Towards a less spherical cow: Species differences dilute the stabilizing effect of higher-order interactions

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(Dated: October 7, 2025)

Ecological models traditionally explain stability and coexistence through pairwise interactions among species. These interactions can also involve groups of three or more species—higher-order interactions—which recent theory suggests can by themselves stabilize communities. However, ecological communities exhibit both pairwise and higher-order interactions, and how their interplay governs stability and coexistence remains unknown. This work addresses this gap by analyzing a model of competitive communities that incorporates a proportion of pairwise and higher-order interactions. Using empirical data, numerical simulations, and analytical methods, we show that higher-order interactions alone cannot guarantee coexistence. We find that, while a small fraction of higher-order interactions can stabilize dynamics in communities of identical species, this effect disappears under more realistic conditions—such as heterogeneity in birth and death rates, empirically derived rates, or explicit interaction structures. Our results challenge the prevailing view of higher-order interactions as a universal stabilizing mechanism, providing quantitative evidence of the joint importance of both pairwise and higher-order interactions, together with network structure and species parameters, for understanding ecological stability.

INTRODUCTION

The question of how different species coexist has captivated researchers beyond ecology, including disciplines like statistical physics and mathematics. The challenge mainly arises from the competitive exclusion principle, which asserts that inferior competitor species should eventually be driven to extinction by better-adapted counterparts. Among other coexistence mechanisms, intransitive competition has garnered attention as a potential bypass of exclusion [1]. Intransitive competition establishes no hierarchy among species, such as in a "rock-paper-scissors" tournament, where species i outcompetes species j, j outcompetes species k, and in turn, k outcompetes i. In intransitive communities, coexistence is reached because species abundances tend to cycle, preventing one species from taking over the whole population. From the theoretical side, models implementing intransitive dominance result in abundances neutrally cycling around an equilibrium point [2]; or asymptotic solutions in which the system cycles from being composed almost entirely of one species to almost wholly by another and so for [3], something that is unlikely to occur in nature. In addition, the presence of large oscillations may turn against coexistence since species could become extinct by external perturbations or stochastic events. Moreover, the number of systems that rely completely on intransitive competition as the *main* mechanism for promoting coexistence is still scarce [1, 4]. Some classic examples of intransitivity in natural systems are the side-blotched lizards [5], and *E. coli* [6], where three strains regulate a toxin's resistance, sensitivity, and production. More recent works include the study of sessile organisms like trees [7] and fungi [8].

Recent theoretical studies aim to (1) overcome the large oscillations by finding conditions for stable coexistence [9] (stability *sensu* May [10]) and (2) explain when intransitivity could be found in nature as a coexistence mechanism [7, 11]. Their approach is to combine intransitivity with auxiliary mechanisms, such as mobility [12], local and structured interactions [13], or higher-order interactions [9]. Structured interactions explicitly consider space, which has an important impact on coexistence [14–16]. The spatial arrangement of individuals can significantly affect the magnitude of their mutual influences, and hence the resulting dynamics [17]. In the case of intransitive competitive interactions, the system stabilizes when the individuals of competing species are embedded in space and can only interact with other individuals within a short distance [13]. On the contrary, large oscillations emerge when these interactions are neither spatially structured nor local.

Stable coexistence has also been achieved in mathematical models where the interactions are higher-order under certain conditions [2]. Higher-order interactions (HOIs) emerge when the presence of a third species influences the interaction between two other species. They attracted much attention in ecological research several decades ago, in part because their nonlinearity promised greater realism than the classic Lotka–Volterra equations [18, 19]. After their popularity waned amid debates over their definition [20, 21] and detection [22, 23], HOIs are enjoying a revival [24, 25], even if previous quarrels remain [26, 27]. New theoretical models now aim to clarify whether and how HOIs influence the coexistence and stability of ecological communities [28]. In particular, for intransitive competition, a model with *only* HOIs stabilizes the dynamics for species with *equal* or very similar physiological rates [9].

However, competition models have predominantly focused on either pairwise interactions or HOIs separately, within ei-

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ther structured or unstructured communities. In reality, those approaches—pairwise or higher-order interactions in isolation, and equivalent species in terms of physiological rates—are too far from natural scenarios. As one would expect to encounter a combination of various types of interactions in environments that vary in complexity [29, 30], the logical next step would be to explore the stability conditions with both orders of interactions simultaneously.

Here, we go one step further in complexity by investigating whether stable coexistence can be achieved in communities with a combination of both pairwise *and* higher-order interactions, even when these are unstructured, with empirical physiological rates. On the one hand, we test the influence of HOIs by varying their proportion in situations where pairwise competition alone cannot stabilize the system. Then, we explore how heterogeneity in physiological rates and the structure of competitive interactions change the dynamics. We use a compilation of empirical birth and mortality rates of more than 500 plant species to do so (Methods). We find that stable coexistence is reached with a small critical proportion of HOIs, which strongly increases with the species differences in physiological rates. A critical proportion of HOIs is also needed for stability when considering interaction networks. In that case, the coexistence can be explained by the distribution of hyperlinks formed by an increasing proportion of HOIs.

We explore the consequences of combining interaction orders with analytical derivations, numerical integration, and Monte Carlo simulations of empirical data. As a starting point, we study a competition model with both pairwise and higher-order interactions involving three species. We then allow species to differentiate not only on their competition skills but also on their physiological rates. Finally, we abandon the well-mixed scenario and define an interaction network, whose nodes are single individuals of different species (Methods). They are connected by links and hyperlinks, representing pairwise and higher-order interactions [31]. Both orders of links are randomly drawn, mimicking unstructured interactions, to test the impact of HOIs without the stabilizing effect of pairwise structured interactions [13]. Our results present a set of conditions in the structure and order of interactions, and on physiological rates that natural communities need to fulfill to have stable coexistence under intransitive competition.

RESULTS

We consider an isolated competitive g-species community and model the effect of combining pairwise and higher-order interactions in two scenarios, growing in complexity. Firstly, the coexistence and stability of our community are studied with the machinery developed for non-linear dynamical systems. In particular, this means we take a well-mixed approach and describe the evolution of species densities with ODEs. Secondly, we place the individuals in a network, whose links determine who competes with whom and the nature of the interaction, pairwise or higher-order.

