Mutualism Destabilizes Communities, but Competition Pays the Price

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Abstract

A classic result in theoretical ecology states that an increase in the proportion of mutualistic interactions in unstructured ecological communities leads to a loss of stability to external perturbations. However, the fate and composition of the species that constitute an unstable ecology community following such perturbations remains relatively unexplored. In this paper, we use an individual-based model to study the population dynamics of unstructured communities following external perturbations to population numbers. We find that while mutualistic interactions do indeed destabilize communities, the entire community is rarely wiped out following a perturbation. Instead, only a subset of the ecological community is driven to extinction, and the species that go extinct are more likely to be those engaged in a greater number of competitive interactions. Thus, the resultant community formed after a perturbation has a higher proportion of mutualistic interactions than the original community. We show that this result can be explained by studying the dynamics of the species engaged in the highest number of competitive interactions: After an external perturbation, those species that compete with such a 'top competitor' are more likely to go extinct than expected by chance alone, whereas those that are engaged in mutualistic interactions with such a species are less likely to go extinct than expected by chance alone. Our results provide a potential explanation for the ubiquity of mutualistic interactions in nature despite the known negative effects of mutualism on community stability.

Keywords: Mutualism; Individual-based model; Interspecific interactions; Ecological stability; Community ecology; Lotka-Volterra;

Introduction

One of the central questions in community ecology asks whether observed patterns of interspecific interactions can be explained using ecological principles (Dobson et al., 2020; Sherratt et al., 2009; Sutherland et al., 2013). An important notion in this regard is the 'stability' of a community i.e., its ability to withstand external disturbances, and how it is affected by interactions between the constituent species (Sherratt et al., 2009). While the effects of interaction patterns on community stability have been extensively studied in the literature (Allesina and Tang, 2012; Coyte et al., 2015; May, 1973; Qian and Akçay, 2020; Serván et al., 2018; Stone, 2020), the question of what happens to unstable communities following a perturbation has received much lesser attention. In this paper, we ask whether all species in a community go extinct after a perturbation, and if not, whether the composition of the community in terms of the interaction patterns is changed following species loss.

The interactions between two species in a community can be broadly classified into three types: competitive, cooperative (mutualistic), and exploitative (Allesina and Tang, 2012). When two competing species interact, both are adversely affected and perform worse than if the other were absent. This could be due to several reasons, including competition for shared resources or the secretion of toxins that harm members of the other species. Contrastingly, mutualistic species help each other grow, for example, by providing each other with essential resources. Finally, exploitation refers to the phenomenon where one of the two interacting species benefits from the interaction, whereas the other is debilitated. This can happen through predation or parasitism, in which individuals of one species actively consume part or whole of individuals of the other species.

Modeling all species interactions in a community through pairwise interactions (as in Lotka-Volterra type models), interspecific effects can be collected in a so-called 'interaction matrix.' The i-j^{th} entry of the interaction matrix quantifies the effect of species j on the growth rate of species i. This, of course, need not be exclusive to pairwise interactions alone, as higher-order interactions among multiple (greater than 2) species may be decomposed into multiple pairwise interactions. Diagonal entries of such a matrix capture intraspecific competition (self-inhibition) of the species. If we assume, as is often done (e.g. (Allesina and Tang, 2012; Coyte et al., 2015; May, 1973)), that interactions within the community are completely random (unstructured), this matrix can be entirely characterized by measuring the fraction of mutualistic (p_m), competitive (p_c), and exploitative (p_e) interactions present. Under such a scenario, the question of how community interaction patterns affect stability reduces to how these three numbers affect stability.

Previous theoretical studies in the infinite species richness limit have shown that for a given magnitude of self-inhibition, communities with a greater fraction of mutualistic interactions (higher p_m) are less likely to be stable (Allesina and Tang, 2012; Coyte et al., 2015) in the sense of being able to return to the same initial configuration of species abundances following an external perturbation. These results were extended to a system with finite (but large) species richness using a computational IBM (Coyte et al., 2015). The latter study also showed that higher p_m decreases the persistence of a community, *i.e.,* the probability that no species within the community will go extinct following random perturbations to species abundances. Since environmental conditions are seldom constant, perturbations are ubiquitous in nature. If communities with a large fraction of mutualistic interactions are unstable, and unstable communities are more likely to experience species loss, mutualistic communities would be less likely to be found in nature. However, this insight is difficult to reconcile with the empirical observation that reasonable number of positive interactions (mutualism and commensalism) are abundant in ecological communities (Kehe et al., 2021), with some communities almost solely comprising of mutualistic interactions (Machado et al., 2021).

Another issue in terms of community composition relates to the relative strengths of the intra-specific and inter-specific interactions. Theoretical studies (Allesina and Tang, 2012; Coyte et al., 2015; May, 1973) suggest that species-rich, randomly assembled communities are overwhelmingly likely to be unstable. This insight is congruent with the observation that the interaction networks of large microbial communities in nature often have low connectivity (Yonatan et al., 2022). If many species-rich communities are likely to be unstable, several questions arise related to their fate. For example, if an external perturbation causes some extinctions in a randomly assembled community, do all species go extinct? If not, then is the identity of the species that go extinct random, or determined by their interactions with other members of the community?

In this paper, we study the effects of interspecific interactions on both community persistence as well as resultant community composition in the face of external perturbations. We employ a stochastic individual-based model (IBM) in which we supply rules at the species level and let population-level patterns emerge spontaneously. While we focus on unstructured communities for the rest of this article, our approach is general and can easily be extended to analyze the stability of communities with arbitrary interaction structures. Our primary results indicate that perturbations to unstable communities do not necessarily result in all species of the community going extinct. Instead, we find that perturbations often result in the extinction of only a few species and the formation of a new "sub-community" with fewer species. We observe that while communities with a greater fraction of mutualistic interactions are more likely to experience extinctions of some species, the resultant community formed after the extinctions is found to have a greater fraction of mutualistic interactions than the original community, implying that species which partake in competitive interactions are more likely to be selectively removed. We then study the community dynamics to answer why species participating in competitive interactions are more likely to go extinct.

Methods

Model Overview

We present a brief overview of the model here, with all the relevant details in the following subsections. This study used an Individual-Based Model based on a previous framework (Coyte et al., 2015). In this framework, every species interacts with every other species either mutualistically, competitively, or exploitatively. Let p_m, p_c, and p_e denote the fraction of total mutualistic, competitive or exploitative interactions, respectively. Following usual conventions (Allesina and Tang, 2012; Coyte et al., 2015; May, 1973; Serván et al., 2018), we assume that all species have the same level of intraspecific competition, denoted by $-s$. To study the effects of species interactions on persistence, we initialize a community with a specified (p_m, p_c, p_e) at equilibrium determined from Lotka-Volterra dynamics. To do this, we generate an interaction matrix such that a randomly drawn interspecific interaction will be mutualism with probability p_m, competition with probability p_c, and exploitation with probability p_e. Interaction strengths are drawn from a gamma distribution. We then initialize the population with a random initial configuration of population densities, and adjust the growth rates of each species such that this initial configuration is a fixed point of the generalized Lotka-Volterra equations. We then perturb this community by killing off a fixed, relatively small number of randomly chosen individuals (for details, see below). The strength of this perturbation was sufficiently small such that no species went extinct due to the perturbation alone. Thus, any subsequent species extinctions would be driven by the dynamics of biotic interactions within the community following the perturbation. We observe how species abundances vary following such a perturbation by allowing the community to stabilize to a new steady state according to the generalized Lotka-Volterra equations.

