



Effects of perturbation on the predator–prey system in a heterogeneous landscape

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ABSTRACT

Environmental perturbations occur in ecosystems as the result of disturbance, which is closely related to ecosystem stability and resilience. To understand how perturbations can affect ecosystems, we constructed a spatially explicit lattice model to simulate the integrative predator–prey–grass relationships. In this model, a predator (or prey) gives birth to offspring, according to a specific birth probability, when it is able to feed on prey (or grass). When a predator or prey animal was initially introduced or newly born, its health state was set at a given high value. This state decreased by 1 with each time step. When the state of an animal decreased to zero, the animal was considered dead and was removed from the system. In this model, the perturbation was defined as the sudden death of some portion of the population. The heterogeneous landscape was characterized by a parameter, H , which controlled the degree of heterogeneity. When $H \geq 0.6$, the predator population size was positively influenced by the perturbation. However, the perturbation had little effect upon the population sizes of prey or grass, regardless of the value of H .

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Introduction

Numerous species are prone to extinction due to natural (e.g., temperature fluctuations, climatic changes) and anthropogenic (i.e., pollution) perturbations (Paine, 1966; Shaffer, 1987; Tilman and Downing, 1994; Lynch et al., 1995; Kamenev et al., 2008). Understanding the effect of such perturbations on ecosystems is essential for comprehending the ecosystem's resilience and stability. For this reason, many researchers have extensively studied the perturbation effects of environmental stochasticity or catastrophes (Yodzis, 1988; Lande, 1993; Tainaka, 1994; Edwards et al., 2005; Lee et al., 2007).

Previous studies have proved helpful for understanding ecosystem responses, such as changes in stability and/or resilience, when ecosystems have been exposed to various types of environmental perturbations for long periods of time. Most of these studies, however, have considered how perturbations modify the biological properties of species, such as mortality rates and other vital rates (Yodzis, 1988) or Gaussian noise (or pulses) (Spagnolo and Barbera, 2002; Lee et al., 2004; Li et al., 2008).

In contrast to the long-term effects stated above, short-term effects of environmental perturbations (such as heavy snowfall, severe fires, or storms) have been frequently observed. These

perturbations are likely to cause sudden death of healthy individuals within a population, which did not exhibit any changes in their biological variables within a population at a stable state. In addition, previous studies have not considered landscape heterogeneity because of the difficulties in characterizing the interaction between species and the landscape, as well as the difficulties involved in mathematically describing a landscape structure.

In the present study, these problems were addressed by constructing an ecosystem model consisting of a heterogeneous landscape with multiple populations in a predator–prey–grass system. This model was used to investigate the effects that short-term perturbations have upon predator–prey–grass dynamics.

Model construction

A square lattice $L \times L$ ($= 100$) with periodic boundary conditions was considered. Each site of the lattice contained predators, prey, and/or grass, or remained empty. Predators and prey could occupy the same site simultaneously. Double occupancy by grass at a site was forbidden. This lattice model was the same as that suggested in our previous studies (Lee, 2010, 2011).

Before the simulation was run, predators, prey, and grass were distributed on the lattice space by assigning 1 or 0 to each lattice site. The assignment of 1 or 0 was determined by $n_w(i, j)$ for predators, $n_r(i, j)$ for prey, and $n_g(i, j)$ for grass, and these parameters denoted the

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number of individuals at the lattice site (i, j) . Initially, only 1 individual of each species was allowed to be present at a single lattice site.

The occupancy of a lattice site by an individual of a species was given by a threshold that was based on the probabilities W , R , and G :

$$n_w(i, j), n_r(i, j), \text{ and } n_g(i, j) = \begin{cases} 1, & \text{when } \text{rand}(i, j) < W(\text{for predator}), R(\text{for prey}), G(\text{for grass}) \\ 0, & \text{otherwise} \end{cases}$$

where $\text{rand}(i, j)$ represents a randomly generated number at site (i, j) . Thus, the initially assigned species densities were represented by the probabilities W , R , and G . In the present study, the values of W and R were in the range of 0.1 to 0.3, with an increment of 0.05, while the value of G was fixed at 0.3. Each combination of W , R , and G was run for 3000 iterations and the results were averaged over 200 independent simulations.

