ECOLOGY

Species richness and redundancy promote persistence of exploited mutualisms in yeast

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Mutualisms, or reciprocally beneficial interspecific interactions, constitute the foundation of many ecological communities and agricultural systems. Mutualisms come in different forms, from pairwise interactions to extremely diverse communities, and they are continually challenged with exploitation by nonmutualistic community members (exploiters). Thus, understanding how mutualisms persist remains an essential question in ecology. Theory suggests that high species richness and functional redundancy could promote mutualism persistence in complex mutualistic communities. Using a yeast system (*Saccharomyces cerevisiae*), we experimentally show that communities with the greatest mutualist richness and functional redundancy are nearly two times more likely to survive exploitation than are simple communities. Persistence increased because diverse communities were better able to mitigate the negative effects of competition with exploiters. Thus, large mutualistic networks may be inherently buffered from exploitation.

Mutualist communities are prevalent in every ecosystem (*1*–*3*), forming the core of food webs and providing critical ecosystem services. Like other communities, mutualist communities must be able to cope with constantly changing conditions, but the factors that help maintain their stability remain under debate (*4*–*6*). Recent efforts to understand mutualistic community dynamics by using network analysis suggest that high species richness could enhance persistence (*4*); however, experimental validations of this hypothesis are needed. Understanding the persistence of mutualist communities is paramount for the management and conservation of ecosystems (*7*), especially given the risk of species loss with climate change (*8*).

To persist, mutualisms need to resist exploitation by organisms that use the exchanged commodities of the mutualism without providing anything in return (*9*). These exploiters can be unrelated to the mutualists or they can be mutualistic species or individuals that have defected from the mutualism ("cheaters") (*10*). Although there is debate about whether exploitation has strong negative fitness consequences in many mutualisms (*11*), exploitation can change the structure of communities (*3*, *12*, *13*), leading to local species loss (*14*). Despite the possible negative effects of exploitation, exploiters or cheaters are present in virtually all mutualistic communities; thus, how mutualistic communities are buffered from the effects of exploitation is unclear.

Similar to the proposed effect of species richness on mutualism persistence (*4*), richness could potentially enhance mutualism persistence under exploitation because rich communities have redundant species with similar functional roles (*4*, *5*). Consequently, if a mutualist goes extinct after exploitation, the community can persist with fewer species because the remaining redundant mutualist species still provide the commodities to sustain the community (*15*, *16*). Simultaneously, however, redundant species have similar niches and may compete strongly with one another for mutualistic commodities and/or other resources. Theory suggests that coexistence of redundant mutualists is hindered by competition for the mutualistic commodity (*17*). Competition could lead to removal of inferior competitors (*17*) and decreased species richness over time (*5*), and influence mutualism persistence. Considering these contrasting effects of species redundancy on communities, in this study we experimentally test how mutualist species richness and functional redundancy contribute to mutualism persistence with and without cheaters.

We created a synthetic mutualism using brewer's yeast, *Saccharomyces cerevisiae*, by engineering asexual strains to overproduce either lysine or adenine but not produce the other resource (Fig. 1A) (*18*). Adenine is required for cell division and lysine for cell growth, making these nutrients essential for yeast fitness. Because the overproduced nutrients are released into the medium and are freely available, the mutualism cannot involve sanctions or partner choice, which are mechanisms used in some mutualisms to restrict cheating, for example, by controlling the amount of commodities exchanged or by avoiding interactions (*19*). Thus, this mutualism is similar to common, diffuse mutualisms such as many generalized pollination systems (*20*). We genetically engineered the strains to function ecologically as different species; as such, the strains are genetically distinct, reproductively isolated, and analogous to species. Additionally, within each mutualist type, the strains have small differences in genotype and phenotype (e.g., yield) (Fig. 1, B and C), making them analogous to closely related, ecologically similar species that would compete strongly with one another because of niche overlap.