Competitive community model with higher-order interactions

To focus on the interplay between pairwise and higher-order interactions (HOIs), we keep the number of processes to a minimum. Each species i has two physiological rates, specifically birth f_i and mortality d_i rates, and competes with the other species. The evolution of species density x_i can be described by replicator dynamics, in the pairwise case, as in [9]:

$$\begin{aligned}\frac{dx_i}{dt} &= \sum_{j=1}^{g} (W_{ij} - W_{ji}) \\ &= x_i \left(\frac{D(x)}{F(x)^2} f_i \sum_j 2H_{ij} f_j x_j - d_i \right),\end{aligned} \tag{1}$$

where W_{ij} is the rate at which individuals of species i replace individuals of species j by means of direct pairwise competition. The equations can be expressed in terms of physiological rates and the dominance matrix H, which encodes competitive interactions. In particular, H_{ij} is the probability species i outcompetes species j, so that $H_{ii} = 0.5$ and $H_{ij} + H_{ji} = 1$. Introducing a probabilistic dominance matrix in this and the subsequent equations allows us to go beyond neutral competition ($H_{ij} = 0.5\,\forall i, j$) and complete ($H_{ij} = 1, H_{j,i} = 0\,\forall i, j$) dominance between species [9]. The developing probability of offspring of species i is $f_i x_i / F(x)$, given that $F(x) = \sum_i f_i x_i$, and $d_i x_i / D(x)$ is the dying probability of an individual belonging to species i, where $D(x) = \sum_i d_i x_i$. Varying these physiological rates also allows us to break neutrality in the classic sense of species with equal probabilities of reproduction and death [32].

Conversely, one could also express the dynamics of a system of *only* higher-order interactions. If we limit ourselves to *triplewise* interactions, i.e. involving 3 competitors, the equations are

$$\frac{dx_i}{dt} = x_i \left(\frac{D(x)}{F(x)^3} f_i \sum_{j,k} B_{ijk} f_j x_j f_k x_k - d_i \right), \tag{2}$$

in which B is a tensor (in the sense of a multidimensional array) whose elements B_{ijk} represent the probability of species i simultaneously winning both species j and k, and hence $B_{ijk} = B_{ikj}$.

Since one would expect the presence of both pairwise and higher-order interactions in a natural community [29], we set a parameter α to define the proportion or intensity of HOIs. The equations of such a system become

$$\begin{aligned}\frac{dx_i}{dt} = (1-\alpha) &\left[x_i \left(\frac{D(x)}{F(x)^2} f_i \sum_j 2H_{ij} f_j x_j - d_i \right) \right] \\ + \alpha &\left[x_i \left(\frac{D(x)}{F(x)^3} f_i \sum_{j,k} B_{ijk} f_j x_j f_k x_k - d_i \right) \right].\end{aligned} \tag{3}$$

If $\alpha = 0$, we recover the pairwise scenario. By increasing α, we can intensify the importance of higher-order interactions in density evolution.

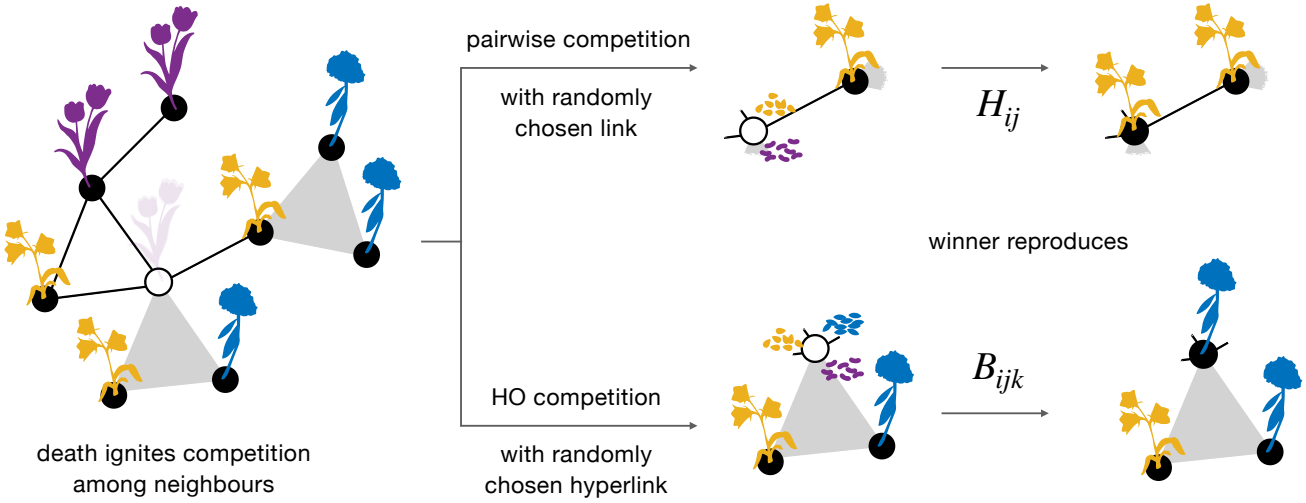

FIG. 1. **Illustration of the competitive dynamics**. When a random plant dies, it leaves a vacant fertile region. The neighbors connected to the empty node by one of its links compete to establish offspring there. Depending on the nature of the link, competition is pairwise or higher-order, and the winner plant is chosen according to the probabilities of the species dominance matrix H, or tensor B, respectively.

The dynamical behavior of pairwise and higher-order interactions considered separately (Eqs(1) and (2)) is very different. Previous results show that the system neutrally oscillates in the pairwise case if the dominance matrix has intransitive cycles ($H_{ij} > H_{jk} > H_{ki} > 0.5$)[6, 33]. Instead, HOIs (Eq (2)) stabilise the community –in the sense that it converges to a stable fixed point– when they also form intransitive cycles so that $B_{ijk} = 2H_{ij}H_{ik} + H_{ij}H_{jk} + H_{ik}H_{kj}$ encodes all possible pairwise combinations and when the physiological rates are equal or very similar [9]. For the complete case of Eq. (3), we varied α to quantify how introducing HOIs influences species coexistence and stability.

Building upon the illustration of sessile organisms –e.g. flowering plants competing for space– with every iteration of our model, a plant dies, creating an opening. One link to the new vacant region is selected at random, and the plants that belong to that link compete to disperse their seedling there (Fig. 1). Depending on the link order, the winner is determined either by the $g \times g$ dominance matrix H for pairwise interactions or by the $g \times g \times g$ dominance tensor B in the case of HOIs (Methods).

Once presented our model, we explore our research questions by first analyzing the temporal evolution of species' densities in the situation of three competing species, $g = 3$. Without loss of generality, we use the dominance matrix as defined in [13]

$$H = \begin{pmatrix} 0.5 & 0.34 & 0.76 \\ 0.66 & 0.5 & 0.25 \\ 0.24 & 0.75 & 0.5 \end{pmatrix}, \tag{4}$$

defining $B_{ijk} = 2H_{ij}H_{ik} + H_{ij}H_{jk} + H_{ik}H_{kj}$ and track the proportion of individuals of each species in the system, $x_i(t)$, where $\sum x_i(t) = 1$ at every t. To characterize the behavior during Monte Carlo simulations, we do not consider directly the amplitude of the oscillations in x_i since they could be misleading due to the stochastic nature of the simulations. Instead, we take advantage of the fact that species densities can be interpreted as a point tracing a trajectory within a $g-1$ simplex covering the space of possible ecological states, where each vertex corresponds to a single-species population. As time evolves, the area encircled by the densities' trajectories on the simplex characterizes the macroscopic state of the system [13]. We then remove the most outlier points encircled in the simplex associated with stochasticity. The trajectory occupies a small area when the system fluctuates with low amplitude around a certain point. In contrast, larger oscillations cover a wider area in the simplex.

