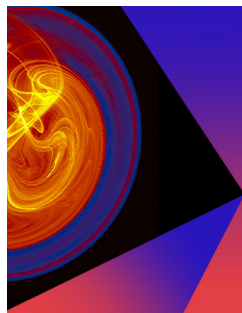# Invasion and interaction determine population composition in an open evolving ecological system ⊘

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Invasion and interaction determine population composition in an open evolving ecological system

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ABSTRACT

It is well-known that interactions between species determine the population composition in an ecosystem. Conventional studies have focused on fixed population structures to reveal how interactions shape population compositions. However, interaction structures are not fixed but change over time due to invasions. Thus, invasion and interaction play an important role in shaping communities. Despite its importance, however, the interplay between invasion and interaction has not been well explored. Here, we investigate how invasion affects the population composition with interactions in open evolving ecological systems considering generalized Lotka–Volterra-type dynamics. Our results show that the system has two distinct regimes. One is characterized by low diversity with abrupt changes of dominant species in time, appearing when the interaction between species is strong and invasion slowly occurs. On the other hand, frequent invasions can induce higher diversity with slow changes in abundances despite strong interactions. It is because invasion happens before the system reaches its equilibrium, which drags the system from its equilibrium all the time. All species have similar abundances in this regime, which implies that fast invasion induces regime shift. Therefore, whether invasion or interaction dominates determines the population composition.

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An ecosystem consists of many interacting species. The generalized Lotka–Volterra equation has described how such interactions determine the abundances of species. Most conventional studies, however, have focused on fixed interaction structures, while real-world ecosystems evolve by constantly introducing new species. Once new species invade a system, the interaction structure changes because the new species induce new interactions. In this paper, we capture the dynamics of the interaction structure considering an open evolving network. Species and pairwise interactions are represented by nodes and links in the network. The interplay between invasion and interaction will shape the abundances of species. If the invasion occurs frequently, new species will invade a system before the system reaches its equilibrium.

As the interaction strength governs the equilibration time, the interaction strength as well as the invasion rate plays an important role in the dynamics. Examining the abundance distributions of species for various invasion rates and interaction strengths, we find that reducing invasion rate and increasing interaction strength affect in a similar way on the abundance distributions. Furthermore, we figure out the role of the invasion rate and the interaction strength by measuring the correlation between abundances and species properties, such as age and the incoming degree strength in the given interaction structure. It sheds light on this invasion, and interaction plays an important role to determine the population composition—diversity and abundance distribution—in an open evolving ecological system.

I. INTRODUCTION

In an ecosystem, many species interact with each other. Some species compete with others for shared resources, inducing adaptation, or death from the competition. On the other hand, flowers provide food for insects, with the help of reproduction from them. As interactions between species affect their death and reproduction, population compositions are determined from them. To understand how such interactions affect populations, the generalized Lotka–Volterra equation has been studied.[1,2] The equation describes the abundance dynamics of species taking interactions into account and has successfully explained the real world.[3–5] However, the literature has focused on the situation where the interaction structures are fixed, while invasions alter the structures all the time in nature.

An ecosystem is an open system that has biological invasions. When a newly invading species enters an ecosystem, it interacts with the resident species, resulting in changes in the interaction structure. Consequently, these changes lead to changes in the population composition.[6–9] If there is no invasion at all, population dynamics with a non-changing interaction structure can be analyzed by investigating fixed points of the dynamical system.[10–17] The system evolves toward stable fixed points as time goes on. However, the open evolving ecological system with new invaders continues to change interaction structures over time. Here, another timescale that comes from the invasion process is involved in population dynamics, and, thus, the equilibration is not guaranteed, where the previously well-developed methodology could not be applied.

