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Coexistence in diverse communities with higher-order interactions

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A central assumption in most ecological models is that the interactions in a community operate only between pairs of species. However, two species may interactively affect the growth of a focal species. Although interactions among three or more species, called higher-order interactions, have the potential to modify our theoretical understanding of coexistence, ecologists lack clear expectations for how these interactions shape community structure. Here we analytically predict and numerically confirm how the variability and strength of higher-order interactions affect species coexistence. We found that as higher-order interaction strengths became more variable across species, fewer species could coexist, echoing the behavior of pairwise models. If interspecific higher-order interactions became too harmful relative to self-regulation, coexistence in diverse communities was destabilized, but coexistence was also lost when these interactions were too weak and mutualistic higher-order effects became prevalent. This behavior depended on the functional form of the interactions as the destabilizing effects of the mutualistic higher-order interactions were ameliorated when their strength saturated with species' densities. Last, we showed that more species-rich communities structured by higher-order interactions lose species more readily than their species-poor counterparts, generalizing classic results for community stability. Our work provides needed theoretical expectations for how higher-order interactions impact species coexistence in diverse communities.

coexistence | species interactions | community assembly | competition

Significance

Some species interactions, termed higher-order interactions, can only emerge when there are many species in an ecological community. These interactions are likely frequent in nature, although their role in shaping the coexistence of species is poorly explored. Here we incorporate higher-order interactions into a mathematical model of the dynamics of diverse communities and show that many of the rules governing the effects of pairwise interactions on coexistence extend to the higher-order case. Our theory requires only a small number of parameters to predict the number of species coexisting at equilibrium. As a result, empiricists can use our framework to generate expectations for how higher-order interactions influence species coexistence in nature.

A fundamental problem in ecology is explaining species coexistence in diverse communities despite the force of competitive exclusion. Because of the inherent complexity of diverse systems, research on this problem has typically advanced by assuming that interactions operate only between pairs of species and that these pairwise interactions then combine to generate the dynamics of the full community (1). Two kinds of interactions uniquely emerge in systems with more than two species. First are interaction chains, which are defined as the indirect effect of one species on another through changes in the abundance of a third (or fourth, fifth, etc.) species (1, 2). Rock-paper-scissors games and intransitive competition more generally are well-studied examples of this type of competitive dynamic (3–5). Importantly, the interactions in these chains remain fundamentally pairwise, even when their effects on species densities propagate through the competitive network. By contrast, the second main type of interaction occurs when a group of two or more species interactively affect a focal species. Such interactions, termed higher-order interactions, are absent from the purely pairwise models that have contributed most to our understanding of species coexistence. Despite longstanding efforts in ecology (6–11) and other fields (12–16), we currently lack coherent theoretical expectations for how higher-order interactions impact coexistence in diverse communities.

Higher-order interactions emerge when species plastically respond to other species in ways that affect their interaction with still other species. For example, consider the idealized case of three plant species with different rooting depths, so that the strength of the competitive interactions among species depends on the rooting depth overlap (1). Suppose the species with the intermediate rooting depth is also phenotypically plastic such that its rooting depth adjusts to avoid competition. In pairwise competition with either the shallow- or deep-rooted species, this intermediate species might experience little competition because its rooting depth adjusts to avoid the roots of its competitor. When competing with both the shallower and deeper rooting species, however, this intermediate species experiences intense competition because it cannot simultaneously avoid both a shallower and deeper rooted species.

Conversely, mutualistic higher-order interactions are also possible. As an example, an antibiotic-degrading bacteria can protect antibiotic-sensitive bacteria from those producing the toxin, promoting the coexistence of three or more strains (17, 18). Interactions of this type are presumably frequent in nature, and empirical evidence for their operation

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in plant and microbial communities is accumulating (19–21). While demonstrating the operation of higher-order interactions is the key first step in this research area, the obvious follow-up question is how higher-order interactions actually shape the dynamics of the community.

Ecologists do know how interactions shape coexistence in the simplest possible case of just two competing species, and these rules form a null expectation for the influence of higher-order interactions (22–25). The following rules generally apply:

1) Coexistence is favored when intraspecific competition is stronger than interspecific competition.
2) Coexistence is disfavored by large variance among species in their intrinsic growth rates and sensitivities to competition.
3) Species abundances grow without bound when interspecific interactions are facilitative rather than harmful and stronger than self-regulating interactions.

Generalizing these rules to diverse ecosystems—even those with only pairwise interactions—is mathematically challenging as the coexistence outcomes depend on the full structure of the competitive network (26). One feasible path forward involves first ignoring this structure and analyzing how the summary statistics of pairwise interactions affect coexistence. Taking this approach, ecologists have shown that the qualitative rules for the dynamics of two competing species can still apply in diverse communities with pairwise interactions (27–33). Understanding how the statistics of higher-order interactions influence coexistence could refine our theories of species diversity in general. Indeed, recent theoretical work studying communities of fixed total abundance (34) suggests that higher-order interactions may upend classical expectations related to diversity and stability, although whether this extends to systems where the total abundance emerges from the interactions themselves remains to be explored.

Here we combine numerical simulation with a technique from statistical physics (30, 35–38) to address three questions: 1) How do the strength and variability of higher-order interactions affect species coexistence in diverse communities? 2) How do these effects compare to the rules for coexistence in pairwise systems? 3) Does considering higher-order interactions alter classical theoretical results relating diversity to the probability of coexistence (27–29)?

Results

We explored our research questions with a simple extension of the generalized Lotka–Volterra model to include third-order interactions (39–41), similar to those used in recent empirical studies (19–21). In a community with S species, the dynamics of species i's density, N_i, is given by

$$\frac{dN_i}{dt} = N_i \left(R_i - \sum_j A_{ij} N_j - \sum_j \sum_k B_{ijk} N_j N_k \right), \quad [1]$$

where R_i is species i's intrinsic growth rate, A_{ii} describes the strength of intraspecific limitation (set to 1 from now on for simplicity), and the coefficient A_{ij} describes the pairwise impact of species j on species i's growth (Fig. 1*A*). We model the higher-order interactions experienced by species i as the product of two other species' densities N_j and N_k. B_{ijk} measures the interactive impact of species j and species k on species i. We initially allow higher-order interactions to include squares (i.e., the term $N_i N_j^2$) but not cubes of abundances ($B_{iii} = 0$ scales N_i^3 for all i) because we assume that species' intraspecific regulation is fully captured by the pairwise parameter A_{ii}. We consider the case of cubic self-regulation later in *Results*. The sign of the coefficients A_{ij} and B_{ijk} can be either positive (and therefore harmful) or negative (and mutualistic).