For well-mixed systems with equal physiological rates, any proportion of HOIs is sufficient for stability

We begin our analysis on how the proportion of higher-order interactions α influences species coexistence and stability by studying the particular case of equal physiological rates ($d_i = f_i = 1\ \forall i$), for which Eq. (3) becomes

$$\begin{aligned} \frac{dx_i}{dt} = (1-\alpha)\left(-x_i + 2\sum_j H_{ij}x_i x_j \right) \\ +\alpha\left(-x_i + \sum_{j,k} B_{ijk}x_i x_j x_k \right). \end{aligned} \tag{5}$$

The equilibrium of Eq. (1) ($2\sum_j H_{ij}x_j^* = 1$) is also an equilibrium of the previous equation and can be used to determine whether the system stands up to disturbances and coexist. To do so, we use the Lyapunov function $V(x)$ as defined in [9],

$$V(x) = -\sum_i x_i^* \log \frac{x_i}{x_i^*}, \tag{6}$$

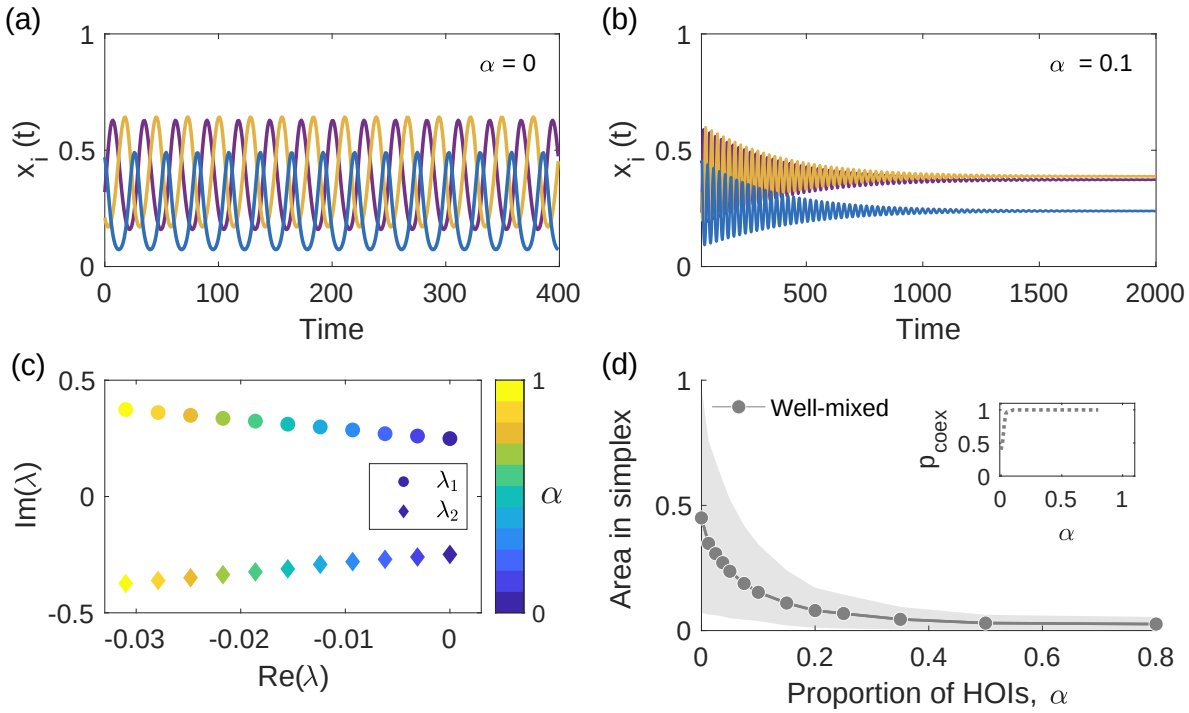

FIG. 2. **Any proportion of higher-order interactions stabilizes the dynamics in well-mixed competitive systems with equal physiological rates.** Numerical integration of the dynamics from the set of ODEs, Eq. (5), for (a) $\alpha = 0$ (no HOIs) and (b) $\alpha = 0.1$. (c) Eigenvalues for different proportions of HOIs (dots color) at the fixed point. For $\alpha > 0$, the pair of complex conjugate eigenvalues cross into the left half-plane, guaranteeing that the fixed point is stable. (d) Average area on the simplex of our 3-species system as a function of different values of α. The areas are calculated over 50 Monte Carlo simulations. Shades indicate the standard deviation. The inset is the probability of coexistence p_{coex} over 100 simulations since the noisy nature of the simulations may lead to extinctions when the oscillations are wide enough. To measure the area in the simplex, we only consider the dynamics of those systems in which all species coexist.

since fortunately, it is still a Lyapunov function for Eq. (3). Deriving Eq. (6) and assuming the feasibility of the equilibrium ($x_i^* > 0,\ \forall i$ [34]), we obtain

$$\begin{aligned}\frac{dV}{dt} &= \sum_i \frac{\partial V}{\partial x_i}\frac{\mathrm{d}x_i}{\mathrm{d}t} = -\sum_i \frac{x_i^*}{x_i}\frac{\mathrm{d}x_i}{\mathrm{d}t} \\ &= \alpha\left[-2\sum_i x_i^*\left(\sum_j H_{ij}\xi_j\right)^2\right],\end{aligned} \tag{7}$$

where we have introduced $\xi_j := x_j - x_j^*$. For $\alpha = 0$, we recover the case of only pairwise interactions, where $dV/dt = 0$ meaning the system follows neutral cycles around the equilibrium (Fig. 2a) [9]. When $\alpha > 0$, we always get $dV/dt \leq 0$, which implies $\vec{x}^*$ is a globally stable fixed point (Fig. 2b). Thus, there is a transition between these two regimes at $\alpha_c = 0$, where neutral-cycle oscillations give way to a stable fixed point. The eigenvalues of the Jacobian matrix at the equilibrium characterize this transition as a Hopf Bifurcation (Fig. 2c).

To corroborate these analytical predictions, we run Monte Carlo simulations of our system with well-mixed population of $g = 3$ species and random initial conditions. During the simulations, extinctions can easily occur for $\alpha = 0$ due to stochastic fluctuations (see inset in Fig. 2d). When $\alpha > 0$, the system stabilizes around the predicted equilibrium, which agrees with our theoretical derivations. In the simulations, the transition between these two regimes occurs smoothly as α increases. Nevertheless, the area covered by the trajectory decreases, and by $\alpha = 0.1$, the system could be considered to have reached a fixed point (Fig. 2d). Hence, we do not need to lose pairwise interactions altogether to stabilize the dynamics: a small proportion of higher-order interactions is enough to obtain the same effect.