To implement the evolving interaction structure, we introduce an evolving network, where nodes represent species and links are pairwise interactions.[7,8,18–21] In the ecosystem, the interactions are directional with weights and signs. The weight indicates how strong the interaction is and the sign does the type of the interaction such as competition, facilitation, mutualism, parasitism, and so on.[22–26] Furthermore, the abundance of each species is denoted as a property of the node. Interactions finally change the abundance of all species and even can cause the extinction of certain species. In this case, extinct species nodes are removed from the system with the connecting/connected links together. Once a new species comes (invades) into the system, a new species node and connecting links (new interactions) are added.

Considering the evolving interaction networks with generalized Lotka–Volterra-type dynamics, we investigate how both invasion and interaction determine the population composition. As the system has two timescales involved in the invasion and equilibration processes, we manipulate the invasion rate and interaction strength. Varying these two parameters, we perform simulations of population dynamics and find two distinct patterns in the observed abundance, determined by the competition between invasion and interaction timescales.

Fast invasion helps the system keep high diversity pushing the settled resident species. It suppresses the emergence of dominant species that take over almost the population if there is enough time to evolve. The high-diversity populations appear if the invasion is fast, even for the quite strong interaction condition, which makes equilibration fast. However, when interactions are strong enough to overcome the invasion effect, the dominant species finally appear. The decreasing invasion rate and increasing interaction strength are effectively the same in the sense of diversity. It only changes the timescale factor. Furthermore, the abundance distributions of each species are similar, which implies that the dominant factor between the invasion rate and the strength of the interaction determines the population composition.

This paper is organized as follows: The Lotka–Volterra-type equation with resource limitation is portrayed in Sec. II A. In Sec. II B, the scheme of an open evolving network system is described. Section III is focused on the correlation between abundance and a network property to infer the boundaries among different regimes that show different population compositions. Further discussion is done in Sec. IV.

II. MODEL

Interactions between species determine the abundance of species telling who will dominate and who will go extinct. On the other hand, invasions perturb the existing population composition because new interactions reshape the interaction structure. To investigate both invasion and interaction effects on population composition, we construct an open evolving model with generalized Lotka–Volterra-type dynamics.

A. Abundance dynamics

$$\frac{dx_i}{dt} = r_i\, x_i \left(1 - \frac{\sum_j^S w_{ij}\, x_j}{K_i}\right), \tag{1}$$

where x_i is the abundance of species i. The intrinsic growth rate and the carrying capacity of species i are denoted by r_i and K_i, respectively. The effect of the interaction from species j to species i is w_{ij}. When species j affects the abundance of species i, $w_{ij} \neq 0$. Otherwise, the interaction weight w_{ij} is zero. If there are no interactions at all, Eq. (1) is equivalent to the logistic growth equation with $w_{ii} = 1$.

The generalized Lotka–Volterra equation has captured the behavior of ecosystems well.[4,5] When the amount of common resources, such as space and shared food, is finite so-called resource limitation, population growth without a bound is unrealistic.[12] Thus, we modify the generalized Lotka–Volterra equation so that the system has the bounded total population size K as follows:

$$\frac{dx_i}{dt} = G_i(\mathbf{x})\, x_i \left(1 - \frac{\sum_j^{S(t)} x_j}{K}\right) + D_i(\mathbf{x})\, x_i, \tag{2}$$

with the abundance vector $\mathbf{x} = \{x_i\}$ in which elements consist of the abundances of all species. The first and the second terms on the right-hand side describe birth and death processes, respectively. Thus, birth occurs only when the total population does not reach the total carrying capacity K. The growth and death rates of species i, $G_i(\mathbf{x})$ and $D_i(\mathbf{x})$, change depending on the interaction weights and the abundance of the interacting species,

