  (a) If type-i has been caught before, the probability to capture type-i prey, P_i increases by ΔP and to capture other prey types, P_j decreases by ΔP, that is,

$$P_i = P_i + \Delta P;\ \ P_j = P_j - \Delta P\ (j = 1 \ldots M \text{ and } j \neq i)$$

  (b) If, instead, type-i has not been caught before, type-i is recorded as one of the M prey types, and then the probability to capture type-i prey increases by ΔP and to capture other prey types decreases by ΔP.

  (c) If the predator individual has already saved M prey types but type-i is not one of them, type-i replaces the least common one among the M types, and then the probability to capture type-i prey increases by ΔP and to capture other prey types decreases by ΔP.

  (d) All capture probabilities $P_k\,(k = 1 \ldots M)$ are bounded by P_{min} and P_{max}, that is,

$$0 \leq P_{min} \leq P_k \leq P_{max} \leq 1\ (k = 1 \ldots M)$$

For all the simulation runs in this chapter, I set $M = 5$, $\Delta P = 0.1$, $P_{min} = 0$ and $P_{max} = 1$. Due to random mutations, the genomes of digital creatures change rapidly, which limits the number of individuals of a specific genotype. On the other hand, digital creatures with the same genome length usually share a very similar genetic structure. If digital prey individuals are grouped by their sizes, each size class, in contrast to each genotype, has significantly more individuals and evolves more slowly. This would allow predators to experience more prey individuals of the same class before they are modified by mutations and thus to effectively execute positive frequency-dependent predation. Therefore, in the above algorithm, prey types are classified by the genome lengths, rather than by the genotypes, of prey individuals. If a predator individual captures a type-i prey individual, its probability to capture the prey individuals which share the same size as type-i prey increases by ΔP. For example, assume there are 3 prey genotypes which are 86 instructions long, 86aaa, 86aab and 86aac (In Tierra, a genotype is named by the size of the creature followed by a three-letter code (Ray, 1998)). If a predator individual catches an individual of 86aaa, then it has a higher probability to catch prey individuals of 86aaa as well as 86aab and 86aac.

4.3 Increase and Maintenance of Genetic Diversity by Positive Frequency-dependent Predation in an Evolving Ecological Community in Tierra

In the original Tierra system, when one or a few successful genotypes emerged through mutations, they usually gained reproductive advantages and rapidly crowded out other existing genotypes. Thus, the soup was repetitively dominated by very few genotypes and the evolving populations exhibited relatively low diversity (Ray, 1994).

The simulation results in the ecological runs in chapter 3 suggest that a predator population with positive frequency-dependent behavior depresses the populations of dominant prey types and thus allows the more competitive prey types to coexist with the less competitive ones. If, regardless of the changes in the genomes of digital predators and prey caused by mutations, predation could persist during an evolutionary run, predator populations may be able to limit the dominant prey types. This would provide more resources to support the survival of other prey types and thus more prey types may have the opportunities to evolve. With this increase in the number of coexisting prey types, more types of food sources may be available to predators which may promote the differentiation of predator types, with each specializing on a certain type of prey. As a result, this evolving ecological community may achieve high diversity.

The digital organisms in Tierra, similar to bacteria, reproduce asexually and thus the traditional concept of species based on reproductive isolation may not be applied to those digital creatures. In the ecological scenario in chapter 3, the genomes of the predator and three prey types differ significantly from one another. Therefore it may be appropriate to view each genotype as a different species. However, in the evolutionary scenario in which genomes of predators and prey constantly change, the evolving community is composed of many genotypes that only differ from one another by a few mutations (those genotypes may not be considered as different species), as well as, a considerable number of genotypes that vary significantly in their genome lengths and structures (those genotypes may be viewed as different species). Currently, there are two popular approaches to measure the diversity in the digital community: one approach focuses on the numerous coexisting genotypes and calculates the genetic diversity by the Shannon-Wiener index (Ray, 1994; Cooper and Ofria, 2002). The other approach is to create an operational definition of species, for example, Chow *et. al* first calculated the phylogenetic distance between each pair of genotypes, which was defined as “the total number of intermediate genotypes along the lines of descent leading to their most recent common ancestor”, and then applied a clustering algorithm to divide all genotypes into different clusters, with each cluster containing the genotypes that had small phylogenetic distances from one another. Chow *et. al* then defined each cluster as a species (Chow *et. al*., 2004; Lenski *et. al*., 2003). In my work, I follow the first approach to measure the diversity in the evolving digital community.

4.3.1 Genetic Diversity in the Evolving Predator and Prey Populations in Tierra

Methods

One of the causes of the cessation of evolution in the original Tierra system was that ecological interactions only emerged when selection favored smaller genomes (when all creatures received equal amounts of CPU time from the system, smaller creatures reproduced faster than larger ones). Selection favoring smaller genomes eventually led to stasis when genomes reduced their sizes as much as possible, and no significant genetic variants were possible. Predation is a mechanism of allowing ecological interactions in the absence of selection for smaller genomes. In this chapter, as predation is introduced into the system, digital creatures evolve under size-neutral selection in which the amount of CPU time that a creature receives from the system is proportional to its genome length. This would allow creatures with different sizes to have a similar reproduction rate, which potentially prevents the dominance of smaller creatures and the resulting loss of complex structures in genomes. Therefore, due to size-neutral selection and predation, an evolutionary process in Tierra may continue longer with interesting ecological interactions between predator and prey populations.

The increase and maintenance of genetic diversity in an evolving community by predators is explored by comparing the results of two simulations. In the experimental run (with predation), I seed the soup with a predator population of 300 individuals and 3 prey types (type-A, type-B and type-C), each with a population of 1000 individuals. As various types of random mutations modify the genomes of digital creatures, new prey and predator genotypes continuously appear. A predator is allowed to capture prey and acquire CPU energy from them but is not allowed to capture other predators. Therefore, the evolving ecological community is essentially a simple two-layer food chain, composed of one prey layer and one predator layer. Each predator searches for prey in its local area and executes positive frequency-dependent predation ($\Delta P = 0.1$) based on its most recent predation history, as described in details in section 4.2. In each predation loop, a predator is allowed to eat at most m ($m = 4$) prey and acquires 40% of CPU time from each prey. The CPU time of a captured prey is reduced to 30% of its original value. To observe predation over an evolutionary run, I record the time when a predator individual captures a prey individual and then I count the number of such predation events occurring in every million instructions executed. In the control run (without predation), I seed the soup with the same prey populations used in the experimental run (type-A, type-B and type-C, with 1000 individuals of each prey type) but I replace the predator population with 300 individuals of pseudo-predators. The genome of a pseudo-predator is the same as that of a predator except for the instruction to execute predation. Due to the lack of the ability to capture prey, pseudo-predators receive CPU time from the system for their reproduction. This community of prey and pseudo-predators evolves as mutations continue changing the genomes of digital creatures. The introduction of pseudo-predators allows the experimental run and the control run to start with the same genetic diversity of the initial community and the only difference between the two simulation runs is the presence or absence of predation.

In both the experimental run and the control run, the simulation lasts until 1500 million instructions have been executed and I record the genetic diversity in the evolving community over time. Genetic diversity is evaluated by the Shannon-Wiener index, one of the most popular measures of community diversity used by ecologists (Hill, 1973). Assume there are S different genotypes in a community, the Shannon-Wiener index is calculated as

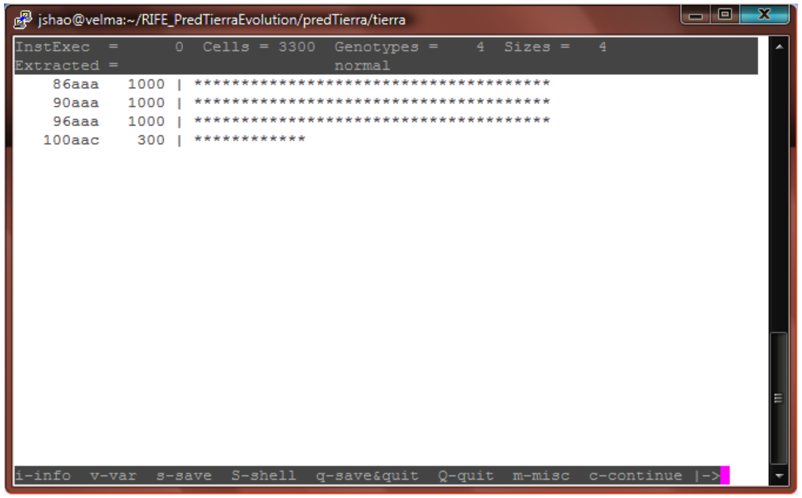
$$H = -\sum_{i=1}^{S} p_i \ln(p_i) \qquad \text{where } p_i = \frac{n_i}{N}$$

p_i represents the relative abundance of a genotype i, measured by the number of individuals in genotype i (n_i) divided by the total number of all individuals in the community (N). Therefore, genetic diversity calculated by the Shannon-Wiener index considers both the number of genotypes and the evenness of their abundances, that is, genetic diversity increases when more genotypes and/or when greater genotype evenness are present in the community.

The genotypes which have just one individual are the mutants that are not able to reproduce. After excluding those genotypes, I calculate the genetic diversity of the community for every 1000 instructions executed and then average those values of genetic diversity over every million instructions executed. Furthermore, I focus on the genotypes which have at least 5 individuals and consider them as successful mutants due to their ability to acquire resources to produce multiple offspring in the highly competitive environment in Tierra. I calculate the genetic diversity of those successful genotypes for every 1000 instructions executed and then average those values of genetic diversity over every million instructions executed. In addition, I use the same approach (calculate the values for every 1000 instructions executed and then average them over every million instructions executed) to measure the average genome size of the genotypes which reproduce at least once and also those which have at least 5 individuals.

Results

Figure 4.1 shows 7 snapshots of the simulator window, when 0, 150, 300, 600, 900, 1200 and 1500 million instructions have been executed, during the control run (left column (a1) – (a7)) and the experimental run (right column (b1) – (b7)), respectively. As shown in Figure 4.1(a1) and (b1), both the control run and the experimental run start with the same prey populations (86aaa, 96aaa and 90aaa are type-A, type-B and type-C prey, respectively, with 1000 individuals of each type) but with a different predator population: 300 individuals of predators (100aaa) are present in the initial community of the experimental run, while those predators are replaced by 300 individuals of pseudo-predators (100aac) in the control run. Due to the same number of genotypes and the same number of individuals in each genotype, the two communities share the same initial genetic diversity. However, the two communities exhibit different patterns during the evolutionary process. In the control run, the community is frequently dominated by one or a few genotypes, as illustrated in Figure 4.1(a2) when 150 million instructions have been executed.



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    90aaa   1000 | **************************************
    96aaa   1000 | **************************************
   100aac    300 | ************
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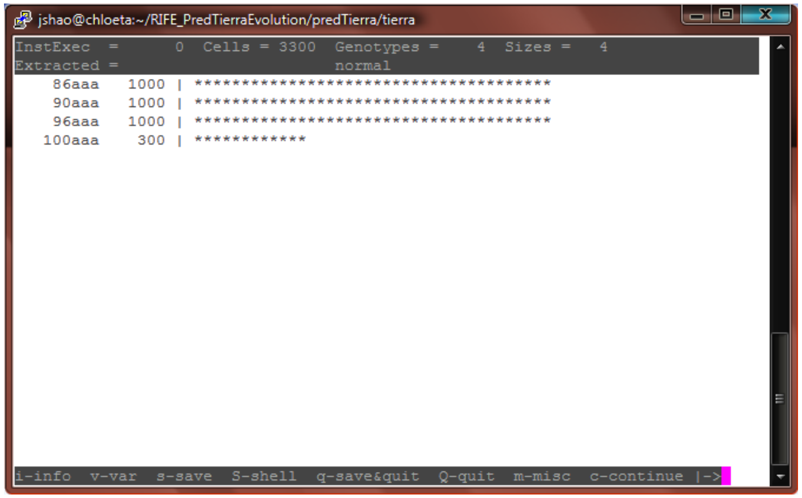
```

(a1)



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Extracted =                          normal
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    90aaa   1000 | **************************************
    96aaa   1000 | **************************************
   100aaa    300 | ************
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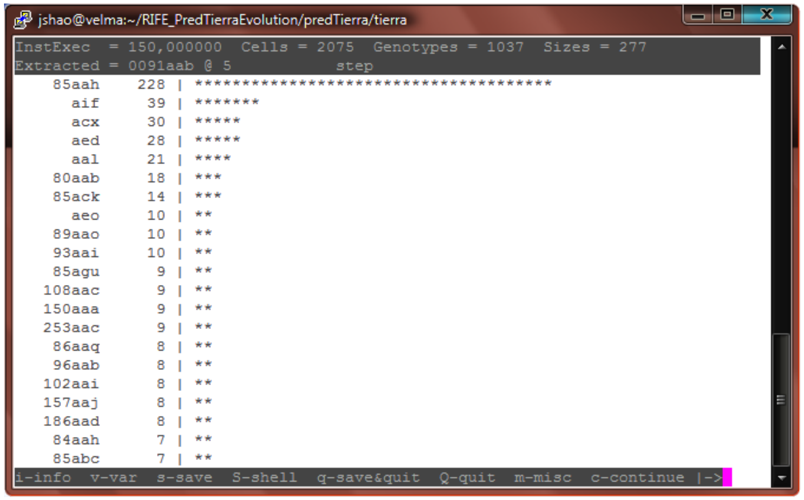
```

(b1)