Stability depends on the variability of physiological rates

So far we have only considered species with equal birth and mortality rates, and thus they only differ in their competitive abilities (encoded in H). To further explore the consequences of adding HOIs, we go beyond this assumption by studying the more realistic scenario of Eq. (3) with different physiological rates. Now, the equilibrium varies with the proportion of

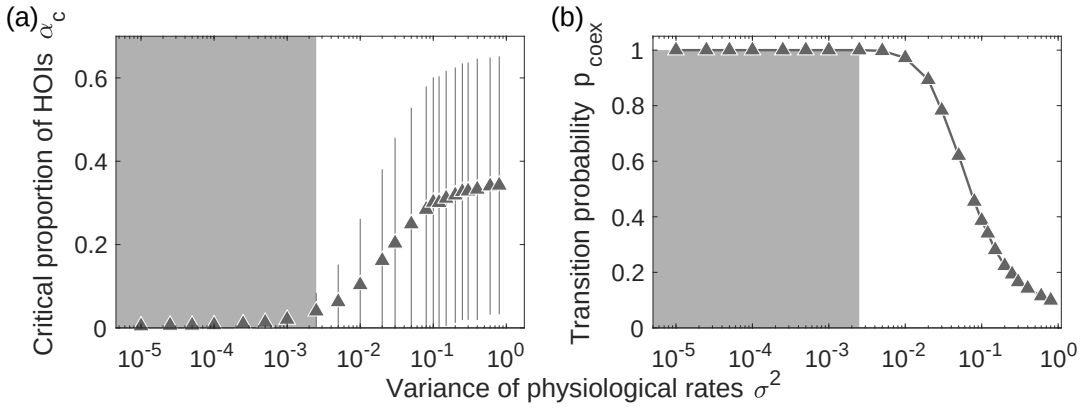

FIG. 3. **As the difference between physiological rates increases, a greater proportion of higher-order interactions is needed to stabilize the dynamics.** Numerical integration of Eq. (3) with normally-sampled physiological rates. (a) Critical higher-order interactions proportion α_c as a function of variance σ^2, averaged over 10^4 simulations with the same dominance matrix H. (b) Probability of the existence of a transition towards a fixed point p_{coex} as a function of variance σ^2 over 10^4 simulations. The shaded regions indicate the area where species always coexisted in our simulations.

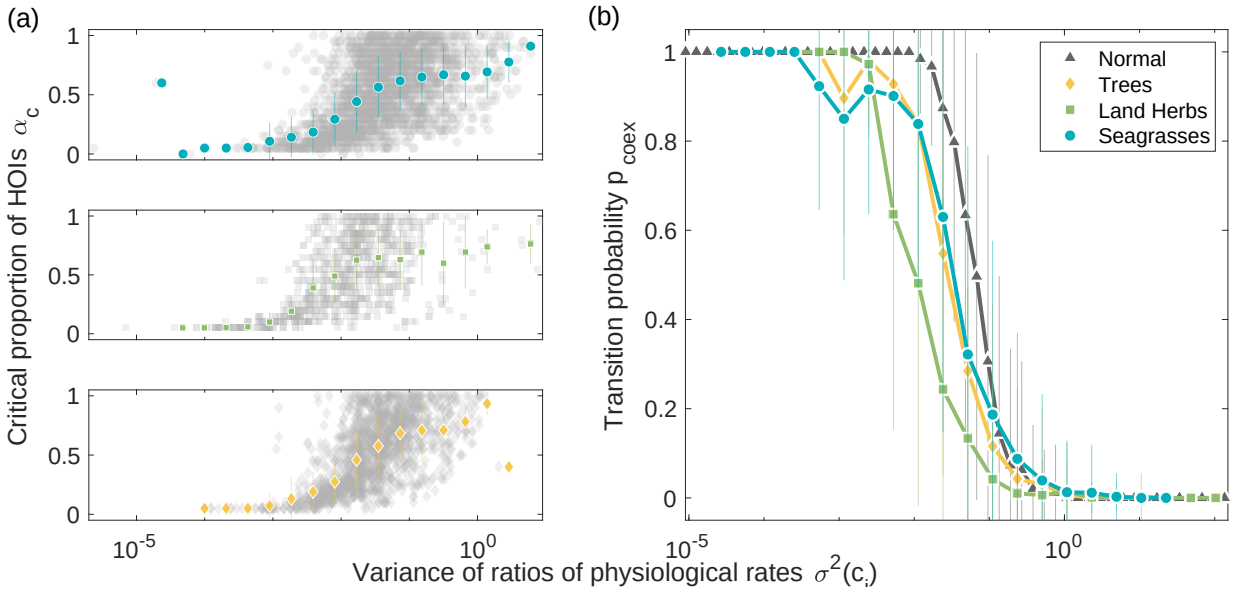

FIG. 4. **Critical proportion of HOIs for physiological rates for different plant species.** (a) Numerical integration of Eq. (3) with empirical physiological rates extracted from [35] for different categories of plants, showing the critical higher-order interactions proportion α_c as a function of the variance of the proportionality among physiological rates $\sigma^2(c_i)$ for 15000 triples of different species with the same dominance matrix H. (b) Probability of the existence of a transition towards a fixed point p_{coex}. For comparison, the probability for the case of normally distributed physiological rates is also plotted, but note that the x-axis differs from that of Fig. 3.

HOIs in the system, α. If we define

$$T_1(\vec{x}) := \frac{D}{F^2}\sum_j 2f_i f_j H_{ij} x_j \quad \text{and}$$
$$T_2(\vec{x}) := \frac{D}{F^3} f_i \sum_j \sum_k 2f_j f_k (H_{ij}H_{jk} + H_{ij}H_{ik}) x_j x_k, \tag{8}$$

(where we have dropped the arguments of $D(x)$ and $F(x)$ for readability) then, the equilibrium must fulfill the expression

$$T_1^*(1-\alpha) = d_i - \alpha\, T_2^*, \tag{9}$$

where and $T^* := T(\vec{x}^*)$. Assuming that $\vec{x}^*$ exists and is feasible, we can define another Lyapunov function $V(x)$ as:

$$\frac{dV}{dt} = -\sum_i \frac{x_i^*}{x_i}\dot{x} \tag{10}$$

and, substituting the equilibrium condition, we have:

$$\frac{dV}{dt} = \frac{1}{F^2 D^*}\left(F^* D - F D^*\right)^2 + \alpha\left[2D\frac{F^*}{F} - \sum_i x_i^* T_2 - \frac{F^{*2}}{F^2}\frac{D}{D^*}\sum_i x_i T_2^*\right] \quad (11)$$

(see Methods section for the full calculation). If the dynamics eventually stabilizes, this derivative must be zero at some point. After some calculations, we find that this transition takes place at

$$\alpha_c = \frac{-\frac{1}{F^2 D^*}\left(F^* D - F D^*\right)^2}{2D\frac{F^*}{F} - \sum_i x_i^* T_2 - \frac{F^{*2}}{F^2}\frac{D}{D^*}\sum_i x_i T_2^*}. \quad (12)$$

We can observe that the dividend part is zero when mortality rates are proportional to birth rates by a constant value for all species, i.e. $f_i = c d_i \ \forall i$. The dividend is always negative otherwise. The divisor can be either positive or negative, depending on the specific values of the physiological rates. Thus, the transition to stability will no longer be at $\alpha_c = 0$. In general, we need to have a non-negligible proportion of HOIs to stabilize the community.