Heterogeneous landscape

A spatially heterogeneous landscape was created in the lattice space using a neutral landscape model (Gardner et al., 1987; With, 1997; Lee and Su, 2009). Each lattice site had a value representing the spatially distributed property of the landscape. Because the details of the complex effects of the landscape properties on the species were unknown, for simplicity, the environmental properties were represented as a value h , ranging from 0.0 to 1.0, with high values representing favorable environmental conditions. An internal parameter H , which controlled the aggregation of lattice sites with high h values, was also assigned a value of 0.0 to 1.0, with high H values corresponding to high levels of aggregation (see Fig. 3).

Species

When a grass site had neighboring sites that included at least one site that was not occupied by grass, the grass could grow into that site according to its growth probability, which was arbitrarily set to 0.2. It was possible for grass to grow into multiple neighboring sites during a single iteration time step Fig. 1a. The growth of grass was not influenced by landscape heterogeneity and the grass could occupy only a single lattice site.

When a predator (or a prey) was surrounded by neighboring sites, it was more likely to move into a site with a higher h value than a site with a lower h value Fig. 1b. For example, in Fig. 1(b), the prey has the highest probability of moving into the top-right site portion of the

figure. The probability value was calculated as $0.7/\text{sum of the } h \text{ values of the neighboring sites}$.

When predator and prey were present within the same site at the same time, the number of prey which were eaten/killed was the same as the number of predators. The prey that was eaten was chosen randomly. This rule was also applied to the relationship between the prey and grass.

The state of health of a predator or prey was represented by a value ranging from 0 to 20. When a predator or prey was initially introduced or newly born, its initial state of health was assigned a value of 20.

When a predator or prey moved a step spatially, its health state decreased by 1. When its health state decreased to below zero, the predator or prey was considered dead, and it was removed from the system.

If a predator or prey consumed food (grass for prey; prey for a predator) before death, its health state was restored to the original value of 20.

When a predator ate a prey individual or a prey ate grass, the predator or prey gave birth to a single offspring according to the birth probability of 0.2. The offspring was located within the same lattice site as its parent (Fig. 2).

Environmental perturbation

Individuals for each species were randomly chosen with a probability M ($= 0.1, 0.2, \dots, 0.5$) at $t = 500$ and immediately removed from the system. This determined the proportion of individuals within a population that suddenly died due to an environmental perturbation. Considering the transient behavior occurring due to the nonlinearity of the predator–prey system in the early stage ($t < 500$), we chose the time at which the perturbation occurred. Preliminarily, we tested the population dynamics for the different perturbation occurring times and confirmed that the dynamics were statistically same, regardless of the time.

Results

Fig. 4 shows the typical population dynamics for predator, prey, and grass, where $H = 0.4$ and $M = 0.4$. The initial densities for predator, prey, and grass were 0.2, 0.2, and 0.3, respectively. The stabilities at different population levels were observed throughout the simulation. The prey and predator populations appeared to fluctuate periodically, while the grass population remained relatively stable, even after the

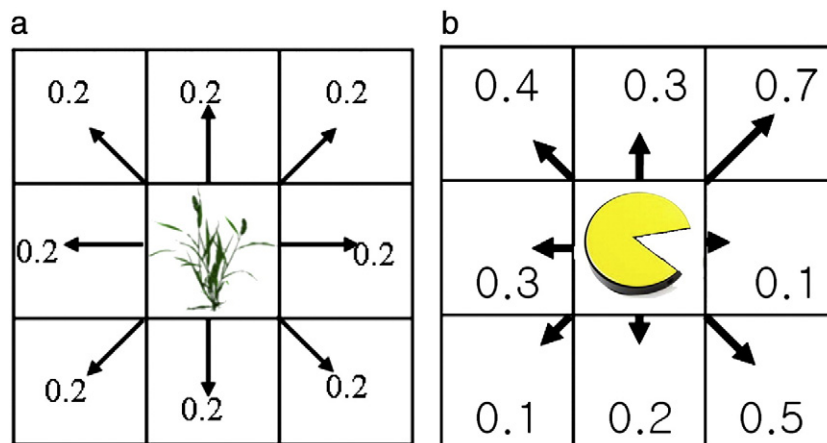


Fig. 1. (a) The growth process of grass with a growth probability of 0.2, (b) an example of a prey (or a predator) surrounded by eight neighboring sites. Each neighboring site is labeled with its associated h value, reflecting the landscape property. The length of an arrow indicates the probability that the prey will move into a specific site.