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      acx     30 | *****
      aed     28 | *****
      aal     21 | ****
    80aab     18 | ***
    85ack     14 | ***
      aeo     10 | **
    89aao     10 | **
    93aai     10 | **
    85agu      9 | **
   108aac      9 | **
   150aaa      9 | **
   253aac      9 | **
    86aaq      8 | **
    96aab      8 | **
   102aai      8 | **
   157aaj      8 | **
   186aad      8 | **
    84aah      7 | **
    85abc      7 | **
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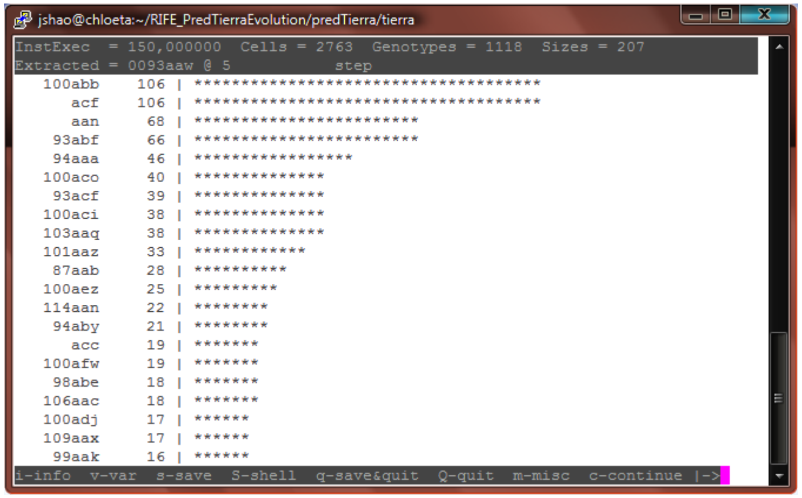
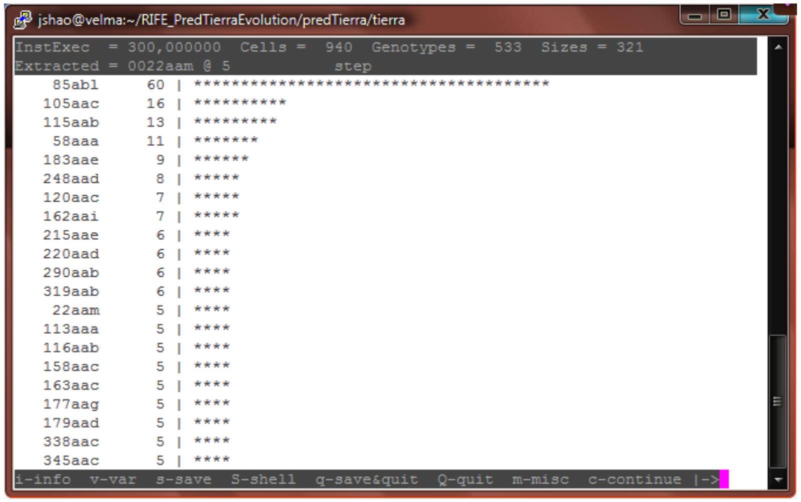
```

(a2)



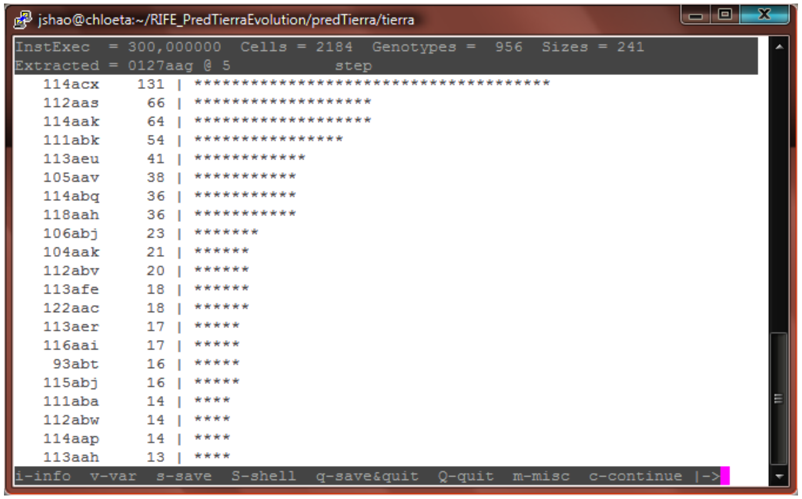
```
InstExec  = 150,000000  Cells = 2763  Genotypes = 1118  Sizes = 207
Extracted = 0093aaw @ 5              step
   100abb    106 | *************************************
      acf    106 | *************************************
      aan     68 | ************************
    93abf     66 | ************************
    94aaa     46 | *****************
   100aco     40 | **************
    93acf     39 | **************
   100aci     38 | **************
   103aaq     38 | **************
   101aaz     33 | ************
    87aab     28 | **********
   100aez     25 | *********
   114aan     22 | ********
    94aby     21 | ********
      acc     19 | *******
   100afw     19 | *******
    98abe     18 | *******
   106aac     18 | *******
   100adj     17 | ******
   109aax     17 | ******
    99aak     16 | ******
i-info  v-var  s-save  S-shell  q-save&quit  Q-quit  m-misc  c-continue |->
```

(b2)



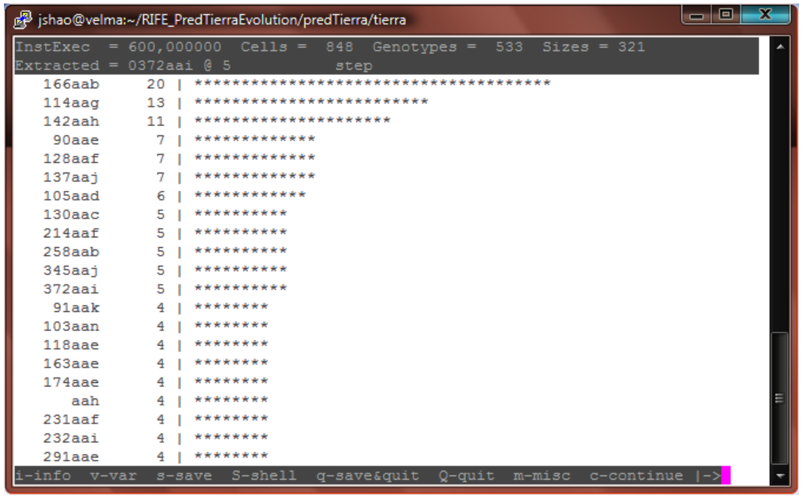
```
InstExec  = 300,000000  Cells =  940  Genotypes =  533  Sizes = 321
Extracted = 0022aam @ 5             step
    85abl     60 | **************************************
   105aac     16 | **********
   115aab     13 | *********
    58aaa     11 | *******
   183aae      9 | ******
   248aad      8 | *****
   120aac      7 | *****
   162aai      7 | *****
   215aae      6 | ****
   220aad      6 | ****
   290aab      6 | ****
   319aab      6 | ****
    22aam      5 | ****
   113aaa      5 | ****
   116aab      5 | ****
   158aac      5 | ****
   163aac      5 | ****
   177aag      5 | ****
   179aad      5 | ****
   338aac      5 | ****
   345aac      5 | ****
i-info  v-var  s-save  S-shell  q-save&quit  Q-quit  m-misc  c-continue |->
```

(a3)



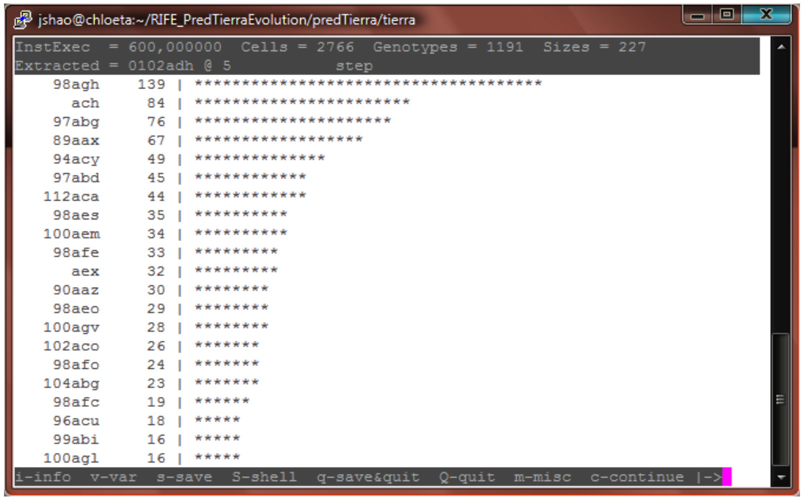
```
InstExec  = 300,000000  Cells = 2184  Genotypes =  956  Sizes = 241
Extracted = 0127aag @ 5             step
   114acx    131 | **************************************
   112aas     66 | *******************
   114aak     64 | *******************
   111abk     54 | ****************
   113aeu     41 | ************
   105aav     38 | ***********
   114abq     36 | ***********
   118aah     36 | ***********
   106abj     23 | *******
   104aak     21 | ******
   112abv     20 | ******
   113afe     18 | ******
   122aac     18 | ******
   113aer     17 | *****
   116aai     17 | *****
    93abt     16 | *****
   115abj     16 | *****
   111aba     14 | ****
   112abw     14 | ****
   114aap     14 | ****
   113aah     13 | ****
i-info  v-var  s-save  S-shell  q-save&quit  Q-quit  m-misc  c-continue |->
```

(b3)



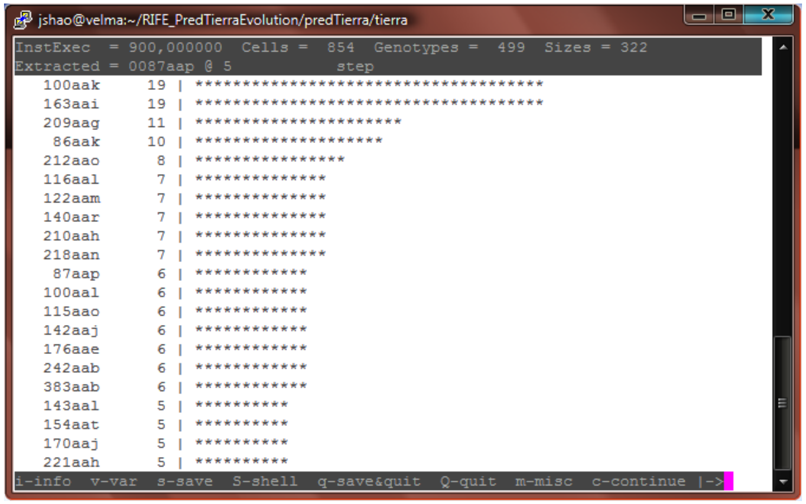
```
InstExec  = 600,000000  Cells =  848  Genotypes =  533  Sizes = 321
Extracted = 0372aai @ 5             step
   166aab     20 | **************************************
   114aag     13 | *************************
   142aah     11 | *********************
    90aae      7 | *************
   128aaf      7 | *************
   137aaj      7 | *************
   105aad      6 | ************
   130aac      5 | **********
   214aaf      5 | **********
   258aab      5 | **********
   345aaj      5 | **********
   372aai      5 | **********
    91aak      4 | ********
   103aan      4 | ********
   118aae      4 | ********
   163aae      4 | ********
   174aae      4 | ********
      aah      4 | ********
   231aaf      4 | ********
   232aai      4 | ********
   291aae      4 | ********
i-info  v-var  s-save  S-shell  q-save&quit  Q-quit  m-misc  c-continue |->
```

(a4)



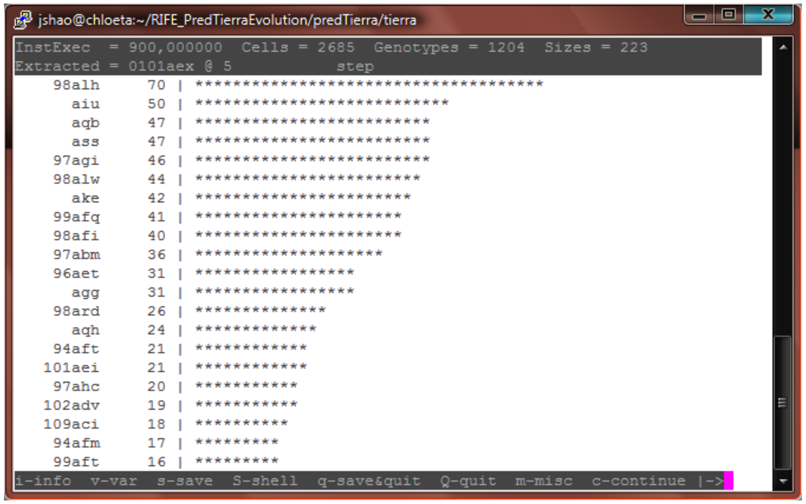
```
InstExec  = 600,000000  Cells = 2766  Genotypes = 1191  Sizes = 227
Extracted = 0102adh @ 5             step
    98agh    139 | *************************************
      ach     84 | ***********************
    97abg     76 | *********************
    89aax     67 | ******************
    94acy     49 | **************
    97abd     45 | ************
   112aca     44 | ************
    98aes     35 | **********
   100aem     34 | **********
    98afe     33 | *********
      aex     32 | *********
    90aaz     30 | ********
    98aeo     29 | ********
   100agv     28 | ********
   102aco     26 | *******
    98afo     24 | *******
   104abg     23 | *******
    98afc     19 | ******
    96acu     18 | *****
    99abi     16 | *****
   100agl     16 | *****
i-info  v-var  s-save  S-shell  q-save&quit  Q-quit  m-misc  c-continue |->
```

(b4)



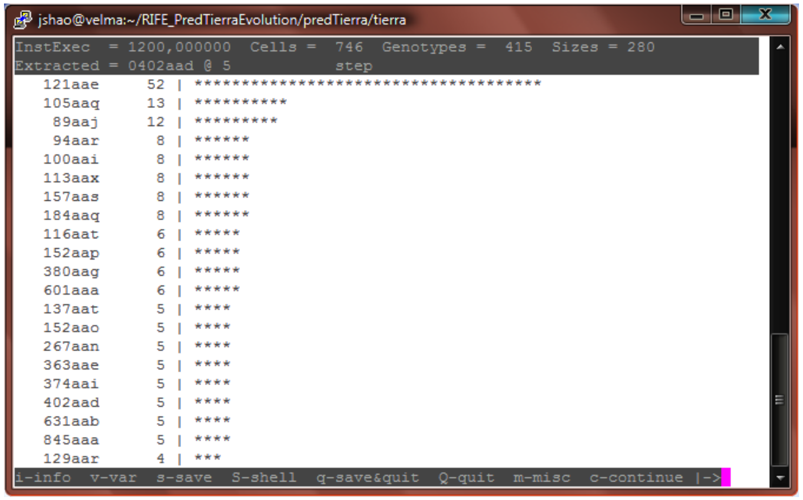
```
InstExec  = 900,000000  Cells =  854  Genotypes =  499  Sizes = 322
Extracted = 0087aap @ 5           step
   100aak     19 | *************************************
   163aai     19 | *************************************
   209aag     11 | **********************
    86aak     10 | ********************
   212aao      8 | ****************
   116aal      7 | **************
   122aam      7 | **************
   140aar      7 | **************
   210aah      7 | **************
   218aan      7 | **************
    87aap      6 | ************
   100aal      6 | ************
   115aao      6 | ************
   142aaj      6 | ************
   176aae      6 | ************
   242aab      6 | ************
   383aab      6 | ************
   143aal      5 | **********
   154aat      5 | **********
   170aaj      5 | **********
   221aah      5 | **********
i-info  v-var  s-save  S-shell  q-save&quit  Q-quit  m-misc  c-continue |->
```

(a5)



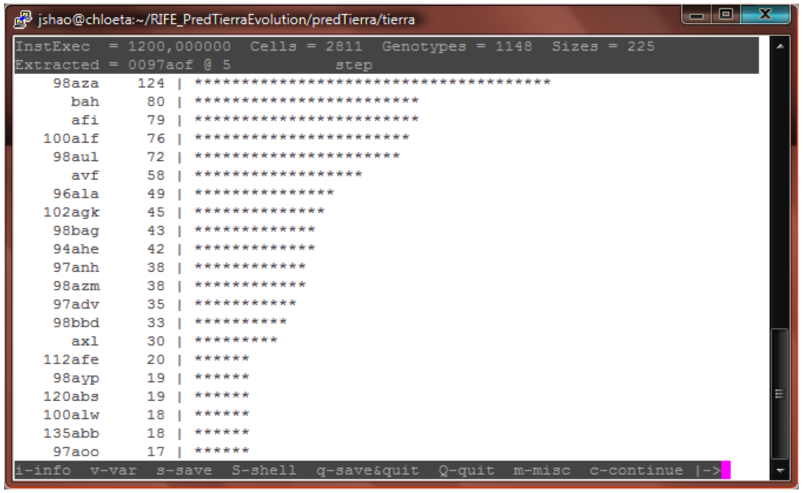
```
InstExec  = 900,000000  Cells = 2685  Genotypes = 1204  Sizes = 223
Extracted = 0101aex @ 5           step
    98alh     70 | *************************************
      aiu     50 | ***************************
      aqb     47 | *************************
      ass     47 | *************************
    97agi     46 | *************************
    98alw     44 | ************************
      ake     42 | ***********************
    99afq     41 | **********************
    98afi     40 | **********************
    97abm     36 | ********************
    96aet     31 | *****************
      agg     31 | *****************
    98ard     26 | **************
      aqh     24 | *************
    94aft     21 | ************
   101aei     21 | ************
    97ahc     20 | ***********
   102adv     19 | ***********
   109aci     18 | **********
    94afm     17 | *********
    99aft     16 | *********
i-info  v-var  s-save  S-shell  q-save&quit  Q-quit  m-misc  c-continue |->
```

(b5)



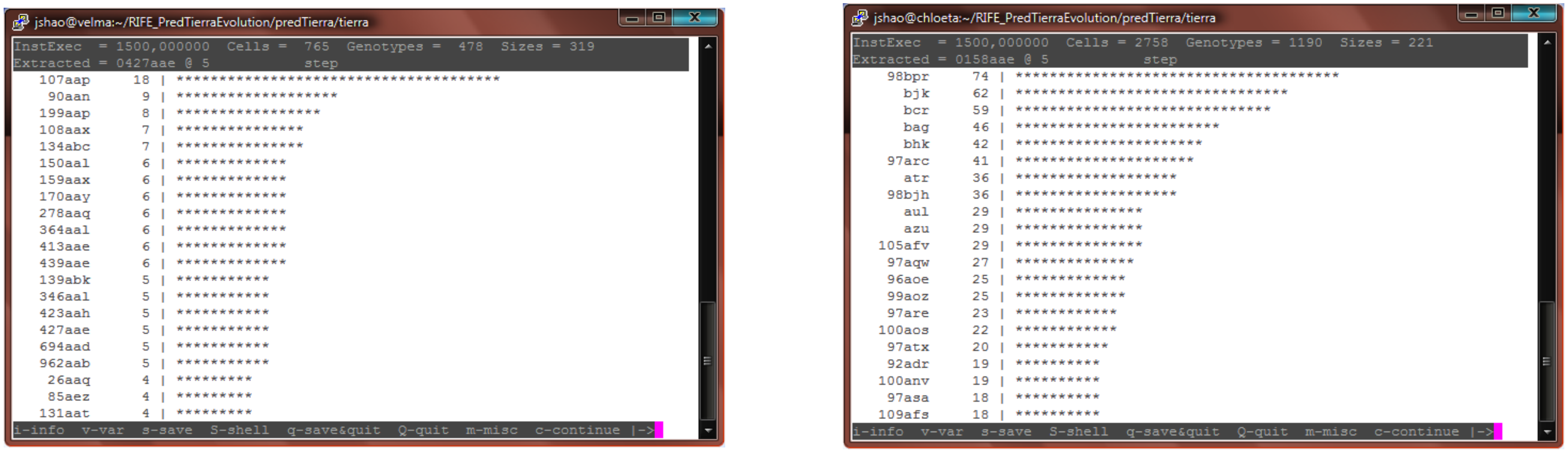
```
InstExec  = 1200,000000  Cells =  746  Genotypes =  415  Sizes = 280
Extracted = 0402aad @ 5           step
   121aae     52 | *************************************
   105aaq     13 | **********
    89aaj     12 | *********
    94aar      8 | ******
   100aai      8 | ******
   113aax      8 | ******
   157aas      8 | ******
   184aaq      8 | ******
   116aat      6 | *****
   152aap      6 | *****
   380aag      6 | *****
   601aaa      6 | *****
   137aat      5 | ****
   152aao      5 | ****
   267aan      5 | ****
   363aae      5 | ****
   374aai      5 | ****
   402aad      5 | ****
   631aab      5 | ****
   845aaa      5 | ****
   129aar      4 | ***
i-info  v-var  s-save  S-shell  q-save&quit  Q-quit  m-misc  c-continue |->
```

(a6)



```
InstExec  = 1200,000000  Cells = 2811  Genotypes = 1148  Sizes = 225
Extracted = 0097aof @ 5           step
    98aza    124 | **************************************
      bah     80 | ************************
      afi     79 | ************************
   100alf     76 | ***********************
    98aul     72 | **********************
      avf     58 | ******************
    96ala     49 | ***************
   102agk     45 | **************
    98bag     43 | *************
    94ahe     42 | *************
    97anh     38 | ************
    98azm     38 | ************
    97adv     35 | ***********
    98bbd     33 | **********
      axl     30 | *********
   112afe     20 | ******
    98ayp     19 | ******
   120abs     19 | ******
   100alw     18 | ******
   135abb     18 | ******
    97aoo     17 | ******
i-info  v-var  s-save  S-shell  q-save&quit  Q-quit  m-misc  c-continue |->
```

(b6)



```
InstExec  = 1500,000000  Cells =  765  Genotypes =  478  Sizes = 319
Extracted = 0427aae @ 5            step
   107aap     18 | **************************************
    90aan      9 | *******************
   199aap      8 | *****************
   108aax      7 | ***************
   134abc      7 | ***************
   150aal      6 | *************
   159aax      6 | *************
   170aay      6 | *************
   278aaq      6 | *************
   364aal      6 | *************
   413aae      6 | *************
   439aae      6 | *************
   139abk      5 | ***********
   346aal      5 | ***********
   423aah      5 | ***********
   427aae      5 | ***********
   694aad      5 | ***********
   962aab      5 | ***********
    26aaq      4 | *********
    85aez      4 | *********
   131aat      4 | *********
i-info  v-var  s-save  S-shell  q-save&quit  Q-quit  m-misc  c-continue |->
```

(a7)

