Maintenance of Species Diversity by Predation in the Tierra System

Jie Shao and Thomas S. Ray

Department of Zoology, University of Oklahoma, Norman, Oklahoma 73019, USA
jshao@ou.edu

Abstract

One of the ecological theories has proposed that high species diversity can be maintained by predation, and several experimental studies showed that a few predator individuals with positive frequency-dependent behavior were able to maintain the coexistence of two prey types. However, in a natural environment, when a single predator species regulates the diversity of prey species, it is likely to be a full population of predators, not just a few individual predators. The role of a predator population in maintaining species diversity has not been carefully investigated in laboratory experiments but has been seriously questioned by computer simulations. In this paper, we introduce predation into the Tierra system and the dynamic relationship between prey and predator populations is examined. The robust appearance of the "Lotka-Volterra-like" cycle in Tierra suggests that the digital creatures may follow the same fundamental principles as their organic counterparts. Moreover, when each predator in a large predator population searches for prey in its neighboring area and performs positive frequency-dependent predation based on local prey abundance, a global pattern of coexistence of prey species emerges. This suggests that positive frequency-dependent predation may be a reasonable mechanism to maintain species diversity in nature.

Introduction

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 poorly understood. One of the ecological theories has proposed that high species diversity can be maintained by predation. A few dominant species grow rapidly and crowd out many of the other species, but this reduction of species diversity due to competitive exclusion can be avoided by the presence of predators. Predators limit the populations of dominant species and thus more resources become available to support the survival of other prey species. Several experimental studies demonstrated that the presence of predator species prevented the diversity of prey species from declining (Paine, 1974; Morin, 1981). At the same time, the coexistence of multiple prey species provides more feeding options for predators. To avoid competing for the same resource, predator species may specialize to adapt to different prey types (Stanley, 1973). Therefore, predation may facilitate the increase of diversity in both prey and predator species.

Further experimental studies on predation mechanisms revealed that a predator may switch among different prey types in response to their abundance and positive frequency-dependent predation was executed by predators. This means that predators disproportionately consumed the more abundant prey type, maintaining the coexistence of two prey types (Allen, 1988; Murdoch, 1969; Murdoch et al., 1975). Although only a few predator individuals were used to conduct the experiments, based on the assumption that a population would have an equivalent behavior as a few individuals, it was concluded that a population of such predators in a natural environment would also be able to maintain the diversity of prey species. But this conclusion was seriously questioned by computer simulations of an individual-based model which showed that over a variety of parameter settings, the duration of the coexistence of two prey phenotypes dramatically decreased as the number of predator individuals increased (Merilaita, 2006).

In this study, we conduct simulations in the well-known Tierra system to explore the predation mechanism for maintaining species diversity in an ecological scenario. In Tierra, self-replicating computer programs continuously evolve in a resource-limiting environment (Ray, 1991). This system of Darwinian evolution inside a computer, besides being applied to many evolutionary challenges (Wilke and Adami, 2002), can also be used to study intriguing ecological problems when we set all the mutation rates to zero. With fast generation times (on the order of seconds) and precise measurements, the ecological processes in Tierra can be accurately repeated and thoroughly examined under various parameter settings. Therefore, the Tierra system provides an alternative but powerful experimental method to explore the general principles in ecology.

In order to investigate the maintenance of species diversity by positive frequency-dependent predation, we first design a digital predator which is able to capture multiple prey and acquire energy (CPU time) from them. Then we evaluate our design by comparing the dynamic relationship between the prey and predator populations in Tierra with that in nature. The simulation results show that a cyclic oscillation, similar to the "Lotka-Volterra" cycle (a fundamental pattern displayed by natural prey and predator populations), robustly appears in Tierra. Next, we apply a set of simple rules to specify the behavior of digital predators as they encounter different prey types and verify that the predation in Tierra is essentially the same as positive frequency-dependent behavior exhibited by real predators in laboratory experiments (Merilaita, 2006). Then we allow each digital predator to search for prey in its neighboring area and perform predation based on local prey abundance. We then explore the conditions under which the

presence of a predator population supports the coexistence of two different types of prey. This mechanism of positive frequency-dependent predation for the persistence of species diversity is further examined as we increase the number of prey species from two to three.