The strength of the higher-order interactions in Eq. **1** is a simple linear function of the product of species densities, allowing the model to capture a broad range of possible interaction patterns. At the same time, this assumption may not always be ecologically realistic (42–45). To understand how this choice of functional form affects our results, we also consider a suite of alternative models where the magnitude of the higher-order interactions saturates as a function of species densities and where the strengths of the pairwise and higher-order interactions are explicitly coupled. Note that we include the coefficients B_{ijk} and B_{ikj} in Eq. **1** even though they multiply the same two abundances and therefore could be absorbed into a single parameter. In the models with more complex functional forms, however, these interactions are no longer mathematically equivalent, so we retain these terms as separate higher-order interactions to facilitate comparisons between the different modeling frameworks.

Because of the complexity of ecological models with large numbers of species, we aim to predict how species coexistence depends on summary statistics of the species' growth rates and interactions, rather than any particular parameterization. To understand how

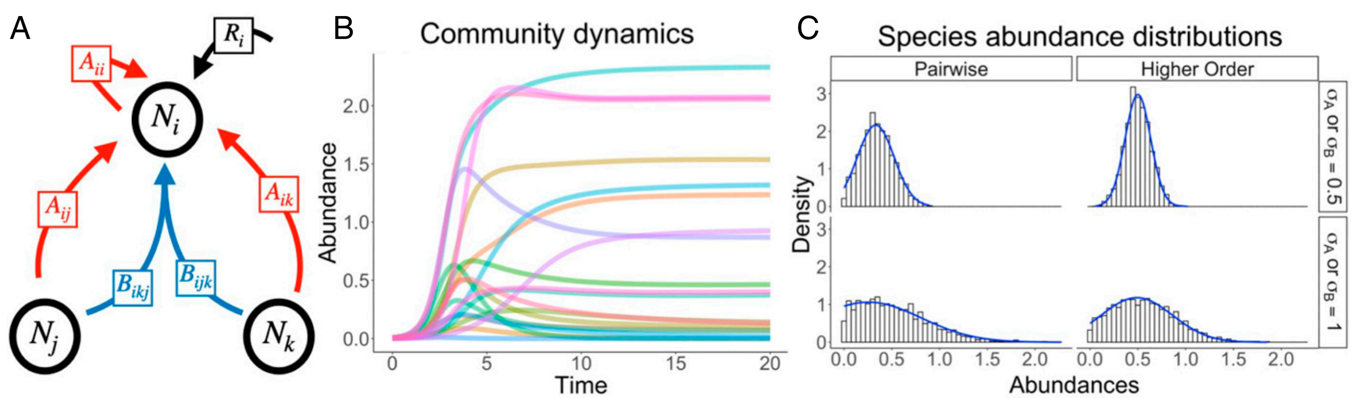

Fig. 1. (*A*) Following Eq. **1**, each species *i* in the community has an intrinsic growth rate R_i, experiences self-limitation through the parameter A_{ii}, and competes with other species through pairwise (red) and higher-order (blue) interactions. The pairwise competition coefficient A_{ij} measures the impact of species *j* on species *i*, while the higher-order coefficient B_{ijk} measures the interactive impact of species *j* and species *k* on species *i*. (*B*) In our simulations, we integrate the dynamics of Eq. **1** with either or both pairwise and higher-order interactions and record the fraction of species that are excluded and the abundances of the coexisting species at equilibrium. (*C*) Plots of the density of species with a given abundance (the species abundance distribution) for communities with either pairwise or higher-order interactions, and with different interaction variances. The solid blue curves denote the predicted species abundance distributions from the cavity method (see *Materials and Methods* for details).

the mean and variance of the growth rates (μ_R and σ_R^2) and pairwise (μ_A and σ_A^2) and higher-order (μ_B and σ_B^2) interactions influence coexistence, we varied these statistics and used both numerical simulations and analytical theory to determine how they influence the fraction of coexisting species. By choosing these statistics appropriately, we concentrate on systems whose interactions are on average harmful but, due to their variance, can sometimes be mutualistic. Because there are many more higher-order interactions than pairwise interactions among the S species, we scale the interaction strengths to account for the number of pairwise or higher-order interactions (see *SI Appendix*, section 1 for a more complete discussion). In our simulations, we drew the growth rates and interactions from normal distributions with the specified means and variances, solved the dynamical system in Eq. **1** numerically, and then recorded the abundances of all species in the community (Fig. 1*B*). This was then repeated many times for different means and variances to understand how these factors influence species coexistence. Here, rather than asking whether the S species equilibrium is stable or feasible, as in previous work (27–29, 31–33, 46, 47), we ask what fraction of the species coexist (ϕ) after the dynamics proceed from positive, randomly assigned initial species densities. This fraction is sometimes referred to as the persistence of the community (48), and it has been studied extensively in the context of mutualistic and trophic networks (48–52).

In addition to the simulation results, we use the cavity method, a technique from statistical physics (35, 36), to generate analytical predictions for how species coexistence depends on the mean and variance of species' growth rates and pairwise and higher-order interactions. The central aim of the cavity method is to characterize the distribution of abundances that a species could achieve after invading a coexisting community. The equilibrium abundances follow a distribution because the interactions themselves are sampled from probability distributions which give rise to variability in species' competitive abilities. The method then equates this distribution of invader abundances to the distribution of coexisting species abundances, permitting the derivation of a set of equations for the statistics of the species abundance distribution in the eventual community (*Materials and Methods* and *SI Appendix*, section 2.A). The resulting community composition is determined by both the species interactions and the equilibrium abundances. In a diverse community, complex interaction patterns in the species pool (like intransitivity, trophic structure, or more complicated empirically observed feedback loops) give rise to the abundances of the coexisting species (5, 53, 54), and similarly, the identity of the abundant species determines the dominant patterns in the interactions of the coexisting community (55). In some sense, the cavity method calculation integrates over the complicated relationship between interactions and species abundances to tell us how these two effects jointly determine the coexistence patterns in our simulations. In recent work, the cavity method has successfully predicted the equilibrium species abundance distributions for a wide variety of ecological models (30, 37, 38, 56–60). Although this method is only theoretically valid in the limit of an infinite number of species ($S \to \infty$), it has been shown to describe the behavior of relatively small Lotka–Volterra communities with pairwise interactions (30, 38). Throughout our work, we implement a correction to the standard cavity method equations so that we are better able to predict coexistence in smaller communities (*Materials and Methods* and *SI Appendix*, section 2.E).

