On the stability of competitive ecological communities with pairwise and higher-order interactions

Marc Duran-Sala,[1] Sandro Meloni,[2,3,4] and Violeta Calleja-Solanas[5]

[1]*Laboratory of Urban and Environmental Systems, École Polytechnique Fédérale de Lausanne (EPFL), Lausanne, Switzerland*
[2]*Institute for Applied Mathematics Mauro Picone (IAC) CNR, Rome, Italy*
[3]*Institute for Cross-Disciplinary Physics and Complex Systems (IFISC), CSIC-UIB, Palma de Mallorca, Spain*
[4]*Centro Studi e Ricerche "Enrico Fermi" (CREF), Rome, Italy**
[5]*Estación Biológica de Doñana (CSIC), Seville, Spain*

Ecological communities intrigue researchers seeking to explain the emergence of biodiversity observed in nature. This raises a fundamental question: What sustains the stability and coexistence of species within these ecosystems? Traditional ecological models have largely been based on the assumption that species primarily engage in pairwise interactions. However, interactions in ecological systems may involve groups of three or more individuals –i.e. higher-order interactions. As a result, the question of how the combined effects of pairwise and higher-order interactions shape the stability of large ecological communities remains unresolved.

This work addresses this gap by analyzing a model of competitive communities that incorporates both pairwise and higher-order interactions. Using analytical techniques and numerical simulations, we find that higher-order interactions alone are not always sufficient to foster and maintain coexistence. When species are identical (i.e., have the same physiological rates), even a small proportion of higher-order interactions can stabilize their dynamics. However, when more realistic factors—such as varied birth and death rates or complex interaction structures—are introduced, a finite fraction of higher-order interactions may not be sufficient to achieve stable coexistence. Our findings challenge the role of higher-order interactions as a universal stabilizing mechanism in ecological communities and open new avenues for research into the interplay of different factors that underpin biodiversity and ecosystem stability.

I. INTRODUCTION

The question of how different species coexist in natural ecosystems has intrigued researchers across fields, including ecology, statistical physics, and mathematics. This challenge largely stems from the competitive exclusion principle, which posits that less competitive species should eventually be driven to extinction by better-adapted counterparts. In response, a range of theories has emerged, with niche and neutral ones being the most prominent [1, 2]. Despite their influence, these theories have limitations, leading researchers to explore alternative or complementary mechanisms for coexistence. One such mechanism that has gained significant attention is intransitive competition [3]. In intransitive competition, no clear hierarchy exists among species; instead, interactions follow a cyclical pattern akin to a "rock-paper-scissors" dynamic, where species i outcompetes species j, species j outcompetes species k, and species k in turn outcompetes species i. Classic examples of intransitivity in natural systems include the side-blotched lizards [4] and the bacterium *E. coli* [5], in which three strains regulate toxin resistance, sensitivity, and production. More recent studies have also documented intransitivity among sessile organisms, such as annual plants [6], tree-soil relationships [7], and fungi [8].

In intransitive communities, coexistence is achieved because species abundances tend to cycle [9], preventing any single species from dominating the entire population. From a theoretical perspective, models that incorporate intransitive dominance often result in species abundances neutrally cycling around an equilibrium point –a scenario unlikely to occur in nature [10]. Additionally, large oscillations in species abundances can undermine coexistence in discrete settings, as species may face extinction due to external disturbances or stochasticity. To address these limitations, recent studies have explored combining intransitivity with auxiliary mechanisms, such as mobility [11] and structured interactions [12].

Structured interactions explicitly consider the spatial context in which species interact, which has a significant impact on coexistence [13–15]. The spatial arrangement of individuals can greatly influence the strength of their mutual effects, thereby shaping the resulting dynamics [16]. In cases of intransitive competitive interactions, the system tends to stabilize when individuals of competing species are spatially embedded and can only interact with others within a short distance [12]. By contrast, large oscillations emerge when these interactions are not spatially structured.

Stable coexistence can also be achieved in mathematical models that incorporate higher-order interactions (HOIs) [10, 17, 18]. Higher-order interactions occur when the presence of one species modifies the relationship between other species, leading to interactions among three or more species simultaneously. This influences species abundances in a way that differs from pairwise interactions alone.

Despite the significant attention the topic received, competition models have predominantly focused on either pairwise interactions or higher-order interactions independently, within either structured or well-mixed communities. In reality, these approaches –considering only pairwise or only higher-order interactions– fall short of representing realistic scenarios, as natural communities are expected to involve combinations of various interaction types with varying levels of complexity [19, 20]. This combined approach has only recently begun to be explored [21, 22].

Given these limitations, we investigate whether stable coexistence can be achieved in communities that combine both

pairwise and higher-order interactions. Specifically, we examine the influence of HOIs by varying their proportion in scenarios that are not stable when considering pairwise intransitive competition alone. In this setting, using a combination of analytical derivations, numerical integration, and Monte Carlo simulations, we explore how heterogeneity in species' physiological rates and the spatial arrangement of individuals also impacts the stability of community dynamics.

