

Research Article

Pattern Dynamics in a Predator-Prey Model with Diffusion Network

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Diffusion plays an essential role in the distribution of predator and prey. We mainly research the diffusion network's effect on the predator-prey model through bifurcation. First, it is found that the link probability and diffusion parameter can cause Turing instability in the network-organized predator-prey model. Then, the Turing stability region is obtained according to the sufficient condition of Turing instability and the eigenvalues' distribution. Finally, the biological mechanism is explained through our theoretical results, which are also illustrated by numerical simulation.

1. Introduction

Turing instability was first investigated in the reaction-diffusion system [1], and it is constantly being promoted to explain the dynamical mechanism [2, 3]. Asllani et al. pointed out that the directed network could induce Turing instability when an indirect network does not work [4, 5]. Meanwhile, tuning the topology structure of the system can create or destroy patterns in a reaction-diffusion system [6]. Mimar et al. proved that the pattern formation's topological properties are determined by complex interaction [7]. Although spontaneous patterns [8] are associated with the dominance of eigenvectors and eigenvalues [9–11], the dynamical mechanism of the random network in pattern formation remains to be uncovered.

Since the Lotka–Volterra model was proposed in the early twentieth century, some biological mechanisms were explained in the predator-prey system [12–18]. Chang et al. researched the dynamics in the predator-prey system on complex networks and found that Turing instability caused by delay can generate spiral waves [19]. Liu et al. showed the effect of network and diffusion on the ecological balance of the predator-prey system [20]. Upadhyay and Bhattacharya studied the differences between the aqueous and terrestrial environments in predator-prey networks and tried to

explain their biological mechanism [21]. Astarloa et al. tried to use the joint species distribution modeling to reveal the coexistence problem of prey and predator in the Bay of Biscay [22]. Although previous work shows that diffusion and randomness influence the Turing pattern significantly, the random network's effect on the distribution of predator and prey should be carefully evaluated.

To reveal the natural mechanism of biological invasion, we intend to investigate the random diffusion network's effect on the network-organized predator-prey model's stability. First, we obtain the conditions under which Turing bifurcation arises. Second, we find an estimated region of all the eigenvalues of the Laplacian matrix, the sufficient stability conditions in the network-organized predator-prey model. Third, we explain the network-organized Turing instability by the mean-field approximation and comparison principle. Also, we estimate the Turing instability range about link probability and diffusion and try to explain the mechanism of biological invasion. Last, we illustrate our theoretical results through numerical simulation.

2. A Network-Organized Predator-Prey Model

For the convenience of subsequent research, we first give some necessary symbolic rules. The network Laplacian

matrix $L = \{L_{ij}\}$ can be treated as $L_{ij} = A_{ij} - k_i \delta_{ij}$, and all the eigenvalues of L are $\Lambda = \{\Lambda_i\}$. The eigenvectors $\phi_i \in R^n$ of Λ_i satisfy $L\phi_i = \Lambda_i \phi_i$, $i = 1, \dots, n$. L is real symmetric, and we choose an orthonormal basis for $\phi_i \phi_j = \delta_{ij}$, where the degree of node i is k_i , and δ_{ij} is the Kronecker delta function.

We consider the following predator-prey system:

$$\begin{aligned} \frac{dx}{dt} &= x[r_1 - a_{11}x - a_{12}y], \\ \frac{dy}{dt} &= y[r_2 + a_{21}x - a_{22}y], \end{aligned} \quad (1)$$

where x and y are prey and predator, respectively. r_1 represents the intrinsic growth rate, a_{12} is the proportionality coefficient of predator and prey, and a_{21} is the growth rate of the predator; the predator increases exponentially with ratio r_2 (actually $r_2 < 0$ means the number of predators decreases exponentially). According to Samuelson's assumptions [23], a_{11} and a_{22} represent increasing returns or decreasing returns, respectively. Among them, $a_{ii} > 0$ (< 0), ($i = 1, 2$)

correspond to increasing returns (decreasing returns). System (1) correspond to the mixed-income when $a_{11}a_{22} \leq 0$.