```
InstExec  = 1500,000000  Cells = 2758  Genotypes = 1190  Sizes = 221
Extracted = 0158aae @ 5            step
    98bpr     74 | **************************************
      bjk     62 | ********************************
      bcr     59 | ******************************
      bag     46 | ************************
      bhk     42 | **********************
    97arc     41 | *********************
      atr     36 | *******************
    98bjh     36 | *******************
      aul     29 | ***************
      azu     29 | ***************
   105afv     29 | ***************
    97aqw     27 | **************
    96aoe     25 | *************
    99aoz     25 | *************
    97are     23 | ************
   100aos     22 | ************
    97atx     20 | ***********
    92adr     19 | **********
   100anv     19 | **********
    97asa     18 | **********
   109afs     18 | **********
i-info  v-var  s-save  S-shell  q-save&quit  Q-quit  m-misc  c-continue |->
```

(b7)

Figure 4.1: Seven snapshots of the simulator window during the control run (a1) – (a7) and the experimental run (b1) – (b7). On the top of a simulator window, "InstExec" shows the number of instructions that have been executed, as a measure of time; "Cells", "Genotypes" and "Sizes" records the number of creatures, the number of different genotypes and the number of different sizes among the genotypes in the soup, respectively. The central area of the window shows the name of each genotype (genome length followed by a three-letter code), the number of individuals in each genotype and the relative abundance of those genotypes, represented by the lengths of the horizontal bars. Due to the limitation of the window size, only the 21 most abundant genotypes are exhibited in the simulator window.

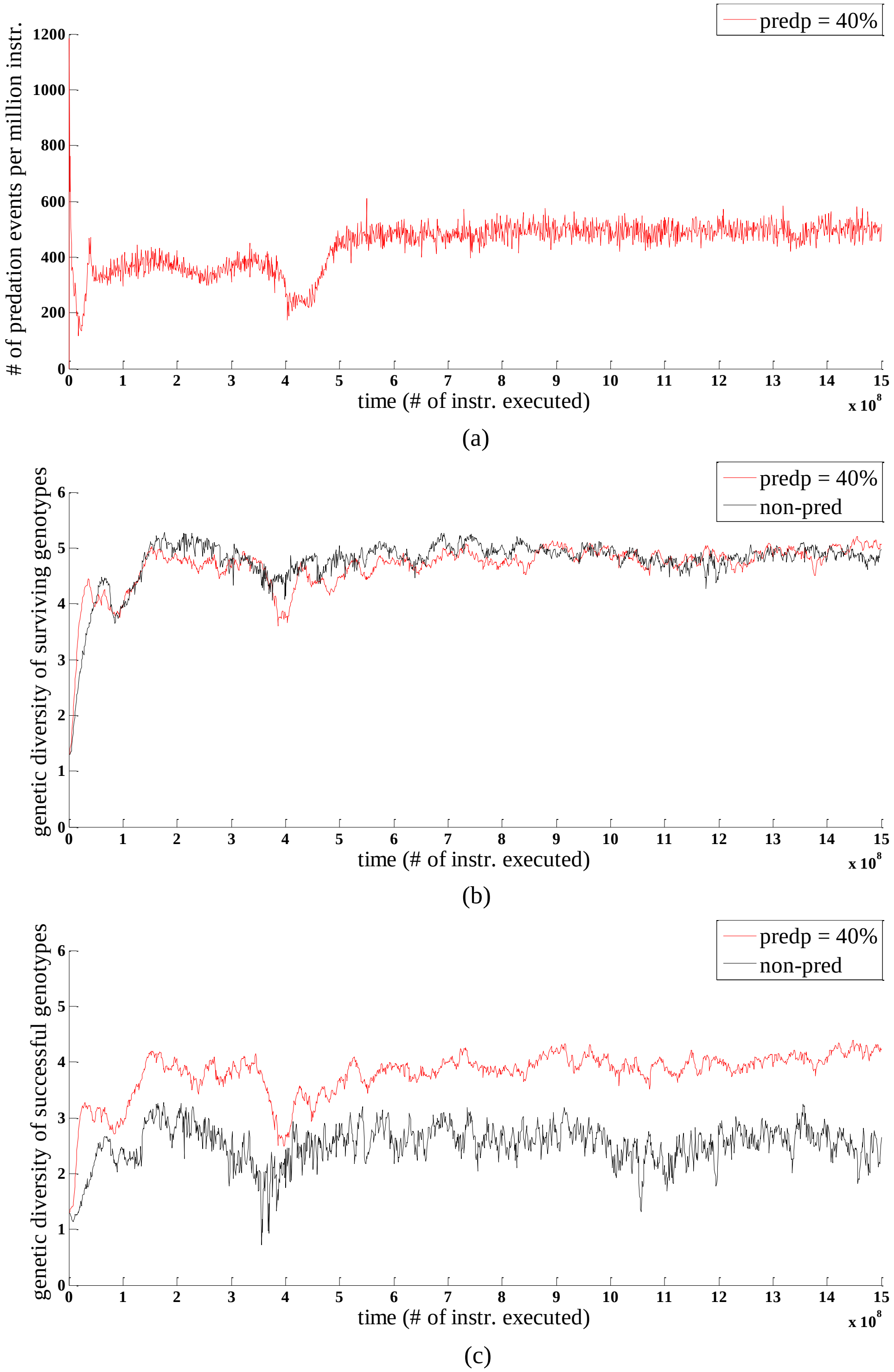
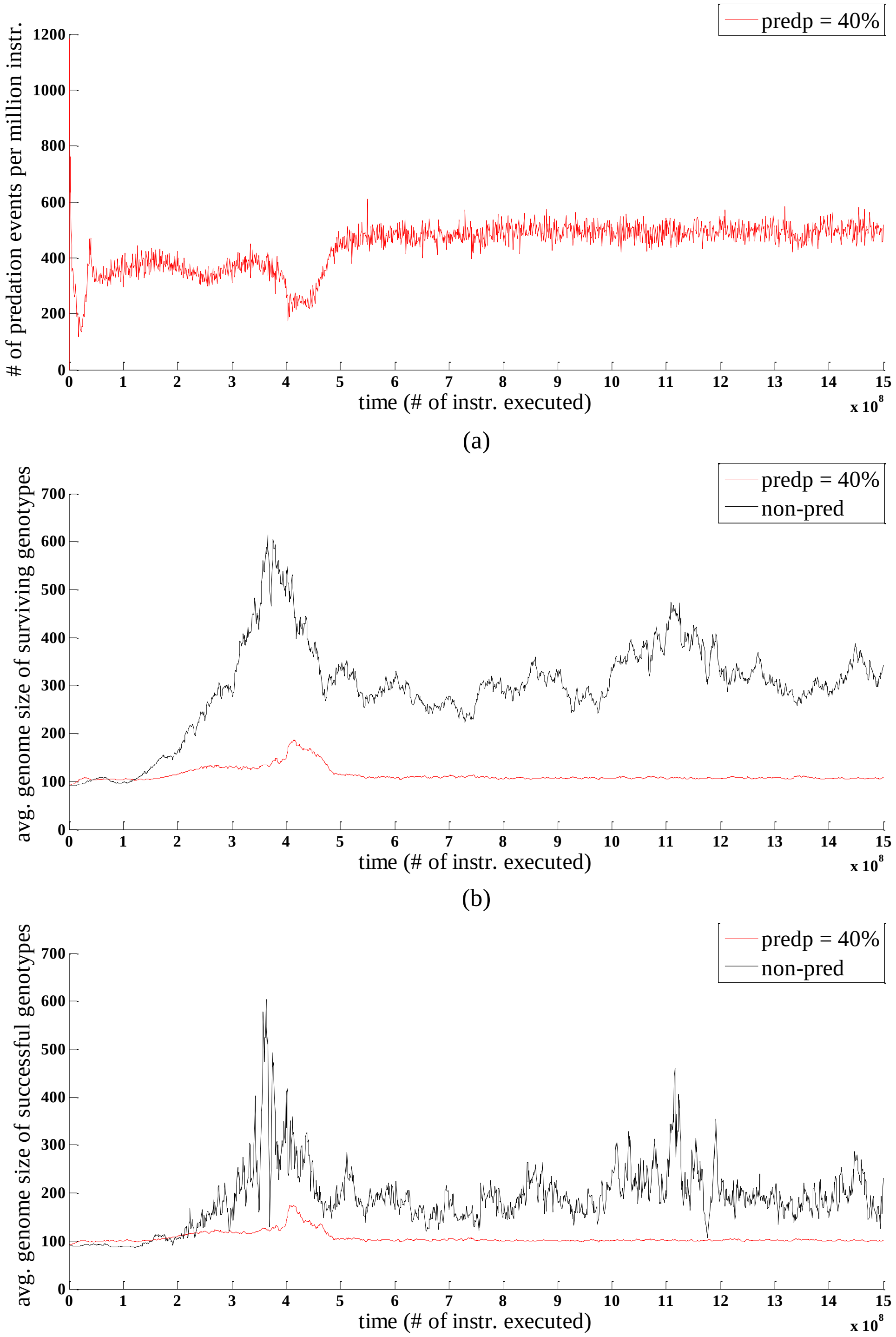


Figure 4.2: Persistence of predation and genetic diversity in an evolving community when 40% of CPU energy is transferred from a captured prey to its predator. (a) After the transient initial stage, intensive predation is stably maintained in the community. (b) Genetic diversity of surviving genotypes in the community with predation and without predation. (c) Genetic diversity of successful genotypes in the community with predation and without predation.



(a)

(b)

(c)

Figure 4.3: Persistence of predation and mean genome size in an evolving community when 40% of CPU energy is transferred from a captured prey to its predator. (a) After the transient initial stage, intensive predation is stably maintained in the community. (b) Mean genome size of surviving genotypes in the community with predation and without predation. (c) Mean genome size of successful genotypes in the community with predation and without predation.

As time passes, as shown in Figure 4.1(a3) – (a7), the creatures may gradually evolve towards larger sizes, which considerably reduce the number of creatures living in the soup. Furthermore, most of the genotypes have a negligible population size and thus may disappear from the community soon after their birth. In contrast, the community in the experimental run usually exhibits high evenness of abundances among different genotypes. Many genotypes survive well and achieve a good population size. The lengths of creatures may not change significantly over the simulation run and thus the number of creatures living in the soup is similar to that in the initial community, as shown in Figure 4.1(b2) – (b7).

The genetic diversity and the sizes of creatures in the evolving community are further examined in Figure 4.2 and Figure 4.3 as they are calculated for every million instructions executed. In the experimental run, intensive predation persists in the ecological community, as shown in Figure 4.2(a): after the initial transient stage, the number of predation events per million instructions executed reaches about 380 and then following a temporary decrease, occurring around 400 million instructions executed, the predation level increases to and stably maintains at about 500 predation events per million instructions executed until the end of the run. In contrast, no predation events occur in the control run because no predators are introduced into the initial community and no creatures are able to become predators through mutations during the run. The genetic diversity, calculated by the surviving genotypes which are able to reproduce at least once, in the experimental run does not differ significantly from that in the control run, as shown in Figure 4.2(b). This negligible difference of the genetic diversity in the two runs may result from the strong influence of mutations on the genetic diversity. In an evolving community, new genotypes continuously emerge through mutations and most of them may produce at least one offspring before death. Therefore, mutations may greatly enhance the number of surviving genotypes in the community and thus may obscure the effect of predation on the genetic diversity. However, the successful genotypes, after being generated through mutations, live in the soup for a certain period of time and highly rely on their biotic environment to achieve a population of at least 5 individuals. Thus, the number of successful genotypes may be much less sensitive to mutations. When the genetic diversity is computed for the successful genotypes, as shown in Figure 4.2(c), the community in which predators actively feed on prey exhibits a much higher genetic diversity than the community lacking in predation. In addition, the temporary decrease in the predation level around 400 million instructions executed in Figure 4.2(a) concurs with the drop in the genetic diversity of the community in the experimental run in Figure 4.2(c). The high genetic diversity achieved and maintained by predation may result from the disproportionate consumption of the most abundant prey genotypes by predators: in the absence of predation, one or a few genotypes quickly dominate the soup and drive other genotypes to go extinct. This can cause an abrupt, dramatic decrease in genetic diversity. Then mutations modify the genomes of the dominant genotypes which causes new genotypes to appear and thus the recuperation of the genetic diversity. This pattern of sudden drop and then rapid restoration of the genetic diversity repetitively appears throughout the control run, as shown in Figure 4.2(c). However, in the experimental run, predators with positive frequency-dependent behavior may depress the dominant prey genotypes and thus allow the less competitive prey to survive for a longer time. Therefore, more prey genotypes have a chance to reach a population of 5 or more individuals before being crowded out of the soup. This increase in the number of successful prey genotypes may also promote the survival of various predator genotypes. With the persistent flourishing of prey and predator genotypes, the genetic diversity of the community may reach and stably maintain a high level, as shown in Figure 4.2(c).

Figure 4.3(a) is a copy of Figure 4.2(a) which shows the persistence of predation in the ecological community in the experimental run. Both the average genome size of the surviving genotypes and the average genome size of the successful genotypes in the control run are significantly larger than those in the experimental run, as shown in Figure 4.3(b) and Figure 4.3(c), respectively. Because the soup has a fixed finite space, as the sizes of creatures increase, the number of creatures living in the soup declines. By preventing an increase in the average genome size of digital organisms, the community with the presence of predation maintains a number of creatures as large as that in the initial community and thus may allow rich ecological interactions to continuously occur among creatures during the evolutionary process.

4.3.2 Robustness to the Variations of Parameter Settings

Methods

The simulation results in section 4.3.1 suggest that with the presence of predation, the genetic diversity of successful genotypes in an evolving ecological community reaches and maintains a high level. One of the most crucial parameters that support predator populations and thus the persistence of predation during an evolutionary run is the amount of energy transferred from prey to predators through predation. To explore the robustness of the influence of predation on genetic diversity, I systematically vary the amount of CPU time that a predator acquires from each of its captured prey from 35%, 45%, 50%, 55% to 60%, while keeping other parameter settings the same as those used in section 4.3.1 when the scenario that a predator receives 40% of CPU time from each prey is studied. Then I compare the genetic diversity of successful genotypes in the evolving populations in the absence and the presence of predation. Moreover, I examine the sizes of creatures during evolutionary runs when the CPU energy acquired by predators varies. Because the number of individuals in the surviving genotypes is significantly more than that in the successful genotypes, the sizes of surviving genotypes have a much stronger impact on the number of creatures living in the soup. Thus, I evaluate the abundance of creatures in the community through the average genome size of surviving genotypes.

The robustness of the influence of predation on genetic diversity is further examined by repeating a simulation run with different random seeds. For each of the 6 experimental runs (the amount of CPU energy transferred from a captured prey individual to its predator varies from 35% to 60% in 5% increments), I perform 10 replicates by using 10 random seeds and record the number of replicates in which predation persists in the evolving community for 1000 million instructions executed. Then I average the genetic diversity of successful genotypes over those replicates with persistent predation and compare it to the one calculated in the control run over the same random seeds. In addition, I record the standard deviation at 0, 250, 500, 750 and 1000 million instructions executed, as a measure of the variations in the genetic diversity of successful genotypes among different replicates.

Results

As shown in Figure 4.4(a), when a predator receives 35% of CPU time from each of its captured prey, predation events only occur at the beginning of the simulation run and rapidly decline to 0 after 30 million instructions executed. This suggests that predator populations may not acquire sufficient energy through predation and thus quickly go extinct. With the disappearance of predators in the evolving community, the genetic diversity of successful genotypes in the experimental run becomes almost indistinguishable with that in the control run, as shown in Figure 4.4(b). The sizes of creatures in the experimental run also significantly increase, being very similar to those in the control run, as shown in Figure 4.4(c).

However, when a predator receives 45%, 50%, 55% and 60% of CPU time from each of its prey, respectively, the patterns of the persistence of predation, genetic diversity and sizes of creatures exhibited in Figure 4.2 and Figure 4.3 robustly reappear. As shown in Figure 4.5 – Figure 4.8, after the initial transient stage, intensive predation stably persists in the evolving community over the entire simulation run of 1500 million instructions executed. With the continuous presence of predators, the genetic diversity of successful genotypes in the experimental run is considerably higher than that in the control run. Moreover, in the experimental run, the average genome size of surviving genotypes in the evolving community remains almost the same as that in the initial community. In contrast, in the control run, the sizes of creatures increase dramatically during the evolutionary process with huge fluctuations.

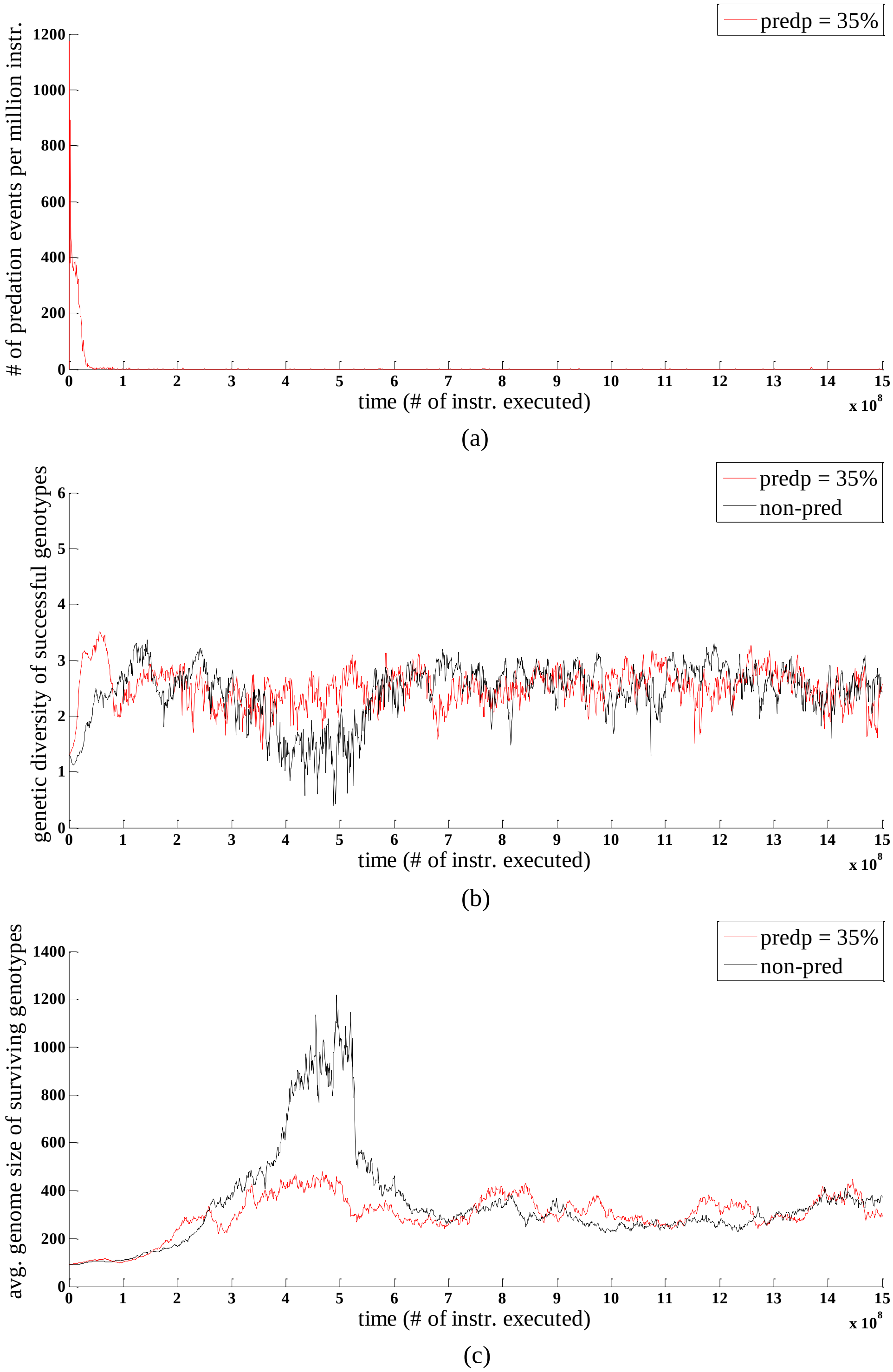
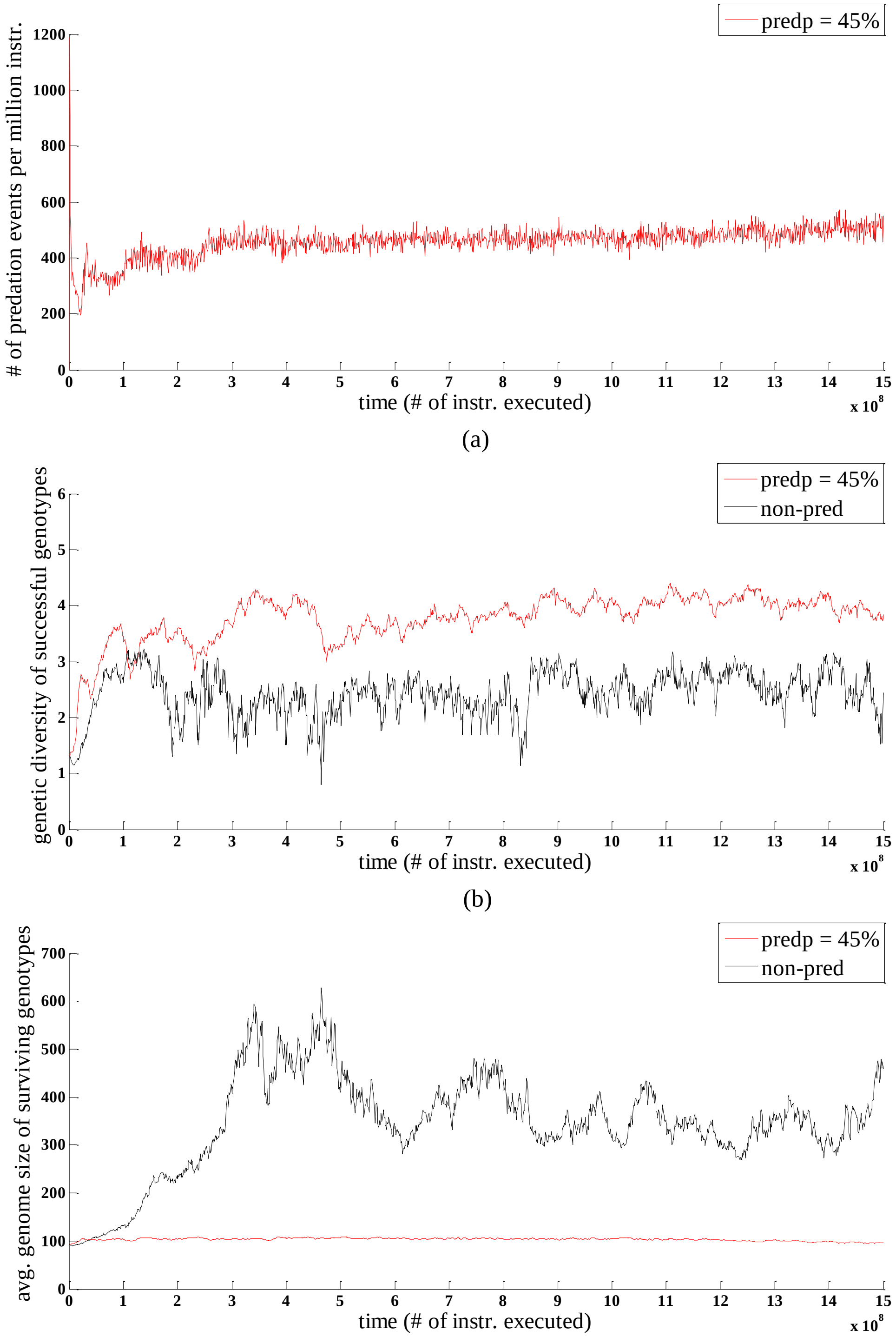


Figure 4.4: Persistence of predation, genetic diversity and mean genome size in an evolving community when 35% of CPU energy is transferred from a captured prey to its predator. (a) Predation is not maintained in the community. (b) Genetic diversity of successful genotypes in the community with predation and without predation. (c) Mean genome size of surviving genotypes in the community with predation and without predation.



(a)

(b)

(c)

Figure 4.5: Persistence of predation, genetic diversity and mean genome size in an evolving community when 45% of CPU energy is transferred from a captured prey to its predator. (a) Predation is stably maintained in the community. (b) Genetic diversity of successful genotypes in the community with predation and without predation. (c) Mean genome size of surviving genotypes in the community with predation and without predation.

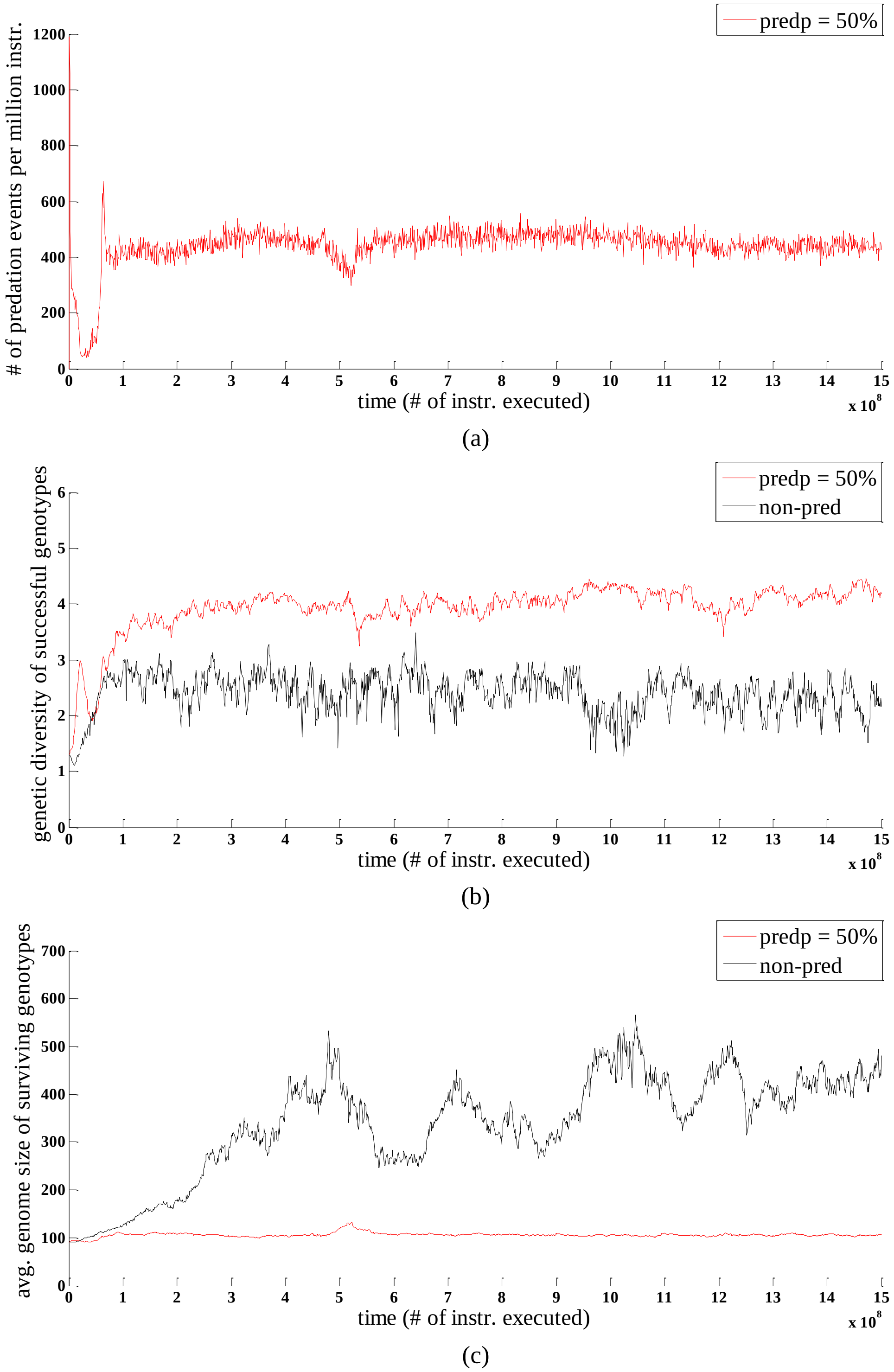


Figure 4.6: Persistence of predation, genetic diversity and mean genome size in an evolving community when 50% of CPU energy is transferred from a captured prey to its predator. (a) Predation is stably maintained in the community. (b) Genetic diversity of successful genotypes in the community with predation and without predation. (c) Mean genome size of surviving genotypes in the community with predation and without predation.

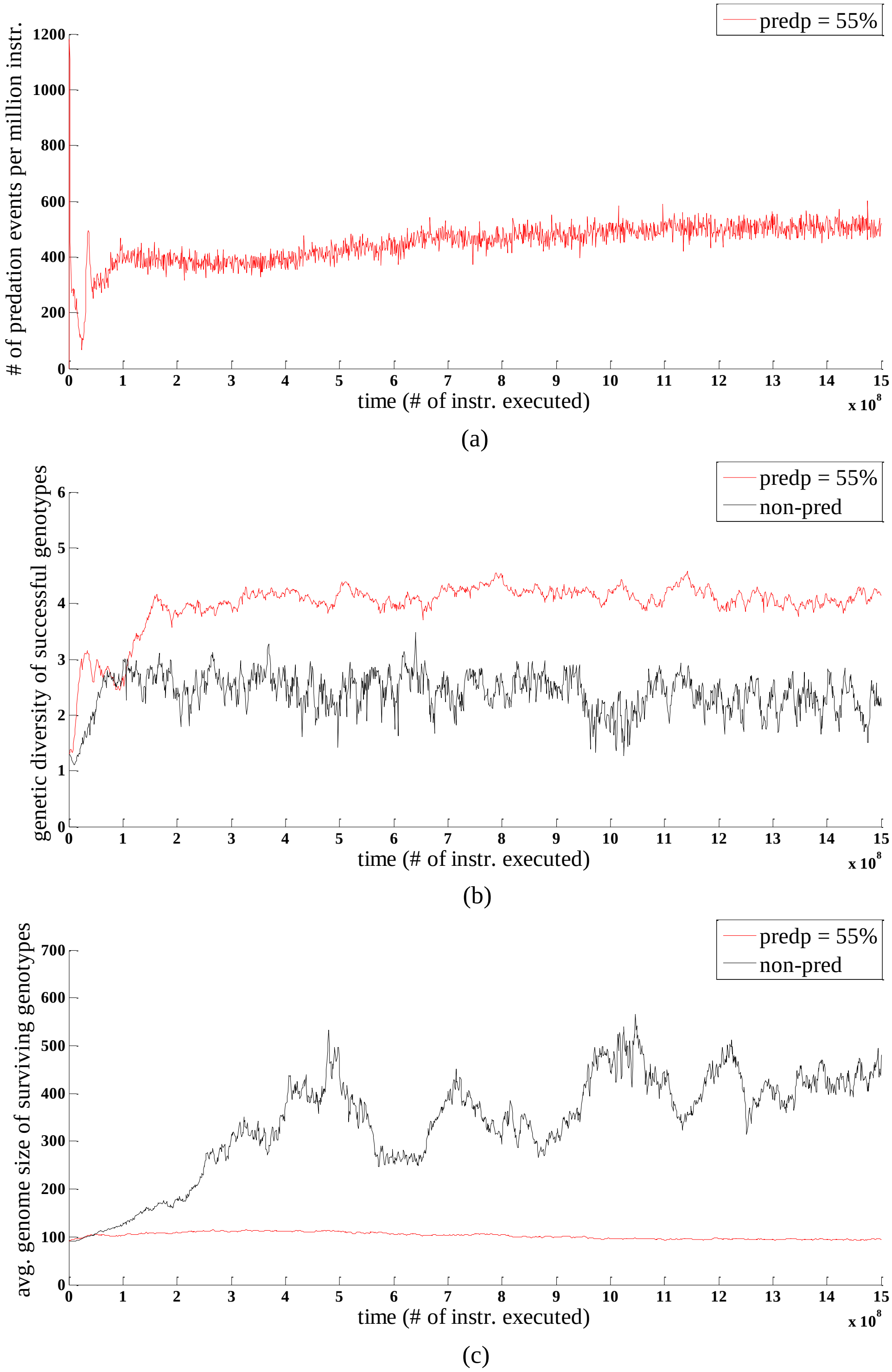
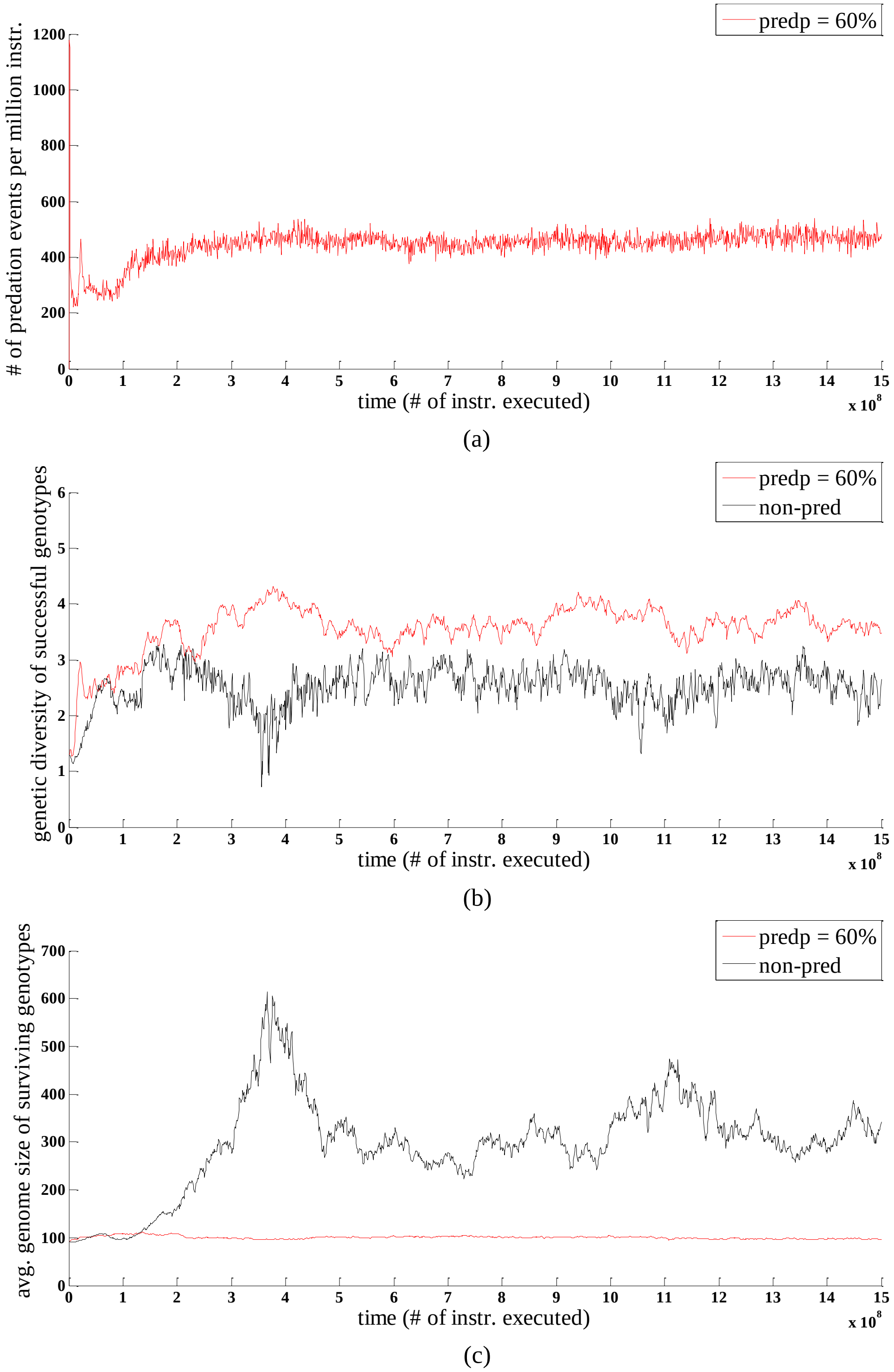


Figure 4.7: Persistence of predation, genetic diversity and mean genome size in an evolving community when 55% of CPU energy is transferred from a captured prey to its predator. (a) Predation is stably maintained in the community. (b) Genetic diversity of successful genotypes in the community with predation and without predation. (c) Mean genome size of surviving genotypes in the community with predation and without predation.



(a)

(b)

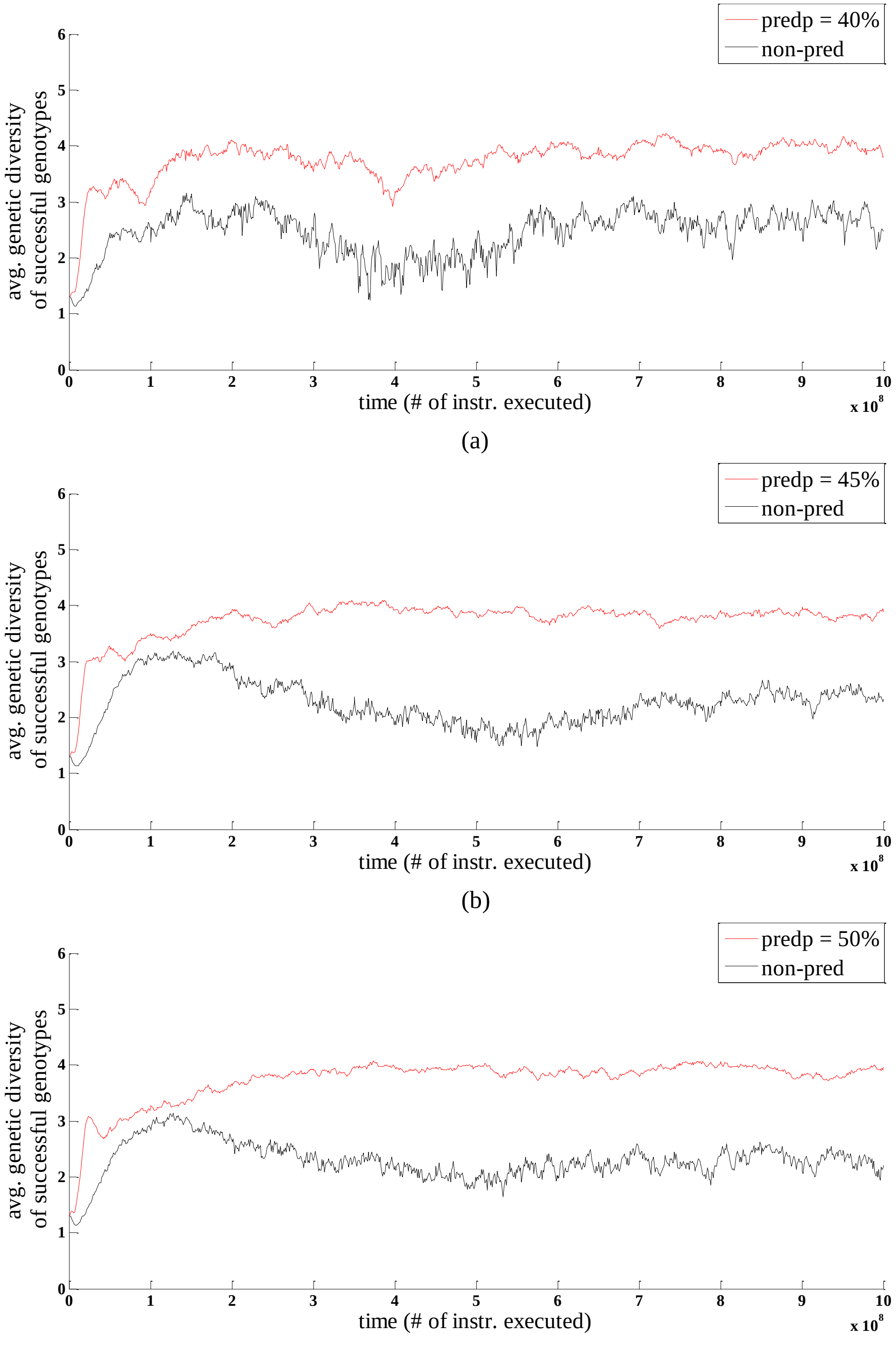
(c)

Figure 4.8: Persistence of predation, genetic diversity and mean genome size in an evolving community when 60% of CPU energy is transferred from a captured prey to its predator. (a) Predation is stably maintained in the community. (b) Genetic diversity of successful genotypes in the community with predation and without predation. (c) Mean genome size of surviving genotypes in the community with predation and without predation.

As I repeat an experimental run with 10 different random seeds, the amount of CPU energy that predators acquire from their prey greatly influences the likelihood of the maintenance of predation in the evolving community. As shown in Table 4.1, when a predator receives 35% of CPU time from each of its prey, no predation persists in the community in any of the 10 replicates. However, a stable, high level of predation starts to appear when 40% of CPU time is transferred from each prey to its predator, as persistent predation occurs in 2 out of 10 replicates. With the further increase of the energy transferred to predator populations, such as a predator receives 45%, 50%, 55% or 60% of CPU time from each of its prey, the stable, continuous predation, which occurs in 6 to 8 out of 10 replicates, may robustly happen in the community. The averages and standard deviations of the genetic diversity of successful genotypes over the replicates in which predation steadily persists for 1000 million instructions executed are shown in Figure 4.9(a) – (e) and Table 4.2. Those results suggest that over a wide range of the amount of energy acquired by predators, the genetic diversity of successful genotypes in the community with intensive predation is clearly much higher than that in the community lacking in predation.