Methods

The 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 implementation (Ray, 1991). However, the predator has an additional predation loop inserted before reproduction. This loop is used to search for multiple prey in the predator's local area. If the predation template in a prey is complementary to the one in the predator and that prey has not been eaten by other predators yet, the predator eats that prey, that is, a certain percent of the prey's CPU time is delivered to the predator and the prey's CPU time is reduced to a small amount. 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. After the predator acquires energy (CPU time) from its prey, 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
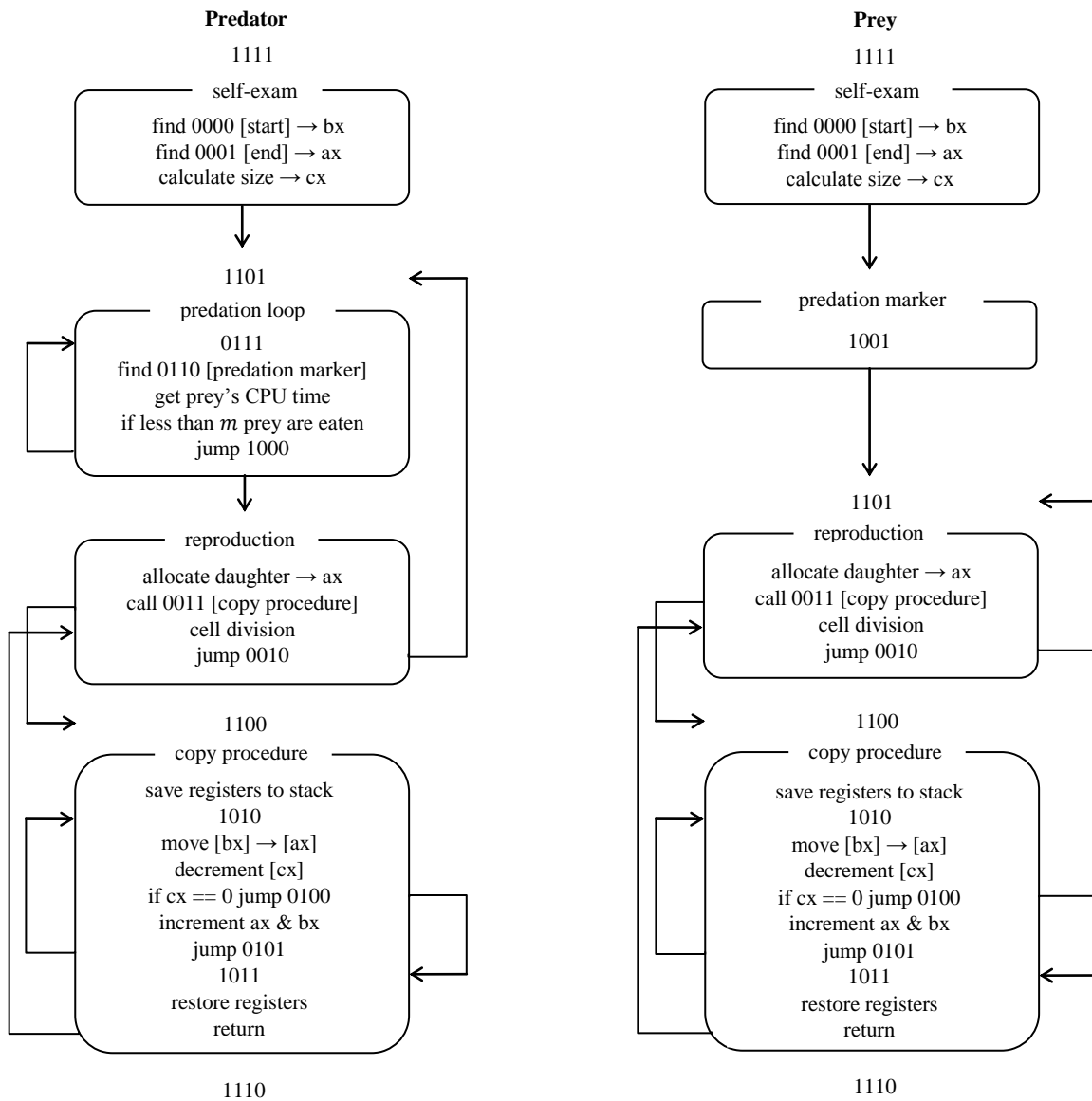
FIGURE 1 Algorithmic flow chart for the predator and prey in the Tierra system. The predation template in the predator (0110) is complementary to the one in the prey (1001), which allows the predator to catch the prey and acquire CPU time from it.

