Research article

Biological control for predation invasion based on pair approximation

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Abstract: Biological invasions have been paid more attention since invasive species may cause certain threats to local ecosystems. When biological control is adopted, selecting control species for effect better becomes the focus of latest studies. A food web system, with one native species, one invasive species as predator, and one introduced control species preying on both native and invasive species, is established based on pair approximation, in which the spatial landscape of biological invasion and control is concerned, and the local and global dispersal strategies of invasive species, in addition to the predation preferences of control species for native and invasive species, are considered. The influence of the initial density and initial spatial structures of the control species is investigated and the effects of control species releasing time are analyzed. Generally, the earlier the species introduction, the better the control effect, especially for invasive species dispersing globally. Interestingly, too low control species predation preference for native species can lead to unsuccessful introduction, while too much predation preference will have a weak control effect. The larger the control species predatory preference for invasive species is, the more conducive it is to biological control. The extinction of the invasive species is closely related to the initial density and concentration of the control species. This study gives some insights on selecting control species, its appropriate releasing time, and the density and spatial aggregation of it. Some real-life examples are elaborated on, which provides references for biological invasion control.

Keywords: biological invasion; biological control; pair approximation; cellular automata; predation preference; dispersion strategy

1. Introduction

Biodiversity loss is a major global environmental issue [1]. The main reasons of the loss include habitat degradation, overexploitation and invasion, among other threats [2]. Now, invasion is considered as one of the major threats to global biodiversity and human livelihoods [3].

Recently, concerns about the potential invasion risks of alien species and the impacts on biodiversity have increased rapidly [4−6], because some non-native species can bring about serious problems for ecosystems, socio-economic and human health [7,8]. Some invasive species will compete for resources with native species [9], feed on native species, lead to the extinction of many native species [10,11], reduce local biodiversity [12,13], and result in ecosystem degradation [14]. Besides ecological impacts, economic costs are also high [15]. For example, the imported red fire ants invaded the United States destroyed local agriculture and environmental hygiene, causing huge economic losses [16]. The invasion of new pathogens also has a negative impact on human health [17,18]. The number of invasive species will increase if no measures are taken, and the negative impact will be serious. At present, ways like blocking incoming, mechanical processing, spraying drugs, and biological control are used to control invasion. This study will focus on the method of biological control.

Biological control is a method of using biological interactions to inhibit or eliminate harmful species, which include microbial control, parasitic natural enemy control and predatory natural enemy control [19]. The application of drugs left residues, while blocking incoming and mechanical processing are impractical on large scale biological invasion, but the introduction of natural enemies for invasive species can reproduce themselves and control pests for a long time, with long-lasting effects and relatively low costs.

Biological invasion happens quite often in recent years, and biological control was successful in some cases. Cases in point include: Locusts and planthoppers were controlled by releasing ducks in sweet potato and rice fields [20]; The introduction of *Chrysoperla sinica Tjeder* to control red spiders in fruit groves and agricultural pests in vegetable sheds [21]; *Chouioia cunea Yang* are stocked in garden to curb the spread of *Hyphantria cunea* by species interactions [22]. It should be noted that when applying biological control methods, in-depth researches on the introduced species need to be conducted to ensure that they do not become new harmful invasive species, making selection of control species a very important issue.

There are studies on biological control [23,24], but most ignore the spatial structure of populations. Pair approximation (PA) is used in this study to investigate the invasion control theory with the spatial structure of species in consideration. Compared with the mean-field approximation (MFA), PA, which is often applied to biological phenomena such as population dynamics and epidemic spread [25,26], and which has obtained good results by its theoretical insights, considers the relationship between adjacent individuals and constructs a set of closed autonomous differential equations to represent the transfer process between patches.

Many factors affect the results of species control, one of which is the timing of the control. Previous research has shown that once invasions are identified, even if they have not yet had an impact, preventive action should be taken. And if potential harms exist, they should be eliminated immediately [27]. A case in point is, only 17 days after the discovery of invasive algae in California coastal waters, measures were taken [28]. Previous studies also discover that species omnivore is one of the factors affecting species density [29−31]. Both predation preference and control starting time will be considered in this research.

Different dispersal patterns can alter the distribution of species in surrounding habitats, and previous studies have shown that dispersal patterns affect the density of species [25,32]. Whether the dispersal strategy of species will affect the control result is a question that have drawn much attention. Some studies have found that initial density may be an important determinant of competitiveness and may influence interactions between species [33−36]. Initial density of the species may also affect the control outcome. It is generally believed that when species invade new habitats due to human transportation or boat fishing, the invader density is small and scattered while the native species density is high. Few studies have explored the effects of initial species density and spatial distribution on control outcomes.

We establish relevant models to explore biological control in this study, considering the situation of one native species and one invasive species. First, the effect of invasive species on native species was studied by pair approximation. Then, control species were introduced at different time nodes to study the effects of time introduction, predation preference, and dispersion strategies of invasive species on the density of species, and to compare the effectiveness of biological control.

2. Model

2.1. Model description

We use the single-species occupation model in a discrete infinite lattice to describe a native species, assuming that the lattice is rotationally symmetric and the landscape is homogeneous, i.e., $\rho_{ij} = \rho_{ji}$, and all patches are suitable for species survival. In addition, von Neumann neighbors are used, and each patch has $z = 4$ neighbors. The second species will be introduced to the landscape as an invader, and the third species will be joined in the system as the control species. More details will be described in the next step on model building. Table gives some symbols used to construct the model.

2.2. Species invasion

Suppose the native species in the landscape can only disperse locally to the nearest empty patch. Species 2 invades the landscape, and it only reproduces by hunting native species 1, colonizing the patch where native species 1 existed by mixed dispersion mechanism, namely dispersing locally and globally. Global dispersion refers to sending offspring to random sites of all lattice, while local dispersion refers to sending offspring to random neighboring sites. If there are native species in the site patch, the invader has successful colonization, otherwise it will be wasted.

The possible states of each patch are 0, 1, and 2 (denoted empty patches, occupied by native species 1, and occupied by invasive species 2). Let ρ_i and ρ_{ij} represent the density of single patch i and pair patches $<ij>$. $<ij>$ is a pair of adjacent patches, one of which is type i and the other is type j. Let $q_{i/j}$ represents the conditional probability of arbitrarily selecting a j-type patch whose neighbor is i-type, and $q_{i/j} = \rho_{ij}/\rho_j$, $i, j \in \{0, 1, 2, 3\}$. Let c_{21} indicates the colonization rate of species 2 by preying on species 1 in its neighbors, dispersing to the site where species 1 is located, and c^*_{21} represents the colonization rate of species 2 by preying on any species 1 in the entire lattice. More symbols and explanations are in Table 1.

Table 1. The symbols and descriptions.

Symbols	Descriptions
b_1	The birth rate of native species 1
d_i	The mortality rate of species i
c_{21}	The local colonization rates of species 2
c^*_{21}	The global colonization rate of species 2
c^*_{31}	The predation preference of species 3 for species 1
c^*_{32}	The predation preference of species 3 for species 2
ρ_i	The density of i-type patch
ρ_{ij}	The probability of pair patches <ij>
$q_{i/j}$	The conditional probability of pair patches <ij>
T_1	Introduction time of species 3

Note: Species 1 is native species, species 2 is invasive species and species 3 is control species.