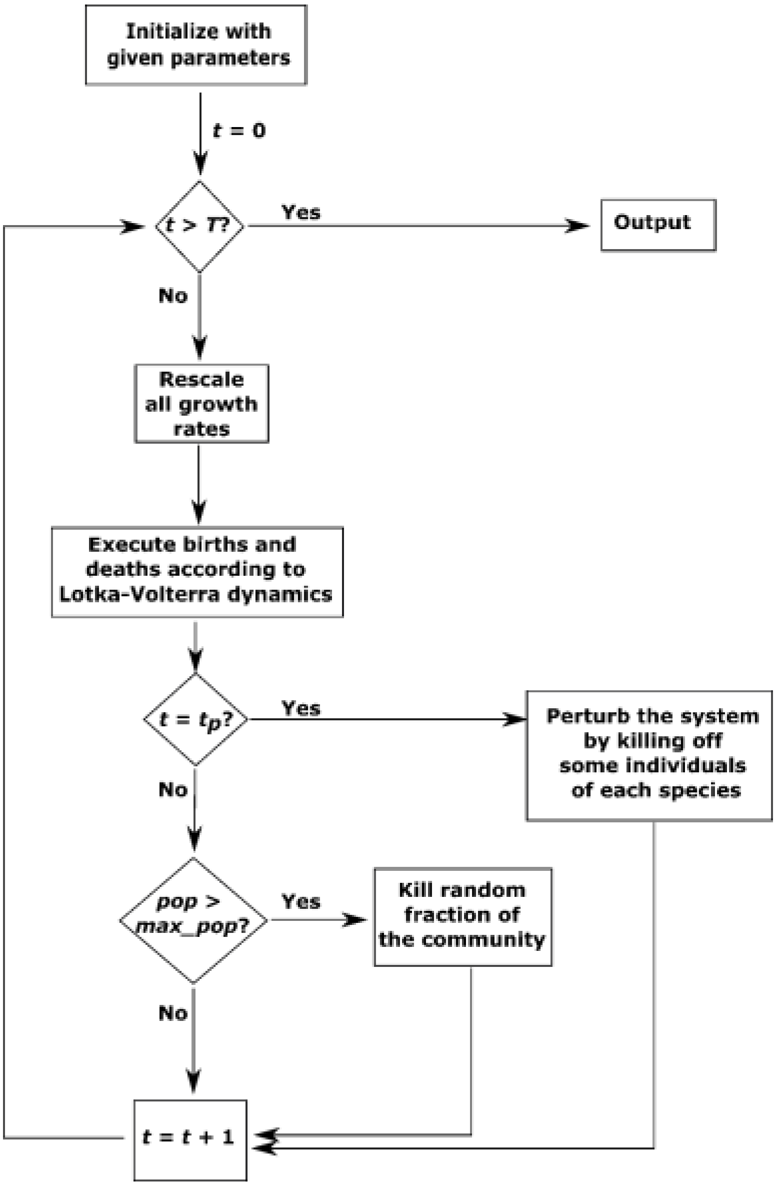

***Figure 1**: **A schematic description of our IBM.** The model is initialized with a set of parameters and a time counter set at t=0. In this diagram, t is the number of time steps in the model (Not to be confused with the actual time for which the dynamics are simulated; the two differ due to adaptive rescaling of the growth rates, see Methods section). The model is allowed to run for a total of T timesteps. The community follows Lotka-Volterra dynamics, except when t_p timesteps have elapsed, at which point the population experiences an external perturbation that kills off some individuals of each species. If at any time the Lotka-Volterra dynamics predict that the total population size $N = \sum_i N_i$ of the community exceeds a maximum allowed size, a random fraction of the community is eliminated until the total population size is below the maximum allowed size. Refer to the main text for details of the model and the parameter values chosen.*

Figure 1 provides a schematic description of our modeling scheme. To avoid the possibility of only observing the effects of specific network topologies, we randomize the specific interactions between species within a community between replicates such that only the effects of the proportion of each interaction type (as opposed to the specific network topology) were kept constant. Since an extinction in a community reduces the species richness of the community and thus reduces the number of interactions, we define a new interaction matrix following extinctions, where the interaction effects from the extinct species have been set to 0. The effects of any potential extinctions on community composition can then be studied by comparing the species richness and the interaction matrix at the beginning and the end of the simulation. For simplicity, we present results for $p_e = 0$ (i.e., communities where all interactions are mutualistic or competitive) in the main text. Results with exploitation are present in the supplementary information (Figs S1-S7).

Initialization and static parameters

The world of the simulation is a 50×50 2D square lattice with periodic boundary conditions. Each lattice site is occupied by, at most, a single individual. Every individual interacts with every other individual, and thus interactions are non-local. An individual can only reproduce if an empty space is adjacent to the focal individual. The community is initialized with S different species, all interacting with each other (this corresponds to setting the connectivity $C = 1$ in the Coyte *et al.* 2015 IBM). The total population size is capped at 90% lattice occupancy at any given time. Thus, our simulations could have a maximum of 2250 individuals coexisting at a given time in a given simulation run. An obvious drawback of this design is a limit on how many species we can include in our community. However, highly species-rich communities require each species to have high self-inhibition, at times orders of magnitude greater than the other interactions, to ensure stability of the community as a whole (Allesina and Tang, 2012; Coyte et al., 2015; May, 1973; Serván et al., 2018). Species-rich communities in which interspecific interactions are non-negligible relative to intraspecific interactions are therefore inherently unstable, and studying the effects of the distribution of interaction patterns (mutualism, competition, and exploitation) in such communities is thus of limited biological use.

Interactions and population dynamics

Population dynamics are assumed to follow the generalized Lotka-Volterra equation, which, in matrix form, reads

$$\frac{dx}{dt} = x(r + Ax) \tag{1}$$

For a community with S species, equation (1) is an S-dimensional equation. Here, r is an S-dimensional vector of intrinsic growth rates, and the interaction matrix A is an $S \times S$ matrix that captures the effects of interspecific interactions. The ij-th entry of the matrix, which we denote by a_{ij}, describes the effect of species j on the growth rate of species i. Diagonal entries of this matrix are $-s$, where s, the self-inhibition, is a parameter that controls the strength of intraspecific competition. For off-diagonal entries, the magnitude of a_{ij} is drawn from a Gamma distribution with a mean of 0.25 and a variance of 0.01. The signs of a_{ij} are determined randomly such that species i and j have a mutualistic interaction (+/+) with probability p_m, have a competitive interaction (-/-) with probability p_c, and an exploitative interaction (+/-) with probability ($1- p_m - p_c$). In the case of an exploitative interaction, each species is equally likely to be the one that is benefited. For all simulations in the main text, we set p_m and p_c such that $p_m+p_c=1$. Thus, there were no exploitative interactions in the community. Since we fill the interaction matrix according to probabilistic rules, p_m, p_c, and p_e are not the realized values in any given simulation but are the parameters used to determine the probability of an interaction being mutualistic, competitive, or exploitative. Each species is assigned a random population density, and the growth vector r is chosen such that the population densities at initialization are a fixed point for the Lotka -Volterra dynamics. Thus, given a realized interaction matrix A and a randomly initialized population vector x_0, we set the growth rate to

$$r = -Ax_0$$

This ensures that the RHS of Eq. (1) becomes zero at the initial community configuration x_0.

Perturbation and extinctions

Following a previous study (Coyte et al., 2015), we implement a perturbation five time steps into the simulation by eliminating 10% of the population of each species. The individuals eliminated are chosen at random. The simulation is then allowed to run until T=750 time steps have passed. For consecutive perturbations, as depicted in Figure 1C, we execute a secondary perturbation at 750 time steps and allow the system to run for an additional 750 time steps (*i.e.,* for a total time of *T*=1500). These particular time steps are chosen as the population attained an equilibrium well before this time in sample simulations. If, at any point in the simulation, the growth rates predicted a population size that exceeded the maximum population size allowed by the simulation, a random fraction of the population is killed off such that the new population size is below the maximum allowed population size.

