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Invasion Consequences in Communities Maintained by Niche and Intransitive Coexistence Mechanisms

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Abstract: Understanding invasion mechanisms or identifying their potential outcomes has been a longstanding objective of invasion biology. Many recent empirical and theoretical works tend to frame a perspective of invasion biology within the field of coexistence theory. With increasing emphasis on indirect competitions, more researches hold that niche departure, intransitive loop structure or the integration of these two would be the potential mechanisms to promote native coexistence. But how invasion dynamics rely on these key properties of native competitive network is seldom investigated. Here, we introduce one alien species to a three-species competition system. By setting the structure of coexistence coefficient matrix, we consider three native coexistence mechanisms. After analyzing the equilibrium consequences of alien species invasion under these three mechanisms, we have found that (1) in the native communities supported by strong niche differentiation, alien species can certainly establish their population but would not pose great destruction to native species. (2) Invasion exclusion would happen in the community maintained by intransitive competition loop. However, whether alien species coexist with or exclude resident populations depends on both intraspecific and interspecific competition of invader. (3) The community assembled by the combination of these two mechanisms are most resistant to invasion, and where invasion consequences are more diverse. (4) Finally, the species long-term steady state and short-term respond always keep consistent. We have explicitly situated invasion process within the recent coexistence framework. Our results would broaden the understanding of invasion mechanisms and provide insights into the combination of invasion and coexistence theory.

Keywords: biological invasion; competitive networks; niche differentiation; intransitivity; species coexistence



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1. Introduction

Since biological invasions pose serious threats to ecological communities, including the erosion of species diversity and the destruction of ecosystem functions, they have attracted extensive attentions from the governments and international community (van Kleunen et al., 2015 [1]; McGeoch and Latombe 2016 [2]; Coates 2016 [3]). Understanding invasion mechanisms or identifying their potential outcomes has been a longstanding objective of invasion biology (Kolar and Lodge 2001 [4]; Keane 2002 [5]). However, the process of invasion is often too complex to be explained by a single theory or hypothesis (Hiero et al., 2005 [6]; Diez et al., 2010 [7]). The successful establishment of alien species is not only due to its own competitive advantage, but also frequently related to the characteristics of local community (Pyšek and Richardson 2007 [8]; Ortega et al., 2014 [9]). When alien species arrive the novel region, they should colonize, survival and spread to successfully establish their population (Hobbs 1989 [10]). During these stages, introduced species will inevitably interact with a subset of native species (Colautti et al., 2004 [11]; Mitchell et al., 2006 [12]) and so that they might encounter potential competitors, mutualists (Traveset and Richardson 2014 [13]; Minoarivelo and Hui 2016 [14]) and novel enemies (Keane 2002 [5]). One perspective of the invading researches has considered this dynamic

within a single trophic level (Mitchell et al., 2006 [12]; Godoy and Thompson 2019 [15]), especially for those species directly competing for limiting factors (e.g., light, nutrient or food) or indirectly through interaction chains (Romanuk et al., 2009 [16]; Hui et al., 2016 [17]). Classical niche theory suggested that species can survive under several limited conditions (Hutchinson 1959 [18]). Great niche overlap under one single environmental limiting factor would present species extinction in communities (Diamond 1975 [19]; MacArthur and Wilson 2016 [20]). Therefore, the invaders which occupying different niche space than native species could successfully establish their populations (Fargione et al., 2003 [21]; Fridley et al., 2007 [22]). By possessing novel phytochemicals, alien species more easily invade those less functionally diverse communities (Mack 2003 [23]; Stachowicz and Tilman 2005 [24]). MacDougall et al. (2009) [25] reviewed the question of how species differences influence the establishment and impact of invaders in light of the recent work of coexistence theory, which shows how niche and fitness differences between native species and invaders co-determine the outcome of invasions. Nevertheless, there were also studies that suggest trait differences between alien and resident species might actually presenting limited power to predict invasion success (Leffler et al., 2014 [26]). The functional properties of invader and resident plants were found to be strikingly similar in some empirical researches (Bruno et al., 2005 [27]). Additionally, niche hypothesis also poorly predicts those invasions with great damage (MacDougall et al., 2009 [25]) and has shown contradictory results. Their shortcomings when being applied to invasion are that most of them have provided little guidance for how alien species establish populations without niche departures (MacDougall et al., 2009 [25]). The non-hierarchical competition structure, such as intransitive competition which being similar to a rock-paper-scissors game, is also expected to promote coexistence (Laird and Schamp 2006 [28]; Allesina and Levine 2011 [29]). Among this kind of native community, species population densities are maintained stable under dynamical constrains, namely there is no universal strong or weak competitor (Lankau and Strauss 2007 [30]). Since the type of scenario could be rather uncommon in nature (Soliveres et al., 2018 [31]), this study view was recently updated a little. Some investigations have demonstrated that intransitive competition structures alone are not able to determine coexistence (Gallien et al., 2017 [32]; Godoy et al., 2017 [33]). Competition should be viewed in a more continuous way (Godoy et al., 2017 [33]; Yang and Hui 2021 [34]), such as when combined with the pairwise niche differentiation. In modern coexistence theory, species would be maintained when intraspecific competition intensity are stronger more than interspecific competition the intensity of intraspecific competition exceeds that of interspecific competition (Chesson 2000 [35]).

All advances in coexistence theory inspire us that native community features, especially for competitive networks, can produce diverse outcomes and effects of invasion (Godoy et al., 2017 [33]). A structure of non-hierarchical interaction might be predicted to resistant to alien species but also conversely be crumbled by invader with particular features, like priority effects (Uricchio et al., 2019 [36]). If resident species are competing for multiple limited factors, exotic species would be expected to successfully coexist with resident species through niche departure rather than competitive exclusion (Levine 1976 [37]; Mitchell and Power 2003 [38]; Bulleri et al., 2008 [39]). This trend could be also modified by another species differences that drive the competitive dominance of invader (Adler et al., 2007 [40]; MacDougall et al., 2009 [25]). In short, different configuration of competing networks, variance in niche differences, in competitive asymmetries, and even match with specific properties of invaders, would result in diverse resistance outcomes when facing invasion (Godoy and Thompson 2019 [15]). Literature should explicitly consider the effect of competitive networks on invasion establishment (Godoy et al., 2017 [33]; Hui and Richardson 2019 [41]; Latombe et al., 2021 [42]) and further explore which competitive networks are more resistant to invasion in natural communities. Here, we focus on simplest competition networks, a three-species dynamic system. We have established a Lotka-Volterra competition model and extended it to the invasion scenario. As we know, the competition matrix of system equations has played vital roles for the dynamical regimes

of the community (Hofbauer and Sigmund 1998 [43]; Laird and Schamp 2006 [28]; Schreiber and Killingback 2013 [44]). Based on the relationship between niche overlap and intraspecific or interspecific competition factors (Chesson 2000 [35]), we construct a competition coefficient matrix controlled by two parameters. The matrix can continuously change the relative intensity of intransitive competition mechanisms and niche differentiation mechanisms under parameter values setting. After stable coexistence of native species was achieved, we select three groups of community parameters with different attributes through the branching results of stability analysis, and added alien species invasion process to these three native communities. After exploring the equilibrium densities of resident species and invaders versus parameter value ranges, and analyzing the dynamic response to the invasion, we want to investigate the following questions: (1) what is the invasion consequence respectively in communities supported by niche departure, strong intransitive competition loop or combinations of the two extremes; (2) how competitive asymmetries moderate these processes; and further (3) whether there is a difference between the predicted results of stable state and species short-term dynamic response trend.

