

Quantification of competition dynamics in multispecies systems using landscape and flux theory

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Multispecies competition models contribute to understanding how various species interact in natural ecosystems and how these interactions influence population dynamics and ecosystem stability. However, achieving a comprehensive and physical understanding behind species competition remains challenging. Based on the nonequilibrium landscape-flux theory, we developed a resource competition model that reveals underlying landscape to quantify global stability. We found that the dynamics of species competing for resources are influenced not only by landscape gradients but also by rotational flux. We further unveiled the underlying thermodynamic and dynamic mechanisms driving species competition. By leveraging the time irreversibility of nonequilibrium systems, we quantified the primary irreversible dynamical pathways and provided early warning indicators for predicting critical transitions. Through global sensitivity analysis of barrier heights, we revealed the critical impact of resource supply on state stability. This study offers a comprehensive physical explanation for understanding species competition at a global perspective.

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I. INTRODUCTION

Species competition models are essential tools in ecology for understanding and predicting the interactions among species and their effects on ecosystems [1–4]. The study of interspecies competition is closely linked to ecosystem stability [5]. Moreover, the diversity of competing species significantly influences both ecosystem functionality and stability [6–8]. Competition, as a fundamental ecological process, is widespread among plants, animals, and microorganisms [9–13]. It profoundly impacts community structure and function, thereby shaping the biodiversity of ecosystems [13,14].

To understand the interactions between species, ecologists have proposed various competition models. These include the predator-prey model [15,16], MacArthur's consumer-resource model [17–19], and Tilman's resource-ratio model [20,21]. The Lotka-Volterra model, relatively simple, generally does not exhibit sustained oscillations [22]. It is important to note that the Lotka-Volterra model is not a mechanistic model, as it primarily describes the effects of interspecies competition through empirical or phenomenological approaches without providing a physical or biological explanation of the resource competition process [23,24]. MacArthur's consumer-resource

model explicitly considers species competing by exploiting shared resources [18,19]. Tilman's resource-ratio hypothesis model, emphasizes the impact of limiting resources and resource supply on species competition, which can be used to explain and predict how plant communities respond to environmental changes and how these changes drive ecological succession [25]. These classic models have laid the foundation for subsequent research and understanding of consumer-resource interactions, being widely applied in ecological studies [4,26–28].

The interactions among species often manifest as competition for limited resources between two or more species [13,29]. The outcome of competition can inhibit the growth, reproduction, or survival of certain species, thus affecting species abundance, distribution, and resource utilization [10,30,31]. In fact, as the number of competing species in a system increases, complex dynamic behaviors such as oscillations and chaos may emerge [32,33]. Huisman and Weissing investigated the biological conditions for oscillations and chaos in multispecies competition involving nonessential abiotic resources, showing that the relationship between species' resource demands and consumption characteristics can lead to dynamic behaviors such as oscillations and chaotic fluctuations [34], with this model being particularly applicable to phytoplankton and terrestrial vegetation. In recent years, significant advancements have been made in resource competition modeling. For example, inspired by studies on the role of trade-offs in phytoplankton diversity [35], research has explored how nutrient trade-offs and environmental shaping jointly promote ecological diversity [27]. Light as a limiting resource has also been incorporated into the theoretical

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studies of resource competition in phytoplankton [36–38]. Additionally, statistical physics approaches have been applied to analyze classic ecological models [39], providing perspectives and tools for understanding the complexity of biological ecosystems. However, extended versions of most resource competition models [4,13,34] often exhibit multistability, chaos, and state transitions, but the underlying physical mechanisms remain unclear. Generally, competition models are based on local stability analysis [2,21,34], making it challenging to quantify the process of species competition for resources on a global perspective.

In the past, landscape theory has been successfully applied to typical ecosystems, including predation, competition, and mutualistic symbiosis [40]. In this study, we propose a stochastic model of resource competition, which, from a global perspective, explores the physical mechanisms required for state transitions in multispecies competition dynamics, based on landscape and flux. We introduce a landscape and flux theoretical framework to quantify the dynamic characteristics of the entire competition system. In the state space, different dynamic states are represented and distinguished based on their relative weight. Competitive states often correspond to higher probabilities and occupy lower potential valleys. Within this framework, the different stable states of the ecosystem can be represented by attractor basins on the landscape, reflecting their probabilities of occurrence. By quantifying the topographical features of the potential landscape, such as the barrier heights between attractor basins, we can assess the global stability of multispecies competition models. We also find that quantifying the landscape topography in multispecies competition helps in understanding the stable states and oscillatory behaviors within the system. The landscape and rotational flux jointly determine the system's dynamic characteristics: The landscape gradient forces attract the system to specific states, while the rotational probability flux drives the system's movement in a spiraling within the state space, leading to complex oscillatory behaviors. Additionally, we will explore the thermodynamic and dynamic origins of species competition oscillations and state transitions. During interspecies resource competition, the system functions as an open system, continuously exchanging energy and matter with the environment. For this purpose, we construct a nonequilibrium dynamic and thermodynamic framework to quantify key thermodynamic and dynamical quantities such as entropy production and average flux, which helps in understanding the underlying driving mechanisms during competition. Moreover, compared with existing study [40], we propose an early-warning indicator based on the time irreversibility of species abundance time series, which enables the prediction of impending critical transitions in ecological competition-resource systems. Unlike conventional methods that rely on complete steady-state distributions or the construction of global potential landscapes, this approach is more experimentally accessible and offers greater practicality and operability, providing a more feasible tool for identifying critical transitions in ecosystems.

II. MODEL

We consider a differential equation model of three species competing for three essential abiotic resources, which is

particularly well suited for describing the dynamics of phytoplankton communities and terrestrial vegetation [34]. This model is based on the following two key assumptions:

(1) The specific growth rate p_{ji} of a species is determined by von Liebig's "law of the minimum" [2,41], meaning it is governed by the most limiting resource. Specifically, if the specific growth rate p_{ji} of species i is determined by resource j , then the species is limited by resource j , satisfying the condition

$$\min[p_{1i}(R_1), \dots, p_{ki}(R_k)] = p_{ji}(R_j), \quad j \in \{1, \dots, k\}. \quad (1)$$

Here, $\min$ denotes the minimum function, R_j represents the availability of resource j , and k represents the number of resources. The growth rate of a species is determined by the most limiting resource, as this resource is the first to reach a critical deficiency, thereby constraining growth. Even if other resources are abundant, the shortage of a single resource can still inhibit growth. Therefore, selecting the minimum value in the model reflects this ecological phenomenon, simulating the growth limitation imposed by the most restrictive resource.

(2) The growth rate follows the Monod equation [42]:

$$p_{ji}(R_j) = \frac{r_i R_j}{K_{ji} + R_j}. \quad (2)$$

Here, r_i represents the maximum specific growth rate of species i and K_{ji} denotes the half-saturation constant of species i for resource j . This equation links the biological growth rate with the concentration of nutrients and is commonly used to model microbial growth [43].

As shown in Fig. 1(a), the three species competing for three different resources, the red line indicates that promotion leads to an increase in species abundance, while the blue solid line indicates that inhibition leads to a decrease in resource quantity. The abundance of each species N_i satisfies Eq. (3), while the evolution of the availability of resource R_j satisfies Eq. (4) [34]:

$$\begin{aligned} \dot{N}_i &= N_i(\min[p_{ji}(R_j), \dots, p_{ki}(R_k)] - m_i), \\ \text{for } i &= 1, \dots, n, \end{aligned} \quad (3)$$

$$\begin{aligned} \dot{R}_j &= G(S_j - R_j) - \sum_{i=1}^n c_{ji} N_i \min[p_{ji}(R_j), \dots, p_{ki}(R_k)], \\ \text{for } j &= 1, \dots, k. \end{aligned} \quad (4)$$

Here, m_i represents the specific loss rate of species i , n represents the number of species, G is the turnover rate of the resources, S_j is the supply of resource j , and c_{ji} is the quantity of resource j in species i , this quantity reflects the species' resource consumption capacity for the resource, with higher values indicating stronger resource consumption capacity. Specifically, if a species has a higher quantity of a particular resource than all other species, it is consuming the highest amount of that resource. Thus, if for all $g \neq i$, it holds that $c_{ji} > c_{jg}$, then species i is consuming the most of resource j . Here, g is used to mark the species, and g runs through all species except the specific species i . Consuming the least amount of a resource can be stated as follows: If a species has a lower quantity of a particular resource than all other species, it is consuming the lowest amount of that resource.

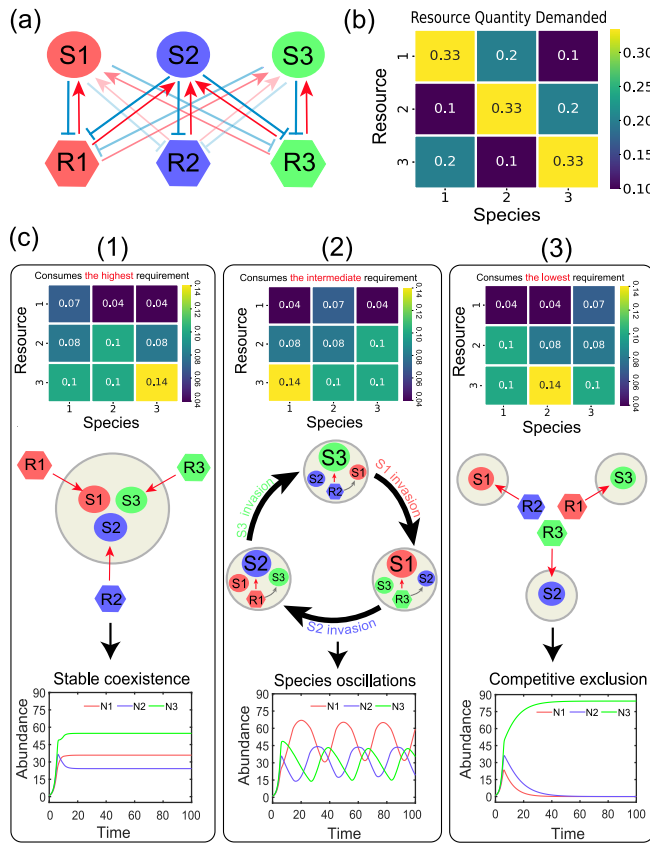


FIG. 1. (a) Schematic diagram of three species competing for three resources. (b) The degree of demand R^*_{ji} of species i for resource j . (c) Three dynamic phases for three consumption cases c_{ji} .

Consequently, if for all $g \neq i$, it holds that $c_{ji} < c_{jg}$, then species i is consuming the lowest of resource j . Regarding intermediate consumption, if a species' consumption of a particular resource is neither the lowest nor the highest, i.e., its resource quantity is neither greater than nor less than that of some other species, we can consider its consumption of that resource to be intermediate. Specifically, if there exist at least one species g and one species l (where $g \neq i$ and $l \neq i$) such that $c_{jg} < c_{ji} < c_{jl}$, then we can say that species i has intermediate consumption of resource j . The specific values of the parameters in the model are provided in the Supplemental Material [44], and these values fall within the typical range for phytoplankton species.

To measure the degree of resource demand, the quantity of resource j required by species i when its growth rate equals its loss rate is defined by Eq. (2) ($p_{ji} = m_i$). Then, the degree of demand is quantified using the following formula:

$$R^*_{ji} = \frac{m_i K_{ji}}{r_i - m_i}, \quad (5)$$

where K_{ji} denotes the half-saturation constant of species i for resource j and r_i is the maximum specific growth rate of species i . The quantity R^*_{ji} quantitatively expresses the demand of species i for resource j . We say that a species has the lowest demand for resource j if its R^*_{ji} is lower than that of other species, meaning for all $g \neq i$, $R^*_{ji} < R^*_{jg}$. This definition allows us to clearly quantify and compare the

degree of demand for specific resources among different species. Conversely, if we say that a species has the highest demand for resource j , it means that its R^*_{ji} is higher than that of other species. In other words, for all $g \neq i$, if $R^*_{ji} > R^*_{jg}$, then species i has the highest demand for resource j . The intermediate demand can be defined as follows: If species i has a demand for resource j that is neither highest nor lowest than the demands of other species, it is said to have an intermediate demand for resource j . In other words, the R^*_{ji} of species i lies between the R^* values of other species. Specifically, if there exist at least $g \neq i$ and $l \neq i$, such that $R^*_{jg} < R^*_{ji} < R^*_{jl}$, then species i can be considered to have an intermediate demand for resource j .

Based on the parameter values provided in the Supplemental Material [44] and in conjunction with Eq. (5), the demand of each species for each resource can be calculated. Figure 1(b) shows the specific values and distribution of the demand R^*_{ji} of species i for resource j in this three-species, three-resource model. It is evident that the levels of demand are consistent with the following order:

$$\begin{aligned} R^*_{11} &> R^*_{12} > R^*_{13}, \\ R^*_{22} &> R^*_{23} > R^*_{21}, \\ R^*_{33} &> R^*_{31} > R^*_{32}. \end{aligned} \quad (6)$$

That is, for resource 1, species 1 has the highest requirement, species 2 has an intermediate requirement, and species 3 has the lowest requirement. For resource 2, species 2 has the highest requirement, species 3 has an intermediate requirement, and species 1 has the lowest requirement. For resource 3, species 3 has the highest requirement, species 1 has an intermediate requirement, and species 2 has the lowest requirement.

Previous studies have shown that the trade-off between resource consumption and demand is a key element in determining the state of multispecies competition systems [34]. The predicted population dynamics largely depend on the relationship between species' resource demands and their resource consumption characteristics. Specifically, if species predominantly consume the resources for which they have the highest demand, stable coexistence will result. If species predominantly consume resources for which they have intermediate demands, oscillations behavior will appear. If species predominantly consume resources for which they have the lowest demand, competitive exclusion will emerge, with the winner depending on the initial conditions. Figure 1(c) shows the three dynamic phases and the evolutionary trajectories of species abundance under the deterministic model when each species consumes its highest, intermediate, and lowest demand resources. Based on the resource demands [Fig. 1(b)] and the quantity of resource of the each species [upper part of Fig. 1(c)], we can observe that when each species consumes its highest needed resource, i.e., when species i has the consumption sequence for resource j as follows [upper part of Fig. 1(c)(1)]:

$$\begin{aligned} c_{11} &> c_{12} \geq c_{13}, \\ c_{22} &> c_{23} \geq c_{21}, \\ c_{33} &> c_{31} \geq c_{32}. \end{aligned} \quad (7)$$

That is, for resource 1, species 1 consumes the most, species 2 consumes an intermediate amount, and species 3 consumes the least. For resource 2, species 2 consumes the most, species 3 consumes an intermediate amount, and species 1 consumes the least. For resource 3, species 3 consumes the most, species 1 consumes an intermediate amount, and species 2 consumes the least. Although each species has a competitive advantage in utilizing the resource it prefers, its competitiveness is relatively weak with respect to other resources. Thus, when a certain species becomes dominant in the ecosystem due to its utilization of the resource it needs the most, the system is in an unbalanced state. At this point, other species can exploit this species' disadvantage in utilizing other resources to "invade" and gain an advantage. Their competitive and invasive behavior will restore the system to a balanced state. This dynamic process drives competition among species toward a dynamic equilibrium, thereby ensuring stable coexistence. Therefore, when each species primarily consumes the resource it needs the most, the entire system will achieve stable coexistence [middle part of Fig. 1(c)(1)].

When all three species consume the resources for which they have an intermediate demand, i.e., when the consumption sequence of resource j for species i is as follows [upper part of Fig. 1(c)(2)]:

$$\begin{aligned} c_{12} &> c_{13} \geq c_{11}, \\ c_{23} &> c_{21} \geq c_{22}, \\ c_{31} &> c_{32} \geq c_{33}. \end{aligned} \quad (8)$$

That is, for resource 1, species 2 consumes the most, species 3 consumes an intermediate amount, and species 1 consumes the least. For resource 2, species 3 consumes the most, species 1 consumes an intermediate amount, and species 2 consumes the least. For resource 3, species 1 consumes the most, species 2 consumes an intermediate amount, and species 3 consumes the least. In this context, the system is likely to exhibit oscillatory behavior.