System (1) always has three equilibria $E_0 \triangleq (0, 0)$, $E_1 \triangleq (r_1/a_{11}, 0)$, and $E_2 \triangleq (0, r_2/a_{22})$. System (1) also have fourth equilibrium point $E_3 \triangleq (x^*, y^*) \triangleq (r_1a_{22} - r_2a_{12}/a_{11}a_{22} + a_{12}a_{21}, r_1a_{21} + r_2a_{11}/a_{11}a_{22} + a_{12}a_{21})$ when $r_1a_{22} - r_2a_{12}/a_{11}a_{22} + a_{12}a_{21} > 0$, $r_1a_{21} + r_2a_{11}/a_{11}a_{22} + a_{12}a_{21} > 0$. On the basis of Hopf bifurcation's definition, we need to satisfy $tr(J_{E_3}) = 0$, $\det(J_{E_3}) > 0$. The critical value for bifurcation is a positive root of $tr(J_{E_3}) = 0$ and the bifurcation parameter is $a_{12} = a_{12}^*$ which satisfies $\det(J_{E_3}) > 0$,

$$\begin{aligned} a_{12} &= \frac{(r_1 + r_2)a_{11}a_{22} + r_1a_{21}a_{22}}{r_2a_{11}} \triangleq a_{12}^*, \\ \frac{r_2(r_1a_{21} + r_2a_{11})}{a_{11} + a_{21}} &< 0. \end{aligned} \quad (2)$$

Then, we give the condition of Hopf bifurcation. Firstly, we verify the transversality condition [24].

$$\begin{aligned} \frac{d}{da_{12}} tr(J(x^*, y^*)) \Big|_{a_{12}=a_{12}^*} &= \frac{a_{22}(a_{11} + a_{21})(r_1a_{21} + r_2a_{11})}{(a_{11}a_{22} + a_{12}a_{21})^2} \Big|_{a_{12}=a_{12}^*} \\ &= -\frac{(r_2a_{11})^2}{a_{22}(a_{11} + a_{21})(r_1a_{21} + r_2a_{11})} \neq 0. \end{aligned} \quad (3)$$

Then, we compute the first Lyapunov coefficient [25]. Let $a_{12} = a_{12}^*$, then $(x^{*c}, y^{*c}) = (-r_2/a_{11} + a_{21}, (r_2a_{11}/a_{22}(a_{11} + a_{21})))$. Making the following shift

$$\begin{aligned} X &= x - x^{*c}, \\ Y &= y - y^{*c}. \end{aligned} \quad (4)$$

(1) becomes

$$\begin{aligned} \dot{X} &= \alpha_{10}X + \alpha_{01}Y + \alpha_{20}X^2 + \alpha_{11}XY, \\ \dot{Y} &= \beta_{10}X + \beta_{01}Y + \beta_{11}XY + \beta_{02}Y^2, \end{aligned} \quad (5)$$

where $\alpha_{10} = -a_{11}x^{*c}$, $\alpha_{01} = -a_{12}x^{*c}$, $\alpha_{20} = -a_{11}$, $\alpha_{11} = -a_{12}$, $\beta_{10} = a_{21}y^{*c}$, $\beta_{01} = -a_{22}y^{*c}$, $\beta_{11} = a_{21}$, $\beta_{02} = -a_{22}$.

The first Lyapunov coefficient at $a_{12} = a_{12}^*$ can be computed by the formula

$$\begin{aligned} l_1 &= \frac{-3\pi}{2\alpha_{01}\Delta^{3/2}} \left\{ \left[\alpha_{10}\alpha_{01}(\beta_{11}^2 - 2\alpha_{20}^2 + \alpha_{20}\beta_{11} + \alpha_{11}\beta_{02}) + \alpha_{10}\beta_{10}(\alpha_{11}^2 - 2\beta_{02}^2 + \alpha_{11}\beta_{02}) \right] \right. \\ &\quad \left. + \alpha_{01}\beta_{10}(\beta_{11}\beta_{02} - \alpha_{11}\alpha_{20}) \right\} - 2\alpha_{10}^2\beta_{11}\beta_{02} + 2\alpha_{10}^2\alpha_{11}\alpha_{20} \\ &= \frac{-3\pi}{2} \left(\frac{a_{11} + a_{21}}{r_2(r_1a_{21} + r_2a_{11})} \right)^{3/2} \frac{(r_1a_{21} + r_1a_{11} + r_2a_{11})a_{22}^2}{a_{11} + a_{21}}, \end{aligned} \quad (6)$$

where $\Delta = \alpha_{10}\beta_{01} - \alpha_{01}\beta_{10} > 0$, $\alpha_{10} + \beta_{01} = 0$, and if $l_1 < 0$ (> 0), the Hopf bifurcation is supercritical (*resp.* subcritical).