then reproduction repeats until death (Figure 1). We also design two types of prey which are the same as the ancestral creature in the original Tierra system except for the predation template before the reproduction loop (Figure 1). The two prey types differ only in their genome lengths and the predator can detect both of them by matching the predation marker. A type-A prey with the length of 86 instructions reproduces faster than a type-B prey with the length of 96 instructions. The Tierra system assigns a standard amount of CPU time to each prey, but a predator receives only a very small amount of CPU time from the system which supports the predator to execute its first predation loop to try to capture a prey. If the predator fails to capture a prey, it does not have CPU time to execute more instructions. Therefore, predators have to catch prey to obtain energy for survival and reproduction.

The dynamics of the interactions of the predators and prey are examined in ecological simulations, in which Tierra is run without mutation. We seed the soup 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 and it receives 15% of CPU time from each prey. The amount of CPU time of a captured prey is reduced to 15% of its original value. In a simulation run, we 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. Then we 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. To confirm that the dynamic pattern between the predator and its prey population results from the predation, rather than random fluctuations in the Tierra system, we design a type-A* prey which shares the same genome length as a type-A prey. Because each prey receives, on the average, the same amount of CPU time from the system, the two prey types with the same length theoretically have the same reproduction rate and thus their population sizes should be maintained at a constant level. Therefore, the variations of the population sizes of type-A and type-A* prey reflect the randomness in the system. We 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. Then we compare the population dynamics between type-A and type-A* prey with those between type-A prey and predators.

To investigate positive frequency-dependent behavior of a predator population, we apply the following rules to each predator as it encounters two types of prey in its neighborhood.
(1) Initially, each predator is assigned an equal probability to eat type-A and type-B prey when encountered, that is
$$P_A = P_B = 0.5$$
(2) If the predator eats a type-A prey, its probability to eat type-A prey is increased by ΔP and to eat type-B prey is decreased by ΔP, that is,
$$P_A = P_A + \Delta P \qquad P_B = P_B - \Delta P$$
(3) If, instead, the predator eats a type-B prey, its probability to eat type-A prey is decreased by ΔP and to eat type-B prey is increased by ΔP, that is,
$$P_A = P_A - \Delta P \qquad P_B = P_B + \Delta P$$

(4) All eating 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 simulation results reported in this paper are obtained when $\Delta P = 0.1, P_{min} = 0$ and $P_{max} = 1$, if not otherwise mentioned.

In a laboratory experiment, positive frequency-dependent behavior of a predator is revealed by computing the percentage of one type of prey in the predator's diet as the percentage of that prey type in environment increases from 0 to 100%. In our simulations, the behavior of a predator population in which each predator obeys the above predation rules is examined through the following setup: we run nine separate simulations and in each simulation, we seed the soup with 3000 prey individuals and 300 predator individuals. In each predation loop, a predator can eat at most m ($m = 4$) prey and acquire 35% of 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 nine simulations is the 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, we should calculate the percentage of type-A prey in the predators' diet while the ratio of type-A in environment remains constant. However, in our simulations, as the predators start to consume different prey types, the proportion of two prey types changes. We 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%, we 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%, we 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).

The maintenance of prey diversity by predators is explored by comparing the results of two simulations. In the control run, we 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 goes extinct. In the experimental run, we introduce a predator population of 300 individuals into the two initial prey populations used in the control run. Each predator searches for prey in its neighboring area and executes positive frequency-dependent predation based on the type of prey actually captured. In each predation loop, a predator is allowed to eat at most m ($m = 4$) prey and acquires 35% of 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 we record the population sizes of the predator and two prey species during the run.

To explore the robustness of positive frequency-dependent predation in maintaining the coexistence of type-A and type-B populations, we 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 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 is varied, the other two remain unchanged. We 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 we 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 set $P_{min} - P_{max}$ back to $0 - 1$, we increase the percentage of type-A prey in the 3000 prey individuals from 10% to 90% in 10% increments. For each parameter setting, we record the duration (the number of instructions that have been executed) that the two prey types coexist.

To further examine the role of positive frequency-dependent predation in maintaining species diversity, we add one more species, type-C prey with a length of 90 instructions. Except that the initial prey populations in the control and experimental runs are type-A, type-B and type-C populations of 1000 individuals each, we use the same procedure and parameter settings as those used in the above case of two prey species. We compare the dynamics of prey populations in the absence of predators with those in the presence of predators.