To gain further insights on the behavior of Eq. (12), we decide to study its behavior when physiological rates become increasing different. To do so, we sample birth and death rates from two normal distributions, namely $\mathcal{N}(\mu_b, \sigma_b^2)$ and $\mathcal{N}(\mu_d, \sigma_d^2)$. This way we can study how the heterogeneity of f_i and d_i affects α_c. Inspecting the numerator in Eq. (12), we see that the expected value of α_c will depend on the difference of the means of each distribution. When $\mu_b = \mu_d = 1$, α_c is predicted to be zero, but it can deviate significantly due to finite sample size for large variances—a proxy of heterogeneity. We explore this situation by simulating communities with increasing values of α for species whose physiological rates are drawn from normal distributions with $\mu_b = \mu_d = 1$ and varying $\sigma_b^2 = \sigma_d^2 \equiv \sigma^2$. We then record the value of α_c at which the transition occurs.

Fig. 3a shows that as the variance of physiological rates becomes larger, α_c increases too, and reaches values close to 0.5 on average. In addition, the proportion of HOIs needed to stabilize the dynamics becomes increasingly variable as differences in physiological rates do, hindering the prediction of the stability of communities comprising species with different rates. Interestingly, another consequence of this result is that there are situations where there is no transition for any value of α—i.e., no fraction of HOIs would be enough to stabilize the dynamics. That occurs above a critical value for the variance (outside of the grey shaded region in Figures 3a and 3b), where the probability of finding a value of α that stabilizes the dynamics $\mathrm{p_{coex}}$ decreases abruptly (Fig. 3b). Hence, coexistence is unlikely when birth and death rates are too different within and between species.

Empirical physiological rates

So far, the physiological rates we considered were based on synthetic data. However, a natural question arises: what will happen in a more realistic setting where physiological rates are based on empirical values found in real-world communities? To answer this question, we now sample the physiological rates from data from an empirical study investigating allometric scaling in plants [35]. Being more specific, we consider data from three different plant types: *Trees*, *Land and salt marsh herbs* and *seagrasses* accounting respectively for 230, 190 and 151 species yielding birth and death rates, which span 6 orders of magnitude. For each type, we sample $g = 3$ different species at time with their respective birth f_i and death d_i rates. We then use Eq. 12 to find the critical value of α at which the transition to stability takes place, if present. Finally, in order to quantify the heterogeneity between the rates, we calculate the variance $\sigma^2(c_i)$ of their ratio ($c_i = f_i/d_i$) among the sampled species.

Our findings show that, as for the case of synthetic rates, when the variance of the ratios of physiological rates becomes larger $\sigma^2(c_i)$, α_c increases too (Fig. 4a). In addition, the proportion of HOIs needed to stabilize the dynamics also becomes increasingly variable, hindering the prediction of the stability of communities. Regarding the probability of transition towards stable coexistence $\mathrm{p_{coex}}$, we observe that it decays for empirical values even earlier than for synthetic rates (Fig. 4b).

Interaction networks

So far, we focused our analysis on the case of well-mixed populations. However, assuming that each individual interacts with the entire population could be unfeasible in most scenarios. To overcome this limitation, in this section we study our competitive community model on random networks with HOIs.

To do that, we are forced to abandon the analytical description of Eq. 3 and rely on mechanistic simulations on random Erdös-Rényi (ER) graphs with a fixed density and an increasing fraction of HOIs, α. In particular, we create ER networks with a fixed average forgetful degree $\langle \tilde{k} \rangle = 20$ – i.e. the sum of a node's connections weighted by their order– with increasing values of α. With $\alpha = 0$ the network is only composed of pairwise links while larger values of α mean that pairwise connections are replaced by higher-order ones retaining $\langle \tilde{k} \rangle$ constant (see the Methods section for details). Moreover, with the aim of testing if HOIs are a plausible mechanism for communities stability, we impose again the simple setting of identical physiological rates.

Fig. 5a shows system's stability against the proportion of HOIs. What is surprising is that for $\alpha < 0.2$ HOIs are not capable of stabilizing the dynamics, when for well-mixed populations we have $\alpha_c = 0$. For $\alpha \simeq 0.2$ instead, a sharp transition occurs with the system immediately reaching stability. The same happens for probability of coexistence (inset of Fig. 5a), reaching one as α approaches 0.2.

To understand the mechanisms behind this transition, we look at how the introduction of HOIs changes the large-scale organization of the network. Specifically, we look at how a giant component of composed only of hyperlinks $GC_\triangle$ appears

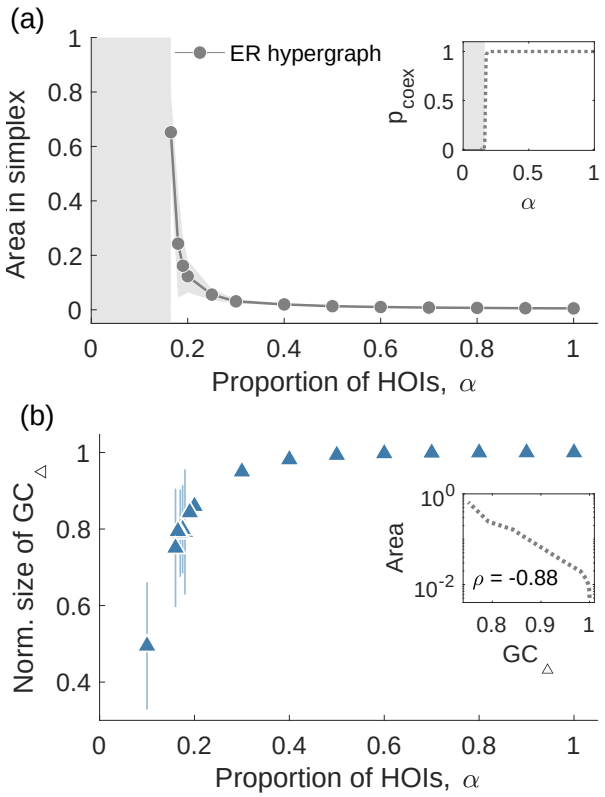

FIG. 5. **HOIs stabilize the dynamics of an unstructured system.** (a) Monte Carlo simulations on Erdős-Rényi (ER) hypergraphs show that the average area of the 3-species system decreases as a function of α. Shades indicate the standard deviation over 50 simulations with $N = 5 \cdot 10^4$ and average forgetful degree $\langle \tilde{k} \rangle = 20$. The inset is the probability of coexistence p_{coex} over 50 simulations. (b) The size of the normalized giant component of hyperlinks ($GC_\triangle$) increases with α in the same fashion as the area in the simplex decreases in the above figure. The dependence of the proportion of HOIs on $GC_\triangle$ tells us that the area is minimal when $GC_\triangle$ fills the whole network, as can be seen in the inset together with their Pearson correlation coefficient ρ.

as α increases. Interestingly, $GC_\triangle$ shows the same transition for $\alpha \simeq 0.2$ observed for the area of the simplex occupied by the system trajectory, reaching one around $\alpha \simeq 0.3$. At the same time, the inset of Fig. 5b shows that the area decreases as $GC_\triangle$ percolates, and reaches its minimum when the $GC_\triangle$ encompasses the whole network. Therefore, the system stabilizes when a giant component composed solely of hyperlinks appears –i.e. each node of the network is reached by, at least, one higher-order link.