The oscillation in species abundance arises from the fact that when a species tends to dominate, it can be invaded by certain species while simultaneously excluding several others [middle part of Fig. 1(c)(2)]. Let us start by discussing species 3. Species 3 primarily consumes resource 2 [upper part of Fig. 1(c)(2); $c_{23} = 0.1$, $c_{23} > c_{21}$, and $c_{23} > c_{22}$], so it quickly becomes limited by resource 2. However, since species 1 has the lowest demand for resource 2 [Fig. 1(b); $R_{21}^* = 0.1$, $R_{21}^* < R_{22}^*$, and $R_{21}^* < R_{23}^*$], species 1 invades and gains an advantage. This leads to an increase in species 1 abundance and a decrease in species 3 abundance. Subsequently, species 1 depletes a large portion of resource 3 [upper part of Fig. 1(c)(2); $c_{31} = 0.14$, $c_{31} > c_{32}$, and $c_{31} > c_{33}$], for which it has an intermediate demand [Fig. 1(b); $R_{32}^* < R_{31}^* < R_{33}^*$], and thus soon becomes limited by resource 3. Since species 2 has the lowest demand for resource 3 [Fig. 1(b); $R_{32}^* = 0.1$, $R_{32}^* < R_{31}^*$, and $R_{32}^* < R_{33}^*$], species 2 invades and gains an advantage. This results in an increase in species 2 abundance and a decrease in species 1 abundance. Next, species 2 depletes a large portion of resource 1 [upper part of Fig. 1(c)(2); $c_{12} = 0.07$, $c_{12} > c_{13}$, and $c_{12} > c_{11}$], for which it has an intermediate demand [Fig. 1(b); $R_{13}^* < R_{12}^* < R_{11}^*$], and thus soon becomes limited

by this resource. Since species 3 has the lowest demand for resource 1 [Fig. 1(b); $R_{13}^* = 0.1$, $R_{13}^* < R_{12}^*$, and $R_{13}^* < R_{11}^*$], species 3 invades and gains an advantage. This leads to an increase in species 3 abundance and a decrease in species 2 abundance. Subsequently, since species 3 primarily consumes resource 2, for which it has an intermediate demand, it soon becomes limited by resource 2 again. This cycle repeats itself indefinitely. In other words, each species is able to invade and replace the preceding species but will in turn be invaded by the next species, forming a sequential dynamic process [middle part of Fig. 1(c)(2)].

When all species consume the resources for which they have the lowest demand, i.e., when the consumption sequence of resource j for species i is as follows [upper part of Fig. 1(c)(3)]:

$$\begin{aligned} c_{13} &> c_{12} \geq c_{11}, \\ c_{21} &> c_{23} \geq c_{22}, \\ c_{32} &> c_{31} \geq c_{33}. \end{aligned} \quad (9)$$

That is, for resource 1, species 3 consumes the most, species 2 consumes an intermediate amount, and species 1 consumes the least. For resource 2, species 1 consumes the most, species 3 consumes an intermediate amount, and species 2 consumes the least. For resource 3, species 2 consumes the most, species 1 consumes an intermediate amount, and species 3 consumes the least.

If species primarily consume resources for which they have the lowest requirement, their utilization efficiency for these resources may not be high. However, they will still significantly deplete these resources. As a result, other species that depend on these resources will struggle to obtain sufficient amounts to sustain their own growth, leading to severe inhibition of their growth, and potentially even extinction. Consequently, these excluded species will eventually be driven out of the ecosystem, leaving only a single dominant species in the system. At this point, the outcome of the competition among species depends on the initial abundances of the species [middle part of Fig. 1(c)(3)].

Through the analysis of resource demands and consumption in multispecies competition, it is possible to elucidate the diverse dynamical behaviors of competitive ecology, which span from straightforward stable states to intricate oscillations, chaotic patterns, and even abrupt transitions. Such complex dynamics are not only responses of ecosystems to fluctuating environmental conditions but also serve as a mechanism for sustaining biodiversity. Grasping these complexities is of paramount importance for the conservation of ecological systems and the management of resources. However, despite elucidating the biological mechanisms behind the complex dynamical behaviors that arise in multispecies competition, the underlying physical principles of species competition dynamics are not yet well understood, and exploring the global stability and dynamics of species competition remains a challenge. Using probabilistic descriptions may provide an answer. Here, we investigate the global properties of species competition using landscape and flux theory approaches.

III. METHODS

A. Landscape and flux theory

Noise is crucial for the dynamics of multispecies competition systems within ecosystems. Research has shown that noise can induce temporal oscillations, spatial pattern formation, and even stochastic resonance—features that are absent in deterministic models [45,46]. Therefore, it is essential to incorporate noise into models of biological competition to predict the spatiotemporal dynamics of populations. In general deterministic descriptions, there is typically no general way that captures the global characteristics of the system. The dynamics of the entire system are deterministic and predictable. However, in stochastic dynamics, a single time-evolution trajectory becomes unpredictable. In a stochastic competition system, each state variable satisfies the Langevin equation [47]:

$$\dot{\mathbf{x}} = \mathbf{F}(\mathbf{x}) + \boldsymbol{\eta}(\mathbf{x}, t), \quad (10)$$

where $\mathbf{F}(\mathbf{x})$ represents the right-hand side of Eqs. (3) and (4), and $\boldsymbol{\eta}$ is the noise term, or the so-called stochastic force. Here, we consider isotropic Gaussian white noise with an autocorrelation function given by $\langle \boldsymbol{\eta}(\mathbf{x}, t) \boldsymbol{\eta}(\mathbf{x}, t') \rangle = 2\mathbf{D}\delta(t - t')$, where $\mathbf{D}$ is a diffusion matrix with only diagonal elements $D_{11} = D_{22} = \dots = D_{nn}$, reflecting the magnitude and heterogeneity of the noise intensity, and $\delta(t - t')$ is a Dirac delta function. The symbol $\langle \cdot \rangle$ denotes the statistical average over many independent realizations of repeated experiments or simulations, referring here to different realizations of stochastic noise. In a more general case, the diffusion matrix $\mathbf{D}(\mathbf{x})$ is spatially dependent and includes off-diagonal elements D_{ij} ($i \neq j$). The corresponding Ito interpretation of the Fokker-Planck equation for the Langevin equation is

$$\frac{\partial P(x_1, x_2, \dots, x_n, t)}{\partial t} = - \sum_{i=1}^n \frac{[\partial F_i(x_1, \dots, x_n) P(x_1, \dots, x_n, t)]}{\partial x_i} + \sum_{i=1, j=1}^{n,n} \frac{\partial^2 D_{ij} P(x_1, \dots, x_n, t)}{\partial x_i \partial x_j}. \quad (11)$$

This equation can be interpreted as the conservation of local probability: $\nabla \cdot \mathbf{J}(\mathbf{x}, t) + \partial_t P(\mathbf{x}, t) = 0$, the probability density distribution of the system's state variables being linear and predictable [48], where $\mathbf{J}(\mathbf{x}, t)$ is the flux, defined as

$$\mathbf{J}(\mathbf{x}, t) = \mathbf{F}(\mathbf{x})P(\mathbf{x}, t) - \nabla \cdot \mathbf{D}(\mathbf{x})P(\mathbf{x}, t). \quad (12)$$

It is important to note that when the entire system evolves to a steady state, i.e., $\partial_t P_{ss}(\mathbf{x}) = 0$, it can be seen from Fokker-Planck that $\nabla \cdot \mathbf{J}_{ss}(\mathbf{x}) = 0$. In this scenario, two situations may arise: One where there is a net flux $\mathbf{J}_{ss}(\mathbf{x}) \neq 0$ within the local infinitesimal element, corresponding to a nonequilibrium state where detailed balance is broken, and another where the incoming and outgoing fluxes are equal, leading to a detailed balance situation with net flux $\mathbf{J}_{ss}(\mathbf{x}) = 0$. Since the divergence of a rotational field is always zero, the broken detailed balance can be expressed as a rotational field, i.e., $\mathbf{J}_{ss}(\mathbf{x}) = \nabla \times \boldsymbol{\psi}(\mathbf{x})$ [here, $\boldsymbol{\psi}(\mathbf{x})$ is a vector field with nonzero curl]. Additionally, noting the expression (12) for $\mathbf{J}(\mathbf{x})$, we can

decompose the force into three terms [49]:

$$\mathbf{F}(\mathbf{x}) = -\mathbf{D}(\mathbf{x}) \cdot \nabla U(\mathbf{x}) + \frac{\mathbf{J}_{ss}(\mathbf{x})}{P_{ss}(\mathbf{x})} + \nabla \cdot \mathbf{D}(\mathbf{x}). \quad (13)$$

Here, the landscape or generalized potential function is defined as [50,51]

$$U(\mathbf{x}) = -\ln P_{ss}(\mathbf{x}). \quad (14)$$

This relationship is analogous to the Boltzmann-Gibbs distribution in equilibrium statistical mechanics ($P_{ss}(\mathbf{x}) = e^{-U(\mathbf{x})}$). The first term in Eq. (13) arises from the gradient of $U(\mathbf{x})$, the second term originates from the existence of net flux, and the third term results from the inhomogeneity of noise. In the case of detailed balance, the driving force of the system can only be expressed as the gradient of the landscape, whereas in the case of broken detailed balance, a rotational force emerges. Thus, under nonequilibrium conditions, the driving force of the dynamics is generally determined by both the landscape gradient force and the rotational force. This is similar to the helical motion of a charged particle in an electromagnetic field under the influence of Lorentz force [49,50].

B. Nonequilibrium thermodynamic and dynamic

The process of species or plants competing for resources typically exists in a state far from thermodynamic equilibrium, characterized by continuous exchanges of matter, energy, and information with the external environment. For example, plants absorb light energy through photosynthesis from the external environment while taking in water and nutrients from the soil and releasing oxygen and organic matter. This exchange of energy and matter prevents the system from being considered a closed system, implying that the system is always in a nonequilibrium state. Here, we can construct a nonequilibrium thermodynamics for the species competition process, starting with the entropy formula:

$$S(\mathbf{x}, t) = - \int P(\mathbf{x}, t) \ln P(\mathbf{x}, t) d\mathbf{x}. \quad (15)$$

Taking the time derivative of the above equation, we obtain [52,53]

$$\dot{S}(\mathbf{x}, t) = \int \mathbf{J}(\mathbf{x}, t) \cdot \mathbf{D}(\mathbf{x})^{-1} P(\mathbf{x}, t)^{-1} \cdot \mathbf{J}(\mathbf{x}, t) d\mathbf{x} - \int \mathbf{J}(\mathbf{x}, t) \cdot \mathbf{D}(\mathbf{x})^{-1} \cdot (\mathbf{F}(\mathbf{x}) - \nabla \cdot \mathbf{D}(\mathbf{x})) d\mathbf{x}. \quad (16)$$

The rate of change of system entropy over time $\dot{S}(\mathbf{x}, t)$ is divided into two parts, the first part is the entropy production rate (EPR) of the entire system and the environment,

$$\text{EPR} = \int \mathbf{J}(\mathbf{x}, t) \cdot \mathbf{D}(\mathbf{x})^{-1} P(\mathbf{x}, t)^{-1} \cdot \mathbf{J}(\mathbf{x}, t) d\mathbf{x}, \quad (17)$$

and the second part,

$$\text{HDR} = \int \mathbf{J}(\mathbf{x}, t) \cdot \mathbf{D}(\mathbf{x})^{-1} \cdot (\mathbf{F}(\mathbf{x}) - \nabla \cdot \mathbf{D}(\mathbf{x})) d\mathbf{x}, \quad (18)$$

represents the heat dissipation or entropy flux to the external environment per unit time. The entropy production rate of the entire system and environment equals the sum of the system's entropy change rate and the environment's entropy change

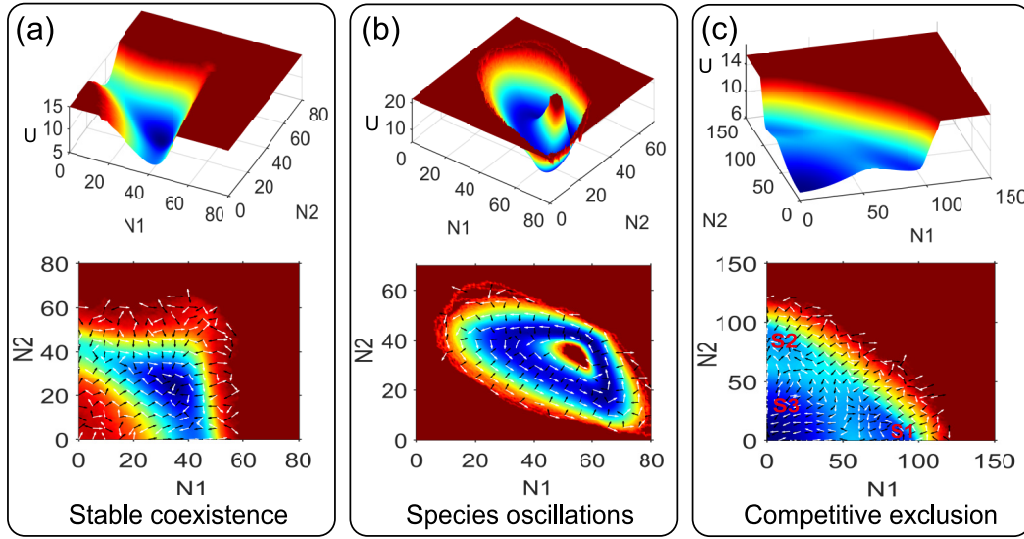


FIG. 2. (a) The landscape under the species coexistence; the diffusion coefficient $D = 10$. (b) The landscape under the species oscillations; the diffusion coefficient $D = 0.3$. (c) The landscape under competitive exclusion; the diffusion coefficient $D = 60$.

rate or dissipation rate, providing the first law of nonequilibrium thermodynamics [52]. The entropy production rate of the system and environment is always greater than or equal to zero, which corresponds to the second law of thermodynamics [52]. The entropy production rate explicitly reflects the time irreversibility of the nonequilibrium system or the degree of detailed balance breaking. Additionally, the average flux can be used to quantify the degree of nonequilibrium in the system. The flux being rotational tends to destabilize the system, providing the dynamical source for nonequilibrium phase transitions [54]:

$$Flux = \int |J_{ss}(x)| dx. \quad (19)$$

C. Time-reversal symmetry breaking

The degree of time-reversal symmetry breaking can be monitored using time series to track changes in cross-correlation differences as the system approaches a bifurcation point [54]. This method can predict continuous transitions. Here, we define the average difference between forward and backward cross-correlations as [55,56]

$$\Delta CC = \sqrt{\frac{1}{t_f} \int_0^{t_f} (C_{XY}(\tau) - C_{YX}(\tau))^2 d\tau}. \quad (20)$$

Here, $C_{XY}(\tau)$ represents the forward cross-correlation function over time, defined as

$$C_{XY}(\tau) = \langle X(0)Y(\tau) \rangle = \sum X^i Y^j P_i^{ss} P_{ij}(\tau). \quad (21)$$

$C_{YX}(\tau)$ is the backward cross-correlation function over time, where X and Y represent the time series of two random variables, τ denotes the lag time between the two series, and t_f denotes the maximum lag time. P_{ij} is the probability of transitioning from state i to state j at time τ .

IV. RESULTS

A. Landscape and flux of multispecies competition

The various dynamic states of the system, such as steady states and oscillatory states, which are determined by the interplay between resource demand and consumption characteristics, are typically represented by attractors in the state space. The system stabilizes in regions of lower U within the state space, with different competitive states exhibiting distinct landscape topologies. To obtain the landscape U that describes the global weight of the system's state, it is necessary to solve the partial differential equation [Eq. (11)]. However, solving the Fokker-Planck equation becomes extremely challenging when the system dimension is very high. Therefore, we obtain the probability distribution function P by solving the corresponding Langevin equation and analyzing statistical random trajectories (see the Supplemental Material [44]). For clarity in the following discussion, the term “system” specifically refers to the system of three species competing for three resources.

Figure 2 shows the quantified three-dimensional (3D) and two-dimensional (2D) landscapes under three situations, respectively, when each species consumes its highest needed resource, all three species coexist stably, and the landscape in the state space takes the form of an attractor basin. When all three species consume the resources for which they have an intermediate demand, all species abundances exhibit oscillatory behavior, and the landscape takes a Mexican hat shape. When all species consume the resources for which they have the lowest demand, the landscape features three attractor basins, each representing a different potential species state. The white arrows around the attractors represent rotational flux $\frac{J_{ss}(x)}{P_{ss}(x)}$, while the black arrows denote gradient forces $-D \cdot \nabla U(x)$. The gradient forces stabilize the three-species system at attractors, while the rotational forces drive the system away from the attractors. When the system is in a three-species oscillatory state, the rotational forces around the limit cycle maintain the periodic oscillations of the system.