Results

Lotka-Volterra-like Cycle between Digital Prey and Predator Populations

In a natural environment, in order to survive and reproduce, predators have to catch prey and acquire energy from them. This energy transfer from prey to predators leads to the famous "Lotka-Volterra" cycle: an abundant prey population provides more food for predators and thus supports a larger predator population. But as the number of predators increases,
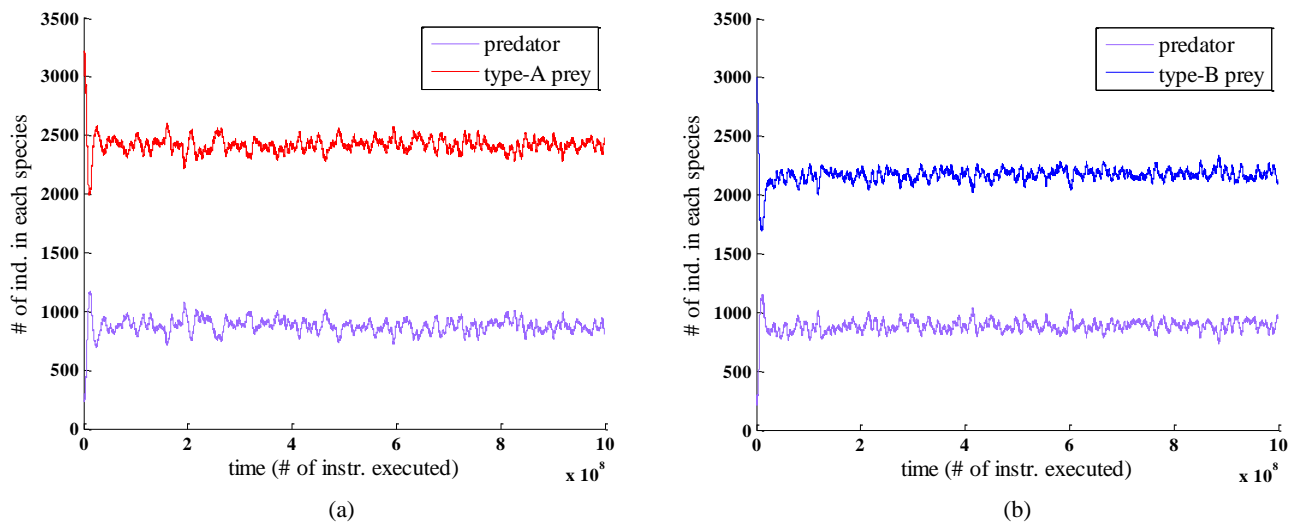

FIGURE 2 Coexistence of a predator population and a prey population in the Tierra system (a) The predator and type-A prey populations stably coexist. (b) The predator and type-B prey populations stably coexist.
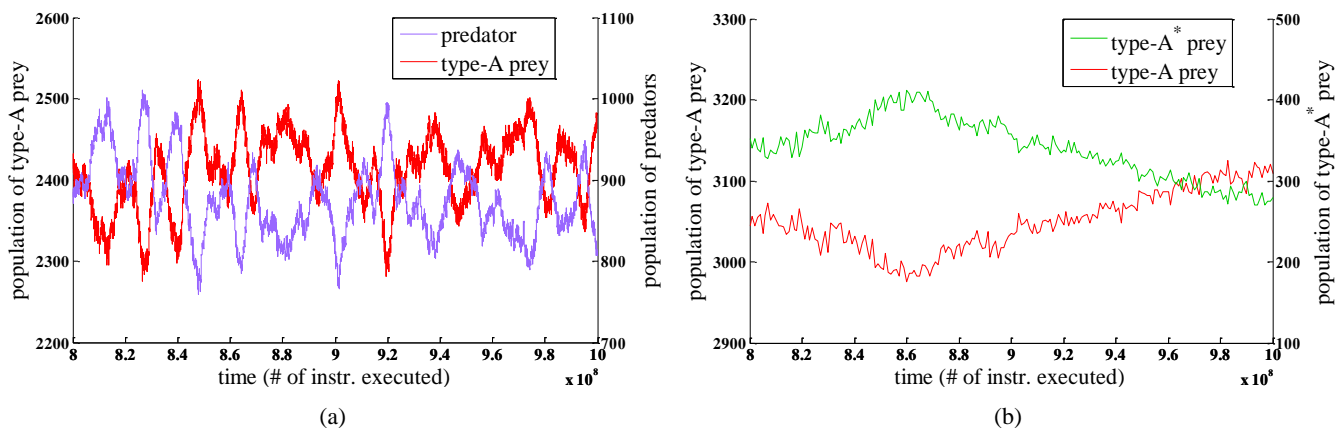

