

## Limiting similarity of competitive species and demographic stochasticity

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The limiting similarity of competitive species and its relationship with the competitive exclusion principle is still one of the most important concepts in ecology. In the 1970s, May [R. M. May, *Stability and Complexity in Model Ecosystems* (Princeton University, Princeton, NJ, 1973)] developed a concise theoretical framework to investigate the limiting similarity of competitive species. His theoretical results show that no limiting similarity threshold of competitive species can be identified in the deterministic model system whereby species more similar than this threshold never coexist. Theoretically, for competitive species coexisting in an unvarying environment, deterministic interspecific interactions and demographic stochasticity can be considered two sides of a coin. To investigate how the “tension” between these two forces affects the coexistence of competing species, a simple two-species competitive system based only on May's model system is transformed into an equivalent replicator equation. The effect of demographic stochasticity on the system stability is measured by the expected drift of the Lyapunov function. Our main results show that the limiting similarity of competitive species should not be considered to be an absolute measure. Specifically, very similar competitive species should be able to coexist in an environment with a high productivity level but big differences between competitive species should be necessary in an ecosystem with a low productivity level.

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### I. INTRODUCTION

The competitive exclusion principle, or the limiting similarity of competitive species, is one of the basic concepts in ecology, which states that species making their living in identical ways cannot coexist [1–3]. This concept not only relates the most fundamental mechanism of long-term coexistence of competitive species (or biodiversity) in an ecosystem but also provides a basic theoretical cornerstone for understanding ecosystem stability and complexity [1–3]. Based on the concept of ecological niche [4], May measured the similarity of competing species in terms of their niche overlap in his model system [1]. His result shows clearly that, when the environment is assumed to be unvarying (or static), the limiting similarity of competing species cannot be identified in his model system.

Specifically, in May's model [1], bell-shaped Gaussian curves are used to represent the utilization functions for each of two competing species, aligned along some one-dimensional resource axis. Each species has a preferred location on the resource axis, a spread of characteristic width,  $\omega$ , about this optimal location, and the two species' optima are separated by a distance,  $d$ . The resource-utilization functions (Gaussian curves) define the species' niches and the niche overlap can be measured by the ratio  $\omega/d$ . Based on these assumptions and definitions, MacArthur and May [5] asked what are the limits to similarity by considering how small  $d$  can be, in relation to  $\omega$ , and yet have the two species persist together. Further, for a set of  $n$  species uniformly spaced at

intervals along the resource continuum and obeying the Lotka-Volterra competition equations, the competition coefficients are calculated from the overlap in the uniformly spaced niches: the competition coefficient  $\alpha_{ij}$  between species  $i$  and  $j$ , whose mean utilizations are separated by  $|i - j|d$ , is  $\alpha^{(i-j)^2}$ , where  $\alpha = \exp(-d^2/4\omega^2)$ . May and MacArthur showed clearly that this system is always stable, no matter how small  $d/\omega$ , since the eigenvalues of the linearized interaction matrix have negative real parts. Moreover, they show that the dominant eigenvalue has a real part which becomes increasingly negative as species numbers,  $n$ , increase, whereas the other  $n - 1$  eigenvalues have negative real parts which creep close to zero [1,5,6]. Thus, as  $n$  increases, with consequent increase in niche overlap and decrease in  $d/\omega$ , individual populations are less stable. However, as apparent from the related literature [7], none of the theoretical results so far that are based only on May's basic model provide a clear answer to MacArthur and May's question [5] without introducing new assumptions to the model or increasing its complexity. In this article, we argue the answer for the basic model can be understood through the relationship between deterministic interspecific interactions and demographic stochasticity.

Theoretically, for the long-term coexistence of competitive species in a static environment, the deterministic interspecific interactions and demographic stochasticity should be considered two sides of a coin. In essence, the competitive exclusion principle (or limiting similarity of competitive species) reflects the balance between deterministic force and random force in an interspecific competition system, i.e., the power contrast between deterministic and random forces. Thus, the key question is not only to show which one of these two sides is more important in determining the coexistence of competitive species but also to reveal how system stability is influenced by

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demographic stochasticity. As an extreme situation, instead of looking for differences between species, Hubbell asked what would be observed if species are exactly the same as one another [6,8,9]. Although Hubbell's neutral community theory is considered to be a modern descendent of the null-hypothesis movement and the corresponding neutral model is highly sensitive to the neutrality assumption [6], we are still interested in why this extreme assumption may actually predict some of the most conspicuous patterns in large-scale ecology [6,8,10].

As mentioned above, in this article, we take only May's basic model system as the foundation [1,2] to reveal how the stability of a two-species competitive system is influenced by demographic stochasticity. As we will see, our underlying mathematical methods are similar to Claussen and Traulsen's study on the dynamic stability of the rock-paper-scissors game [11].