We start by studying a competition model where both pairwise and higher-order interactions form intransitive cycles in a well-mixed scenario and all species have the same birth and death rates. We then allow species to differentiate by considering different physiological rates. Finally, we abandon the well-mixed scenario and define an interaction network, whose nodes are single individuals of different species connected by links and hyperlinks –representing pairwise and higher-order interactions, respectively.

Our results show that stable coexistence is reached with any amount of HOIs only in a neutral case (when species have identical physiological rates). In the more realistic setting of heterogeneous physiological rates, we find that a finite fraction of HOIs could not be sufficient to achieve coexistence. A critical proportion of HOIs also appears when interactions take place on a network. In that case, coexistence can be reached only with the emergence of a giant cluster of hyperlinks for an high proportion of HOIs. A condition unlikely to occur in real communities.

II. HIGHER-ORDER INTRANSITIVE COMPETITION MODEL

We start by considering an isolated competitive g-species community with a well-mixed population. To focus only on the interplay between pairwise and higher-order interactions (HOIs), we keep the number of ecological processes to a minimum. Each species i has two physiological rates, specifically, birth f_i and death d_i rates, and species compete in an intransitive tournament. The evolution of species density x_i can be described, for the pairwise case, by a Replicator Dynamics:

$$\frac{dx_i}{dt} = x_i \left(\frac{D(x)}{F(x)^2} f_i \sum_j 2H_{ij}f_j x_j - d_i \right), \quad (1)$$

The equations can be expressed in terms of physiological rates and the probabilistic 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 deterministic ($H_{ij} = 1, H_{j,i} = 0, \forall i,j$) dominance between species. 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 al-

lows us to break neutrality in the classic sense of species with equal probabilities of reproduction and death [23].

Conversely, one could also model the dynamics of the same system with *only* higher-order interactions. If we limit ourselves to *triplewise* interactions, i.e. involving $g = 3$ competitors, the equations, as introduced in [17], become:

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

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 can be simplified as a combination of all the possible pairwise competition terms: $B_{ijk} = 2H_{ij}H_{ik} + H_{ij}H_{jk} + H_{ik}H_{kj}$.

Since one would expect the presence of interactions of different orders at the same time in a natural community [20], we combine the previous equations together. In particular, we introduce a parameter, α, that weights the fraction of HOIs present in the system with respect to pairwise interactions. Thus, the expression for the full system becomes:

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

If $\alpha = 0$, we recover the pairwise scenario. In contrast, $\alpha = 1$ leads to a complete HOIs system.

The dynamical behavior of Eqs.(1) and (2) considered separately is very different. In the pairwise case, the system neutrally oscillates if the dominance matrix has intransitive cycles ($H_{ij} > H_{jk} > H_{ki} > 0.5$) or leads to extinctions if it does not [5, 24]. Instead, in a full HOIs system densities converge to a stable fixed point when the physiological rates are equal or very similar [17].

A. Interaction networks

To consider a more realistic scenario, we also studied the case in which species' individuals do not interact with all the other individuals at the same time –i.e. the well-mixed hypothesis– but the locality of interactions is taken into account. We place each individual in a node of an hypergraph, which symbolizes a fixed spatial location. Individuals compete to place their offspring in an empty node only if there is a link between them. Links can be of two different types, based on the number of individuals involved: the order of the interaction. Pairwise links connect only two individuals, and hyperlinks connect three individuals at the same time.