Computing realized growth rates following a perturbation and an adaptive timestep

Following the perturbation, the community is no longer at the density x_0 and is thus no longer at equilibrium for the Lotka-Volterra dynamics defined by Eq. (1). While computing the resultant population dynamics, we rescale the growth rates to allow for an adaptive timestep using a method introduced in a previous study (Coyte et al., 2015). We first define a parameter g_{cap} which is the maximum magnitude of growth rate allowed in a single time step. We then rescale the realized growth rate of every species to be in $[-g_{cap}, g_{cap}]$. This rescaling lets us naturally define an adaptive time step that enables the model to simulate long times if differences in growth rates between species are large, while also allowing us to determine the fine-scale dynamics if the differences in growth rates is small (Coyte et al. 2015). More explicitly, our model can be described as follows: At each time step, we first compute the realized per-capita growth rate of species *i,* g_i, as

$$g_i(t) = r_i + Ax_i(t) - diag(A)$$

The $-diag(A)$ term simply serves to remove the effect of an individual on itself. We then find the maximum growth rate (in absolute value), $g_{max}(t) = \max_i |g_i(t)|$, and rescale the growth rate of each species as

$$g_i'(t) = \frac{g_i(t)}{g_{max}(t)} g_{cap}$$

We then advance time according to the formula

$$t' = t + \frac{1}{g_{max}}$$

The population density of species *i* at time t' is then given by

$$x_i(t') = x_i(t) g_i{}'(t)$$

which is simply the right hand side of Eq. (1) after rescaling growth rates. This constitutes one 'time step' of the model. Thus, though the model runs for only 750 (or 1500) time steps, the true 'in world' time is considerably greater than 750 (or 1500), since time is rescaled dynamically at every step. The extent of the difference between time steps of the model and simulated time within the model is controlled both by the parameter g_{cap} and by the difference between the realized growth rates g_i of the different species.

At the end of the simulation, we store the number of extant species and the new p_m, and p_c values, computed only using the extant species. We vary p_m from 0 to 1 (this automatically varies p_c from 1 to 0) and *s* from 0.15 to 1.65. Since our simulations are stochastic, we run 100 independent realizations of the simulation for any given combination of parameter values to obtain an estimate of expected (average) behavior. All parameters that are held constant for all simulations run in this paper are summarized in Table 1. All simulations were run in Python 3.6 on the PARAM-Brahma supercomputer of IISER Pune. Plots were made using either Python 3.11.4 (packages numpy 1.24.2, pandas 1.5.3, matplotlib 3.7.1, and seaborn 0.12.2) or R 4.2.2 (packages dplyr 1.1.1, rstatix 0.7.2, ggplot2 3.4.1, and ggpubgr 0.6.0). Statistical tests were run in R 4.2.2. For effect size calculations, we used the *wilcox_effsize* function from the rstatix package.

Fixed Parameter	**Value**
Total time of simulation (T)	750 (1500 for two perturbations)
Time of perturbation (t_p)	5
Proportion of each species killed in a perturbation	10%
Side Length of lattice (controls total population size)	50
Maximum allowed occupancy (% of lattice that can be occupied)	90%
Interaction strength mean	0.25
Interaction strength variance	0.01
Maximum allowed growth rate in one time step (g_{cap})	0.25

***Table 1**: Parameters that were held constant across all simulation runs. The interaction strengths were drawn from a Gamma distribution with the specified mean and variance.*

Results

To briefly recapitulate our modeling approach: we use an IBM to study the stability and dynamics of finite-species communities after perturbations. We consider communities with 7 or 15 species interacting with every other species through mutualism or competition. Our model also includes self-inhibition or intra-specific competition, i.e., when members of each species compete with con-specifics. We initiate communities in equilibrium and simulate a perturbation, where a fraction of all community individuals is killed off randomly. We then study the stability and composition of the post-perturbation community. If the original community were stable, the species composition would remain unchanged after perturbation.

Unstable communities do not usually lose all their species following a perturbation

In our study, we perturb the communities in such a way that the strength of the perturbation in itself does not lead to species extinctions. Under such a scenario, the community does not lose its entire assemblage of species to extinctions but instead forms a smaller community with fewer species (Fig 2A). We also found that following a perturbation, more species-rich communities (Fig 2A. compare red and yellow curves) and communities with a greater fraction of mutualistic interactions (i.e., higher p_m) (Fig 2A, 2B) tended to lose more species. However, community extinctions happened only when the fraction of mutualistic species was very high (Fig 2B). In line with previous studies, we found that increasing self-inhibition (intraspecific competition) promoted coexistence – all else being equal, communities with higher self-inhibition tended to retain a higher fraction of species following a perturbation (Fig 2B). Following these extinctions, the resultant community is stable, and a second perturbation did not lead to any major changes in the community composition. This is demonstrated by the fact that the number of species in the community following one perturbation was not significantly different from that of species following two perturbations (Fig 2C. Wilcoxon rank-sum text, $W = 5193, p = 0.63$). Broadly the same results hold for communities with exploitation (Figs S1, S2). To assess how the community composition changes after a fraction of the species is lost, we studied whether the proportion of interactions of each type in the post-perturbation community significantly differed from that of the original community.