We also engineered cheater strains that provide no resources but consume either adenine (hereafter, "adenine cheater") or lysine ("lysine cheater"). We call them cheaters because they are derived from the mutualists, simulating cheaters that share recent evolutionary history with mutualists. Because no lysine or adenine is available in the medium except for that released by the mutualists, the cheaters cannot exist independently of the mutualists, and community persistence critically depends on the presence of both types of overproducing mutualists. Thus, when one or both mutualist types went extinct, we considered these communities as having collapsed. To test the hypothesis that species richness enhances mutualism persistence, we created symmetrical communities that varied in richness with and without the two types of cheaters (Fig. 1A). Communities were grown for 4 weeks, and we assessed their survival and community composition weekly (1679 communities) (*18*).

Persistence of mutualistic communities was highly dependent on community composition. All mutualist-only communities survived the entire experiment. Communities with cheaters, however, went extinct at different rates depending on the type of cheater. The lysine cheater led to the collapse of 55% of the mutualistic communities, whereas the adenine cheater caused <5% collapse (Fig. 2A), thus demonstrating that the effect of cheaters on mutualism persistence is context dependent. This context dependency may help explain why some cheaters, but not others, can have strong negative effects on natural mutualistic communities. The negative effect of the lysine cheater on community persistence was buffered by the higher initial number of mutualist strains in the community, as persistence rates nearly doubled in the richest communities (Fig. 2A). Because the richest communities were not independently replicated, as the mutualist strains were sampled from a pool of eight total strains, we also tested for changes in persistence by excluding the eight-strain communities, thus eliminating communities that were not independently replicated. This analysis confirmed that species richness buffers mutualist communities that are experiencing substantial negative effects from cheaters (χ^2 = 17.96, df = 2, P = 0.0001).

The results suggest that species richness is an important component of persistence with cheaters, yet increasing richness also adds

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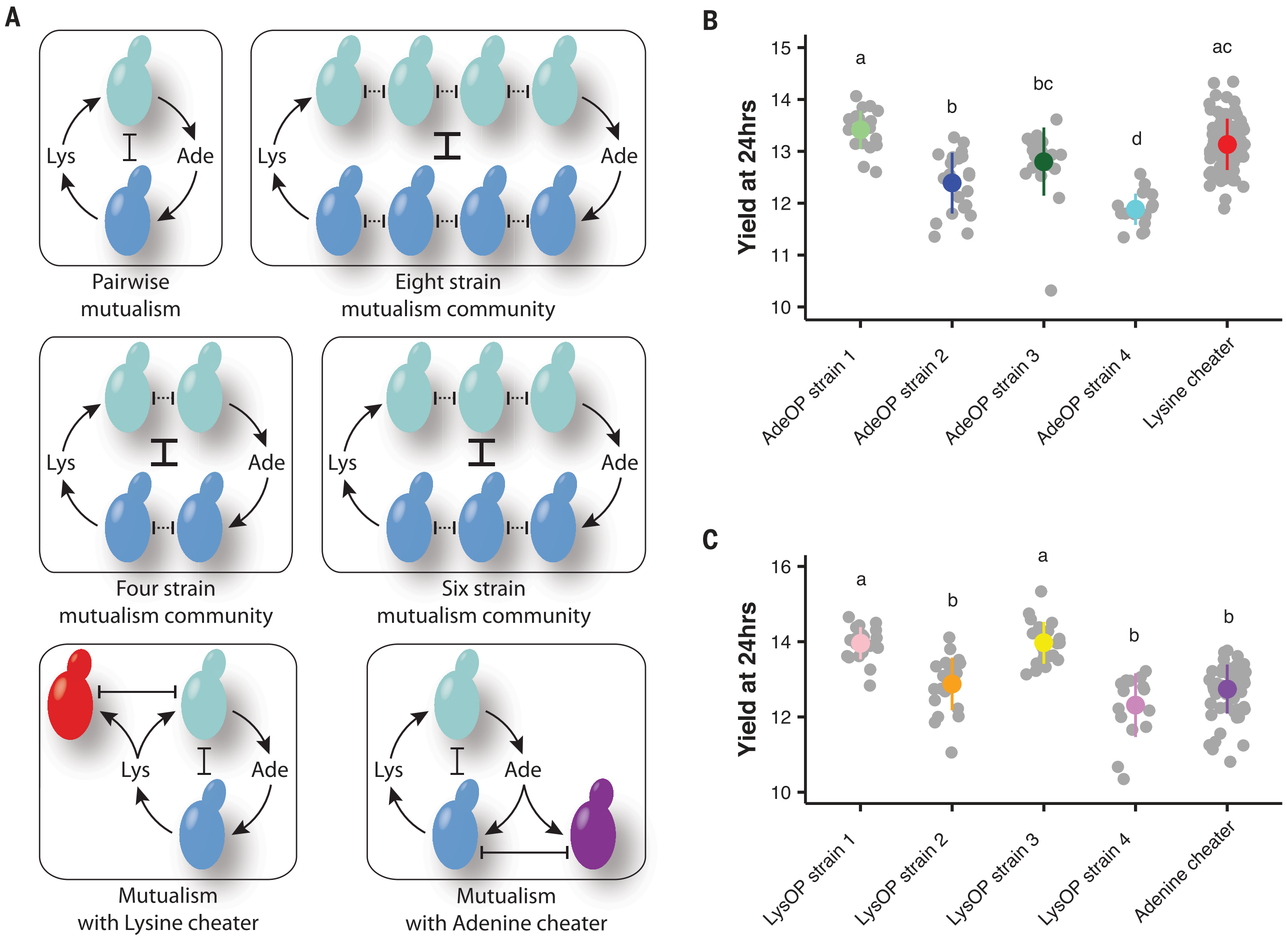