2. Methods

2.1. Native Dynamic Model

2.1.1. Model Construction

The three-species competition system is given by the classical Lotka-Volterra model framework (Leung 2013 [45]; Pao 2012 [46]; Takeuchi 1996 [47]). As an ecological model representing the interaction between competing species, it has been widely used in the field of ecology (Waltman 1983 [48]). The coexistence theory based on this model framework emphasizes that the degree of differences between intraspecific and interspecific competition determines species stable coexistence or exclusion (Lotka 1925 [49]; Volterra 1928 [50]). Specifically, population dynamics are expressed by a series of ordinary differential equations. Consider three variables N_1, N_2, N_3 , which respectively conveys the population density of species 1, species 2 and species 3. The dynamic variation of the system is as follows:

$$\frac{dN_i}{dt} = r_i N_i \left(1 - \sum_{j=1}^S \alpha_{ij} N_j \right), \quad i = 1, 2, 3, \quad (1)$$

where r_i is the intrinsic growth rate of species i , $S = 3$ represents the number of species in community, α_{ij} are the competition strength from species j to i . When α_{ij} are being assigned with different magnitudes, we would gain different population dynamic characteristics and species coexistence results. Next, we set up the competition matrix accordingly.

2.1.2. Competition Matrix

In this paper, we mainly consider two kinds of coexistence mechanisms, namely intransitive competition coexistence and niche differentiation coexistence (i.e., intraspecific competition intensity is much higher than interspecific competition intensity). Usually in natural communities, species coexistence may be caused by either of the two mechanisms, or the combination of them. In order to quantitatively describe the species coexistence mode in native community, we utilize the method proposed by Yang and Hui (2021) [34] to set the elements of competition matrix. Such as $\alpha_{21} - \alpha_{12} = \alpha_{32} - \alpha_{23} = 1 - \theta$ and $\alpha_{31} - \alpha_{13} = 1 - \theta_3$, where $\theta \in [0, 1]$. If $\theta = 0$, the competition between species 1, 2, and 2, 3 are asymmetrical and competitiveness show the largest difference. When $\theta = 1$, since $1 - \theta = 0$, species 1, 2, and 2, 3 present symmetrical competitions. In this case, competition effects are cancelled each other and there is no difference in competitiveness.

In our model, we fix the value of θ and change θ_3 to continuously modify the intransitive degree of competing system (Figure 1). For example, $1 - \theta_3 = 0$ represents chain competition, that is, species 1 is more competitive than species 2, and species 2 is more competitive than species 3, so that species 1 is the dominant competitor in the system. When $1 - \theta_3$ increases and beyond 0, the competition difference between species 1 and 3 is positive, resulting in intransitive competition. $1 - \theta_3 = 1 - \theta$ means the highest in-

transitive competition, which is the cyclic competition in the normal sense. Therefore, $0 \leq 1 - \theta_3 \leq 1 - \theta$ and then the range of θ_3 here is $\theta \leq \theta_3 \leq 1$.

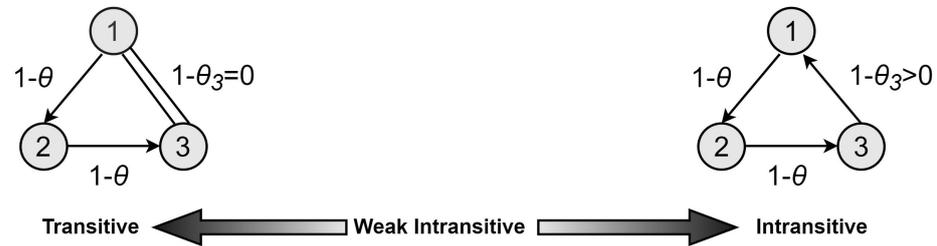


Figure 1. The spectrum of transitive–intransitive continuum in the three-species system. Arrows represent the net competition direction between two species, which point from the stronger to weaker competitor. Double lines represent equal net competition. From left to right, intransitivity $1 - \theta_3$ increases from 0 to $1 - \theta$, shifting a transitive network to an intransitive loop.

In addition to the intransitive competitive coexistence, our paper also considers the niche differentiation mechanism. According to theoretical frameworks from Chesson et al. (2000) [35], the degree of niche overlap between species i and j can be expressed as $\sqrt{(\alpha_{ij}\alpha_{ji}) / (\alpha_{ii}\alpha_{jj})}$. In the three-species competition matrix, in order to fix the niche overlap degree $\sqrt{(\alpha_{ij}\alpha_{ji}) / (\alpha_{ii}\alpha_{jj})} \equiv k$ and control the niche differentiation level of the system $(1 - k)$ from low to high (the range of k is $[0, 0.9]$), we set the coefficient of intraspecific competition as $\alpha_{11} = \sqrt{\theta_3}/k, \alpha_{22} = \theta / (k\sqrt{\theta_3}), \alpha_{33} = \sqrt{\theta_3}/k$. The interspecific competition matrix is as follow:

$$M = \begin{pmatrix} \frac{\sqrt{\theta_3}}{k} & \theta & 1 \\ 1 & \frac{\theta}{k\sqrt{\theta_3}} & \theta \\ \theta_3 & 1 & \frac{\sqrt{\theta_3}}{k} \end{pmatrix}.$$

In summary, if the intrinsic growth rates of the three species are set as $r_1 = r_2 = r_3 = r$, with the value of competition intensity θ fixed in the model, the competition system can be controlled by only two parameters: intransitive degree $1 - \theta_3$ and niche overlap degree k . We can explore the effect of intransitivity and niche differentiation mechanisms on species coexistence through the three parameter values.

2.1.3. Coexistence Mechanisms Analysis

The positive equilibrium point $N_i^* > 0$ represents native species have positive population density in the steady state. We first find the positive equilibrium point $N_i^* (i = 1, 2, 3)$ by setting the right-hand formula of system (1) as 0. They are the function of parameters θ, k and θ_3 . Since θ is fixed, the value of $N_i^* (i = 1, 2, 3)$ is determined only by k and θ_3 . Then the existence conditions for positive equilibrium point are obtained by solving inequalities $N_i^* > 0$. Besides, in order to guarantee the steady state do not move away from steady state by small perturbations, we still need to do local stability analysis.

Local stability analysis is an effective method to judge whether species can coexist stably in competitive networks. The principle of local stability analysis is based on Lyapunov stability (Lyapunov 1992 [51]). When the equilibrium state of the system satisfies Lyapunov stability, the system will never leave the stable state and can approach or return to the original equilibrium state no matter what disturbance it is subjected to. Then we apply the Lyapunov stability analysis to our system. Lyapunov’s condition for the local asymptotic stability of N^* is:

$$Re\lambda_i(J) < 0, i = 1, 2, \dots, n \tag{2}$$

where $Re\lambda_i(J)$ is the real part of the eigenvalue of the system Jacobian matrix λ_i . Inequation (2) can be calculated using Routh-Hurwitz criterion (Gantmacher 1959 [52]). It is also the function of intransitive degree $1 - \theta_3$ and niche overlap degree k , and competitive asymmetry θ . Our final coexisting conditions are obtained by the intersection of area where $N_i^* > 0$ and $Re\lambda_i(J) < 0$. See for more details in Appendix A.

