A Species Invasion Model with Detritus

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Abstract

We present a lattice model of food web with alien plants invasion and analyze the model via Monte Carlo simulations and Mean Field Theory. The original food web contains herbivore, plant and detritus. Our results reveal that the alien species invasion will cause different consequences under different conditions. There are five kinds of phenomenon at most in our experiment. The system’s status could be only detritus exists, only alien plants exists, all plants exist harmoniously, initial plants die out while other ingredients still be alive with the alien plants, or the alien plants become extinct while the original system keeps working. In these consequences, people should pay attention to the system collapse caused by the unsuccessful species invasion. Probably it is the reason to some ecosystems break down.

Keywords: species invasion, Monte Carlo simulations, predator–prey systems, detritus, means field theory

1. Introduction

Species invasion is a key factor of global environmental changes today. The huge threaten and destruction to ecosystem from the species invasion have caught worldwide attention [5, 14]. The invasion is considered as one of the major reasons for the loss of species and genomic diversity [7, 15, 16, 20, 22]. Elton [4], who introduced the concept of food webs, first claimed that the species invasion is dangerous for local ecosystems. His workmates also put effort to the research of
species invasion, including the invasion patterns; intervene from nature or human and the damage to original ecosystem by the invasion.

Food webs (FW), meaning the feeding relationships among species in ecological systems, are applied in the research of species invasion [2]. In recent years, a lot of efforts have been put into the study of food webs, both from the theoretical and the experiment ways [4, 17]. The previously prevailing belief of ecologists was that highly complex ecosystems were much more stable than simpler ones [3, 18]. But May [19] showed mathematically that large and complicated ecosystems were inherently unstable. His contribution has been one of the drivers of both theoretical and experimental ecology in the last few decades [14, 15]. According to the presented works, a simple model is often extracted to illustrate the interaction in the food web, and the characteristics of the food web could be depicted appropriately [8].

In the past, the plants were regarded as the premier energy source of entire food web. It means the detritus is always neglected. But recently, the function of detritus has been considered in the food web models [1, 9-13, 23]. In these articles, it is proved that both the intermediate and top level species play crucial roles in maintaining the structure of the system [11-13]. And it also indicates that a food web with detritus is more stable [1].

The paper is organized as follows. In Section 2, we construct a model which contains herbivore, plant and detritus. Then a new kind of plant invades the ecosystem and the results of numerical simulations are discussed. Section 3 is the analysis of our experiment by using Mean Field Theory. Finally, in Section 4, conclusions are drawn.

2. Model and results

2.1 Basic model

First, we consider a food web with three components, which is presented in figure 1.

![Food Web Diagram](image)

Fig.1 A two-level food web with a closed nutrient cycle. Consumers C feed on $R_i$. Remains of dead C’s, i.e. detritus D, constitute the nutrients for the species $R_i$. The arrows indicate the flow of nutrient in the food web. The dashed lines are related to the dead organic matter.

In Fig.1, the herbivore (consumer) C feeds on the bottom level resource $R_i$. The species $R_i$ feeds on the detritus D of upper level individuals. The food web under consideration will be simulated with an agent-based Monte Carlo method on a square
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lattice with the linear dimension $L$. In the model, we assume the individuals do not move during their lifetimes. Spreading of the agents is realized only via putting progeny in the neighborhood of the parents. A given number of agents of each type are put in stochastic positions on the lattice. For each site, we set the rule that there will be only two states in the model. The lattice could be occupied by one agent for a certain species or the lattice is empty, which is labeled by $E$. All individuals will interact with other individuals in the stochastic neighborhood of their von Neumann neighborhood. Other rules of our simulation are below.

\[
\begin{align*}
R_i & \xrightarrow{d_R} E, \\
C & \xrightarrow{d_C} D, \\
C + R_i & \xrightarrow{b_R} C + C, \\
C + R_i & \xrightarrow{1-b_R} C + E, \\
R_i + D & \xrightarrow{b_R} NR_i \quad (N \leq 7), \\
R_i + D & \xrightarrow{1-b_R} R_i + E.
\end{align*}
\]

1. Consumer $C$ dies with a probability $d_C$. Its remains $D$ stays at the node. The resource $R_i$ dies with a probability $d_R$ as well.