Finally, these results reveal two complementary insights. First, in the more realistic scenario of interaction networks, stable coexistence can be achieved only when a quite large proportion of HOIs are present. Second, to be effective HOIs need a very specific structural arrangement involving a very large fraction of, if not all, the individuals in the community. These findings suggest that HOIs alone cannot be responsible for the coexistence in real communities. Our results also suggest that models focusing solely on one mechanism may miss crucial dynamics that can promote stability through the interplay of more complex interaction patterns.

DISCUSSION

Understanding the mechanisms that enable species coexistence within ecological communities is critical for biodiversity maintenance, ecosystem functioning, and conservation. Recent theoretical models suggest that HOIs create conditions for coexistence. This work was motivated by the need to clarify this claimed potential of higher-order interactions as stabilizing factors. Here, we demonstrate that the theoretical power of HOIs as a stabilizing mechanism weakens when parameters and models assumptions are constrained more realistically. Till now, theoretical results supporting these claims considered communities composed only by HOIs [9] or interactions drawn at random [36, 37]. Our results demonstrate that these results do not hold once you introduce more realistic interaction structures. For instance, if HOIs cluster in specific trophic motifs or their signs correlate with pairwise effects [28], or if species differ in their physiological rates as we modeled, the supposed stabilizing influence of HOIs vanishes. In other words, the stability in those models may be an artifact of simplifying assumptions.

In particular, we focus on the role of higher-order interactions in intransitive competitive communities. We have analyzed different proportions of pairwise and HOIs, and different values of physiological rates, ranging from equivalent to distinct species. Our results show that a critical proportion of HOIs can explain stability when the competitive community cannot be stable by pairwise interactions alone. However, this proportion α_c depends on the similarity of physiological rates among the species. When physiological rates become more dissimilar, the transition disappears.

We believe that our results redefine the stabilizing effect of HOIs. In fact, in most cases their effect is lost or demands additional conditions when we incorporate more ecological complexity, such as variation in physiological rates. In reality, species do differ in their birth and mortality rates, and this heterogeneity plays a significant role in community dynamics. This dependence on heterogeneity was something that models based on random interactions could not foresee. In such cases, HOIs guarantee coexistence, but only if pairwise interactions are weak or facilitative [25].

We also study the role of HOIs in a case where interactions take place on a network. By taking space into account explicitly, our findings reveal that stable coexistence can be reached only when HOIs span the entire network –i.e. a giant component of hyperlinks emerges. This result also suggests that models focusing solely on one mechanism may miss crucial dynamics that can promote stability through the interplay of more complex interaction patterns.

However, our study also has several limitations. First of all, our model is far from being realistic; missing several details of real ecological communities. However, the fact that HOIs not always stabilize the dynamics even in this simplified set-

ting suggests that their effect would be also negligible in more complex model. To isolate the effect of physiological rate heterogeneity, we used synthetic dominance matrices H as real interaction data are practically impossible to estimate. We also assumed that each sampled triplet could potentially coexist in nature, something at least unlikely. Although our species come from different geographic regions and may not naturally interact, we limited the simulations to plants within the same functional category. However, the trends observed in α_c suggest that physiological heterogeneity would likely yield similar results among spatially co-occurring species. Finally, we constructed the higher-order dominance tensor B by aggregating the pairwise outcomes in H (following [9]). However, this tournament-based method can overlook genuine three-species (or higher) effects that are not reducible to pairwise combinations. In principle, one could replace this tournament-derived method with a direct parametrization of higher-order effects without losing analytical traceability. However, obtaining empirical estimates for these modified interactions is currently challenging.

Along this line and building on the need for empirical studies of higher-order effects, [38] offers a compelling case that combines HOIs with network structure to predict species persistence. In their multitrophic experiments, they show that incorporating HOIs in the model description alters the strength and even reverses the sign of per-capita interactions among plants, leading to substantially different predictions of coexistence than non-HOIs models (in agreement with [39, 40]). Incidentally, these works also support that HOIs in a well-mixed model alone are insufficient: only when embedded within the pairwise interactions and spatial experiments do models achieve reliable predictions of each species' persistence probability. They thus emphasize our message that higher-order coefficients must go hand in hand with other coexistence mechanisms to faithfully predict coexistence.

In the spirit of these empirical works and limitations, our results thus suggest two next steps: first, quantifying how the values of the higher-order dominance tensor B are distributed in natural communities [27, 41] (whose theoretical predictions are suggested [28]), and second, testing whether HOIs spatially arrange according to the patterns found in our results.

While adding realism decreases the stabilizing effect, this does not allow us to categorically dismiss the importance of HOIs. Despite the potential of combining mechanisms to promote coexistence, we still lack the knowledge needed to disentangle HOIs' importance for coexistence in nature. Progress requires coupling empirical data and observations to our models. In this line, the longstanding debate between theoretical and field ecologists over the value of mathematical abstractions reminds us that the law of parsimony—Occam's razor—favors simpler models when they perform equally well [20]. Since the mere act of adding higher-order (or nonlinear) terms boosts explanatory power [42], any claimed biological role for a mechanism must be weighed against that baseline. But Occam retaliates: if adding complexity clearly improves explanatory or predictive power, simplicity should be abandoned. Therefore, we must assemble compelling evidence that invoking HOIs as auxiliary mechanisms is indeed the most effective way to explain species coexistence.

METHODS

Lyapunov function for different physiological rates

When we consider a well-mixed competitive system with pairwise and higher-order interactions combined, the evolution of species abundances is written as:

$$\begin{aligned}\frac{dx_i}{dt} &= (1-\alpha)\left[x_i\left(\frac{D(x)}{F(x)^2}f_i\sum_j 2H_{ij}f_jx_j - d_i\right)\right] \\ &+ \alpha\left[x_i\left(\frac{D(x)}{F(x)^3}f_i\sum_{j,k}B_{ijk}f_jx_jf_kx_k - d_i\right)\right].\end{aligned} \tag{13}$$

To study this case, let's introduce the notation:

$$\begin{aligned}T_1 &:= T_{1_i} = \frac{D}{F^2}\sum_j 2f_if_jH_{ij}x_j \\ T_2 &:= T_{2_i} = \frac{D}{F^3}f_i\sum_j\sum_k 2f_jf_k(H_{ij}H_{jk}+H_{ij}H_{ik})x_jx_k\end{aligned} \tag{14}$$