2.2. Invasion of Alien Species

Here we introduce one alien species to the competition. The extended model system is as follows:

$$\frac{dN_i}{dt} = r_i N_i \left(1 - \sum_{j=1}^S \alpha_{ij} N_j \right), \quad i = 1, 2, 3, 4; \quad s = 4 \tag{3}$$

the competition matrix M_I is set as:

$$M_I = \begin{pmatrix} \frac{\sqrt{\theta_3}}{k} & \theta & 1 & \alpha_{14} \\ 1 & \frac{\theta}{k\sqrt{\theta_3}} & \theta & \alpha_{24} \\ \theta_3 & 1 & \frac{\sqrt{\theta_3}}{k} & \alpha_{34} \\ 1 & 1 & 1 & \alpha_{44} \end{pmatrix},$$

In this competition matrix, the competition between native species and invasive species are fixed as $\alpha_{41} = \alpha_{42} = \alpha_{43} = 1$ while α_{i4} ($i = 1, 2, 3$) determine the difference of competition intensity between invasive and native species. $\alpha_{i4} > 1$ indicates that invasive species has a competitive advantage over resident species i , whereas $\alpha_{i4} \leq 1$ suggests invader is at a competitive disadvantage compared to natives.

As we known, species coexistence happens under equalizing (similar fitness abilities) and stabilizing (unique niche requirements) mechanisms (Chesson 2000 [35]). If introduced alien species equipping with either a fitness advantage or a distinct niche requirement (more intraspecific competition), they may destabilize coexistence. Therefore, here we mainly explored the parameter value of competitive ability of invasive against native species α_{i4} , $i = 1, 2, 3$ and the intraspecific competitive ability of invader α_{44} . They jointly determine the invasion consequences.

We get the equilibrium point N_i^* ($i = 1, 2, 3, 4$) by setting the right-hand formula of system (3) as zero. The final invasion consequence are divided into three categories for discussion: (1) $N_i^* > 0$ ($i = 1, 2, 3, 4$), all population densities, including both invasive and native species, are positive, which indicates invasive species have successfully established their population, and there is invasion coexistence between native and invasive species; (2) $N_4^* > 0 \cap (N_1^* \leq 0 \cup N_2^* \leq 0 \cup N_3^* \leq 0)$, where invasive population density at equilibrium state is positive, but native community has extinctions. In this case, the alien species successfully invade and has a certain degree of harmful effect on native community, which here considered as invasion exclusion; (3) $N_4^* \leq 0$. If the invasive population density at equilibrium state is zero or negative, then the invasion fails.

Based on the analysis method, we have explored three invasion scenarios on the whole: We respectively examined the results when alien species compete with one (e.g., $\alpha_{i4} > 1, \alpha_{j4} = 1, \alpha_{k4} = 1$), two (e.g., $\alpha_{i4} > 1, \alpha_{j4} > 1, \alpha_{k4} = 1$) and three native species (e.g., $\alpha_{i4} > 1, \alpha_{j4} > 1, \alpha_{k4} > 1$), where $i, j, k = 1, 2, 3$ & $i \neq j \neq k$.

2.3. Metrics for Species Short-Term Response to Invasion

As we know, during interactions between alien and native species, native community system may tend to be destabilized. The usual question would be whether alien species can establish and invade. At this point, there should be a particular estimator to forecast species-level invasion performance and response. In fact, some researches have been proposed feasible estimators to quantify the short-term dynamic response of native species to invasion (Hui and Richardson 2019 [41]). By calculating the estimator, we can know how

the native system deviates from the current stable state when facing the invasion process, and thus reveal the dynamic trajectory of various groups.

Specifically, we first standardized N_i by $n_i = N_i - N_0$, where N_0 is the initial population density at the beginning of invasion (here the value of N_0 was uniformly set). Then n_i can be regarded as the modification of population densities after invasion processes. By considering the dynamical system $\dot{n}_i = F(n_i) = F(N_i - N_0)$, we transform original network Equation (3) into the follow new one:

$$\frac{dn_i}{dt} = r_i(n_i + N_0) \left(1 - \sum_{j=1}^s \alpha_{ij}(n_j + N_0) \right), \quad i = 1, 2, 3, 4; s = 4 \quad (4)$$

The linearized approximation of (4) is $\dot{\vec{n}} = J'\vec{n}$, $\vec{n} = (n_1, n_2, n_3, n_4)^T$. Jacobian matrix J' here transforms the abundance vector \vec{n} into a new vector space. We have $JV = V\Lambda$, where $V = v_1, v_2, \dots$ is eigenvector matrix composed of vertical eigenvectors v_i of eigenvalues λ_i (λ_i satisfy $Jv_i = v_i\lambda_i$). Λ is an eigenvalue matrix with diagonal elements of λ_i and other elements of zero. After solving the linearized equations $\dot{\vec{n}} = J'\vec{n}$ (details of this derivation are in Appendix B), we have each $n_i(t) = \sum_j v_{ji}c_j e^{\lambda_j t} = e^{\lambda_m t} \sum_j v_{ji}c_j e^{(\lambda_j - \lambda_m)t}$, $i = 1, 2, 3, 4$, where v_{ji} is the i th element of the eigenvector v_j and λ_m is the leading eigenvalue (largest eigenvalue) of the Jacobian matrix J .

As time t going to infinity, we can see $n_i \rightarrow v_{mi}c_m e^{\lambda_m t}$. Since term $c_m e^{\lambda_m t}$ are the same for all species, the species level dynamic difference would only result from the term v_{mi} . As such, the short-term response of species i (how species i changes), both in direction and magnitude, depends entirely on v_{mi} . If $v_{mi} > 0$, the species i would increase; When $v_{mi} < 0$, the population density of species i tend to decrease. $v_{mi} = 0$ means less sensitive of species i to invasion disturbance. Here, we compare the short-term reaction between each resident and alien species.

3. Results

3.1. Native Coexistence Mechanisms

We uniformly set the intrinsic growth rate of three species in the model as $r_1 = r_2 = r_3 = 0.02$. To explore the robustness of results under different levels of competition asymmetry which is proportional to $1 - \theta$, we repeated the analyses of our system at different levels of $\theta = 0.3, 0.5, 0.7$ (Figure 2). Figure 2a shows the bifurcation conditions for local stability of nonzero equilibrium while Figure 2b is the result combined with the existence area of coexistence equilibrium points ($N_1^* > 0, N_2^* > 0, N_3^* > 0$). From Figure 2b we know, the parameter axis is divided into two parts, species coexistence (yellow color range) and extinction (blue areas). Native species cannot stably coexist when no intransitivity and extremely high niche overlaps. The parameter zone for extinction (yellow area) steadily enlarged when moving from a neutral community (no competition asymmetry with θ close to 1) to a community dominated by asymmetric competition (θ close to 0).

If competition asymmetry θ is fixed, the coexistence of native species was mainly determined by competitive transitivity (θ_3) and niche overlap (k). We note that for communities with enough niche differentiation ($k < 0.3$ in the first panel of Figure 2b), species can coexist regardless of the presence or absence of intransitive competition. This is consistent with the niche theory that niche differentiation promotes species coexistence (Chesson 2000 [35]). When high niche overlap ($k = 0.8$), there are strong competitions among species so that on the system will quickly appear competing exclusion. However, if species has intransitive interacting structure, there is no absolutely dominant species. No one species will exclude the others. When strong intransitive competition force, all species could coexist stably. Finally, native species can also coexist under the combined effect of niche differentiation and intransitive competition.

From the above division of parameter area, we chose three different coexisting scenarios as the native community to introduce invasion process: (1) strong niche differentiation;

(2) combination of niche differentiation and intransitive competition; and (3) intransitive competition. We want to know how invasion effect differ in the communities obtained under these three mechanisms.