Fig. 1. Representation of symmetrical yeast communities and yield differences among strains used to build the communities. (**A**) Symmetrical mutualist communities. (Top left) Simplest community, with one strain of adenine (Ade) mutualist (top, green) that releases adenine into the medium, which is taken up by the lysine (Lys) mutualist (bottom, blue) that releases lysine, which is used by the adenine mutualist. Although these strains are mutualists, they compete for other resources (blunt-ended line). We added pairs of mutualist types to create symmetrical communities of up to eight strains (top right) in which there was also competition within mutualist types (blunt-ended dashed lines). Besides mutualist-only communities, we created communities with a lysine cheater (red) that competed with the adenine mutualists for lysine and communities with an adenine cheater (purple) that competed for adenine with the lysine mutualists. (**B**) Yield at 24 hours of growth for the adenine overproducing mutualists (AdeOP) and the lysine cheater. (**C**) Yield at 24 hours of growth for the lysine overproducing mutualists (LysOP) and the adenine cheater. Yield was measured when strains were growing alone in complete medium. Letters represent Tukey's honest significant difference (HSD) comparisons.

functional redundancy of mutualists. To disentangle the effects of species richness and redundancy, we compared the persistence of asymmetrical communities with and without the lysine cheater. We created mutualist-only communities and a replicate set including the lysine cheater in which one adenine mutualist was matched with either two, three, or four lysine mutualists, as well as the converse (1431 total communities) (*18*).

Results from the asymmetrical communities showed that the positive effect of species richness on community persistence was driven by mutualist functional redundancy, and this redundancy was critical when mutualists use the same mutualistic commodity as the lysine cheater. For the mutualist-only communities, there was no change in persistence, with increasing redundancy of either mutualist type, as the communities did not experience collapse (Fig. 2B). Similarly, changes in redundancy of the lysine mutualists that do not compete for mutualistic commodities with the lysine cheater led to no change in persistence, as these communities suffered ~65% collapse regardless of the initial number of strains. By contrast, increases in functional redundancy of the adenine mutualists that compete with the lysine cheater led to a 25% increase in community persistence when we compared communities with two versus three or four adenine mutualists (from 43 to 67% survival) (Fig. 2B). Thus, functional redundancy of the mutualist type that directly competes with the cheater for the mutualistic resource had a notable impact on community persistence. These results suggest a key role for functional redundancy in mutualism and that having a greater number of redundant mutualist species that compete with a strong cheater increases the likelihood that the mutualism will persist despite the negative effects of cheaters.