In order to construct a predation system by pair approximation, using the dynamic of ρ_{12} in Eq (4) as an example, the two parts will cause the growth: (a1) Species 1 of the right site of pair sites <11> is occupied by species 2 through global and local predation, which can be denoted by ρ_{11} ($c^*_{21}\rho_2$ + $c_{21}q_{2/11}$ (z-1)/z). (a2) The empty site of pair sites <02> is occupied by the offspring from its neighboring sites occupied by species 1, denoted by $b_1\rho_{02}q_{1/02}$ (z-1)/z. Three parts will reduce ρ_{12}: (b1) The death of pair sites <12>, denoted by -$\rho_{12}(d_1 + d_2)$. (b2) Species 1 of pair sites <12> is killed by neighbor species 2, denoted by -$\rho_{12}c_{21}(1/z+ q_{2/12}(z-1)/z)$. (b3) Species 1 of pair sites <12> is killed by arbitrary species 2 of all lattice, denoted by -$\rho_{12}c^*_{21}\rho_2$. The dynamic structure of other pair sites is the same as that of ρ_{12} (see Appendix for details).

Depending on the relationship between single sites and pair sites, combined with the modeling methods of previous PA models [26,31], the corresponding equations can be obtained:

$$\frac{d\rho_1}{dt} = b_1\rho_1(1 - q_{1/1} - q_{2/1}) - (d_1\rho_1 + c^*_{21}\rho_1\rho_2 + c_{21}\rho_1 q_{2/1}), \tag{1}$$

$$\frac{d\rho_2}{dt} = c^*_{21}\rho_2\rho_1 + c_{21}\rho_2 q_{1/2} - d_2\rho_2, \tag{2}$$

$$\frac{d\rho_{11}}{dt} = 2b_1\rho_{10}(\tfrac{1}{z} + \tfrac{z-1}{z}q_{1/01}) - 2\rho_{11}(d_1 + c^*_{21}\rho_2 + c_{21}\tfrac{z-1}{z}q_{2/11}), \tag{3}$$

$$\frac{d\rho_{12}}{dt} = \rho_{11}\left(c^*_{21}\rho_2 + c_{21}\tfrac{z-1}{z}q_{\frac{2}{11}}\right) + \rho_{02}b_1\tfrac{z-1}{z}q_{\frac{1}{02}} - \rho_{12}[d_1 + d_2 + c^*_{21}\rho_2 + c_{21}(\tfrac{1}{z} + \tfrac{z-1}{z}q_{2/12})], \tag{4}$$

$$\frac{d\rho_{22}}{dt} = 2\rho_{12}[c_{21}(\tfrac{1}{z} + \tfrac{z-1}{z}q_{2/12}) + c^*_{21}\rho_2] - 2\rho_{22}d_2. \tag{5}$$

Taking into account the population spatial distribution, according to lattice rotational symmetry, the pair approximation relationship ($q_{i/jk} \approx q_{i/j}$, the spatial structure of two adjacent patches is approximate to that of three adjacent patches), the sum of the single sites is 1 ($\sum_i\rho_i = 1$), and the sum of the density of the pair sites is equal to the corresponding the density of the single site ($\rho_i = \sum_j\rho_{ij}$). All other pair sites can be represented by these five quantities. Apparently Eqs (1)−(5) constitutes a

closed autonomous system on which the invasion process is analyzed.

2.3. Biological control

Since invasive species feed on native species, if not controlled, the local ecosystem may be affected, so we adopted a predatory natural enemy control strategy and introduced species 3 as controller. Assuming that control species 3 globally hunt invasive and native species, with predation preferences. Let c^*_{31} indicates the predation preference of species 3 for species 1, and c^*_{32} represents the predation preference of species 3 for species 2. Since new species need to adapt to the local environment, we assume that native species have stronger reproductive capacity and have lower mortality rates than the other species.

According to the orthogonal neighborhood correlation algorithm given by Hiebeler, the density and spatial connectivity of control species should follow an inequality $2-1/\rho_3 < q_{3/3} < 1$ [25], otherwise, species introduction is considered invalid. After introduction, the possible states of each site are 0, 1, 2, and 3 (indicating unoccupied empty site, occupied by native species 1, occupied by invasive species 2, and occupied by control species 3, respectively). Based on the previous study [26], we can infer that at the moment of introduction of species 3, the dynamics of single site and pair sites satisfy the following constraints (Appendix for details):

$$\begin{cases} \rho_i^+ = \rho_i(1 - \rho_3), & i = 1,2 \\ \rho_3^+ = \rho_3. \end{cases} \quad \begin{cases} \rho_{ij}^+ = \rho_{ij}(1 - 2\rho_3 + \rho_3 q_{3/3}), & i,j = 1,2 \\ \rho_{i3}^+ = \rho_i \rho_3(1 - q_{3/3}), & i = 1,2 \\ \rho_{33}^+ = \rho_3 q_{3/3}. \end{cases} \quad (6)$$

Based on above facts and assumptions, combined with the PA methods [26], a dynamic equation of nine variables is obtained, and the constraint (6) is substituted to finally obtain the system:

$$\frac{d\rho_1}{dt} = b_1(\rho_1 - \rho_{11} - \rho_{12} - \rho_{13}) - \rho_1(d_1 + c^*_{21}\rho_2 + c^*_{31}\rho_3) - c_{21}\rho_{12}, \quad (7)$$

$$\frac{d\rho_2}{dt} = c^*_{21}\rho_1\rho_2 + c_{21}\rho_{12} - c^*_{32}\rho_2\rho_3 - d_2\rho_2, \quad (8)$$

$$\frac{d\rho_3}{dt} = c^*_{31}\rho_1\rho_3 + c^*_{32}\rho_2\rho_3 - \rho_3 d_3, \quad (9)$$

$$\frac{d\rho_{11}}{dt} = 2b_1(\rho_1 - \rho_{11} - \rho_{12} - \rho_{13})\left(\frac{1}{z} + \frac{z-1}{z}\frac{\rho_1 - \rho_{11} - \rho_{12} - \rho_{13}}{1 - \rho_1 - \rho_2 - \rho_3}\right) - 2\rho_{11}\left(d_1 + c^*_{21}\rho_2 + c^*_{31}\rho_3 + c_{21}\frac{z-1}{z}\frac{\rho_{12}}{\rho_1}\right), \quad (10)$$

$$\frac{d\rho_{12}}{dt} = \rho_{11}\left(c^*_{21}\rho_2 + c_{21}\frac{z-1}{z}\frac{\rho_{12}}{\rho_1}\right) + b_1\frac{z-1}{z}(\rho_2 - \rho_{12} - \rho_{22} - \rho_{23})\frac{\rho_1 - \rho_{11} - \rho_{12} - \rho_{13}}{1 - \rho_1 - \rho_2 - \rho_3} - \rho_{12}\left[d_1 + d_2 + c^*_{32}\rho_3 + c^*_{31}\rho_3 + c^*_{21}\rho_2 + c_{21}\left(\frac{1}{z} + \frac{z-1}{z}\frac{\rho_{12}}{\rho_1}\right)\right], \quad (11)$$

$$\frac{d\rho_{13}}{dt} = b_1 \frac{z-1}{z}(\rho_3 - \rho_{13} - \rho_{23} - \rho_{33})\frac{\rho_1 - \rho_{11} - \rho_{12} - \rho_{13}}{1 - \rho_1 - \rho_2 - \rho_3} + \rho_{12}c_{32}^*\rho_3 + \rho_{11}c_{31}^*\rho_3 - \rho_{13}\left(d_1 + d_3 + \right.$$

$$\left. c_{21}^*\rho_2 + c_{31}^*\rho_3 + c_{21}\frac{z-1}{z}\frac{\rho_{12}}{\rho_1}\right), \tag{12}$$

$$\frac{d\rho_{22}}{dt} = 2\rho_{12}\left[c_{21}\left(\frac{1}{z} + \frac{z-1}{z}\frac{\rho_{12}}{\rho_1}\right) + c_{21}^*\rho_2\right] - 2\rho_{22}(d_2 + c_{32}^*\rho_3), \tag{13}$$

$$\frac{d\rho_{23}}{dt} = \rho_{13}\left(c_{21}^*\rho_2 + c_{21}\frac{z-1}{z}\frac{\rho_{12}}{\rho_1}\right) + \rho_{12}c_{31}^*\rho_3 + \rho_{22}c_{32}^*\rho_3 - \rho_{23}(d_2 + d_3 + c_{32}^*\rho_3), \tag{14}$$

$$\frac{d\rho_{33}}{dt} = 2\rho_{13}c_{31}^*\rho_3 + 2\rho_{32}c_{32}^*\rho_3 - 2\rho_{33}d_3. \tag{15}$$

It can be seen that Eqs (7)−(15) constitute a closed system for the control process. Compared with the invasion process (1)−(5), (7)−(15) consider the effects of species 3 hunting species 1 and 2, as well as the intrinsic mortality of species 3.