## II. MODEL AND ANALYSIS

### A. Stochastic simulation of a two-species competitive system

Here we focus our attention on the simplest two-species competitive system described by the classic Lotka-Volterra equation:

$$\begin{aligned} \frac{dN_1}{dt} &= N_1 r_1 \left( 1 - \frac{N_1 + \alpha_1 N_2}{K_1} \right), \\ \frac{dN_2}{dt} &= N_2 r_2 \left( 1 - \frac{\alpha_2 N_1 + N_2}{K_2} \right), \end{aligned} \quad (1)$$

where  $N_i$ ,  $r_i$ , and  $K_i$  are the population size, intrinsic growth rate, and environmental carrying capacity of species  $i$ , respectively ( $i = 1$  and  $2$ ), and  $\alpha_1$  ( $\alpha_2$ ) is the competition coefficient of species 2 (species 1) [1,2]. This deterministic system is one of the most important theoretical models in ecology, which in the most general sense describes the characteristics of interspecific competition. Following May's model [1,2], we also assume that  $r_1 = r_2 = r$ ,  $K_1 = K_2 = K$ , and  $\alpha_1 = \alpha_2 = \alpha$ , where the competition coefficient  $\alpha$  is taken as  $\alpha = \exp(-d^2/4\omega^2)$ , which lies in the interval  $0 \leq \alpha \leq 1$  [1,2]. Clearly, the parameter  $\alpha$  also measures the similarity of species 1 and species 2; i.e., species 1 and species 2 are independent of each other if  $\alpha = 0$ , and they are completely identical in ecology if  $\alpha = 1$ . It is easy to see that the equilibrium point  $(N_1^*, N_2^*)$  with  $N_1^* = N_2^* = K/(1 + \alpha)$  of this simple two-species competition system is globally asymptotically stable for all possible  $\alpha < 1$ . In particular, the eigenvalues of the Jacobian matrix about  $(N_1^*, N_2^*)$  are  $\lambda_{1,2} = r(-1 \pm \alpha)/(1 + \alpha)$ , which, as pointed out by May [1,2], are both negative and satisfy  $\lim_{\alpha \rightarrow 1} \lambda_1 = 0$  and  $\lim_{\alpha \rightarrow 1} \lambda_2 = -r$ .

When demographic stochasticity is added to this simple two-species competitive system, the stochastic simulations described below that are based on the one-step process [12] and Moran's process [13], respectively, reveal how the long-term coexistence of competing species depends on the species similarity and environmental carrying capacity. For the one-step process, we assume that the total system size is not fixed and that, at each time step, only one new individual is produced, or one existing individual dies. This implies that the stochastic fluctuations in  $N_1$  and  $N_2$  can be characterized by a birth-and-death Markov process with the

following events:

$$\begin{aligned} N_1 &\xrightarrow{rN_1} N_1 + 1, \\ N_1 &\xrightarrow{rN_1(N_1 + \alpha N_2)/K} N_1 - 1, \\ N_2 &\xrightarrow{rN_2} N_2 + 1, \\ N_2 &\xrightarrow{rN_2(\alpha N_1 + N_2)/K} N_2 - 1, \end{aligned}$$

where the birth rate,  $rN_1$ , and the mortality rate,  $rN_1(N_1 + \alpha N_2)/K$ , of species 1 represent the relative transition probabilities of  $N_1$ ; and, similarly, the birth rate,  $rN_2$ , and the mortality rate,  $rN_2(\alpha N_1 + N_2)/K$ , of species 2 represent the relative transition probabilities of  $N_2$  [12]. For convenience, let  $W_1 = r(N_1 + N_2)$ ,  $W_2 = rN_1(N_1 + \alpha N_2)/K + rN_2(\alpha N_1 + N_2)/K$ ,  $T_1^+ = rN_1/W_1$ ,  $T_2^+ = rN_2/W_1$ ,  $T_1^- = rN_1(N_1 + \alpha N_2)/K/W_2$ , and  $T_2^- = rN_2(\alpha N_1 + N_2)/K/W_2$ . Then, we can define that, at each time step, the probability that a new individual of species 1 (or species 2) is produced is  $W_1 T_1^+/(W_1 + W_2)$  [or  $W_1 T_2^+/(W_1 + W_2)$ ], or the probability that an existing individual of species 1 (or species 2) dies is  $W_2 T_1^-/(W_1 + W_2)$  [or  $W_2 T_2^-/(W_1 + W_2)$ ]. On the other hand, for the Moran process, we assume that the total system size is fixed, which is defined as  $N_1 + N_2 = 2K/(1 + \alpha)$  at any time  $t$ , and that, at each time step, one new individual is produced and one existing individual dies, where we define a new individual of species 1 (or species 2) is produced with probability  $T_1^+$  (or  $T_2^+$ ) and an existing individual of species 1 (or species 2) dies with probability  $T_1^-$  (or  $T_2^-$ ). At the initial time, we set both species 1 and species 2 to the same size  $K/(1 + \alpha)$ . The coexistence probability of competing species in the simulation is defined as the probability that neither species is excluded within a given time interval, where the observed time scale is taken as  $10^5$  (which is the total length of time steps [14]).