2. We randomly choose two neighbors every time and take relative actions. If a $C$ meets an $R_i$, $C$ eats $R_i$ and $R_i$ disappears at the node. Then a progeny of $C$ is created with a probability $b_R$ at the node $R_i$ occupied before. This may correspond to an herbivore eating a plant.

3. If an $R_i$ appears with a $D$, it feeds. Hence $D$ is removed from the lattice and $R_i$ produces offspring, with a probability $b_R$, at $N$ empty lattices in the neighborhoods. $N$ is at most seven including the position $D$ occupied before and six neighborhoods among $R_i$ and $D$.

2.2 A species invasion model

Then we consider the species invasion model which derives from the basic food web model. A new kind of plant $R_2$ is introduced to the local ecosystem, constructing a food web model with species invasion and detritus. Here we assume the species $R_2$ with unlimited food resources do not rely on the detritus $D$ completely. The new model is described below in Fig. 2.
Fig. 2 The species invasion model with detritus. A new kind of plant $R_2$ is introduced into the basic model in Fig. 1. Consumers $C$ feed on the species $R_1$ and $R_2$. The species $R_2$ do not completely rely on the detritus $D$ and it has unlimited food resources which differs with $R_1$. The dashed lines are related to the dead organic matter.

Notice the species $R_2$ is partly different from $R_1$, the rules related to $R_1, C$ and $D$ are the same as the rules in basic model, and new rules on $R_2$ are below.

\begin{align}
R_2 & \rightarrow^{d_{R_2}} E, \\
C + R_1 & \rightarrow^{b_{R_1}} C + C, \\
C + R_1 & \rightarrow^{1-b_{R_1}} C + E, \\
R_2 + E & \rightarrow^{b_{R_2E}} R_2 + R_2, \\
R_2 + E & \rightarrow^{1-b_{R_2E}} R_2 + E, \\
R_2 + D & \rightarrow^{b_{R_2D}} NR_2 \quad (N \leq 7), \\
R_2 + D & \rightarrow^{1-b_{R_2D}} R_2 + E. 
\end{align}

1. The resource $R_1$ dies with a probability $d_{R_1}$.
2. If a $C$ meets an $R_2$, then $C$ eats $R_2$ and $R_2$ disappears at the site. $C$ can produce a progeny with a probability $b_{c_2}$ at the site $R_2$ occupied before.
3. If an $R_2$ appears with $E$, Then a progeny of $R_2$ is created with a probability $b_{R_2E}$ at the node $E$ occupied before.
4. While an $R_2$ meets a $D$, it feeds .Hence $D$ is removed from the lattice and $R_2$ produces offspring, with a probability $b_{R_2D}$, at $N$ empty nodes in the neighborhoods. $N$ is at most seven including the node $D$ occupied before and six neighborhoods among $R_2$ and $D$.

2.3. Results and discussion

We start from the basic food web model. Taking $L=200$, and the proportion of $R_1, C, D$ and $E$ are equal, $d_{R_1}=0.001, \ b_{c_1}=0.6, \ b_{R_1}=0.9, \ d_c=0.2$, we observe the population fluctuation of the three ingredients, getting the results in figure 3.
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Fig. 3 (Color online) Time evolution of D, R₁ and C densities. Parameters of the simulation: L=200, $d_{R_1}=0.001$, $b_{C_1}=0.6$, $b_{R_1}=0.9$, $d_c=0.2$. The curves were obtained from a single run.

The population size of three species gets stable in short time and the fluctuation will be in a small scale. The bottom resource $R_1$ has the largest amount while the detritus D has the smallest population size. At this time, the entire system is a coexisting one, in which densities of all species are non-zero.