2.4. Simulation process

Due to the complexity of the model, we use MATLAB to calculate the above differential equations. And when the population density is less than 0.00001, this species is considered to be extinct. We set parameters based on mass simulations. Firstly, the four dispersion strategies of invasive species 2 were set as follows: global dispersion ($c_{21}^* = 0.5$, $c_{21} = 0$), partial global dispersion ($c_{21}^* = 0.4$, $c_{21} = 0.1$), partial local dispersion ($c_{21}^* = 0.1$, $c_{21} = 0.4$), and local dispersion ($c_{21}^* = 0$, $c_{21} = 0.5$) (see Appendix Figures B1 and B2). Based on the assumption of reproduction rates and mortality rates let $b_1 = 0.7$, $d_1 = 0.1$, $d_2 = 0.15$, and $d_3 = 0.2$ (other parameter space situations see Appendix Figures B7−B10). In order to prevent invasive species from overly affecting native species, control should not start too late. So we set the introduction time $T_1 = 10, 20, 40$ respectively. In order to explore the influence of the predation preference of control species, we suppose that control species prefer to prey on invasive species ($c_{31}^* < c_{32}^*$), so we fixed the predation preferences of species 1 and 2 as $c_{31}^* = 0.3$ and $c_{32}^* = 0.6$, respectively (see Appendix Figures B3−B6 for other situations). Based on the above parameters, we study the effects of the initial density and initial spatial structure of introduced species on results. These parameters are biologically significant. And there are other available parameter values, so we changed multiple parameter values in the simulation and determined that they would not change our general results and conclusions (see Appendix Figures B1−B6).

3. Results

In order to visually observe the effect of biological control, we simulated the procedure on a lattice of 100×100 and drew landscapes of the invasion process of species 2 and the introduction process of species 3 by cellular automata (Figure 1). Set the initial densities of species 1 and 2 to 0.8 and 0.5. When species 2 invades into a landscape where only species 1 exists, if left uncontrolled, we find that the density of species 1 decreases to approximately 0.1, and species 2 occupies most of the habitat (Figure 1(I)). After that, we introduce species 3, set the initial density and initial aggregation

of species 3 to $\rho_3 = 0.2$ and $q_{3/3} = 0.8$ (Figure 1(II)), then the graph (Figure 1(III)) will be formed instantaneously, at which time three species coexist. After the three species reached equilibrium (IV), compare with Figure 1(III), the number of species 2 after control became significantly smaller, and the number of species 1 increased significantly, indicating that biological control was effective.
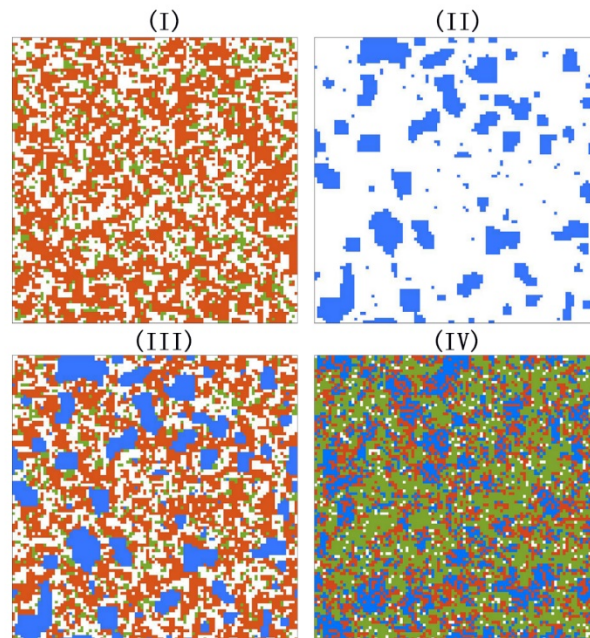

Figure 1. Landscapes for species invasion and biological control. Green represents native species 1, red indicates invasive species 2, blue is control species 3, and white is empty sites. (I): Landscape after invasion of species 2. (II): Distribution of control species 3, setting $\rho_3 = 0.2$, $q_{3/3} = 0.8$. (III): Instantaneous landscape of introduction of species 3. (IV): landscape after stabilization.

Our aim is to explore the effects of the introduction of control species against invasive species based on different dispersal strategies, and to provide suggestions for the selection of control species. Figure 1 has shown that biological control is useful in certain cases, but in order to make the control effect better, the established differential equations are analyzed considering predatory preferences and invasive species dispersal strategies.

The relationship between the predation preference of species 3 to species 1 and population density was studied by fixing the predation preference of species 3 to species 2, that is, $c^*_{32} = 0.6$ (Figure 2). Comparing Figure 2(a−d) reveals an interesting phenomenon in which species 3 does not survive when its predation preference for species 1 is very small, which may be because species 3 preys on too little to meet its own survival conditions. When the living conditions of species 3 are satisfied, with the increase of the predation preference of species 3 to species 1, the density of species 2 gradually decreases, and the density of species 1 increases, indicating when $c^*_{31} > 0.1$ approximately, the control species can effectively control the development of species 2, playing a role in protecting native species and preventing invasive species, and the control effect is best at $c^*_{31} \approx 0.3$. However, when the predation preference of species 3 to species 1 exceeds 0.3, although the invasive species is eliminated, the density of native species will decrease, indicating that the high

predation preference of species 3 over species 1 would be detrimental to biological control. When the predation preference for species 1 is greater than the predation preference for species 2 ($c^*_{31} > 0.6$), the density of native species is already lower than the critical situation in which the introduced species satisfies survival ($c^*_{31} = 0.1$), possibly because species 3 overfished species1 becomes a harmful invasive species, which will not be suitable as the target species for control. In addition, comparing the four maps, it can be found that when species 2 is more partially dispersed, the lower the critical value for the extinction of invasive species. It may be that the distribution is more clustered when invasive species take local dispersion, and the neighbors of species 2 are mostly distributed with species 2, while only invasive species at the edge of the cluster can disperse, so the effective fecundity is low and extinction is more probable.
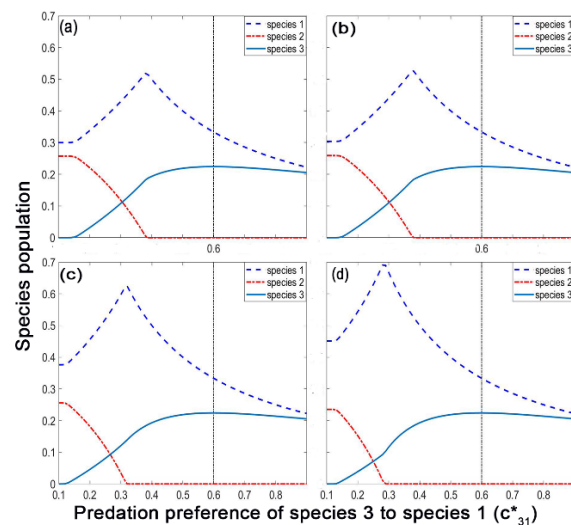
Figure 2. Relationship between predation preference of introduced species 3 to species 1 and population density. The four subgraphs represent four dispersal methods of species 2, (a): global dispersion ($c^*_{21} = 0.5$, $c_{21} = 0$), (b): partial global dispersion ($c^*_{21} = 0.4$, $c_{21} = 0.1$), (c): partial local dispersion ($c^*_{21} = 0.1$, $c_{21} = 0.4$), (d): local dispersion ($c^*_{21} = 0$, $c_{21} = 0.5$). Other parameters: $b_1 = 0.7$; $d_1 = 0.1$; $d_2 = 0.15$; $d_3 = 0.2$; $T_1 = 20$; $c^*_{32} = 0.6$.