We use the cavity method to calculate the species abundance distribution at equilibrium for a range of means and variances describing the pairwise and higher-order interactions in the community. The fraction of species with positive abundances yields the fraction of coexisting species ϕ (see *Materials and Methods* for the equations and *SI Appendix*, section 2.A for the full calculation). Importantly, our predicted abundance distributions closely match their simulated counterparts (Fig. 1*C*). To facilitate comparisons between our analytical theory and simulation results, we concentrate on the case of fully random interactions with specified statistics, but the cavity method calculations could be generalized to incorporate additional structure in the interaction network (38).

Our first main result is that the cavity method does an excellent job predicting the fraction of coexisting species for the Lotka–Volterra model with higher-order interactions. When the community was very small (only five species), we found considerable divergence between the simulation outcomes and the cavity method predictions, and thus, our theory is not predictive for such small systems (Fig. 2). At the other extreme, when the system began with 30 species, or with much larger species pools ($S = 300$) as shown in *SI Appendix*, Fig. S3, we found excellent agreement between our simulations and the cavity method predictions (Fig. 2). Importantly, even when there were only 10 species, the cavity method captured the average behavior of the simulated communities.

We first explored the effects of the pairwise interaction strengths and variances on species coexistence to provide a baseline against which to compare the effects of higher-order interactions. In pairwise systems, increasing the variance in the interaction strength reduces the fraction of species that coexist. This happens because just like in models with only two competitors, variability in the interspecific interaction strengths favors some competitors over others (some get a better draw of interactions than others), driving the losers to exclusion (Fig. 3*A*) (30, 37, 38). Increasing

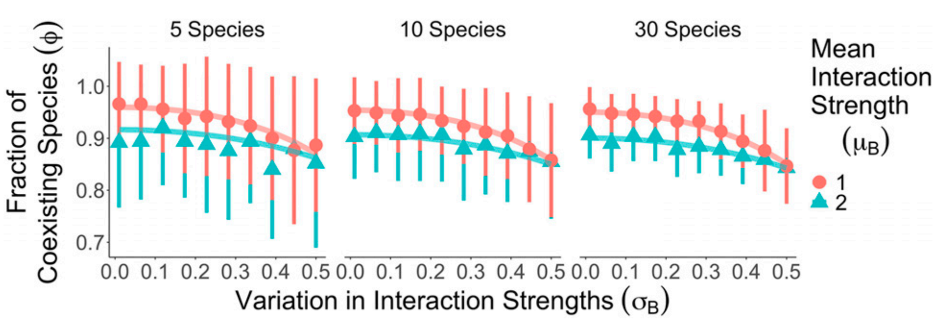

Fig. 2. Comparison between the average simulated fraction of coexisting species, shown by symbols and error bars with ±1 SD, and cavity method predictions of that fraction, shown by the continuous lines. Results are shown for different community sizes—(*Left*) 5 species, (*Middle*) 10 species, and (*Right*) 30 species—and different mean interaction strengths (colors and shapes) across a range of variances in the higher-order interaction strengths. Simulation means and SDs were obtained for 100 realizations of the interactions per parameter combination. In all panels, the mean intrinsic growth rate was $\mu_R = 1.5$, and its SD was $\sigma_R = 0.5$.