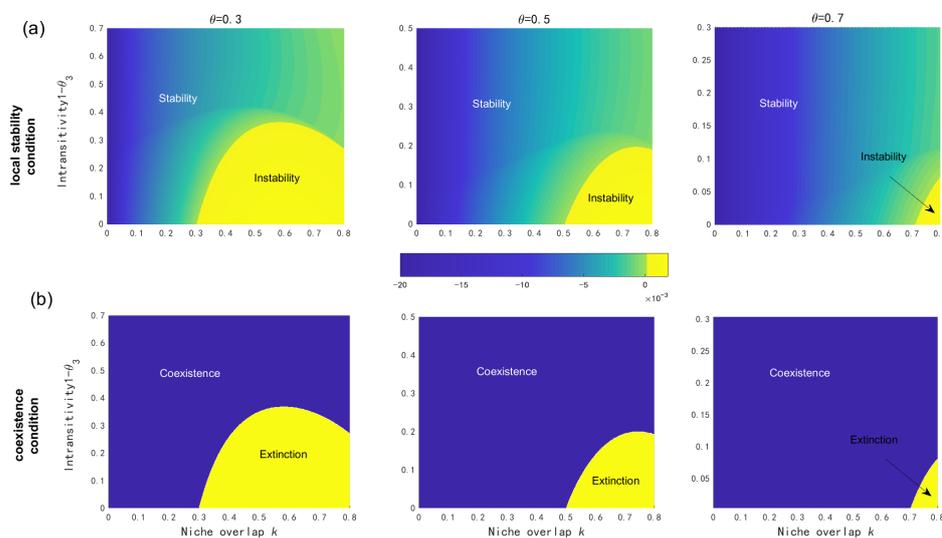


Figure 2. Coexistence area at different levels of competitive symmetry ($\theta = 0.3, 0.5, 0.7$). (a) Stability analysis results of three species system at nonzero equilibrium point. In the parameter range of $Re\lambda_i < 0$, nonzero equilibrium point N_i^* would be locally stable. There were two kinds of ranges: blue and green colors (stable coexistence at N_i^*), yellow colors (unstable at N_i^*). (b) Final coexistence condition, which derived by the intersection of local stability conditions and existence conditions for nonzero equilibrium point N_i^* . The final entire parameter space was still divided into two areas: coexistence (nonzero equilibrium point N_i^* exist and stable) and extinction (not exist or locally unstable). Intransitivity $1 - \theta_3$ was from $[0, 1 - \theta]$. $r_1 = r_2 = r_3 = 0.02$.

3.2. Invasion Consequences

3.2.1. Three Coexistence Mechanisms

The influence of invading events varies with the attribute of native communities. We investigated the consequences after spreading of alien species under three different kinds of native coexistence scenarios (see Table 1). By calculating the values of equilibrium N_i^* ($i = 1, 2, 3, 4$), the consequences were divided into three types of invasion outcomes (referred in Method part). We first considered the invasion where alien species only compete with one native. Then, the other scenarios, like invaders with competitive advantages over two or three native species, were included as well.

Table 1. Three coexistence mechanisms.

Scenario	The Meaning of Different Scenarios	Parameter Range
Case1	Strong niche differentiation	$(k, 1 - \theta_3) = (0.05, 0.1)$
Case2	Combination of niche differentiation and intransitive competition	$(k, 1 - \theta_3) = \left(0.4, \frac{1-\theta}{2}\right)$
Case3	Intransitive competition	$(k, 1 - \theta_3) = (0.75, 1 - \theta)$

3.2.2. Invasion When Only Competing with One Native Species

Our alien species is species 4 and we take the invasive competition with species 1 as example (Figure 3). As it shown, the invasion outcomes in three types of native communities (case 1–3) were indeed different. For the coexistence under niche departure (case 1 and Figure 3a), there are only two kinds of invasion results, invasion coexistence

(blue area) and invasion exclusion (green area), which of these two occur mainly depends on the intraspecific competition of invader α_{44} rather than interspecific competing force α_{14} . In this case, alien species could successfully establish their populations but would not harm native individuals and cause extinctions. On the other hand, for intransitivity-maintained coexistence (case 3 and Figure 3c), there were still two kinds of invasion results. However, how invasion influence native community is the consequence of both intraspecific competition α_{44} and interspecific competition α_{14} . In particular, when the competitiveness of alien species was greater than that of native species ($\alpha_{14} > 1$), the stronger the competing force was, the more harmful the alien species was. Finally, if native community was constructed by the combination of these two coexistence mechanisms (case 2 and Figure 3b), a new invasion outcome, invasion failure (yellow area in axis) occurs. How the three consequences distribute among the parameter axis dramatically depend on intraspecific competition of invader α_{44} . Invasion extinctions would be caused by the alien species with medium intraspecific population competition. We could see alien species may not be able to successfully established their population under the same intraspecific competition when the level of native competitive asymmetry θ change. For example, invader arrived in a highly competitive community, (big competitive asymmetry $\theta = 0.3$), invaders with weaker intraspecific competition ($\alpha_{44} < 1$) were more likely to invade. Whereas when the competition asymmetry was small ($\theta = 0.5$ or 0.7), relatively strong competing force within alien population ($\alpha_{44} > 1$) would be more possible to make successful establishments.

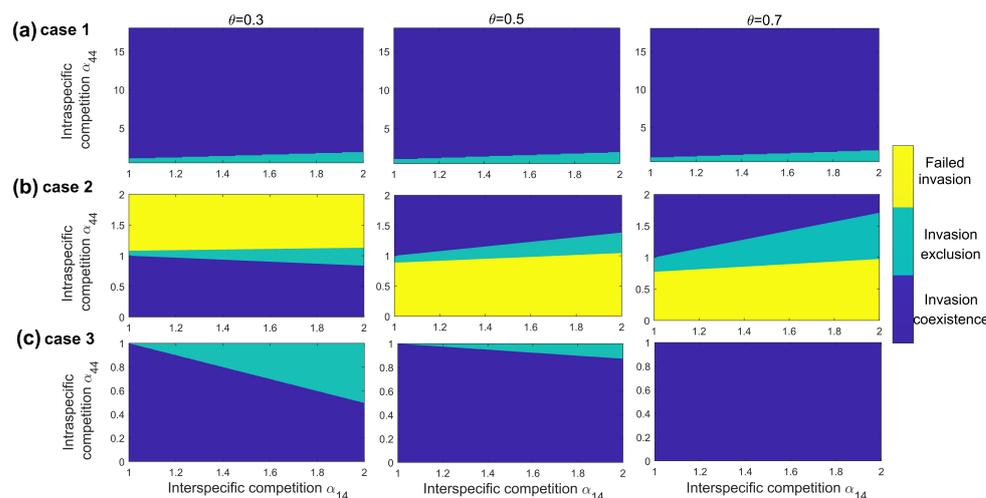


Figure 3. Parameter ranges for different invasive consequences (assuming alien species can only compete with species 1). Different figure rows correspond to three different native communities, which supported by (a) strong niche departure (case 1), (b) the combination of niche differentiation and intransitive competition (case 2), and (c) intransitive competition (case 3). Each columns exhibit three levels of competitive symmetry $1 - \theta = 0.7, 0.5, 0.3$. X axis represents the interspecific competition intensity between alien species and native species 1, α_{14} . Y axis is intraspecific competition intensity of alien species α_{44} . The parameter space is divided into several parts. Blue color area represents successful establishment of invader. Green color region suggests the conditions when alien species pose destructive effect and cause native extinctions; yellow color area identify the invasion failure. $r_1 = r_2 = r_3 = 0.02$.

3.2.3. Long-Term Population Evolution and Short-Term Response

To present the invasion long-term evolution in detail, we numerically solved our Equations (1) and (3). Taking the case 1, case 2 and $\theta = 0.3, 0.7$ as the example, each population density over time was presented in Figures 4 and 5. Besides, we also used the estimator provided by Hui and Richardson (2019) [41] namely the lead eigenvalue for the joint matrix of linearized approximation of system (4), to indicate species short-term

response when facing initial invasion. This index value for each species was shown in the last column of Figure 4.