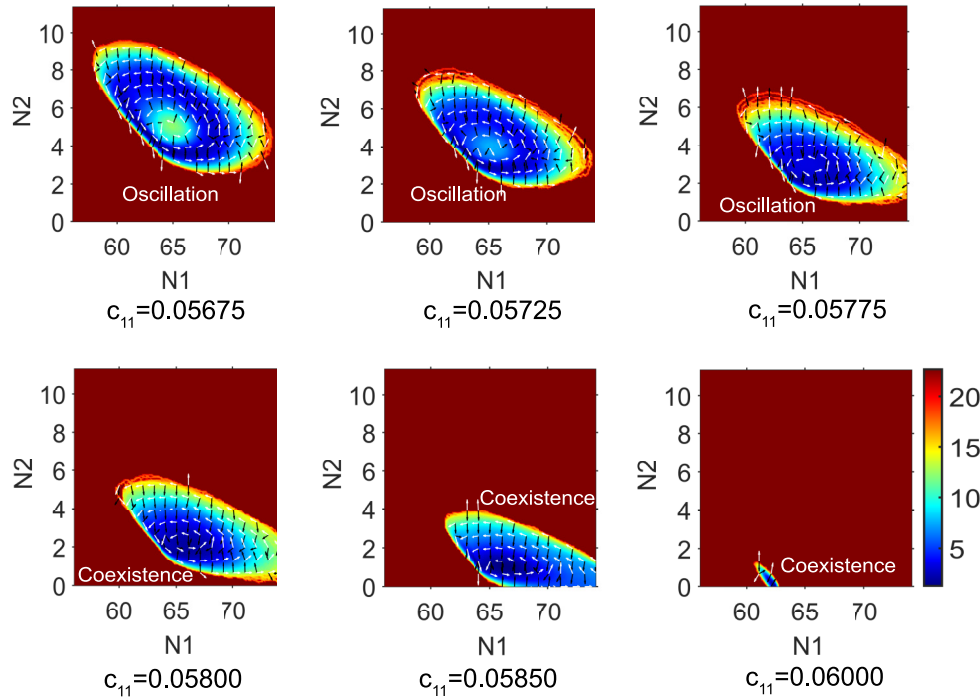


FIG. 3. The two-dimensional projection of the landscape under different parameter c_{11} . The diffusion coefficient $D = 0.005$.

In real species competition for resources, the environment has a significant impact on species competition. The control parameters in Eqs. (3) and (4) reflect how external environments influence the system. Changes in these control parameters can profoundly impact the overall evolution of the competition system, ultimately determining the system's final outcome. Our analysis of various parameter variations reveals that the average flux, entropy production rate, and the average cross-correlation difference between forward and backward in time (ΔCC) are closely associated with shifts in the dynamic states of species competition.

B. Thermodynamic and dynamical sources of multispecies competition

1. The results of changes in the quantity of resource 1 in species 1 (c_{11}) under the species oscillations

We conducted a quantitative analysis of the landscape under varying c_{11} parameter (c_{11} is the quantity of resource 1 in species 1). As shown in Fig. 3, with increases in resource 1 in species 1 (c_{11}), the landscape topology transitions from the initial Mexican hat shape to a single stable point attractor basin (the 3D landscape diagrams can be found in Fig. S4 in the Supplemental Material [44]).

Figure 4 presents a schematic diagram of the system's transition from periodic oscillation to a stable state as c_{11} changes. Correspondingly, Fig. 5(a) presents the phase diagram with changes in the c_{11} parameter. As the resource 1 quantity in species 1 increases, the three-species competition system transitions from an oscillatory state to a single stable coexistence state, which is known as the Hopf bifurcation phenomenon. The red dashed line in the figure indicates the position of the Hopf bifurcation point $c_{11} = 0.05788$. As species 1's consumption capacity for resource 1 increases (i.e., the quantity

of resource 1 in species 1, c_{11}), species 1 gains a competitive advantage. By consuming more of resource 1, the competitive strength of the other species for this resource is weakened. This shift in resource allocation alleviates the intensity of excessive resource competition, enabling the system to move toward a more balanced state. In this equilibrium, the demand of each species for different resources is better satisfied, suppressing oscillations and leading to a stable coexistence state. Therefore, the system gradually approaches a stable attractor, where the abundances of the species tend to stabilize.

However, as the quantity of resource 1 in species 1 (c_{11}) further increases ($c_{11} > 0.059$), species 1 gradually gains dominance by consuming more resource 1 than the other species. This competitive advantage diminishes the ability of the other species to acquire sufficient resource 1 for survival, thereby increasing their survival pressure. Since species 2 has a higher demand for resource 1, compared to species 3, which has a lower demand [in Fig. 1(b); $R_{12}^* = 0.2$ and $R_{13}^* = 0.1$], species 2 becomes more dependent on resource 1. Consequently, as c_{11} increases (i.e., the quantity of resource 1

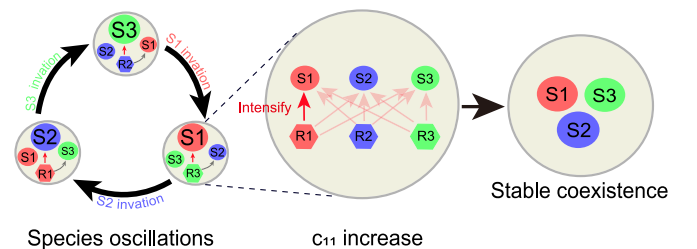


FIG. 4. An increase in the quantity of resource 1 in species 1 (c_{11}) leads to a phase transition from oscillatory dynamics to stable coexistence of the three species.

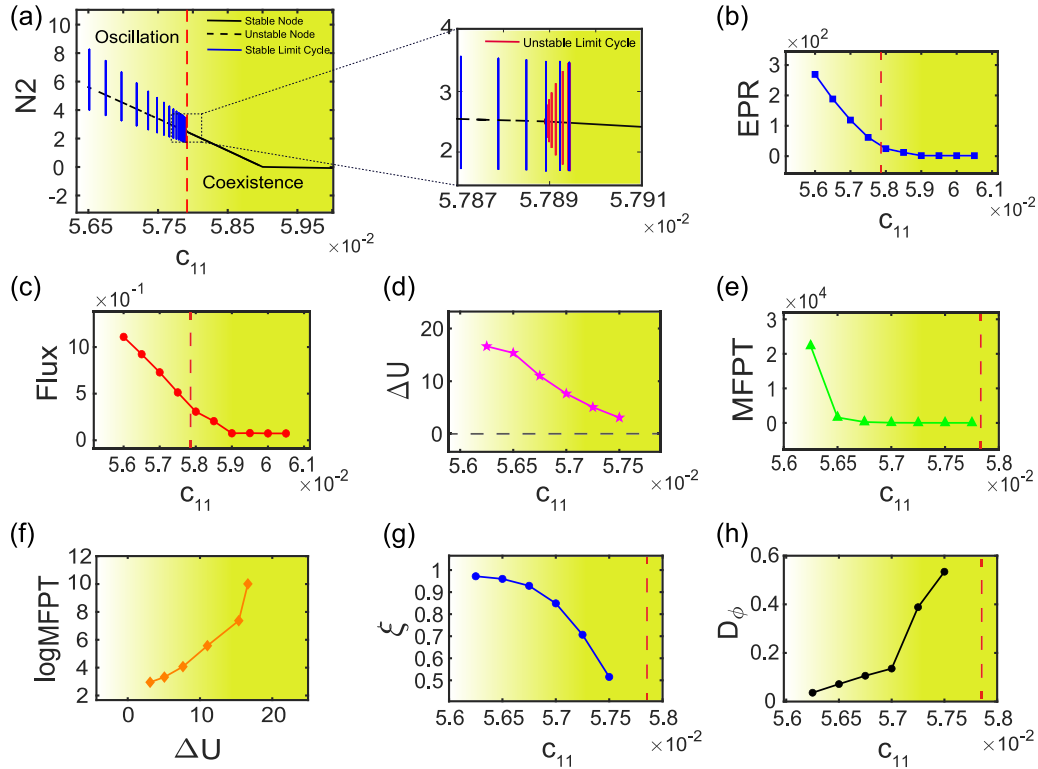


FIG. 5. (a) Phase diagram vs parameter c_{11} . (b) The entropy production rate vs parameter c_{11} . (c) The average flux vs parameter c_{11} . (d) The barrier height vs parameter c_{11} . (e) The mean first passage time vs parameter c_{11} . (f) Mean first passage time vs barrier heights for different parameter c_{11} . (g) The coherence vs parameter c_{11} . (h) The phase diffusion vs parameter c_{11} . The diffusion coefficient $D = 0.005$.

in species 1, c_{11}), species 2 becomes more likely to go extinct. Conversely, when species 1's ability to consume resource 1 weakens (i.e., c_{11} decreases), species 1 no longer holds a significant competitive advantage for resource 1. As a result, the other species become more competitive for resource 1, intensifying the competition among species. This heightened competition disrupts the previously stable distribution of resources. As the competition for limited resources reignites, the instability in resource allocation increases, and the species abundances start to fluctuate periodically in response to the variations in resource availability, leading the system into an oscillatory state.

During the transition of the system from oscillation to stable coexistence, both the entropy production shown in Fig. 5(b) and the average flux shown in Fig. 5(c) exhibit a decreasing trend. This indicates that maintaining the three-species oscillatory state requires higher costs and flux. The flux enhances the stability of the limit cycle oscillation and provides the dynamic source for species oscillations, while entropy production provides the thermodynamic source. As the system approaches the bifurcation point, the global Mexican hat-shaped landscape reflecting species oscillations becomes increasingly flattened, weakening the oscillations of the three-species system, and thus becoming more unstable (see Fig. 3, and Fig. S4 in the Supplemental Material [44]). The accompanying flux also decreases [Fig. 5(c)], and the thermodynamic cost required by the system diminishes [Fig. 5(b)].

The landscape quantifies the global stability of the biological competition system's state, while the barrier height reflects the difficulty of transitioning between different states. We

define the barrier height as the difference $\Delta U = U_{\max} - U_{\min}$ between the top of the Mexican hat and the lowest point of the limit cycle trough (see Fig. S6(a) in the Supplemental Material [44]). By solving the stochastic Langevin differential equations [Eq. (10)], we found that the escape time or mean first passage time (MFPT) from the limit cycle trough of oscillatory states decreases as the system transitions from an oscillatory state to a single stable state, as shown in Fig. 5(e) (the calculation details are shown in Fig. S2 in the Supplemental Material [44]). This is because, as c_{11} increases, the system approaches the bifurcation point, leading to a gradual reduction in the barrier height (Fig. 5(d), and Fig. S4 in the Supplemental Material [44]), thereby decreasing the system's stability and making it easier to escape from the groove in the Mexican hat landscape. Moreover, Fig. 5(f) shows a positive correlation between the logarithm of the mean first passage time and the barrier height $\text{MFPT} \sim e^{\Delta U}$, further indicating that higher barrier heights correspond to greater system stability and, consequently, longer escape times for state changes.

We further observed that, as the system approaches the Hopf bifurcation point, the coherence of the three-species oscillatory state gradually decreases, whereas the phase diffusion increases (Figs. 5(g) and 5(h), and Figs. S9 and S10 in the Supplemental Material [44]). Both quantities were computed based on stochastic time series generated from the Langevin equations (details of the calculation and representative time series are provided in Figs. S3 and S7 in the Supplemental Material [44]). Coherence characterizes the stability and regularity of the system's oscillations: Higher coherence indicates more stable and orderly oscillatory behavior, while

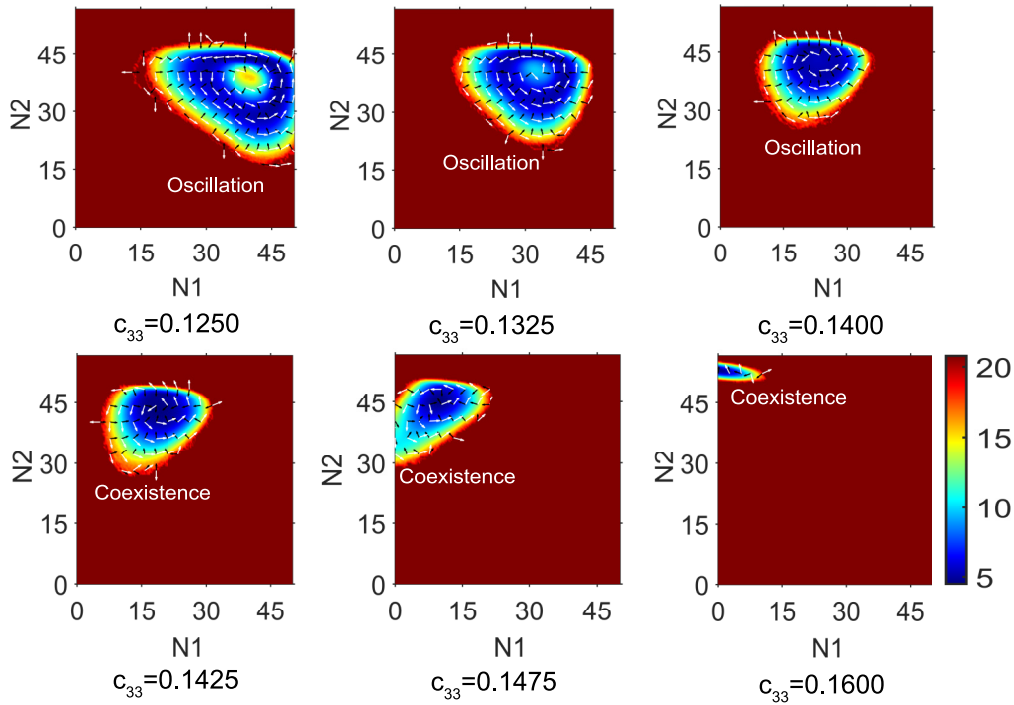


FIG. 6. The two-dimensional projection of the landscape under different parameter c_{33} . The diffusion coefficient $D = 0.3$.

lower coherence reflects reduced stability and increased irregularity. In contrast, phase diffusion quantifies the extent of phase variability in the oscillations, capturing the rate of stochastic phase drift under noise perturbations. It serves as a measure of the system's ability to sustain periodic dynamics in the presence of fluctuations. Larger phase diffusion implies greater deviations in phase and diminished capacity to maintain periodicity, whereas smaller diffusion corresponds to more robust and coherent oscillations.

As shown in Fig. 5(g), at lower values of c_{11} , the potential landscape of the system exhibits a Mexican-hat-like structure with a relatively high barrier (see Figs. 3 and 5(d), and Fig. S4 in the Supplemental Material [44]), which supports stable and well-organized oscillations in species abundances. As c_{11} increases, the barrier height gradually decreases, leading to increasingly irregular and unstable oscillatory behavior, accompanied by a decline in coherence [Fig. 5(g)]. In addition, coherence is closely related to the system's probability flux and entropy production. The average flux and entropy production provide the dynamical and thermodynamic sources for species oscillations, respectively. When c_{11} is relatively low, their values are higher, which helps maintain stable oscillations. In contrast, as the system approaches the bifurcation point, both the average flux and entropy production decrease significantly, thereby reducing the coherence of oscillations and enhancing phase diffusion [see Figs. 5(b), 5(c), 5(g), and 5(h)]. Therefore, the barrier height, average flux, and entropy production play critical roles in maintaining the stability of oscillations in multispecies systems. A higher barrier limits state transitions, while stronger probability flux and greater entropy production help sustain periodic dynamics and suppress phase diffusion, thereby enhancing the stability of oscillatory behavior.

2. The results of changes in the quantity of resource 3 in species 3 (c_{33}) under the species oscillations

Similar to the analysis of the change in the quantity of resource 1 in species 1 (c_{11}), we also studied the landscape changes when the quantity of resource 3 in species 3 changes (c_{33}). Figure 6 shows the transition of the three-species competition system from a Mexican hat-shaped landscape to a stable single attractor basin landscape under different c_{33} values (the 3D landscape diagrams can be found in Fig. S5 in the Supplemental Material [44]). The white arrows represent rotational flux, while black arrows denote gradient forces.

Figure 7 presents a schematic diagram of the system's transition from periodic oscillation to a stable state as c_{33} changes. Figure 8(a) shows the phase diagram as c_{33} varies, with the red dashed line indicating the position of the Hopf bifurcation point $c_{33} = 0.141\,315\,71$. The system initially undergoes a limit cycle attractor with species oscillations and then transitions to a coexistence state. As species 3's consumption capacity for resource 3 increases (i.e., the quantity

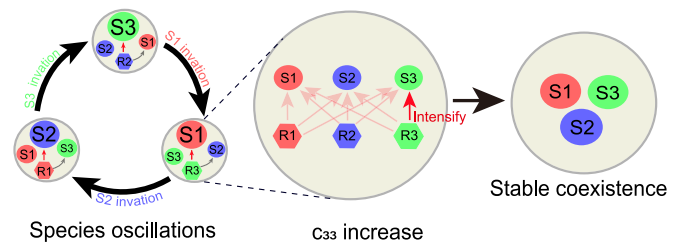


FIG. 7. An increase in the quantity of resource 3 in species 3 (c_{33}) leads to a phase transition from oscillatory dynamics to stable coexistence of the three species.