For the one-step process, the simulation results show clearly that the coexistence probability has a clear separating band on the  $K$ - $\alpha$  plane [Fig. 1(a), where the initial state of the system is taken as  $(N_1^*, N_2^*)$ ] and that the coexistence probability is very low on the upper left of the separating band, and, conversely, the coexistence probability is very high on the lower right of the separating band. This implies that for both species similarity and environmental carrying capacity, the coexistence probability has obvious critical characteristics. Specifically, for a given environmental carrying capacity ( $K$ ), the coexistence probability will decrease with an increase of species similarity ( $\alpha$ ) [see Fig. 1(b)], and, for a given species similarity ( $\alpha$ ), the coexistence probability will increase as the environmental carrying capacity increases ( $K$ ) [see Fig. 1(c)]. All of these simulation results strongly imply that, under May's theoretical framework [1,2], the coexistence of competing species depends not only on species similarity but also on the environmental carrying capacity. The simulations also provide a theoretical intuition for understanding how demographic stochasticity acts on the stability of a competitive system.

Moreover, we can also see that the simulation results of the Moran process are exactly similar to the results of the one-step process [see Figs. 1(d)–1(f)]. This implies that we can use the Moran process with fixed population size to approximate the one-step process although the latter is more close to the

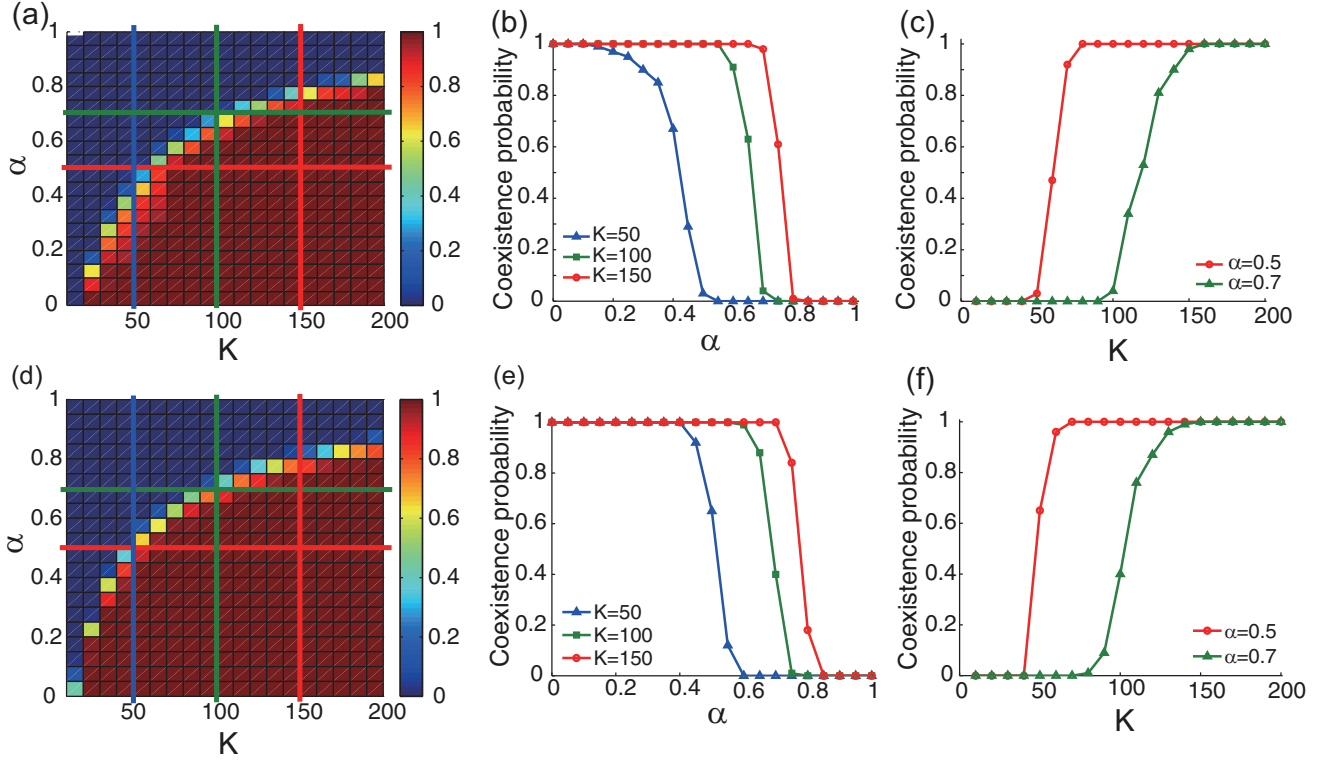


FIG. 1. Stochastic simulations for the effects of species similarity ( $\alpha$ ) and environmental carrying capacity ( $K$ ) on the coexistence probability. Panels (a), (b), and (c) show the simulation results of the one-step process, and panels (d), (e), and (f) show the simulation results of the Moran process. Panels (a) and (d): The coexistence probability (indicated by the color corresponding to the vertical bar on the right) has a rapid transition between 0 and 1 across a separating band in the  $K$ - $\alpha$  plane, where for each pair  $(K, \alpha)$  the observed time scale is  $10^5$ . Panels (b) and (e): For a given  $K$ , the coexistence probability decreases with the increase of  $\alpha$ . For example, when we take  $K = 50$ ,  $K = 100$ , and  $K = 150$ , respectively, panels (b) and (e) show how the coexistence probability drops rapidly from near 1 to near 0, in which the blue, green, and red curves in panel (b) [or in panel (e)] correspond to the blue, green, and red vertical lines in panel (a) [or in panel (d)], respectively. Panels (c) and (f): For given  $\alpha$ , the coexistence probability increases with the increase of  $K$ . For example, when we take  $\alpha = 0.5$  and  $\alpha = 0.7$ , respectively, panels (c) and (f) show how the coexistence probability increases rapidly from near 0 to near 1, in which the red and green curves in panel (c) [or in panel (f)] correspond to the red and green horizontal lines in panel (a) [or in panel (d)], respectively.

real system. On the other hand, we have to point out that for our stochastic simulation results in Fig. 1, the thresholds will change somewhat for longer or shorter time intervals. For example, when we take  $10^4$  time steps (or  $10^6$  time steps), the critical characteristics of coexistence probability on the  $\alpha$ - $K$  plane will not change but the positions of the thresholds will have a small parallel movement toward the left (or right). Theoretically, for all possible  $K$  and  $\alpha$ , if the time is infinite, then the thresholds will disappear but coexistence will not be possible because of random drift (where both the boundaries  $N_1 = 0$  and  $N_2 = 0$  are absorbing states).

### B. Effect of demographic stochasticity on coexistence stability

Previous studies [15, 16] have shown that the Lotka-Volterra equation can be equivalently expressed as a replicator equation under the framework of evolutionary game dynamics. For our simple two-species competitive system, let  $N_3$  be an instrumental variable with  $N_3 \equiv 1$ . Then, the frequencies of species 1 and species 2 can be given by  $x_1 = N_1/(N_1 + N_2 + 1)$  and  $x_2 = N_2/(N_1 + N_2 + 1)$ , respectively, and the frequency of

the instrumental variable is  $x_3 = 1/(N_1 + N_2 + 1)$ . Based on these definitions, we have that

$$\begin{aligned} \frac{dx_1}{dt} &= \frac{d}{dt} \left( \frac{N_1}{N_1 + N_2 + 1} \right) \\ &= x_1 \frac{r}{K} [(1 - x_1)(K - N_1 - \alpha N_2) \\ &\quad - x_2(K - \alpha N_1 - N_2)], \\ \frac{dx_2}{dt} &= \frac{d}{dt} \left( \frac{N_2}{N_1 + N_2 + 1} \right) \\ &= x_2 \frac{r}{K} [(1 - x_2)(K - \alpha N_1 - N_2) \\ &\quad - x_1(K - N_1 - \alpha N_2)], \\ \frac{dx_3}{dt} &= \frac{d}{dt} \left( \frac{1}{N_1 + N_2 + 1} \right) \\ &= -x_3 \frac{r}{K} [x_1(K - N_1 - \alpha N_2) + x_2(K - \alpha N_1 - N_2)], \end{aligned}$$

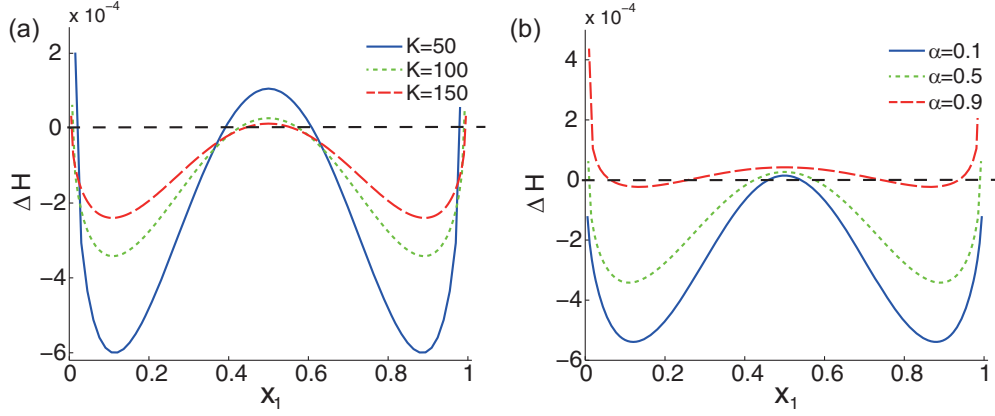


FIG. 2. The effects of  $K$  and  $\alpha$  on  $\Delta H(\mathbf{x})$ . (a) For  $\alpha = 0.5$  and  $K = 50, 100$ , and  $150$ ,  $\Delta H(\mathbf{x})$  is plotted as the function of  $x_1$ . (b) For  $K = 100$  and  $\alpha = 0.1, 0.5$ , and  $0.9$ ,  $\Delta H(\mathbf{x})$  is plotted as the function of  $x_1$ .