When $r_1a_{22} - r_2a_{12}/a_{11}a_{22} + a_{12}a_{21} > 0$, $r_1a_{21} + r_2a_{11}/a_{11}a_{22} + a_{12}a_{21} > 0$, E_3 changes its stability, and Hopf bifurcation occurs if $a_{12} = a_{12}^*$.

Typically, the distribution of individuals is spatially heterogeneous. So, we research (1) with a reaction-diffusion and network as follows:

$$\begin{aligned} \frac{dx_i}{dt} &= x_i[r_1 - a_{11}x_i - a_{12}y_i] + d_1\nabla^2 x_i, \\ \frac{dy_i}{dt} &= y_i[r_2 + a_{21}x_i - a_{22}y_i] + d_2\nabla^2 y_i, \end{aligned} \quad (7)$$

where d_1, d_2 are the diffusion constants.

Generally, we can regard diffusion as an interplay between network nodes. In this article, we consider a distinctive interaction between nodes. So the network-organized system (7) is

$$\frac{dx_i}{dt} = x_i[r_1 - a_{11}x_i - a_{12}y_i] + d_1 \sum_j L_{ij}x_j, \quad (8)$$

$$\frac{dy_i}{dt} = y_i[r_2 + a_{21}x_i - a_{22}y_i] + d_2 \sum_j L_{ij}y_j.$$

The linearized network-organized system of the system (8) is

$$\frac{dx_i}{dt} = \alpha_{10}x_i + \alpha_{01}y_i + d_1 \sum_j L_{ij}x_j, \quad (9)$$

$$\frac{dy_i}{dt} = \beta_{10}x_i + \beta_{01}y_i + d_2 \sum_j L_{ij}y_j.$$

The general solution of the linear network-organized system can be expressed as [3].

$$x_i = \sum_{k=1}^N c_k \beta_k e^{\lambda_k t} \phi_i^k, \quad (10)$$

$$y_i = \sum_{k=1}^N c_k e^{\lambda_k t} \phi_i^k,$$

where $\sum_j L_{ij} \phi_j^k = \Lambda_i \phi_i^k$.

Substituting the general solution into system (9), the Jacobian matrix $B_i (i = 1, \dots, n)$ is

$$B_i = \begin{pmatrix} \alpha_{10} + d_1 \Lambda_i & \alpha_{01} \\ \beta_{10} & \beta_{01} + d_2 \Lambda_i \end{pmatrix}, \quad (11)$$

where all the eigenvalues of matrix L can be represented as $\Lambda_i (0 = \Lambda_1 > \Lambda_2 > \dots > \Lambda_N)$. Then, system (8) has the following characteristic function:

$$\lambda^2 + p_{\Lambda_i} \lambda + q_{\Lambda_i} = 0, \quad (12)$$

where $p_{\Lambda_i} = -(\alpha_{10} + \beta_{01}) - (d_1 + d_2)\Lambda_i$, $q_{\Lambda_i} = d_1 d_2 \Lambda_i^2 + (\alpha_{10} d_2 + \beta_{01} d_1) \Lambda_i + \alpha_{10} \beta_{01} + \alpha_{01} \beta_{10}$. Turing instability occurs when there is a Λ_i with $\text{Re} \lambda > 0$. From (12),

$$4d_1 d_2 (\alpha_{10} \beta_{01} + \alpha_{01} \beta_{10}) + (\alpha_{10} d_2 + \beta_{01} d_1)^2 = 0. \quad (13)$$

We can get the Turing instability's critical value about Λ (Skim $d_1 = 0.1562d_2$) in the reaction-diffusion system Figure 1. Note $k_{1c}^2, k_{2c}^2 (k_{1c}^2 < k_{2c}^2)$ as two solutions of $\text{Re} \lambda(k^2) = 0$, $\text{Re} \lambda(k^2) > 0$ holds if $k^2 \in B = \{\lambda | k_{1c}^2 < \lambda < k_{2c}^2\}$ Figure 2 ($d_2 = 2$). Turing instability of the reaction-diffusion system is the Turing instability's prerequisite in the network-organized system. Based on the Gershgorin circle theorem [9, 10], we have.