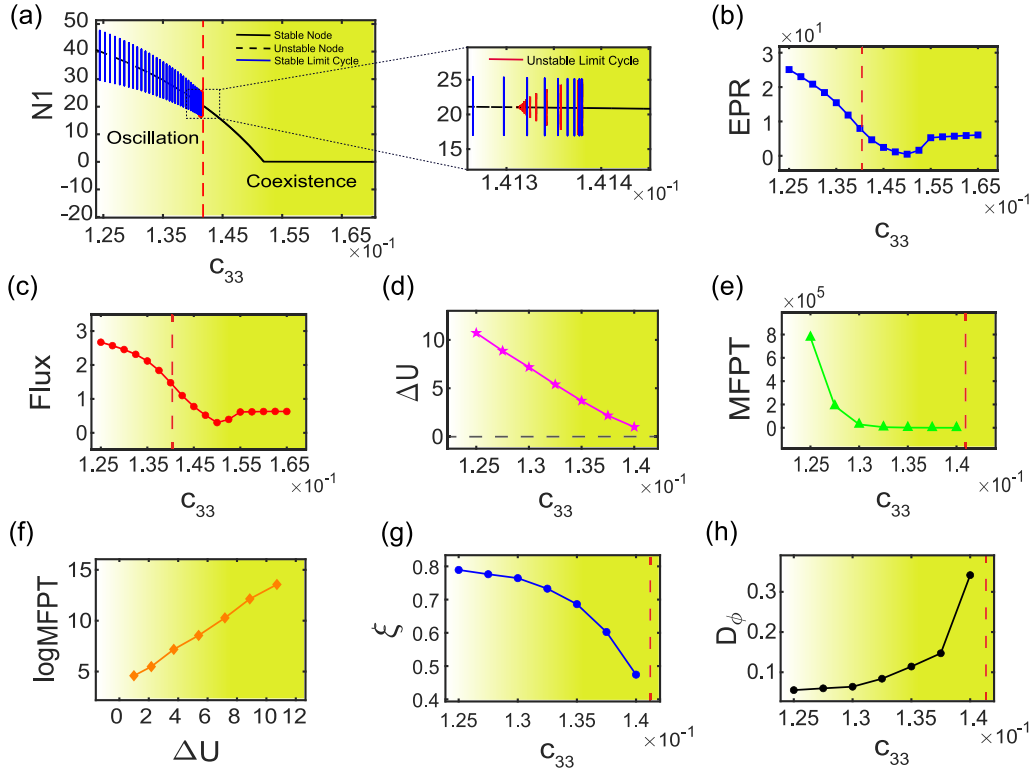


FIG. 8. (a) Phase diagram vs parameter c_{33} . (b) The entropy production rate vs parameter c_{33} . (c) The average flux vs parameter c_{33} . (d) The barrier height vs parameter c_{33} . (e) The mean first passage time vs parameter c_{33} . (f) Mean first passage time vs barrier heights for different parameter c_{33} . (g) The coherence vs parameter c_{33} . (h) The phase diffusion vs parameter c_{33} . The diffusion coefficient $D = 0.3$.

of resource 3 in species 3, c_{33}), species 3 gains a competitive advantage. By consuming more of resource 3, the competitive strength of the other species for this resource is weakened. This shift in resource allocation alleviates the intensity of excessive competition for resources, allowing the system to move toward a more balanced state of coexistence among the three species. However, as the quantity of resource 3 in species 3 further increases ($c_{33} > 0.1519$), species 3 begins to consume more resource 3 than the other species. This competitive advantage diminishes the ability of the other species to acquire sufficient resource 3, thus increasing the survival pressure on both species 1 and species 2. Since species 1 has a higher demand for resource 3 than species 2 [in Fig. 1(b); $R_{31}^* = 0.2$ and $R_{32}^* = 0.1$], the continued increase in species 3's consumption capacity for resource 3 will ultimately lead to the extinction of species 1.

Conversely, as the quantity of resource 3 in species 3 decreases (c_{33} decrease), the availability of resource 3 decreases, intensifying competition for this resource among species 1 and species 2. Species 1 and species 2 will compete to acquire the reduced resource 3, and this scramble disrupts the previously stable distribution of resources, leading to uneven resource allocation and instability in competitive dynamics, ultimately resulting in limit cycle oscillations.

It is important to note that under the deterministic conditions described by Eqs. (3) and (4), at a parameter value of $c_{11} = 0.059$, species 2 has gone extinct [Fig. 5(a)]. However, under stochastic conditions, there is a certain probability that species 2 does not go extinct (Fig. 3; $c_{11} = 0.06$), and all three species coexist in a basin of attraction. Similarly, when

the parameter c_{33} is set to 0.1519, species 1 has gone extinct under deterministic conditions [Fig. 8(a)], but in stochastic scenarios, species 1 does not go extinct (Fig. 6; $c_{33} = 0.16$), and all three species coexist in a basin of attraction. This is a difference between stochastic and deterministic models.

In stochastic models, the probabilistic weight of the dynamical states of species competition changes with increasing c_{33} . As c_{33} increases, the entropy production and flux, shown in Figs. 8(b) and 8(c), decrease from high to low, or conversely, when c_{33} decreases, entropy production and flux gradually increase. This is because species oscillatory states consume more thermodynamic costs compared to coexistence states, and flux provides the driving force for the transition from stable to oscillatory states. Greater flux enhances the stability of the limit cycle oscillations and provides the dynamic source for the system's transition from a stable coexistence state to an oscillatory state, while greater entropy production supplies the thermodynamic source required for oscillations.

Similar to the changes observed with the c_{11} parameter, as c_{33} increases, the transition from limit cycle oscillations to a single stable state results in a decreasing barrier height as the system approaches the Hopf bifurcation point (see Figs. 6 and 8(d), and Fig. S5 in the Supplemental Material [44]). The mean first passage time for escaping from the Mexican hat-shaped landscape groove also decreases gradually [Fig. 8(e)]. Barrier height determines the stability of the system's dynamical states; higher barriers indicate higher stability. As the system is near the bifurcation point, state transitions become easier. Additionally, Fig. 8(f) shows an almost linear relationship between the logarithm of the MFPT and the barrier

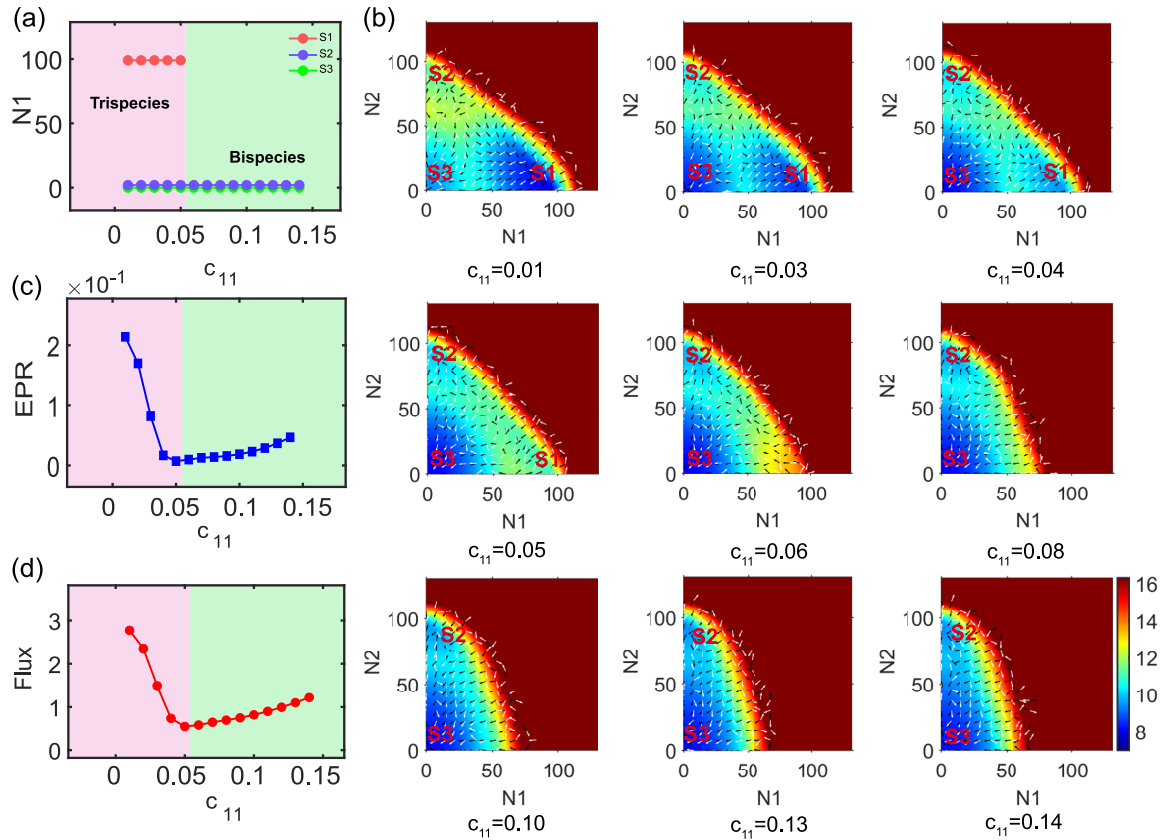


FIG. 9. (a) Phase diagram vs parameter c_{11} . (b) The two-dimensional projection of the landscape vs parameter c_{11} . (c) The entropy production rate vs parameter c_{11} . (d) The average flux vs parameter c_{11} . The diffusion coefficient $D = 40$.

height $\text{MFPT} \sim e^{\Delta U}$, further indicating that barrier height determines the time for state changes and significantly affects the stability of species competition states.

Furthermore, as c_{33} increases and the system approaches the Hopf bifurcation point, the coherence of the three-species oscillatory state decreases [Fig. 8(g)], while phase diffusion increases [Fig. 8(h)]. Initially, when c_{33} is low, the barrier height is high, and species oscillations are more ordered and stable. As c_{33} increases, the barrier height of the Mexican-hat-like oscillatory state gradually decreases, leading to less ordered and less stable oscillations (see the time series in Fig. S8 in the Supplemental Material [44]). Consequently, coherence declines as the system approaches the Hopf bifurcation point. The flux plays a critical role in maintaining species oscillations. With increasing c_{33} , the flux decreases, meaning that lower flux reduces oscillatory stability and leads to increased phase diffusion, whereas higher flux helps sustain stable oscillations and results in decreased phase diffusion [Figs. 8(c), 8(g), and 8(h)].

3. The results of changes in the quantity of resource 1 in species 1 (c_{11}) under competitive exclusion

When all three species consume their minimum required resources, the winning species depends on the initial abundances of the species, with the abundance of the winning species being significantly higher than those of the other two species in state space. For instance, if species S_1 wins the

competition, the location of the winning state for species 1 would be $S_1 = (N_1, N_2, N_3)$, where the abundances follow the order $N_1 > N_2 \geq N_3$. If species S_2 wins, the location of the winning state will be $S_2 = (N_1, N_2, N_3)$, with the abundances following the order $N_2 > N_1 \geq N_3$. If species S_3 wins, the location of the winning state will be $S_3 = (N_1, N_2, N_3)$, with the abundances following the order $N_3 > N_1 \geq N_2$.

We quantified the landscape for different values of parameter c_{11} . Figure 9(a) shows the phase diagram as the quantity of resource 1 in species 1 changes (c_{11}). When the quantity of resource 1 in species 1 is relatively low, the system exists in a state where all three species have the potential to prevail. However, as the quantity of resource 1 in species 1 increases, the system transitions to a state where only species S_2 and S_3 can prevail.

Figure 10 provides a schematic diagram explaining why an increase in c_{11} leads to a bistable coexistence state, where both species S_3 and S_2 have the potential to prevail. The competitive dynamics within the system are influenced by feedback interactions among species. With a fixed supply of resource S_1 , S_2 , and S_3 , a higher c_{11} indicates that species 1 consumes more resource 1 to sustain its growth. Consequently, the depletion of resource 1 accelerates, leading it to become a limiting factor more rapidly. Ultimately, the supply of resource 1 becomes insufficient to meet the demands of species 1, resulting in its inability to compete successfully. In contrast, species S_2 and S_3 are less dependent on resource 1, allowing them to gain a competitive advantage when c_{11}

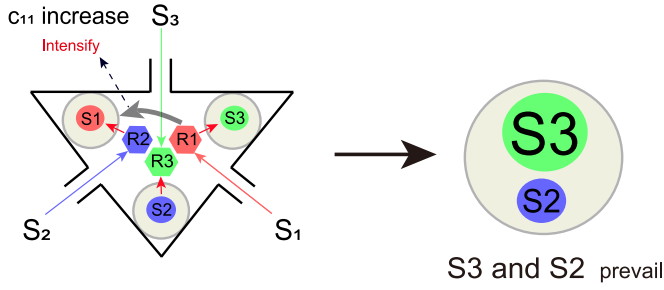


FIG. 10. An increase in the quantity of resource 1 in species 1 (c_{11}) leads to a phase transition from stable coexistence of three species to stable coexistence of two species.

is higher. The overconsumption of resource 1 by species 1 not only inhibits other species from accessing this resource but also increases the survival pressure on species 2 and 3. This dynamics can potentially lead to a bistable coexistence of species 2 and 3. Therefore, under the intense competition from species 1 for resource 1, species 2 and 3 may gradually adapt by developing more efficient resource utilization strategies, especially as the competition for resource 1 (c_{11}) intensifies. They may shift their focus to consuming other resources, thereby finding survival opportunities under the pressure exerted by species 1. Meanwhile, as species 1 depletes a significant amount of resource 1, its demand for this resource continues to increase, making it increasingly difficult for species 1 to survive in conditions of resource scarcity. As a result, species 1 will eventually go extinct, leading to a bistable state where both species 2 and species 3 have the potential to prevail.

Figure 9(b) shows that for varying c_{11} values, the system initially exhibits a state where any species could potentially win, and then transitions to a bistable state where only two species (S2 and S3) have the possibility of winning (the 3D landscape diagrams can be found in Fig. S13 in the Supplemental Material [44]). During the transition from a tristable to a bistable state, both entropy production and flux decrease sharply [Figs. 9(c) and 9(d)], indicating that maintaining a tristable state requires more thermodynamic costs than a bistable state. Conversely, when c_{11} decreases from a high value, the system transitions from a bistable attractor basin to a tristable attractor basin. During this transition, the flux increases significantly [Fig. 9(d)], providing the dynamic driving force for the state change, while entropy production serves as the thermodynamic source [Fig. 9(c)]. Additionally, we predicted the critical transition points in species competition dynamics based on time irreversibility. Under competitive exclusion, the system initially shows in a tristable state (S1, S2, S3), where any one of the three species could win (c_{11} is relatively low). We obtained the stochastic time series of species abundances by solving the stochastic differential equation [Eq. (10)]. Then, using the abundance time series of species 1 and species 2 within the attraction basin corresponding to the winning state of species S1, we calculated the average cross-correlation difference ΔCC between forward and backward time trajectories (Fig. 11, see also the Supplemental Material for more details [44]). In conjunction with Fig. 9(a), we observed that before the system approaches

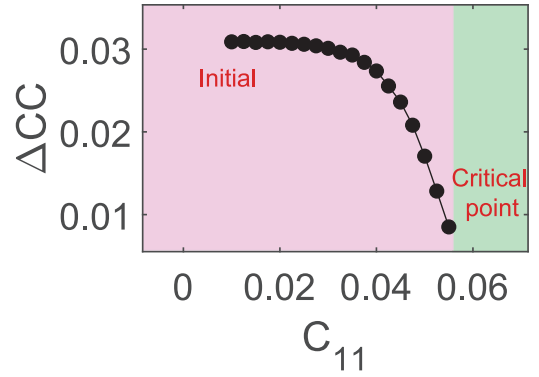


FIG. 11. The average cross-correlation difference ΔCC between forward and backward time vs the parameter c_{11} .

the critical point of the transition from a tristable to a bistable state at $c_{11} \approx 0.057$, ΔCC exhibits a distinct decline before the critical point (Fig. 11), indicating that ΔCC can serve as a predictor for the onset of critical transitions. Furthermore, we noted that both ΔCC and the average flux in Fig. 9(d) show similar changes before the critical point, suggesting a strong correlation between flux and time irreversibility, and both can be used as indicators for predicting the critical transition. For zero flux, $C_{XY}(\tau)$ and $C_{YX}(\tau)$ are equal, which corresponds to time reversibility in a system at equilibrium. Under nonequilibrium conditions, since time irreversibility is directly linked to the degree of detailed balance breaking [55], the cross-correlation difference can quantify the extent of nonequilibrium and serve as a predictor for critical points. The observed differences in cross-correlation between forward and backward time in the real-time trajectories of the system provide a practical method for predicting critical points in complex systems, especially as flux is not easily quantified directly in experiments.

4. The results of changes in the resource supply S_1 under competitive exclusion

The quantity R_{ji}^* is one key indicator for measuring a species' competitive ability. Specifically, the R^* of a species for resource j represents its ability to survive and maintain its population when resource j is at its lowest sustainable level [57,58]. Therefore, a species with a lower R^* indicates that it can continue to grow even when resources are scarce, signifying a higher efficiency in utilizing that resource in competition. In conditions of limited resources, the species with the lowest R^* can deplete the resource to a level where other species cannot sustain themselves, giving it a competitive advantage over others. Thus, the magnitude of R^* directly reflects a species' competitive ability with respect to a specific resource.