The initial configuration is set by randomly distributing individuals in a $N = 5 \cdot 10^4$ hypergraph. We then connect nodes at random with links or hyperlinks, according to the proportion of HOIs in the network defined by α. We do so by preserving the *forgetful* degree of the nodes ($\tilde{k}_i$) –i.e. keeping the
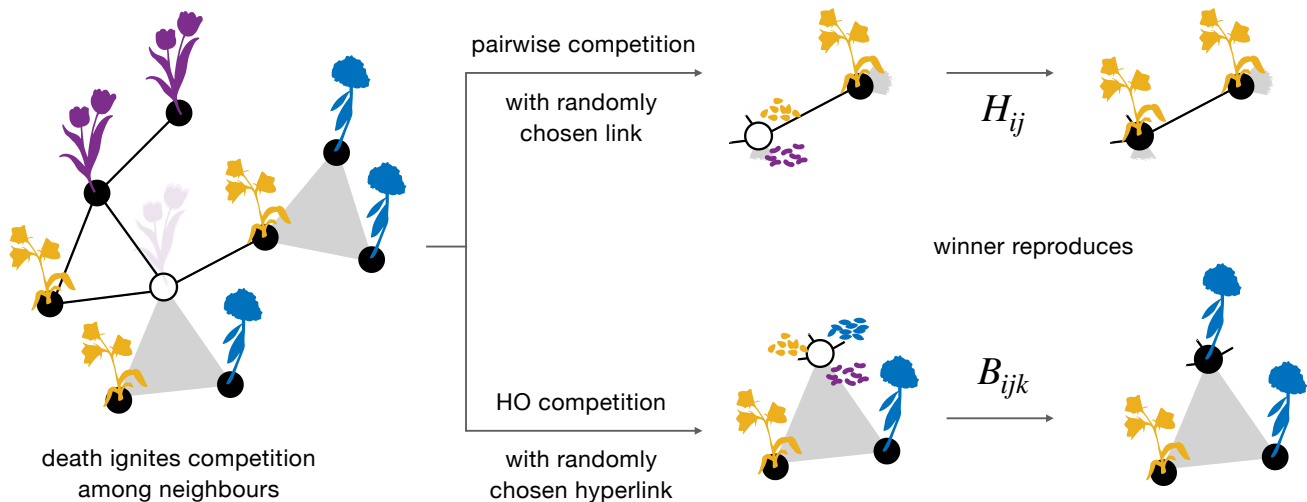
FIG. 1. **Illustration of the competitive dynamics**. When a random plant dies, it leaves a vacant fertile region. The neighbors connected to the empty node by one of its links compete to establish offspring there. One link is selected at random and, depending on the nature of the link, competition is pairwise or higher-order. Finally, the winner plant is chosen according to the probabilities of the species dominance matrix H, or tensor B, respectively.

network density constant– to compare 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 hyperlink adds two to $\tilde{k}_i$. For example, the empty node in Figure 1 has $\tilde{k} = 5$. In our simulations we fix the average forgetful degree $\langle \tilde{k} \rangle = 20$ for all the generated networks.

In Figure 1 we represent a sketch of our model. Building upon the illustration of sessile organisms, for example flowering plants competing for space, with every iteration a plant dies, creating an opening. Then, one link to the new vacant region is selected at random, and the plants connected to that link compete to disperse their seedlings there. Depending on the link's type, the winner is determined either by matrix H or tensor B. The well-mixed model follows exactly the same dynamics except for the fact that competitors are randomly chosen among the entire population. With α dictating whether competition will involve two or three individuals.

III. RESULTS

Once defined our model, we start by studying the temporal evolution of species' densities for different values of α. Without lost of generality, we define a dominance matrix that assures an intransitive tournament:

$$H = \begin{pmatrix} 0.5 & 0.34 & 0.76 \\ 0.66 & 0.5 & 0.25 \\ 0.24 & 0.75 & 0.5 \end{pmatrix} \qquad (4)$$

and track the density 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 the densities of the species can be interpreted as a point that follows a trajectory on the 2-simplex. The simplex represents the $g - 1$ 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 [12]. When the system reaches a fixed point, its trajectory in the simplex occupies a small area. In contrast, neutral circles will cover a large portion of the total area.

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

We begin our analysis by studying the case of equal physiological rates ($d_i = f_i = 1$, $\forall i$), for which Eq. (3) becomes

$$\frac{dx_i}{dt} = (1 - \alpha)\left(-x_i + 2\sum_j H_{ij} x_i x_j \right)$$
$$+ \alpha\left(-x_i + \sum_{j,k} (2H_{ij}H_{ik} + H_{ij}H_{jk} + H_{ik}H_{kj}) x_i x_j x_k \right). \qquad (5)$$

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 stabilizes and species coexist. To do so, we use the Lyapunov function $V(x)$ as defined in [17],