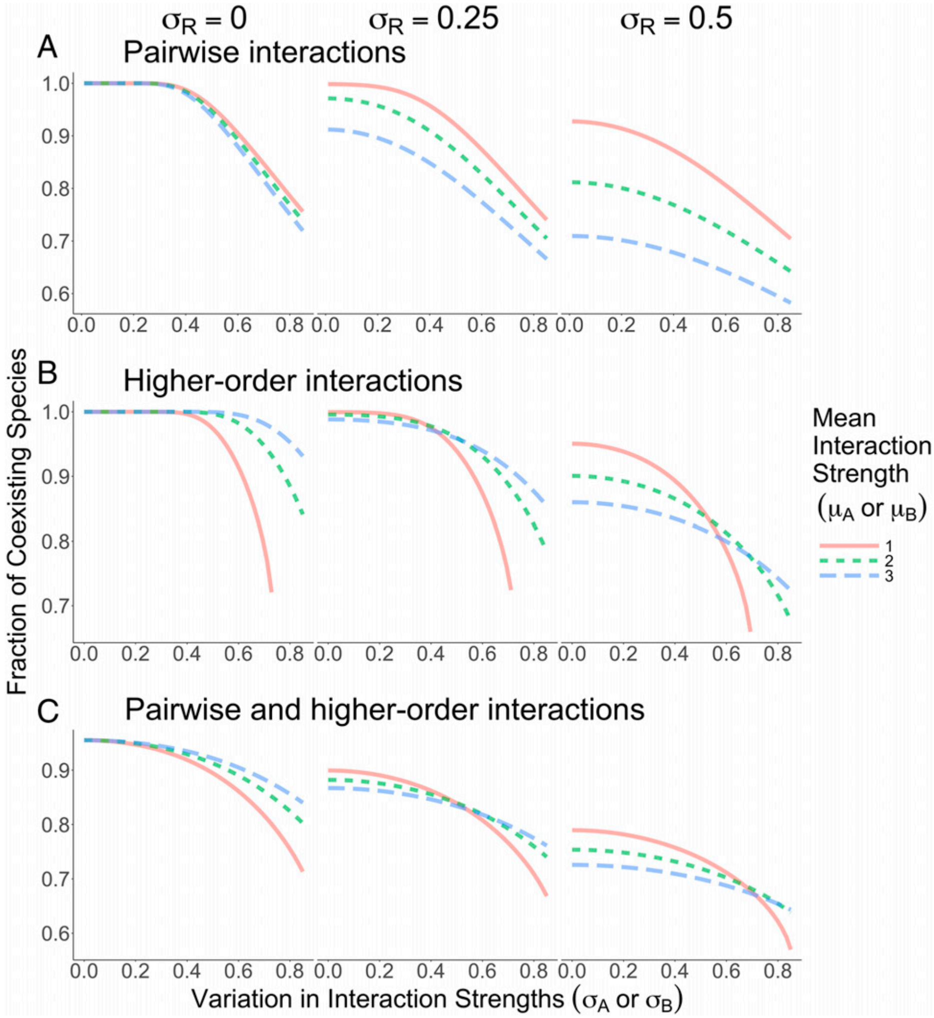

Fig. 3. Predictions for how the fraction of coexisting species (ϕ) depends on the variation in interaction strengths assuming (*A*) only pairwise, (*B*) only higher-order, or (*C*) both types of interactions in the system. We plot results for three different variations in intrinsic growth rates (σ_R) and three different mean interaction strengths (μ_A or μ_B). In *C*, the pairwise interaction statistics are $\mu_A = 1$ and $\sigma_A = 0.5$. In *A*–*C*, the mean growth rate is $\mu_R = 1.5$. Simulation results in *SI Appendix*, Figs. S4 and S5 closely match these predictions.

the variation in growth rates has an analogous effect, which can be seen, for example, by comparing the blue lines (where mean interaction strength is fixed) across Fig. 3*A* (30, 37, 38).

Increasing the mean pairwise interaction strength, while keeping the intraspecific interaction strength constant ($A_{ii} = 1$), reduces coexistence because the interspecific interactions become on the whole more competitive (Fig. 3*A*) (30, 37, 38). With more species exerting greater effects on others than on themselves, the system exhibits less coexistence. This decrease in coexistence becomes most apparent when species' competitive imbalances increase, either through variation in the intrinsic growth rates or variation in interaction strengths. We can attribute this behavior to the relative strength of intraspecific to interspecific interactions because if instead species with a common intrinsic growth rate experience a concomitant increase in self-regulation as their interspecific interactions become more competitive, the mean competition strength has no impact on coexistence (*SI Appendix*, section 2.D) (30, 37).

Our second main result is that some of the lessons from how pairwise interactions affect coexistence translate over to the effects of higher-order interactions. For example, increased variability in higher-order interaction strength (and intrinsic growth rates) reduced species coexistence (Fig. 3*B*) because, just as in the pairwise case, this variability favors some species over others, and the losers get excluded. Similarly, as long as the variation in higher-order interaction strength was relatively low, and species differed in their intrinsic growth rates, more harmful higher-order interactions along with constant self-regulation reduced coexistence.

However, our third main result is that higher-order interaction strength differed markedly from pairwise interaction strength in its effects on species coexistence in one important way. Note that when species shared identical intrinsic growth rates or variation in the higher-order interaction strength was high, more harmful higher-order interactions increased, rather than decreased coexistence (Fig. 3*B*). This coexistence-promoting effect of more harmful higher-order interactions contrasts with the effect of more harmful pairwise interactions and extends to systems with a mix of pairwise and higher-order interactions (Fig. 3 *B* and *C*; see also *SI Appendix*, Fig. S6, where we explicitly plot how the fraction of coexisting species depends on the mean interaction strength).

The beneficial effect of more harmful higher-order interactions emerges because such interactions reduce the likelihood of a mutualism that can cause some species to become highly abundant. When higher-order interactions are only weakly harmful on average but highly variable, some species experience net facilitation from the most abundant species, creating runaway abundances when the mutualisms are reciprocal. This is analogous to the behavior that can emerge in two-species systems when

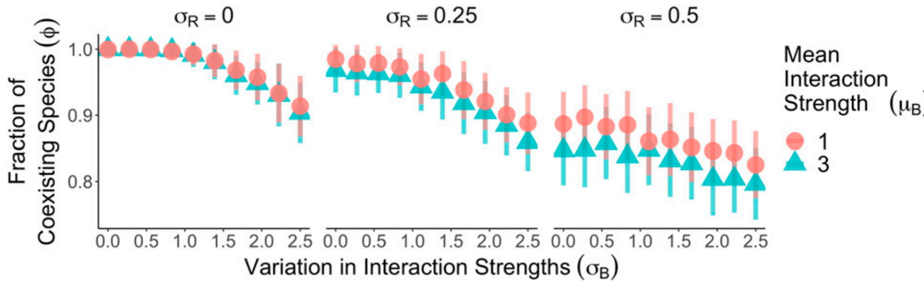

Fig. 4. The fraction of coexisting species for three variations in intrinsic growth rate (σ_R) when the level of saturation is $h = 3$. These plots are analogous to Fig. 3*C*, except now with saturating higher-order interactions. The symbols show the mean of the simulation results for over 100 replicate communities, and the error bars denote 1 SD. In all panels, the number of species $S = 30$, the mean growth rate $\mu_R = 1.5$, the mean pairwise interaction strength $\mu_A = 1$, and the variation in pairwise interaction strengths $\sigma_A = 0.25$.

the interspecific mutualisms are stronger than the self-regulating terms. Indeed, the dominant species in communities with only weakly harmful higher-order interactions tended to be those that facilitate one another, while differentially harming the species with lower abundances (*SI Appendix*, section 3.D). This effect occurs for both pairwise and higher-order interactions (55, 61) (*SI Appendix*, section 3.D), but because higher-order interactions scale with the square of the average abundance, the effect of strong interspecific mutualism becomes more pronounced. In fact, when higher-order interactions are on average mutualistic and self-regulation is relatively weak, the mean abundance grows indefinitely. In sum, even though more harmful interspecific interactions should decrease coexistence by overpowering intraspecific regulation, they simultaneously decrease the likelihood of runaway mutualisms, which greatly benefits coexistence.