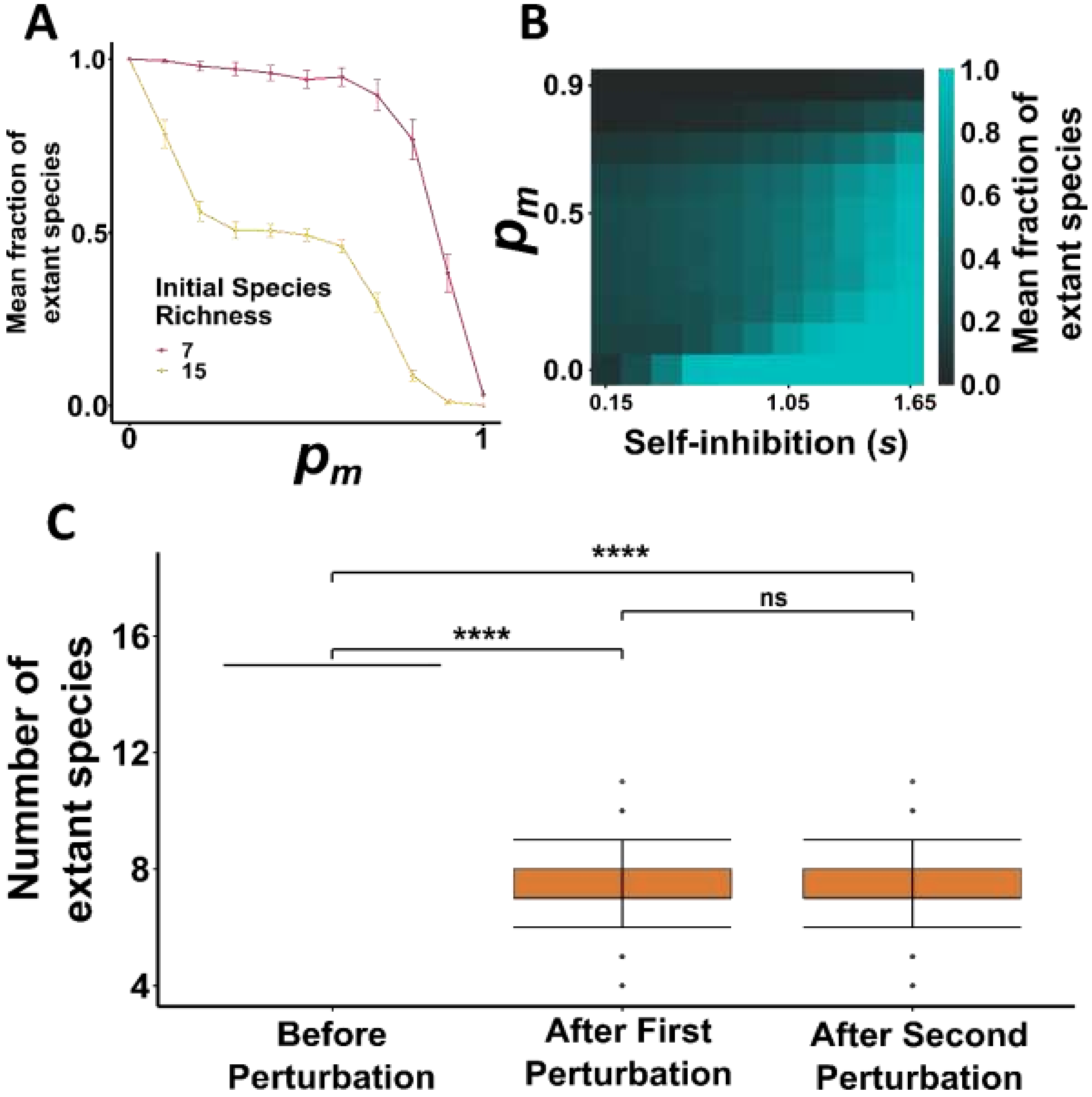

Figure 2: Fraction of extant species left after perturbation. *In all simulations, interaction strengths are drawn from a Gamma distribution such that the mean is 0.25 and the variance is 0.01.* ***(A)*** *For a given self-inhibition (here, s=1.05), the mean fraction of extant species reduces with increasing* p_m *but takes non-zero values for most values of* p_m. *The fraction of extant species is higher for a smaller community (here, seven spp) compared to a larger community (here, 15 spp). Each point is the mean of 100 realizations, and error bars represent 95% CIs.* ***(B)*** *Mean fraction of extant species (averaged over 100 realizations) increases with a higher self-inhibition across different values of* p_m *for a community of 15 species.* ***(C)*** *The number of species in an unstable community falls after one perturbation, but this does not change following subsequent perturbations. (Wilcoxon rank-sum test, W = 4892.5, p > 0.1).*

Selective Removal of Competitive Interactions

If all species have equal probabilities of going extinct after a perturbation, then, on average, we expect the proportion of competitive (or mutualistic) interactions in our randomly assembled communities to remain unchanged by the end of the simulation. Our results reveal that this is not the case. The stable communities formed after species loss had a larger fraction of mutualistic interactions and a lower fraction of competitive interactions than the initial starting communities (Fig 3A). In other words, if some species go extinct in a community following a perturbation, the overall amount of competition in the community, measured in terms of the fraction of competitive interactions, tends to reduce. In communities without exploitation, this implies that despite mutualism having been associated with decreased stability in earlier studies, the fraction of surviving mutualistic interactions would be higher than in the original community prior to perturbation. Indeed, our results indicate that communities found after perturbation have a significantly higher fraction of mutualistic interactions, as measured by a Wilcoxon rank-sum test (Fig 3A, W = 1737, $p < 0.001$), and effect size calculations indicate that this bias has a large effect (Wilcoxon effect size $r = 0.564$). This broad result is valid for a large array of p_m (Fig 3B, 3C) and self-inhibition (Fig 3C) values, suggesting that the result is robust to variation in initial community composition. Thus, even though 'more mutualistic communities' (i.e., communities with a greater fraction of mutualistic interactions between species) are less stable, perturbation-driven-extinctions in these communities do not lead to communities with a lower proportion of mutualistic interactions. However, at high p_m and high self-inhibition, the trend is reversed and, albeit for a small fraction of the parameter space, competitive interactions are lost less often than expected by chance alone (Fig 3C). Broadly the same results hold for communities with exploitation, except that it is exploitation that is lost less often than expected by chance alone, whereas both mutualism and competition may be lost either more often or less often than expected by chance alone (Figs S3-S7). Though competitive interactions may be lost either more or less often than expected by chance alone in communities with exploitation, the magnitude of the bias away from chance expectations is greater when competition is selectively lost (Fig S6).