Next, we simulate the impact of species invasion. At the time MCS=10000, the species $R_2$ is introduced. The proportion of $R_2$ could be 60% the size of the empty lattice E at 10000 MCS in Fig. 3. The death rate of $R_2$ is set to 0.001 for all the simulations in order to reduce the number of model parameters. The values of $b_{C_2}$, $b_{R_{12}}$, $b_{R_{22}}$ are changed and different results are depicted in Fig. 4.
Fig. 4. (Color online) Results of simulations with different parameters after the invasion of species $R_2$. At time $T=10000$, $R_2$ is introduced. ($b_{c2}, b_{R1}, b_{R22}$) take the following values (a) $(b_{c2}, b_{R1}, b_{R22}) = (0.2, 0, 0.9)$, (b) $(b_{c2}, b_{R1}, b_{R22}) = (0.2, 1.0, 0.9)$, (c) $(b_{c2}, b_{R1}, b_{R22}) = (0.2, 0, 0.78)$, (d) $(b_{c2}, b_{R1}, b_{R22}) = (0.58, 0, 0.9)$, (e) $(b_{c2}, b_{R1}, b_{R22}) = (0.8, 1.0, 0.9)$. The curves were obtained from single runs.

Totally five different consequences emerge when we change the parameters in Fig. 4. The subgraph (a) indicates the system is destroyed because of the $R_2$ invasion, and only detritus is left in the environment. In subgraph (b), the original ecosystem is also destroyed by $R_2$. However, $R_2$ spreads to the whole land while $R_1$, C and D step into the extinction eventually. In subgraph (c), we find this condition leads to a coexistence state but the population size of $R_1$ and $R_2$ fluctuate in a large scale. In subgraph (d), species $R_2$ defeats $R_1$ in the survival competition, leading to the result that $R_2$, C and D coexist with each other harmoniously. The subgraph (e) shows the invasion of $R_2$ has little effect on the system. The system is disturbed for a short time and then back to the original status by self-regulation. It means $R_2$ could not survive under this condition.

For a further study, we set $b_{R1} = 0$ and change values of $b_{c2}$ and $b_{R22}$, ranging from 0 to 1.00 with the step 0.01. The status is observed in 100000 MCS. Results
are shown in Fig. 5(a). Four different areas appear in figure 5 with the change of $b_{c_2}$ and $b_{r_{22}}$. Area I is the largest one, meaning the invasion is a tiny disturbance to the ecosystem under most circumstances. The system returns to stability by its self-regulation. When $b_{c_1}$ is small, with the increase of $b_{r_{22}}$, it comes to area II where $R_1$, $R_2$, C and D coexist with each other. If $b_{r_{22}}$ keeps increasing, there will be a fierce competition between $R_1$ and $R_2$. They both die out in this situation because of the lack of space, and only detritus is left in the environment. This situation is indicated by area III. When the growing $b_{c_2}$ comes to some threshold, and $b_{r_{22}}$ is also large enough, the invasion of $R_2$ will be success and the original system will be damaged, turning to a new ecosystem in which $R_2$, C and D could coexist. Moreover, if $b_{c_1}$ is large enough, the ecosystem will not be destroyed and it will keep stable no matter how $b_{r_{22}}$ changes. From the aforementioned results, we draw the conclusion that the more contribution intruder makes to consumers C, the less likely there will be a successful invasion.

Setting $b_{r_{22}}=1$, we change the values of $b_{c_1}$ and $b_{r_{22}}$, ranging from 0 to 1.00 with the step 0.01, and observe the status in 100000 MCS. Results can be seen in Fig.5 (b). Obvious boundary lines divide the plane into several parts. No matter how the value of $b_{r_{22}}$ changes, $R_2$ spreads to the whole land if $b_{c_1}$ is small and it is demonstrated in area V. With the value of $b_{c_1}$ increasing, the system status will be modified by the invasion, and $R_2$ will become extinct while $R_2$, C and D coexist in the environment. In this stage, the larger $b_{r_{22}}$ is, the more beneficial it is to the coexistence of species. However, if $b_{c_1}$ comes to a threshold, $R_2$ could not survive in the environment. The invasion is regarded as a tiny disturbance to the system at this time, and the system will return to original status by self-regulation. On the boundary line between area I and IV, there are several spots which mean the four species coexist under some conditions, but these coexistence are rare in the simulation. According to the results above, it implies that $b_{c_2}$ is a key factor to determine the state of the ecosystem.
Fig. 5. (Color online) The classification maps of status at 100000 MCS after the invasion of species $R_2$. (a) $b_{R_1}$ is set to 0. $b_{C_1}$ and $b_{R_2}$ change from 0 to 1.0, with the step 0.01. (b) $b_{R_1}$ is set to 1.0. $b_{C_2}$ and $b_{R_2}$ change from 0 to 1.0, with the step 0.01. (c) $b_{R_1}$ is set to 0.9. $b_{C_2}$ and $b_{R_2}$ change from 0 to 1.0, with the step 0.01. (d) $b_{C_1}$ is set to 1.0. $b_{R_1}$ and $b_{R_2}$ change from 0 to 1.0, with the step 0.01. The area I, II, III, IV, V imply the ecosystem’s status are $R_1$, C, D coexist, $R_1$, $R_2$, C, D coexist, only D left, $R_1$, C, D coexist and only $R_2$ left.