- (i) Result 1: $k_{\max} = \max\{k_i\}$, $k_{\min} = \min\{k_i\}$ and Λ_i is the eigenvalue of the Laplacian matrix L , then, $\Lambda_i \in C = \{\Lambda_i | -2k_{\max} < \Lambda_i \leq 0\}$.
- (ii) Result 2: in a network-organized system, a system remains stable when no eigenvalue of L stays at the instability range $\Lambda \cap B = \Phi$, Turing instability occurs when $\Lambda \cap B \neq \Phi$, and $B \cap C \neq \Phi$ (C is the set of the

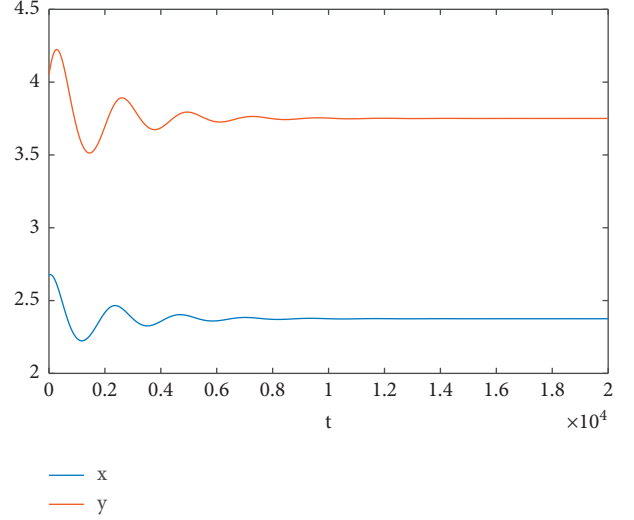


FIGURE 1: The stability of the system (1) without diffusion when $r_1 = 1, r_2 = -1, a_{11} = -1.158, a_{12} = 1, a_{21} = 2, a_{22} = 1$.

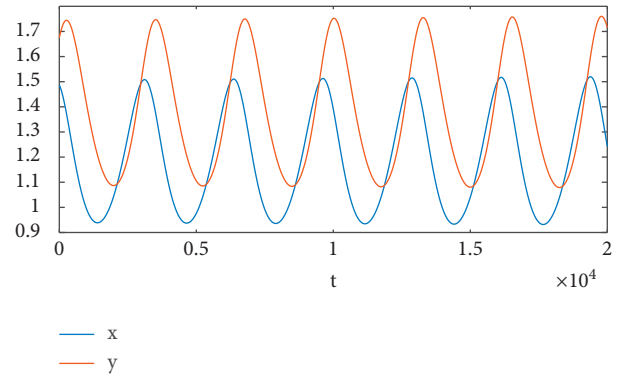


FIGURE 2: The stability of the system (1) without diffusion when $r_1 = 1, r_2 = -1, a_{11} = -1.158, a_{12} = 1.7271, a_{21} = 2, a_{22} = 1$.

eigenvalues of Laplacian matrix) induces the occurring of instability.

To study the mechanism of the network-organized system's stability, we research (8) through the comparison principle: let $x_i = x^* + \varepsilon \hat{x}_i$ and $y_i = y^* + \varepsilon \hat{y}_i$, where $0 < \varepsilon \ll 1$. Substituting x_i, y_i in (9), expanding in ε , we can get the linearized system:

$$\frac{d\hat{x}_i}{dt} = \alpha_{10} \hat{x}_i + \alpha_{01} \hat{y}_i + d_1 L \hat{x}_i, \quad (14)$$

$$\frac{d\hat{y}_i}{dt} = \beta_{10} \hat{x}_i + \beta_{01} \hat{y}_i + d_2 L \hat{y}_i.$$

We resolve the first-order perturbations into ϕ_i 's eigenfunction expansions, to consider the system's stability. Let

$$\hat{x}_i = \hat{X}_i \phi_i, \hat{y}_i = \hat{Y}_i \phi_i, \text{ for each } i = 1, \dots, n. \quad (15)$$

Substituting (15) into (20) and noting the properties of ϕ_i , we obtain

$$\begin{aligned} \frac{d\widehat{X}_i}{dt} &= \alpha_{10}\widehat{X}_i + \alpha_{01}\widehat{Y}_i + d_1\Lambda_i\widehat{X}_i, \\ \frac{d\widehat{Y}_i}{dt} &= \beta_{10}\widehat{X}_i + \beta_{01}\widehat{Y}_i + d_2\Lambda_i\widehat{Y}_i. \end{aligned} \quad (16)$$