$$G_i(\mathbf{x}) = \sum_j w_{ij}^+ x_j, \tag{3}$$
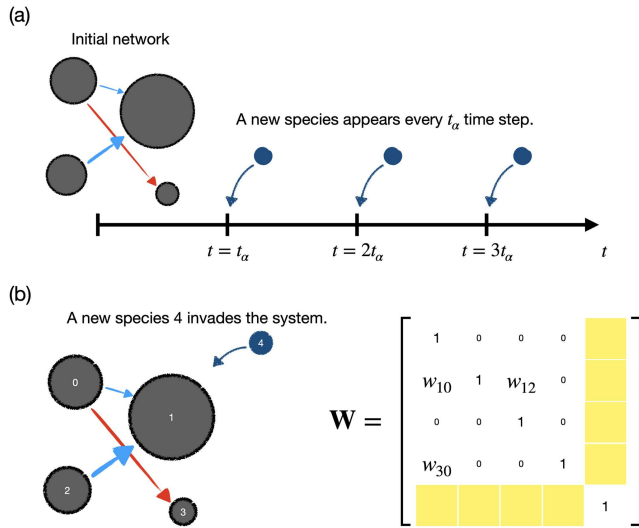
FIG. 1. A schematic figure of an open evolving network model. Species are represented by nodes and pair interactions are denoted by directional links with a sign. The direction of a link from j to i is drawn if node (species) j affects node (species) i. The positive and negative interactions are denoted by the blue and red colors of the links. With those interactions, a generalized Lotka–Volterra-type equation describes the abundance dynamics of species [see Eq. (5)]. (a) Invasion events. A new species invades the system every t_α time step, where the interval between two invasions is $t_\alpha \equiv K/\alpha$. (b) New interactions. A new species interacts with randomly chosen m resident species. We set $m = 5$ because the previous study with a simpler dynamical rule showed that the system can achieve high diversity under the same "open and evolving" condition for $4 < m < 19$.[8] Interaction weight w_{ij} from species j to i is sampled from the normal distribution with zero mean and standard deviation σ. If there are no interactions from j to i, weight w_{ij} is zero. We set intraspecific interaction weight w_{ii} as unity because isolated species can survive by themselves by taking resources.

and

$$D_i(\mathbf{x}) = \sum_j w_{ij}^- \, x_j. \tag{4}$$

A matrix $\mathbf{W}^+$ denotes only positive interactions, $w_{ij}^+ = w_{ij}$ for $w_{ij} > 0$. Otherwise, $w_{ij}^+ = 0$. Similarly, the elements of $\mathbf{W}^- = [w_{ij}^-]$ are nonzero only when the interaction is negative.

For simplicity, we use the normalized abundance of species i with respect to carrying capacity K, $f_i \equiv x_i/K$. Then, Eq. (2) is reduced as

$$\frac{df_i}{dt} = G_i(\mathbf{f}) \, f_i \left(1 - \sum_j^{S(t)} f_j\right) + D_i(\mathbf{f}) \, f_i, \tag{5}$$

rescaling the time as $Kt \to t$ as the growth and death rates are rescaled. Here, $\mathbf{f} = \{f_i\}$ is the normalized abundance vector. Hereafter, we call this normalized abundance, f_i, as abundance for simplicity.

We assume that an invading species carries an initial abundance f_0. Once new interactions are drawn between a new species and residents, the abundance dynamics follows Eq. (5) with the given interaction structure $[w_{ij}^\pm]$ before the next invasion event.
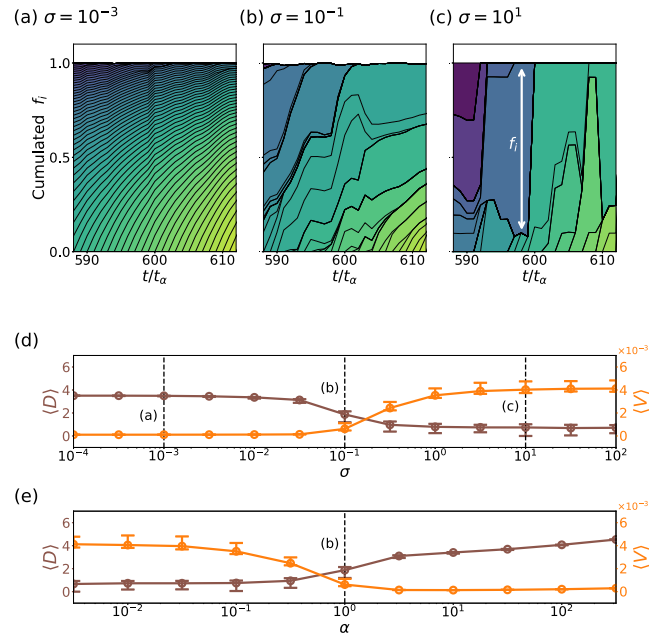