Next, we set $b_{R_1}$ = 0.9. Similarly, we change the values of $b_{C_2}$ and $b_{R_2}$, ranging from 0 to 1.00 with the steps 0.01. The status of our simulations at 100000 MCS is exhibited in Fig. 5 (c). Under this circumstance, there are five different results in our simulation. When we fix $b_{C_2}$ = 0.6 and change the values of $b_{R_1}$ and $b_{R_2}$, ranging from 0 to 1.00 with the step 0.01, four different situations are observed in Fig. 5 (d). It can be seen that the invasion will be success when the value of $b_{R_1}$ is big enough to some extent.
3 Theoretical discussions

For a further analysis, we apply the Mean Field Theory to validate our model. Let \( x_i(t) \), \( x_2(t) \), \( x_3(t) \), \( x_4(t) \) denote the densities of subpopulations \( D \), \( R_1 \), \( C \) and \( R_2 \) respectively. To summarize the reactions, we define the equations as follows.

\[
\begin{align*}
\frac{dx_1(t)}{dt} &= dx_3(t) - (x_2(t) + x_4(t))x_1(t), \\
\frac{dx_2(t)}{dt} &= \left[1 + 6\left(1 - \sum_{i=1}^{4} x_i(t)\right)\right]b_{R_1}x_1(t) - x_3(t) - d_{R_1}x_2(t), \\
\frac{dx_3(t)}{dt} &= \left(b_{C_2}x_2(t) + b_{C_1}x_4(t) - d_{C}\right)x_3(t), \\
\frac{dx_4(t)}{dt} &= \left(b_{R_31}\left(1 - \sum_{i=1}^{4} x_i(t)\right) + \left[1 + 6\left(1 - \sum_{i=1}^{4} x_i(t)\right)\right]\right) b_{R_22}x_1(t) - x_3(t) - d_{R_1}x_4(t).
\end{align*}
\]

To illustrate the stability of equations Eq.(3) briefly, we assume the equilibrium point is \( M(x^*_1, x^*_2, x^*_3, x^*_4) \), where \( 0 \leq x^*_i \leq 1, i = 1, 2, 3, 4 \). Except the point \( M_6(0, 0, 0, 0) \), theoretically, there exists five types of equilibrium points at most, which are denoted by \( M_1(x^*_1, 0, 0, 0) \), \( M_2(0, 0, 0, 1 - \frac{d_{R_1}}{b_{R_1}}) \), \( M_3(x^*_1, x^*_2, x^*_3, x^*_4) \), \( M_4(x^*_1, x^*_2, x^*_3, x^*_4) \) and \( M_5(x^*_1, x^*_2, x^*_3, x^*_4, 0) \), where \( x^*_i > 0, i = 3, 4, 5; j = 1, 2, 3, 4 \) is an expression containing \( b_{C_2}, b_{R_31} \) and \( b_{R_22} \). With different parameters, we get different cases in equilibrium points, which are depicted as follows.

Case 1, \( b_{C_1} = 0.6, b_{R_1} = 0.9, b_{C_2} = 0.2, b_{R_31} = 0.9, d_{R_1} = 0.2, d_{R_2} = 0.001 \), the equilibrium point of Eq.(3) is \( m_1 = (0.01, 0, 0, 0) \). It belongs to type \( M_1 \).