FIGURE 3 (a) "Lotka-Volterra-like" cycle between the predator population and type-A prey population at the steady state from 800 to 1000 million instructions executed in the Tierra system. (b) Population sizes of two prey species with the same genome length slowly drift from 800 to 1000 million instructions executed in the Tierra system.

the growing predation pressure depresses the prey population. When less prey are available, the predator population decreases which reduces the predation pressure and leads to the rebound of the prey population. 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 between the prey and predator populations forms. As shown in Figure 2(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. As we examine the population dynamics at the steady state between 800 and 1000 million instructions executed, as shown in Figure 3(a), we find that following the increase of type-A prey population, the predator population increases, which ceases the expansion of the prey population and causes it to decline. Likewise, the decrease of the prey population causes the predator population to decrease, which leads to the rebound of the prey population. In contrast, the population dynamics caused by the randomness in the Tierra system exhibit a completely different pattern. As shown in Figure 3(b), between 800 and 1000 million instructions executed, the population sizes of type-A and type-A* prey species slowly drift without visible cycling. Therefore, the coupled cyclic oscillation between the prey and predator populations in Figure 3(a) is not the result of random fluctuations in the system, but rather results from the energy dependence of the predators on their prey, the very critical component which supports the "Lotka-Volterra" cycle in nature. Similarly, in Figure 2(b), the type-B prey population of about 2200 individuals steadily coexists with the predator population through the establishment of the "Lotka-Volterra-like" cycle. Moreover, as we vary the number of prey that a predator can eat in each predation loop in the range of 3 to 6 ($m = 3, 4, 5, 6$) and adjust the amount of CPU time transferred from a prey to its predator in the range of 15% to 35%, the "Lotka-Volterra-like" cycle robustly appears in Tierra. This suggests that our 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 prey and predator populations observed in nature.

Positive Frequency-dependent Behavior of Predators at a Population Level

Positive frequency-dependent predation means that the predation risk of a prey individual correlates positively with the frequency of that prey type in environment. That is, a predator is more likely to eat the common prey type than the rare one. In Tierra, each predator has a higher probability of eating a previously encountered prey type, as specified by the rules in the "Methods" section. As shown in Figure 4, 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 becomes the abundant prey type (>50%), the predator population disproportionately consumes more type-A prey. The switch of the preferable prey type occurs exactly when the type-A prey change from a rare type to a common one (50%). Therefore, although each digital

predator exhibits prey preferences 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.
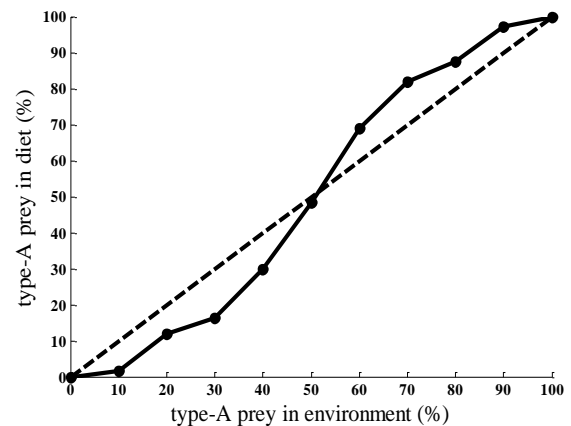

FIGURE 4 A predator population in the Tierra system exhibits positive frequency-dependent behavior. The dashed line indicates the hypothetical situation in which the relative frequency of a prey type in the environment does not affect the predators' eating preference.

Maintenance of Two Prey Species by Positive Frequency-dependent Predation

Many field experiments showed that in the absence of predators, two prey species which shared the same limiting resource 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). 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 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 5(a).