FIG. 2. Abundance dynamics (a)–(c) for the given invasion rate $\alpha = 1$ and various interaction strengths $\sigma = 10^{-3}$, 10^{-1}, and 10^1. Using different colors for different species, we stack abundance f_i so that the height of each color indicates the abundance of each species at time t/t_α. Colors indicate the relative age of each species, not the absolute age, such that blue and yellow are for the oldest and newest species, respectively, within the given time window $t/t_\alpha \in [590, 610]$. Therefore, the lifetime of a species is represented by the width of each stacked color. (d)–(e) Shannon's diversity index D and variability V are measured in the steady state for 100 independent simulations. The error bars indicate a 95% confidence interval. The dashed lines indicate the parameter sets used in (a)–(c), respectively. Increasing interaction strength σ gives a similar result with decreasing invasion rate α. We used the total carrying capacity $K = 100$ for the visualization [the trends in (d)–(e) are robust for larger K]. Note that we also measure various population-level quantities in the steady state (see Sec. B in the supplementary material for details).

We numerically integrate Eq. (5) to get $f_i(t)$. During integration, if the abundance f_i becomes smaller than $1/K \equiv f_{\text{th}}$, we consider that species i goes to extinction and set $f_i = 0$. We use $f_0 = 10 \cdot f_{\text{th}}$ for simulations.

B. Evolving interaction network

If we treat species as nodes, the interaction w_{ij} can be mapped into a link from j to i with a direction and a sign. Thus, the interaction structure can be represented by a network. This network structure changes over time due to invasions and extinctions of species. We suppose that a new species comes into the system with the invasion rate α. It means that a new species appears in the system every $t_\alpha \equiv K/\alpha$ on average. The smaller α is, the less frequent new species come into the system. For simplicity, we add a new species to the system every t_α [see Fig. 1(a)].