Using the comparison principle from [26], we note

$$\frac{d^2Y}{dt^2} + P(t)\frac{dY}{dt} + Q(t)Y = 0, \quad (17)$$

where $Q(t) < 0$. We eliminate one of \widehat{X}_i or \widehat{Y}_i from (16), then

$$\begin{aligned} \frac{d^2\widehat{X}_i}{dt^2} + p_{\Lambda_i}\frac{d\widehat{X}_i}{dt} + q_{\Lambda_i}\widehat{X}_i &= 0, \\ \frac{d^2\widehat{Y}_i}{dt^2} + p_{\Lambda_i}\frac{d\widehat{Y}_i}{dt} + q_{\Lambda_i}\widehat{Y}_i &= 0, \end{aligned} \quad (18)$$

where $p_{\Lambda_i}, q_{\Lambda_i}$ are as in (12). Then, we obtain the generalized condition:

$$\alpha_{10}\beta_{01} + \alpha_{01}\beta_{10} + (d_1\beta_{01} + d_2\alpha_{10})\Lambda_i + d_1d_2\Lambda_i^2 < 0. \quad (19)$$

Assume that the instability condition (19) holds. Then, the homogeneous state $(x_k, y_k) = (x^*, y^*)$ is unstable under the i th Turing mode (15).

We also consider the system (8) through the mean-field theory:

$$\begin{aligned} \frac{dx_i}{dt} &= f(x_i, y_i) + d_1(H^x - k_ix_i), \\ \frac{dy_i}{dt} &= g(x_i, y_i) + d_2(H^y - k_iy_i), \end{aligned} \quad (20)$$

where $H^x = \sum_{j=1}^n A_{ij}x_j, H^y = \sum_{j=1}^n A_{ij}y_j$ and k_i is the network's degree. We let other nodes stay at equilibrium (x^*, y^*) , and rewrite the single-node system,

$$\begin{aligned} \frac{dx_i}{dt} &= x_i[r_1 - a_{11}x_i - a_{12}y_i] + d_1(x^* - k_ix_i), \\ \frac{dy_i}{dt} &= y_i[r_2 + a_{21}x_i - a_{22}y_i] + d_2(y^* - k_iy_i). \end{aligned} \quad (21)$$

Therefore, it is easy to obtain the characteristic equation:

$$\lambda^2 + p_k\lambda + q_k = 0, \quad (22)$$

where $p_k = -(\alpha_{10} + \beta_{01}) + d_1k_i + d_2k_i, q_k = \alpha_{10}\beta_{01} + (\alpha_{10}d_2 + \beta_{01}d_1)k_i + d_1d_2k_i^2$. Assume λ_1 and λ_2 are two eigenvalues of system (22). Then system (21) is stable when $d_1 = d_2 = 0$, namely $p_k > 0$, so $\lambda_1 + \lambda_2 = -p_k < 0$. If $q_k > 0$ ($q_k < 0$). Then, the system (21) is stable(unstable). To sum up, we can use the comparison principle(the mean-field theory) to conclude that the system (8) is unstable when $q_{\Lambda_i} < 0$ ($q_k < 0$).

3. Numerical Simulation

We give some numerical analysis based on the earlier theoretical analysis. From Figure 3, if we choose

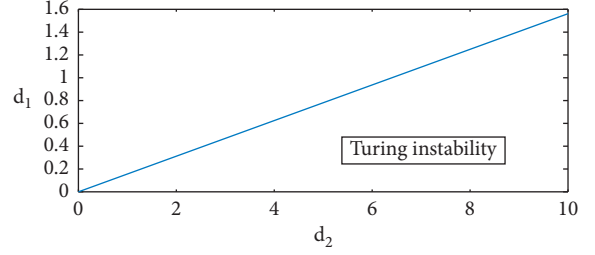


FIGURE 3: Turing bifurcation about d_2 and d_1 in the continuous system.

$r_1 = 1, r_2 = -1, a_{11} = -1.158, a_{12} = 1, a_{21} = 2, a_{22} = 1$, the equilibrium point (x^*, y^*) is asymptotically stable, namely, ecological balance persists as long as there is no biological invasion. That means the predator and the prey can coexist. The equilibrium $(x^{*c}, y^{*c}) = (1.1326, 1.2651)$ is unstable, and Hopf bifurcation occurs Figure 4, when a_{12} passes through the critical value $a_{12}^* = 1.7271$. Because $l_1 = 8.2123 > 0$, the Hopf bifurcation is subcritical, the prey-predator system shows periodic changes; thus, this state is easy to destroy. The equilibrium point (x^*, y^*) becomes unstable, when $a_{12} = 1.8271 > a_{12}^*$.