Case 2, \( b_{C_1} = 0.6, b_{R_1} = 0.9, b_{C_2} = 0.2, b_{R_31} = 1.0, b_{R_32} = 0.9, d_{C} = 0.2, d_{R_1} = d_{R_2} = 0.001 \), the equilibrium points of Eq.(3) is \( m_2 = (0, 0, 0, 0.999) \). It belongs to type \( M_2 \)

Case 3, \( b_{C_1} = 0.6, b_{R_1} = 0.9, b_{C_2} = 0.6, b_{R_31} = 0, b_{R_32} = 0.9, d_{C} = 0.2, d_{R_1} = d_{R_2} = 0.001 \), the equilibrium points of Eq.(3) is \( m_3 = (0.1964, 0.2, 0.3273, 0.1333) \). It belongs to type \( M_3 \)
Case 4, \(b_{c_1} = 0.6, b_{R_1} = 0.9, b_{c_2} = 0.6, b_{R_2} = 1.0, b_{R_{c_2}} = 0.9, d_c = 0.2, d_R = d_{R_2} = 0.001\), the equilibrium points of Eq.(3) is \(m_4 = (0.2209, 0, 0.3681, 0.3333)\). It belongs to type \(M_4\).

Case 5, \(b_{c_1} = 0.6, b_{R_1} = 0.9, b_{c_2} = 0.8, b_{R_{c_2}} = 1.0, b_{R_{c_2}} = 0.9, d_c = 0.2, d_R = d_{R_2} = 0.001\), the equilibrium points of Eq.(3) is \(m_5 = (0.1964, 0.3333, 0.3273, 0)\). It belongs to type \(M_5\).

From the calculation, obviously, we draw the conclusion that all five types of equilibrium points exist under different parameters. The results in theoretical analysis confirm that there should be five consequences at most in figure 4.

4. Conclusion

A model of species invasion with detritus is presented and analyzed by means of Monte Carlo simulations and Mean Field Theory. In the simulation part, the invasion has different effects to the ecosystem under different conditions and five outcomes can be observed. In the Mean Field Theory analysis part, it shows that there are at most five possible states after the invasion of species \(R_2\).

The ecosystem after the invasion could be:

1. the alien plants destroy the original ecosystem completely, but they survive for a short time, and finally there is only detritus left;
2. the alien plants destroy the original ecosystem completely, and they spread to the whole land finally;
3. the alien plants do not destroy the original system, and the new species coexist with others harmoniously during our simulation;
4. the ecosystem comes to stable, but the original plants are replaced by alien plants, and a new food web is constructed;
5. the alien plants can not destroy the ecosystem, they disappear in short time and have no influence on the stability of the ecosystem.

In case 1, 2 and 4, the original plants finally die out. This phenomenon illustrates the loss of diversity of the ecosystem caused by species invasion, which is claimed in Ref. [4].

In Fig. 5 (a), we assume the alien species’ reproduction rate without the detritus is zero and change values of \(b_{c_1}\) and \(b_{R_{c_2}}\) only. In most situations, the invasion is unsuccessful because of the huge advantage of original plants. But we still find that sometimes the alien species could destroy the ecosystem completely and lead to the situation that only detritus is left in the environment. This extinction could provide a reasonable explanation to how the ecosystem breaks down without any evidence of species invasion. In Fig. 5 (b), an appropriate increasing for reproductive rate of consumers after eating the alien plants (\(b_{c_1}\)) will be beneficial to the invasion. However, the invasion will be weakened if \(b_{c_2}\) is
too much bigger than the reproductive rate of consumers after eating the original plants. It may lead to the conclusion that the more the plants contribute to the consumers, the harder the plants will survive. In Fig. 5 (d), we find a larger reproductive rate after eating the detritus will be helpful to survive in the environment.

In our paper, we do not consider the migration of species. Also, we do not discuss the stability of Eq.(3) in depth because of the extreme complexity of equilibrium in calculation. In our future work, more detailed theoretical analysis will be presented.

References


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