When an invasion event happens, the number of nodes in the network increases by one, and m new interactions with this new
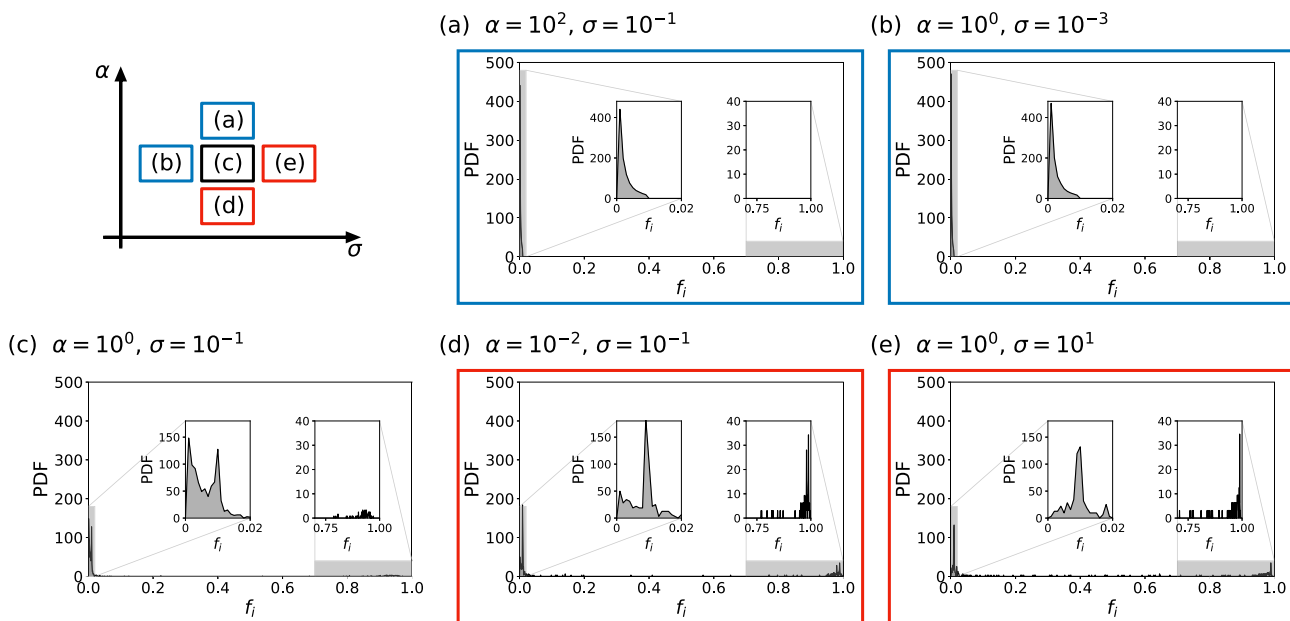
FIG. 3. Abundance distributions at the steady state for various invasion rates $\alpha = 10^2$, 10^0, and 10^{-2} and interaction strengths $\sigma = 10^{-3}$, 10^{-1}, and 10^1. Ranges $f_i \in [0, 0.02]$ and $f_i \in [0.7, 1]$ are zoomed in the insets to check the distribution shapes in very small and large abundances. If the invasion occurs too frequently to reach the equilibrium of the system, the distribution will have no dominant species. On the other hand, when the interaction strength is strong enough to reach equilibrium within two successive invasion events, dominant species can emerge. The color of a panel frame indicates which effect dominates at the given parameter set. The blue color means the invasion is dominant and the red one indicates the interaction is dominant in the system. We used the total carrying capacity $K = 1000$. For obtaining the distributions, 100 independent simulations are used.

species appear [see Fig. 1(b)]. To assign the new interaction weights, we sample the weights w_{ij} from the normal distribution $\mathcal{N}(0, \sigma^2)$, except for the intraspecific interaction weight ($w_{ii} = 1$). That is, the larger σ is, the stronger the interactions become. The sign of w_{ij} indicates the effect of species j on the abundance of species i. After an invasion event, the system follows the dynamics as described in Eq. (5). When species go extinct, the nodes and the links attached to those nodes are removed.

We initially construct a random network with S_0 nodes and m links for each node and randomly assign the direction and the weight of all links. To investigate how invasion and interaction shape the population composition, we constantly add a new species until the system has a saturated number of surviving species. The number of nodes is denoted by $S(t)$. We call this regime *steady* when $[S(t + \Delta t) - S(t)] / \Delta t \sim 0$ and observe how the abundance of surviving species changes over time depending on invasion rate α and interaction strength σ (see Sec. A in the supplementary material for details).

III. RESULT

Depending on interaction strength σ, abundance dynamics shows different behaviors in the steady state at a given invasion rate α [see Figs. 2(a)–2(c)]. In a weak-interaction limit among species, the invasion rate solely determines the whole abundance. In this case, existing species are gradually pushed out of the system due

to constant invasions. A similar scenario happens for low σ where the invasion dominates interactions [see Fig. 2(a)]. In contrast, for large σ, the interactions are strong enough to induce the species with large abundance, reducing the diversity of the system [see Figs. 2(b) and 2(c)]. At the same time, new interactions introduced by an invader are also strong enough to kill such dominant species. Thus, the dominant species keep changing over time [see Fig. 2(c)].