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

since it is still a Lyapunov function for Eq. (3). Deriving Eq. (6) and assuming the feasibility of the equilibrium ($x_i^* >$
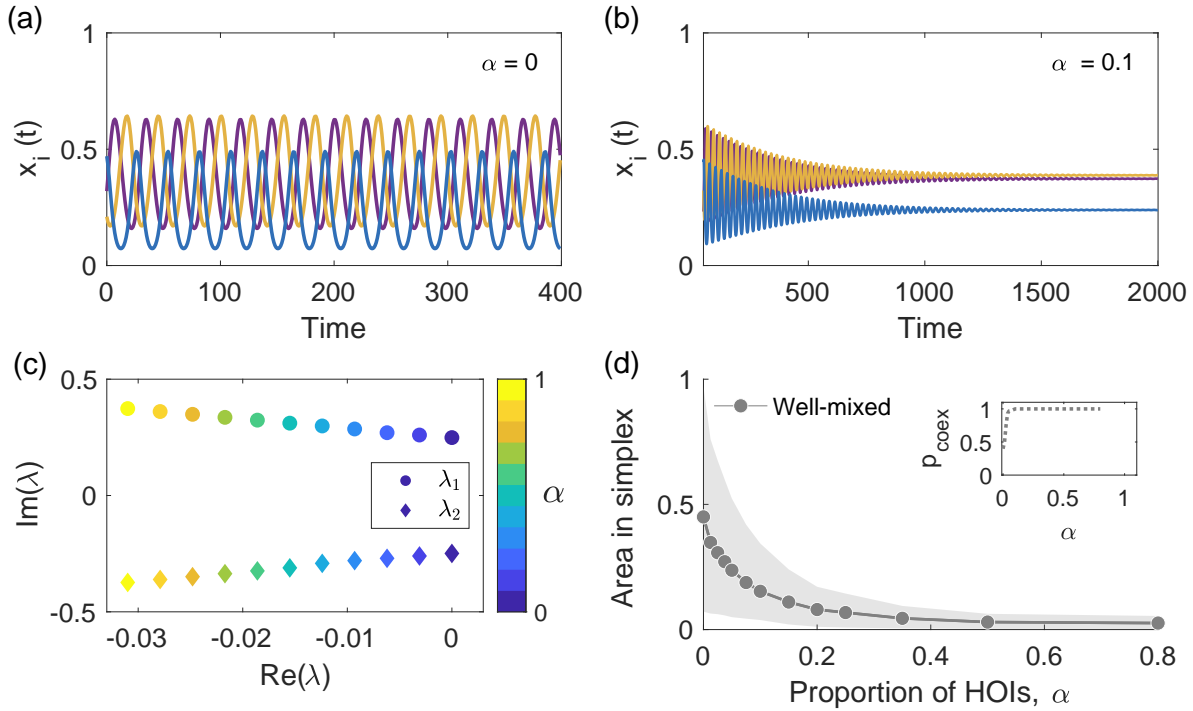
FIG. 2. **Any proportion of higher-order interactions stabilize the dynamics in well-mixed competitive systems with equal physiological rates.** (Panels a and b) Numerical integration of the dynamics from the set of ODEs (Eq. (5)), for (a) $\alpha = 0$ (no HOIs) and (b) $\alpha = 0.1$. (Panel c) Eigenvalues 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. (Panel 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 Carlos simulations with $N = 10^4$. 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.

$0, \forall i)$, we obtain

$$\frac{dV}{dt} = \sum_i \frac{\partial V}{\partial x_i} \frac{dx_i}{dt} = -\sum_i \frac{x_i^*}{x_i} \frac{dx_i}{dt}$$
$$= \alpha \left[-2 \sum_i x_i^* \left(\sum_j H_{ij} \xi_j \right)^2 \right], \quad (7)$$

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 (Figure 2a) [17]. When $\alpha > 0$, we always get $dV/dt \leq 0$, which implies $\vec{x}^*$ is a globally stable fixed point as demonstrated in Figure 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 (Figure 2c).

To corroborate these analytical insights, we reproduce the system's dynamics with Monte Carlo simulations with an asynchronous update scheme. We find that extinctions can easily occur for $\alpha = 0$ due to stochastic fluctuations (see inset in Figure 2d). Instead, when $\alpha > 0$, the system stabilizes around the predicted equilibrium. In the numerical

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 is already at the equilibrium (Figure 2d). Hence, a small proportion of higher-order interactions is enough to maintain coexistence for species with the same physiological rates.

B. Stability depends on the variability of physiological rates

So far we have only considered species with equal birth and death rates, and thus they only vary in their competitive fitness (encoded in H). To explore further the consequences of adding HOIs, we go beyond this neutrality by studying the model of Eq. (3) with different physiological rates. In this case, the equilibrium densities vary with the proportion of HOIs, α. If we define

$$T_1(\vec{x}) := \frac{D}{F^2} \sum_j 2 f_i f_j H_{ij} x_j$$

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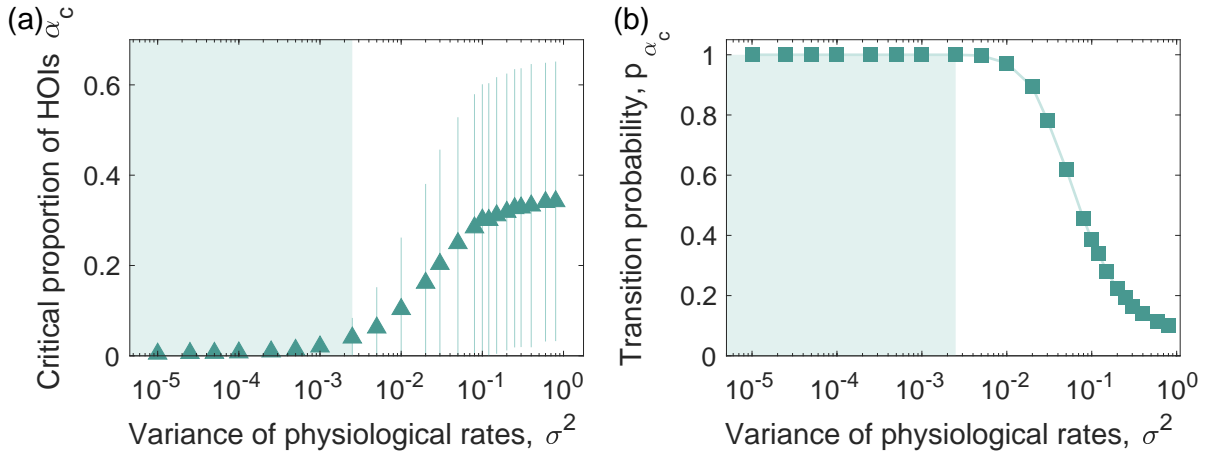
$$(8)$$