However, after a predator population of 300 individuals which exhibits positive frequency-dependent behavior is introduced into the two prey populations of 1500 individuals of each type, the dynamics of the prey populations change dramatically. As shown in Figure 5(b), 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. The stable population size of each prey type indicates that the diversity of prey species may persist forever under positive frequency-dependent predation.
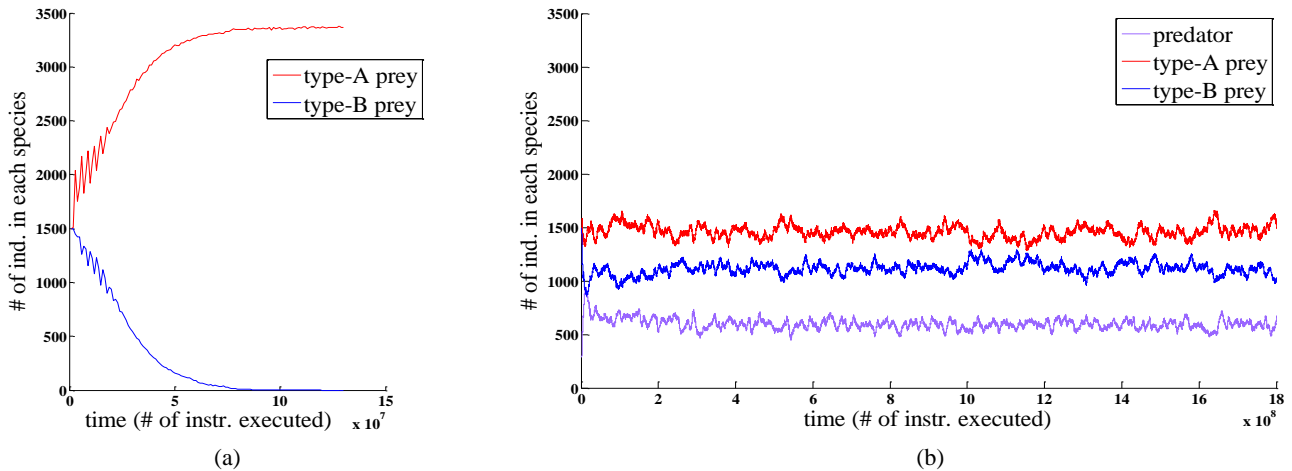
(a)

(b)

FIGURE 5 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) Type-A and type-B prey stably coexist under the predation from a predator population.

Robustness of Frequency-dependent Predation on Maintaining the Coexistence of Two Prey Species

The adjustment rate ΔP directly affects the strength of positive frequency-dependent predation. When $\Delta P = 0$, a predator always has the same probability, $P_A = P_B = 0.5$, to eat type-A and type-B prey regardless of the abundance of those two prey types in its local area. As ΔP increases, a predator can more effectively adjust its probability of eating different types of prey based on the prey it actually captures. As shown in Figure 6(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 eating 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 $P_A = P_B = 0.5$, that is, a predator fails to adjust its eating probabilities based on local prey abundance even if $\Delta P = 0.1$. However, this limitation is gradually relaxed as the adjustment range extends towards $P_{min} - P_{max} = 0 - 1$. As shown in Figure 6(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 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 6(c), when the percentage of type-A prey in
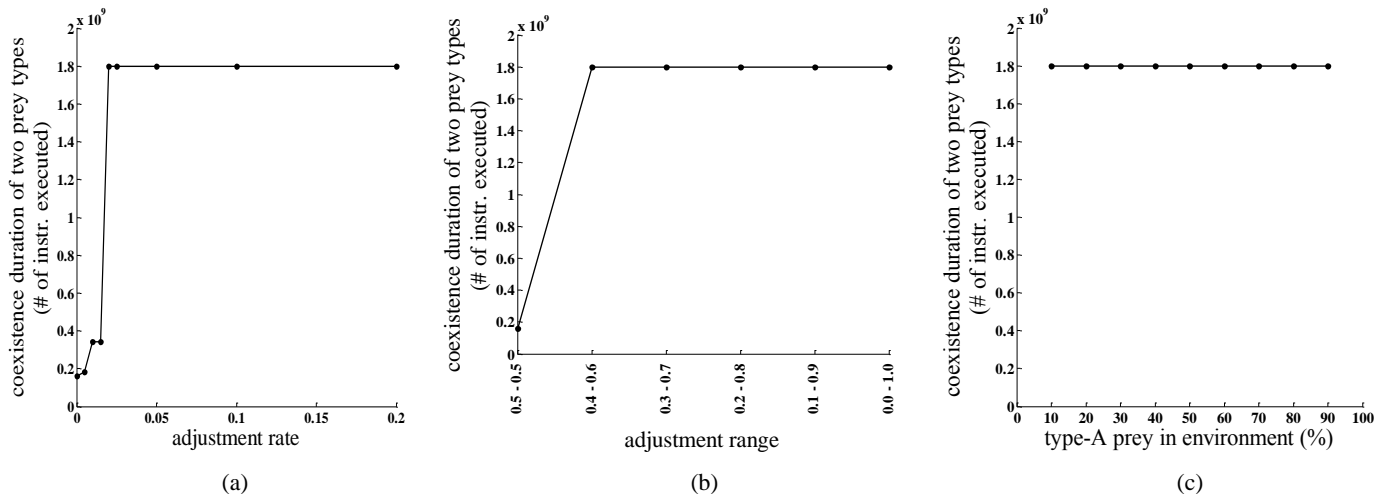