In equilibrium, we have

$$T_1^*(1-\alpha) = d_i - \alpha T_2^* \tag{15}$$

where the star denotes that $x_i = x_i^*$ in the expression of T_1 and T_2. Notice that the solutions of systems with only pairwise or only higher-order interactions do not solve this equation since the equilibrium depends on the number of species involved. After finding this equilibrium condition, we focus on obtaining the expression for the derivative of the Lyapunov function. Assuming the feasibility of the fixed point (all $x_i^* > 0$), we introduce the Lyapunov function $V(x)$ as:

$$\frac{dV}{dt} = -\sum_i \frac{x_i^*}{x_i}\dot{x}. \tag{16}$$

Substituting Eq. (13), we get

$$\frac{dV}{dt} = -\sum_i x^*T_1 + D^* - \alpha\sum_i x_i^*T_2 + \alpha\sum_i x^*T_1 \tag{17}$$

Our objective now is to see the sign of this function or whether we can find a constant of motion for the system. The last term can be expressed as

$$\sum_i x^*T_1 = \sum_i x_i^*\frac{D}{F^2}\sum_j 2f_if_jH_{ij}x_j \tag{18}$$

using that $H_{ij} = 1 - H_{ji}$, we obtain

$$\begin{aligned}\sum_i x^*T_1 &= \sum_i x_i^*\frac{D}{F^2}\sum_j 2f_if_jx_j - \sum_i x_i^*\frac{D}{F^2}\sum_j 2f_if_jH_{ji}x_j \\ &= \frac{2D}{F^2}\left(F^*F - \sum_i x_i^*\sum_j f_if_jH_{ji}x_j\right)\end{aligned} \tag{19}$$

Rearranging factors in the last term, find the expression of T_1^*, Eq. (14), obtaining:

$$\sum_i x^* T_1 = \frac{2DF^*}{F} - \frac{F^{*2}D}{F^2 D^*} \sum_j x_j T_1^* \tag{20}$$

When we revisit Eq. (17), after some calculations we now have

$$\begin{aligned} \frac{dV}{dt} = (1-\alpha) \sum_j T_1^* x_j \frac{F^{*2}D}{F^2 D^*} + D^* - \\ \alpha \sum_i x_i^* T_2 + (\alpha - 1) \frac{2DF^*}{F} \end{aligned} \tag{21}$$

Taking the equilibrium condition (15), we arrive at

$$\begin{aligned} \frac{dV}{dt} &= \frac{F^{*2}D}{F^2 D^*} \sum_j x_j (d_j - \alpha T_2^*) + D^* - \\ &\alpha \sum_i x_i^* T_2 + (\alpha - 1) \frac{2DF^*}{F} \\ &= \frac{1}{F^2 D^*} \left(F^* D - F D^*\right)^2 + \\ &\alpha \left(2D \frac{F^*}{F} - \sum_i x_i^* T_2 - \frac{F^{*2}}{F^2} \frac{D}{D^*} \sum_i x_i T_2^* \right) \end{aligned} \tag{22}$$

Competitive communities model on interaction networks

To relax the well-mixed assumption in our model we extend it to considered interactions taking place on a network with an increasing fraction of higher-order interactions.

We place each individual in a node, which symbolizes a fixed spatial location (Fig. 1). Individuals compete to place their offspring in an empty node only if there is a link between them. These links can now be of two different types based on the number of individuals involved (i.e., the interaction order). Pairwise, connecting only two individuals, and higher-order links with three individuals at time.

The initial configuration is set by randomly distributing the species around $N = 5{\cdot}10^4$ nodes. Then, we connect the nodes at random with links or hyperlinks, according to the fraction of hyperlinks in the network defined by the parameter α, creating an Erdős-Rényi hypergraph. We construct these hypergraphs preserving the so-called *forgetful* degree of nodes ($\tilde{k}_i$) to compare results for networks with different α. The forgetful degree is the sum of all the links that are incident to a node i weighted by their order, so that each of our hyperlinks adds two to $\tilde{k}_i$. For example, the empty node in Fig. 1 has $\tilde{k}_i = 5$. Higher α values lead to more hyperlinks per node, reducing the density of pairwise connections.

ACKNOWLEDGMENTS

We thank S. Suweis for fruitful discussions. This work was partially supported by the María de Maeztu project CEX2021-001164-M funded by the MICIU/AEI/10.13039/501100011033. S.M. and V.C-S. acknowledge the Spanish State Research Agency through Project No. PID2021-122256NB-C22 funded by MCIN/AEI/10.13039/501100011033/FEDER, UE. S.M. also acknowledges support from project "CODE – Coupling Opinion Dynamics with Epidemics", funded under PNRR Mission 4 "Education and Research" - Component C2 - Investment 1.1 - Next Generation EU "Fund for National Research Program and Projects of Significant National Interest" PRIN 2022 PNRR, grant code P2022AKRZ9, CUP B53D23026080001. V.C-S. acknowledges "Europa Excelencia" 2023 Project No. EUR2023-143472/AEI/10.13039/501100011033 funded by the Spanish State Research Agency and Recovery plan "NextGenerationEU".

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Supporting Information of: Towards a less spherical cow: Species differences dilute the stabilizing effect of higher-order interactions

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CONTENTS

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I. CALCULATING AREAS IN THE SIMPLEX

We characterize the behavior of the community by considering the area encircled by the system's trajectory on the simplex. Because of the noisy character of the dynamics in the stochastic simulations, the amplitude of the oscillations is not a robust indicator. Instead, if the system fluctuates with small amplitude around some equilibrium abundances, the trajectory occupies a small area (main Figure 1b), whereas larger oscillations would cover broader areas (Figure 1a). Here, we explain the details on how we compute the area encircled by the trajectory.

For each simulation, the trajectory can be interpreted as points in a 3D space (gray dots in Figure 1, where the averaged density triplet $(\overline{x}_1, \overline{x}_2, \overline{x}_3)$ is the middle cross). To characterize the trajectory, we aim to measure the area covered by those points.

For programming convenience, it is more practical to change to a two-dimensional space (y_1, y_2). The chosen space is the one defined by the $x + y + z = 1$ plane, as the density triplets always lie on it because $\sum_i^g x_i(t) = 1$ at all times. Let $(\hat{u}, \hat{v})$ be two vectors in that plane that form an orthonormal basis. In particular:

$$\hat{u} = \sqrt{\frac{1}{2}} \begin{pmatrix} -1 \\ 1 \\ 0 \end{pmatrix}, \; \hat{v} = \sqrt{\frac{2}{3}} \begin{pmatrix} -1/2 \\ -1/2 \\ 1 \end{pmatrix}. \tag{1}$$

The areas in each space are conserved because the transformation is isometric. In turn, the change of coordinates of our points is given by:

$$y_1 = (x_1, x_2, x_3)\sqrt{\frac{1}{2}} \begin{pmatrix} -1 \\ 1 \\ 0 \end{pmatrix}, \; y_2 = (x_1, x_2, x_3)\sqrt{\frac{2}{3}} \begin{pmatrix} -1/2 \\ -1/2 \\ 1 \end{pmatrix}. \tag{2}$$

During the simulation, heavy fluctuations may occur, but the densities there do not represent the typical behavior of the ecosystem. These extreme densities are the outermost points of the set of points that populate the two-dimensional space. To get a representative area, we eliminate those boundary points, more precisely, we remove the 5% of outlier points. We then calculate the area enclosed by the polygon defined by the new outermost points (green line in Figure 1) using `MATLAB`'s function `polyarea` [1].