Here, we analyze the state transitions in a multispecies system by examining the species' resource requirements R_{ji}^* in relation to changes in external resource supply S_i . Figure 12(a) shows the phase diagram under different resource 1 supply (S_1). At different S_1 values, the system initially exhibits a state where only species S3 can win, then transitions to a bistable state where only species S3 and S2 can win, and eventually to a state where all three species (S1, S2, and S3)

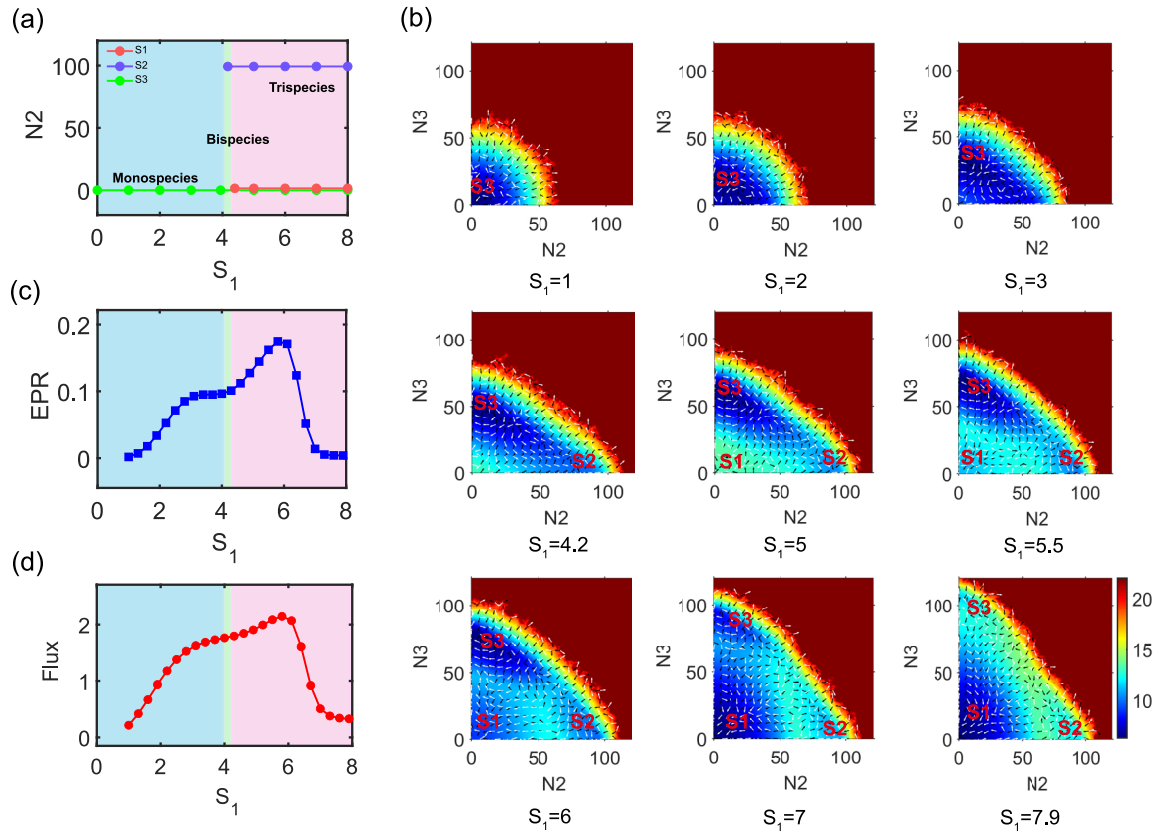


FIG. 12. (a) Phase diagram vs parameter S_1 . (b) The two-dimensional projection of the landscape vs parameter S_1 . (c) The entropy production rate vs parameter S_1 . (d) The average flux vs parameter S_1 . The diffusion coefficient $D = 35$.

could potentially win. Figure 13 presents a schematic diagram of the system's state changes as the supply of resource 1 (S_1) is altered.

When the resource supply S_1 is very low ($S_1 < 4.1$), the availability of resource R_1 is extremely limited, preventing all species from obtaining sufficient resources from R_1 to sustain rapid growth. In this scenario, the species that can most efficiently utilize the limited resource R_1 will have a competitive advantage. Species S_3 , with a low demand for resource 1 [$R_{13}^* = 0.1$; Fig. 1(b)], indicates that it can maintain a relatively high growth rate even under very low resource supply levels. Therefore, despite the low supply of resource S_1 , species S_3 is able to acquire resources more effectively than other species and survive. In contrast, species S_1 and S_2 have higher demands for resource R_1 , with $R_{11}^* = 0.33$ and $R_{12}^* = 0.2$, respectively [Fig. 1(b)]. They are unable to efficiently utilize resources under low resource conditions, and thus cannot maintain population abundance in such a resource scarce environment. As a result, when the parameter S_1 is low, species S_3 can outcompete others and dominate the niche.

As the resource supply S_1 increases ($4.1 < S_1 < 4.3$), resource R_1 becomes more available. At this point, species S_2 is also able to utilize resource R_1 and survive. Although species S_2 may require a slightly higher level of resource 1 to maintain its population abundance (with a moderate demand for resource 1, $R_{13}^* < R_{12}^* < R_{11}^*$), the increased availability of R_1 due to the rise in S_1 allows S_2 to coexist with S_3 . Therefore, in an environment with moderate resource supply S_1 , both species S_2 and S_3 can effectively utilize the limited resource

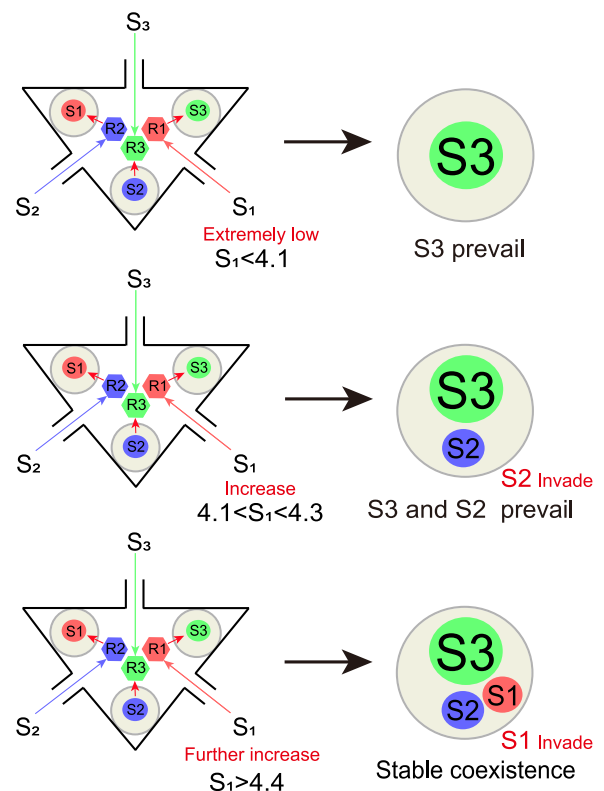


FIG. 13. A diagram explaining the mechanism of phase transition under increased resource supply S_1 .

R_1 . Species S_3 , however, still retains a certain advantage in this process, as it remains competitive even at lower resource levels (with the lowest R_{13}^* , $R_{13}^* < R_{12}^*$). In contrast, species S_1 is still unable to effectively utilize resource R_1 to sustain growth due to its higher demand for R_1 (with the largest R_{11}^*). Thus, when the control parameter S_1 is within a certain range ($4.1 < S_1 < 4.3$), both species S_2 and S_3 can prevail and establish themselves in the system, leading to a bistable state.

As the resource S_1 increases further ($S_1 \geq 4.4$), the availability of resource R_1 becomes abundant enough to meet the level required by species S_1 . Consequently, S_1 can invade and enter the competition, coexisting with species S_2 and S_3 . In this scenario, resource availability is no longer the primary limiting factor in the competition between species, and all species have sufficient resources to support their growth. Therefore, when the resource S_1 is very high, species S_1 , S_2 , and S_3 all have the potential to prevail, and the entire system is in a tristable state.

We investigated the thermodynamic and dynamic sources required for state changes in the model under different parameters S_1 , S_2 , and S_3 . Figure 12(b) shows the corresponding changes in the landscape under different resource supply S_1 values (the 3D landscapes can be found in Fig. S14 in the Supplemental Material [44]). When S_1 is very small, the system has only one attractor basin where species S_3 wins. As S_1 increases, a stable basin for species S_2 appears ($S_1 = 4.2$). With further increase in S_1 , the system eventually transitions to a state where all species have the potential to win. Entropy production and flux show similar patterns of change with S_1 [Figs. 12(c) and 12(d)], providing both thermodynamic and dynamic sources for the topological changes in the landscape. When S_1 is very small ($S_1 = 1$), the weight of state S_3 is initially very small, with correspondingly low thermodynamic and dynamic costs. As the resource supply S_1 increases, entropy production and flux increase, which leads to a greater weight for state S_3 [Fig. 12(b); $S_1 = 2$ and $S_1 = 3$]. Consequently, at around $S_1 \approx 4.1$, a state S_2 emerges from the S_3 state [Fig. 12(b)]. As S_1 further increases to $S_1 \approx 4.3$, entropy production and flux continue to rise [Figs. 12(c) and 12(d)], providing thermodynamic and dynamic origins for the emergence of the S_1 state [Fig. 12(b); $S_1 = 5$]. With further increase in S_1 ($S_1 > 6$), the weights of attractor basins for S_2 and S_3 gradually decrease [Fig. 12(b)], resulting in reduced thermodynamic and dynamic costs, and hence a decrease in entropy production and flux [Figs. 12(c) and 12(d)].

Figure 14 shows the variation of ΔCC with changes in resource supply S_1 , calculated based on the abundance time series of species 1 and species 2 within the attraction basin corresponding to the winning state of species S_1 . The system initially resides in a tristable state, and as it approaches the bistable critical point at $S_1 \approx 4.4$, a peak in ΔCC is observed, indicating its potential as a predictive indicator for the critical transition. Additionally, the entropy production and flux in Figs. 12(c) and 12(d) exhibit a sharp decline before the critical point ($S_1 < 6$), suggesting that flux can also serve as an indicator for predicting critical points. The increase in entropy production rate and flux reflects the deepening degree to which the system is moving away from equilibrium, while the sharp rise in ΔCC indicates an enhancement in

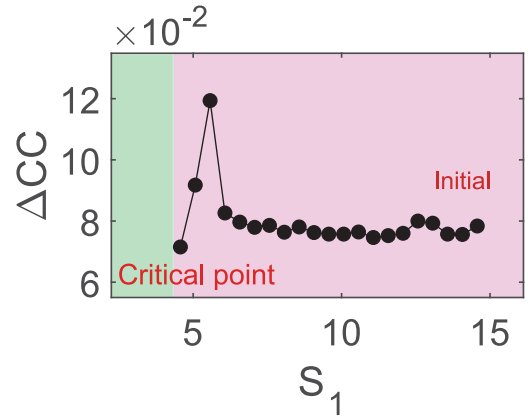


FIG. 14. The average cross-correlation difference ΔCC between forward and backward time vs the parameter S_1 .

the system's temporal irreversibility. As the system transitions from a tristable to a bistable state and approaches the critical transition point, these three quantities reach peaks prior to the critical point, highlighting the high dissipation characteristics and nonequilibrium extent of the system in maintaining multiple competitive states. Specifically, EPR and flux represent the thermodynamic and dynamic costs required for the system to maintain its current state or undergo transitions. As the system nears the critical point, it requires more cost to sustain an stable state, resulting in an increase in both EPR and flux, along with a peak value. Meanwhile, ΔCC serves as a measure of temporal irreversibility, reflecting the differences between forward and backward time series, the further the system is from equilibrium, the greater ΔCC becomes, leading to another significant peak before approaching the critical point. Additionally, near the critical transition point, the system's state becomes highly unstable, causing a sharp change in corresponding entropy production and flux. Consequently, both flux, EPR, and ΔCC will rapidly decline, indicating the system's tendency to stabilize toward a bistable equilibrium.

5. The results of changes in the resource supply S_2 under competitive exclusion

Figure 15(a) presents the phase diagram under varying resource 2 supply (S_2). At different S_2 values, the system initially displays a state where only species S_1 prevails, then transitions to a bistable state where both species S_1 and S_3 can win, and subsequently evolves into a tristable state where all three species can win (S_1 , S_2 , and S_3). As S_2 increases further, the system eventually reaches a bistable state where both species S_2 and S_3 prevail. Figure 16 presents a schematic diagram of the system's state changes as the supply of resource 2 (S_2) is altered.

When the resource supply S_2 is very low ($S_2 < 6.5$), it indicates that the supply of resource R_2 is scarce. In this case, only species with low demand for resource R_2 can survive. Species S_1 , having the lowest resource demand under resource-limited conditions is able to maintain growth and reproduction even with extremely limited R_2 supply [Fig. 1(b); $R_{21}^* < R_{22}^*$ and $R_{21}^* < R_{23}^*$]. Therefore, species S_1 gains a competitive advantage when the resource S_2 is low, becoming the only species

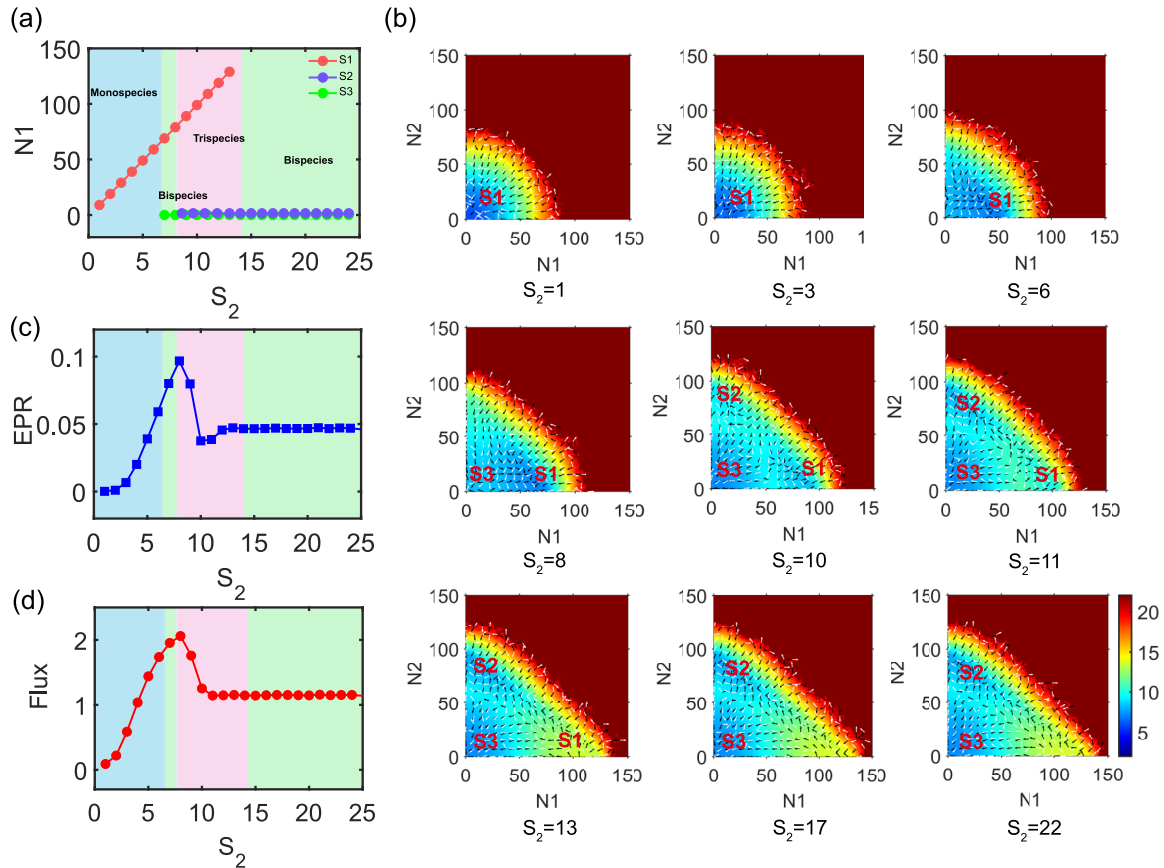


FIG. 15. (a) Phase diagram vs parameter S_2 . (b) The two-dimensional projection of the landscape vs parameter S_2 . (c) The entropy production rate vs parameter S_2 . (d) The average flux vs parameter S_2 . The diffusion coefficient $D = 60$.

capable of maintaining abundance and winning the competition. In contrast, species S_2 and S_3 , which have higher demands for resource R_2 ($R_{22}^* = 0.33$ and $R_{23}^* = 0.2$), are unable to survive under such low resource supply conditions.

As the resource S_2 increases ($6.6 < S_2 < 8.1$), the availability of resource R_2 improves. Since requirement of species S_3 for resource 2 is at a moderate level ($R_{21}^* < R_{23}^* < R_{22}^*$). This enables species S_3 to coexist with species S_1 , while S_3 still maintains its competitive advantage ($R_{23}^* < R_{22}^*$). Therefore, as the resource supply S_2 increases, both species S_1 and S_3 can coexist, leading to a bistable state.