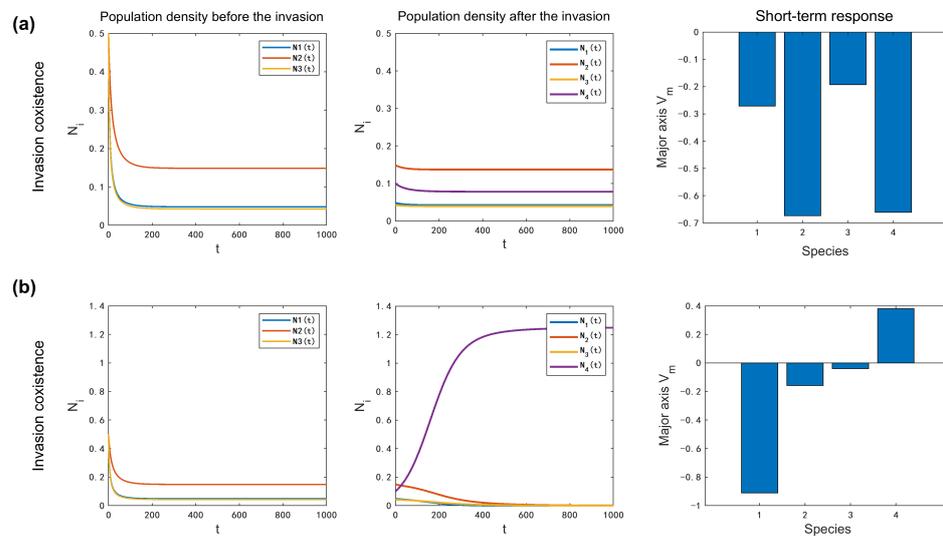


Figure 4. The long-term evolution dynamics and short-term response of all species in case 1 and $\theta = 0.3$. We respectively choose parameter values from obtained two invasion consequences, (a) invasion coexistence and (b) invasion exclusion of this scenario. The first two columns respectively show long-term population evolution before and after invasion. The last column corresponds to the major axis (i.e., the eigenvector of the lead eigenvalue) of the joint matrix, revealing how each species dynamically responds to the invasion (species 1–3 are the original resident species; species 4 is the newly introduced species). $r_1 = r_2 = r_3 = 0.02$. α_{14} and α_{44} are randomly selected in the corresponding invasion result area.

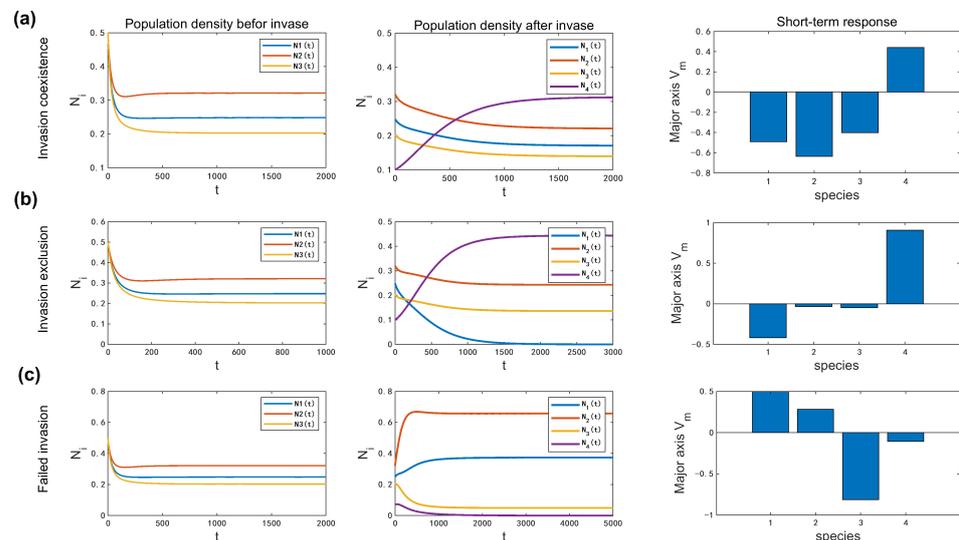


Figure 5. The long-term evolution dynamics and short-term response of all species in case 2 and $\theta = 0.7$. There are three kinds of consequence in this scenario. We choose the parameter values from (a) invasion coexistence (b) invasion exclusion and (c) failed invasion. The first two columns show long-term population evolution before and after invasion. The last column suggests the major axis (i.e., the eigenvector of the lead eigenvalue) of the joint matrix, revealing how each species dynamically responds to the invasion. Other parameters are same with Figure 4.

When parameter values are chosen from the blue area of Figure 3a, small invader population has finally maintained their density (Figure 4a). As for short-term responses, we find most native species are insensitive to initial invasion process. Since alien species

has more negative dynamic direction force, they were not greatly invasive and coexistent with native populations at equilibrium state. For parameter values in green area of case 1 (Figure 4b), alien species had positive direction while resident species responded negatively to invasion. Therefore, native extinction happened in the end. As for case 2 and $\theta = 0.7$ (Figure 5), we know in the previous analysis there would be three kinds of invasion results, invasion coexistence, invasion exclusion and invasion failure. If respectively fixing the parameter values under these different equilibrium condition areas, species long-term evolution trends all fit the equilibriums results perfectly. And short-term reactions for each species also be consistent with their long-term tendencies. Therefore, during the process from initial invasion to system equilibrium state, the direction and magnitude of population density change can be predicted and judged by the results of dynamic response.

3.2.4. Invasion Consequence for the Other Scenarios

For those more universal invaders, like species which have competing advance over all native species, the invasion consequences are different and mostly differ in case 2 and case 3 (Figure 6). In case 2, unlike the distinct invader (Figure 3), the invasion results for more universal invader were affected not only by intraspecific competition among alien species α_{44} , but also by interspecific competition between alien species and native species α_{i4} , $i = 1, 2, 3$. Bigger interspecific and small intraspecific competition ability of invader was likely to establish their population ($\theta = 0.3$ in Figure 6). But counterintuitively, when invading a community with weak competition asymmetry ($\theta = 0.5$ or 0.7), extremely strong competing invader would fail to spread. Additional difference for case3 is that, there is no exclusion occur and alien species generally coexist with native species in this occasion.

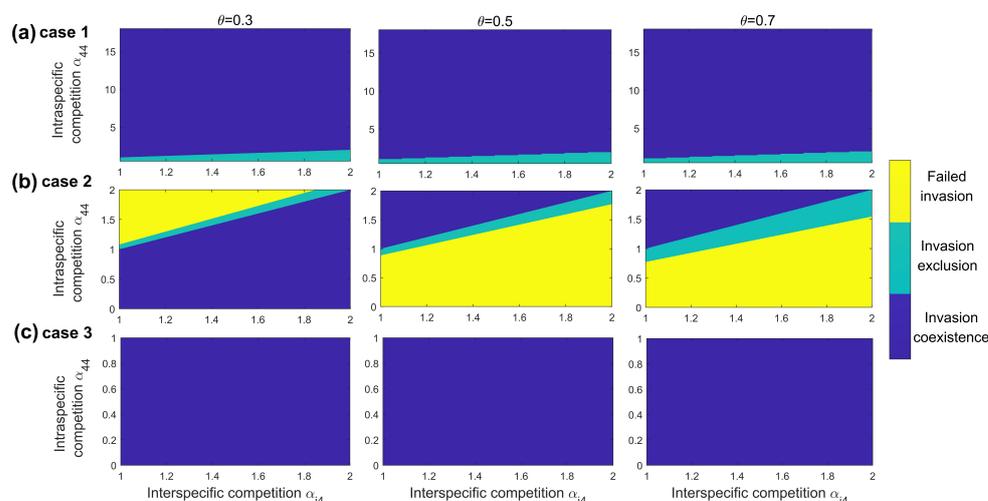


Figure 6. Parameter ranges for different invasive consequences (assuming alien species compete with all three native species). Different figure rows represent native communities which supported by (a) strong niche departure (case 1), (b) the combination of niche differentiation and intransitive competition (case 2), and (c) intransitive competition (case 3). Each columns exhibit three levels of competitive symmetry $1 - \theta = 0.7, 0.5, 0.3$. X axis represents the interspecific competition intensity between alien species and native species i, α_{i4} $i = 1, 2, 3$. Here we assume $\alpha_{14} = \alpha_{24} = \alpha_{34}$. Y axis is intraspecific competition intensity of alien species α_{44} . The parameter space is divided into several parts. Blue color area represents successful establishment of invader. Green color region suggests the conditions when alien species pose destructive effect and cause native extinctions; yellow color area identify the invasion failure. Other parameters are set the same with Figure 3.