Next, we fixed the predation preference of control species to native species 1, i.e., $c^*_{31} = 0.3$, to explore the relationship between the predation preference of control species for invasive species and population density (Figure 3). Figure 3(a−d) indicate that species 3 cannot survive when the predatory preference of species 3 to species 2 is small, consistent with conclusions from Figure 2. And the four charts all show that when meeting the living conditions of the control species, with the increase of the predation preference of species 3 over species 2, the density of species 2 decreased, and that of species 1 increased, indicating that the greater the predation preference of species 3 to species 2, the better the control effect, which is consistent with our conjecture. In addition, comparing Figure 3(a) and 3(d), when species 2 disperses locally and the predatory preference of species 3 to species 2 reaches around 0.4, species 2 is extinct. After that, species 3 and species 1 exist in a stable state. And the density of native species reaches the maximum, indicating that locally dispersed invasive species are more easily controlled, which is consistent with the results shown in Figure 2.
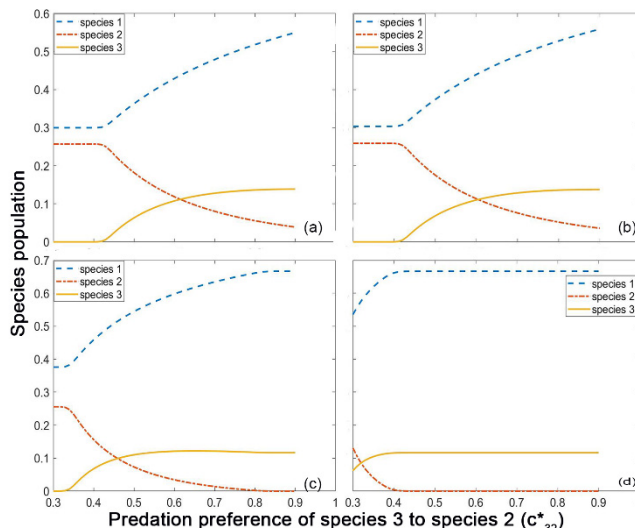
Figure 3. Relationship between predatory preferences of control species towards invasive species and population density. The four subgraphs represent four dispersal methods, (a): global dispersion, (b): partial global dispersion, (c): partial local dispersion, (d): local dispersion. c_{21}, c_{21}^* is consistent with Figure 2. Other parameters: $b_1 = 0.7$; $d_1 = 0.1$; $d_2 = 0.15$; $d_3 = 0.2$; $T_1 = 20$; $c_{31}^* = 0.3$.
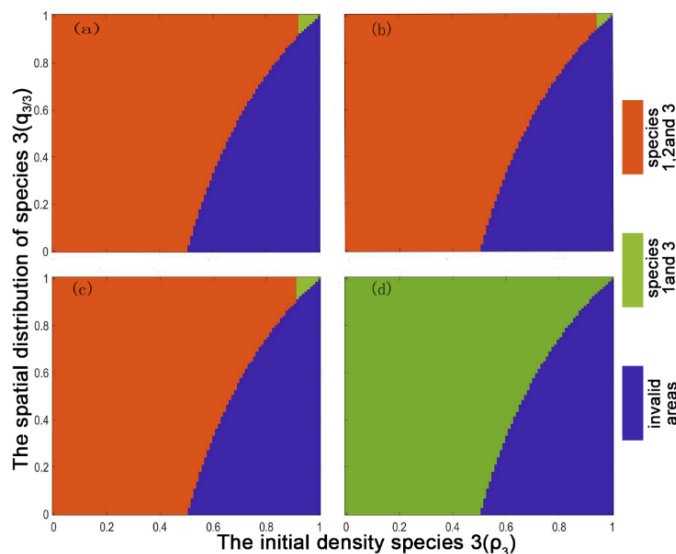

Figure 4. Control effects under different initial densities and initial spatial distributions of control species. Blue indicates invalid areas, i.e., the range that does not satisfy inequality $2-1/\rho_3 < q_{3/3} < 1$ [25]; red indicates the coexistence of species 1−3; and green indicates that species 2 are extinct and species 1 and 3 coexist. The four subgraphs represent four dispersal methods, (a): global dispersion, (b): partial global dispersion, (c): partial local dispersion, (d): local dispersion. c_{21}, c_{21}^* are consistent with Figure 2. Other parameters: $b_1 = 0.7$; $d_1 = 0.1$; $d_2 = 0.15$; $d_3 = 0.2$; $T_1 = 20$; $c_{31}^* = 0.3$; $c_{32}^* = 0.6$.

The effects of the initial density and initial spatial distribution of control species on species density are explored (Figure 4). The time for releasing species 3 is set to $T_1 = 20$. It can be seen from Figure 4(a−c) that when species 2 does not fully adopt local dispersion, species 2 will only become extinct when the initial density and aggregation of species 3 are high. It can be concluded that the extinction of the invasive species is closely related to the initial density and concentration of the control species. But Figure 4(d) shows that when species 2 adopts completely local dispersion strategy, invasive species 2 will become extinct when it reaches a steady state, regardless of the initial density and aggregation of species 3. It shows that the dispersion strategy of invasive species 2 is also closely related to the control effect, which is consistent with the relevant conclusions shown in Figures 2 and 3.
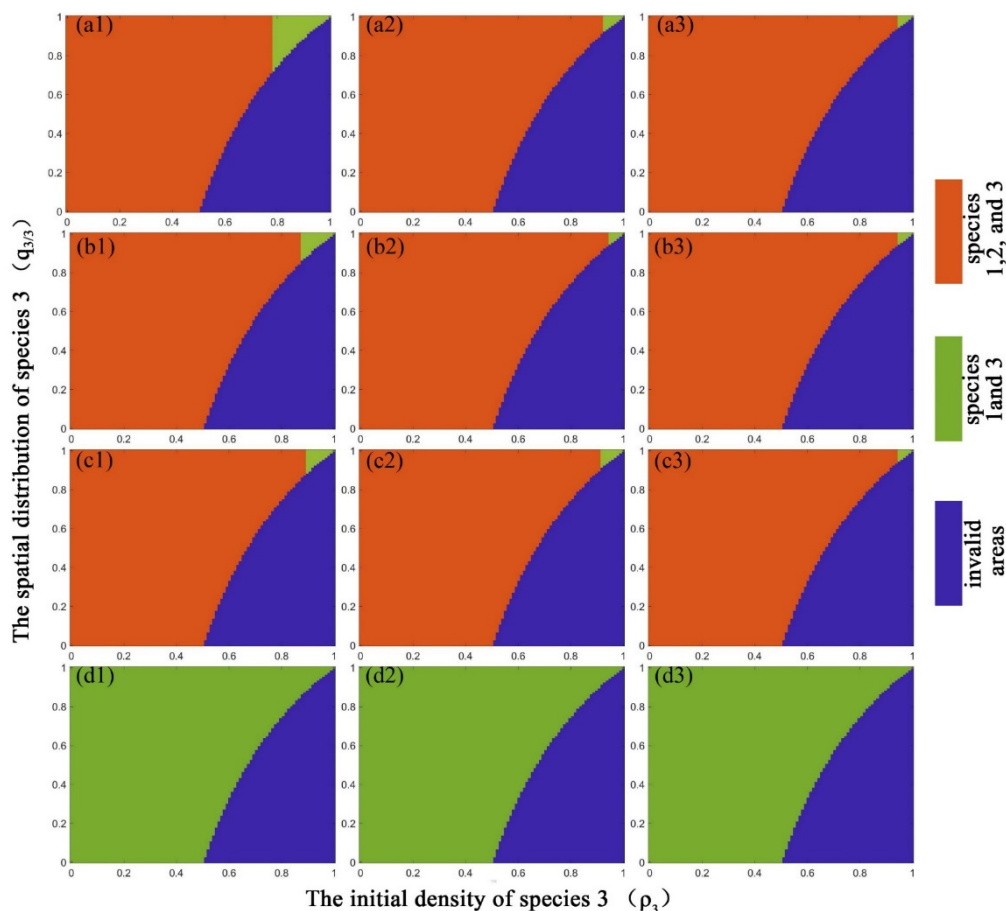