As diffusion is a vital factor in the distribution of predator and prey, we should not ignore migration. So we construct the random network and transform it into the Laplacian matrix L_{ij} . And we consider how the random network affects the equilibrium point's stability when (7) is stable.

Based on the above theoretical analysis, the Turing instability in the reaction-diffusion equation is a precondition for Turing instability in a network-organized system. Turing instability occurs in a reaction-diffusion equation when Turing bifurcation parameters d_2 and d_1 are in a certain range Figure 1. Namely, diffusion behavior is universal and allowed, but the relative diffusion rate needs to be within a specific range; otherwise, the ecosystem will be out of balance and destroyed.

To observe Turing instability in the network-organized, we should guarantee $d_1 < 0.1562d_2$ while changing p . However, the Laplacian matrix eigenvalues are $\Lambda_1, \Lambda_2, \dots, \Lambda_N, N$ is the number of nodes, and k^2 is continuous in a reaction-diffusion system. In other words, the distribution of $-\Lambda_i$ determines the system stability. The critical point is $d_{1c} = 0.3124$ when $d_2 = 2$. The range of eigenvalues Λ_i could be obtained by result 1. The eigenvalues of L are discrete and included in the continuous region Figure 2.

The red region shows the estimated range of Turing instability about (p, d_1) in Figure 5. Besides, we obtain the estimated range of p , $(d_2 \ln N/d_{1c}N) > p > (1/N^2)$, which determines the system dynamical behavior and network characteristics. Moreover, $p = \ln N/N$ is the critical value between the connected network and sparse network [27]. Anyway, the invasive rate of species and p in the predator-prey network play a vital role in balancing the native biological system.

Let the value of (p, d_1) lie in the blue region shown in Figure 5 (here, we set $p = 0.00006, d_1 = 0.1124$), then,

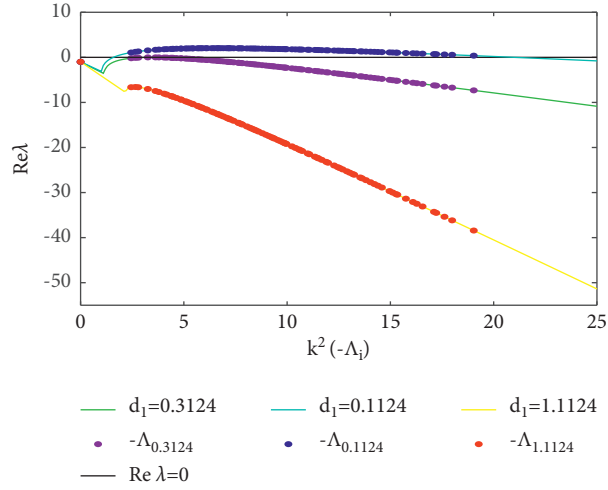


FIGURE 4: Linear stability analysis. The relationship between $\text{Re}\lambda$ about $-\Lambda_i(k^2)$ when $r_1 = 1, r_2 = -1, a_{11} = -1.158, a_{12} = 1, a_{21} = 2, a_{22} = 1,$ and $p = 0.1, d_2 = 2$. The critical values are $\Lambda_c = -3.35, d_{1c} = 0.3124$.