Although we found that functional redundancy can buffer the negative effects of a strong cheater (Fig. 2B), redundancy can be disadvantageous as well because similar mutualist species should also compete strongly with one another (*17*). Our results show that starting species richness had a negative effect on individual strain retention in all multimutualist communities (Fig. 3). Despite that, when we examined the final composition of surviving communities, we observed that coexistence among mutualists usually occurred in at least

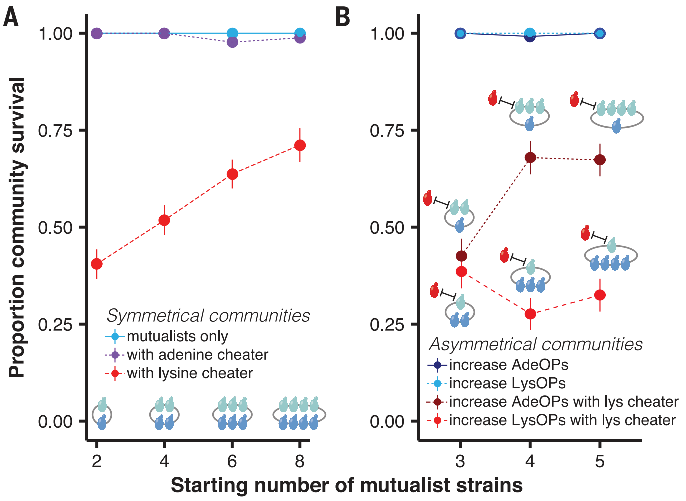

Fig. 2. Effect of species richness and functional redundancy on community persistence. (**A**) Symmetrical communities with mutualists only and with the adenine cheater had high survival, whereas communities with the lysine cheater had 40 to 75% survival rate, depending on the starting number of mutualistic strains ($\chi^2 = 27.47$, df = 3, $P < 0.0001$). (**B**) Asymmetrical communities containing only mutualists had high survival. By contrast, communities with the lysine cheater and variable numbers of strains of the adenine mutualist (AdeOPs) increased community persistence from ~40 to 70% as the number of adenine mutualists increased ($\chi^2 = 25.29$, df = 2, $P < 0.0001$; excluding the most diverse communities that were not independently replicated: $\chi^2 = 17.78$, df = 1, $P < 0.0001$). Communities with the lysine cheater and increasing numbers of lysine mutualists (LysOPs) did not differ ($\chi^2 = 2.94$, df = 2, $P = 0.23$). Points on graphs represent mean ± SE.