To further evaluate this hypothesis, we simulate two additional models where higher-order interactions might not generate runaway abundances because their effect saturates with species density. In the first model form, the scalar B_{ijk} of Eq. **1** was replaced by $\frac{B_{ijk}}{1+hN_jN_k}$ so that higher-order interactions saturate at a rate controlled by the parameter h. If $h = 0$, we recover the model in Eq. **1**, while if $h > 0$, the higher-order interaction strengths level off with increasing densities. With this modification, the higher-order interaction properties affect coexistence in a manner identical to the pairwise interactions. Namely, more harmful higher-order interactions simply lead to less coexistence (Fig. 4). In the second model form, we explicitly tie the strength of each higher-order interaction to a particular pairwise interaction. We now interpret the higher-order interaction measured by the parameter B_{ijk} as modifying the underlying pairwise interaction with coefficient A_{ij}. Then, we constrain the total effect of all higher-order interactions acting on the pairwise interaction between i and j to have at most the same magnitude as the pairwise effect. Mathematically, this means that the net interaction species i experiences through the pairwise interaction with species j and all of the higher-order interactions modifying this pairwise interaction (i.e., the term $-A_{ij}N_j - \sum_k B_{ijk}N_jN_k$) cannot exceed $2A_{ij}N_j$ in absolute value. In some sense, higher-order interactions also saturate with species densities in this model because when large densities cause very strong higher-order interactions, these higher-order interactions are replaced with either no interaction or twice the strength of the pairwise interaction they modify. With this second model form, more harmful higher-order interactions once again lead to fewer coexisting species because beneficial higher-order interactions ameliorate pairwise competition but cannot not give rise to net facilitation (Fig. 5). In sum, modeling higher-order interactions with saturating functional responses eliminated the counterintuitive effect of mean higher-order interaction strength, while preserving the effects of variation in the growth rates and interactions. In the *SI Appendix*, section 3.E, we show that introducing cubic self-regulation has a similar effect on coexistence as saturating higher-order interactions.

Our final result is that the classic finding that the probability of coexistence of all S species declines with species richness in systems with pairwise interactions (27–29, 62) also holds in systems with higher-order interactions. Theory predicts that as the number of species increases, communities can tolerate less variability in their interactions before losing their first species (28, 31, 33, 63, 64). We call the value of the interaction variability at which the first species goes extinct the "critical interaction variability," denoted $\tilde{\sigma}_A$ and $\tilde{\sigma}_B$ for pairwise and higher-order interactions respectively. Notably, recent theory found that under three-way higher-order interactions, this critical interaction variability exhibited no systematic dependence on the number of species (34), albeit using a different mathematical framework from the one we have considered. By contrast, in simulations of our model, the critical interaction variability for both pairwise and higher-order interactions decreased as a function of the number

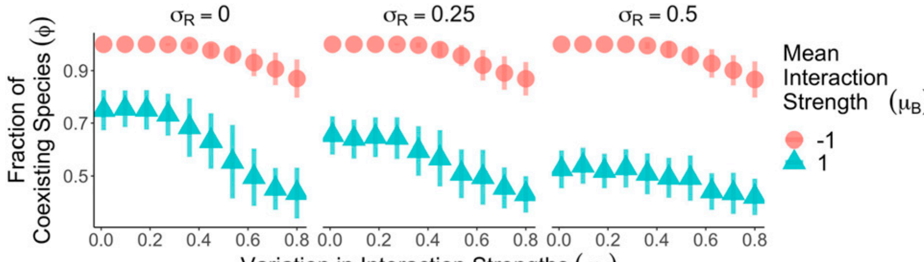

Fig. 5. The fraction of coexisting species for three variations in intrinsic growth rate (σ_R) when higher-order interactions cannot exceed the strength of the pairwise interactions. These plots are analogous to Fig. 3*C*, except now the strengths of the higher-order interactions are constrained by the pairwise interactions. The symbols show the mean of the simulation results for over 100 replicate communities, and the error bars denote 1 SD. In all panels, the number of species $S = 30$, the mean growth rate $\mu_R = 1.5$, the mean pairwise interaction strength $\mu_A = 2$, and the variation in pairwise interaction strengths $\sigma_A = 0.5$.

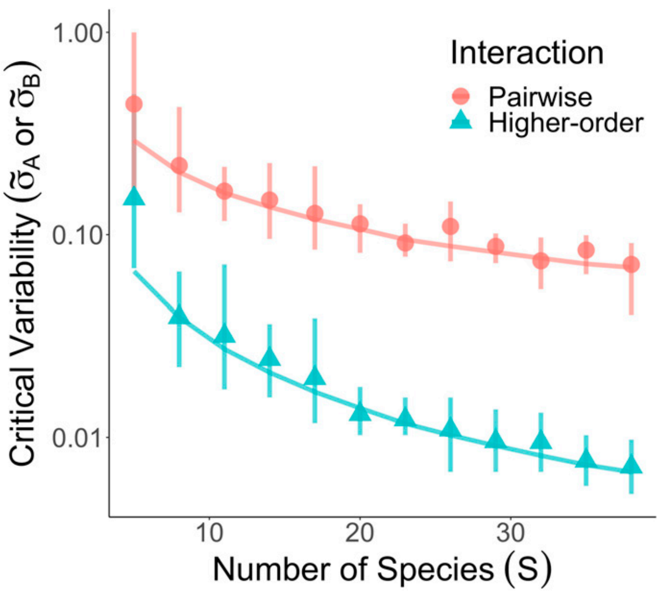

Fig. 6. The critical interaction variability as a function of the number of species in the community with either only pairwise or only higher-order interactions. The critical interaction variability is the smallest value of the variability in the pairwise interactions ($\tilde{\sigma}_A$) or the higher-order interactions ($\tilde{\sigma}_B$) at which the first species goes extinct. The circles and triangles show the average of simulation results for 10 replicate communities, and the error bars denote the minimum and maximum value found in all 10 simulations. The lines are predictions based on our cavity method framework in Eq. **4**. We set $\sigma_R = \mu_A = \mu_B = 0$ to make the comparison with previous theory more direct, and we set the mean growth rate to be $\mu_R = 1.5$.

of species in the community (Fig. 6). In fact, the critical higher-order interaction variability decreased more quickly with species richness than the pairwise variability. Note that to obtain this result, we removed the scalings on the interaction statistics thus far imposed to remove any effect of diversity on the total effect of the interactions. Predictions for the critical variability from our cavity method framework closely matched the simulation results (see the lines in Fig. 6 and *Materials and Methods* for the corresponding equations).

Discussion

Through the analysis of models for two competing species, ecologists have derived simple rules for species coexistence (spelled out in the Introduction) (22, 23). We know that these rules do not formally apply to systems with more than two species, including those with purely pairwise interactions (26). Nonetheless, our findings here suggest that these simple rules may strongly guide expectations for the interpretation of coexistence in large systems, even those organized by higher-order interactions, as long as the network of interactions has a random structure. Moreover, the cavity method can be used to develop theory for how higher-order interactions impact species coexistence in such systems.