(a)

(b)

(c)

FIGURE 6 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 as $\Delta P \geq 0.02$. (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 nine different initial ratios of the two prey populations.
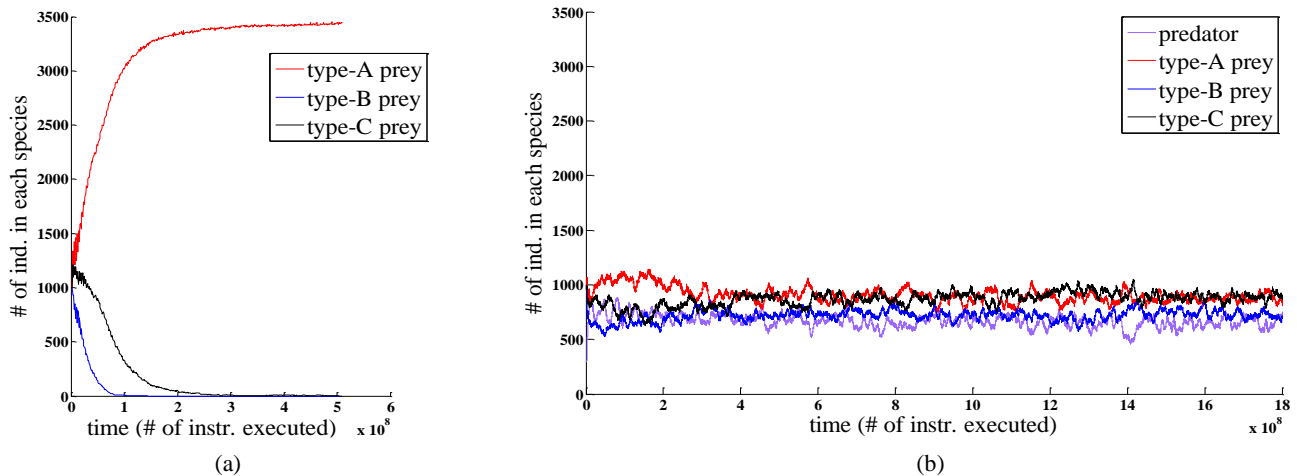
FIGURE 7 Coexistence of three prey species is maintained by a predator population with positive frequency-dependent behavior (a) Competitive exclusion among three types of prey; type-B prey and then type-C prey go extinct. (b) Type-A, type-B and type-C prey stably coexist under the predation from a predator population.

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 nine initial ratios of the two prey populations over the simulation run of 1800 million instructions executed. Those simulation results suggest that positive frequency-dependent predation may robustly support the coexistence of two prey species.

Maintenance of Three Prey Species by Positive Frequency-dependent Predation

We increase the number of prey species by adding one more species, type-C prey which is 90 instructions long. In the absence of predators, 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. 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, as shown in Figure 7(a). However, after a predator population of 300 individuals is introduced into the three prey populations of 1000 individuals of each type, as shown in Figure 7(b), all three prey types stably coexist. This result further supports the idea that positive frequency-dependent predation is able to maintain the diversity of prey species.

Discussion

In the original Tierra implementation, a form of predation emerged through evolution of hyper-parasites which 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 rely on the existence of parasites, the predation relationship between hyper-parasites and parasites may not be consistent with that between organic predator and prey populations. 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 which suggests that the digital predators and prey may be suitable for exploring predator-prey population dynamics.