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. (Panel a) Critical higher-order interactions proportion α_c as a function of variance σ^2, averaged over 10000 simulations with the same dominance matrix H. (Panel b) Probability of the existence of a transition towards a fixed point p_{α_c} as a function of variance σ^2 over 10000 simulations. The shaded regions indicate the area where species always coexisted in our simulations.

then, the equilibrium point must fulfill the expression

$$T_1^*(1 - \alpha) = d_i - \alpha T_2^*, \qquad (9)$$

where we have dropped the arguments of $D(x)$ and $F(x)$ for readability, and $T^* := T(\vec{x}^*)$. Assuming that $\vec{x}^*$ exists and is feasible ($x_i^* > 0\,\forall i$), the derivative of the Lyapunov function is (see Appendix A for the full calculation):

$$\frac{dV}{dt} = \frac{1}{F^2 D^*}\left(F^* D - F D^*\right)^2$$
$$+ \alpha\left[2D\frac{F^*}{F} - \sum_i x_i^* T_2 - \frac{F^{*2}}{F^2}\frac{D}{D^*}\sum_i x_i T_2^*\right]. \qquad (10)$$

If the dynamics eventually stabilizes, this derivative must be zero at some point. After some calculations, we find that this transition takes place at:

$$\alpha_c = \frac{-\frac{1}{F^2 D^*}\left(F^* D - F D^*\right)^2}{2D\frac{F^*}{F} - \sum_i x_i^* T_2 - \frac{F^{*2}}{F^2}\frac{D}{D^*}\sum_i x_i T_2^*}. \qquad (11)$$

We can observe that the numerator is zero when birth rates are equal for all species but different from death rates by a constant value – i.e. they are proportional ($d_i = c f_i$, $\forall i$). The numerator is always negative otherwise. The divisor can be either positive or negative, depending on the specific values of the physiological rates. This implies that the existence of a transition relies on the values of the physiological rates. It will no longer be at $\alpha_c = 0$, except in simpler situations like proportional physiological rates (see appendix B for further details). In general, we need to have a non-negligible proportion of HOIs to stabilize the dynamics.

To gain further insights on the behavior of Eq. (11), we decide to study its behavior when physiological rates become increasing different. To do so, we sample the physiological rates following a normal distribution. This way we can study

how the heterogeneity of f_i and d_i determines α_c. Inspecting the numerator in Eq. (11), we see that the expected value of α_c will depend on the difference of the means of each distribution. When $\mu_f = \mu_d = 1$, 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 $\mu = 1$ and varying σ^2. We then record the α at which the transition occurs for each σ^2.

Results in Figure 3a show that as the variance of physiological rates becomes larger, α_c increases too reaching values close to $\alpha_c = 0.4$. 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 perspective of this result is that there are situations where there is no transition for any α –i.e. any fraction of HOIs would not be enough to stabilize the dynamics. That occurs above a critical value for the variance (outside of the green shaded region in Figures 3a and 3b), where the transition probability p_{α_c} decreases abruptly (Figure 3b). Hence, coexistence is unlikely when birth and death rates are too different within and between species.

C. Interaction networks

Once characterized the well-mixed case, we conclude our analyses by studying the more realistic setting in which interactions are defined by a network substrate.