The central question of our study was how the strength and variability in higher-order interactions influence species coexistence (question 1 from the Introduction). We found that as higher-order interaction strengths become more variable between the species, fewer species coexisted. When interactions are heterogeneous and randomly assigned to species, species differ in their sensitivity to competition, and the poorest competitors get excluded. This behavior is directly analogous to results from pairwise interactions (27–31). The average strength of higher-order interactions, on the other hand, exhibited a more complex effect on coexistence. When species differed considerably in their intrinsic growth rates and interaction strengths had little variation, more harmful interspecific higher-order interactions generated less coexistence. This result follows from the two-species rule that more harmful interspecific interactions relative to intraspecific regulation are destabilizing (30, 31).

However, when the variation in higher-order interactions was large relative to the variation in intrinsic growth rates, we found the opposite dependence—more harmful higher-order interactions counterintuitively produced more coexistence. Even here, though, the two-species rules prove useful. Less harmful mean higher-order interactions introduced more mutualistic interactions, which even in two-species systems can cause abundances to grow without bound when they overwhelm self-regulation. The subset of species engaged in this mutualistic rise were the most abundant (*SI Appendix*, section 3.D) and greatly harmed species that happened to engage in harmful higher-order interactions with these species. When the strength of higher-order interactions instead saturated as a function of species abundance, more harmful higher-order interactions once again produced less coexistence because the likelihood of strong mutualistic interactions, and hence groups of highly dominant species, was reduced.

While variation in higher-order interactions harmed coexistence regardless of whether or not these interactions saturated with species densities, the effect of the mean interaction strength depended strongly on the model form. As a result, increased variation in both pairwise and higher-order interactions reduced coexistence, but the strength of linear higher-order interactions had qualitatively new effects on coexistence relative to pairwise interactions, thereby answering question 2 in the Introduction. In principle, higher-order interactions likely saturate with species densities in natural communities (42–45), but it is unclear whether species abundances in nature lie in a regime where a linear functional response is a reasonable description of these saturating curves. It is worth noting that the higher-order interactions currently fit to data usually involve this linear assumption (mainly as a byproduct of very reasonable data limitations), and if it is valid, our theory suggests that more harmful higher-order interactions may favor coexistence (19). However, this linear description of higher-order interactions may not be a good one, in which case we suspect that the predicted dynamics from these fitted models would not be realistic (19, 65). If indeed, better data supported higher-order interactions that saturate with species abundances or are tightly coupled to pairwise interaction strengths, more harmful higher-order interactions could favor fewer not more coexisting species. The possibility of empirical support for higher-order interactions constrained by the pairwise effects is interesting given that such constraints are central to previous theoretical work showing widespread coexistence resulting from higher-order interactions (17, 66). All of this points to the fact that determining both the parameter values and the functional forms of higher-order interactions supported by empirical data is a crucial next step in this research area.

Thus far, we have argued that higher-order interactions with specific functional forms and constraints can favor coexistence but that more generic, randomly sampled higher-order interactions have similar effects on coexistence as pairwise interactions. This latter message also holds when exploring how species richness affects opportunities for coexistence. Consistent with classic studies modeling pairwise interactions (27–29), we found a loss of coexistence with increasing diversity in our model, for both pairwise and higher-order interaction systems. Importantly, this effect arose from fewer species having positive equilibrium abundance rather than an increasingly unstable equilibrium with all species present. Previous theoretical studies have also found that feasibility is lost before stability in Lotka–Volterra models (33, 63, 64), and we have found the same behavior when incorporating higher-order interactions. Although these feasibility- and stability-based approaches differ quantitatively in their requirements for the coexistence of all species, they have identified the same qualitative relationship between interaction variability and species richness—namely, that communities tolerate less variability in pairwise interspecific interactions as they become more diverse (27–29). This makes the recent findings of Bairey et al. (34), showing that species diversity has no effect on the variability of three-way, higher-order interactions required to disrupt coexistence, particularly surprising. In contrast, not only did we find that the critical variability of both pairwise and higher-order interactions declines with species richness, this decrease was more severe with higher-order interactions. We believe the discrepancy lies in the different modeling frameworks. In the replicator equation used by Bairey et al. (34), all abundances must sum to one, and thus, higher-order interactions become weaker as the number of species increases because the products of relative abundances near zero quickly become very small. In the generalization of the Lotka–Volterra model we consider, every species has an abundance that is fixed by its intrinsic growth rate and its self-regulation. As a result, the variability in higher-order interactions and species richness affects opportunities for coexistence in the same qualitative way that pairwise interactions do, answering question 3 from the Introduction.

Our results also suggest that the number of interactions in a community plays an important role in determining their effects on coexistence. When we removed the scalings which accounted for the larger number of higher-order than pairwise interactions, we found that higher-order interactions had a stronger impact on coexistence simply because there were more of them. This fact suggests that higher-order interactions involving more than three species should have even smaller critical variabilities than those we predicted for three-way higher-order interactions. On the other hand, if in nature the measured strength of higher-order interactions tends to decrease as a function of the number of species involved, then our theory that scales out the number of interactions may be a more accurate representation of real systems. In this case, it is less clear how the order of the interactions (i.e., the number of species they involve) will affect the critical variability because the clear effect of the number of possible interactions is muted. The relationship between the order of an interaction and its empirically derived strength is therefore an important outstanding question for both theoreticians deriving higher-order interactions from mechanistic underpinnings and empiricists tackling the problem in nature. We have focused here on three-way higher-order interactions, both to maintain analytical tractability and because interactions of larger orders are exceedingly difficult to measure empirically (19). A principal direction for future work is to understand which interaction orders ought to be included in phenomenological models and how the orders of these interactions impact macroecological properties.