Table 4.1: Predation is more likely to persist in an evolving community as predator populations acquire more CPU energy from their prey.

Amount of CPU time that a predator acquires from each of its prey (predp)	Number of replicates that predation persists in the evolving community for 1000 million instructions executed, among 10 replicates
35%	0
40%	2
45%	6
50%	7
55%	8
60%	7

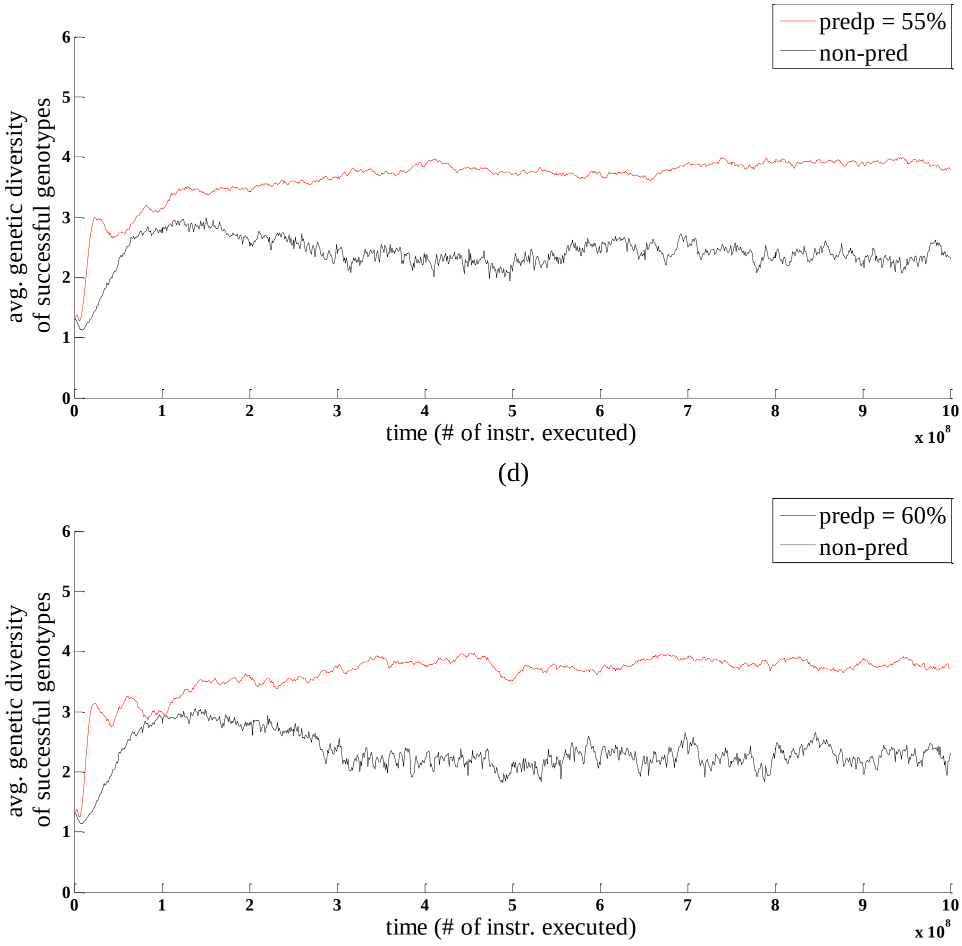


(a)

(b)

(c)

Figure 4.9: Average genetic diversity of successful genotypes over the replicates in which intensive predation is stably maintained in the evolving community, compared to that in the community without predation. (a) 40 % of CPU energy is transferred from a captured prey to its predator. (b) 45 % of CPU energy is transferred from a captured prey to its predator. (c) 50 % of CPU energy is transferred from a captured prey to its predator.



(d)

(e)

Figure 4.9 (continue): Average genetic diversity of successful genotypes over the replicates in which intensive predation is stably maintained in the evolving community, compared to that in the community without predation. (d) 55% of CPU energy is transferred from a captured prey to its predator. (e) 60 % of CPU energy is transferred from a captured prey to its predator.

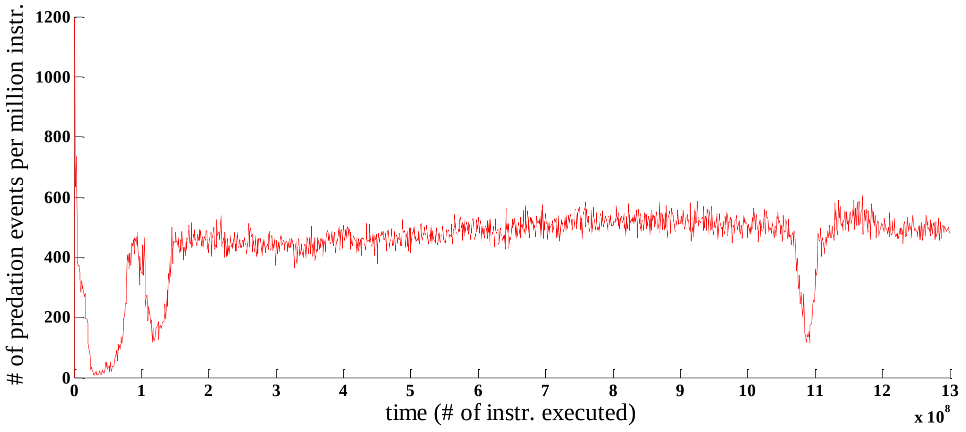
Table 4.2: Standard deviation of the genetic diversity of successful genotypes over the replicates in which intensive predation is stably maintained in the evolving community (pred), compared to that in the community without predation (Npred). The standard deviation is recorded at 0, 250, 500, 750 and 1000 million instructions executed, respectively.

Time (million instr. executed)	Standard Deviation									
	predp = 40%		predp = 45%		predp = 50%		predp = 55%		predp = 60%	
	pred	Npred	pred	Npred	pred	Npred	pred	Npred	pred	Npred
0	0	0	0	0	0	0	0	0	0	0
250	0.175	0.076	0.268	0.283	0.216	0.316	0.186	0.449	0.295	0.348
500	0.073	0.795	0.321	0.674	0.180	0.738	0.389	0.341	0.559	0.805
750	0.153	0.129	0.232	0.306	0.039	0.667	0.201	0.408	0.247	0.644
1000	0.064	0.061	0.403	0.542	0.353	0.509	0.275	0.538	0.366	0.458

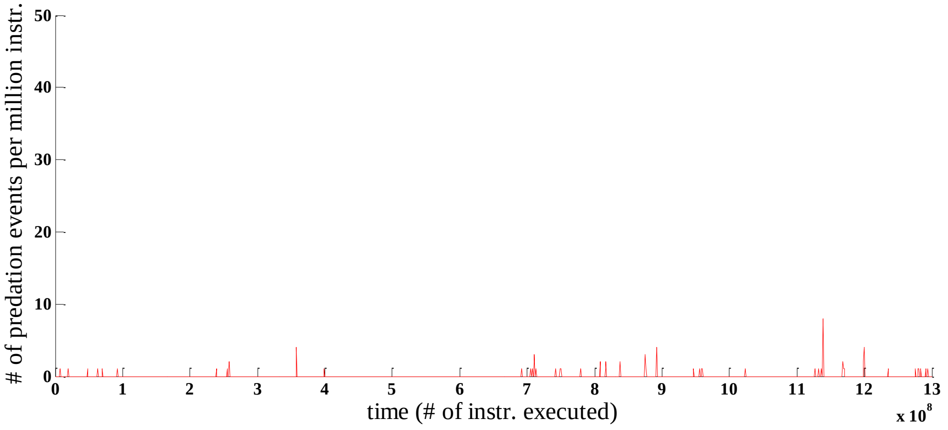
4.4 Coevolution between Digital Predator and Prey Populations in Tierra

The process of coevolution describes the reciprocal evolutionary adaptations of two species that interact ecologically. One of the most extensively studied coevolutionary scenarios is the antagonistic interaction between predator and prey species: through predation, predators exert selective pressures on prey which facilitates the evolution of escaping attributes in prey, such as fast speed, protective coloration and toxic chemical defenses, to deter predation. The prey individuals with efficient escaping mechanisms have better chance to survive and reproduce, passing on their attributes to future generations. On the other hand, with the development of escaping adaptations in prey species, predators experience selective pressures to improve their ability to capture prey. The predators with better feeding mechanisms acquire more food and thus produce more offspring which inherit the predation characteristics, such as acute detection and efficient attack, to circumvent the escaping strategies newly evolved in prey. Such a coevolutionary relationship between prey and predators may cause the two species to continuously evolve, as each species tries to increase its own fitness, at the expense of the other (Rausher 2001).

Similar to the ecological interactions between prey and predator species in nature, digital prey and predators in Tierra also shape the biotic environment of each other. As beneficial mutations occur in digital prey which enhance their ability to escape predation and thus to produce more offspring, digital predators may evolve adaptive response to exploit those newly thriving prey types. Here, I attempt to explore the coevolution patterns between predator and prey populations in Tierra.



(a)



(b)

Figure 4.10: Mutations on predator genomes, rather than on prey genomes, cause new types of predators to emerge. The two simulation runs in (a) and (b) are performed under the same parameter settings, except for the initial predator population: a predator population of 300 individuals is introduced into the initial prey community in the run in (a), but not in the run in (b). Therefore, any predators that appear in the run in (b) come from prey mutants. (a) Stable and intensive predation persists in the evolving ecological community. The sudden, dramatic change of the predation level, during the period of 1060-1120 million instructions executed, may indicate the occurrence of coevolution between predator and prey populations. (b) When predators are generated purely from prey mutants, the number of predation events is negligible (the maximum value of the vertical axis in (b) is 50, rather than 1200).

4.4.1 Coevolution between Predators and Prey Observed at the Genome Level

During an evolution run in Tierra, occasionally, the stable persistence of intensive predation in the evolving ecological community is interrupted by a brief period of significant decline of predation. As illustrated in Figure 4.10(a), after the initial transient stage, the number of predation events per million instructions executed is steadily maintained around 500, however, this predation level suddenly drops to about 100 and then quickly returns to about 500 in the period of 1060 to 1120 million instructions executed. This huge decrease of the predation level may indicate that the majority of prey populations in the community evolve some escaping strategies to avoid being found by predators. And the following increase of the predation level may suggest that predators evolve novel capture mechanisms to exploit the newly evolved prey.

By acquiring the predation instruction through mutations, potentially, with very low probability, a prey individual could become a predator. To verify that a predator population with a reasonable size could not result from prey mutants, I start a simulation run with pure prey populations and allow prey to mutate to predators. Except for the initial predator population, this simulation run uses exactly the same parameter settings as the run that produces Figure 4.10(a). As shown in Figure 4.10(b), when predators are generated purely from prey mutants, the number of predation events is negligible (the maximum value of the vertical axis in Figure 4.10(b) is 50, rather than 1200). This result supports that in Figure 4.10(a), when predation drops to a very low level around 1090 million instructions executed, the majority of the predators, rather than all the predators, go extinct, then mutations on the surviving predators result in the emergence of new types of predators which may feed on the recently evolved prey.

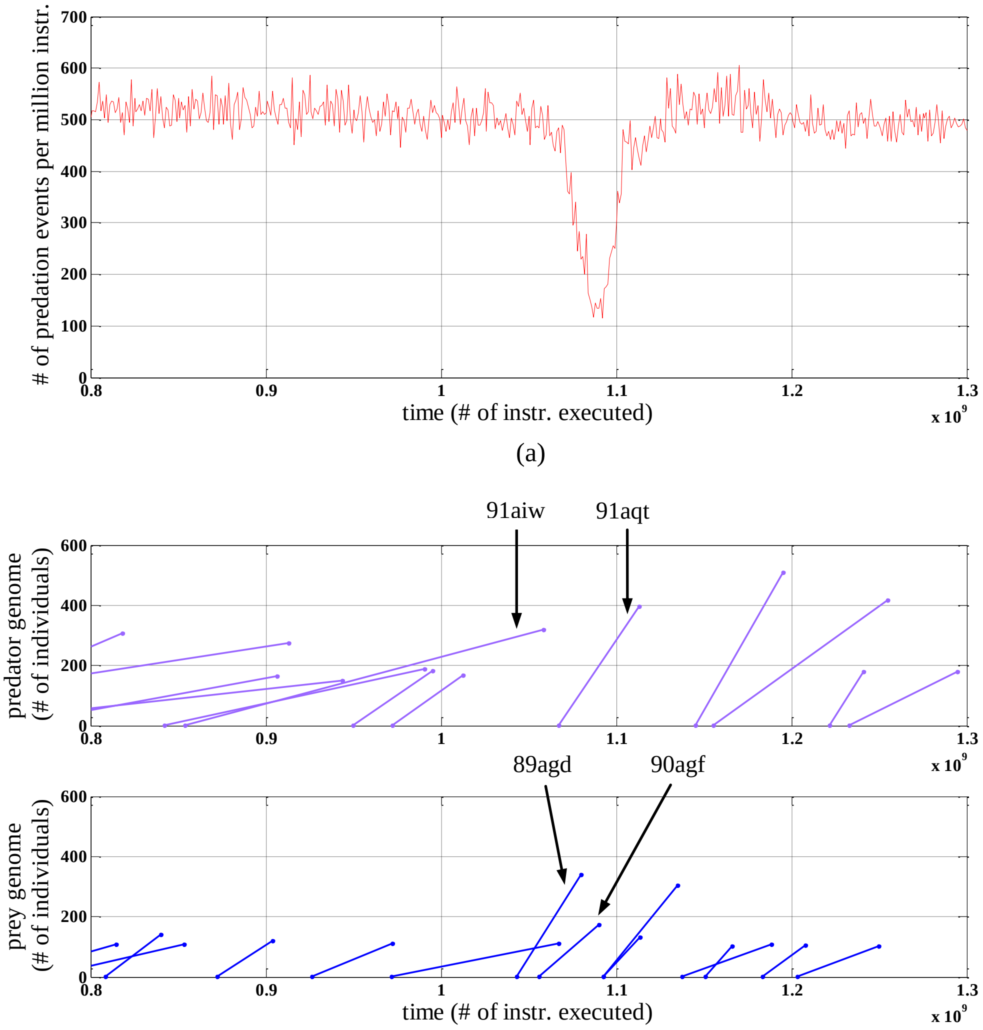
Here, I perform a detailed analysis on the genomes of digital creatures that appear in the period when the dramatic change of predation level occurs, to investigate whether or not coevolution exists between predator and prey populations.

Methods

I use a built-in software tool in Tierra, called “Probe” (Ray, 1998), to find the genomes, in the period of 800 to 1300 million instructions executed, whose maximum population size reaches or exceeds 100 individuals. For each of those major genomes, I record its name, the time that it first appears in the soup, its maximum population size and the time that the maximum population size is achieved, and whether this genome is a prey or a predator. After identifying 13 major predator genomes and 14 major prey genomes, I plot those genomes in separate graphs to observe the time periods that their populations thrive in the soup and reach the maximum sizes. To detect the prey genomes that a predator genome mainly feeds on, for each of the 13 predator genomes, I count the number of individuals in each of the 14 prey genomes that are captured by the predator. In addition, I record the predation template in each predator genome but for each prey genome, I record those templates which are complementary to the predation templates in the 13 predator genomes (different predator genomes may use distinct predation templates to search for prey).

Results

Figure 4.11(a) shows the portion of Figure 4.10(a) in the period of 800 to 1300 million instructions executed. The dramatic decrease of the predation intensity in an ecological community could result from a decline of prey populations or a decline of predator populations.



(a)

(b)

Figure 4.11: Predation level in the evolving ecological community and the thriving major predator and prey genomes during the period of 800 – 1300 million instructions executed. (a) The dramatic change of predation level. (b) Major predator and prey genomes whose maximum population size exceeds 100 individuals. Each line represents one genome with the starting point indicating the time that the genome first appears in the soup with 1 individual and the ending point indicating the time that the genome reaches its maximum population. In the order of the time that each genome reaches its maximum population, from left to right, the 13 predator genomes are 91aba, 91afh, 91abo, 91adt, 91aid, 91ana, 92aeg, 91aiw, 91aqt, 91agf, 91arc, 91amx and 91aqg, and the 14 prey genomes are 88abu, 86add, 89acc, 90afi, 90aie, 91aei, 89agd, 90agf, 89aip, 87aeh, 87afq, 86adm, 90alu and 90ame.

However, Figure 4.11(b) shows that during the period of sudden drop in the predation level, 2 major prey genomes (89agd and 90agf) flourish in the soup, achieving large population sizes. Therefore, the low predation level is most likely caused by the decrease of predator populations, rather than lack of prey. That is, there are plenty of prey individuals available in the soup but predators fail to capture them. For example, as shown in Figure 4.11(b), predator genome 91aiw and prey genome 89agd coexist in the soup for a while and both of them have large population sizes, therefore, they have good chance to encounter each other. However, the population of predator 91aiw starts to decrease when the population of prey 89agd increases rapidly. This may indicate that predator 91aiw is unable to find prey 89agd, in other words, prey 89agd may have evolved some escape strategy to hide from predator 91aiw. On the other hand, predator genome 91aqt emerges after the presence of prey genomes 89agd and 90agf in the soup and then the population of predator 91aqt increases with the populations of prey 89agd and 90agf. This may suggest that predator 91aqt feeds on prey 89agd and 90agf, which may result in the rise of the predation level after the drop.

The predation relationship between a predator genome and a prey genome is further examined by the template matching that a predator uses to capture its prey. As shown in Table 4.3, based on the predation template in a predator genome, the 13 major predator genomes are divided into 4 groups,: the predator genomes in group #1 (91aba, 91afh, 91abo and 91adt), in group #2 (91aid, 91ana, 92aeg and 91aiw), in group #3 (91aqt) and in group #4 (91agf, 91arc, 91amx and 91aqg) use 001, 011, 01 and 010 as the predation template, respectively. The 14 major prey genomes are divided into 2 groups: the prey genomes in group #1 (88abu, 86add, 89acc, 90afi, 90aie and 91aei) have templates 1100 and 101; the prey genomes in group #2 (89agd, 90agf, 89aip, 87aeh, 87afq, 86adm, 90alu and 90ame) have template 101 but not template 1100. As a predator individual searches for its prey, it tries to find a template in prey which is complementary to its predation template. This complementary template in prey could be either a single template or contained in a longer template. The templates which are complementary to the predation templates in predator group #1 and group #2 are 110 and 100, respectively and both are contained in template 1100, therefore, the predators in group #1 and group #2 could potentially feed on prey group #1. Similarly, the templates which are complementary to the predation templates in predator group #3 and group #4 are 10 and 101, respectively and are either contained in or equal to template 101, therefore, the predators in group #3 and group #4 could potentially feed on prey group #2. As digital creatures continuously evolve in the soup, prey and predator genomes may emerge, survive and go extinct at different times. Therefore, besides template matching, the actual execution of predation also depends on whether or not a predator genome encounters its prey in the soup. Based on the number of predation events that occur between each pair of predator and prey genomes, I identify the prey genomes that each predator genome actually feeds on. As shown in Table 4.3, the predators which share the same predation template may actually capture different prey genomes. This feeding difference of the predators may result from their different thriving periods in the soup. For example, due to template matching, predator genome 91aba could potentially capture all the prey genomes in prey group #1, however, 91aba only feeds on prey genomes 88abu, 86add and 89acc. The failure of 91aba to capture prey genomes 90afi, 90aie and 91aei in prey group #1 may be because 91aba population has become extinct before 90afi, 90aie and 91aei appear in the soup.

Table 4.3: The prey genomes that each major predator genome actually feeds on during the period of 800 – 1300 million instructions executed. The first column lists the 13 major predator genomes which are divided into 4 groups, indicated by the 3 horizontal double-lines, based on their predation templates. That is, the predator genomes in group #1, #2, #3, #4 have predation template 001, 011, 01 and 010, respectively. The first row lists the 14 major prey genomes which are divided into 2 groups, indicated by the vertical double-line. The prey genomes in group #1 have template 1100 and 101, but template 1100 disappears in prey group #2. An "X" indicates an actual predator-prey pair. For example, the 3 "X" in the second row suggest that predator genome 91aba feeds on prey genomes 88abu, 86add and 89acc.

Prey Predator	88abu 1100/101	86add 1100/101	89acc 1100/101	90afi 1100/101	90aie 1100/101	91aei 1100/101	89agd 101
91aba 001	X	X	X				
91afh 001	X	X	X	X			
91abo 001	X	X	X	X	X		
91adt 001			X		X		
91aid 011			X		X	X	
91ana 011					X	X	
92aeg 011						X	
91aiw 011			X		X	X	
91aqt 01							X
91agf 010							X
91arc 010							
91amx 010							X
91aqg 010							

Prey Predator	90agf 101	89aip 101	87aeh 101	87afq 101	86adm 101	90alu 101	90ame 101
91aba 001							
91afh 001							
91abo 001							
91adt 001							
91aid 011							
91ana 011							
92aeg 011							
91aiw 011							
91aqt 01	X	X	X	X			
91agf 010	X		X	X	X	X	X
91arc 010						X	X
91amx 010	X		X	X	X	X	X
91aqg 010							X

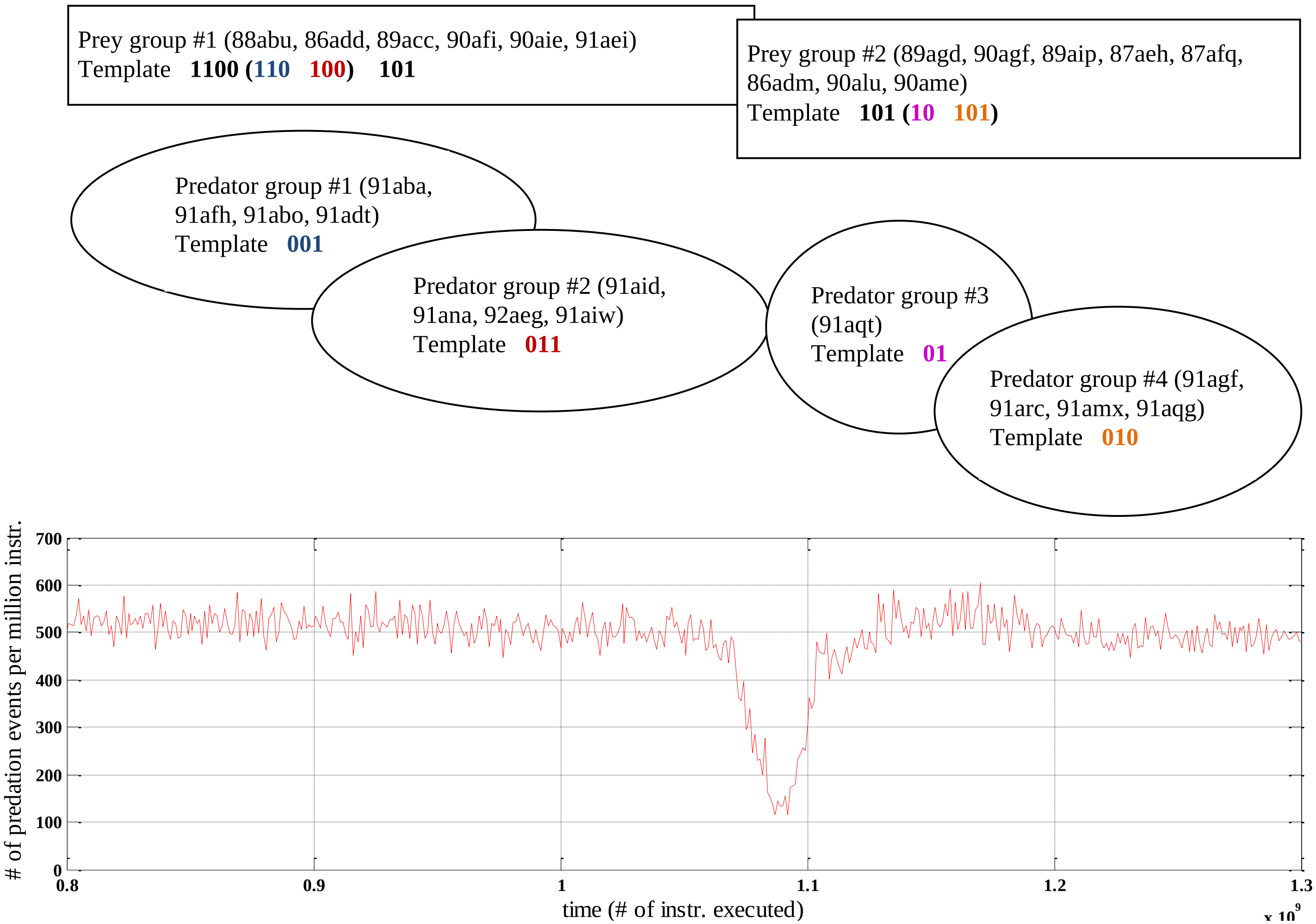