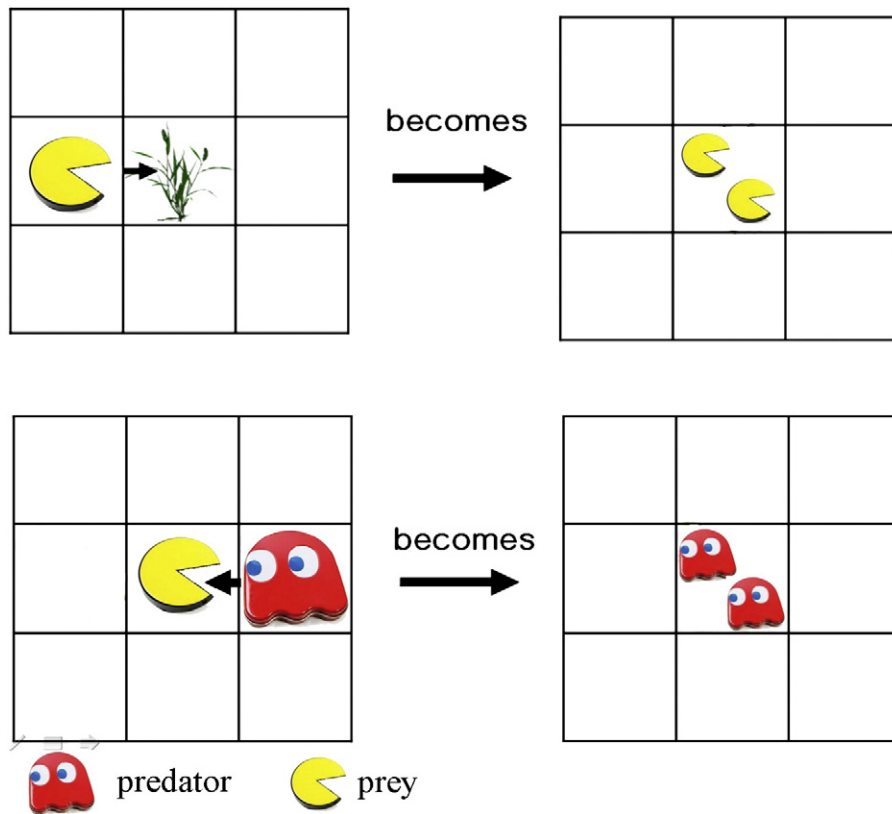


Fig. 2. Possible configurations encountered by a predator and prey at a site. When the prey eats the grass (or the predator eats the prey), the prey (or predator) gives birth to a single offspring.

perturbation. The stability of the grass population was due to its rapid growth rate. As a simulation rule, the grass at a site could grow into multiple neighboring sites during one iteration time step, which, in turn, reduced the fluctuation caused by the environmental perturbation or the consumption by prey.

In order to understand the overall effects of the perturbation on the ecosystem in the heterogeneous landscape across different levels of H and M , we investigated the final population sizes of the species for $H=0.1, 0.2, \dots, 1.0$, where $M=0.1, 0.2, \dots, 0.5$ (Fig. 5). The final population size was calculated by averaging the varying population sizes in the range of $2500 < t < 3000$. In the case of the predator, the final population size increased and reached the equilibrium state with increasing H . When $H \geq 0.6$, the perturbation positively affected the final population size. At an appropriate degree of perturbation ($M=0.2$), population size was maximum. However, for $H < 0.6$,

there was no effect of the perturbation on the predator population size Fig. 5a. The final population sizes of the prey and grass were not influenced by the perturbation (Figs. 5b, c).