When the resource supply S_2 continues to increase ($S_2 \geq 8.2$), the supply of resource R_2 becomes even more abundant, allowing species S_2 to also utilize R_2 to sustain survival. Therefore, with ample resource supply, species S_1 , S_2 , and S_3 are all able to utilize R_2 , and their abundances can be maintained. In such a resource rich environment, the three species can coexist and prevail, forming a tristable state.

When the resource supply S_2 reaches a very high level ($S_2 > 14.3$), the competition among species undergoes significant changes. At this point, resource R_2 is no longer a critical limiting factor, and competition among species may shift to their ability to utilize other resources. While species S_1 performs well under low resource supply, it may gradually lose its competitive advantage at extremely high S_2 levels due to its lower efficiency in resource utilization or weaker competitiveness for other resources such as R_1 and R_3 . Consequently, as the resource supply S_2 further increases

($S_2 > 14.3$), species S_1 is eventually replaced by species S_2 and S_3 , resulting in a stable bistable state.

Figure 15(b) displays the 2D landscape changes under different S_2 values (the 3D landscapes can be found in Fig. S15 in the Supplemental Material [44]). When S_2 is very small ($S_2 < 6$), the system has only one stable attractor basin for species S_1 . As S_2 increases ($S_2 \approx 8$), a stable basin for species S_3 emerges. Further increase in S_2 results in the appearance of a basin for species S_2 ($S_2 \approx 10$). Entropy production and flux provide the thermodynamic and dynamic sources for state changes [Figs. 15(c) and 15(d)]. When S_2 is very small ($S_2 < 6$), the weight of state S_1 is initially very small, with low thermodynamic and dynamic costs. As the resource supply S_2 increases, entropy production and flux increase, leading to a greater weight for state S_1 [Fig. 15(b); $S_2 = 3$ and $S_2 = 6$].

When the entropy production rate and flux increase, it reflects the system's enhanced ability to maintain or transition to certain states, as this indicates more dynamical and thermodynamic resources are available to drive these processes. Although the increase in flux may render state S_1 more unstable, it simultaneously promotes state transitions, leading to a tendency for the weight of state S_1 to increase. Therefore, the combination of high EPR and flux provides greater weight to state S_1 . Conversely, a high weight corresponds to a higher entropy production rate and flux, as a greater weight for state S_1 within the system implies that more cost are required to maintain its stability or drive its transitions. This necessitates greater dynamical and thermodynamic inputs, manifested as

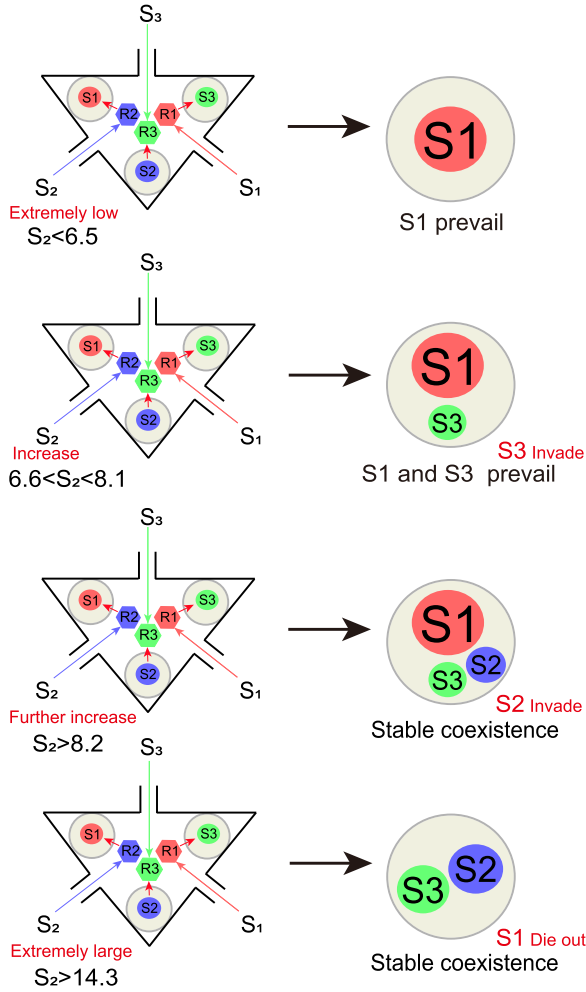


FIG. 16. A diagram explaining the mechanism of phase transition under increased resource supply S_2 .

increased flux and entropy production rate. Consequently, at around $S_2 = 6.6$, a state S_3 emerges from the S_1 state [Fig. 15(a)].

As S_2 further increases to $S_2 = 8$, the entropy production rate and flux reach their maximum values before the critical point at $S_2 = 8.1$, and then gradually decrease. This indicates that a state S_2 will form, as the increased entropy production rate and flux provide the thermodynamic and dynamic driving forces for the formation of the tristable states S_1 , S_2 , and S_3 . As S_2 continues to increase ($S_2 > 10$), the weights of attractor basins for S_1 , S_2 , and S_3 first decrease and then stabilize (Fig. 15(b), and Fig. S15 in the Supplemental Material [44]), resulting in minimal changes in thermodynamic and dynamic costs. Therefore, after $S_2 = 8.1$, entropy production and flux decrease after reaching a peak and then stabilize [Figs. 15(c) and 15(d)].

Figure 17 shows the variation of ΔCC with changes in resource supply S_2 , calculated based on the abundance time series of species 1 and species 2 within the attraction basin corresponding to the winning state of species S_2 . The system initially resides in a tristable state, as S_2 gradually decreases and approaches the bistable critical point at $S_2 \approx 8.1$, ΔCC reaches a peak and then gradually decreases, indicating its

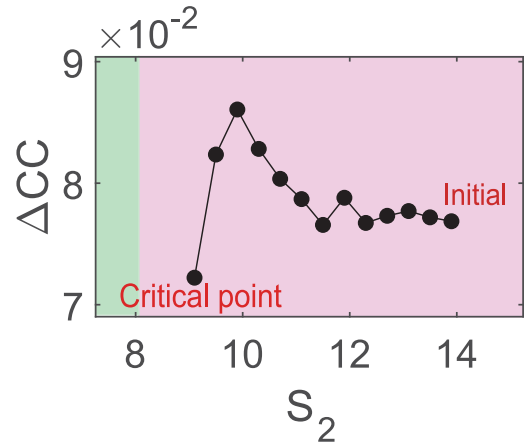


FIG. 17. The average cross-correlation difference ΔCC between forward and backward time vs the parameter S_2 .

potential as a predictive indicator for critical transitions. As a measure of time irreversibility, ΔCC reflects the extent to which the system is away from equilibrium. The greater the instability of the system, the larger the differences between the forward and backward time series, leading to an increase in ΔCC . When the system approaches the critical transition point, its stability becomes highly unstable, resulting in a peak in ΔCC . However, beyond the critical point, the system gradually transitions to a more stable state, such as moving from a tristable to a bistable state. At this point, less cost is required to maintain the previously unstable state, causing ΔCC to decrease. Therefore, after reaching its peak, ΔCC declines, reflecting the system's trend toward a more stable and balanced state. Similarly, in Figs. 15(c) and 15(d), both entropy production and flux exhibit transitions near the critical point at $S_2 \approx 8.1$, suggesting that they, along with ΔCC , can serve as predictive indicators. Furthermore, ΔCC reflects time irreversibility and is more easily observed through time series analysis.

6. The results of changes in the resource supply S_3 under competitive exclusion

Figure 18(a) displays the phase diagram under different resource 3 supply S_3 . At different S_3 values, the system initially shows a state where only species S_2 can win, then transitions to a bistable state with species S_2 and S_3 at around $S_3 = 8.4$, and finally shifts to a tristable state where all three species (S_1 , S_2 , and S_3) can win near $S_3 = 9.9$. Figure 19 presents a schematic diagram of the system's state changes as the supply of resource 3 (S_3) is altered. When the supply of resource S_3 is very low ($S_3 < 8.3$), resource R_3 becomes a major limiting factor. In this situation, species S_2 has the lowest demand for resource R_3 [Fig. 1(b); $R_{32}^* = 0.1$, $R_{32}^* < R_{31}^*$, and $R_{32}^* < R_{33}^*$], enabling it to maintain growth and reproduction in a resource scarce environment. Therefore, species S_2 holds a competitive advantage when the resource supply S_3 is low, while the other species S_1 and S_3 are unable to survive due to their higher demands for resource R_3 ($R_{31}^* = 0.2$ and $R_{33}^* = 0.33$).

As the supply of resource S_3 increases ($8.4 < S_3 < 9.8$), the availability of resource R_3 also rises, allowing species S_3

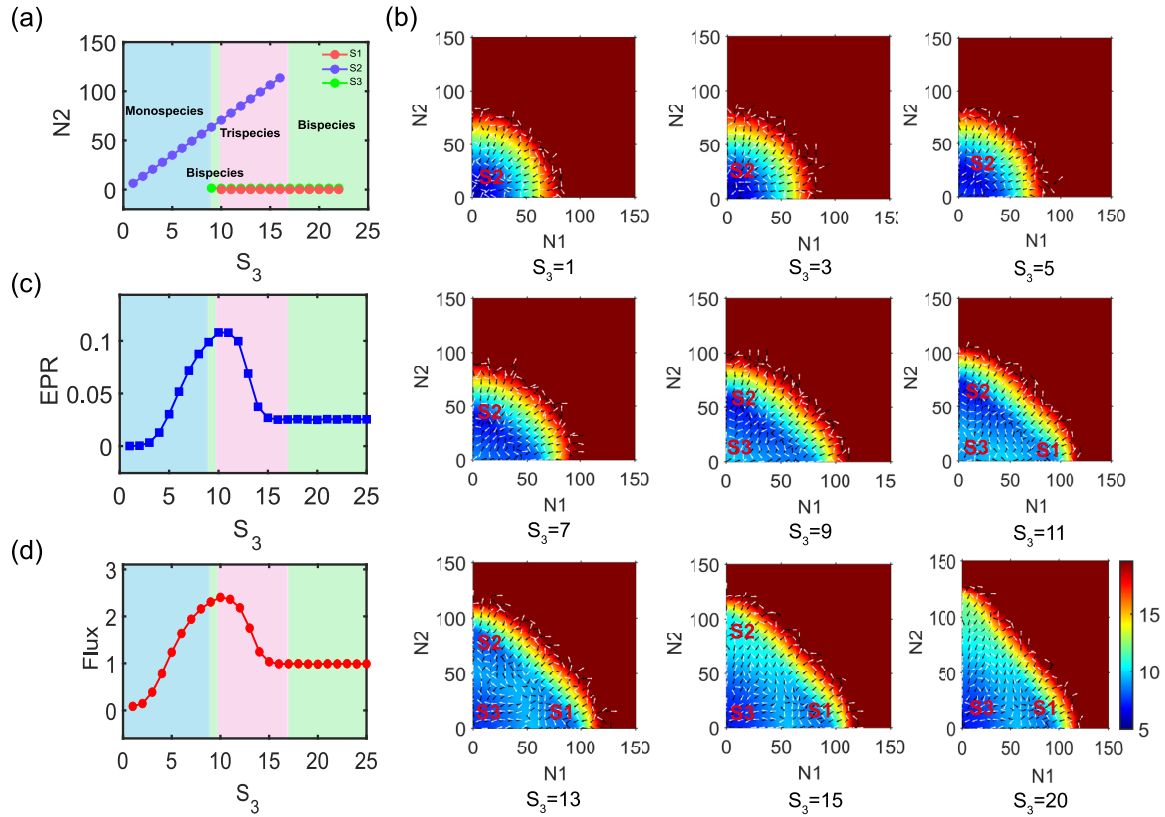


FIG. 18. (a) Phase diagram vs parameter S_3 . (b) The two-dimensional projection of the landscape vs parameter S_3 . (c) The entropy production rate vs parameter S_3 . (d) The average flux vs parameter S_3 . The diffusion coefficient $D = 60$.

to benefit. Consequently, when the supply of S_3 reaches a certain level, species S_2 and S_3 can form a bistable state.

When the supply of resource S_3 continues to increase ($S_3 > 9.9$), the abundance of resource R_3 enables species S_1 to fully utilize this resource as well. At this point, all three species S_1 , S_2 , and S_3 can benefit from the rich supply of resource R_3 , allowing their abundances to be maintained. This creates an opportunity for all three species to coexist and potentially prevail, resulting in a tristable state.

When the supply of resource S_3 reaches a very high level ($S_3 > 17.1$), resource R_3 is no longer the primary limiting factor for species growth. In this scenario, competition among species increasingly depends on the availability and utilization efficiency of other resources R_1 and R_2 . At this point, species S_2 may gradually lose its advantage due to insufficient competitive ability for other resources, while species S_1 and S_3 can continue to grow and reproduce under abundant resource conditions. Therefore, when the supply of S_3 is very high, only species S_1 and S_3 are likely to continue surviving and potentially prevail, forming a bistable state. Figure 18(b) shows the 2D landscape changes under different S_3 values (the 3D landscapes can be found in Fig. S16 in the Supplemental Material [44]). When S_3 is very small, the system has only one attractor basin for species S_2 . As S_3 increases, an attractor basin for species S_3 appears ($S_3 = 9$). Further increase in S_3 leads to the emergence of an attractor basin for species S_1 ($S_3 = 11$). During this process, entropy production and flux initially increase, then decrease, and finally stabilize [Figs. 18(c) and 18(d)]. Similar to the analysis for

parameter S_2 , when S_3 is very small, the weight of state S_2 is initially very small, with low thermodynamic and dynamic costs ($S_3 = 1$). As the resource supply S_3 increases, thermodynamic and dynamic costs gradually increase, with entropy production and flux rising, leading to a greater weight for state S_2 [Fig. 18(b); $S_3 = 5$ and $S_3 = 7$]. Consequently, a state S_3 emerges from the S_2 state ($S_3 = 9$). As S_3 further increases to $S_3 \approx 9.9$, a state where S_1 can win emerges from the bistable state of S_2 and S_3 [Figs. 18(a) and 18(b); $S_3 = 11$], with the system reaching maximum thermodynamic and dynamic costs and maximum entropy production and flux. As S_3 further increases ($S_3 > 11$), the system gradually shifts from a tristable state to a bistable state, reducing the thermodynamic and dynamic costs, which leads to a decrease in the entropy production rate and flux [Figs. 18(c) and 18(d)]. Consequently, this causes the weight of the tristable attractor basins to gradually decrease after $S_3 \approx 13$ [Fig. 18(b)]. As S_3 continues to increase to around $S_3 = 15$, the landscape topology of attractor basins for S_1 , S_2 , and S_3 stabilizes, with minimal changes in thermodynamic and dynamic costs, resulting in nearly unchanged entropy production and flux after $S_3 = 15$ [Fig. 18(d)]. Figure 20 shows the variation of ΔCC with changes in resource supply S_3 , calculated based on the abundance time series of species 1 and species 2 within the attraction basin corresponding to the winning state of species S_1 . The system initially resides in a tristable state, as it gradually decreases and approaches the bistable critical point at $S_3 \approx 9.9$, a sharp increase in ΔCC is observed. The rise in ΔCC and flux [Fig. 18(d)] reflects the process by which

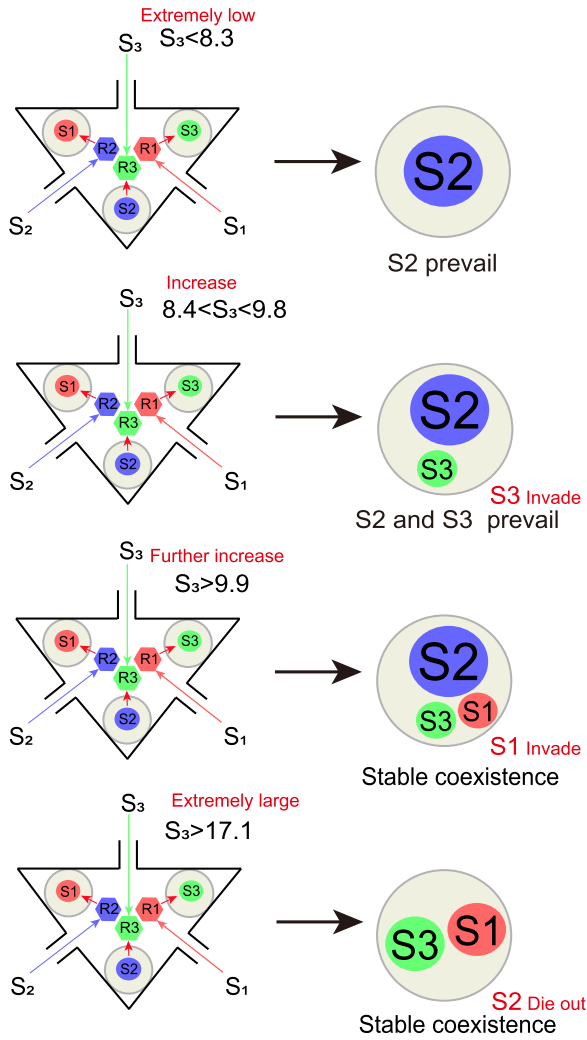


FIG. 19. A diagram explaining the mechanism of phase transition under increased resource supply S_3 .

the system becomes increasingly unstable as it approaches the critical point. As the system nears this point, the transitions between different states intensify, leading to an increase in

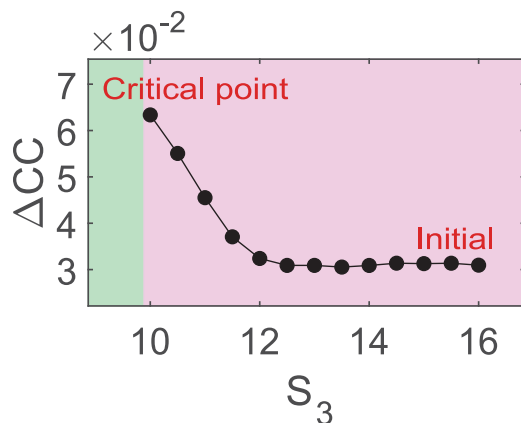


FIG. 20. The average cross-correlation difference between forward and backward in time ΔCC vs parameter S_3 .