Figure 4.12: Coevolution between predator and prey populations is essentially the coevolution between the predation templates in predators and their complementary templates in prey. The horizontal length of each square/oval roughly represents the time period that each prey/predator group thrives in the soup.

Combining the information present in Figure 4.11(b) and in Table 4.3, I attempt to reveal the coevolution of predator and prey populations during the period of 800 to 1300 million instructions executed. Figure 4.12 illustrates the flourishing periods of the 2 prey groups and 4 predator groups, and the complementary template matching between the prey and predator groups. During the period of 800 to 1060 million instructions executed, prey genomes (prey group #1) maintain the templates 1100 and 101 as they evolve. Although predator genomes change their predation template from 001 (predator group #1) to 011 (predator group #2) during evolution, each of those predation templates has its complementary template contained in 1100. Therefore, the predators in group #1 and #2 are able to capture the prey genomes in prey group #1 and thus a high level of predation persists in the evolving community. During the period of 1060 to 1090 million instructions executed, prey may mutate template 1100 as they evolve. As a result, template 1100 is no longer contained in the prey genomes in prey group #2. Predators which use predation template 011 to search for their prey are unable to feed on the existing prey in the soup which contain template 101. Therefore, the predator populations in predator group #2 may decline rapidly, causing the sudden, dramatic decrease of predation level. The newly evolved prey genomes, by removing the template (1100) attacked by predators, escape predation and thrive in the soup with very weak predation pressures. However, this low predation period does not last very long. As abundant prey genomes with template 101 survive in the soup, predators quickly evolve their predation template to exploit this new food source. The predator genome in group #3 uses a shorter predation template 01 to search for prey and successfully feeds on the prey genomes with template 101, resulting in the rapid increase of predation level during the period of 1090 to 1150 million instructions executed. The high predation level is then further maintained as predators evolve a more complete predation template 010 in group #4 to capture the prey genomes in prey group #2, during the period of 1150 to 1300 million instructions executed. The increase in the size of the predation template from 2 to 3 suggests that predators do not evolve a cheating strategy, by continuously reducing the size of their predation template, which potentially allows predators to find the complementary templates in more prey individuals.

In summary, the dramatic change of the predation level, during the period of 1060 to 1120 million instructions executed, may clearly demonstrate the coevolution between predator and prey populations: by mutating templates, prey avoid being found by predators and thus escape predation. This adaptation evolved in prey severely reduces the fitness of their predators (predator group #2). Then predators evolve their predation templates to attack the templates contained in the newly evolved prey, circumventing the escape mechanisms developed in prey (predator group #3 and #4). Therefore, the coevolution between predator and prey populations in Tierra may essentially be the coevolution between the predation templates in predators and their complementary templates in prey. Moreover, the coevolution process may consistently occur throughout the entire simulation run: a significant decrease of predation level may occur when the majority of prey populations in the soup escape predation around the same time; however, if different prey populations evolve escape strategies at different times, the predators that feed on distinct prey types may alternately thrive in the soup, which may maintain a high stable predation level.

4.4.2 Coevolution between the Predation Templates in Predators and Their Complementary Templates in Captured Prey

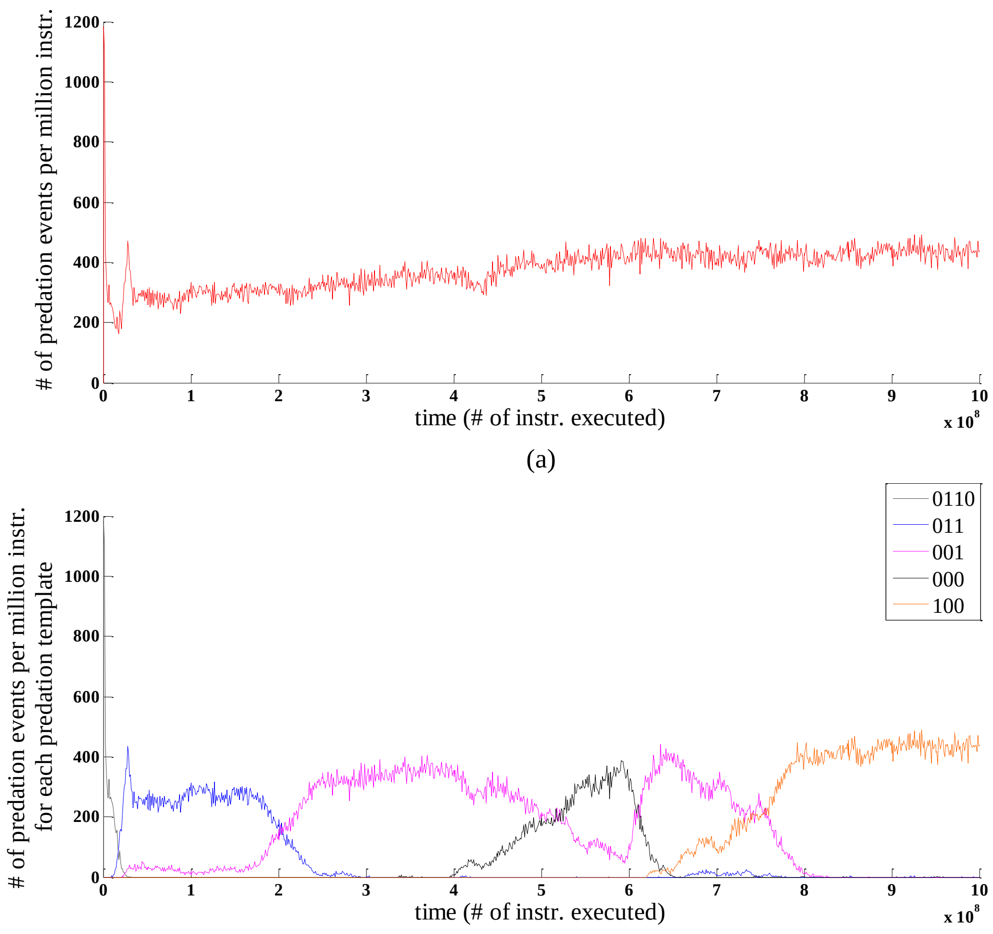
By identifying the genomes of major predators and prey and then examining the predation templates in predators and their complementary templates in prey, I demonstrate one example of coevolution between predators and prey at a particular period of time (when the predation level dramatically drops) in section 4.4.1 and conclude that the coevolution between predator and prey populations may be driven by the predation templates in predators and their complementary templates in prey, rather than by specific predator and prey genotypes. Here, by focusing on the changes in predation templates and their complementary templates, I attempt to study the coevolution between predators and prey throughout the entire simulation run.

Methods

Similar to the simulation setup used in section 4.3.1, I seed the soup with a predator population of 300 individuals and 3 prey types (type-A, type-B and type-C), each with a population of 1000 individuals. Those genomes of digital creatures are continuously modified by mutations during the simulation run. Each predator searches for prey in its local area and executes positive frequency-dependent predation ($\Delta P = 0.1$) based on its most recent predation history, as described in detail in section 4.2. In each predation loop, a predator is allowed to eat at most m (m = 4) prey. The results in Table 4.1 suggest that intensive predation is most likely to persist in an evolving community when the amount of CPU time that a predator acquires from each of its prey is in the range of 45% – 60%. To observe more examples of coevolution between predators and prey, I vary the amount of CPU energy transferred from a captured prey individual to its predator from 45% to 60% in 5% increments. The CPU time of a captured prey is reduced to 30% of its original value. The evolution of templates is investigated by the changes of their abundances in the soup over time: when a predator individual captures its prey, I record the predation template in that predator and its complementary template in the prey. Then I count the number of each predation template and its complementary template, respectively, in every million instructions executed. I focus on the major predation templates which are used by predators more than 2000 times during a simulation run of 1000 million instructions executed.

Results

Figure 4.13(a) exhibits the persistence of predation in an evolving community, measured by the number of predation events per million instructions executed. As I decompose those predation events based on the predation templates that predators use to capture prey, the evolutionary patterns of different predation templates emerge. As shown in Figure 4.13(b), template 0110 in the ancestor predators rapidly declines and disappears at the beginning of the simulation run. Then the soup is dominated by the predators with template 011, which are later replaced by the predators with template 001. The predators with template 000 thrive and coexist with those with template 001 during the period of 500 – 600 million instructions executed. Finally, the predators with template 100 appear and dominate the soup. More examples of the evolution of predation templates are shown in Figure 4.14, as I vary random seeds and the amount of CPU energy transferred from prey to predator populations.

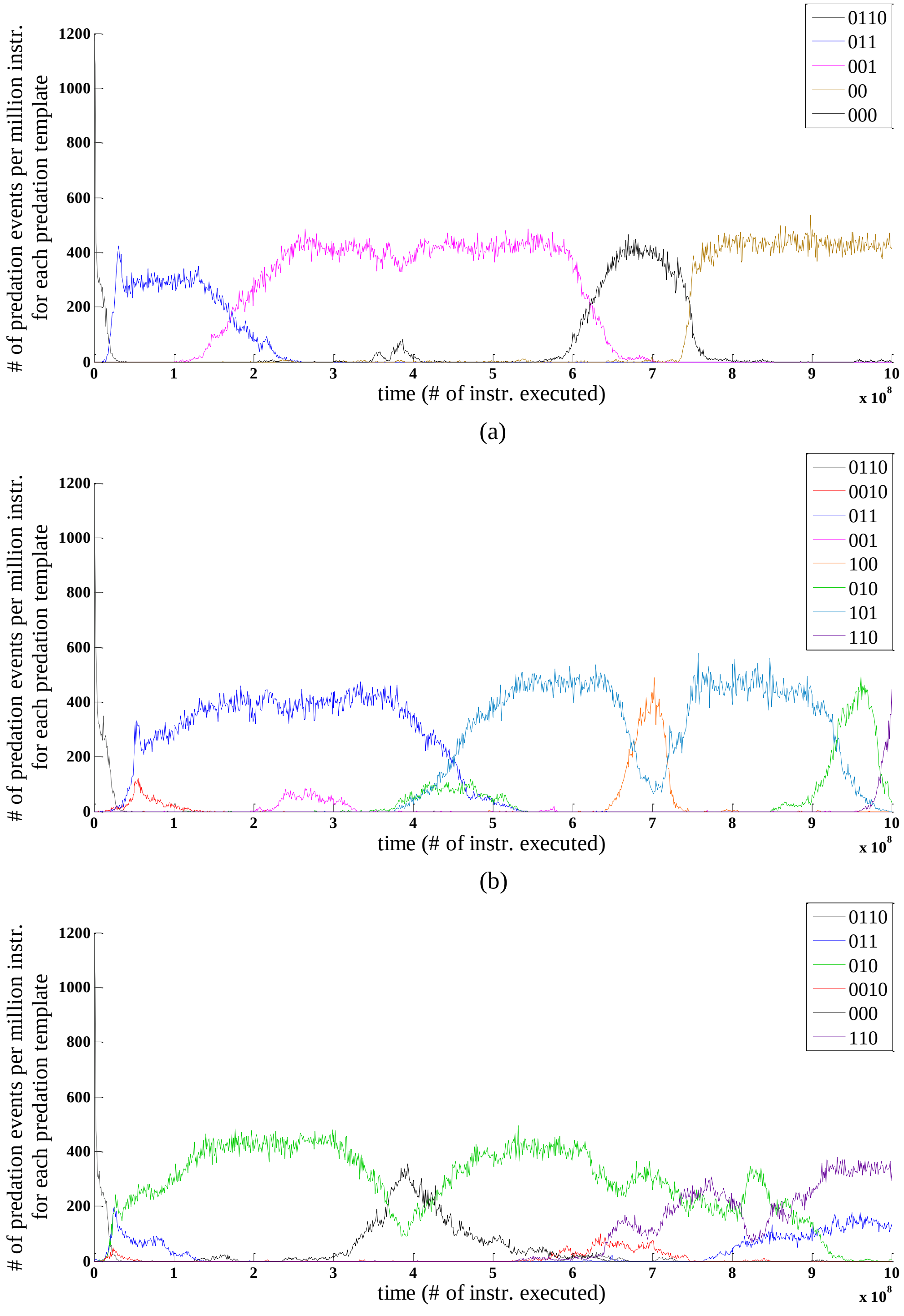


(a)

(b)

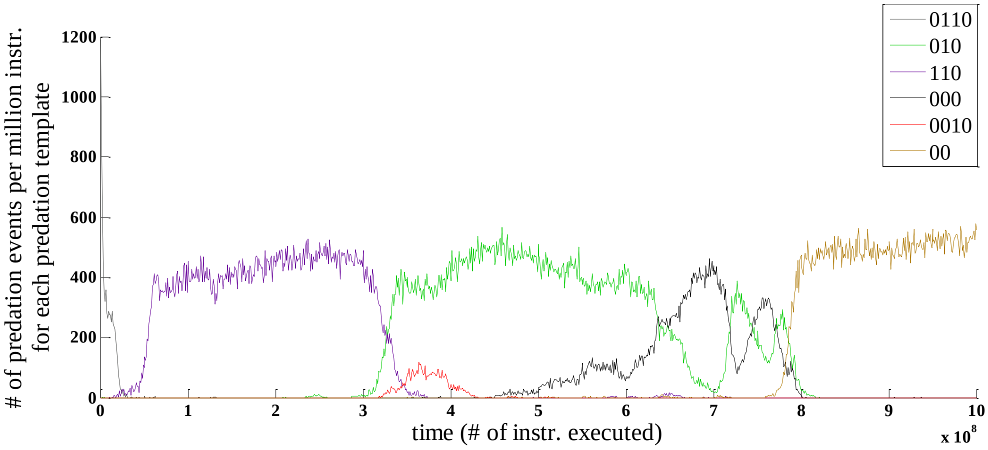
Figure 4.13: Evolution of predation templates in predators during a simulation run of 1000 million instructions executed. (a) Intensive predation stably persists in the evolving community. (b) Five different predation templates successively emerge during the evolutionary process.

Figure 4.14(a) exhibits a continuous transition of 5 predation templates as one template completely replaces another without much periods of coexistence of two templates. However, in Figure 4.14(b), despite the dominance of predation template 011, three templates (0010, 001 and 010) successively emerge and coexist with template 011 for a certain period of time.

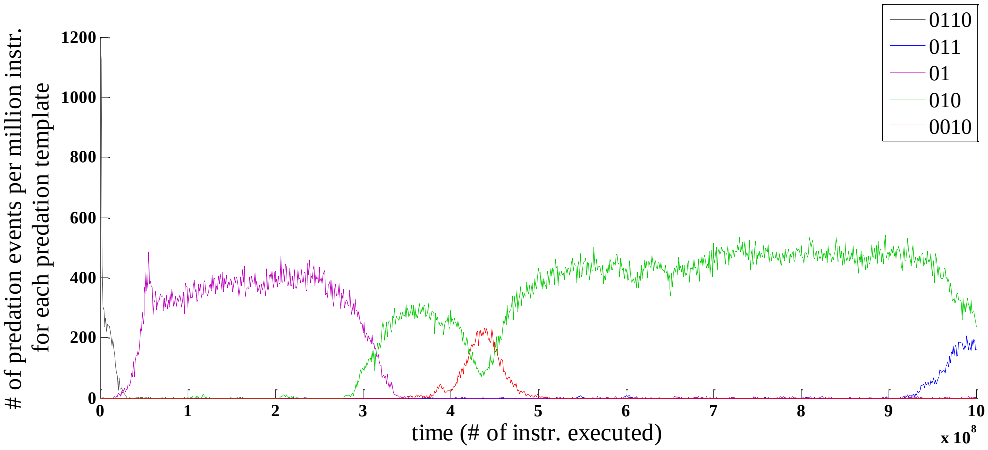


(c)

Figure 4.14: Evolution of predation templates in predators in an evolving ecological community. (a) Five different predation templates sequentially emerge, with one replacing another. (b) Eight different predation templates emerge and some templates coexist in the soup. (c) Six different predation templates emerge and multiple templates coexist in the soup, especially during the period of 650 – 900 million instructions executed.



(d)



(e)

Figure 4.14 (continue): Evolution of predation templates in predators in an evolving ecological community. (d) Six different predation templates emerge: some templates coexist in the soup and a more complex template emerges from simple templates. (e) Five different predation templates emerge and more complex templates evolve after the soup has been dominated by simple templates for a long period of time.

The more apparent coexistence of two predation templates occurs around 700 million instructions executed in Figure 4.14(b) and around 400 million instructions executed in Figure 4.14(c). During the period of 650 – 900 million instructions executed in Figure 4.14(c), three predation templates persistently coexist in the soup, although with the replacement of template 0010 by 011. Moreover, the two templates, 011 and 110, seem to reach a relatively stable coexistence at the end of the simulation run. This coexistence of multiple predation templates may indicate the differentiation of predators, with each using a different strategy to catch prey. Besides the sequential replacement of predation templates over time and the coexistence of two templates, 010 and 000, during the period of 550 – 780 million instructions executed, Figure 4.14(d) also shows that a more complicated predation template, 0010, could emerge and survive after the soup has been dominated by shorter predation templates for a long time. This potential to evolve longer predation templates is more clearly demonstrated in Figure 4.14(e): the ancestor predators are replaced by those with a very simple predation template, 01 and those predators dominate the soup for about 300 million instructions executed. However, this does not prevent the later emergence of longer, more sophisticated predation templates — the predators with template 010 appear and flourish, which completely removes those with template 01. Moreover, the predators with template 0010 reach a considerable population size and coexist with the predators with template 010 during the period of 400 – 480 million instructions executed. With a reasonable template size, predators are able to evolve a variety of different predation templates, which enriches the potential predation strategies that predators could develop to capture their constantly evolved prey.

The evolution of each complementary template in prey exhibits exactly the same pattern as its corresponding predation template in predators. For example, in Figure 4.13(b), the lines that represent the predation templates 0110, 011, 001, 000 and 100 also represent the complementary templates 1001, 100, 110, 111 and 011, respectively. Due to the mismatching of templates, prey may escape predation from previous predators, for example, the prey with complementary template 011 may not be found by the predators with predation template 000. However, it is also possible that the predators with predation template 000 and 100 may share the same type of prey with template 0111, by matching different parts of the template. In this case, the escape strategies may not be evolved in prey. On the other hand, the continuous evolution of predation templates in predators is presumably driven by the evolution of prey. Moreover, a detailed study on all the templates contained in prey genomes in the evolving community reveals that the overwhelming majority of the templates are shorter than 5 binary digits. Therefore, it is extremely unlikely that 3 or more different predation templates attack the same template in prey. As shown in Figure 4.13 – 4.14, 5 or 6 different predation templates, even 8 predation templates in Figure 4.14(b), have evolved in the soup during the simulation run of 1000 million instructions executed. This strongly suggests that prey may modify the template attacked by predators to escape predation, which promotes the changes in the predation template as predators try to capture the evolved prey by locating another template in prey.

4.5 Conclusion and Discussion

In this chapter, I investigate the influence of positive frequency-dependent predation on the genetic diversity in an evolving ecological community. The simulation results show that in the absence of predators, the community is repetitively dominated by a few genotypes, which causes the frequent, dramatic diversity loss. However, after a predator population with positive frequency-dependent behavior is introduced into the community and the intensive predation persists despite the constant changes in predator and prey genomes, the genetic diversity in the community significantly increases and steadily maintains a high level. The stable persistence of predation and the high genetic diversity robustly occur in the evolving community over a wide range of the amount of CPU energy that predators acquire from their prey. Therefore, in a simple, spatially homogeneous environment in Tierra, positive frequency-dependent predation may be a mechanism to support the coexistence of a variety of different genotypes in the community during an evolutionary process.

The evolution of an ecological community in Tierra has been studied under the selection favoring smaller genomes and under the size-neutral selection, respectively. In the first scenario, many intriguing ecological interactions among digital creatures spontaneously emerged throughout the simulation run but the sizes of digital creatures continuously shrunk over time. This reduction in sizes caused a severe loss of complex structures in genomes and eventually no significant genetic variants could be generated (Ray, 1991; Ray, 1994). In the second scenario, although smaller genomes emerged and thrived in the soup from time to time, most digital creatures in the community evolved towards larger sizes, which greatly decreased the number of creatures living in the soup and thus reduced the possible ecological interactions in the community (Ray, 1994). The simulation results presented in this chapter suggest that when a predator population with positive frequency-dependent behavior is introduced into the initial community, the evolution of the community under the size-neutral selection exhibits a completely different pattern — the sizes of digital creatures remain almost the same during the evolutionary process, which prevents the loss of genetic information in genomes as well as promoting rich ecological interactions by allowing abundant creatures to survive in the soup. Therefore, this community of predator and prey populations may evolve longer with interesting ecological dynamics.