Discussion

In this study, a lattice model was constructed to simulate an ecosystem consisting of three community levels, predators, prey, and grass, and a heterogeneous landscape, in order to explore the effect of an environmental perturbation on the ecosystem. In the model, a perturbation was introduced at $t=500$ by removing some portion of each population. The simulation results demonstrated that the perturbation was beneficial to the final population size (calculated by averaging the varying population sizes in the range of $2500 < t < 3000$) of the predator species in heterogeneous landscapes with high H values. These results

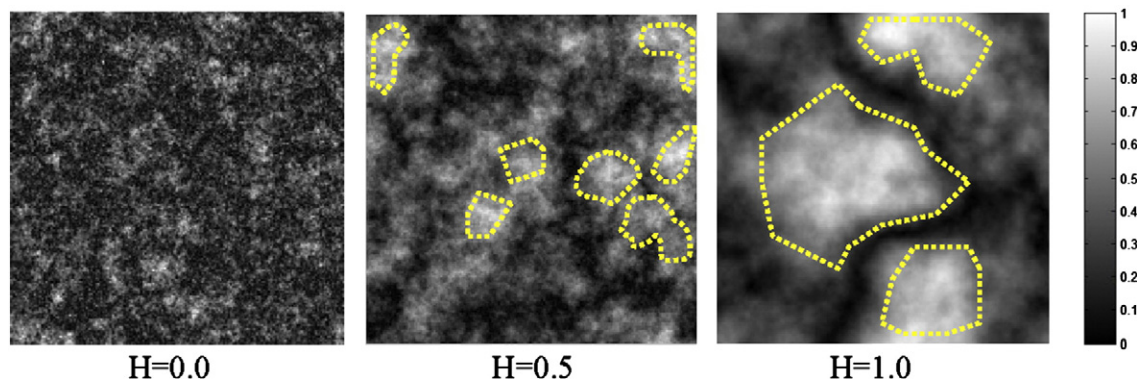


Fig. 3. Heterogeneous landscapes. The landscape varies in the value of H ($=0.0, 0.5$, or 1.0), which produces a gradient of fragmentation. The gray color represents the value of h . Brighter colors correspond to higher h values.

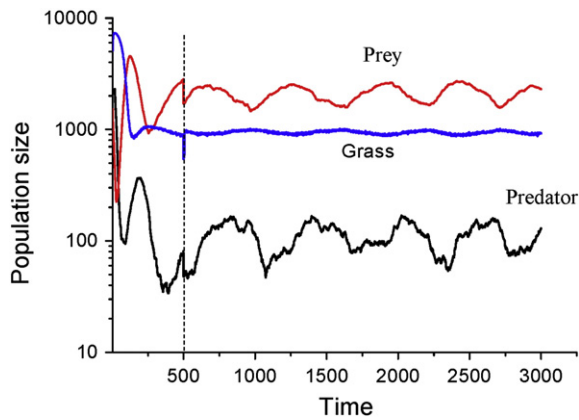


Fig. 4. Typical population dynamics of prey, grass, and predator species, where the degree of perturbation is $M = 0.4$ and the landscape heterogeneity is $H = 0.4$. The initial densities of predator, prey, and grass were 0.2, 0.2, and 0.3, respectively.

support a previous study (Robert, 2006), which reported that negative environmental perturbations may paradoxically improve middle- and long-term species persistence for realistic frequency distributions of perturbation occurrence and severity. For prey and grass, the perturbation effect was not observed regardless of the level of perturbation. The reasons why the maximum effect upon the predator population size occurs at an intermediate perturbation range will be studied in detail in a future study.

It would be interesting to investigate the reasons for the increase and the saturation of the final population size of the predator, which is observed with an increase in H Fig. 5a, as well as the reason for the low final population size of prey at $H = 0.0$ Fig. 5b. A possible

explanation for this effect could be that, as H increased, clusters with higher values of h were formed and increased in size (indicated by dotted lines in Fig. 3), and these clusters acted as attractors for predator and prey (Lee, 2010). Thus, the predator population increased due to the supply of prey individuals in the clusters, but when the predator population exceeded a certain size, the population increase ceased because of the lack of prey in the clusters. Lee (2010) reported that the heterogeneity of a landscape positively affects the predator and prey population densities in a predator–prey system, which could explain why, when $H = 0.0$, the final population sizes for predators and prey is low. The relationship between cluster size/frequency and population size appears to be complicated. More detailed investigations are required to understand this relationship.