When we only consider pairwise interactions on a random network, our model presents, as expected, the same neutral circles observed in the all-to-all case [12]. Thus, we again test the stability of coexistence for increasing fractions of HOIs. To isolate the effect of the network structure from the hetero-
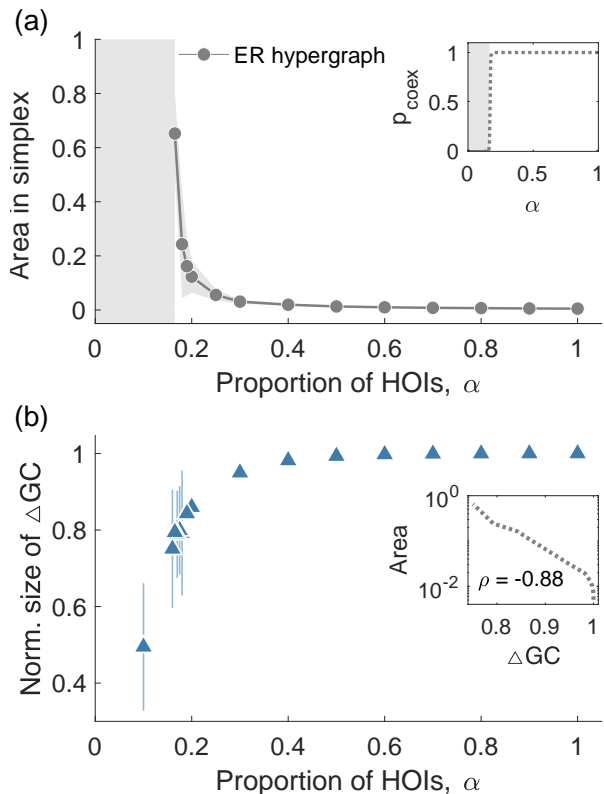
FIG. 4. **Dynamics of our model on a network.** (Panel a) Monte Carlo simulations on Erdős-Rényi (ER) hypergraphs show that the average area of the 3-species system decreases as a function of α. Shades indicate the standard deviation over 50 simulations with $N = 5 \cdot 10^4$. The inset is the probability of coexistence p_{coex} over 50 simulations. (Panel b) The size of the normalized giant component of hyperlinks ($\triangle GC$) 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 $\triangle GC$ tells us that the area is minimal when $\triangle GC$ percolates, as can be seen in the inset together with their Pearson correlation coefficient.

geneity of the physiological rates, we consider the case where all the rates are equal, which in the well-mixed assumption leads to $\alpha_c = 0$.

We generate ER hypergraphs with an average forgetful degree $\langle k \rangle = 20$ and vary α to increase the density of hyperlinks.

Figure 4a shows that, even with equal physiological rates, the dynamics stabilizes only after α reached a finite value close to $\alpha = 0.2$. In the same point the coexistence probability has a sharp transition from 0 to 1 (inset of Figure 4a) showing that only after $\alpha = 0.2$ stable coexistence is possible. Hence, also in this case we find a critical value $\alpha_c > 0$.

To understand the origins of this behavior, we look at how the introduction of HOIs changes the overall connectivity patterns of the network. Specifically, since we suspect that the regions of the network reached by higher-order links are likely to stabilize, we look at the giant component of just hyperlinks ($\triangle GC$) to see how it relates to the emergence of small areas

in the simplex. First, we see that the size of $\triangle GC$ rapidly increases with α and percolates for $\alpha > 0.2$ (Figure 4). Moreover, the inset of Figure 4b demonstrates a strong correlation between the area in the simplex and $\triangle GC$, suggesting that the whole system stabilizes only when each node is reached by, at least, one HOI.

IV. CONCLUSIONS

Understanding the mechanisms that enable species coexistence within ecological communities is critical for maintaining biodiversity, ecosystem functions, and conservation. Recently higher-order interactions have been suggested to play an important role in guaranteeing stable coexistence. However, their effect has only been tested in isolation and specific setups. This work was motivated by the need to delve deeper into different coexistence mechanisms, focusing on the more realistic setting of pairwise and higher-order interactions acting at the same time in intransitive competitive communities. By addressing this combination, we aimed to evaluate the potential HOIs as stabilizing factor.

We have studied a model where multiple species compete in intransitive dominance cycles. We have analyzed different proportions of pairwise and HOIs, and different values of physiological rates, ranging from neutral to distinct species. Our results support only in part the narrative that HOIs enable stable coexistence. In fact, even if we show that a small amount of HOIs allows stability when the competitive community cannot be stable with pairwise interactions alone, this fraction α_c depends on the similarity of physiological rates among the species. Meaning that HOIs are only able to stabilize the dynamics if species are unrealistically equivalent. Instead, as physiological rates become more dissimilar, no amount of HOIs could assure coexistence.

Something similar happens when we consider interactions taking place on a network substrate mimicking the spatial distribution of individuals. When we introduce HOIs in the network via hypergraphs, our results show that the distribution of hyperlinks among individuals is the key to stable coexistence. It is reached only when a giant cluster of hyperlinks percolated the entire network. A condition that is unlikely to be found in a broad range of natural communities.

Taken together our results redefine the relevance of HOIs in ecological communities. Even if our model is far from being realistic and several ecological processes are not included, it already demonstrates that higher-order interactions contribute to stability only under specific and ideal conditions. Their stabilizing effect is lost or requires additional conditions when we incorporate more ecological complexity, for example when we simply include variation in physiological rates. Species do have different birth and death rates indeed. Moreover, the fact that more diverse communities required an higher fraction of HOIs suggests the presence of other mechanisms besides intransitive competition, spatial interactions, or HOIs to maintain stability in real ecological communities. Finally, our results suggest that models focusing solely on one mechanism may miss crucial dynamics that are generated by

the interplay of more complex interaction patterns.