The coevolution between prey and predator populations is observed in the digital community as I examine the genomes of digital creatures during the period of a dramatic decrease in the predation level: prey mutate the template attacked by predators and thus escape predation and predators modify their predation template to match another template in the newly evolved prey. Further simulations on the evolution of predation templates in predators and their complementary templates in prey suggest that the coevolution between prey and predators may continuously occur throughout the simulation run and predators, by maintaining a reasonable size of predation templates, may have the potential to evolve a variety of different predation strategies.

The current approach of, when a predator individual captures its prey, recording the predation template in the predator and its complementary template in the prey, clearly demonstrates that as new prey types continuously emerge in the soup, predators are capable to mutate their predation templates to exploit the recently evolved prey. However, because this approach focuses on the prey being captured, rather than those escaping predation, the evolution of escape strategies in prey may only be studied indirectly: the template in prey attacked by the current predators is not complementary to the predation template in the immediate ancestral predators. Moreover, the length of most templates in prey genomes is shorter than 5 binary digits, which restricts the chance that predators with different predation templates may share the same type of prey. Therefore, along with the successive occurrence of at least 5 predation templates in predators, the escape strategies in prey may be developed multiple times during a simulation run. In the future, I would like to directly observe when those escape strategies are evolved in prey by following the changes of the template in prey that is currently attacked by predators but disappears in the genomes of immediate descendant prey.

Chapter 5: Conclusions and Future Research

In this chapter, I summarize the main conclusions of my research work based on the simulation results presented in chapters 2, 3 and 4. Then I lay out two possible future research directions.

5.1 Conclusions

In this dissertation, I use the Tierra system to study the influence of positive frequency-dependent predation on the diversity of an ecological community. In order to introduce active predation into the Tierra system, I design a digital predator which is able to capture multiple digital prey individuals in its local area and obtain a certain amount of CPU energy from each prey. Unlike digital prey which constantly receive CPU energy from the system, digital predators acquire CPU energy for their survival and reproduction only through predation. This energy dependence of predators on their prey robustly generates a coupled cyclic oscillation between the predator and prey populations in Tierra, which has a pattern similar to the "Lotka-Volterra" cycle in nature. Therefore, the design of digital prey and predators may capture some essential properties of the predation relationship observed in nature and thus may be suitable to study predator-prey population dynamics.

With predation built into the Tierra system, I study two predation strategies that predators may use when encountering two different types of prey, namely, proportional predation and positive frequency-dependent predation. Proportional predation means that predators feed on different prey types in proportion to their relative abundances in the environment, that is, predators show no preference for one prey type over the other. Positive frequency-dependent predation means that predators consume disproportionately more of the common prey type than of the rare one, that is, predators strongly favor the abundant prey type. I block all the mutations in Tierra so that predators and prey interact with each other in an ecological scenario, without evolution. The simulation results show that in the absence of predation, two competing prey types could not coexist as the prey type that reproduces faster drives the other type to go extinct. When a predator population with proportional predation behavior is introduced into the prey populations, the two prey types coexist for a longer time but a stable coexistence of prey types is not achieved. However, when the prey populations are under the predation of a predator population with positive frequency-dependent behavior, the two prey types stably coexist and this coexistence is robust to the variations of the parameters that affect either the predation behavior of predators or the initial relative proportion of the two prey types in the environment. Further studies on the underlying mechanisms of the maintenance of prey diversity reveal that predators with positive frequency-dependent behavior consume disproportionately fewer individuals of a rare prey type, which facilitates the rapid population growth of that type. Meanwhile, those predators consume disproportionately more individuals of a common prey type and thus severely depress its population. Therefore, positive frequency-dependent predation provides a strong negative feedback regulation on the prey populations, which tends to equalize the abundances of different prey species and thus results in a stable persistence of prey diversity. Moreover, as the number of prey types increases from two to three, a predator population with positive frequency-dependent behavior also successfully maintains the stable coexistence of three prey species. Therefore, in contrast to previous studies which showed that the coexistence duration of two prey species dramatically decreased as the number of predator individuals increased and thus proposed that a population of frequency-dependent predators in nature may fail to maintain a stable coexistence of multiple prey species, the simulation results in this dissertation strongly support that positive frequency-dependent predation may be a reasonable mechanism to maintain the diversity of prey species in nature.

Besides their effects on maintaining prey diversity in a community, the two predation strategies are further examined from the perspective of enhancing the reproductive success of predators as they feed on two different types of prey. Because in Tierra, digital predators acquire the CPU energy from their prey, the availability of digital prey forms a dynamic biotic environment for predators. This biotic environment is constantly modified by predators and converges to different patterns as predators execute different predation strategies. For example, when the predators with proportional predation (PP-predator) dominate the predator population, one prey type becomes significantly more abundant than the other, which creates a favorable environment for the predators with positive frequency-dependent predation (PFDP-predator) and thus results in a rapid growth of the PFDP-predator population. On the other hand, when PFDP-predators dominate the predator population, the two prey types tend to approach a similar abundance, an environment which enhances the competitive ability of PP-predators. Therefore, the dominant predator type, by executing its predation strategy, changes the relative abundance of two prey types in such a way that favors, rather than depresses, the other predator type. This mutual support, rather than exclusion, allows the two predation strategies to be comparably competitive and thus the two predator competitors may coexist in the population or either one of them may go extinct. In addition to demonstrating that the fitness of predators highly depends on the biotic environment where they live, this ecological community composed of two predator types and two prey types also exhibits one of the most fundamental principles of competition — competition within the same trophic level is much more severe than that between different trophic levels.

Positive frequency-dependent predation, in addition to being a mechanism to maintain prey diversity in an ecological scenario, is also predicted to have the potential to increase community diversity during evolution. However, very little research has been conducted to study this prediction. After observing that a predator population with positive frequency-dependent behavior successfully maintains a stable coexistence of multiple competing prey types in an ecological setup in Tierra, I turn on various types of mutations to allow digital prey and predators to evolve freely and investigate the changes of community diversity by the populations of frequency-dependent predators in an evolutionary scenario. The simulation results show that in the absence of predators, the community is repetitively dominated by a few genotypes, which causes frequent, dramatic diversity loss. However, with the introduction of predators which generate intensive predation in an evolving ecological community, many prey and predator genotypes persistently flourish in the soup and thus the genetic diversity in the community rapidly achieves and steadily maintains a relatively high level. This increase and maintenance of genetic diversity by frequency-dependent predators robustly occurs over a wide range of the amount of CPU energy transferred from prey to predator populations. Therefore, those simulation results strongly suggest that positive frequency-dependent predation may be a mechanism to support the coexistence of a variety of different genotypes in the community during an evolutionary process. In addition, unlike previous studies in which the sizes of digital creatures in an evolving community either continuously shrunk or continuously increased, in the current community composed of prey and predator populations, the sizes of digital creatures remain almost the same during evolution, which prevents the loss of genetic information in genomes as well as promoting rich ecological interactions among abundant coexisting creatures. Therefore, this community of prey and predators may maintain interesting ecological dynamics through longer periods of evolution.

One of the intriguing ecological interactions present in the evolving digital community is the continuous coevolution between predator and prey populations: prey mutate the template attacked by predators and thus escape predation and predators modify their predation template to match another template in the recently evolved prey and thus exploit new available food sources. These reciprocal evolutionary adaptations of prey and predators consistently develop multiple times during a simulation run. In the future, I would like to study the coevolutionary dynamics in more detail by examining the exact moments that coevolution occurs and the changes of the templates in prey and predator genomes that cause the occurrence of coevolution.

5.2 Future Research

5.2.1 Coevolution between Predation Templates in Predators and Template Resources in Prey

As shown in Figure 2.2, in addition to the predation marker, a prey individual contains several other templates which specify its beginning and ending locations and direct the reproduction loop and the copy procedure in its genome. When any one of those templates (or a shorter template contained in it) is complementary to the predation template in a predator, this prey could be potentially found by the predator. Therefore, all the templates in prey genomes may be viewed as available food sources for predators to exploit and those food sources consistently evolve with prey populations.

To study the evolutionary relationship between predators and their food sources, I can record the template information of each creature that ever survives in the soup. For example, if the creature is a predator individual, I record its predation template and the complementary template that it finds in its prey; if the creature is a prey individual, I record all the templates in its genome. By acquiring complete information on all the templates in prey genomes, I may observe the period of existence of each template in prey in the soup and thus may clearly detect when escape strategies evolve in prey. For example, if none of the templates (and the shorter templates contained within them) in major prey genomes are complementary to the predation templates which have just become extinct, it may strongly suggest that selection favors the mutated variations of prey templates, which leads to a dramatic decrease in frequency of prey templates that match the predation templates in predators.

Furthermore, with rich information on the templates in prey, I may also study the patterns of predation strategies developed in predators, such as, are predators more likely to attack the most abundant templates in prey populations? Could predators differentiate, with each specializing on a different food source (that is, could several predation templates coexist in the soup, with each attacking a different type of prey)? Could a predator type feed on several food sources (that is, could a predator evolve one predation template to match the templates in different types of prey)? In contrast to previous studies in which digital creatures were provided with several predefined, fixed food sources (Cooper and Ofria, 2002; Chow *et al*., 2004), here, the evolution of feeding strategies is examined when predators are facing a dynamic environment in which the available prey types continuously change over time and prey types may also constantly develop adaptations to escape predation. Therefore, this research may provide better insight into the survival of predators in their ever-changing biotic environment in nature.

5.2.2 A Food Chain with More Than Two Layers

In the current design in which predators are allowed to eat prey but not other predators, the food chain in Tierra has only two layers, a prey layer and a predator layer. One of the future research directions may be to build a longer, more complicated food chain by allowing predation among predators: besides capturing prey, larger predators may also feed on smaller predators, for example, a predator genotype 100aaa may consume a predator genotype 85aaa, by obtaining a certain amount of CPU time from them and reducing the CPU time of a captured predator to a low level. Similar to the scenario in nature in which the creatures that feed on both plants and herbivores may acquire plants more easily than catch herbivores, the larger predators in Tierra may have a higher chance to capture prey than to capture smaller predators. This design of allowing predation among predators increases the complexity of the internal structure of an ecological community and I would like to explore whether a high level of genetic diversity could be achieved and stably maintained during evolution in this more sophisticated community. Furthermore, by comparing the genetic diversity of two communities, one in which predators are only allowed to feed on prey and the other in which larger predators are allowed to consume prey and smaller predators, I may be able to study whether an increase in the complexity of ecological interactions among creatures could lead to a higher genetic diversity in the community.

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Appendices

Appendix A: Assembler Source Code for the Digital Predator