Figure 5. Control effects of species 3 at different introduction times. The three columns represent three different introduction times, (a1−d1): $T_1 = 10$; (a2−d2): $T_1 = 20$; (a3−d3): $T_1 = 40$. The four rows represent four diffusion methods, (a): global dispersion, (b): partial global dispersion, (c): partial local dispersion, (d): local dispersion. c_{21}, c^*_{21} are consistent with Figure 2. Other parameters: $b_1 = 0.7$; $d_1 = 0.1$; $d_2 = 0.15$; $d_3 = 0.2$; $c^*_{31} = 0.3$; $c^*_{32} = 0.6$.

The control effects of control species on invasive species at different time nodes are explored (Figure 5). The four rows represent four dispersal methods, and the three columns represent three nodes of introducing species 3. By comparing the three maps in each row of Figure 5, it can be found that regardless of the dispersal strategy of invasive species, the earlier species 3 is introduced, the larger

the area of extinction of invasive species, indicating the better the effect of biological control, which is consistent with the actual situation. By comparing the degree of change in every row, we found that when the invasive species took global dispersion (Figure 5(a1−a3)), the starting time had the greatest impact on the control effect, so for invasive species with global dispersion, the starting time was important. But when invasive species take local dispersion, no matter when the control begins, the invasive species will eventually become extinct (d1−d3). In addition, comparing Figure 5(a1−c1), we found that when time to start prevention $T_1 = 10$, globally dispersed invasive species were more likely to become extinct, probably because the distribution of invasive species with global dispersal is more scattered, while the control species are released quickly, and interspecific competition is relatively large. However, compared with Figure 5(a2−c2), and (a3−c3), when time to start prevention $T_1 = 20$ or 40, the difference in the control effect of different dispersal strategies was very small, indicating that the later the control starts, the smaller the impact of the dispersal strategy of invasive species on the outcome, probably because species 3 is released late, and there are many species2, and more control species are needed to eliminate species 2.

4. Discussion

The main reasons for the success of species invasions are the environment suitability and the lack of natural enemies. Globalization causes biological invasions occurring more frequently, rabbits invading Australia, Asian carp and tongue fish invading the United States being 2 examples. Of course, invasions are not always successful, such as the crayfish, bullfrogs, tilapia and other species on our dining table, but for those invasive species with strong fertility and great harm, prevention and control measures must be taken.

In order to model the invasion process and the prevention process, some assumptions were made. First, some studies have shown that the higher the trophic level of a population, the more likely it is to disperse over long distances [37,38]. Therefore, this study assumes that native species, invasive species, and control species disperse locally, mixed, and globally, respectively. Second, according to the hypothesis of the nutritional cascade [39,40], the omnivorous nature of species affects interactions within the food web, so it is assumed that control species have a predation preference. Third, considering spatial structure, the density and aggregation of the control species can be described by Hiebeler's algorithm [25,41]. Based on the above assumptions, the complex invasion and control process is shown in Figure. Selecting the right natural enemy can not only effectively control the invasion, but also reduce possible pollution of drugs to the environment due to drugs spraying.

Obviously, control species with appropriate predation preferences for native species should be selected (Figure 2). When the predation preference of the control species to the native species is low, the control species cannot survive and cannot play a role, whereas when the predation preference of the control species for the native species is too high, the control species will become a new harmful invasive species, which will have a serious impact on the local ecology. Jamaica introduced too much *Herpestes javanicus* to control house rats, eventually the number of house rats decreased less than expected, and *Herpestes javanicus* nibbled on a large number of crops, becoming a new harmful species, with indelible effects on the local ecology [42], consistent with the conclusions of this study (Figure 2(a−d)). Besides, the predatory preference of *Beroe ovatas* for *Mnemiopsis leidyis* is large enough to control the growth of *Mnemiopsis leidyis* [43] without causing ecological damage. Therefore, before implementing biological control, it is necessary to conduct researches on the predation

preferences of introduced species to avoid unforeseen consequences.

The more locally dispersed the strategy of an invasive species, the smaller the extinction threshold for the species (Figure 2). For biological interference, invasive species with a local dispersion strategy are easier to control. There may be two reasons. First, invaders can only breed by preying on native species, so the larger the range they can prey, the more likely they are to reproduce successfully, which means that global predation strategies are more beneficial to invasion. This guess echoes the result obtained by Johst et al. [44], who found that long-distance dispersion has a positive effect on species persistence in the landscape. Second, local dispersion strategies will largely lead to the aggregation of invasive species, which will become extinct more quickly due to the relatively strong intraspecific competition [45].

We found that the greater the predation preference of control species for invasive species, the easier they are to be targeted species for control (Figure 3). Some invasion facts can be explained by the results of this model. For example, when planthoppers invade rice fields, ducks or fish put to the field after rice grows to a certain height helps. The rice at this time is relatively tall, and fish and ducks have less negative impact on rice. It can be considered that fish and ducks have a higher predation preference for planthoppers, so as to achieve a good control effect [46]. There is also the case of *Mosquitofish*, when *Mosquitofish* invade the habitat of *Oryzias latipes*, people will introduce birds or fish to control the number of *Mosquitofish*, but the introduction of birds does not effectively control the situation [47], largely because birds do not have a large preference in predation on *Mosquitofish* and other fish. In addition, because ladybug have predation specificity, they are often used to control *Aphis gossypii* [48]. Therefore, species with stronger specific predation to invasive species are more suitable as candidate species for biological control, which is consistent with the previous findings [49].

When and how many to release the target species after being selected is under discussion. First of all, for the time of introduction, as we expected, the earlier the introduction, the better the prevention and treatment effect, which is the same as the conclusion of the drug release [32]. This conclusion may also explain the following example, where invasive seagrass was discovered in the Mediterranean Sea and no measures taken, it spread over a total of more than 100 square kilometers around it in the following decade [50]. Therefore, we must achieve early detection and early control of invasive species. For the initial number of introduced species, the greater the initial density of the control species, the more possible the invasive species on the verge of extinction (Figure 5). But when the initial density is not very sufficient, even if the invasive species are not exterminated, it will be smaller than density of the native species (Figures 2 and 3), at which time we also think that the control is effectual. For the initial concentration, the greater the initial concentration of the control species, the more possible the invasive species on the verge of extinction (Figures 4 and 5).

This study gives some suggestions on how to select the target species for biological control, how to determine the amount and time released by the target species: 1) Early detection and early control; 2) Compared with global dispersion, local dispersing invasive species are easier to control; 3) Natural enemies with higher predation preference for invasive species are best choice as control species, especially species with specificity predation; 4) For introduced species that hunt globally, the initial release density and aggregation has a positive impact on the control effect. These conclusions provide some insights into solving the problem of biological invasion, which is of practical significance.