Appendix A: 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 described by Eq. (3). To help readability , let's introduce the following notation:

$$T_1 := T_{1_i} = \frac{D}{F^2} \sum_j 2 f_i f_j H_{ij} x_j$$

$$T_2 := T_{2_i} = \frac{D}{F^3} f_i \sum_j \sum_k 2 f_j f_k (H_{ij} H_{jk} + H_{ij} H_{ik}) x_j x_k \tag{A1}$$

At the equilibrium, we have

$$T_1^*(1 - \alpha) = d_i - \alpha T_2^* \tag{A2}$$

where the star denotes that $x_i = x_i^*$ in the expression of T_1 and T_2. Notice that the solutions of a system with only pairwise or only higher-order interactions it is not a solution of this equation since the equilibrium densities depend on the number of species involved. After finding this equilibrium condition, we focus on obtaining the expression for $\frac{dV}{dt}$ in Eq. (10). Assuming the feasibility of the fixed point (all $x_i^* > 0$), we introduce the Lyapunov function $V(x)$ as equation (6)

$$\frac{dV}{dt} = -\sum_i \frac{x_i^*}{x_i} \dot{x} \tag{A3}$$

Substituting Eq. (3), we get

$$\frac{dV}{dt} = -\sum_i x^* T_1 + D^* - \alpha \sum_i x_i^* T_2 + \alpha \sum_i x^* T_1 \tag{A4}$$

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

$$\sum_i x^* T_1 = \sum_i x_i^* \frac{D}{F^2} \sum_j 2 f_i f_j H_{ij} x_j \tag{A5}$$

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

$$\sum_i x^* T_1 = \sum_i x_i^* \frac{D}{F^2} \sum_j 2 f_i f_j x_j - \sum_i x_i^* \frac{D}{F^2} \sum_j 2 f_i f_j H_{ji} x_j$$

$$= \frac{2D}{F^2} \left(F^* F - \sum_i x_i^* \sum_j f_i f_j H_{ji} x_j \right) \tag{A6}$$

Rearranging factors in the last term, we find the expression of T_1^* (Eq. (8)), obtaining

$$\sum_i x^* T_1 = \frac{2DF^*}{F} - \frac{F^{*2} D}{F^2 D^*} \sum_j x_j T_1^* \tag{A7}$$

Revising Eq. (A4) after some calculations we now have:

$$\frac{dV}{dt} = (1 - \alpha) \sum_j T_1^* x_j \frac{F^{*2} D}{F^2 D^*} + D^* - \alpha \sum_i x_i^* T_2 + (\alpha - 1) \frac{2DF^*}{F} \tag{A8}$$

Taking the equilibrium condition (A2), we arrive at

$$\frac{dV}{dt} = \frac{F^{*2} D}{F^2 D^*} \sum_j x_j (d_j - \alpha T_2^*) + D^* - \alpha \sum_i x_i^* T_2 + (\alpha - 1) \frac{2DF^*}{F}$$

$$= \frac{1}{F^2 D^*} (F^* D - F D^*)^2 + \alpha \left(2D \frac{F^*}{F} - \sum_i x_i^* T_2 - \frac{F^{*2}}{F^2} \frac{D}{D^*} \sum_i x_i T_2^* \right) \tag{A9}$$

Appendix B: 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

$$f_i = c d_i, \forall i \tag{B1}$$

In that case we also have $F = cD$ and $F^* = cD^*$. Defining

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

$$\frac{1}{FF^*} \sum_i x_i f_i \sum_j \sum_k 2 f_j f_k (H_{ij} H_{jk} + H_{ij} H_{ik}) x_j^* x_k^*, \tag{B2}$$

Eq. (10) can be rewritten as

$$\frac{dV}{dt} = \frac{c}{F^2 F^*}\left(\frac{F^* F}{c} - \frac{F F^*}{c}\right)^2 + \alpha\left(2\frac{F^*}{c} - \frac{E}{c}\right)$$
$$= \frac{\alpha}{c}\left(2F^* - E\right)$$

(B3)

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.

[1] S. P. Hubbell, *The unified neutral theory of biodiversity and biogeography*, nachdr. ed., Monographs in population biology No. 32 (Princeton Univ. Press, Princeton, NJ, 2001).

[2] S. Azaele, S. Suweis, J. Grilli, I. Volkov, J. R. Banavar, and A. Maritan, Statistical mechanics of ecological systems: Neutral theory and beyond, Reviews of Modern Physics **88**, 10.1103/RevModPhys.88.035003 (2016), arXiv: 1506.01721.

[3] S. Soliveres and E. Allan, Everything you always wanted to know about intransitive competition but were afraid to ask, Journal of Ecology **106**, 807 (2018), _eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1111/1365-2745.12972.

[4] B. Sinervo and C. M. Lively, The rock–paper–scissors game and the evolution of alternative male strategies, Nature **380**, 240 (1996), number: 6571 Publisher: Nature Publishing Group.