To quantify the decrease in diversity for strong interactions, we measure Shannon's diversity index D for various σ as

$$D = -\sum_i f_i \log f_i. \tag{6}$$

Another feature of the abundance dynamics for strong interactions is fast changes in dominant species [see Fig. 2(c)]. As a new dominant species emerges all the time, the fluctuation of the abundance is large. To quantify changes in abundance over time, we measure variability V as follows:

$$V = \left\langle \mathrm{Var}_t(f_i) \right\rangle_S, \tag{7}$$

where $\mathrm{Var}_t(f_i)$ indicates the variance of abundance f_i over time and $\langle \cdot \rangle_S$ means the average over the number of species that survived at the steady state. The large variability V indicates frequent turnover of dominant species. As increasing interaction strength σ, diversity decreases while variability becomes higher at a fixed invasion rate [see Fig. 2(d)].
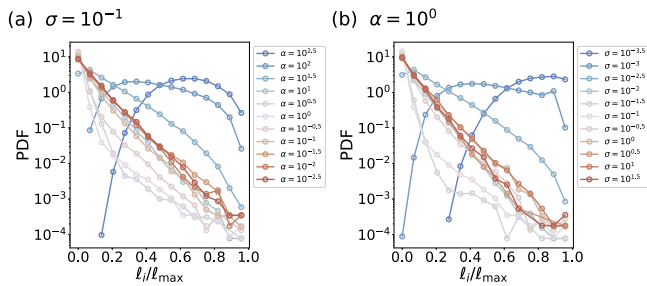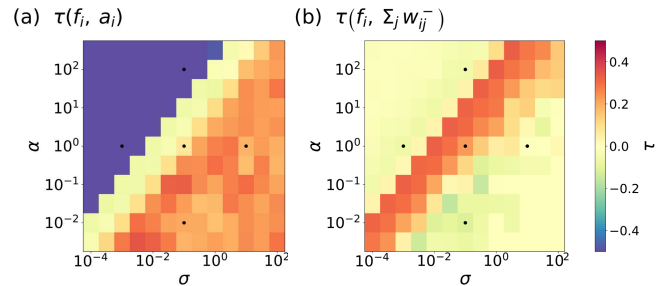
FIG. 4. Lifetime distributions (a) for various invasion rates α from $10^{-2.5}$ to $10^{2.5}$ at fixed interaction strength $\sigma = 10^{-1}$ and (b) interaction strengths σ from $10^{-3.5}$ to $10^{1.5}$ at fixed invasion rate $\alpha = 10^{0}$. We normalized the lifetime with respect to the maximum lifetime at a given parameter set, ℓ_i/ℓ_{max}, to plot the distributions in the same scale. The color of each line indicates the dominating effect at the given parameter set (blue: invasion effect dominates, red: interaction effect dominates). As either decreasing invasion rate α or increasing interaction strength σ (from blue to red), the lifetime distributions change from a bell-shaped distribution to an exponential distribution. In the intermediate, a heavy-tailed distribution appears indicating a long-lived species. We used 100 independent configurations for each distribution.

FIG. 5. Kendall's tau-b correlation coefficients τ between abundance f_i and age a_i in (a), and the correlation coefficients between the abundance f_i and the negative incoming weight sum $\sum_j w_{ij}^-$ in (b), respectively. The correlation coefficients are measured at the steady state. In the invasion-dominant regime (upper left), the abundance negatively correlates with its age because each invasion event pushes down all resident species abundances. Moreover, the interaction weights are not correlated with the abundance because the interaction effect is not enough to change the observed abundance dynamics. In the lower right of the panels, however, the interaction effect is much more dominant than the invasion effect on the dynamics. Once an invading species has lots of positive links from others, the species have a higher abundance. Then, the species dominantly survive until new dominant species appear while other invading species with not enough positive links are pushed out immediately. For this reason, the abundance of species positively correlates with the age in the interaction-dominant regime because we measure the correlation coefficient for surviving species at the steady state. In the lower right in (b), the interaction-dominant regime, species with negative incoming links cannot survive. As a result, the correlation between abundances and negative incoming links cannot be captured as the surviving species do not have negative incoming links [see Fig. S2(g) in the supplementary material]. Black dots correspond to the parameter sets used in Fig. 3. The total carrying capacity is set to $K = 1000$.