One important caveat of our cavity method results that they are only valid when species coexist at a stable equilibrium (67). Species may instead coexist in limit cycles (68) or exhibit chaotic dynamics (69, 70), in which case it is no longer clear how the mean and variance of the interactions affect coexistence. In the parameter regimes we focused on, nonequilibrium dynamics were rare (but see *Materials and Methods* and *SI Appendix*, section 3.B for a complete discussion of where they can appear). Nevertheless, complex dynamics with widespread coexistence have been shown to emerge in diverse models with randomly sampled interactions when intraspecific competition is similar to interspecific competition (71) or in the regime with multiple equilibria when there is also external immigration (59). We did find multiple equilibria when higher-order interactions are saturating (*Materials and Methods* and *SI Appendix*, section 3.B), suggesting that nonequilibrium coexistence may appear in model communities with higher-order interactions of specific functional form.

Our theory generates a null expectation for how higher-order interactions influence species coexistence assuming they are on average harmful (mutualistic, nonsaturating higher-order interactions simply cause abundances to explode), and there is no structure to the higher-order interaction network. Indeed, we have shown with the cavity method that when higher-order interactions are sampled at random, they do not generate ecosystems with perfect coexistence. However, ecological interactions in nature are likely to be nonrandom. If the network of higher-order interactions has some complex structure, then it may have a fundamentally different effect on coexistence than suggested here. For example, we assumed that higher-order interactions involving the square of abundances [the intraspecific higher-order interactions (19)] follow the same distribution as all other higher-order interaction terms. If instead the intraspecific higher-order interactions are stronger than their interspecific counterparts, they might be broadly stabilizing (39). Similarly, higher-order interaction strength may be correlated with the underlying pairwise interactions in the system and thereby give rise to more or less coexisting species than predicted here. At this point, however, it is unclear how to impose additional constraints on the parameters of the model we consider without specifying a mechanism for the interactions in the ecosystem (72, 73). Moreover, deviations from truly random interactions may not alter the qualitative conclusions we have focused on. If specific interaction structures were found to change our main conclusions, it is possible to incorporate these structures into the cavity method (37, 61), allowing one to understand the mechanisms by which nonrandom interaction structures benefit or harm coexistence.

In this context, a central challenge in this field is to derive phenomenological higher-order interaction parameters either from 1) nature or 2) an underlying mechanistic process in a model. Although both approaches could refine the conclusions we have derived based on randomly sampled interactions, an empirically determined interaction network can be used to interrogate specific patterns in the structure of the interactions. At the same time, the number of possible higher-order interactions grows quickly with the number of species and the order of the interactions themselves, making it very difficult to estimate all possible interactions experimentally and necessitating new empirical approaches to circumvent this challenge. This is where the cavity method may prove particularly useful in an empirical context. To predict coexistence with the cavity method, one only needs estimates of the mean and variability of the interactions (61). In other words, not every interaction needs to be measured. As a result, the cavity method provides a powerful framework for empiricists to compare the potential effects of higher-order interactions across different ecosystems. The theory can be used to generate a baseline level of coexistence expected from randomly assigned higher-order interactions, and thus, deviations from such predictions can be indicators of more complex ecological structure in nature.

Materials and Methods

Simulation Details. In our simulations, we used the Livermore Solver for Ordinary Differential Equations (LSODA) from the deSolve v1.25 package (74) in R version 3.6.1. We sample the species' growth rates and interaction parameters from normal distributions with the statistics we specified in *Results*. In *SI Appendix*, Fig. S8, we show that our predictions still perform well for uniformly distributed interactions. We start each simulation with all species present at randomly selected abundances in the interval [0, 1]. We integrate the dynamics for 10^7 time steps and then record the abundances. We designate species with abundance smaller than 10^{-14} to be extinct. We then test whether or not we have reached equilibrium by computing each of the coexisting species per capita growth rates and comparing them to a cutoff of 0.01. We also test if any of the excluded species can invade the equilibrium using the same growth rate threshold. If the dynamics did not reach equilibrium or an excluded species can invade, we remove the simulation run for our data. This occurs rarely and only for large values of σ_A or σ_B (see *SI Appendix*, section 3 for further discussion of our simulation methods). The code used to run simulations and generate figures is available on GitHub at https://github.com/theogibbs/CavityHOIs (75).

Cavity Method Equations. In *SI Appendix*, section 2.A, we provide the cavity method calculation in detail. In this and the following sections, we discuss the calculation without the finite-size corrections that we mentioned in the main text, but see *SI Appendix*, section 2.E for the complete analysis. The predicted distribution for the coexisting species is a truncated normal distribution (Fig. 1*C*). We use μ_0 and σ_0 to denote the mean and SD of this distribution before truncating it. We derive equations in *SI Appendix*, section 2.A for how these statistics relate to the growth rate and interaction statistics. Specifically, we find that

$$\begin{aligned}\mu_0 &= \mu_R - \mu_A\phi\langle N\rangle - \mu_B\phi^2\langle N\rangle^2 \\ \sigma_0^2 &= \sigma_R^2 + \sigma_A^2\phi\langle N^2\rangle + \sigma_B^2\phi^2\langle N^2\rangle^2,\end{aligned} \qquad [2]$$

where ϕ is the fraction of coexisting species (as in *Results*), $\langle N\rangle$ is the mean of the coexisting species, and $\langle N^2\rangle$ is the second moment of the coexisting species. In *SI Appendix*, section 2.A, we actually treat a more general case in which the pairwise interaction coefficients can be correlated across the diagonal (i.e., $\langle A_{ij}A_{ji}\rangle - \langle A_{ij}\rangle^2 = \rho_A\sigma_A^2/S$), but we report the simpler formulas in which $\rho_A = 0$ here. Eq. **2** can be interpreted as the average and variance in abundances of a given coexisting species. Specifically, we can solve Eq. **1** for a focal abundance N_i and then compute the mean and variance of the resulting solution using both the unknown properties of the coexisting species (ϕ, $\langle N\rangle$, and $\langle N^2\rangle$) as well as the statistics of the growth rates and interactions. In fact, previous work (76, 77) used this method to predict the equilibrium properties of the Lotka–Volterra model without invoking the cavity method. In Eq. **2**, ϕ, $\langle N\rangle$, and $\langle N^2\rangle$ are all unknowns, but they are related to μ_0 and σ_0. Let $P(N_0|\,\mu_0, \sigma_0)$ be the nontruncated normal distribution with mean μ_0 and SD σ_0. Then, ϕ is the integral of $P(N_0|\,\mu_0, \sigma_0)$ over the positive abundances. Similarly, $\langle N\rangle$ is the average of $P(N_0|\,\mu_0, \sigma_0)$ over the positive abundances. We find that

$$\begin{aligned}\phi &= \int_0^\infty P(N_0|\,\mu_0, \sigma_0^2)\, dN_0 \\ \langle N\rangle &= \frac{1}{\phi}\int_0^\infty N_0 P(N_0|\,\mu_0, \sigma_0^2)\, dN_0 \\ \langle N^2\rangle &= \frac{1}{\phi}\int_0^\infty N_0^2 P(N_0|\,\mu_0, \sigma_0^2)\, dN_0,\end{aligned} \qquad [3]$$

where the factors of $1/\phi$ normalize the integral. All in all, we have three equations for three unknowns that we can solve numerically to determine the species abundance distribution.