[5] B. Kerr, M. A. Riley, M. W. Feldman, and B. J. Bohannan, Local dispersal promotes biodiversity in a real-life game of rock–paper–scissors, Nature **418**, 171 (2002), publisher: Nature Publishing Group.

[6] O. Godoy, D. B. Stouffer, N. J. B. Kraft, and J. M. Levine, Intransitivity is infrequent and fails to promote annual plant coexistence without pairwise niche differences, Ecology **98**, 1193 (2017), _eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1002/ecy.1782.

[7] M. Pajares-Murgó, J. L. Garrido, A. J. Perea, Á. López-García, J. M. Bastida, J. Prieto-Rubio, S. Lendínez, C. Azcón-Aguilar, and J. M. Alcántara, Intransitivity in plant–soil feedbacks is rare but is associated with multispecies coexistence, Ecology Letters **27**, e14408 (2024).

[8] D. S. Maynard, M. A. Bradford, D. L. Lindner, L. T. van Diepen, S. D. Frey, J. A. Glaeser, and T. W. Crowther, Diversity begets diversity in competition for space, Nature ecology & evolution **1**, 1 (2017), publisher: Nature Publishing Group.

[9] R. M. May and W. J. Leonard, Nonlinear Aspects of Competition Between Three Species, SIAM Journal on Applied Mathematics **29**, 243 (1975).

[10] J. M. Levine, J. Bascompte, P. B. Adler, and S. Allesina, Beyond pairwise mechanisms of species coexistence in complex communities, Nature **546**, 56 (2017), number: 7656 Publisher: Nature Publishing Group.

[11] T. Reichenbach, M. Mobilia, and E. Frey, Mobility promotes and jeopardizes biodiversity in rock–paper–scissors games, Nature **448**, 1046 (2007), number: 7157 Publisher: Nature Publishing Group.

[12] V. Calleja-Solanas, N. Khalil, J. Gómez-Gardeñes, E. Hernández-García, and S. Meloni, Structured interactions as a stabilizing mechanism for competitive ecological communities, Phys. Rev. E **106**, 064307 (2022), publisher: American Physical Society.

[13] F. Valladares, C. C. Bastias, O. Godoy, E. Granda, and A. Escudero, Species coexistence in a changing world, Frontiers in Plant Science **6**, 866 (2015), publisher: Frontiers.

[14] U. Dieckmann, R. Law, and J. A. J. Metz, eds., *The Geometry of Ecological Interactions* (Cambridge University Press, Cambridge, 2000).

[15] N. V. Lowery and T. Ursell, Structured environments fundamentally alter dynamics and stability of ecological communities, Proceedings of the National Academy of Sciences of the United States of America **116**, 379 (2019).

[16] S. Kéfi, V. Guttal, W. A. Brock, S. R. Carpenter, A. M. Ellison, V. N. Livina, D. A. Seekell, M. Scheffer, E. H. van Nes, and V. Dakos, Early Warning Signals of Ecological Transitions: Methods for Spatial Patterns, PLoS ONE **9**, e92097 (2014), iSBN: 10.1371/journal.pone.0092097.

[17] J. Grilli, G. Barabás, M. J. Michalska-Smith, and S. Allesina, Higher-order interactions stabilize dynamics in competitive network models, Nature 10.1038/nature23273 (2017), arXiv: NIHMS150003 ISBN: 0008-5472 (Print)\r0008-5472 (Linking).

[18] E. Bairey, E. D. Kelsic, and R. Kishony, High-order species interactions shape ecosystem diversity, Nature Communications **7**, 12285 (2016).

[19] S. Kéfi, E. L. Berlow, E. A. Wieters, L. N. Joppa, S. A. Wood, U. Brose, and S. A. Navarrete, Network structure beyond food webs: mapping non-trophic and trophic interactions on Chilean rocky shores, Ecology **96**, 291 (2015), _eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1890/13-1424.1.

[20] A. J. Golubski, E. E. Westlund, J. Vandermeer, and M. Pascual, Ecological Networks over the Edge: Hypergraph Trait-Mediated Indirect Interaction (TMII) Structure, Trends in Ecology and Evolution **31**, 344 (2016), publisher: Elsevier Ltd.

[21] T. Gibbs, G. Gellner, S. A. Levin, K. S. McCann, A. Hastings, and J. M. Levine, *Can higher-order interactions resolve the species coexistence paradox?*, preprint (Ecology, 2023).

[22] D. García-Callejas, R. Molowny-Horas, and M. B. Araújo, The effect of multiple biotic interaction types on species persistence, Ecology **99**, 2327 (2018).

[23] A. M. Leroi, B. Lambert, J. Rosindell, X. Zhang, and G. D. Kokkoris, Neutral syndrome, Nature Human Behaviour **4**, 780 (2020).

[24] S. Allesina and J. M. Levine, A competitive network theory of species diversity, Proceedings of the National Academy of Sciences **108**, 5638 (2011).