To simplify the model, the predator and prey were assumed to have the same health state and dispersal speed characteristics. In addition, both species were assumed to be equally influenced by landscape heterogeneity. Although these assumptions may not be realistic for animals in natural populations, our study is valuable because the simulation results highlighted possible consequences of environmental perturbations for predator–prey–grass systems. Accordingly, this study could serve as a baseline for future empirical work on the dynamics of multi-species communities that are exposed to unexpected environmental perturbations.

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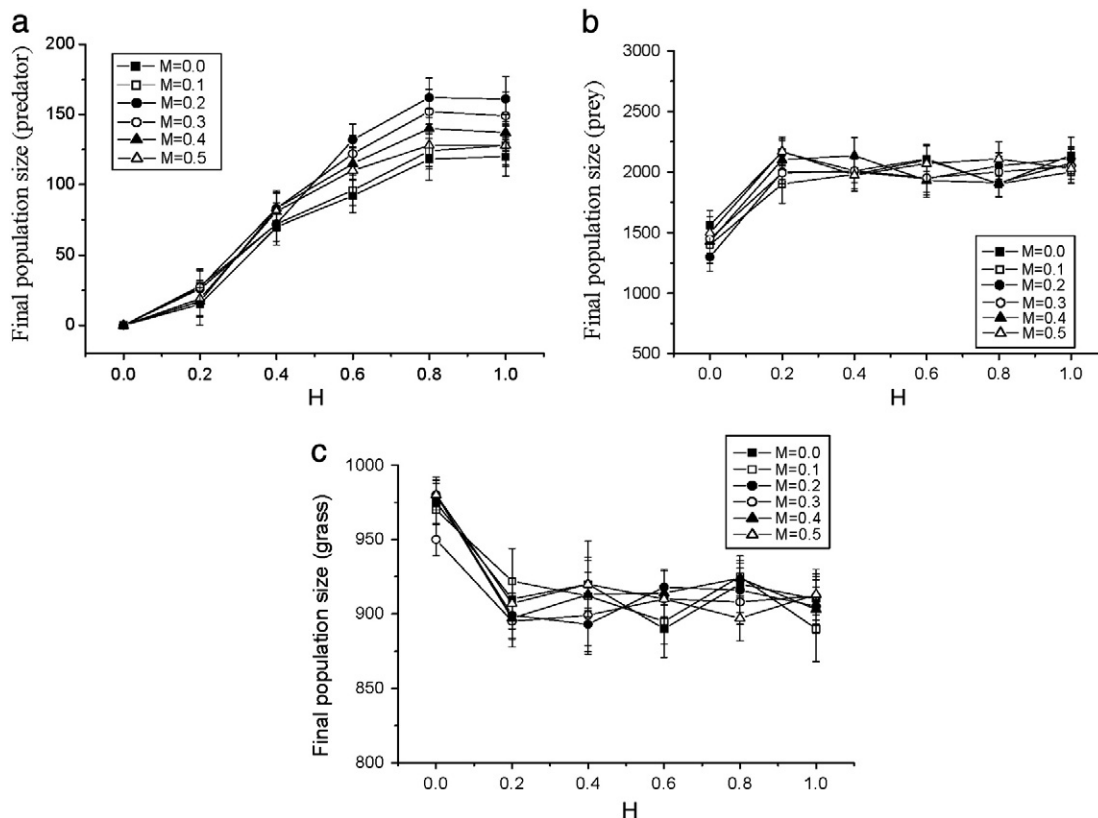


Fig. 5. Plots of final population sizes for (a) predator, (b) prey, and (c) grass against landscape heterogeneity H , where the degree of perturbation ranged from $M = 0.1$ to 0.5 .

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