Feasting yeast and the sweetness of diversity

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The idea that a spreading species can lose genetic diversity goes back to early work by Ernst Mayr in 1942 on founder effects for introduced populations (1). Here, reduced diversity of a spreading population arises from the small number of individuals who are initially introduced into a region (founders). A small number of founders will not represent the full genetic diversity of the population, and then the diminished diversity will be propagated as these few individuals grow and spread, passing on their genotypes.

The question arises, however, as to the outcome for genetic diversity if small groups of individuals do not fare well and only larger groups manage to thrive and spread. Perhaps the smaller groups will die out and the larger groups will be sufficient in size to pass on their population diversity to successive generations. While theoreticians (2, 3) and mathematicians (4–6) have postulated that such an effect should exist, and there has been some empirical support from field studies (7), it has been difficult to connect the theory to experimental observation. However, a recent paper by Gandhi et al. (8) sheds light on how cooperation can preserve diversity. Their work investigates the genetic diversity of expanding yeast (*Saccharomyces cerevisiae*) populations. By manipulating the food substrate for spreading populations of yeast cells on test plates, Gandhi et al. experimentally demonstrated how cooperative feeding dynamics can actually help combat declines in genetic diversity when populations undergo spatial expansion. Using a number of ingenious techniques, the authors were able to connect the experimental results closely to theoretical predictions.

The idea that larger groups thrive when smaller ones do not, referred to as an Allee effect by ecologists, can arise from something as simple as requiring a mate for reproduction. However, for these experiments with yeast strains, an Allee effect arose from cooperative feeding dynamics, which were manipulated from being fully individual to cooperative by changing the sugar substrate for growth. The simple sugar galactose permitted individual feeding whereas the complex sugar sucrose required cooperative feeding and so induced an Allee effect. It was shown that glucose yielded a very small Allee effect.

Building on the work of ref. 9, the relationship between food substrate, cooperation, and the Allee effect was used meticulously to change spreading waves of yeast on a test plates. When galactose was provided, feeding was individual, requiring no help from neighbors. Here the spreading waves were "pulled" by a few individuals at the leading edge that pioneered the spread. When sucrose was provided, the feeding was cooperative, requiring help from neighbors and giving rise to the Allee effect. Here the waves were "pushed" by larger numbers of individuals spilling over from high-density regions and colonizing the empty regions in densities sufficient to overcome the Allee effect. Glucose had an intermediate effect, giving rise to a small Allee effect and weakly pushed waves. While the transition from pulled to pushed waves has been a subject long analyzed by mathematicians (10), evidence that such a transition could be induced in yeast waves by changes in sugar substrate was only just recently discovered by some of the same authors in another PNAS paper (9).

The innovative step in the experimental work for this current paper (8) was to link the pulled versus pushed wave dynamics to the issue of maintenance of genetic diversity. The authors focused on a particular form of genetic diversity, that is, neutral genetic diversity that does not convey a selective advantage. The researchers required a simple method to both modify and track the neutral genetic diversity of the yeast strains. For this they used 2 otherwise identical genotypes with different fluorescent markers, whose frequency could be tracked over time.

The researchers found that when spreading population waves are pulled, via individuals feeding on