with  $N_1 = x_1/x_3$  and  $N_2 = x_2/x_3$ . Thus, Eq. (1) becomes the replicator equation

$$\frac{dx_i}{dt} = x_i[(\mathbf{A}\mathbf{x})_i - \mathbf{x} \cdot \mathbf{A}\mathbf{x}] \quad (2)$$

for  $i = 1, 2$ , and  $3$ , where  $\mathbf{x} = (x_1, x_2, x_3)$  and

$$\mathbf{A} = \begin{pmatrix} -r/K & -r\alpha/K & r \\ -r\alpha/K & -r/K & r \\ 0 & 0 & 0 \end{pmatrix}$$

is called the payoff matrix for the evolutionary game dynamics [15,16]. Under the evolutionary game dynamics, the term  $(\mathbf{A}\mathbf{x})_i = \sum_{j=1}^3 x_j a_{ij}$  in Eq. (2) can be also called the expected payoff of species  $i$  for  $i = 1$  and  $2$ . It is easy to see that the interior equilibrium of this replicator equation,  $\mathbf{x}^* = (N_1^*, N_2^*, 1)/(N_1^* + N_2^* + 1) = (K, K, 1 + \alpha)/(2K + 1 + \alpha)$ , is globally asymptotically stable for all possible  $0 < \alpha < 1$ . On the other hand, from the theory of evolutionary game dynamics [15,17], the stable interior equilibrium of Eq. (2),  $\mathbf{x}^*$ , is an evolutionarily stable strategy (ESS) for the payoff matrix  $\mathbf{A}$  (the straightforward proof is shown in the Appendix). Thus, the Lyapunov function of the replicator equation, Eq. (2), can be given by

$$H(\mathbf{x}) = - \prod_{i=1}^3 x_i^{x_i^*}, \quad (3)$$

since  $dH(\mathbf{x})/dt < 0$  for all possible  $\mathbf{x}$  but  $\mathbf{x} \neq \mathbf{x}^*$  [15].  $H(\mathbf{x}) - H(\mathbf{x}^*)$  is interpreted as a measure of how far the system is from equilibrium.

To show the effect of demographic stochasticity on the system stability, based on the Moran process, we assume that the total system size is a fixed constant, which is taken to be the equilibrium size  $N_1 + N_2 = 2K/(1 + \alpha)$ . According to this assumption, the change of system state can be considered to be a birth-and-death process. That is, the change from  $(N_1, N_2)$  to  $(N_1 \pm 1, N_2 \mp 1)$  is equivalent to the change from  $(x_1, x_2, x_3)$  to  $(x_1 \pm x_3, x_2 \mp x_3, x_3)$ . Thus, the drift of  $H(\mathbf{x})$  at each time step is

$$\Delta H(\mathbf{x}) = [H(x_1 + x_3, x_2 - x_3, x_3) - H(\mathbf{x})]T_1^+ T_2^- + [H(x_1 - x_3, x_2 + x_3, x_3) - H(\mathbf{x})]T_1^- T_2^+. \quad (4)$$

[11]. Obviously, the strong deterministic interspecific interaction should tend to make  $\Delta H(\mathbf{x})$  negative, and the strong stochastic effect should tend to make  $\Delta H(\mathbf{x})$  positive.

The numerical results of  $\Delta H(\mathbf{x})$  [where  $\Delta H(\mathbf{x})$  is taken as the function of  $x_1$  since  $x_2 = 1 - x_1 - x_3$  with  $x_3 \equiv (1 + \alpha)/(2K + 1 + \alpha)$ ] show clearly how  $\Delta H(\mathbf{x})$  is influenced by the parameters  $K$  and  $\alpha$  [see Fig. 2(a), in which we take  $\alpha = 0.5$  and  $K = 50, 100$ , and  $150$ , and see Fig. 2(b), in which we take  $K = 100$  and  $\alpha = 0.1, 0.5$ , and  $0.9$ ]. That is, they show how demographic stochasticity acts on the coexistence stability of competitive species under different system states. More specifically, when the system state  $\mathbf{x}$  is at the equilibrium  $\mathbf{x}^* = (x_1^*, x_2^*, x_3^*)$ , species 1 and species 2 must have the same expected payoff, i.e.,  $(\mathbf{A}\mathbf{x}^*)_1 = (\mathbf{A}\mathbf{x}^*)_2$ ; and when  $\mathbf{x}$  is near  $\mathbf{x}^*$ , the absolute difference  $|(\mathbf{A}\mathbf{x})_1 - (\mathbf{A}\mathbf{x})_2|$  is small. Thus, when  $\mathbf{x}$  is at, or near,  $\mathbf{x}^*$ , the effect of deterministic interspecific interaction on the system dynamics should be weaker than that of the demographic stochasticity. This is why  $\Delta H(\mathbf{x}) > 0$  if  $\mathbf{x}$  is at, or near,  $\mathbf{x}^*$ . On the other hand, when the system state  $\mathbf{x}$  is near the boundary  $x_1 = 0$ , or  $x_1 = 1$ , although the absolute difference  $|(\mathbf{A}\mathbf{x})_1 - (\mathbf{A}\mathbf{x})_2|$  could be not small, the deterministic interspecific interaction is unable to make the rare species resist the disturbance of demographic stochasticity. So, we have also  $\Delta H(\mathbf{x}) > 0$  if the system state is near the boundary  $x_1 = 0$  or  $x_1 = 1$ .