ΔCC . This indicates a reduction in system stability as it gradually moves away from the initial tristable state. At the same time, as the critical point approaches, both the flux, which reflects the degree of system nonequilibrium, and the entropy production, representing thermodynamic costs, reach their peaks [Figs. 18(c) and 18(d)]. Therefore, the simultaneous rise in entropy production, flux, and ΔCC highlights significant dynamical and thermodynamic changes in the system near the critical point, characterizing the system's tendency toward an unstable transitional state.

In conclusion, the entropy production rate and flux complement each other by providing thermodynamic and dynamic resources for state changes in species competition systems, while the increases in both ΔCC and flux near the critical point can serve as predictive indicators of critical transitions.

C. The impact of noise on multispecies competition systems

The above discussion focuses on the dynamical and thermodynamic analysis of the system under a fixed noise intensity, characterized by the magnitude of the diffusion coefficient. It is important to emphasize that noise intensity can significantly affect the system's dynamical behavior, probabilistic landscape, average flux, entropy production rate, and other physical quantities. However, it should be noted that although the noise intensity adopted in simulations may not exactly match that of real biological systems (such as phytoplankton communities), this does not mean that these physical quantities lose their significance at other noise levels. We illustrate the effect of noise on the system by considering the case of three species competing for three resources under a competitive exclusion regime, with external resource supply as a control variable.

Figure 21 shows the landscape variations under different noise intensities in the three-species, three-resource competition system. Three attractor basins are observed, each corresponding to a competitive advantage state of a particular species. When the noise intensity is low ($D = 20$), the attractor basins are relatively narrow with sharp boundaries, and the barrier heights between the basins are high. This suppresses transitions between dominant states, enhances the stability of individual basins, and thereby strengthens the competitive advantage of each species. As the noise intensity increases, the system behavior becomes more stochastic. The basins on the landscape gradually expand, and the barrier heights between them decrease, leading to a flatter landscape with less distinguishable attractor states. This progressively obscures the underlying landscape structure and reduces species-specific advantages. When the noise intensity becomes extremely high ($D = 180$), the attractor basins are completely flattened, losing their structural characteristics. Therefore, a moderate noise level helps to reveal structural features of the landscape, contributing to a globally stable configuration. Excessively high noise results in strong stochasticity, flattening the landscape and blurring structural distinctions, which is detrimental to species dominance. Conversely, lower noise levels enhance the stability of individual attractors and thus reinforce competitive advantage. Hence, only within an appropriate noise intensity range can the landscape exhibit a clear evolutionary trend.

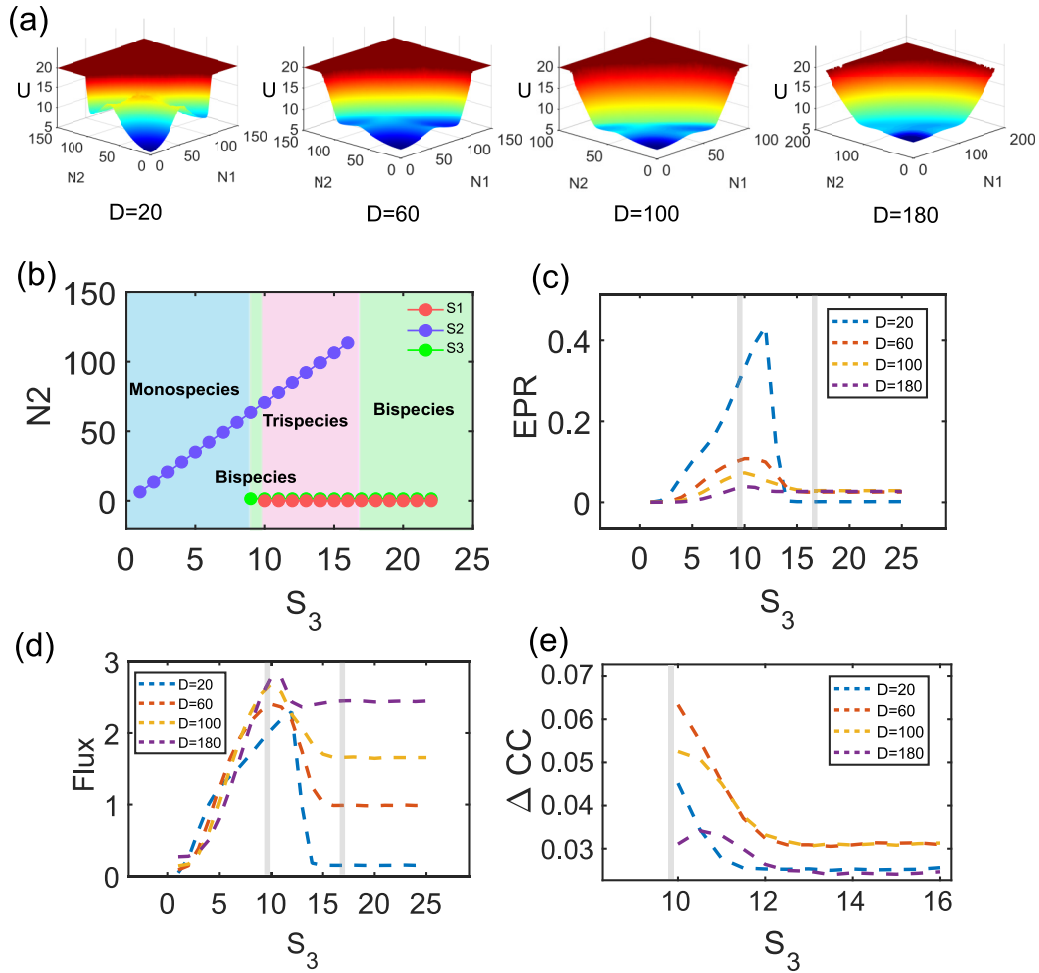


FIG. 21. (a) Landscape variation under different noise intensities. (b) Phase diagram vs parameter S_3 . (c) The entropy production rate vs parameter S_3 . (d) The average flux vs parameter S_3 . (e) The average cross-correlation difference between forward and backward in time ΔCC vs parameter S_3 . In panels (c)–(e) of the figure, the gray shading delineates the position of the critical point.

In addition, noise also significantly influences entropy production and average flux. Figures 21(c) and 21(d) show the changes in entropy production and average flux under different noise levels as the external resource supply S_3 is varied [see phase diagram, Fig. 21(b)] in the context of competitive exclusion among the three species. It is observed that both physical quantities exhibit noticeable changes near the system's critical transition point. Around $S_3 = 10$, both flux and entropy production rise and reach a peak, followed by a decrease around $S_3 = 15$. These results provide both thermodynamic and dynamical evidence for phase transitions in multispecies competition systems. Moreover, the average cross-correlation difference ΔCC between forward and backward time trajectories also exhibits significant changes near the critical point under different noise levels [Fig. 21(e)], indicating that it can be used as a practical early-warning indicator across varying noise conditions.

At fixed external resource supply S_3 , flux increases as noise level increases. Fluctuation increases the chances of moving around in state space and therefore enhances the spread and delocalized spread in state space, which is facilitated by the increase of noise. Since the entropy production

expression depends on flux and noise level in an opposing way ($EPR = \int \mathbf{J} \cdot \mathbf{D}^{-1} \mathbf{P}^{-1} \cdot \mathbf{J} d\mathbf{x}$), thus when noise increases, the entropy production decreases. There is less thermodynamic cost for moving state around when fluctuations can help to do so. The time irreversibility quantified by cross-correlation difference between forward and backward time increases first and then decreases as noise level increases. According to fluctuation theorem, the entropy production is related to time irreversibility. At reasonable noise level and higher noise level, increasing noise decreases entropy production and thus the time irreversibility.

In summary, our method remains applicable within a certain range of noise intensities. The nonequilibrium quantities—such as the landscape, average flux, and entropy production—retain their potential to interpret dynamic changes in ecological systems under different noise levels. Furthermore, considering the complexity of high-dimensional ecological systems, where noise may originate from diverse sources and its intensity is difficult to measure directly, the landscape and associated physical quantities may not be easily quantified or analytically resolved. In future work, we plan to incorporate experimental or observational data to estimate

noise levels in natural systems, thereby further assessing the applicability and robustness of our theoretical framework in real ecological contexts.

D. The global sensitivity analysis for barrier height reveals the key role of resource supply

In our developed multispecies competition model, barrier height can reflect a species' competitive advantage or disadvantage under a given resource allocation. When we say that the barrier height of a species' winning state increases, it means that the stability of that species' winning state is enhanced, making it more difficult for other species to replace it by altering their states or improving their competitive abilities. Conversely, if the barrier height decreases, the stability of the species' winning state is less, making it easier for other species to win in competition. We define the barrier height in the case of tristable attractors (where each species consumes its minimum required resources under competitive exclusion) as the difference between the value U at the saddle point between the two basins and the value U at the minimum point of each basin, i.e., $\Delta U = U_{\text{saddle}} - U_{\text{min}}$ (see Fig. S6(b) in the Supplemental Material [44]). To determine which parameters have the greatest impact on the stability of the competition system, we increased each parameter by 10% to explore their importance in the overall biological competition system. The results indicate that the resource supply S_i for the species significantly impact competition. The resource supply directly determines the availability of resources and the competitive environment [59,60]. When resources are abundant, competition between species may be less intense, however, when resources are scarce, competition becomes fiercer, and even small changes in resource supply can significantly affect species' relative competitive advantages [61]. Additionally, each species has different needs and dependencies on specific resources. A species may be particularly sensitive to or dependent on a certain resource. This quantity of resource use may deprive other species of sufficient resources, putting them at a competitive disadvantage. When the supply of that resource increases, the species relying on it may gain significant growth and reproductive advantages, potentially leading to imbalances in resource distribution within the ecosystem.

In practice, it is generally expected that increasing the resource supply S_2 for species S_2 would enhance its competitive advantage, making it more likely to win, while placing other species at a disadvantage. As shown in Fig. 22(a), the analysis of barrier heights between species S_1 and S_2 reveals that increasing the resource supply for species S_2 leads to an increase in the barrier height of S_2 's winning state, making this state more stable and giving it a competitive advantage. Conversely, the barrier height of S_1 's winning state decreases, decreasing its stability and making S_1 less likely to win. Increasing the resource supply S_3 for species S_3 results in an increase in the barrier height of S_1 's winning state while decreasing the barrier height of S_2 's winning state. This change makes S_1 more advantageous in resource competition while putting S_2 at a disadvantage. This effect may be due to the increased resource supply for species S_3 altering the resource balance, enhancing competition between S_3 and S_2 , and ultimately

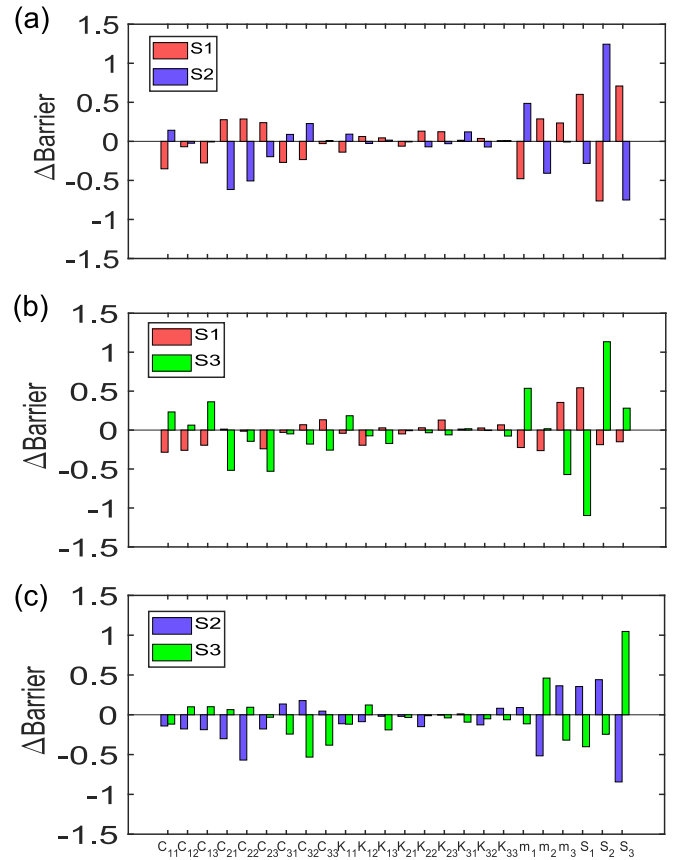


FIG. 22. Global sensitivity analysis for the barrier height of different state. Using the landscape at $S_3 = 13$ as a reference, each parameter is increased by 10%. (a) Sensitivity analysis of the barrier height between the winning state of species S_1 and the winning state of species S_2 . (b) Sensitivity analysis of the barrier height between the winning state of species S_1 and the winning state of species S_3 . (c) Sensitivity analysis of the barrier height between the winning state of species S_2 and the winning state of species S_3 . The diffusion coefficient $D = 60$.

leading to the exclusion or weakening of species S_2 , while species S_1 benefits from this resource environment.

Figure 22(b) shows that increasing the resource supply S_1 for species S_1 results in an increase in the barrier height of S_1 's state, while decreasing the barrier height of S_3 's state. This makes S_1 's state more stable and S_3 's state more unstable, thus benefiting species S_1 in resource competition while disadvantaging species S_3 . Increasing the resource supply S_2 for species S_2 leads to an increase in the barrier height of S_3 's state and a decrease in S_1 's barrier height. This indicates that increasing S_2 's resource supply may alter the resource balance, enhancing competition between S_1 and S_3 , resulting in the exclusion or weakening of S_1 and benefiting S_3 in this resource environment.

Figure 22(c) shows that increasing the resource supply S_3 for species S_3 results in an increase in the barrier height of S_3 's state while decreasing the barrier height of S_2 's state. This increases the stability of S_3 's state and decreases the stability of S_2 's state, making species S_3 more likely to win in resource competition and decreasing the probability of species S_2 winning. Therefore, the resource supply for each species

significantly impacts the likelihood of that species winning, with higher resource supply for a species being more favorable for its competitive success.

E. Nonequilibrium dynamic path of species transition

In the context of species competition, the path integral method can be employed to quantify multispecies competition dynamical process. We can use a path integral functional to describe the population dynamics probability from the initial state x_{initial} at time $t = 0$ to the final state x_{final} at time t [62]:

$$P(x_{\text{final}}, t | x_{\text{initial}}, 0) = \int \mathcal{D}\mathbf{x}(t) e^{-S[\mathbf{x}(t)]}, \quad (22)$$

$$\begin{aligned} S[\mathbf{x}(t)] &= \int L(x(t)) dt \\ &= \int dt \left(\frac{1}{2} \nabla \cdot \mathbf{F}(\mathbf{x}) + \frac{1}{4} (\dot{\mathbf{x}} - \mathbf{F}(\mathbf{x})) \cdot \frac{1}{\mathbf{D}(\mathbf{x})} \cdot (\dot{\mathbf{x}} - \mathbf{F}(\mathbf{x})) \right). \end{aligned} \quad (23)$$

Here, $\mathcal{D}\mathbf{x}(t)$ represents the summation over all possible paths from x_{initial} at $t = 0$ to x_{final} at t . The action $S[\mathbf{x}(t)]$ in the exponent provides the weight for each path, while $L(x(t))$ is the Lagrangian of each path. On one hand, since the action depends on each path, the contribution of each path will differ. On the other hand, as paths are weighted exponentially, the contributions of secondary paths are generally negligible compared to the optimal path. For multidimensional problems, identifying the dominant path often presents a technical challenge due to the boundary value problem at different final times, in contrast to the relatively simpler initial value problem. To find the optimal path, one can transform the action into a line integral along a specific one-dimensional path l in length space within the Hamilton-Jacobi (HJ) framework [62,63]:

$$S_{\text{HJ}} = \int_{x_i}^{x_f} \left(\sqrt{\frac{E_{\text{eff}} + V(\mathbf{x})}{\mathbf{D}(\mathbf{x})}} - \frac{1}{2\mathbf{D}(\mathbf{x})} F_l \right) dl. \quad (24)$$

The effective Hamiltonian E_{eff} is a constant and the effective potential $V(\mathbf{x})$ is given as $V(\mathbf{x}) = \frac{1}{4\mathbf{D}(\mathbf{x})} \mathbf{F}(\mathbf{x})^2 + \frac{1}{2} \nabla \cdot \mathbf{F}(\mathbf{x})$. The action can then be computed using the Monte Carlo method to determine the action and the corresponding optimal paths. Figure 23 shows the nonequilibrium optimal paths for the victory states of each species. In deterministic models, species dominance in the three-species competition system under competitive exclusion is determined by the initial abundance of each species. In contrast, in a nonequilibrium stochastic model, we observed that when all three species have the potential to win, there is a certain probability of transitioning between different states. In other words, a species that is in a winning state at a given time has a certain likelihood of transitioning to another species' winning state. Furthermore, the transition paths between different species' states are irreversible. For instance, the path from the S1 winning state to the S2 winning state does not coincide with the path from the S2 winning state to the S1 winning state. This irreversibility arises from the breakdown of detailed balance in the nonequilibrium system, introducing a rotational flux in the force F_l .