Acknowledgments

Conflict of interest

All authors declare no conflicts of interest in this paper.

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Appendix

A. The dynamic structure of pair sites

The dynamic of ρ_1 in Eq (1) is explained as follows, a part will cause the growth: (a) Empty sites are colonized in adjacent species 1, which denoted by $b_1\rho_1 (1 - q_{1/1} - q_{2/1})$. Three parts will reduce ρ_1: (b1) The intrinsic death of species 1, which denoted by $-d_1\rho_1$. (b2) Species 1 is killed by neighbor species 2. Denoted by $-c_{21}\rho_1 q_{2/1}$. (b3) Species 1 is killed by arbitrary species 2 of all lattice. Denoted by $-c^*_{21}\rho_1\rho_2$.

The dynamic of ρ_2 in Eq (2) is explained as follows, two parts will cause the growth: (a1) Species 1 is killed by neighbor species 2. Denoted by $c_{21}\rho_2 q_{1/2}$. (a2) Species 1 is killed by arbitrary species 2 of all lattice. Denoted by $c^*_{21}\rho_2\rho_1$. A part will reduce ρ_2: (b) The intrinsic death of species 2, which denoted by $-d_2\rho_2$.

The dynamic of ρ_{11} in Eq (3) is explained as follows, the two parts will cause the growth: (a1) Empty site of pair sites <10> is occupied by species 1 of the left of empty site, and <01> was the same as <10>, which denoted by $2b_1\rho_{10}(1/z)$. (a2) The empty site of <10> is occupied by species 1 in the neighborhood except for the left neighbor, as is <01>, which denoted by $2b_1\rho_{10}q_{1/01}(z-1)/z$. Three parts will reduce ρ_{11}: (b1) The death of pair sites <11>, which denoted by $-2\rho_{11}d_1$. (b2) Species 1 of pair sites <11> is killed by neighbor species 2. Denoted by $-2\rho_{11}c_{21}q_{2/11}(z-1)/z$. (b3) Species 1 of pair sites <11> is killed by arbitrary species 2 of all lattice. Denoted by $-2\rho_{11}c^*_{21}\rho_2$.

The dynamic of ρ_{22} in Eq (5) is explained as follows, the three parts will cause the growth: (a1) Species 1 of pair sites <12> is killed by species 2 of the right of species 1, as is <21>, which denoted by $2\rho_{12}c_{21}(1/z)$. (a2) Species 1 of pair sites <12> is killed by species 2 in the neighborhood except for the right neighbor, as is <21>, which denoted by $2\rho_{12}c_{21}q_{2/12}(z-1)/z$. (a3) Species 1 of pair sites <12> is killed by arbitrary species 2 of all lattice, which denoted by $2\rho_{12}c^*_{21}\rho_2$. A part will reduce ρ_{11}: (b) The death of pair sites <22>, which denoted by $-2\rho_{22}d_2$.

After the introduction of species 3, the structure of the food chain has changed since species 3 feeds on species 1 and 2, assuming that at the moment of introduction of species 3, species 1 and species 2 in the area where species 3 is located will be eaten, so that ρ_i^+ and ρ_{ij}^+ represent the density of single site and pair sites at the moment of the introduction of species 3. The density of species 1 and 2 will become:

$$\rho_i^+ = \rho_i(1 - \rho_3) \quad i = 1,2. \tag{A1}$$

Let $\rho_{3^-3^-}$ indicate the density of pair sites that are not occupied by species 3 at the moment of the introduction of species 3, then:

$$\rho_{ij}^+ = \rho_{ij}\rho_{3^-3^-} \quad i,j = 1,2. \tag{A2}$$

Based on the fact that the sum of the densities of pair sites is equal to the density of the corresponding single site, we can obtain:

$$\rho_{13}^+ = \rho_1^+ - \rho_{10}^+ - \rho_{11}^+ - \rho_{12.}^+ \tag{A3}$$

From Eq (6) to know constraint $\rho_1 = \rho_{10} + \rho_{11} + \rho_{12}$, substituting (A1 and A2) into (A3), simplifying to get the density of sites <13>:

$$\rho_{13}^+ = \rho_1(1 - \rho_3 - \rho_{3^-3^-}). \tag{A4}$$

The same can be obtained to the density of sites <23>:

$$\rho_{23}^+ = \rho_2(1 - \rho_3 - \rho_{3^-3^-}). \tag{A5}$$

According to the ideas of Liao et al. (2016), there are:

$$\rho_{3^-3^-} = \rho_{3^-} - \rho_{3^-3} = 1 - \rho_3 - (\rho_3 - \rho_{33}) = 1 - 2\rho_3 + \rho_3 q_{3/3}. \tag{A6}$$

where $\rho_{33} = \rho_3 q_{3/3}$, substituting (A6) into (A2) (A4-5) yields the (6).

B. Simulation of multiple parameter values

To prove that the results obtained in this study are general, we selected multiple parameter values that are biologically significant and found that they do not change our general conclusions.

First, the parameter values of the dispersal strategy of invasive species were changed (Figures B1−B4), and compared with Figures 2 and 3, it was obvious that although the population density changed, the conclusions in Figures B1−B4 are consistent with those in Figures 2 and 3.
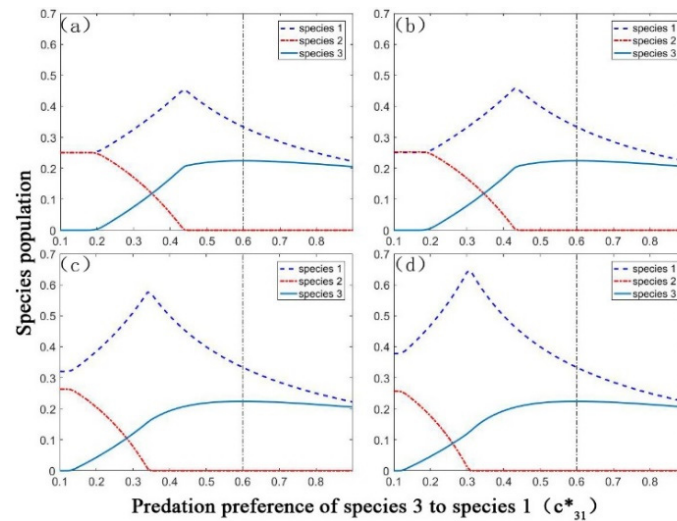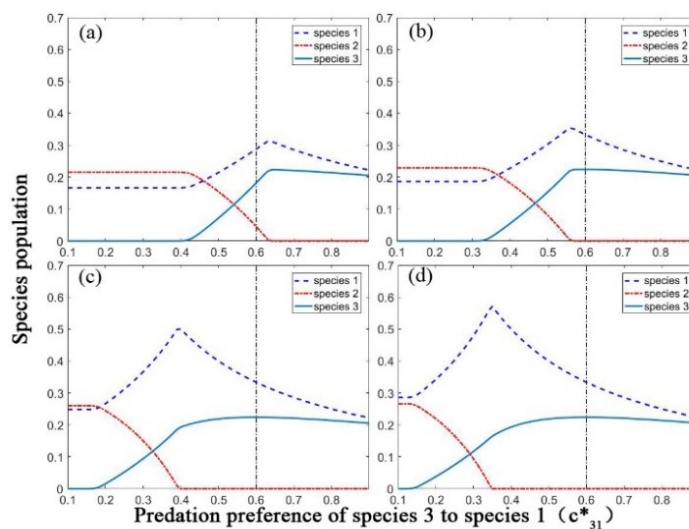
Figure B1. The relationship between the predation preference of introduced species to species 1 and species density. (a): Species 2 takes global dispersion ($c^*_{21} = 0.6$, $c_{21} = 0$). (b): Species 2 is partially global dispersed ($c^*_{21} = 0.5$, $c_{21} = 0.1$). (c): Species 2 is partially local dispersed ($c^*_{21} = 0.1$, $c_{21} = 0.5$). (d) Species 2 takes local dispersion ($c^*_{21} = 0$, $c_{21} = 0.6$). The other parameters are the same as Figure 2.
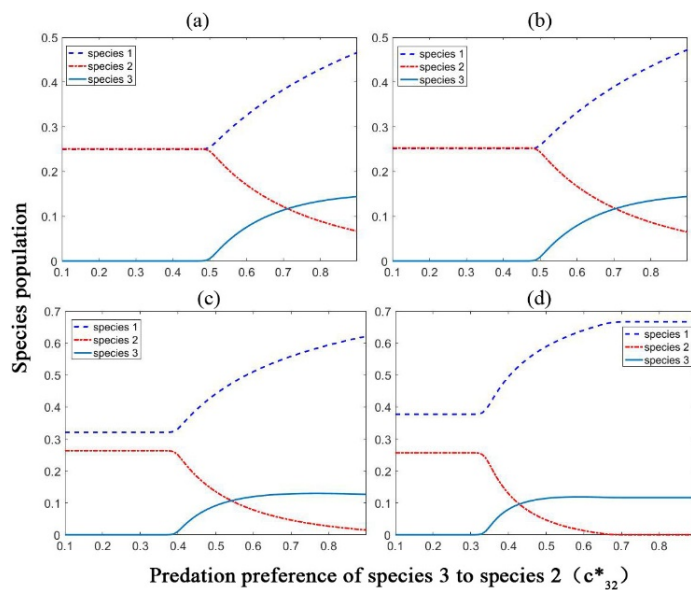