Let  $\phi(x_1; t)$  denote the probability density distribution that the system state is at  $(x_1, x_2, x_3)$  at time  $t$  with  $x_3 = (1 + \alpha)/(2K + 1 + \alpha)$  and  $x_2 = 1 - x_1 - x_3$ . Furthermore, for convenience in the mathematical analysis, we also assume that there is a very small mutation rate between species 1 and species 2, denoted by  $\mu$  (with  $\mu \rightarrow 0$  but  $\mu \neq 0$  at any time  $t$ ). Then, as shown in the Appendix, the stationary distribution  $\phi(x_1)$  can be approximated as

$$\phi(x_1) = \mathcal{N}e^{-U(x_1)}, \quad (5)$$

where the potential is given by

$$U(x_1) = \ln \left[ \frac{x_3}{2} (T_1^+ T_2^- + T_1^- T_2^+) \right] - \frac{2}{x_3} \int^{x_1} \frac{T_1^+ T_2^- - T_1^- T_2^+}{T_1^+ T_2^- + T_1^- T_2^+} ds, \quad (6)$$



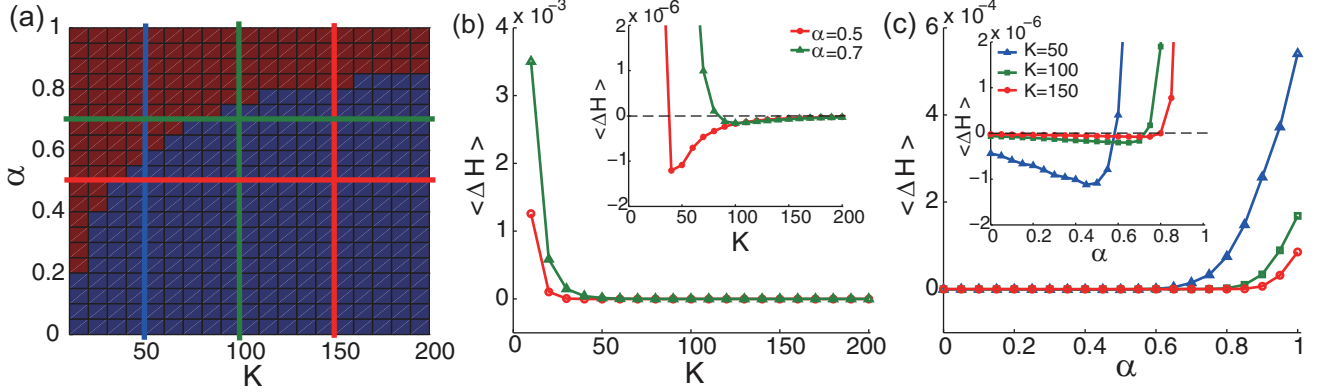


FIG. 3. The limiting similarity of competing species based on the sign change of  $\langle \Delta H(\mathbf{x}) \rangle$ . (a) The threshold characteristics of  $\langle \Delta H(\mathbf{x}) \rangle$  are shown in the  $K$ - $\alpha$  plane, where the color red (upper) denotes  $\langle \Delta H(\mathbf{x}) \rangle > 0$ , and the color blue (lower) denotes  $\langle \Delta H(\mathbf{x}) \rangle < 0$ . (b) For given  $\alpha$ , there is a threshold of  $K$  such that  $\langle \Delta H(\mathbf{x}) \rangle = 0$ . This shows how system stability is influenced by the environmental carrying capacity. (c) On the other hand, for a given  $K$ , there is also a threshold of  $\alpha$  such that  $\langle \Delta H(\mathbf{x}) \rangle = 0$ . This threshold can be considered to be the limiting similarity of competitive species for a given environmental carrying capacity.

and the normalization constant  $\mathcal{N}$  is given by  $\mathcal{N} = [\int_0^{1-x_3} e^{-U(x_1)} dx_1]^{-1}$ . Thus, for all possible  $x_1$ , the expectation of  $\Delta H(\mathbf{x})$  with respect to the stationary distribution  $\phi(x_1)$ , denoted by  $\langle \Delta H(\mathbf{x}) \rangle$ , is given by

$$\langle \Delta H(\mathbf{x}) \rangle = \int_0^{1-x_3} \Delta H(\mathbf{x}) \phi(x_1) dx_1. \quad (7)$$