Then we have also investigated other scenarios, such as when invader competing only with one species but with species 2 or 3 (Figure 7a) and when invaders threaten any two of native species (Figure 7b). Since in niche differentiated (case 1) or intransitive loops (case 3) communities, species would either be highly restricted by intraspecific competition

or all species are at the same competitive hierarchy, the type of target competing species become less important to the outcome of invasion in these both cases. Therefore, here we mainly focus on the analysis for case 2. Specifically, we quantified the image difference for region of each invasion consequence. From Figure 7a, we knew that if native species exist more competition asymmetries ($\theta = 0.3$), the invasion results for scenarios when invader competing with species 1, species 2 or species 3 would differ mostly. As for the invaders that threaten two native species, there existed similar results (Figure 7b). This might be due to that high competition asymmetry $1 - \theta$ has enhanced the heterogeneous of competition hierarchies, which made the invasion outcomes fluctuated greatly. Therefore, we should pay more attentions to the original species competition hierarchies when native community has more competition asymmetries.

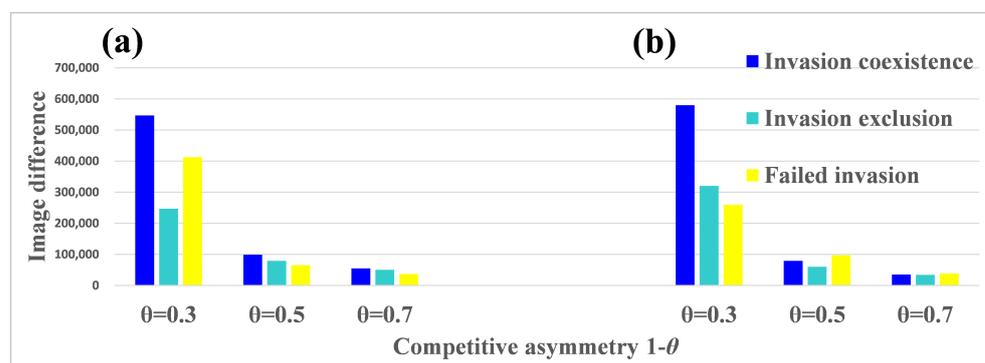


Figure 7. Comparison of competitive invasion results in case 2. (a) suggests the mean difference of each type of invasion consequence across the scenarios when invaders only competing with one resident species. (b) represents the mean gap of each invasion consequence over the scenarios when invaders competing with two of native species. We quantify the comparison by image difference of invasion consequence regions (region details as shown in Supplementary information). It is calculated by counting the number of pixels at the same competitive asymmetry level and calculating the difference and average value of the pixel number. We assume competing force $\alpha_{14} = \alpha_{24}$ or $\alpha_{14} = \alpha_{34}$ or $\alpha_{24} = \alpha_{34}$. Bars with different colors are for different invasion consequences. Competitive asymmetry $1 - \theta = 1 - 0.3$ or $1 - 0.5$ or $1 - 0.7$. Other parameter values are the same with Figures 5 and 6.

4. Discussion

In order to explore the invasion to the competitive network, we here take the simple three-species interaction dynamics as an example. By setting the structures of coexistence coefficient matrix, we have obtained three kinds of native coexistence mechanisms: strong niche differentiation, intransitive competition, and interplays of the two. After exotic species introduction, the equilibrium consequences of invasion under above three mechanism cases are investigated. Our study emphasizes that the properties of competitive networks may produce opposing effects on the invasion outcomes and impacts. Where the type of invasion consequence appears in parameter space mainly depends on the degree of intra and inter specific competition. Additionally, we find that invasion long-term steady-state and species short-term reaction trend also fit well.

For resident community, we first obtained the conditions when species stably coexistence through pairwise features, like niche departures. High niche differentiation can maintain all native species with a positive population density at equilibrium state regardless of how interaction network structured. This agrees with the “modern coexistence theory”, which suggests if species limits themselves much more than they limit the other (e.g., niche differentiation occurs), species has the possibility to coexist (Chesson 2000 [35]). When the other extreme, species niche departure being extremely small, hierarchical interaction could have caused competitive exclusion (Miller 1994 [53]). But if species competing network are cyclic structured (e.g., occurs when species utilizing multiple limited factors), any decrease

in the abundance of competitors in the loop causes a feedback pattern to propagate through the network that is conducive to disturbing the species recovery (Levine et al., 2017 [54]). Similar to previous studies, native populations can be maintained positive by intransitivity (Lankau and Strauss 2007 [30]). We find strong enough competitive intransitivity of system has the ability to keep biodiversity and competitive asymmetry also plays quite important roles for this effecting process. Although there are theoretical conclusions, those communities sustained only by intransitive competition might be rather uncommon in nature (Soliveres et al., 2018 [55]). Recent works proposed that the species diversity still depends on pairwise features of community, so that intransitive competition should be considered together with the pairwise features (Gallien et al., 2017 [32]; Godoy et al., 2017 [33]; Yang and Hui 2021 [34]). Therefore, we finally view our system in a more continuous way and obtained the parameter range for merged mechanism.

Based on the obtained three cases of bifurcation results, we respectively introduce alien species into these communities. Our equilibrium findings show that no matter for universal or distinct invader (e.g., only compete with one native species), if species of native community are maintained by niche differentiation (case 1) or intransitive competition loop (case 3), the invasion process that happen in such communities would similarly have two kinds of consequence: invasive coexistence which only causes native abundance change rather than extinction (Gallardo et al., 2016 [56]) and invasion exclusion. Unlike the case 3, for niche differentiation dominant community (case 1), native species limit themselves more than others (Barabas et al., 2016 [57]). As such, structure of interspecific interaction network does not matter for population dynamics. And this principle has increased species' per capita growth rates at low relative abundance (Adler et al., 2007 [40]; MacDougall et al., 2009 [25]). Therefore, most alien species would establish their populations but cause no resident extinction in case 1, even though they might be highly competitive. Whereas for only intransitivity (namely rock–paper–scissors competition structure) supported community, none of the species could be a permanent strong or weak competitor (Lankau and Strauss 2007 [30]). Species are dynamically kept under their interspecific interacting loops. If introducing alien species, we find those invaders being with particular competitive features, like higher intra and interspecific competitive ability, crumbles the stable state of resident community. From MacDougall et al. (2009) [25], we know that niche differentiation factor (like invaders limiting themselves more here) allows the invader to establish, and fitness difference factors (such as invader being with a higher competitive ability) favors the dominance of the invader. Thus, alien species successfully spread and drives competitive exclusion in this scenario. Since intransitive community more likely occurs in heterogeneous and unproductive conditions (Soliveres et al., 2018 [31]), invasion introduction in this type of communities would become more harmful.