Figure B2. The relationship between the predation preference of introduced species to species 1 and species density. (a): Species 2 takes global dispersion ($c^*_{21} = 0.8$, $c_{21} = 0$). (b): Species 2 is partially global dispersed ($c^*_{21} = 0.7$, $c_{21} = 0.1$). (c): Species 2 is partially local dispersed ($c^*_{21} = 0.1$, $c_{21} = 0.7$). (d): Species 2 takes local dispersion ($c^*_{21} = 0$, $c_{21} = 0.8$). The other parameters are the same as Figure 2.

Figure B3. The relationship between the predation preference of species 3 to species 2 and species density. Let $c^*_{31} = 0.3$, other parameters are the same as Figure B1.
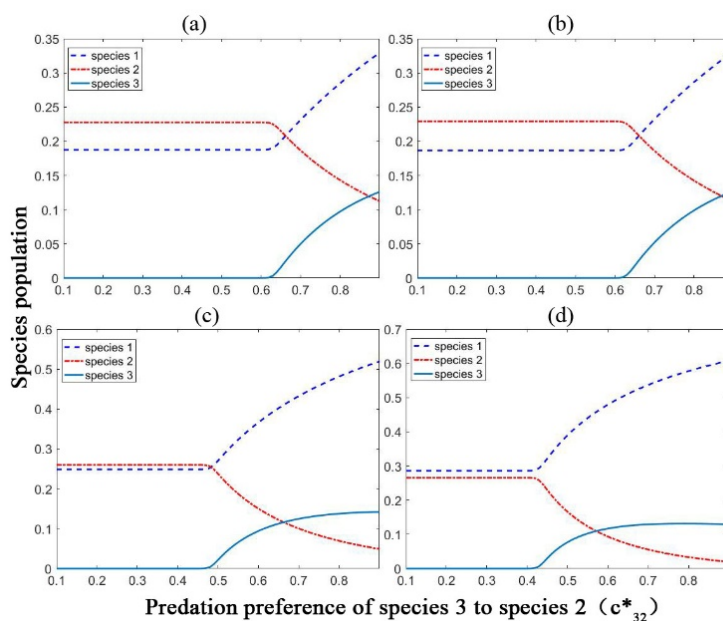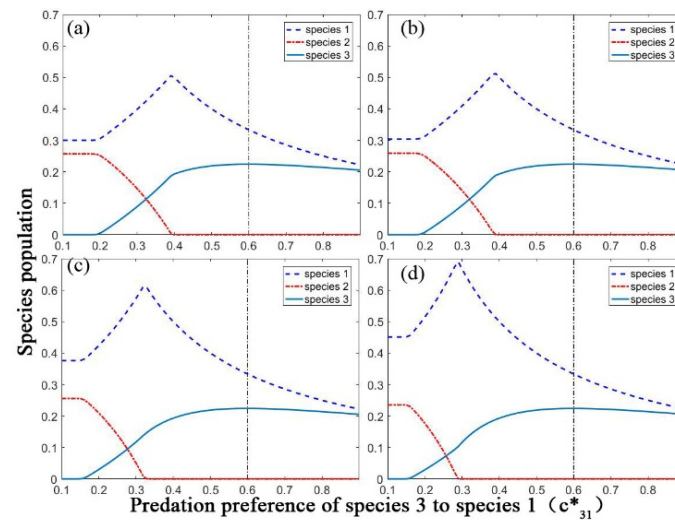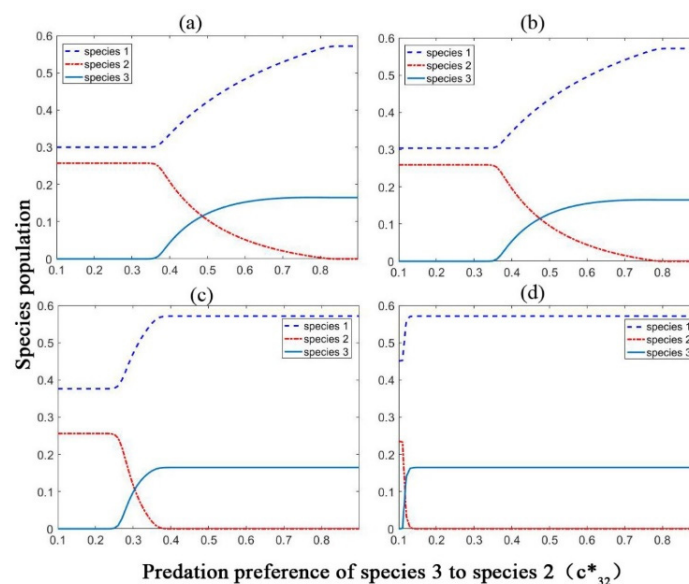

Figure B4. The relationship between the predation preference of species 3 to species 2 and species density. Let $c^*_{31} = 0.3$, other parameters are the same as Figure B2.

Then, the predation preference of the introduced species was changed to $c^*_{32} = 0.55$ and $c^*_{31} = 0.35$, respectively (Figures B5 and B6), and the trends were also consistent with Figures 2 and 3.

Figure B5. The relationship between the predation preference of species 3 to species 1 and species density. Let $c^*_{32} = 0.55$, other parameters are the same as Figure 2.

Figure B6. The relationship between the predation preference of species 3 to species 2 and species density. Let $c^*_{31} = 0.35$, other parameters are the same as Figure 3.