Here we can take  $\langle \Delta H(\mathbf{x}) \rangle$  as a measure of system stability under demographic stochasticity, reflecting how deterministic interspecific interactions resist the effect of demographic stochasticity on the coexistence of competitive species. This means that the system can be considered to be stable (or unstable) under the demographic stochasticity if  $\langle \Delta H(\mathbf{x}) \rangle < 0$  (or  $\langle \Delta H(\mathbf{x}) \rangle > 0$ ). That is, for a given environmental carrying capacity  $K$ ,  $\langle \Delta H(\mathbf{x}) \rangle$  can be used to identify a measurable limiting similarity of competitive species, denoted by  $\tilde{\alpha}$ , such that  $\langle \Delta H(\mathbf{x}) \rangle = 0$  when  $\alpha$  exactly equals  $\tilde{\alpha}$ , and  $\langle \Delta H(\mathbf{x}) \rangle < 0$  (or  $\langle \Delta H(\mathbf{x}) \rangle > 0$ ) if  $\alpha$  is smaller (or larger) than  $\tilde{\alpha}$ . On the other hand, according to May's definition [1,2], the limit of  $d$  corresponding to  $\tilde{\alpha}$  can be expressed as  $\tilde{d} = 2\omega\sqrt{-\ln \tilde{\alpha}}$  since  $\alpha = \exp(-d^2/4\omega^2)$ . This also provides a very important theoretical intuition for why the number of competitive species that can coexist stably in a given environment must be limited.

It should also be noted that a previous study [11], which investigated the stability of a rock-scissors-paper game dynamics in a finite population, uses the average of  $\Delta H(\mathbf{x})$  for all possible  $\mathbf{x}$  to measure the influence of demographic stochasticity on the system stability. However, for our model, we can see that the stationary distribution  $\phi(x_1)$  depends on the system state or on the deterministic interspecific interaction [see Eqs. (5) and (6)]. Thus, the expectation  $\langle \Delta H(\mathbf{x}) \rangle$  based on the stationary distribution  $\phi(x_1)$  should be considered to be a more reasonable measure for revealing how the demographic stochasticity acts on the system stability.

The numerical results of Eq. (7) reveal the threshold characteristics of  $\langle \Delta H(\mathbf{x}) \rangle$  on the  $K$ - $\alpha$  plane [Fig. 3(a)]. Specifically, for any given  $K$ , there must exist a threshold value of  $\alpha$ , denoted by  $\tilde{\alpha}$ , such that  $\langle \Delta H(\mathbf{x}) \rangle > 0$  (or  $< 0$ ) if  $\alpha > \tilde{\alpha}$  (or  $\alpha < \tilde{\alpha}$ ), and the threshold value  $\tilde{\alpha}$  increases with

the increase of  $K$ ; and, similarly, for any given  $\alpha$ , there also must exist a threshold value of  $K$ , denoted by  $\tilde{K}$ , such that  $\langle \Delta H(\mathbf{x}) \rangle > 0$  (or  $< 0$ ) if  $K < \tilde{K}$  (or  $K > \tilde{K}$ ), and  $\tilde{K}$  will increase with the increase of  $\alpha$ . For example, for a given  $\alpha$  (or  $K$ ),  $\langle \Delta H(\mathbf{x}) \rangle$  will decrease (or increase) with the increase of  $K$  (or  $\alpha$ ) [Figs. 3(b) and 3(c)]. These results not only accord well with the results of stochastic simulations [see Fig. 1(d)] but also profoundly reveal why very similar competitive species can coexist stably in an environment with large  $K$  and why a big difference between competitive species is needed for the long-term coexistence in an environment with a small  $K$ . Thus, for long-term stable coexistence of competitive species under May's theoretical framework [2], the limiting similarity of competitive species should strongly depend on the environmental productivity levels.

### III. DISCUSSION

In ecology, a fundamental question is what determines how many species are to be found in a given place. For example, May *et al.* [6] asked why we find roughly 700 species of breeding birds in North America, rather than 7 or 70 000. Similarly, MacArthur [18] asked why five species of warblers coexist in trees in Vermont. Why not more or fewer similar species? Our theoretical analysis implies that very similar competing species are able to coexist for a long time in an environment with a relatively high productivity level (e.g., limestone, grasslands, tropical forests, and coral reefs [19]) but that big differences between competing species are necessary in an ecosystem with a relatively low productivity level (e.g., boreal forests, bogs, and heathland [19]). Thus, the concept of limiting the similarity of competing species based on the sign change of  $\langle H(\mathbf{x}) \rangle$  may provide a fundamental insight to understand in general why species abundance is proportional to the productivity level of an ecosystem [20].

On the other hand, our results also mean that the characteristic distribution of species abundance in an ecosystem with large total system size could be approximated well by Hubbell's neutral theory [8,9,21]. Specifically, when many species coexist in an ecosystem with a large total system size,

demographic stochasticity has a much more significant effect on the coexistence of competing species with high species similarity. This may be why neutral theory can correctly characterize the distribution of species abundance in tropical rain forests [8,9,21].