As for communities maintained by interplay of the two mechanisms (or partial intransitivity), there are more diverse invasion consequences. Except for invasion coexistence and native extinctions, the consequence of invasion failure occurred for certain parameter ranges. Some recent investigations have also indirectly suggested the facilitating effect on invasion when increasing the number of resource and native species (Northfield et al., 2018 [58]). But since the literature about competitive networks effect on invasion are seldom (Godoy and Thompson 2019 [15]), people did not explicitly explore the influence of niche departure and intransitive competition or even their interplay. Here, we further show that the phase of repelling invasion occurs depends dramatically on the extent to which they limit themselves and competitive asymmetries. Community containing big competition asymmetries favors invaders of lower intraspecific competition while the opposite is true for small competing asymmetry communities. We may explain this from how competition asymmetries modulate levels of the two coexistence mechanisms in our system. For example, small competition asymmetry ($1 - \theta$) promotes system tend to have more homogeneous fitness differences and so that enhancing intraspecific density regulation (the degree of niche difference). Alien species without enough intra-group competition would not be able to establish their populations. Whereas greater competition

heterogeneous (bigger value of $1 - \theta$) tend species densities to be more balanced under partial intransitive loop. If invasion happens and invader limit more themselves, this balance would not be disrupted, leading to strong resistance to invasion. This invasion which is failed by less intraspecific limitation could happen in certain community sites. Warren et al. (2019) [59] once found, in their observational and experimental researches, that the decrease of intraspecific competition invader (e.g., caused by ‘friendly release’) would allow ant invader *Myrica rubra* successfully established. Additionally, universal or distinct invader may propose significant different parameter range of invasions. Invasion outcomes in this scenario, especially when interplay of the two mechanisms and high competition asymmetry occurs, are found more sensitive to features of invader.

The index λ_m and \vec{V}_m , our estimator to quantify the short-term response of each species, make us possible to compare species long-term evolution dynamics to their dynamic response when facing invasion. Our findings indicate the species short-term response to invasion would be consistent with the long-term stable state of population density. In fact, there have existed studies focusing on the estimation of λ_m and its potential role in system resilience (Allesina and Tang 2012 [60]; Suweis et al., 2015 [61]; Villa Martin et al., 2015 [62]). λ_m determines the magnitude of trajectory change for species (native or alien) while certain element of \vec{V}_m represent both directions and speed of population change. Villa Martin et al. (2015) [62] believe \vec{V}_m indicates the effective potential of dynamic system in the direction of steepest descent. For more extend, we do not need to calculate the adjacency matrix for the full recipient species (Hui and Richardson 2019 [41]), but just consider an optional small matrix which depicting a focal species-centric network in more complex intransitive loop. Finally, for future application, this matrix \vec{V}_m can also be equivalent to the major axis from a principal component analysis (PCA) of the adjacency matrix. As we know, PCA is a statistical tool that reduces multicollinearity by converting multiple vectors into spaces with orthogonal unrelated axes (Jolliffe 2002 [63]). From the perspective of ecology, the first principal component \vec{V}_m of the Jacobian matrix can intuitively show how dynamic system deviate from the long-term survival point in the face of invasion. Once the Jacobian matrix is quantified, we can use principal component analysis to treat the first principal component as the dynamic response trajectory of the invasive ecological network.

Here, we explicitly evaluate the invasion to competition network with two properties, niche differentiation and intransitivity. The intransitive dynamic results mainly arise from changes in the density of a third species that interacts with both species of the focal pair. However, as increasing emphasis on diverse competitive networks (Levine et al., 2017 [54]) in coexistence theory, the other trait-mediated indirect interactions among networks, like higher-order interactions (Billick and Case 1994 [64]; Grilli et al., 2017 [65]) also should be linked with invasion performance (Godoy and Thompson 2019 [15]). Given lack of the knowledge about invasion to above systems (Valentin et al., 2017 [66]; Latombe et al., 2021 [42]), future studies necessarily pay more attentions to this issue.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d15040554/s1>, Figure S1: Assuming alien species can only compete with species 2, there are various invasive consequences. Figure S2: Assuming alien species can only compete with species 3, there are various invasive consequences. Figure S3: Assuming alien species can compete with species 1 and 2, there are various invasive consequences. Figure S4: Assuming alien species can compete with species 1 and 3, there are various invasive consequences. Figure S5: Assuming alien species can compete with species 2 and 3, there are various invasive consequences. Figure S6: Under the circumstance involving the combination of niche differentiation and intransitive competition, invasive species exhibit a competitive advantage over only single species, resulting in various invasive consequences. Figure S7: Under the circumstance involving the combination of niche differentiation and intransitive competition, invasive species exhibit a competitive advantage over two species, resulting in various invasive consequences.

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Appendix A. Calculation of Native Coexistence Conditions

Appendix A.1. The Existence of Positive Equilibrium Point

We get the equilibrium point N_i^* ($i = 1, 2, 3$) by setting the right-hand formula of system (1) in the main text as zero. N_i^* ($i = 1, 2, 3$) are functions of parameters θ, k and θ_3 . Since θ is fixed, the value of N_i^* ($i = 1, 2, 3$) is determined only by k and θ_3 . The existence region of each positive equilibrium points under different levels of competitive asymmetry ($1 - \theta = 0.7, 0.5, 0.3$) is shown in the Figure A1a–c. The positive equilibrium point $N_i^* > 0$ represents native species have positive population density in the steady state. But in order to guarantee the steady state do not change too much under small perturbations, we still need to do local stability analysis (refers to the next following part). Our coexistence area is obtained by the intersection of these two kinds of regions.

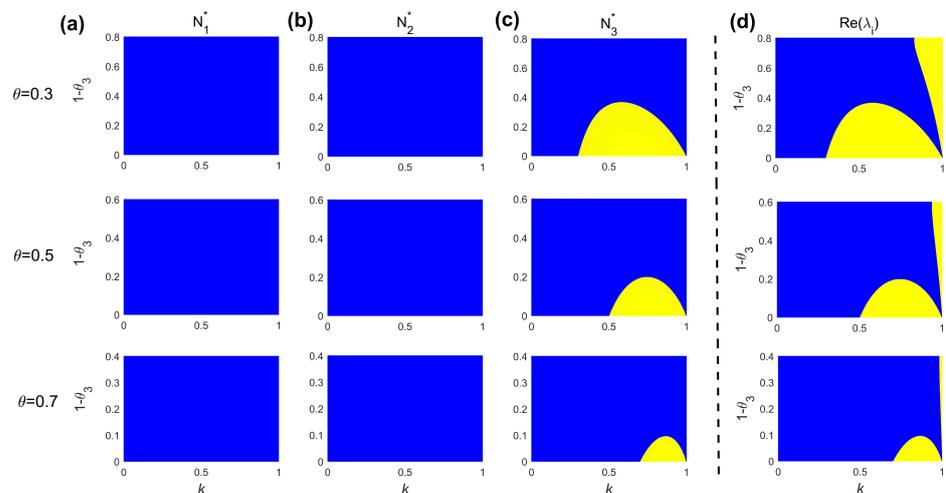


Figure A1. Detail parameter ranges for positive equilibrium states (a–c) and for locally asymptotic stable analysis (d). Different figure rows correspond to three levels of competitive symmetry $1 - \theta = 0.7, 0.5, 0.3$. There were two kinds of ranges: blue colors ($N_1^* > 0, N_2^* > 0, N_3^* > 0$ and $Re(\lambda_i) < 0$), yellow colors ($N_1^* < 0, N_2^* < 0, N_3^* < 0$ and $Re(\lambda_i) > 0$). We select the intersection of all figures in each row to represent the final coexistence area for each competitive symmetry $1 - \theta$ (Figure 2b of main text). Other parameters are $r_1 = r_2 = r_3 = 0.02$.