Finally, the corresponding parameter values were determined by simulating the effects of different birth and death rates of the three species. we changed the birth rate of native species ($b1 = 0.5$) and explored the control effects under different initial densities and initial spatial distribution of control species (Figure B7). Figure B7(d) found that invasive species with local dispersion are not always extinct, which is somewhat different from Figure 5(d). This may be due to the higher birth rates of native species, and according to the bottom-up cascade effect, the density of invasive species increased accordingly, keeping invasive species from going extinct, but other conclusions are unanimous. As for the selection of birth and death rates of native species, the stable population density of the native

population under different death rates and birth rates without the influence of invasion was considered, as shown in Figure B8. As the predation invasion model was established in the paper, the medium and high population density was selected, i.e., $b1 = 0.7$, $d1 = 0.1$. Then the birth and death rates of invasive species were determined, and the population density corresponding to different predation rates and death rates of invasive species under different dispersal modes was explored, as shown in Figure B9. In selecting the mortality rate of introduced species, the influence of the mortality rate of introduced species was studied by fixing the predation preference for native and invasive species and considering different dispersal modes of invasive species, as shown in Figure B10.
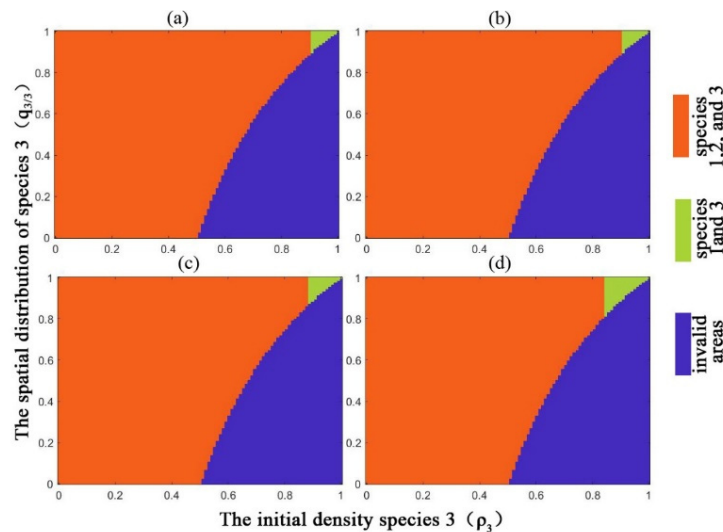

Figure B7. Control effects of control species under different initial densities and initial spatial distributions. Let $b_1 = 0.5$, other parameters are consistent with Figure 2.
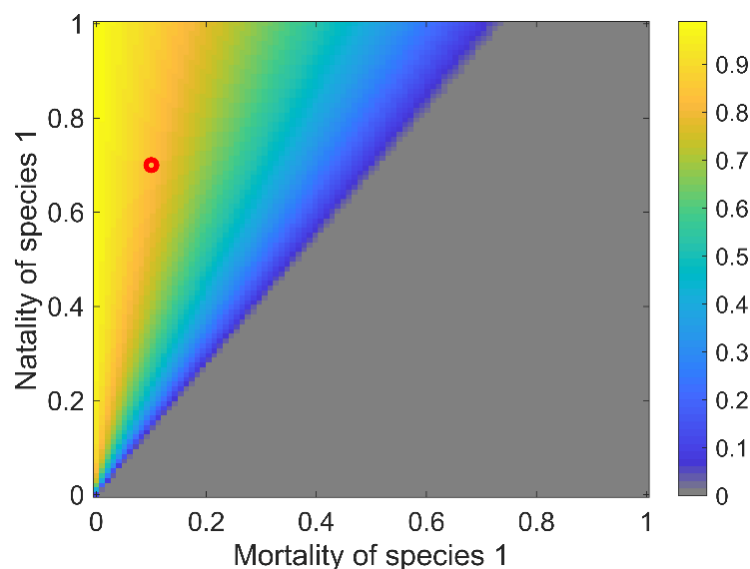

Figure B8. Final population densities for different mortality and birth rates of native species without invasive effects. Different colors represent different densities of native species. The red circle is the parameter group selected in this paper ($b_1 = 0.7$, $d_1 = 0.1$).
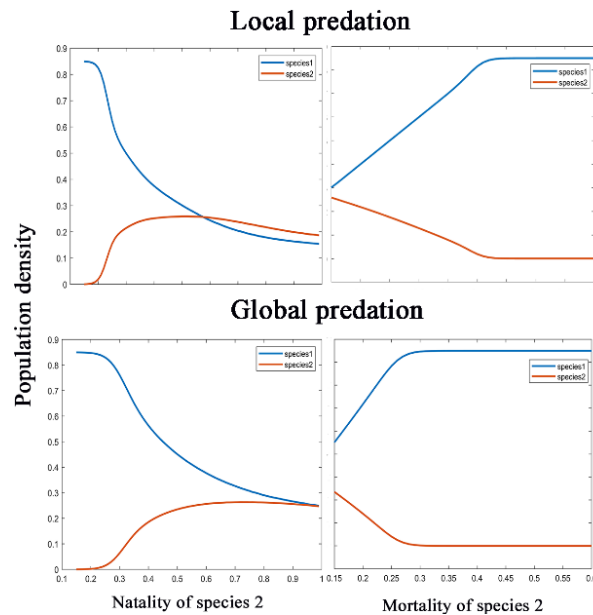
Figure B9. Effects of mortality and birth rate of invasive species on density under different predation strategies. The two figures on the left: $d_2 = 0.15$; on the right: $c^*_{21} = 0.5$, $c_{21} = 0$ (bottom), $c_{21} = 0.5$, $c^*_{21} = 0$ (top). Other parameters: $b_1 = 0.7$, $d_1 = 0.1$.
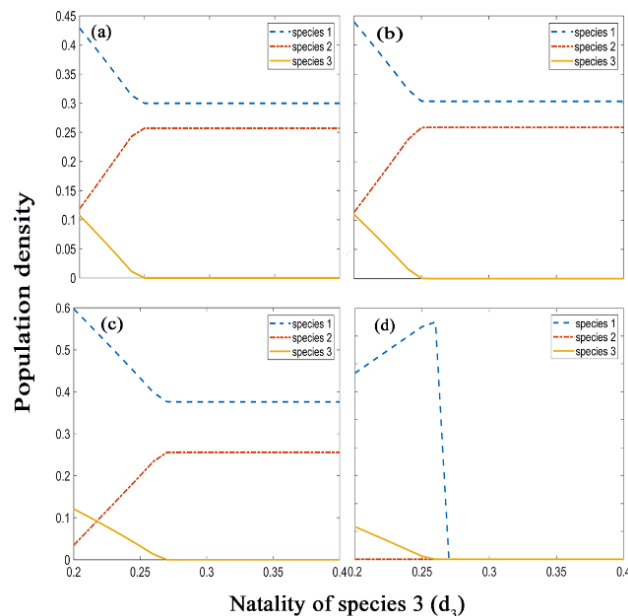

Figure B10. The effect of introduced species mortality on the final density of the three species. (a): global dispersion ($c^*_{21} = 0.5$, $c_{21} = 0$), (b): partial global dispersion ($c^*_{21} = 0.4$, $c_{21} = 0.1$), (c): partial local dispersion ($c^*_{21} = 0.1$, $c_{21} = 0.4$), (d): local dispersion ($c^*_{21} = 0$, $c_{21} = 0.5$). Other parameters: $c^*_{31} = 0.3$; $c^*_{32} = 0.6$; $b_1 = 0.7$; $d_1 = 0.1$; $d_2 = 0.15$.

It can be seen from the figures above that the selection of parameters only affects the final density of the population without affecting the overall trend. The same conclusion can be obtained by selecting different parameter groups, so we choose global dispersion ($c^*_{21} = 0.5$, $c_{21} = 0$), partial

global dispersion ($c^*_{21} = 0.4$, $c_{21} = 0.1$), partial local dispersion ($c^*_{21} = 0.1$, $c_{21} = 0.4$), and local dispersion ($c^*_{21} = 0$, $c_{21} = 0.5$), $b_1 = 0.7$, $d_1 = 0.1$, $d_2 = 0.15$, $d_3 = 0.2$, $c^*_{31} = 0.3$ and $c^*_{32} = 0.6$.