Finally, we would like to say that although the concept of the limiting similarity of competitive species has been discussed by many authors since 1970s [7], our study based only on May's [1,2] simple model system mainly focuses on how the coexistence stability of competitive species is influenced by the demographic stochasticity. Our theoretical results also strongly imply that the loss of coexistence stability of a competitive system is largely due to the decline in the environmental productivity level, or when the level of environmental productivity drops to a certain degree, the original coexistence relationship of competitive species will be unable to resist the disturbance of demographic stochasticity.

Of course, the stability of a real competitive system will be affected by many factors, but, in all of these effects, the relationship between competitive species similarity and demographic stochasticity should be the most fundamental.

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**APPENDIX**

**1. The interior equilibrium of Eq. (2),  $\mathbf{x}^*$ , is an ESS**

For Eq. (2),  $\mathbf{x}^*$  corresponds to a minimum of

$$F(x_1, x_2) = \mathbf{x}^* \cdot \mathbf{Ax} - \mathbf{x} \cdot \mathbf{Ax} = \frac{r}{K}(x_1^* - x_1)(Kx_3 - x_1 - \alpha x_2) + \frac{r}{K}(x_2^* - x_2)(Kx_3 - \alpha x_1 - x_2),$$

if  $\alpha < 1$  since

$$\left. \frac{\partial F(x_1, x_2)}{\partial x_1} \right|_{(x_1^*, x_2^*)} = \left. \frac{\partial F(x_1, x_2)}{\partial x_2} \right|_{(x_1^*, x_2^*)} = 0, \quad \frac{\partial^2 F(x_1, x_2)}{\partial x_1^2} = \frac{\partial^2 F(x_1, x_2)}{\partial x_2^2} = \frac{2r}{K}(K + 1), \quad \frac{\partial^2 F(x_1, x_2)}{\partial x_1 \partial x_2} = \frac{2r}{K}(K + \alpha),$$

and

$$\left[ \frac{\partial^2 F(x_1, x_2)}{\partial x_1 \partial x_2} \right]^2 - \frac{\partial^2 F(x_1, x_2)}{\partial x_1^2} \frac{\partial^2 F(x_1, x_2)}{\partial x_2^2} < 0.$$

Thus  $\mathbf{x} \cdot \mathbf{Ax}^* = \mathbf{x}^* \cdot \mathbf{Ax}^*$  and  $\mathbf{x}^* \cdot \mathbf{Ax} > \mathbf{x} \cdot \mathbf{Ax}$  for all possible  $\mathbf{x}$  with  $\mathbf{x} \neq \mathbf{x}^*$  [22]. Thus,  $\mathbf{x}^*$  is an ESS [17,22].

**2. The derivation of Eq. (5)**

Let  $\pi^\pm(x_1)$  denote the transition probabilities from  $x_1$  to  $x_1 \pm x_3$ . Since we assume that the mutation rate  $\mu$  is small enough,  $\pi^\pm(x_1)$  can be approximated as  $\pi^\pm(x_1) \approx T_1^\pm T_2^\mp$ . When the time step is taken as  $x_3$ , then

$$\begin{aligned} \phi(x_1; t + x_3) - \phi(x_1; t) &= \phi(x_1 - x_3; t)\pi^+(x_1 - x_3) + \phi(x_1 + x_3; t)\pi^-(x_1 + x_3) \\ &\quad - \phi(x_1; t)\pi^-(x_1) - \phi(x_1; t)\pi^+(x_1). \end{aligned}$$

[23]. From the Taylor expansions of  $\phi(x_1; t + x_3)$ ,  $\phi(x_1 \pm x_3; t)$ , and  $\pi^\pm(x_1 \mp x_3)$  about  $t$  and  $x_1$ , the Fokker-Planck

equation of  $\phi(x_1; t)$  is given by

$$\frac{\partial \phi(x_1; t)}{\partial t} = -\frac{\partial}{\partial x_1} D^{(1)}(x_1)\phi(x_1; t) + \frac{\partial^2}{\partial x_1^2} D^{(2)}(x_1)\phi(x_1; t),$$

where

$$\begin{aligned} D^{(1)}(x_1) &= \pi^+(x_1) - \pi^-(x_1), \\ D^{(2)}(x_1) &= \frac{x_3}{2}[\pi^+(x_1) + \pi^-(x_1)]. \end{aligned}$$

The stationary distribution is then

$$\phi(x_1) = \mathcal{N}e^{-U(x_1)},$$

where

$$U(x_1) = \ln D^{(2)}(x_1) - \int^{x_1} \frac{D^{(1)}(s)}{D^{(2)}(s)} ds,$$

and the normalization constant  $\mathcal{N}$  is given by  $\mathcal{N} = [\int_0^{1-x_3} e^{-U(x_1)} dx_1]^{-1}$ .

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