The Limit in Which All Species Coexist. The formulas in Eq. **2** cannot easily be solved since μ_0 and σ_0^2 are not the same as $\langle N\rangle$ and $\langle N^2\rangle - \langle N\rangle^2$, respectively, because the values of $\langle N\rangle$ and $\langle N^2\rangle - \langle N\rangle^2$ both depend on the fraction of species that are excluded. However, when $\phi = 1$, $\mu_0 = \langle N\rangle$, and $\sigma_0^2 = \langle N^2\rangle - \langle N\rangle^2$ and the equations in Eq. **2** simplify considerably. Because our theory is only justified in the $S \to \infty$ limit, this calculation is not fully consistent with the cavity method, since when S is large enough, a nonzero fraction of species will always be excluded. Nonetheless, we find that it still captures the qualitative dependence of the fraction of coexisting species on the mean and variance in species abundances reasonably well. In fact, in the next section, we use this limit to quantitatively predict the results of our simulation results for the critical variabilities.

When every species has the same growth rate ($\sigma_R = 0$) and there are only pairwise interactions in the ecosystem $\mu_B = \sigma_B = 0$, we find that $\mu_0 = \frac{\mu_R}{1+\mu_A}$ and $\sigma_0^2 = \frac{\sigma_A^2}{1-\sigma_A^2}\mu_0^2$. As a result, we find that σ_0 is directly proportional to μ_0. Because the ratio μ_0/σ_0 determines ϕ (*SI Appendix*, section 2.B), this calculation suggests that, at least in the limit where all species coexist, μ_A should have no impact on coexistence (up to finite-size corrections, which we are neglecting here). Interestingly, this dependence is true throughout the full range of σ_A values we consider, rather than just for small σ_A values when we are close to the $\phi = 1$ limit. A straightforward calculation (which we include in *SI Appendix*) shows that the same analysis predicts the effect of mean pairwise competition strength when species do not have identical growth rates ($\sigma_R > 0$). When there are higher-order interactions (when μ_B and σ_B are nonzero), we must now solve quadratics in Eq. **2** to get μ_0 and σ_0^2. In *SI Appendix*, section 2.C, we find the behavior that we report in *Results*–namely, that the qualitative effect of the mean higher-order interaction strength changes for different values of σ_0, which is in turn determined by σ_R and σ_B. Moreover, as μ_0 becomes smaller, the ratio μ_0/σ_0 actually increases because σ_0 depends on μ_0. At the same time, when $\sigma_R > 0$, this dependence is reversed, and the ratio μ_0/σ_0 increases as μ_0 increases.

Deriving the Critical Variabilities. To find the critical variabilities for pairwise and higher-order interactions, we once again consider the limit where $\phi = 1$. We use our solutions for μ_0 and σ_0 to compute the expected minimum of S samples from the normal distribution with mean μ_0 and SD σ_0. Let $\kappa(S)$ be the expected maximum value of S samples from the standard normal distribution. Then, the expected minimum of our predicted normal distribution is $\mu_0 - \kappa(S)\sigma_0$. In our formulas, we also include the approximation $\kappa(S) \lesssim \sqrt{2\log(S)}$, so that we can interpret the functional behavior more easily, but we use computationally determined estimates of $\kappa(S)$ in Fig. 6 because they are significantly more accurate. By setting the expected minimum to zero and solving for $\tilde{\sigma}_A$ or $\tilde{\sigma}_B$, we find that the (average) critical variabilities are given by

$$\begin{aligned}\tilde{\sigma}_A &= \frac{1}{\sqrt{S}}\frac{1}{\sqrt{\kappa(S)^2+1}} \gtrsim \frac{1}{\sqrt{S}}\frac{1}{\sqrt{2\log(S)+1}} \\ \tilde{\sigma}_B &= \frac{1}{S\mu_R}\frac{\kappa(S)}{1+\kappa(S)^2} \gtrsim \frac{1}{S\mu_R}\frac{\sqrt{2\log(S)}}{1+2\log(S)},\end{aligned} \qquad [4]$$

where the first factors of $S^{-1/2}$ and S^{-1} come from the interaction scalings that we removed in this analysis. These predictions work well (Fig. 6), even though they are based on a series of approximations. Note that the prediction for $\tilde{\sigma}_B$ involves the mean growth rate μ_R because σ_0 depends on μ_0 which in turn depends on μ_R, as we discussed in the previous section.

Multiple Equilibria. Previous work on communities with only pairwise interactions showed that in the regime where σ_A is large, multiple stable equilibria are possible (30, 38). We find the same behavior here (*SI Appendix*, section 3.B). By contrast, we show that when σ_B is large in communities with only higher-order interactions, there are not multiple equilibria, because the dynamics undergo unbounded growth in this regime. This unbounded growth is an unrealistic feature of the multilinear model we have considered. It also occurs in some regimes of the pairwise Lotka–Volterra model (30). In a model with only higher-order interactions, however, the unbounded growth regime appears to occur at a smaller value of σ_B than the regime where there could be multiple equilibria, meaning that we do not observe multiple equilibria in our simulations of Eq. **1** (*SI Appendix*, Fig. S9). However, when we modify Eq. **1** to use saturating higher-order interactions, we once again find multiple stable equilibria (*SI Appendix*, Fig. S10), suggesting that these more complicated dynamics may still occur in models with higher-order interactions as long as unbounded growth is prevented.

Data, Materials, and Software Availability. Simulation code and data have been deposited in GitHub (https://github.com/theogibbs/CavityHOIs) (75). All other study data are included in the article and/or *SI Appendix*.

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