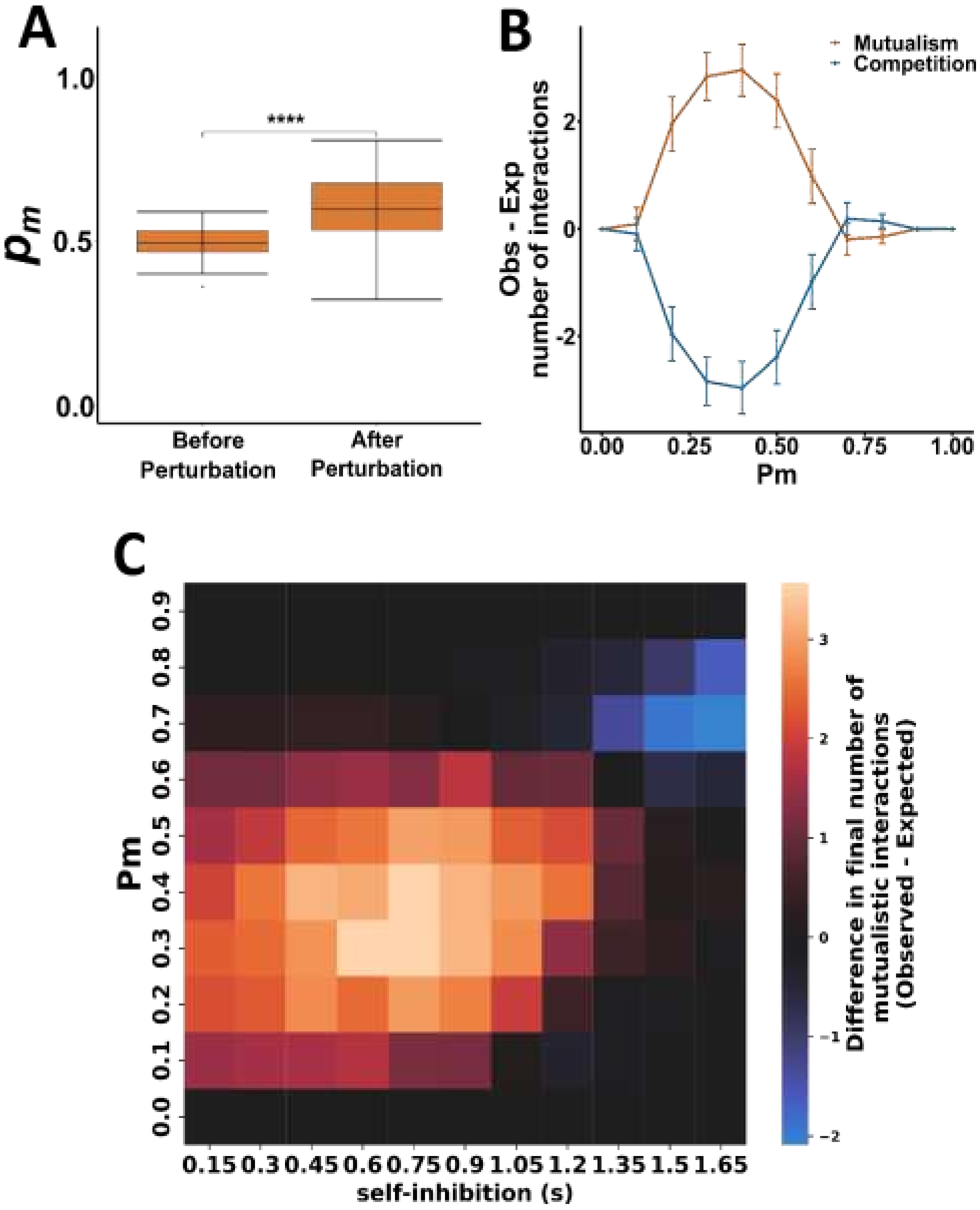

***Figure 3: The fate of mutualistic and competitive interactions after species loss**. In all simulations, S=15 before perturbations. Interaction strengths are drawn from a Gamma distribution such that the mean is 0.25 and the variance is 0.01. By plotting the difference between the observed and expected values of the number of interactions of each type, we can examine whether some interaction types tend to be preserved after extinction events. Here, the expected values are the values of the original community, while the observed values are those measured after equilibrium attainment following the induced perturbation. If this value is greater than 0, fewer interactions of that type are being lost than would be expected by chance alone, and if the value is less than 0, then more interactions are being lost than expected by chance alone. **(A)** The difference in the proportion of interactions before and after a perturbation is statistically significant, as tested by a Wilcoxon rank-sum test ($W = 1737$, $p < 0.001$, effect size $r = 0.564$). In this plot, $s = 1.05$. **(B)** For a fixed value of s (here, $s = 1.05$), regardless of the value of p_m, on average, mutualistic interactions tend to be lost less often than expected by chance alone. In contrast, chance alone loses competitive interactions more often than expected. In this plot, the points represent the mean over 100 realizations, and error bars represent 95% CIs. **(C)** This qualitative result is valid for a large fraction of the parameter space, as indicated by heatmaps in which p_m is varied along the y-axis and s is varied along the x-axis. In these plots, the color represents the mean difference (over 100 realizations) between the observed and expected number of interactions following a perturbation. Warmer / Redder colors indicate that the difference is greater than zero (more mutualists are retained), and cooler / bluer colors indicate that the difference is less than zero (i.e., more competitors are retained). For a large region of the parameter space, mutualism tends to be preferentially retained, whereas competition tends to be preferentially lost.*

The greater loss of competitive interactions can be understood through the following reasoning. Given any two species i and j, the net effect of species j on the growth rate of species i depends on both their interaction type and strength (α_{ij}) and on the population density of species j (N_j). Thus, for a given species i, if the magnitude of interspecific interaction strengths ($|\alpha_{ij}|$) are approximately similar, the strongest interspecific effect will be from that species with the highest population density (N_j). In other words, if interaction strengths are similar, the most significant interspecific effect on species i will be caused by the species j, which has the largest number of individuals. Immediately following a perturbation (*i.e.*, random killing of a fraction of the individuals in the community), highly competitive species are likely to experience a larger growth rate, and species that are more mutualistic are likely to experience a lower growth rate. Mechanistically, the reduced growth rate of mutualists is because the benefit that a species gets from its mutualists is reduced following a perturbation due to reduced numbers of these mutualists. Thus, mutualistic species tend to drive themselves to ever-lower numbers through positive feedback loops (Coyte et al., 2015).

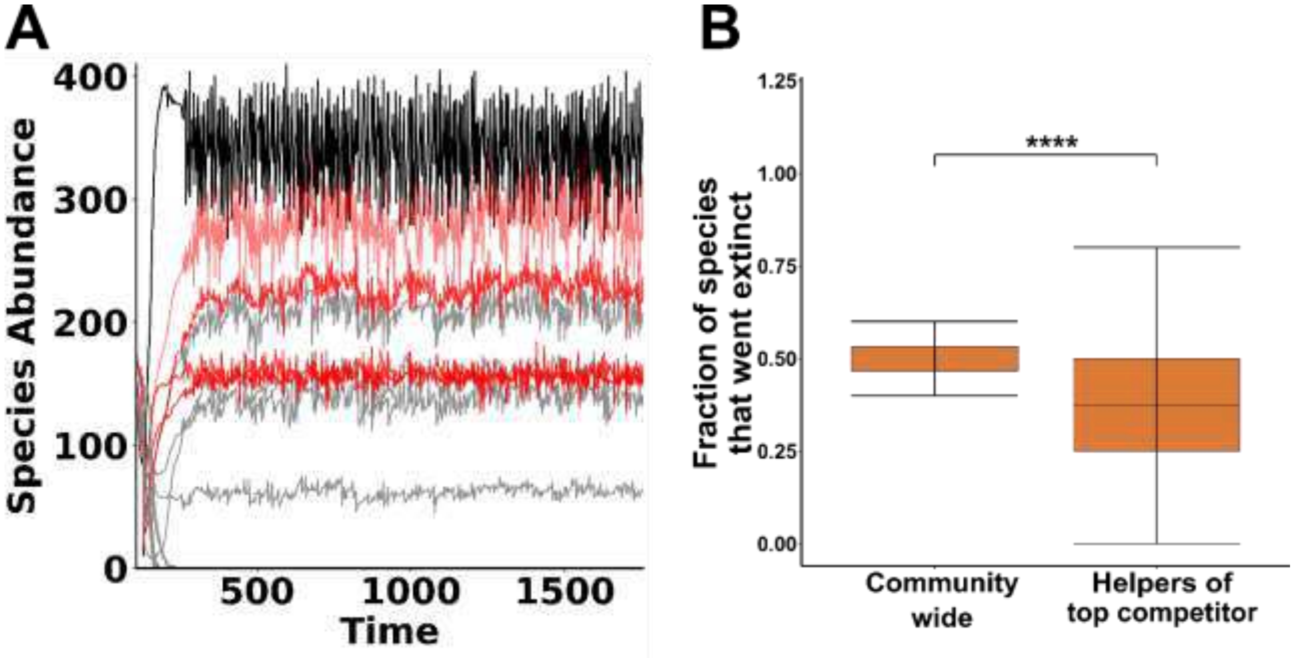

Figure 4: Mechanism for the stability of communities induced by extinctions in unstable communities. (A) *The trajectories of individual populations of each species for a single realization of the IBM with* $S = 15$, $p_m = 0.5$, $s = 1.05$ *are plotted. The species with the largest number of competitive interactions (the 'alpha competitor') is colored in black, species engaged in mutualisms with the alpha competitor are colored in red, and all other species are colored in grey. Following a perturbation, the alpha competitor quickly increases in numbers and 'pulls along' those species engaged in mutualisms while driving the others to extinction.* ***(B)*** *Statistical analysis of 100 independent realizations reveals that for this set of parameters (S = 15, pm = 0.5, s = 1.05) if the alpha competitor does not go extinct, the extinction probability of species that are engaged in mutualisms with the alpha competitor is significantly less than the background extinction probability of the community as a whole. (Wilcoxon rank-sum test, W = 6945.5, p < 0.0001, effect size r = 0.338). The center of the box plot denotes the median, and the edges of the box indicate the upper and lower quartile.*

Conversely, the first species to rise to a large population size will likely be those primarily engaged in competitive interactions (Fig 4A, black trajectory). However, even this species will likely have some (small number of) mutualistic interactions. Once a small number of such competitive species have risen to relatively large population sizes, they will then 'pull up' those species which are engaged in mutualistic interactions with them (Fig 4A, red trajectories) while 'pushing down' other competitors and driving them closer to extinction (Fig 4A, grey trajectories). Thus, species engaged in positive interactions with highly competitive species tend to go extinct less often than expected by chance alone (Fig 4B. Wilcoxon Rank-sum test, $W = 6113.5$, $p < 0.001$), and effect size calculations indicate that the reduction in extinction rate is moderately large(Wilcoxon effect size $r = 0.338$). Since we study random, unstructured communities, species engaged in a higher number of mutualistic interactions are more likely to be engaged in mutualistic interactions with the top competitors. In contrast, species engaged in a higher number of competitive interactions are more likely to be engaged in competitive interactions with the top competitors (probabilistically). Thus, species engaged in more mutualistic interactions are more likely to get a boost in growth rate due to being engaged in positive interactions with highly competitive species. On the other hand, more competitive species are likely to be engaged in competitive interactions with the top competitor and are thus pushed to extinction. This mechanism does not work if the proportion of mutualism is very high because all competitors, in this case, are likely supported by a large number of mutualistic interactions, which explains the trend reversal at high p_m values. This explanation reveals that species engaged in a large number of exploitative interactions enjoy two distinct benefits following a perturbation --- species that are exploited by many species obtain a large increase in growth rate immediately following a perturbation due to release from exploitation/predation, whereas species that exploit a large number of species experience an increase in growth rate through a mechanism similar to that explained for mutualists above. Indeed, in communities with exploitative interactions, simulations reveal that the proportion of exploitative interactions always increases following a perturbation (Figs S4, S7).