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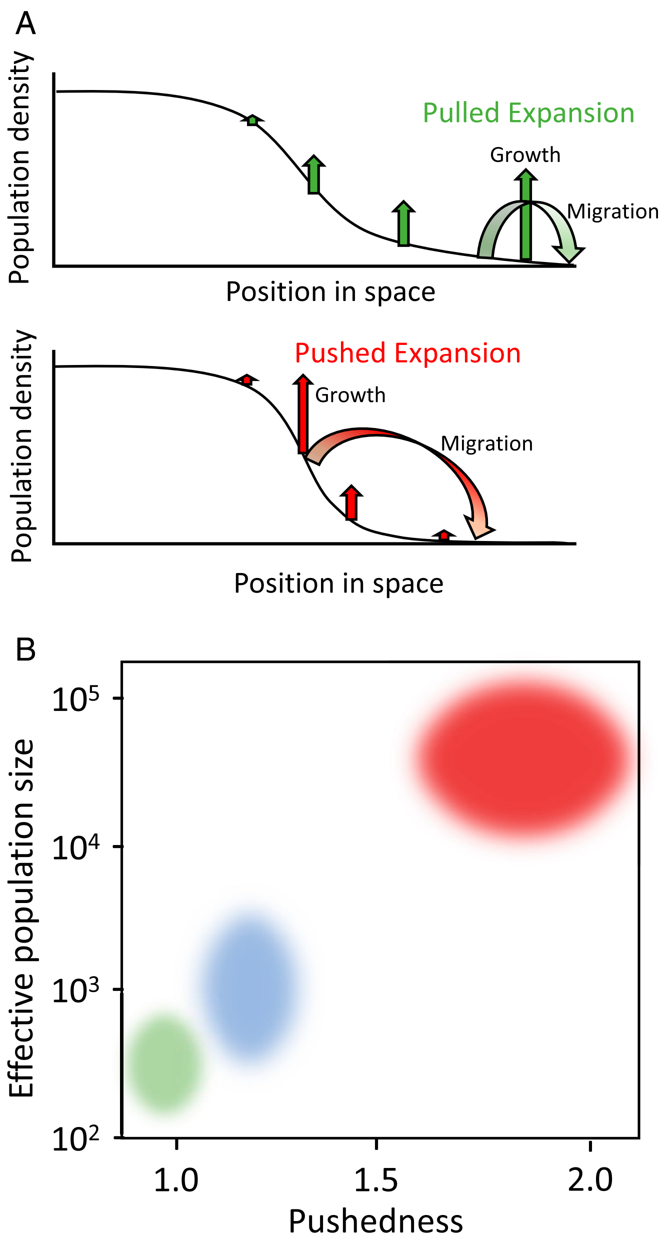

Fig. 1. Pushed versus pulled expansions lead to very different effective population sizes. (*A*) Pulled expansions have highest per capita growth rates at the leading edge and are pulled forward by a mixture of growth and migration at the leading edge. Pushed expansions have highest per capita growth rates at intermediate densities and are pushed forward by growth at intermediate densities spilling over via migration to fill in the leading edge. (*B*) Effective population size versus pushedness for spreading yeast populations grown on galactose (green), glucose (blue), and sucrose (red) solutions over a wide variety of experimental conditions (summarized and redrawn from ref. 8).

galactose, the populations lose substantial genetic diversity because of a founder effect at the leading edge of the wave. The loss of genetic diversity is tremendous, leading to an effective population size 4 orders of magnitude lower than the actual population size. However, when population waves are pushed, via cooperative feeding on sucrose, the spreading populations maintain far more genetic diversity than in the pulled situation. The case with a weakly pushed wave, via feeding on glucose, leads to intermediate loss of genetic diversity (Fig. 1).

Outside of controlled experimental circumstances, the question could arise as to whether the takeover of a population by a given genotype is not from a founder effect but is, rather, from a selective advantage by one of the genotypes. Although the experiments by Gandhi et al. (8) were carefully controlled to focus on founder effects, some mutations actually occurred within strains and thus takeovers based on mutations conferring a selective advantage were also observed experimentally. Perhaps surprisingly, the researchers found a way to distinguish between the spatial signatures of the founder effect versus selective advantage processes by analyzing their trajectories over time and space.

The idea that Allee effects could increase neutral genetic diversity via pushed waves has already been predicted and analyzed by both theoreticians (2, 3) and mathematicians (4–6). However, the results from these theoretical analyses have remained theoretical, relying on complex simulations (2, 3) or on the abstract analysis of partial differential equations (4, 5) and related models (6). To be able to experimentally test the theory in an elegant, repeatable experimental setting represents a major step forward in the study of evolutionary ecology of spreading populations.

The hope for ecologists and evolutionary biologists is that lessons learned from the experimentally manipulated yeast–sugar system are more broadly applicable to understanding the mechanisms of maintenance of genetic diversity in populations, even in the presence of selection. Of course the issue of spatial scale must be considered. While the experimental setup for this work involved strains of yeast on a test plate, the question of diversity in expanding populations occurs on much broader scales: Range shifts on continental scales are expected as endemic species adapt to climate change by spreading spatially into regions that match their thermal tolerance, and invasive species are notorious for carving out new geographical ranges when they are introduced to pristine habitats. Thus, the implications of this work could be widespread if they could be extrapolated to geographical range spread.

There is also the possibility for further experimental tests of the diversity of yeast populations subject to changing environmental condition, such as those arising from shifts in environmental conditions due to climate change. Here there are existing theoretical predictions of the impacts on genetic diversity (11, 12), and it would be exciting to see if these hold in an experimental setting.

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