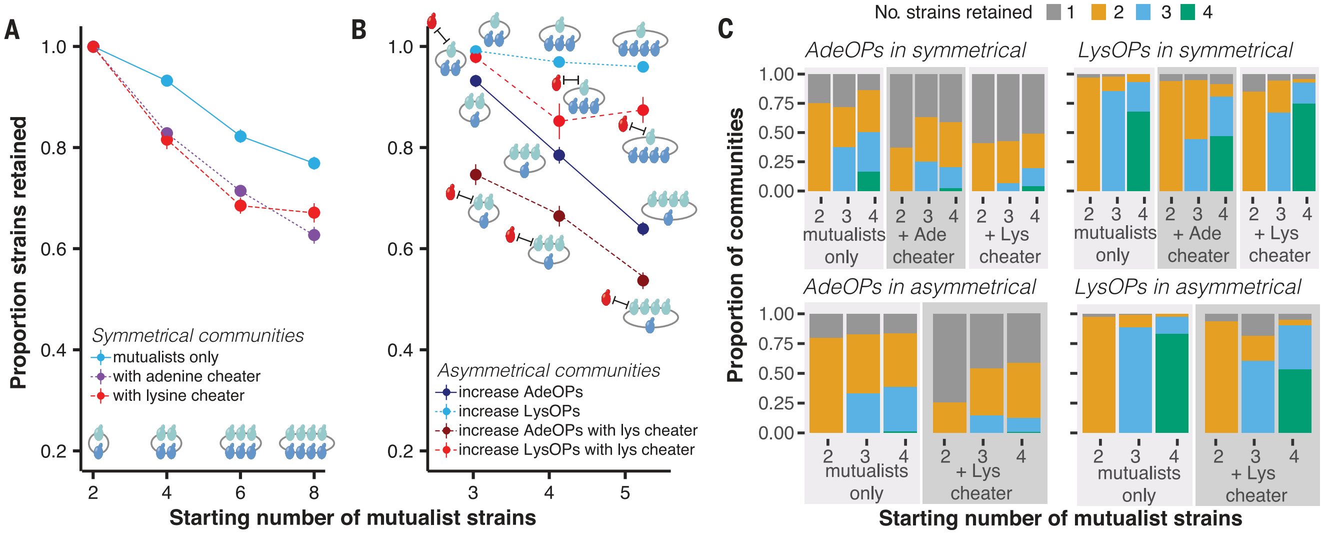

Fig. 3. Effect of richness on strain loss in persistent communities. (**A**) Mutualist strain retention in symmetrical communities decreased with the starting number of mutualistic strains (mutualists only: $t = -14.47$, df = 1328, $P < 0.0001$; with lysine cheater: $t = -14.8$, df = 1328, $P < 0.0001$, with adenine cheater: $t = -23.87$, df = 1328, $P < 0.0001$). Communities with cheaters had greater loss than communities with mutualists only (Tukey's test: mutualists only versus with lysine cheater: $t = 3.06$, df = 1328, $P = 0.006$; mutualists only versus with adenine cheater: $t = 6.02$, df = 1328, $P < 0.0001$; with lysine cheater versus with adenine cheater: $t = 2$, df = 1328, $P = 0.11$). (**B**) Strain retention decreased with the starting number of mutualist strains in asymmetrical communities ($F_{2,992} = 100.9$, $P < 0.0001$); within each community type, all pairwise comparisons differed with increasing richness ($P < 0.001$) except for communities with increasing number of lysine mutualists (light red and light blue). In these communities, there was no difference in strain loss with starting numbers of four or five mutualists, regardless of the presence of the lysine cheater (with cheater: $z = 0.52$, $n = 123$, $P = 0.859$; without cheater: $z = -0.69$, $n = 285$, $P = 0.765$). Points on graphs (A) and (B) represent mean ± SE. (**C**) Coexistence of mutualists as a proportion of communities, showing the number (No.) of strains of adenine mutualists (AdeOPs) and lysine mutualists (LysOPs) retained to the end of the experiment for each community type.

half of the communities and was even more frequent among lysine mutualists and in mutualist-only communities (Fig. 3C). In addition, strain loss was more pronounced when either cheater was present (Fig. 3), likely because cheaters removed mutualistic commodities without contributing any resources to the environment.

Together, the results suggest that competition for the shared resources among mutualists and between mutualists and cheaters is driving the patterns of strain loss. For instance, the negative effect on community survival caused by the lysine cheater but not the adenine cheater suggests that there is likely a difference in the intensity of competition for the mutualistic commodities being exchanged. This idea is further supported by our finding that strain loss was higher among redundant adenine mutualists than among redundant lysine mutualists (Fig. 3B). Furthermore, in contrast to the adenine mutualists, the lysine mutualists were less likely to be excluded from communities (Fig. 3C). Competition for lysine could be more intense than for adenine because lysine availability is delayed but adenine is readily available. Lysine is stored in vacuoles and is released as the lysine-producing mutualists die, whereas adenine is continuously secreted by the adenine mutualists (*21*). Consequently, lysine availability was nearly unmeasurable for the first 48 hours, whereas adenine availability increased over time (Fig. 4A). Thus, this difference in resource availability might be leading to stronger competition for lysine than for adenine, both among adenine mutualist strains