Our explanation of how competitive interactions are selectively removed while mutualistic interactions are maintained hinges on the assumption that the community is unstructured and can be modeled as a random matrix of interactions between species. Communities in nature, of course, may not necessarily satisfy these criteria. For example, there may be a community where the most competitive species do not engage in any mutualistic interactions. In such a community, even though some highly competitive species may see a sharp rise in population density following a perturbation, they may not pull up the numbers of species that participate in mutualistic interactions. Our analysis does not attempt to model such exceptional cases and is meant to interpret the results for typical random, unstructured communities. Strictly speaking, exceptional cases, such as those mentioned above, can arise despite a random assignment of interactions between species. However, the probability of such communities in our design is extremely low and therefore are unlikely to play a critical role in driving the general trends.

Discussion

Our results indicate that when a community is unstable (i.e., likely to lose species after a perturbation), only a subset of the species in the community goes extinct before the community becomes stable again (Fig 2C). Furthermore, species engaged in more mutualistic interactions are less likely to go extinct, suggesting that the extinction patterns in randomly assembled communities are non-random with respect to interaction type. The effects we uncover represent systematic biases in extinction probability that will consistently affect resultant community dynamics following any external perturbation that is strong enough to lead to species loss. These dynamics suggest a potential explanation for the prevalence of mutualism in natural communities (Kehe et al., 2021; Machado et al., 2021) – a community can harbor reasonably high levels of mutualism if it is formed due to species loss from a larger randomly interacting community. Community assembly is often thought to occur by random dispersal followed by environmental filtering and subsequent exclusion of some species due to biotic interactions (Begon et al., 2006; Molles, 2015). This is precisely the kind of process for which our results would be relevant. Thus, our model highlights the importance of assembly processes in determining community structure.

A recent modeling study of assembly processes in communities also suggests that when species sequentially invade a community, a balance of interaction types is vital for community stability, with higher fractions of mutualistic interactions corresponding to increased species persistence as well as increased stability of the community as a whole to external invasions (Qian and Akçay, 2020). Such so-called 'ecological selection' (Qian and Akçay, 2020) for community structure during assembly has also been observed in dispersal models (Denk and Hallatschek, 2023) and eco-evolutionary community models (Nell et al., 2022). Our study highlights that ecological selection of this form can operate not only through a sequential assembly of communities but also through extinctions from initially assembled unstable communities. In nature, a situation mirroring our model is often encountered in communities such as microbiomes, where empirical data suggests that many species are randomly assembled through dispersal processes and environmental filtering (Sieber et al., 2019; Venkataraman et al., 2015). Empirical studies of microbial communities also suggest that positive interactions, in the sense of exploitations as well as mutualisms, are ubiquitous in culturable bacteria (Kehe et al., 2021) (but see (Palmer and Foster, 2022)). Our study provides a mechanistic hypothesis for reconciliation of such empirical results with theory regarding the destabilizing effects of mutualism (Allesina and Tang, 2012; Coyte et al., 2015).

Our model also predicts an emergent non-random interaction structure from an initially unstructured, unstable community. Since competitive interactions with the top competitor are selectively lost, the stable community so formed is likely to have a small number of 'central' species (previously the 'top competitors') engaged in positive interactions with most community members. Competitive interactions with this 'central' species should be relatively weak. This aligns with a previous analytical study, which predicts that assembly processes should lead to ecological networks with weaker competition and stronger mutualism than the original species pool (Bunin, 2016). A similar phenomenon has also been observed in an analytical model of unstructured communities with higher-order interactions (Gibbs et al., 2022). In this study, the authors found that when interaction strengths in their model were low, the dominant species in communities with higher-order interactions tended to be those engaged in positive interactions with each other and engaged in negative interactions with species that have lower species density. By studying the dynamics of unstable communities, our results underscore the need to go beyond the question of whether communities are stable: to study the fate of unstable communities. While such studies are often complex to conduct analytically, computational methods, laboratory experiments, and long-term field observations provide potential avenues to address this vital question.

Though we have only looked at randomly assembled communities, a previous simulation study (García-Callejas et al., 2018) suggests similar results may hold for structured trophic networks. These authors found that positive interactions such as mutualism and commensalism promoted persistence in trophic networks with low species richness. However, this effect was less pronounced at higher species richness. Our study neglects environmental or spatial heterogeneity, which is known to affect coexistence and stability (Allen et al., 2013; Durrett and Levin, 1994; Gordon et al., 2015; Hauert and Doebeli, 2021; Krakauer and Pagel, 1995; Stein et al., 2014; Ursell, 2021; Yu et al., 2001). Another factor that can potentially affect community stability is demographic stochasticity, which has been shown to promote mutualism/cooperation in many model systems (Chotibut and Nelson, 2015; Constable et al., 2016; Houchmandzadeh, 2015; Houchmandzadeh and Vallade, 2012; McLeod and Day, 2019). By neglecting these factors, we do not mean to imply that they are unimportant. Instead, we illustrate that they cannot *solely* be responsible for explaining the occurrence of mutualism since, as we have shown, mutualism may persist purely through non-random extinction processes during initial community assembly.

Our model also assumes that all direct community interactions are pairwise and allows higher-order interactions to only manifest as emergent properties of the simulation. Analytical studies suggest that many classic results from pairwise interaction models carry over to models with higher-order interactions (Gibbs et al., 2022). In particular, May's classic results on the diversity-stability relation carry over to models with higher-order interactions (Gibbs et al., 2022). Therefore, there is a possibility that such models may lead to results analogous to those presented in this study. A recent paper has argued on analytic grounds that mutualism is not destabilizing in Lotka-Volterra communities if studies use the so-called 'community matrix', which differs from the more commonly used 'interaction matrix' by accounting for species densities (Stone, 2020). Our explanation for the non-random loss of competitive interactions from an unstable community following a perturbation also crucially relies on the observation that species densities play a large role in determining community dynamics. However, in contrast to the analytical study, our model predicts a decrease in stability with an increase in mutualism, but nevertheless, provides a potential explanation for the prevalence of mutualistic interactions in nature, namely 'ecological selection'.

Lastly, our simulations are over ecological timescales and do not allow for evolution via speciation or evolution in traits (interaction strengths and/or intrinsic growth rates). Incorporating evolution is known to qualitatively alter the predictions of purely ecological models (Kokko et al., 2017; Schoener, 2011; Yamamichi et al., 2022). A suite of empirical studies increasingly indicates that the separation of timescales between ecology and evolution can often be blurred, especially in the case of organisms such as microbes (Schoener, 2011). Including evolutionary processes in ecological coexistence theory and the mutualism-competition debate thus provides an attractive avenue for future studies.

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Data and Code availability

All scripts used in the study will be uploaded to a public GitHub repository upon acceptance of the manuscript.

Author contributions

ASB: Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing – Original Draft, Writing – Review & Editing, Visualization; **SN**: Conceptualization, Methodology, Formal analysis, Investigation, Validation, Writing – Original Draft, Writing – Review & Editing; **SD**: Conceptualization, Methodology, Resources, Writing – Review & Editing, Supervision, Funding Acquisition.