Even though the interaction strength σ is large, the system can have high diversity and low variability when the invasion rate α is large enough. It is because the species expected to be dominant is pushed out before reaching its equilibrium due to the high invasion rate. Thus, increasing α has the opposite effect of increasing σ [see Fig. 2(e)]. As a high invasion rate can inhibit the effect of interactions, the interplay between invasion rate α and interaction strength σ determines the abundance dynamics.

The species with small abundance (around the initial abundance) result from invasions, while strong interaction is essential to observe the species with large abundance (much larger than the initial abundance f_0). If the invasion effect is dominant, all abundances will be around initial values. On the other hand, species with a large abundance can appear for higher interaction strength. Figure 3 shows the steady-state abundance distributions for various invasion rates α and interaction strength σ. Increasing α and decreasing σ give the same effects on abundance distributions [see Figs. 3(a) and 3(b)]. In the same way, decreasing α and increasing σ show similar trends of abundance distributions [see Figs. 3(d) and 3(e)]. Invasion rate α and interaction strength σ have the opposite effects on abundance distributions.

When the invasion events happen too frequently, no dominant species appear [see Figs. 3(a) and 3(b)]. In this regime, species have abundances less than or equal to the initial value ($f_i \leq f_0$ in the figure). Once a new species comes into the system, all abundances are reduced proportionally to their abundances due to resource limitations. Thus, a portion of each abundance remains in the system. A newly added species undergoes such a reduction once, while the residents already experienced several dilutions. Thus, the later invading species have the larger abundance, showing decreasing distribution function of f_i.

Conversely, in the interaction-dominant regime [see Figs. 3(d) and 3(e)], dominant species appear with non-zero probability. Species with small abundances can hardly survive except for new

invading species. That is the reason why the peak around $f_i = f_0$ remains.

The lifetime distributions tell us the consistent scenario. In the invasion-dominant regime, a unimodal distribution appears because all species have a similar lifetime on average as they behave in a similar way regardless of interactions (see the blue colored lines in Fig. 4). On the other hand, the distribution becomes exponential when the interactions are too strong as almost species instantaneously go to extinction (see the red colored lines in Fig. 4). In the intermediate regime that shows an interesting behavior, a winning species, which takes almost the total carrying capacity, survives for a long time while the others have shorter lifetimes due to lower fitness than the winner. As a result, the lifetime distribution has a heavy tail (see the gray colored lines in Fig. 4). This is, therefore, the lifetime distributions change from a unimodal distribution through a heavy tail distribution to an exponential distribution as the invasion effect diminishes and the interaction effect in the system intensifies (see Sec. C in the supplementary material for details).

To examine how invasion rate α and interaction strength σ determine the patterns of the observed abundance dynamics, we imagine two extreme cases: one is the case of zero interactions given at a constant invasion rate, and the other is strong interactions that ensure the equilibration of the system before new invasions (see Sec. D in the supplementary material for a detailed

calculation). Without interactions ($\sigma = 0$), each species is independent and identical. There are no differences between species except for their age—how long the species stay in the community. Once a new invasion event occurs, this invader pushes down all residents' abundances due to the limited population size [see Eq. (5)]. Thus, elder species that undergo more invasion events are likely to have a smaller abundance compared to others, giving a smooth gradient of abundances between species. Therefore, negative correlations between abundances and ages appear for large α and small σ [see Fig. 5(a)]. On the contrary, young species tend to have smaller abundances for small α and large σ as dominant species emerge and invaders usually die out.