```
genotype:  100 aaa    genetic:  0,100    parent genotype:  human
ploidy:  1    track:  0
; comments:  the predator ancestor, written by human

CODE

nop1       ; 01      0   beginning marker
nop1       ; 01      1   beginning marker
nop1       ; 01      2   beginning marker
nop1       ; 01      3   beginning marker
zero       ; 04      4   put zero in cx
not0       ; 02      5   put 1 in first bit of [cx]
shl        ; 03      6   shift left [cx] ([cx] = 2)
shl        ; 03      7   shift left [cx] ([cx] = 4)
movDC      ; 18      8   move [cx] to [dx] ([dx] = 4)
adrb       ; 1c      9   get (backward) address of beginning marker -> ax
nop0       ; 00     10   complement to beginning marker
nop0       ; 00     11   complement to beginning marker
nop0       ; 00     12   complement to beginning marker
nop0       ; 00     13   complement to beginning marker
subAAC     ; 07     14   subtract [cx] from [ax], result in [ax]
movBA      ; 19     15   move [ax] to [bx], bx now contains start address of mother
adrf       ; 1d     16   get (forward) address of end marker -> ax
nop0       ; 00     17   complement to end marker
nop0       ; 00     18   complement to end marker
nop0       ; 00     19   complement to end marker
nop1       ; 01     20   complement to end marker
incA       ; 08     21   increment [ax], to include dummy instruction at end
subCAB     ; 06     22   subtract [bx] from [ax] to get size, result -> cx
nop1       ; 01     23   reproduction loop marker
nop1       ; 01     24   reproduction loop marker
nop0       ; 00     25   reproduction loop marker
nop1       ; 01     26   reproduction loop marker
ifz        ; 05     27   dummy instruction to separate templates
ifz        ; 05     28   dummy instruction to separate templates
nop0       ; 00     29   predation loop complement
nop1       ; 01     30   predation loop complement
nop1       ; 01     31   predation loop complement
nop1       ; 01     32   predation loop complement
adrp       ; 1b     33   search for complementary predation marker in another organism
nop0       ; 00     34   predation marker
nop1       ; 01     35   predation marker
nop1       ; 01     36   predation marker
nop0       ; 00     37   predation marker
predat     ; 14     38   get prey's time slice
ifp        ; 15     39   if exit predation loop, skip next instruction
jmpo       ; 13     40   jump to template below (predation loop)
nop1       ; 01     41   predation loop template
nop0       ; 00     42   predation loop template
nop0       ; 00     43   predation loop template
nop0       ; 00     44   predation loop template
mal        ; 1e     45   allocate space ([cx]) for daughter, address to ax
```