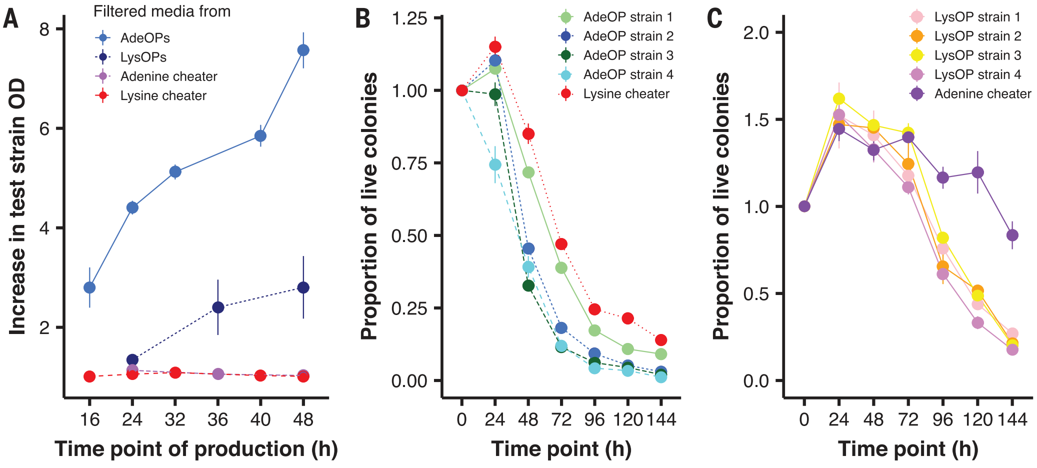

Fig. 4. Mechanism of strain loss and community collapse. (**A**) Estimates of lysine and adenine produced by mutualists and cheaters over time (compared with the first time point: 8 hours adenine mutualists and lysine cheater, 12 hours lysine mutualists and adenine cheater). Production of adenine by mutualists increases over time ($F_{4,35}$ = 40.4, P < 0.0001), whereas production did not differ for cheaters and lysine mutualists (LysOPs: $F_{2,20}$ = 2.5, P = 0.107; adenine cheater: $F_{4,5}$ = 2.36, P = 0.186; lysine cheater: $F_{2,3}$ = 0.71, P = 0.56). Production was measured indirectly by assessing the growth of a test strain that could not produce adenine or lysine, and the only lysine or adenine available was that produced by the mutualists. OD, optical density. (**B**) Starvation resistance of adenine mutualists and the lysine cheater. The lysine cheater was more resistant to 48 hours of starvation than the adenine mutualists (Tukey's HSD between lysine cheater and AdeOPs had P < 0.05). (**C**) Starvation resistance of lysine mutualists and adenine cheater. All strains had similar starvation resistance at 48 hours ($F_{4,10}$ = 0.72, P = 0.6). Points on graphs represent mean ± SE.

as well as between the adenine mutualists and the lysine cheater.

One important competitive trait for the lysine cheater and adenine mutualists would be starvation resistance that would allow survival during periods when lysine is limiting. Strains that have more individuals surviving a period of starvation would have higher initial population density when the resource becomes available, leading to priority effects. If lysine cheaters are more resistant to starvation than the adenine mutualists, it could explain the severity of their impact on mutualist communities. To test this hypothesis, we grew the strains alone and measured starvation resistance to the mutualistic commodity that they require. At 48 hours, 85% (±3.5 SE) of the lysine cheater population survived lysine starvation, whereas only 47.3% (±4.6 SE) of the adenine mutualist populations survived (Fig. 4B). In comparison, the lysine mutualists and the adenine cheater had similar starvation resistance at 48 hours (Fig. 4C); however, these strains probably do not starve for adenine because adenine is continuously released in relatively high quantities (Fig. 4A). We hypothesized that the superiority in starvation resistance of the lysine cheater would cause shifts in composition ratios toward the lysine cheater, as would be expected under a model of priority effects. To test this, we assembled a small set of pairwise mutualist communities with and without cheaters and quantitatively tracked the population size of each species. Lysine cheaters quickly became dominant in 25% of the communities, and these communities eventually went extinct (table S3). By contrast, communities containing the adenine cheater shifted in favor of the mutualists, and the cheater was eventually excluded, possibly because of a competitive trait other than starvation resistance (e.g., yield) (Fig. 1B). For the mutualist-only communities, the ratio of lysine and adenine mutualists remained constant. Thus, differences in starvation resistance appear to be linked to shifts in population ratio favoring the lysine cheater, ultimately resulting in community collapse.