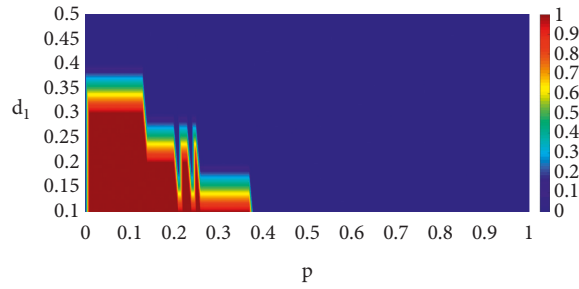
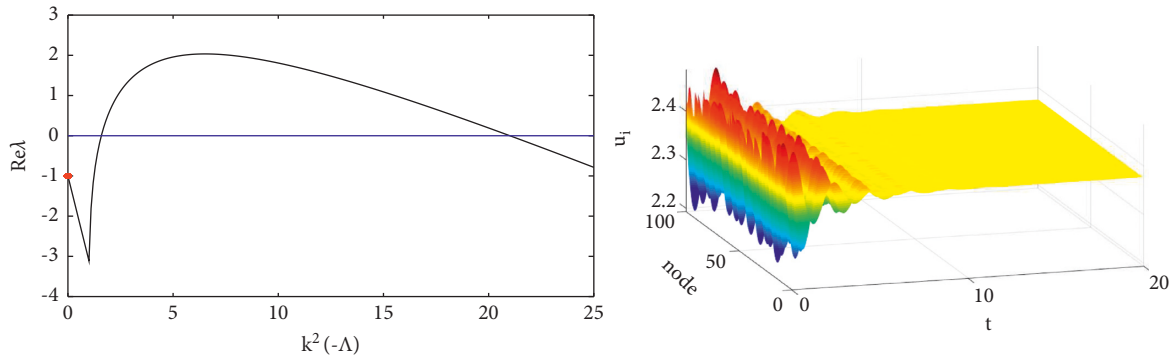
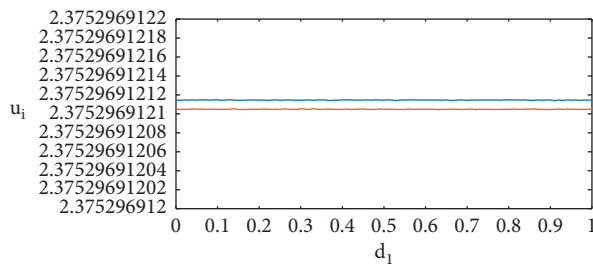


FIGURE 5: The region of instability about d_1 and p .



— k^2
 • $-\Lambda$
 — $\text{Re}\lambda=0$

(a)



(b)

FIGURE 6: (a) Instability region (left) of random network and pattern formation (right) in random network when $p = 0.00006, d_1 = 0.1124$. (b) The bifurcation about d_1 when $p = 0.00006$.