Furthermore, we find that species abundances are highly correlated with the sum of negative incoming weights only in the intermediate regime between invasion-dominant and interaction-dominant regimes. The positive correlations between abundances and the sum of negative incoming weights in the interaction-dominant regime are expected because the derivatives of abundances are highly dependent on their interaction structure at the steady-state [see Eq. (5)]. However, too strong an interaction leads to almost immediate deaths of the other species, and all observed species and interactions are transient [see Fig. S2(g) in the supplementary material]. The calculated correlation coefficients for various α and σ support that there are two regimes where either invasion or interaction dominates (see Sec. E in the supplementary material for details).

IV. DISCUSSION

Interacting species can hardly form a high-diversity community because the fittest species takes all resources. However, with a high invasion rate, ecosystems can show high diversity. When invasion events occur before the system reaches its equilibrium, multiple species can coexist. In other words, the interaction strength controls the equilibrium time of the dynamics, while the invasion rate interrupts reaching equilibrium by changing the interaction structure. Therefore, invasion and interaction play an important role in shaping the population composition.

To describe the dynamics according to the invasion rate α and the interaction strength σ, we consider the Lotka–Volterra-type equation with an open evolving interaction network [see Eq. (5)]. As a new invader enters the system with a fixed time interval, new interactions between the invader and the residents are drawn. Because the system undergoes invasions and extinction of species, the growth and death rates of all species change over time. We found that the invasion rate α and the interaction strength σ have opposite effects on the population composition. The system has a high diversity and low variability for high invasion rate α and small interaction strength σ. In contrast, when the interaction strength σ is sufficiently strong, dominant species appear. The composition is almost homogeneous when the invasion effect is dominant, while the interaction effect makes the population composition become heterogeneous.

There are several interesting directions for future research. The first is to consider the effect of abundance on interactions.[20] We can directly modify the interaction term in the dynamics or consider the abundance effects on invasions, which would be more realistic. For example, new invaders tend to be more competitive for species with lower abundance than those with higher abundance. Moreover, the interaction itself can be drawn based on abundances, rather than assuming that a new species interacts with residual species randomly. The second interesting direction for future research is to consider higher-order interactions, involving more than three species. For instance, in microbial communities, by-product metabolites can induce higher-order interactions that affect the environment and, in turn, the interactions between species. Previous studies have shown that incorporating higher-order terms into Lotka–Volterra-type equations can stabilize ecosystems.[27] Thus, we would investigate whether the higher-order interactions can stabilize open evolving ecosystems as well. Our simple model can be extended to study more realistic ecosystems, providing a basic toolbox to investigate the impact of abundances on interactions or the role of higher-order interactions.

To put it all together, our finding shows that fast invasion events not only provide temporal coexisting species with small abundances but shift the regime, governing the observed abundance dynamics with interaction strength. Thus even if strong competition tends to result in the emergence of dominant species, fast invasion events prevent the growth of species, which is expected to be dominant. It means that not only the interaction strength but also the invasion rate is important in shaping the population composition. It is because invasions introduce a new time scale in the system, the invasion time scale.

SUPPLEMENTARY MATERIAL

See the supplementary material for detailed information on the studied evolving open system.

AUTHOR DECLARATIONS

Conflict of Interest

The authors have no conflicts to disclose.

Author Contributions

Youngjai Park: Conceptualization (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Project administration

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(equal); Validation (equal); Visualization (equal); Writing – original draft (lead). **Takashi Shimada:** Conceptualization (equal); Investigation (equal); Writing – review & editing (equal). **Seung-Woo Son:** Conceptualization (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Writing – review & editing (lead). **Hye Jin Park:** Conceptualization (equal); Formal analysis (equal); Funding acquisition (lead); Investigation (equal); Methodology (equal); Resources (equal); Supervision (equal); Writing – original draft (supporting); Writing – review & editing (lead).

DATA AVAILABILITY

The data that support the findings of this study are openly available in github at https://github.com/youngjai/OpenEvolvingSystem, Ref. 28.

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