Community persistence increased with richness regardless of strain composition (figs. S1 and S2), suggesting that the patterns of community survival were not driven by the presence of competitively superior strains. As more mutualist strains are added, there is an increased probability that one of those strains will be competitively superior to the lysine cheater. Consequently, we tested (i) whether communities containing the superior adenine mutualist competitor were more likely to survive, (ii) whether the strongest mutualist competitor was numerically dominant in the surviving communities, and (iii) whether coexistence with the cheater was rare. These tests showed that survival and abundance of different adenine mutualist strains varied from one community to the next (figs. S3 and S4), and there was no specific strain that dominated all of the communities. In addition, coexistence of the mutualists and lysine cheater was as likely as the exclusion of the cheater for most of the surviving communities (fig. S5). Thus, the outcome of competition among mutualist strains and between mutualists and the lysine cheater was context dependent and was not solely predictable on the basis of the identity of the mutualist strains in the communities. These results show that although competition is an important factor in all communities, competitive exclusion alone does not determine the persistence of mutualist communities that are exploited.

Our results provide evidence for the feasibility of the coexistence of functionally redundant species in multimutualistic communities. In non-neutral models that assume niche differentiation, coexistence occurs either when intraspecific competition is stronger than interspecific competition, when there is a trade-off between colonization and competitive abilities, or when there is spatial or temporal heterogeneity in resource availability coupled with trade-offs in competitive abilities for different resources or for environmental tolerances (*22*, *23*). The mutualist species that we used in our experiments closely resemble one another and were growing together in a mixed, homogenous, closed environment. These conditions should promote competitive exclusion, yet we commonly observed coexistence among mutualists as well as between mutualists and cheaters. Johnson and Bronstein (*17*) suggested that coexistence can be facilitated in multimutualist communities if mutualist species can partition the shared mutualistic commodity as well as another nonmutualistic resource. The redundant mutualist strains in our system likely have trade-offs in their competitive ability for different resources, and this, combined with temporal resource heterogeneity due to mutualistic resource production and nonmutualistic resource consumption, may allow coexistence of multiple mutualist strains. How the temporal dynamics of competition and resource availability drive coexistence in mutualisms requires further experimentation. Our results, however, highlight the importance of context dependency in determining coexistence in multimutualist communities with and without exploitation.

Together, our results show that species richness can ameliorate mutualistic community collapse caused by cheaters. Mutualist functional redundancy allowed the mutualism to persist even with extinction of some mutualist species. The positive effect of functional redundancy was pronounced for mutualist species that directly competed with cheaters for the most limiting mutualistic commodity. Although only one type of cheater markedly affected community survival, both had negative effects on the communities in terms of species loss, possibly because they reduce the availability of the mutualistic resources. Thus, our results show that cheaters in general can have negative effects on mutualist communities even when they do not cause community collapse.

In terms of understanding the persistence of multispecies mutualistic communities, our results suggest three key findings. First, exploitation can have strong negative effects on multimutualist communities by affecting community persistence and species loss. However, the negative effects of cheaters are context dependent and vary greatly with the strength of competition for mutualistic commodities [e.g., (*24*)]. Second, for mutualist communities experiencing exploitation, the fate of the community is determined largely by the effect of cheaters on mutualist population dynamics [e.g., (*25*)]. Cheaters that use resources more efficiently or that better survive periods of low resource availability will have an advantage over mutualists. Third, in complex, diffuse mutualistic networks, regulatory mechanisms such as host sanctions, partner choice, and positive partner feedbacks [e.g., (*26,27*)] may not be required to explain community stability. Regulatory mechanisms are unlikely to work in diffuse mutualisms because these communities have many species that differ in life history, behavior, and the benefit they provide. Competition, however, is one mechanism that is universal across species and communities and offers a general framework to explain the stability of diverse types of mutualistic communities under exploitation. In the face of inevitable competition among redundant mutualist species and exploiters, maintenance of high richness in natural systems is necessary to promote persistence of mutualist communities.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Figs. S1 to S5
Tables S1 to S4
References (*29–35*)

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Species richness maintains mutualisms

Mutualistic communities of species that benefit each other are ubiquitous in ecosystems and are important for ecosystem functioning. However, the relationship between the persistence of mutualisms and species richness has remained unclear. Vidal *et al.* used a synthetic mutualism in brewer's yeast to experimentally test whether species richness buffers mutualistic communities against exploitation by species that do not provide benefits in return. They showed that richer mutualist communities survive exploitation more often than pairwise mutualisms and that higher species richness and functional redundancy allow mutualist communities to persist in the presence of exploiters. These results provide experimental support for the hypothesis that species richness is necessary for the function and maintenance of mutualistic communities.

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