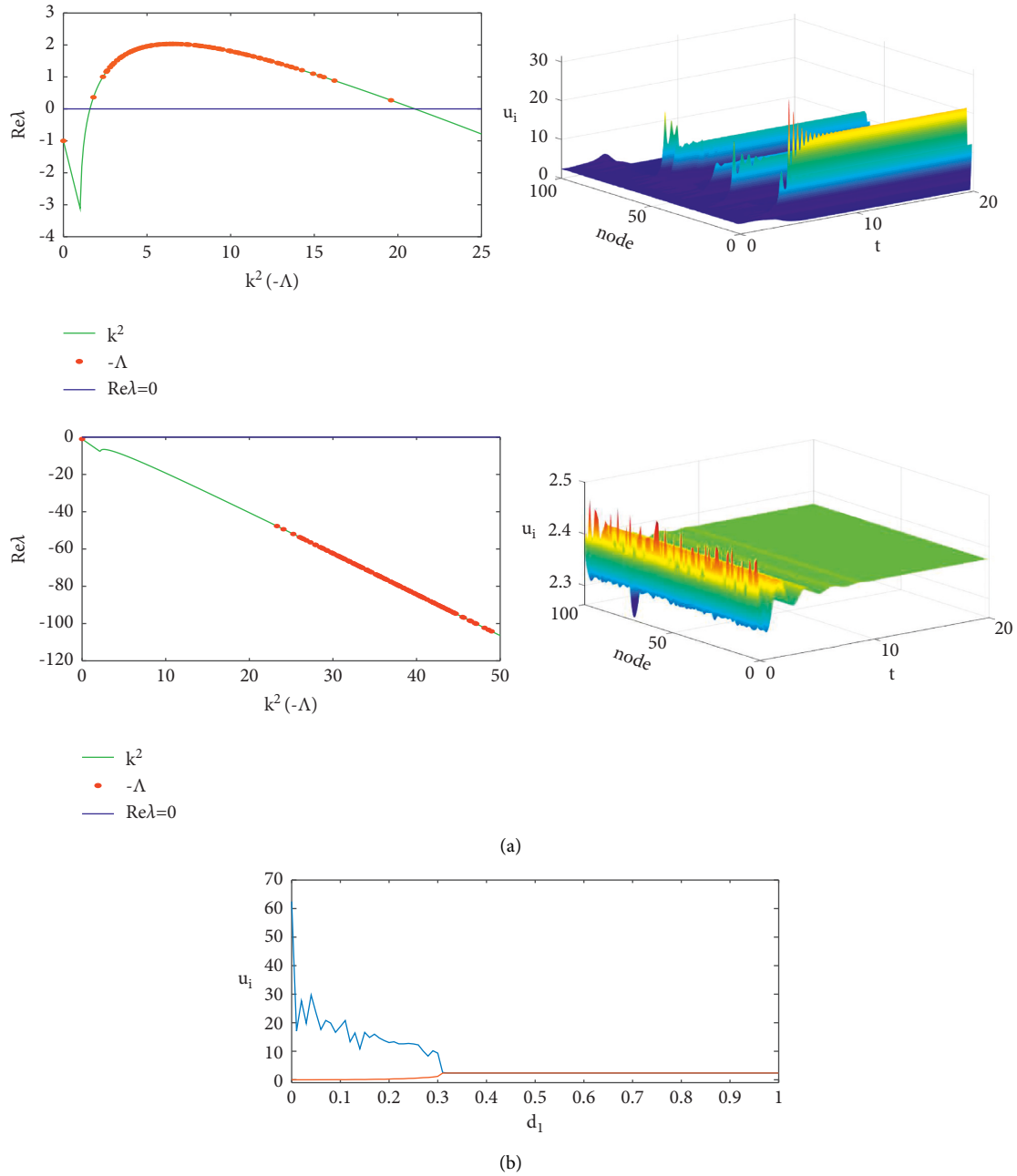


FIGURE 7: (a) The relationship between $\text{Re}\lambda$ about $-\Lambda_i(k^2)$ (left) and the pattern formation of system (3) (right). Top: when $p = 0.08, d_1 = 0.1124$, almost all points $\Lambda_i(k^2)$ lie in the instability region and the Turing instability occurs. Bottom: when $p = 0.08, d_1 = 1.1124$, no point $\Lambda_i(k^2)$ lies in the instability region and the system is stable. (b) The bifurcation occurs about d_1 when $p = 0.08$.

there is no point $\Lambda_i(k^2)$ in the instability region $\Lambda \cap (1.7, 21.1) = \Phi$ (result 2) (Figure 6(a)) and the equilibrium is stable (Figure 6(a)). We verified the correctness of the previous analysis with bifurcation diagrams (Figure 6(b)). We can conclude that with a fixed predator invasion rate and a fixed prey invasion rate, the link probability between two different systems will negatively impact the entire predator-prey network stability. Even the predator-prey network's diffusion induces the species extinction.

Figure 7 shows an example of p that belongs to the red region in Figure 5, such as $p = 0.08, d_1 = 0.1124 < d_{1c} = 0.3124$, almost all of $\Lambda_i(k^2)$ in instability region Figure 7(a) left(up) and 7(a) right(up) shows that Turing instability occurs. If $p = 0.08$ and $d_1 = 1.1124 > d_{1c} = 0.3124$ (i.e., (p, d_1) in the blue region in Figure 5), there is no point $\Lambda_i(k^2)$ in the instability region (Figure 7(a), left(down)), the system is stable (Figure 7(a), right(down)). We also verified the correctness of the previous analysis with a bifurcation diagram (Figure 7(b)).

The ecological interpretation is that the system is less stable when the invasion rate of the prey is lower when the link probability of predator-prey systems is fixed. Conversely, if we want to keep the predator-prey system stable, the invasion rate of the prey needs to be decreased.

4. Conclusion

This paper theoretically derives Turing instability conditions [28–31] in a predator-prey network and carries out a detailed numerical study. We study the effects of diffusion and link probability on pattern formation in a random system. The smaller the invasion rate d_1 of the prey undergoes, the easier the predator-prey network Turing instability. Meanwhile, Turing instability occurs when the link probability p falls in the approximate region $(d_2 \ln N/d_{1c}N) > p > (N^2/1)$, which depends on the system characteristics.

Regarding an explanatory biological mechanism, the link probability and the invasion rate significantly influence the entire predator-prey network stability. The lower the invasion rate of the prey is, the less stable it is. Conversely, the prey invasion rate can be increased if we want to keep the predator-prey system stable. That means we can find an equilibrium point between native and invasive species by adjusting the diffusion probability and species' invasion rate. Finally, we obtain the estimated region of p , $(d_2 \ln N/d_{1c}N) > p > (1/N^2)$. Thus, invasion rate of species and the link probability in the predator-prey network play a key role in balancing the native biological system.

Data Availability

All data and codes can be found on Baidu Wangpan (password: reff) and Baidu.

Conflicts of Interest

The authors declare that there are no conflicts of interest.

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