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Supplementary Information: Mutualism Destabilizes Communities, but Competition Pays the Price

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This document contains supplementary figures for the study ‘Mutualism destabilizes communities, but competition pays the price’. The main text contains the results of simulations in which $p_e = 0$ (*i.e.* all interspecific interactions are either mutualistic or competitive). In this supplementary file, we present the corresponding plots for communities in which exploitation is present in equal proportion as competition (*i.e.* $p_c = p_e$). As in the main text, all means are over 100 independent realizations, and in plots with varying p_m, p_m is varied from 0 to 1.

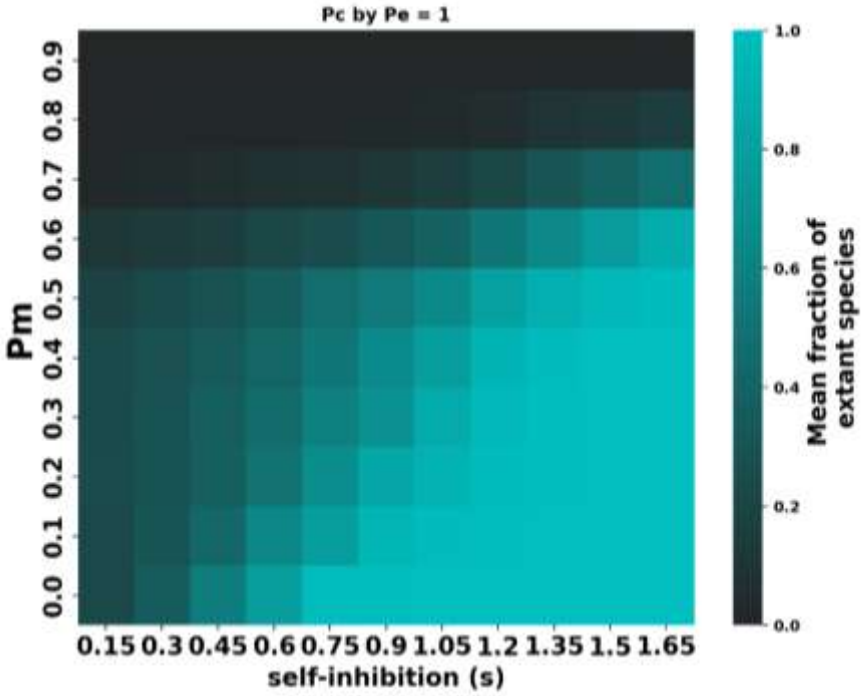

Fig S1: Proportion of extant species as a function of amount of mutualism (p_m) and intraspecific competition (s). Compare with Fig 2B in the main text.

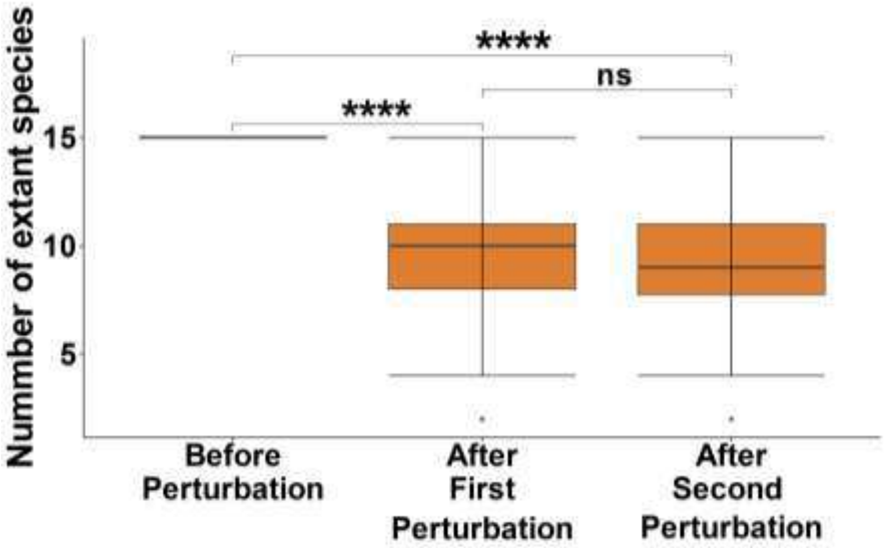

Fig S2: Proportion of extant species following one perturbation and two perturbations for communities in which $p_c = p_e$. *Following a perturbation, communities experienced significant species loss (Wilcoxon rank sum test, W=9700, p < 0.0001). However, the number of species left extant in the community following a single perturbation was not significantly different from that after two perturbations (Wilcoxon rank sum test, W = 5559.5, p = 0.17). Compare with Fig 2C in the main text. Legend is same as for Fig 2C.*

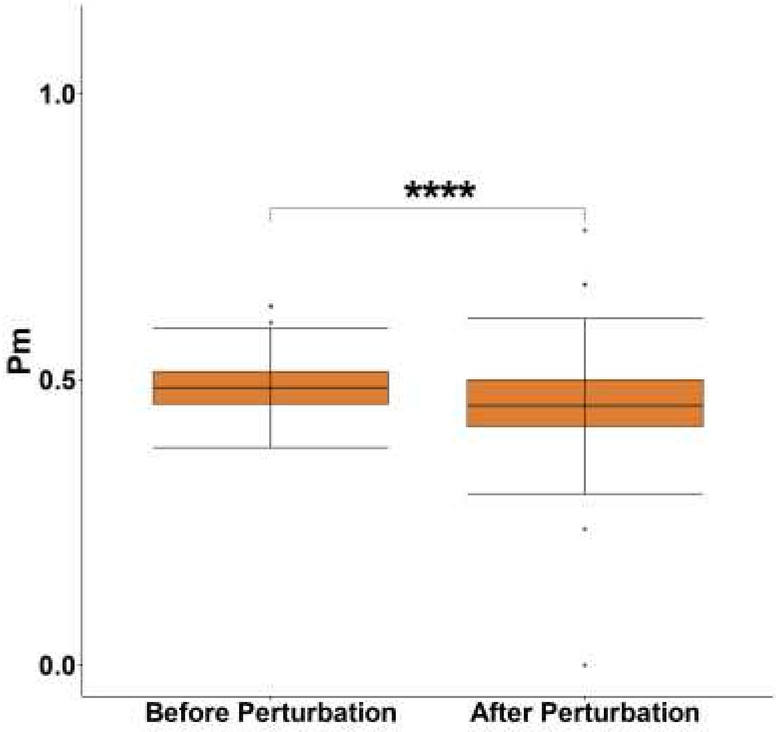

Fig S3: Proportion of mutualistic before and after perturbation for communities in which $p_c = p_e$*. In this case,* p_m *slightly decreases (Wilcoxon rank sum test,* $W = 6594.5$*,* $p < 0.0001$*). However, the effect is small (Wilcoxon effect size* $r = 0.276$*) and is not a general trend, as will be revealed upon examining the full parameter space in Figs S5-S7. Here,* $s = 1.05$*. Compare with Fig 3A in the main text. Legend is same as for Fig 3A.*