Positive frequency-dependent predation is one of the proposed mechanisms for maintaining species diversity in nature (Gendron, 1987). It has been supported by several laboratory experiments in which one or a few predators that constantly consumed the more common prey type were able to maintain the coexistence of two prey phenotypes (Allen, 1988). But in a natural environment, it is likely to be a full predator population, rather than a few predator individuals, to regulate prey populations. In the paper (Merilaita, 2006), the author used an individual-based model to explore the dynamics of positive frequency-dependent predation at a population level with one predator species and two prey species. The simulation results showed that although one or two predator individuals could maintain the diversity of prey species, which was consistent with the laboratory experiment 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. However, the setup of the simulations in the paper (Merilaita, 2006) may not agree with the natural behavior of a predator population. In the laboratory experiment 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. The author in the paper (Merilaita, 2006) 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) Because each predator in the ten-predator case lacked global information on prey type frequencies, those ten predators could not maintain prey diversity as efficiently and accurately as a single predator individual. But 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 frequency 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. Our simulation results show that when each predator in Tierra, similar to its organic counterpart, 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 proportion of the two prey types in the environment. Furthermore, as we increase the number of prey types from two to three, the predator population also successfully maintains the coexistence of three prey species. Therefore, our results strongly suggest that positive frequency-dependent predation may be a reasonable mechanism to maintain species diversity in nature.

The simulation results we report here are obtained under an ecological scenario in which all mutations are blocked. Our future research will explore the hypothesis that positive frequency-dependent predation may facilitate the increase and maintenance of species diversity in an evolutionary scenario. It is a more complex but more intriguing situation: when various types of random mutations are introduced into the Tierra system, the genomes of digital creatures will be modified and thus new types of prey and predator species will continuously emerge. Therefore, unlike the ecological scenario in which the prey types are known and the number of prey types is fixed, in the evolutionary scenario the prey types that can be detected by predators change over time. In the original Tierra system, when one or a few successful species emerged through mutation, they usually gained reproductive advantages either by effectively exploiting other creatures or by shortening their own lengths and rapidly crowded out other existing species. Thus, the soup was repetitively dominated by very few species. However, with the introduction of positive frequency-dependent predation, the dominant prey species may be depressed by predators. This may provide resources to support the populations of other prey species and thus more

prey species may have the opportunities to evolve. With this increase in the number of coexisting prey species, more food sources may be available to predators which may promote the differentiation of predator species, with each specializing on a certain type of prey. Moreover, in order to produce more offspring, new prey species may evolve novel escape strategies to avoid being eaten and new predator species may develop innovative predation tactics to acquire more energy from prey. Therefore the co-evolution between prey and predator species may be observed in the Tierra system. Additionally, the introduction of predation may elongate an evolutionary process in Tierra. 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). 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, and thus may allow evolution to continue longer.

References

Allen, J. A. (1988). Frequency-dependent selection by predators. *Philosophical Transactions of the Royal Society B*, 319: 485-503.

Gause, G. F. (1934). *The struggle for existence*, Williams & Wilkins, Baltimore, MD.

Gendron, R. P. (1987). Models and mechanisms of frequency-dependent predation. *The American Naturalist*, 130: 603-623.

MacArthur, R. H. (1958). Population ecology of some warblers of northeastern coniferous forests. *Ecology*, 39: 599-619.

Merilaita, S. (2006). Frequency-dependent predation and maintenance of prey polymorphism. *Journal of Evolutionary Biology*, 19: 2022-2030.

Morin, P. J. (1981). Predatory salamanders reverse the outcome of competition among three species of anuran tadpoles. *Science*, 212: 1284-1286.

Murdoch, W. W. (1969). Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecological Monographs*, 39: 335-354.

Murdoch, W. W., Avery, S., and Smyth, M. E. B. (1975). Switching in predatory fish. *Ecology*, 56: 1094-1105.

Paine, R. T. (1974). Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia*, 15: 93-120.

Ray, T. S. (1991). An approach to the synthesis of life. In Langton, C. *et al*., editors, *Artificial Life II*, pages 371-408. Addison-Wesley publishing company, Redwood City, CA.

Stanley, S. M. (1973). An ecological theory for the sudden origin of multicellular life in the late Precambrian. *Proceedings of the National Academy of Sciences*, 70: 1486-1489.

Wilke, C. O. and Adami, C. (2002). The biology of digital organisms. *Trends in Ecology & Evolution*, 17: 528-532.