```
call      ; 16     46   call template below (copy procedure)
nop0      ; 00     47   copy procedure complement
nop0      ; 00     48   copy procedure complement
nop1      ; 01     49   copy procedure complement
nop1      ; 01     50   copy procedure complement
divide    ; 1f     51   release mature daughter cell
jmpo      ; 13     52   jump to template below (reproduction loop)
nop0      ; 00     53   reproduction loop complement
nop0      ; 00     54   reproduction loop complement
nop1      ; 01     55   reproduction loop complement
nop0      ; 00     56   reproduction loop complement
ifz       ; 05     57   dummy instruction to separate templates
ifz       ; 05     58   dummy instruction to separate templates
nop1      ; 01     59   copy procedure template
nop1      ; 01     60   copy procedure template
nop0      ; 00     61   copy procedure template
nop0      ; 00     62   copy procedure template
pushA     ; 0c     63   push [ax] onto stack
pushB     ; 0d     64   push [bx] onto stack
pushC     ; 0e     65   push [cx] onto stack
nop1      ; 01     66   copy loop template
nop0      ; 00     67   copy loop template
nop1      ; 01     68   copy loop template
nop0      ; 00     69   copy loop template
movii     ; 1a     70   move the instruction at [bx] to [ax] (copy one instruction)
decC      ; 0a     71   decrement [cx] (size)
ifz       ; 05     72   if [cx] == 0 perform next instruction, otherwise skip it
jmpo      ; 13     73   jump to template below (copy procedure exit)
nop0      ; 00     74   copy procedure exit complement
nop1      ; 01     75   copy procedure exit complement
nop0      ; 00     76   copy procedure exit complement
nop0      ; 00     77   copy procedure exit complement
incA      ; 08     78   increment [ax] (address in daughter to copy to)
incB      ; 09     79   increment [bx] (address in mother to copy from)
jmpo      ; 13     80   bidirectional jump to template below (copy loop)
nop0      ; 00     81   copy loop complement
nop1      ; 01     82   copy loop complement
nop0      ; 00     83   copy loop complement
nop1      ; 01     84   copy loop complement
ifz       ; 05     85   dummy instruction to separate templates
ifz       ; 05     86   dummy instruction to separate templates
nop1      ; 01     87   copy procedure exit template
nop0      ; 00     88   copy procedure exit template
nop1      ; 01     89   copy procedure exit template
nop1      ; 01     90   copy procedure exit template
popC      ; 12     91   pop [cx] off stack (size)
popB      ; 11     92   pop [bx] off stack (start address of mother)
popA      ; 10     93   pop [ax] off stack (start address of daughter)
ret       ; 17     94   return from copy procedure
nop1      ; 01     95   end template
nop1      ; 01     96   end template
nop1      ; 01     97   end template
nop0      ; 00     98   end template
ifz       ; 05     99   dummy instruction to separate creature
```

Appendix B: Assembler Source Code for the Digital Prey

(a) Type-A prey (86 instructions long)

```
genotype:  0086aaa    genetic:  0,86    parent genotype:  0666god
ploidy:  1    track:  0
; comments:  the prey ancestor, written by a human

CODE

nop1      ; 01     0   beginning marker
nop1      ; 01     1   beginning marker
nop1      ; 01     2   beginning marker
nop1      ; 01     3   beginning marker
zero      ; 04     4   put zero in cx
not0      ; 02     5   put 1 in first bit of cx
shl       ; 03     6   shift left cx (cx = 2)
shl       ; 03     7   shift left cx (cx = 4)
movDC     ; 18     8   move cx to dx (dx = 4)
adrb      ; 1c     9   get (backward) address of beginning marker -> ax
nop0      ; 00    10   complement to beginning marker
nop0      ; 00    11   complement to beginning marker
nop0      ; 00    12   complement to beginning marker
nop0      ; 00    13   complement to beginning marker
subAAC    ; 07    14   subtract cx from ax, result in ax
movBA     ; 19    15   move ax to bx, bx now contains start address of mother
adrf      ; 1d    16   get (forward) address of end marker -> ax
nop0      ; 00    17   complement to end marker
nop0      ; 00    18   complement to end marker
nop0      ; 00    19   complement to end marker
nop1      ; 01    20   complement to end marker
incA      ; 08    21   increment ax, to include dummy instruction at end
subCAB    ; 06    22   subtract bx from ax to get size, result in cx
adrp      ; 1b    23   search predation marker in another creature -> ax
nop1      ; 01    24   predation marker
nop0      ; 00    25   predation marker
nop0      ; 00    26   predation marker
nop1      ; 01    27   predation marker
ifz       ; 05    28   dummy instruction to separate templates
nop1      ; 01    29   reproduction loop marker
nop1      ; 01    30   reproduction loop marker
nop0      ; 00    31   reproduction loop marker
nop1      ; 01    32   reproduction loop marker
mal       ; 1e    33   allocate space (cx) for daughter, address to ax
call      ; 16    34   call template below (copy procedure)
nop0      ; 00    35   copy procedure complement
nop0      ; 00    36   copy procedure complement
nop1      ; 01    37   copy procedure complement
nop1      ; 01    38   copy procedure complement
divide    ; 1f    39   create independent daughter cell
jmpo      ; 13    40   jump to template below (reproduction loop)
nop0      ; 00    41   reproduction loop complement
nop0      ; 00    42   reproduction loop complement
nop1      ; 01    43   reproduction loop complement
nop0      ; 00    44   reproduction loop complement
ifz       ; 05    45   dummy instruction to separate templates
```

```
nop1     ; 01    46  copy procedure template
nop1     ; 01    47  copy procedure template
nop0     ; 00    48  copy procedure template
nop0     ; 00    49  copy procedure template
pushA    ; 0c    50  push ax onto stack
pushB    ; 0d    51  push bx onto stack
pushC    ; 0e    52  push cx onto stack
nop1     ; 01    53  copy loop template
nop0     ; 00    54  copy loop template
nop1     ; 01    55  copy loop template
nop0     ; 00    56  copy loop template
movii    ; 1a    57  move contents of [bx] to [ax] (copy one instruction)
decC     ; 0a    58  decrement cx (size)
ifz      ; 05    59  if cx == 0 perform next instruction, otherwise skip it
jmpo     ; 13    60  jump to template below (copy procedure exit)
nop0     ; 00    61  copy procedure exit complement
nop1     ; 01    62  copy procedure exit complement
nop0     ; 00    63  copy procedure exit complement
nop0     ; 00    64  copy procedure exit complement
incA     ; 08    65  increment ax (address in daughter to copy to)
incB     ; 09    66  increment bx (address in mother to copy from)
jmpo     ; 13    67  bidirectional jump to template below (copy loop)
nop0     ; 00    68  copy loop complement
nop1     ; 01    69  copy loop complement
nop0     ; 00    70  copy loop complement
nop1     ; 01    71  copy loop complement
ifz      ; 05    72  this is a dummy instruction to separate templates
nop1     ; 01    73  copy procedure exit template
nop0     ; 00    74  copy procedure exit template
nop1     ; 01    75  copy procedure exit template
nop1     ; 01    76  copy procedure exit template
popC     ; 12    77  pop cx off stack (size)
popB     ; 11    78  pop bx off stack (start address of mother)
popA     ; 10    79  pop ax off stack (start address of daughter)
ret      ; 17    80  return from copy procedure
nop1     ; 01    81  end template
nop1     ; 01    82  end template
nop1     ; 01    83  end template
nop0     ; 00    84  end template
ifz      ; 05    85  dummy instruction to separate creature
```

(b) Type-B prey (96 instructions long)

```
genotype:  0096aaa    genetic:  0,96    parent genotype: 0668god
ploidy:  1    track:  0
; comments:  the prey ancestor, written by a human

CODE

nop1     ; 01     0  beginning marker
nop1     ; 01     1  beginning marker
nop1     ; 01     2  beginning marker
nop1     ; 01     3  beginning marker
zero     ; 04     4  put zero in cx
not0     ; 02     5  put 1 in first bit of cx
shl      ; 03     6  shift left cx (cx = 2)
```

```
shl         ; 03      7   shift left cx (cx = 4)
movDC       ; 18      8   move cx to dx (dx = 4)
adrb        ; 1c      9   get (backward) address of beginning marker -> ax
nop0        ; 00     10   complement to beginning marker
nop0        ; 00     11   complement to beginning marker
nop0        ; 00     12   complement to beginning marker
nop0        ; 00     13   complement to beginning marker
subAAC      ; 07     14   subtract cx from ax, result in ax
movBA       ; 19     15   move ax to bx, bx now contains start address of mother
adrf        ; 1d     16   get (forward) address of end marker -> ax
nop0        ; 00     17   complement to end marker
nop0        ; 00     18   complement to end marker
nop0        ; 00     19   complement to end marker
nop1        ; 01     20   complement to end marker
incA        ; 08     21   increment ax, to include dummy instruction at end
subCAB      ; 06     22   subtract bx from ax to get size, result in cx
nop1        ; 01     23   reproduction loop marker
nop1        ; 01     24   reproduction loop marker
nop0        ; 00     25   reproduction loop marker
nop1        ; 01     26   reproduction loop marker
ifz         ; 05     27   dummy instruction to separate templates
nop0        ; 00     28   predation loop complement
nop1        ; 01     29   predation loop complement
nop1        ; 01     30   predation loop complement
nop1        ; 01     31   predation loop complement
adrp        ; 1b     32   search for predation template in another organism
nop1        ; 01     33   predation marker
nop0        ; 00     34   predation marker
nop0        ; 00     35   predation marker
nop1        ; 01     36   predation marker
ifp         ; 15     37  if exit predation loop, skip next instruction
jmpo        ; 13     38   jump to template below (predation loop)
nop1        ; 01     39   predation loop template
nop0        ; 00     40   predation loop template
nop0        ; 00     41   predation loop template
nop0        ; 00     42   predation loop tmeplate
mal         ; 1e     43   allocate space (cx) for daughter, address to ax
call        ; 16     44   call template below (copy procedure)
nop0        ; 00     45   copy procedure complement
nop0        ; 00     46   copy procedure complement
nop1        ; 01     47   copy procedure complement
nop1        ; 01     48   copy procedure complement
divide      ; 1f     49   create independent daughter cell
jmpo        ; 13     50   jump to template below (reproduction loop)
nop0        ; 00     51   reproduction loop complement
nop0        ; 00     52   reproduction loop complement
nop1        ; 01     53   reproduction loop complement
nop0        ; 00     54   reproduction loop complement
ifz         ; 05     55   dummy instruction to separate templates
nop1        ; 01     56   copy procedure template
nop1        ; 01     57   copy procedure template
nop0        ; 00     58   copy procedure template
nop0        ; 00     59   copy procedure template
pushA       ; 0c     60   push ax onto stack
pushB       ; 0d     61   push bx onto stack
pushC       ; 0e     62   push cx onto stack
```

```
nop1     ; 01    63   copy loop template
nop0     ; 00    64   copy loop template
nop1     ; 01    65   copy loop template
nop0     ; 00    66   copy loop template
movii    ; 1a    67   move contents of [bx] to [ax] (copy one instruction)
decC     ; 0a    68   decrement cx (size)
ifz      ; 05    69   if cx == 0 perform next instruction, otherwise skip it
jmpo     ; 13    70   jump to template below (copy procedure exit)
nop0     ; 00    71   copy procedure exit complement
nop1     ; 01    72   copy procedure exit complement
nop0     ; 00    73   copy procedure exit complement
nop0     ; 00    74   copy procedure exit complement
incA     ; 08    75   increment ax (address in daughter to copy to)
incB     ; 09    76   increment bx (address in mother to copy from)
jmpo     ; 13    77   bidirectional jump to template below (copy loop)
nop0     ; 00    78   copy loop complement
nop1     ; 01    79   copy loop complement
nop0     ; 00    80   copy loop complement
nop1     ; 01    81   copy loop complement
ifz      ; 05    82   dummy instruction to separate templates
nop1     ; 01    83   copy procedure exit template
nop0     ; 00    84   copy procedure exit template
nop1     ; 01    85   copy procedure exit template
nop1     ; 01    86   copy procedure exit template
popC     ; 12    87   pop cx off stack (size)
popB     ; 11    88   pop bx off stack (start address of mother)
popA     ; 10    89   pop ax off stack (start address of daughter)
ret      ; 17    90   return from copy procedure
nop1     ; 01    91   end template
nop1     ; 01    92   end template
nop1     ; 01    93   end template
nop0     ; 00    94   end template
ifz      ; 05    95   dummy instruction to separate creature
```

(c) Type-C prey (90 instructions long)

```
genotype:  0090aaa    genetic:  0,90    parent genotype:  0666god
ploidy:  1    track:  0
; comments:  the prey ancestor, written by a human

CODE

nop1     ; 01     0   beginning marker
nop1     ; 01     1   beginning marker
nop1     ; 01     2   beginning marker
nop1     ; 01     3   beginning marker
zero     ; 04     4   put zero in cx
not0     ; 02     5   put 1 in first bit of cx
shl      ; 03     6   shift left cx (cx = 2)
shl      ; 03     7   shift left cx (cx = 4)
movDC    ; 18     8   move cx to dx (dx = 4)
adrb     ; 1c     9   get (backward) address of beginning marker -> ax
nop0     ; 00    10   complement to beginning marker
nop0     ; 00    11   complement to beginning marker
nop0     ; 00    12   complement to beginning marker
nop0     ; 00    13   complement to beginning marker
```

```
subAAC  ; 07    14  subtract cx from ax, result in ax
movBA   ; 19    15  move ax to bx, bx now contains start address of mother
adrf    ; 1d    16  get (forward) address of end marker -> ax
nop0    ; 00    17  complement to end marker
nop0    ; 00    18  complement to end marker
nop0    ; 00    19  complement to end marker
nop1    ; 01    20  complement to end marker
incA    ; 08    21  increment ax, to include dummy instruction at end
subCAB  ; 06    22  subtract bx from ax to get size, result in cx
adrp    ; 1b    23  search predation marker in another creature -> ax
nop1    ; 01    24  predation marker
nop0    ; 00    25  predation marker
nop0    ; 00    26  predation marker
nop1    ; 01    27  predation marker
ifz     ; 05    28  dummy instruction to separate templates
nop1    ; 01    29  reproduction loop marker
nop1    ; 01    30  reproduction loop marker
nop0    ; 00    31  reproduction loop marker
nop1    ; 01    32  reproduction loop marker
mal     ; 1e    33  allocate space (cx) for daughter, address to ax
call    ; 16    34  call template below (copy procedure)
nop0    ; 00    35  copy procedure complement
nop0    ; 00    36  copy procedure complement
nop1    ; 01    37  copy procedure complement
nop1    ; 01    38  copy procedure complement
divide  ; 1f    39  create independent daughter cell
jmpo    ; 13    40  jump to template below (reproduction loop)
nop0    ; 00    41  reproduction loop complement
nop0    ; 00    42  reproduction loop complement
nop1    ; 01    43  reproduction loop complement
nop0    ; 00    44  reproduction loop complement
ifz     ; 05    45  dummy instruction to separate templates
ifz     ; 05    46  dummy instruction to separate templates
ifz     ; 05    47  dummy instruction to separate templates
nop1    ; 01    48  copy procedure template
nop1    ; 01    49  copy procedure template
nop0    ; 00    50  copy procedure template
nop0    ; 00    51  copy procedure template
pushA   ; 0c    52  push ax onto stack
pushB   ; 0d    53  push bx onto stack
pushC   ; 0e    54  push cx onto stack
nop1    ; 01    55  copy loop template
nop0    ; 00    56  copy loop template
nop1    ; 01    57  copy loop template
nop0    ; 00    58  copy loop template
movii   ; 1a    59  move contents of [bx] to [ax] (copy one instruction)
decC    ; 0a    60  decrement cx (size)
ifz     ; 05    61  if cx == 0 perform next instruction, otherwise skip it
jmpo    ; 13    62  jump to template below (copy procedure exit)
nop0    ; 00    63  copy procedure exit complement
nop1    ; 01    64  copy procedure exit complement
nop0    ; 00    65  copy procedure exit complement
nop0    ; 00    66  copy procedure exit complement
incA    ; 08    67  increment ax (address in daughter to copy to)
incB    ; 09    68  increment bx (address in mother to copy from)
jmpo    ; 13    69  bidirectional jump to template below (copy loop)
```

```
nop0      ; 00     70   copy loop complement
nop1      ; 01     71   copy loop complement
nop0      ; 00     72   copy loop complement
nop1      ; 01     73   copy loop complement
ifz       ; 05     74   this is a dummy instruction to separate templates
ifz       ; 05     75   this is a dummy instruction to separate templates
ifz       ; 05     76   this is a dummy instruction to separate templates
nop1      ; 01     77   copy procedure exit template
nop0      ; 00     78   copy procedure exit template
nop1      ; 01     79   copy procedure exit template
nop1      ; 01     80   copy procedure exit template
popC      ; 12     81   pop cx off stack (size)
popB      ; 11     82   pop bx off stack (start address of mother)
popA      ; 10     83   pop ax off stack (start address of daughter)
ret       ; 17     84   return from copy procedure
nop1      ; 01     85   end template
nop1      ; 01     86   end template
nop1      ; 01     87   end template
nop0      ; 00     88   end template
ifz       ; 05     89   dummy instruction to separate creature
```