The Locally Asymptotic Stable Analysis

We linearize system (1) of main text to get $\dot{N} = JN$, where J is the Jacobian matrix. Then, we analyze the stable state of the system at equilibrium point $N^* = (N_1^*, N_2^*, N_3^*)$, and the following characteristic equation can be obtained by $|\lambda I - J| = 0$:

$$\lambda^3 + A\lambda^2 + B\lambda + C = 0, \tag{A1}$$

where $\lambda = (\lambda_1, \lambda_2, \lambda_3)$ is the eigenvalue for Jacobian matrix J . By transforming the equation above, we can get:

$$A = \alpha_{11}N_1^* + \alpha_{22}N_2^* + \alpha_{33}N_3^*, \tag{A2}$$

$$B = (\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21})N_1^*N_2^* + (\alpha_{11}\alpha_{33} - \alpha_{13}\alpha_{31})N_1^*N_3^* + (\alpha_{22}\alpha_{33} - \alpha_{23}\alpha_{32})N_2^*N_3^*, \tag{A3}$$

$$C = (\alpha_{11}\alpha_{22}\alpha_{33} + \alpha_{12}\alpha_{23}\alpha_{31} + \alpha_{13}\alpha_{21}\alpha_{32} - \alpha_{11}\alpha_{23}\alpha_{32} - \alpha_{12}\alpha_{21}\alpha_{33} - \alpha_{13}\alpha_{22}\alpha_{31})N_1^*N_2^*N_3^*, \tag{A4}$$

where α_{ij} are the elements of the competition matrix M . They represent the competition strength from species j to i . After substituting the above equation with specific setting values in main text, we can get the following equation:

$$A = (\sqrt{\theta_3}/k)N_1^* + (\theta/k\sqrt{\theta_3})N_2^* + (\sqrt{\theta_3}/k)N_3^*, \tag{A5}$$

$$B = \left((\theta/k^2) - \theta \right) N_1^*N_2^* + \left((\theta_3/k^2) - \theta_3 \right) N_1^*N_3^* + \left((\theta/k^2) - \theta \right) N_2^*N_3^*, \tag{A6}$$

$$C = \left((\theta\sqrt{\theta_3}/k^3) + \theta^2\theta_3 + 1 - 3(\theta\sqrt{\theta_3}/k) \right) N_1^*N_2^*N_3^*, \tag{A7}$$

where $k \in [0, 0.9]$ is the degree of niche overlap, $\theta \in [0, 1]$ is the intensity of interspecific competition and $\theta_3 \in [0, 1]$. And let us express $N_i^* (i = 1, 2, 3)$ the same way:

$$N_1^* = (k\theta - k^3\theta + k^3 + k^3\theta^2 - (k^2\theta) / \sqrt{\theta_3} - k^2\theta\sqrt{\theta_3}) / (\theta\sqrt{\theta_3} + k^3 + k^3\theta^2\theta_3 - 3k^2\theta\sqrt{\theta_3}), \tag{A8}$$

$$N_2^* = (k(\theta_3 - k^2\theta_3 - k\sqrt{\theta_3} + k^2 + k^2\theta\theta_3 - k\theta\sqrt{\theta_3})) / (\theta\sqrt{\theta_3} + k^3 + k^3\theta^2\theta_3 - 3k^2\theta\sqrt{\theta_3}), \tag{A9}$$

$$N_3^* = (k(\theta - k\sqrt{\theta_3} - k^2\theta + k^2 + k^2\theta\theta_3 - k\theta\sqrt{\theta_3})) / (\theta\sqrt{\theta_3} + k^3 + k^3\theta^2\theta_3 - 3k^2\theta\sqrt{\theta_3}), \tag{A10}$$

the system is locally asymptotically stable at the equilibrium point if satisfying:

$$Re\lambda_i(J) < 0, i = 1, 2, 3 \tag{A11}$$

That is $\lambda_1 < 0, \lambda_2 < 0$ and $\lambda_3 < 0$, which are three roots corresponding to the characteristic Equation (5). We get $\lambda_i (i = 1, 2, 3)$ by taking the roots of the cubic Equation (5), and $\lambda_i (i = 1, 2, 3)$ are functions of parameters θ, k and θ_3 . Since θ is fixed, the value of $\lambda_i (i = 1, 2, 3)$ is determined only by k and θ_3 . The regions where native species reach Lyapunov stability ($Re\lambda_i(J) < 0$) under different competitive asymmetries ($1 - \theta = 0.7, 0.5, 0.3$) is shown in the Figure A1d.

Appendix B. Calculation of Matrix for Species Short-Term Response

Specifically, we first define $n_i = N_i - N_0$ and transform original network system (3) of main text into a new system (4) of main text, where N_0 is the initial population density at the beginning of the invasion (the initial population density of invasive species is uniformly set), So n_i is standardization of N_i and can be regarded as the difference between the population density of the new system at any time after the invasion and the initial population density at the beginning of the invasion, namely the change of population density of each species after invasion. Then, let us consider the dynamical system of the ecological network $\dot{n}_i = F(n_i) = F(N_i - N_0)$ and its linearization $\dot{\vec{n}} = J'\vec{n}$. In mathematics, the matrix J is an operator that transforms the abundance vector n into a new vector space, also known as a Jacobian matrix. According to the definition, we have $J'V = V\Lambda$, where $V = v_1, v_2, \dots$ is eigenvector matrices composed of vertical eigenvectors v_i of eigenvalues λ_i (λ_i satisfy $J'v_i = v_i\lambda_i$). Λ is an eigenvalue matrix with diagonal elements of λ_i and other

elements of zero, after the equation transformation, $V^{-1}J' = \Lambda V^{-1}$ can be obtained. Let $n = V\varepsilon$, where ε is the new vector space whose derivative is:

$$\dot{\varepsilon} = V^{-1}\dot{n} = V^{-1}J'n = \Lambda V^{-1}n = \Lambda\varepsilon, \quad (\text{A12})$$

therefore:

$$\varepsilon_i = c_i e^{\lambda_i t}, \quad (\text{A13})$$

where $c_i = \varepsilon_i(0)$ is a constant, indicating the initial value of the system disturbance. Then, we can obtain the dynamics of species i :

$$n_i(t) = \sum_j V_{ji} c_j e^{\lambda_j t}, \quad (\text{A14})$$

where V_{ji} is the i th element of the eigenvector V_j . We can expand and analyze the above formula:

$$n_i(t) = V_{1i}c_1 e^{\lambda_1 t} + V_{2i}c_2 e^{\lambda_2 t} + \dots + V_{mi}c_m e^{\lambda_m t} + \dots, \quad (\text{A15})$$

$$n_i(t) = e^{\lambda_m t} \left(V_{1i}c_1 e^{(\lambda_1 - \lambda_m)t} + V_{2i}c_2 e^{(\lambda_2 - \lambda_m)t} + \dots + V_{mi}c_m + \dots \right), \quad (\text{A16})$$

where λ_m is the leading eigenvalue (the largest eigenvalue of the real part) of the Jacobian matrix J' of the system. As time t goes to infinity, we can see that $n_i \rightarrow V_{mi}c_m e^{\lambda_m t}$, namely $\Delta N_i \sim V_{mi}e^{\lambda_m t}$ (ΔN_i is the change in population density of species i). Thus, the short-term response of species i (how species i changes), both in direction and magnitude, depends entirely on V_{mi} . If $V_{mi} > 0$, the species i will increase; If $V_{mi} < 0$, the species i will decrease; If $V_{mi} = 0$, the species i is less sensitive to disturbance.

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