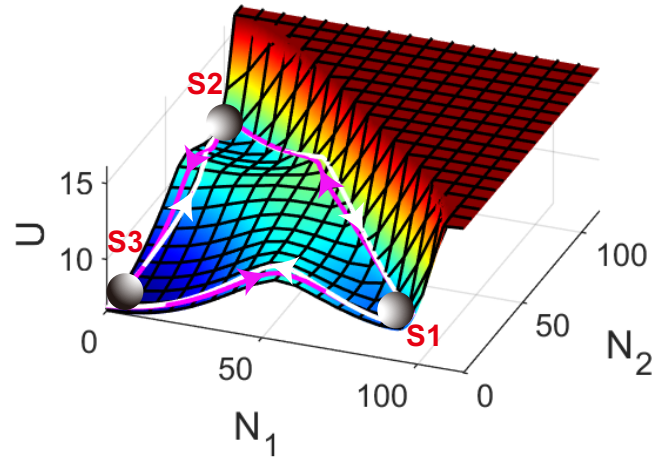


FIG. 23. Nonequilibrium optimal dynamic transition path. The diffusion coefficient $D = 40$.

F. Scalability of the theoretical framework: Competition among five species for five resources

Figure 24(a) shows the quantified landscape of a system comprising five species competing for five resources. In agreement with previous predictions [34], when each species predominantly consumes the resource for which it has the second-highest requirement, the system exhibits species-pair oscillations among species (the species' resource demand levels R_{ji}^* can be found in Sec. S1 in the Supplemental Material [44]). The corresponding steady-state landscape displays a “Mexican hat” topology. When each species primarily consumes the resource for which it has the lowest requirement, the system exhibits competitive exclusion dynamics, where the eventual winner depends sensitively on the initial species abundances. The corresponding landscape consists of multiple attraction basins, among which three basins overlap at the origin, each representing a stable state where one of three species dominates, respectively (the 3D landscape diagrams can be found in Fig. S17 in the Supplemental Material [44]). The driving forces underlying the system dynamics can still be decomposed into the gradient of the landscape (black arrows) and the rotational flux (white arrows), reflecting the nonequilibrium nature of the system.

To further explore the capability of the landscape and flux theory in describing resource competition dynamics in higher-dimensional ecological systems, we constructed a phase diagram under varying supply levels of resource S_1 , based on extensive simulations initialized with 10 000 random points in state space for each parameter setting [Fig. 24(b)]. At low values of S_1 , species S5 dominates due to its minimal requirement for resource R_1 ($R_{15}^* = 0.06$; see Sec. S1 in the Supplemental Material [44]). As the supply of S_1 increases, the availability of resource R_1 improves, allowing species S3 and S4, which have moderate demands for R_1 , to also successfully compete, resulting in the emergence of bistability and tristability ($R_{13}^* = 0.13$, $R_{14}^* = 0.10$, with $R_{15}^* < R_{13}^*$, $R_{15}^* < R_{14}^*$). Further increases in S_1 render resource R_1 sufficiently abundant to support species S2 and S1, which have relatively high requirements for this resource ($R_{12}^* = 0.26$ and $R_{11}^* = 0.33$), leading to the emergence of five stable states.

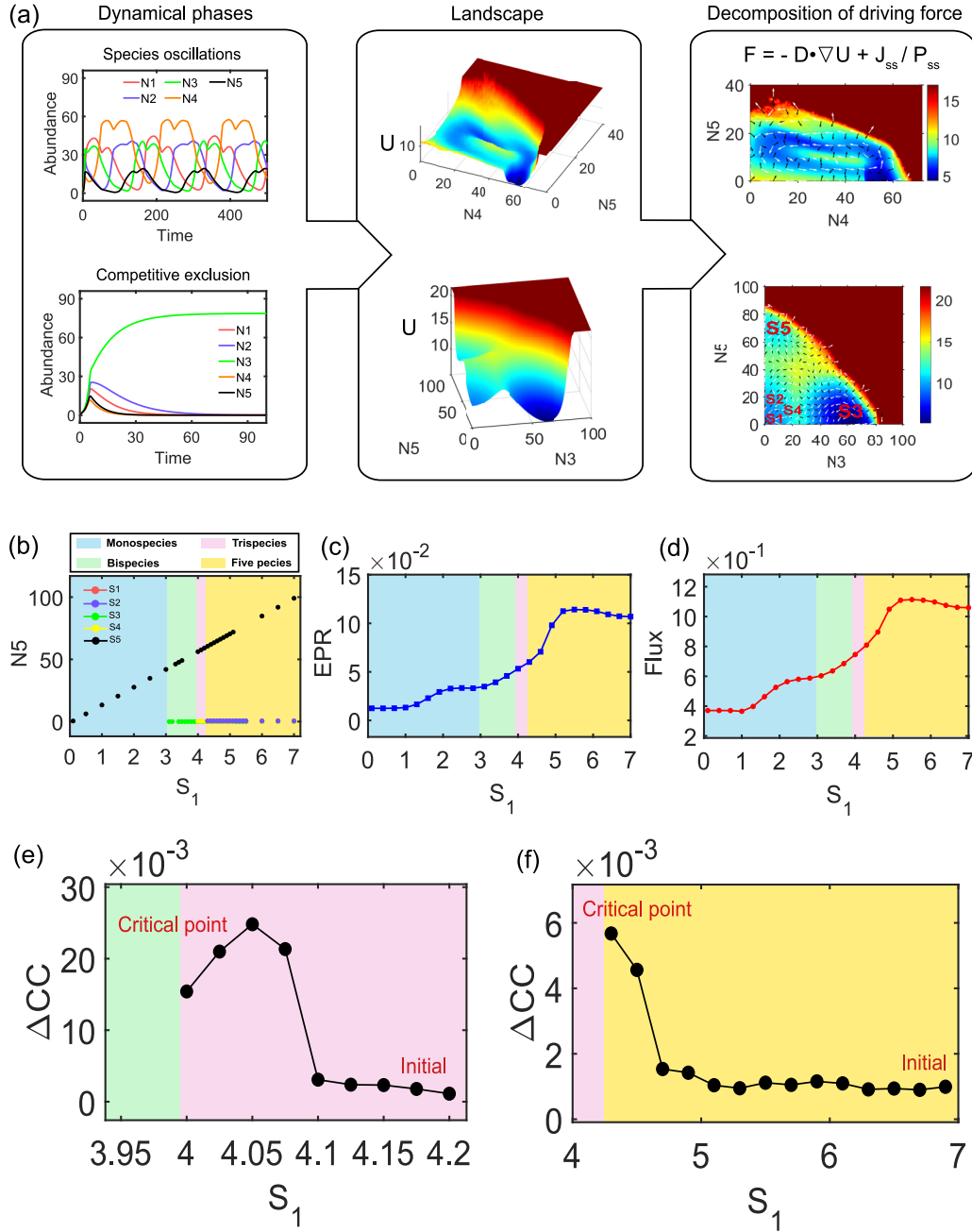


FIG. 24. (a) Dynamical phases and the quantified global landscape. (b) Phase diagram vs parameter S_1 . (c) The entropy production rate vs parameter S_1 . (d) The average flux vs parameter S_1 . (e), (f) The diffusion coefficient $D = 12$. (e), (f) The average cross-correlation difference ΔCC between forward and backward time vs the parameter S_1 . The diffusion coefficient $D = 0.001$.

Figures 24(c) and 24(d) show the corresponding variations in entropy production rate and average flux, respectively. As the system progresses from monostability to bistability, then to tristability, and eventually to five stable states, both quantities tend to exhibit a generally increasing trend. These results indicate that entropy production and flux serve as the thermodynamic and dynamical sources required for phase transitions in the system. In addition, the time-irreversibility indicator ΔCC was calculated based on the species abundance time series under low-noise conditions. Figure 24(e) shows the variation of ΔCC with resource supply S_1 , calculated based on the abundance time series of species 4 and species 5

within the attraction basin corresponding to the winning state of species S_4 , and exhibits a pronounced peak prior to the critical point at $S_1 = 4.0$. Figure 24(f) presents the variation of ΔCC with resource supply S_1 , computed from the time series of species 2 and species 5 within the basin corresponding to the winning state of species S_2 , and shows a noticeable increase in ΔCC prior to the critical point at $S_1 = 4.2$. In summary, a pronounced change in ΔCC was observed prior to the onset of critical transitions, indicating its potential as a reliable early-warning indicator of impending critical points.

At present, we are only able to quantify the projection of the landscape onto a lower-dimensional subspace. In

low-dimensional ecological systems, physical quantities such as potential landscapes and flux are generally more tractable to analyze and visualize, owing to the numerical controllability and reduced complexity of the state space. However, such quantification becomes substantially more challenging in high-dimensional systems and is beyond the scope of the current study. As the dimensionality increases (e.g., due to the inclusion of more species or resource types), the expansion of the state space significantly complicates the accurate computation of steady-state distributions, fluxes, and potential barriers. Moreover, the structure of the system itself may also become more complex. For example, resource preference relationships among species can become more intertwined, and interaction networks more tightly coupled, thereby giving rise to richer dynamical behaviors, such as multistability or even chaos. These factors together pose substantial numerical challenges for constructing and interpreting the landscape-flux structure in high-dimensional systems. The feasibility and accuracy of such analyses strongly depend on the structural complexity of the model and the characteristics of its steady states.

Nonetheless, this does not diminish the theoretical significance of the landscape and flux approach in understanding the stability and transition mechanisms of high-dimensional ecological systems. On the contrary, with advances in computational techniques and the application of dimensionality reduction methods, the landscape-flux framework remains capable of offering qualitative and, in some cases, semiquantitative insights—particularly in identifying critical transition pathways and characterizing time irreversibility. Therefore, the applicability of landscape and flux theory is not limited to low-dimensional models; with appropriate methodological support, it holds promise for extension to more complex, high-dimensional ecological systems. In summary, while our approach performs well in systems of moderate dimensionality, its application to real-world high-dimensional ecological systems requires the integration of dimensionality reduction strategies and approximation algorithms to overcome numerical bottlenecks.

V. DISCUSSION

In complex ecosystems, interactions between species can lead to the emergence of multiple dynamic phases [13,34,64]. These phases reflect the dynamic changes in species competition, predation, and symbiosis, which represent the intricate relationships among species. Traditionally, these complex phenomena have been described using deterministic differential equations that capture the temporal evolution of the system's state [16,34,64]. However, resource competition among species is inherently an open system, influenced by both external environmental factors and internal dynamics. This implies that its dynamic behavior should not only be considered deterministic but also as a stochastic dynamic process.

Most deterministic models rely on local stability analysis near equilibrium points [2,21,34], which cannot fully reveal the global properties of the system. For instance, the stability of competitive species states and the relative weights between different species states are not adequately addressed. In contrast, global stability analysis focuses on the dynamic behavior

across the entire state space, allowing for the quantification of the system's global attraction domain and providing a more comprehensive perspective [40,49,63]. Additionally, species often transition from one state to another, a process typically driven by interspecies interactions. However, understanding the mechanisms of these interactions and how they influence population dynamics remains a challenging issue.

Building on previous research [14,34], we developed a simple three-species, three-resource model to quantify the global landscape and flux properties of the system. The results demonstrate that the resource competition system, under the combined effects of gradient forces and rotational fluxes, facilitates transitions between different competitive modes. This provides deeper insights into the mechanisms underlying species competition in ecosystems. Our model reveals additional dynamic features, such as the quantification of species oscillation coherence, entropy production associated with transitions from oscillatory to stable states, barrier heights, and dynamical fluxes, all of which can be calculated quantitatively.

Moreover, by analyzing the time series of species abundance evolution, we observed that time irreversibility exhibits sharp changes at critical points of species multistability, suggesting its potential as an early-warning signal for predicting critical transitions in complex ecosystems, which has not been fully explored in previous study on competition ecosystems [40]. However, the extent to which this time irreversibility applies to various types of real-world ecosystems is still unclear. The interaction mechanisms among species, resource allocation patterns, and characteristics of environmental fluctuations may vary across ecosystems, potentially affecting the model's predictive capabilities. Therefore, further experimental validation is needed.

The specific steps are as follows. First, by incorporating the actual physical quantities provided in Tables S1 and S2 in the Supplemental Material [44], ecological parameters measured in experiments can be fitted within the parameter range of the model [34], enabling parameter calibration and establishing an effective link between the model and real ecological systems. Second, by adjusting controllable factors such as resource supply, one can observe changes in species coexistence patterns and competitive dominance, which can be used to test whether the model-predicted population-level dynamics (e.g., oscillatory behavior) actually emerge, and whether these changes are accompanied by variations in key quantities such as entropy production and average flux. Furthermore, it allows for the assessment of whether early-warning indicators such as ΔCC respond prior to critical transitions. These experimental observations can be used to systematically evaluate the model's ecological interpretability and predictive power. In addition, in practical applications, physical quantities such as entropy production and average flux primarily depend on the system's steady-state probability distribution, which is generally difficult to measure directly in the experiments [65]. Their estimation typically requires long-term, continuous, and high-resolution time series of species abundances. In contrast, the time-irreversibility metric is more experimentally accessible. It does not rely on prior knowledge of the system's detailed model structure or the location of dynamical critical points, nor does it require access to the steady-state distribution.

Instead, it can be inferred directly from observed time-series data, making it a more feasible and practical indicator for identifying early-warning signals in ecological systems. The practical steps for measuring flux and entropy production are as follows: First, the system's driving force can be reconstructed from the time series, and the noise term can also be estimated [66]:

$$\langle \dot{x} \rangle = F(x), \quad \langle (\dot{x} - F)(\dot{x} - F) \rangle = 2D \quad (25)$$

($\langle \cdot \rangle$ denotes time averaging when the system reaches the steady state). By collecting long-term statistics, one can obtain the steady-state probability distribution P_{ss} . Using force decomposition, the steady-state probability flux can then be determined as

$$\frac{J_{ss}}{P_{ss}} = F + D \nabla U, \quad \text{where } U = -\ln P_{ss}. \quad (26)$$

Finally, the EPR of the system can be calculated as

$$\text{EPR} = \int J \cdot D^{-1} P^{-1} \cdot J dx. \quad (27)$$

Given the relative simplicity of the three-species, three-resource and five-species, five-resource systems, it is both interesting and of significant research value to further explore the generalizability of this landscape theory approach to higher-dimensional, multispecies, multiresource systems.

VI. CONCLUSION

Since the time of Darwin, there has been a profound interest in the theory of natural selection. This theory has had a significant impact on biology by examining how organisms adapt to their environments and compete with one another, thereby aiding our understanding of the vast diversity of species and their evolution over time. However, the study of species competition has generally lacked a physical perspective. To address this gap, we have developed a comprehensive physical theory of species-resource competition using stochastic dynamics and have quantified the probabilistic potential landscapes and fluxes involved in the competition among three species and three resources.

The stable coexistence of species, competitive exclusion, and competitive oscillations correspond to attractor basins and Mexican hat-shaped landscapes, respectively. The dynamics of species competition are driven by both gradient forces and rotational fluxes, with the flux providing the driving force for phase transitions between different competitive states and entropy production serving as the thermodynamic source. Additionally, we proposed an effective method for detecting critical points in species competition systems by using the average cross-correlation difference between forward and backward time series.

The barriers on the landscape characterize the difficulty of state transitions, quantifying the global stability of various competitive states. Through a global sensitivity analysis of barrier heights, we found that resource supply play a crucial role in determining competitive outcomes among species, indicating the feasibility of managing ecosystems by adjusting resource supply.

In summary, our model offers an ecological theoretical perspective, contributing to a better understanding of multispecies competition dynamics. This theoretical framework helps deepen our insight into the intrinsic mechanisms of multispecies competition and provides a broader and more physical understanding.

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DATA AVAILABILITY

All data and code used in this study are publicly available on Github [67].

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