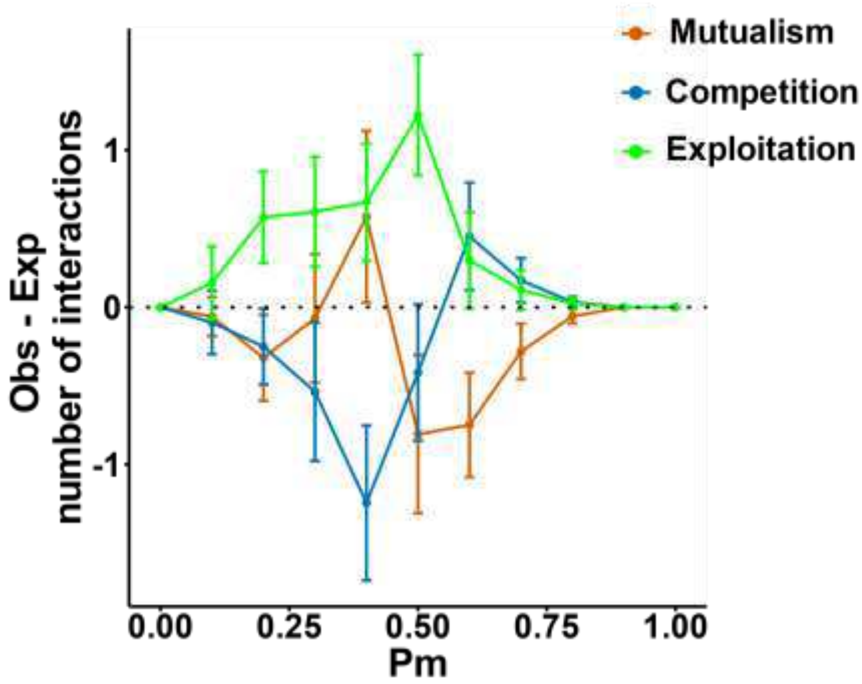

Fig S4: The difference between observed and expected number of interactions of each type for communities in which $p_c = p_e$. In this case, the dynamics are more complicated than those of communities with no exploitation. Broadly, exploitation is always lost less than expected by chance alone, whereas both mutualism and competition may be lost either more often or less often than expected by chance alone, though in opposite regions of parameter space. In this plot, the intraspecific competition strength is $s = 1.05$. Error bars represent standard errors, and points are mean values. Compare with Fig 3B in the main

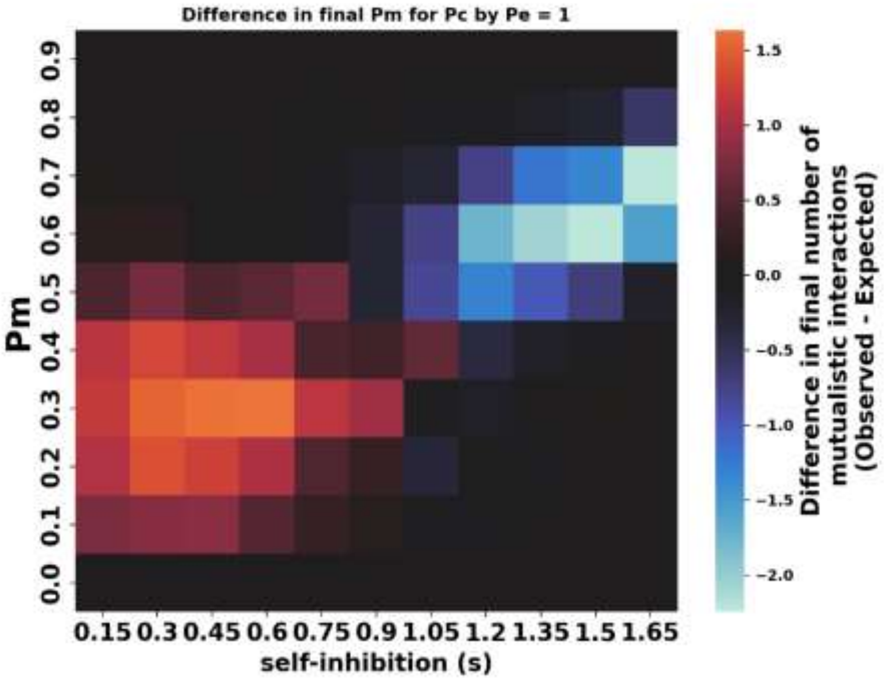

Fig S5: Observed vs expected number of mutualistic interactions following a perturbation. In communities with exploitation, there is also a significant range of parameter space in which mutualism is lost more often than expected by chance alone. However, the effects are generally rather weak (compare limits of color bar with those of Fig 3C in the main text). Legend is same as in Fig 3C.

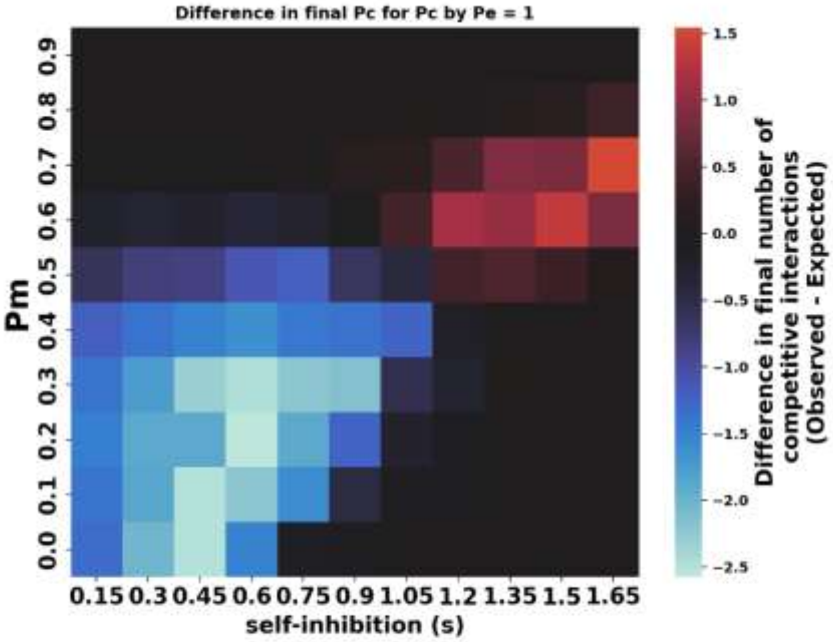

Fig S6: Observed vs expected number of competitive interactions following a perturbation. Competition may be lost less often or more often than expected by chance alone. However, the gain in competition is weaker in effect than the loss (compare red limit vs blue limit in color bar). Legend is same as in Fig 3C.

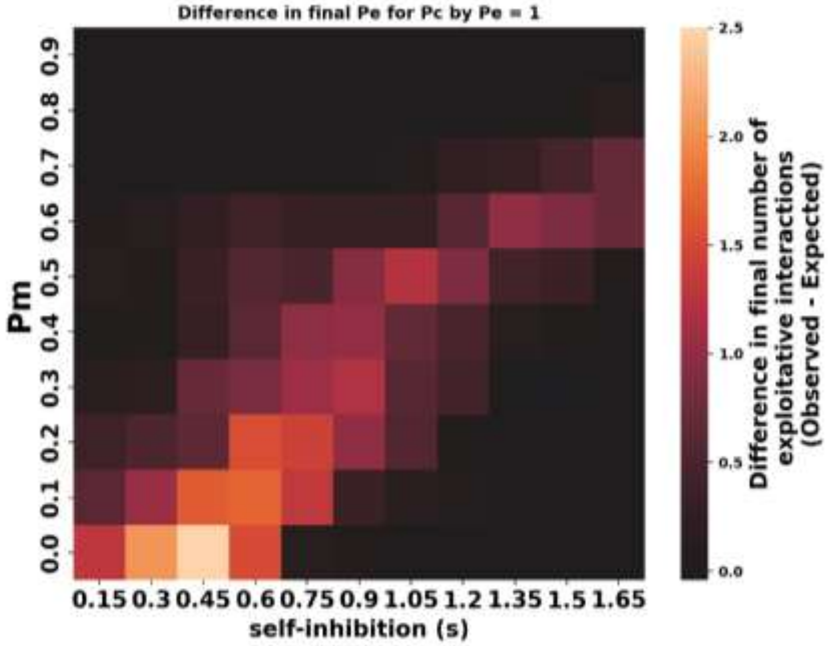

Fig S7: Observed vs expected number of exploitative interactions following a perturbation. Exploitative interactions are always lost less often than expected by chance alone. Legend is same as in Fig 3C.