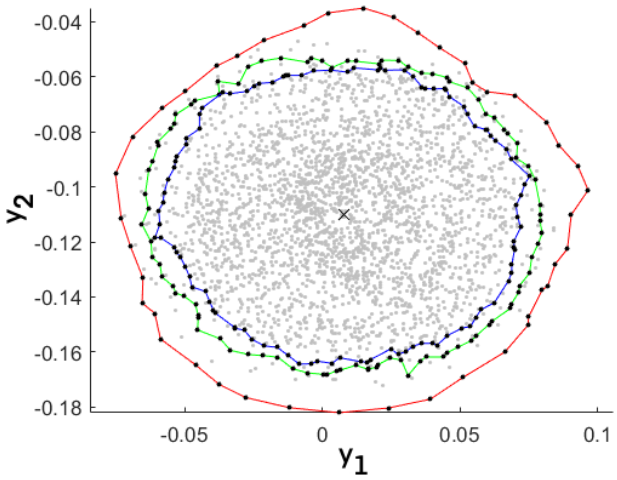

FIG. 1. Trajectory points projected in 2D. The red line encloses all the points. Green and blue lines enclose the 95% and 90% of the points, respectively.

II. LYAPUNOV FUNCTION FOR DIFFERENT PHYSIOLOGICAL RATES

When we consider a well-mixed competitive system with pairwise and higher-order interactions combined, the evolution of species abundances is written as:

$$\begin{aligned}\frac{dx_i}{dt} = (1-\alpha)\left[x_i\left(\frac{D(x)}{F(x)^2}f_i\sum_j 2H_{ij}f_jx_j - d_i\right)\right] \\ + \alpha\left[x_i\left(\frac{D(x)}{F(x)^3}f_i\sum_{j,k}B_{ijk}f_jx_jf_kx_k - d_i\right)\right].\end{aligned} \tag{3}$$

To study this case, let's introduce the notation:

$$\begin{aligned}T_1 := T_{1_i} &= \frac{D}{F^2}\sum_j 2f_if_jH_{ij}x_j \\ T_2 := T_{2_i} &= \frac{D}{F^3}f_i\sum_j\sum_k 2f_jf_k(H_{ij}H_{jk}+H_{ij}H_{ik})x_jx_k\end{aligned} \tag{4}$$

In equilibrium, we have

$$T_1^*(1-\alpha) = d_i - \alpha T_2^* \tag{5}$$

where the star denotes that $x_i = x_i^*$ in the expression of T_1 and T_2. Notice that the solutions of systems with only pairwise or only higher-order interactions do not solve this equation since the equilibrium depends on the number of species involved. After finding this equilibrium condition, we focus on obtaining the expression for the derivative of the Lyapunov function. Assuming the feasibility of the fixed point (all $x_i^* > 0$), we introduce the Lyapunov function $V(x)$ as:

$$\frac{dV}{dt} = -\sum_i \frac{x_i^*}{x_i}\dot{x}. \tag{6}$$

Substituting Eq. (3), we get

$$\frac{dV}{dt} = -\sum_i x^*T_1 + D^* - \alpha\sum_i x_i^*T_2 + \alpha\sum_i x^*T_1 \tag{7}$$

Our objective now is to see the sign of this function or whether we can find a constant of motion for the system. The last term can be expressed as

$$\sum_i x^*T_1 = \sum_i x_i^*\frac{D}{F^2}\sum_j 2f_if_jH_{ij}x_j \tag{8}$$

using that $H_{ij} = 1 - H_{ji}$, we obtain

$$\begin{aligned}\sum_i x^*T_1 &= \sum_i x_i^*\frac{D}{F^2}\sum_j 2f_if_jx_j - \sum_i x_i^*\frac{D}{F^2}\sum_j 2f_if_jH_{ji}x_j \\ &= \frac{2D}{F^2}\left(F^*F - \sum_i x_i^*\sum_j f_if_jH_{ji}x_j\right)\end{aligned} \tag{9}$$

Rearranging factors in the last term, find the expression of T_1^*, Eq. (4), obtaining:

$$\sum_i x^*T_1 = \frac{2DF^*}{F} - \frac{F^{*2}D}{F^2D^*}\sum_j x_jT_1^* \tag{10}$$

When we revisit Eq. (7), after some calculations we now have

$$\begin{aligned}\frac{dV}{dt} = (1-\alpha)\sum_j T_1^* x_j \frac{F^{*2}D}{F^2 D^*} + D^* - \\ \alpha \sum_i x_i^* T_2 + (\alpha - 1)\frac{2DF^*}{F}\end{aligned} \tag{11}$$

Taking the equilibrium condition (5), we arrive at

$$\begin{aligned}\frac{dV}{dt} &= \frac{F^{*2}D}{F^2 D^*}\sum_j x_j(d_j - \alpha T_2^*) + D^* - \\ &\alpha \sum_i x_i^* T_2 + (\alpha - 1)\frac{2DF^*}{F} \\ &= \frac{1}{F^2 D^*}\left(F^* D - F D^*\right)^2 + \\ &\alpha\left(2D\frac{F^*}{F} - \sum_i x_i^* T_2 - \frac{F^{*2}}{F^2}\frac{D}{D^*}\sum_i x_i T_2^*\right)\end{aligned} \tag{12}$$

III. SPECIAL CASE OF PROPORTIONAL RATES

To investigate what happens when the physiological rates are not equal, let's suppose first that they are proportional in such a way that

$$f_i = cd_i, \forall i \tag{13}$$

This assumption is inspired by the fact that these physiological rates usually are related. So-called slow species survive and reproduce little, and fast species reproduce a lot and die soon –a phenomenon named "the fast-slow continuum" [2]. In that case we have $F = cD$ and $F^* = cD^*$. Defining

$$E := \frac{1}{F^2}\sum_i x_i^* f_i \sum_j \sum_k 2f_j f_k (H_{ij}H_{jk} + H_{ij}H_{ik}) x_j x_k + \frac{1}{FF^*}\sum_i x_i f_i \sum_j \sum_k 2f_j f_k (H_{ij}H_{jk} + H_{ij}H_{ik}) x_j^* x_k^*, \tag{14}$$

Eq. (12) can be rewritten as

$$\begin{aligned} \frac{dV}{dt} &= \frac{c}{F^2F^*}\left(\frac{F^*F}{c} - \frac{FF^*}{c}\right)^2 + \alpha\left(2\frac{F^*}{c} - \frac{E}{c}\right) \\ &= \frac{\alpha}{c}\left(2F^* - E\right) \end{aligned} \tag{15}$$

This expression shows that the proportionality of physiological rates c does not cause the derivative of the Lyapunov function to become zero if it is the same for all the species. Still, a transition exits at $\alpha_c = 0$ for all different values of c.

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