Finding the sweet spot for invasion theory

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Human activities, such as trade, agriculture, and recreation, have relocated much of the world's flora and fauna across geographical space. Although some newly introduced species have faltered, many have thrived and spread spatially, modifying their new environments. Notorious invaders, such as zebra mussels or gypsy moths, have wreaked ecological and economic havoc (1). The vast, uncontrolled experiment that constitutes the introduction, spread, and impact of alien species across continental scales has fascinated biologists since the time of Charles Elton (2), a pioneer in the subject. Invasion biology has now emerged as a discipline in its own right, with experimental, theoretical, and management components (3).

A key element for an invader's success is the speed at which it spreads spatially once established in a new environment. High spreading speeds yield rapid spatial coverage and the possibility of large geographical impacts. Ideally, an estimate for the spreading speed would be available beforehand, allowing biologists and managers to prepare for and manage the consequences. This is where mathematical theory has an unexpected role to play: it can come up with a formula for the spreading speed, based on details of life history and movement behavior, long before an actual invasion takes place.

Models may be in continuous or discrete time; they may track the density of a single species or of multiple interacting species. Among this variability in model structure, mathematical theory has shown that there are two key types of population waves associated with biological invasion. "Pulled waves" are driven by growth and dispersal processes at the leading edge of the invasion where densities are low. "Pushed waves" are driven by the growth and dispersal processes further back in the wave where densities are higher.

For their PNAS paper, Gandhi et al. (4) undertook an ingenious set of carefully controlled experiments to investigate pulled and pushed waves in the spatial invasion of budding yeast populations, cultured in linear arrays of wells on plates. Here, the exchange of small volumes of growth media between adjacent wells simulated spatial dispersal, whereas manipulations of the sugar type in the underlying culture were sufficient to switch the dynamics from pulled to pushed waves. The authors were able to connect their experimental results to theoretical predictions that go back 40 y regarding the speed and shape of pulled and pushed waves. Although these predictions have formed a mainstay of invasion theory, until this present work they had never been adequately tested in a controlled environment.

To fully understand the Gandhi et al. (4) paper, it is necessary to take into account a historical perspective on the mathematical theory of population spread associated with biological invasions. Developments can be traced back to the well-known Fisher-KPP (Kolmogorov-Petrovsky-Piscounov) equation, originally used to track the geographical advance of an advantageous allele into a new environment in the late 1930s (5, 6), and then later reapplied in ecological contexts to invasion biology in the 1950s (7). This equation, which couples logistic population growth to a spatial diffusion process, yields an appealing and tractable formula for the spreading speed: $c = 2\sqrt{rD}$, where r is the per capita growth rate at low densities and D is the diffusion coefficient. It is fascinating that the carrying capacity arising from competition in logistic growth plays no role in this formula for the spreading speed. The relevant quantity for per capita growth, r, is measured at low population densities. Mathematically, the wave of advance is pulled across the landscape, driven by growth and dispersal processes at the leading edge of the invasion where per capita growth rates are highest and densities are low, rendering nonlinear interactions negligible. This spreading speed formula has been widely tested, starting with the work of Skellam (7) and continuing to this day. These tests have shown that theoretically predicted speeds compare well to those observed from geographical case studies for invasions, ranging from the bubonic plague to insect pests to mammals (8).

Although hailed as a success story in theoretical ecology (8), tests of the Fisher-KPP spreading speed theory have been subject to major shortcomings. First, these tests have been primarily retrospective, explaining

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Table 1. Effects of sugar types on growth and invasion dynamics in budding yeast

Growth medium	Carrying capacity	Growth rate	Density dependence	Invasion wave type
Galactose	High	Low	Negative	Pulled
Glucose	Low	High	Negative	Pulled
Sucrose	—	—	Positive/negative	Pushed

historical observations rather than predicting future outcomes. Second, there has been little possibility for replication; indeed, preventing repetition of significant invasions is essential to protecting the environment. Third, the actual form of nonlinear density-dependence described by logistic growth is too simplistic for many populations. Social interactions, such as cooperative feeding or sexual reproduction, produce so-called "Allee effects": diminished per capita population growth rates at low densities because of a lack of partners. Allee effects can cause a breakdown in the celebrated Fisher-KPP spreading speed formula. In this case, rather than being pulled, the wave of advance is actually pushed, with populations that are well behind the leading edge having the highest per capita growth, and then spilling over via diffusion to push the wave forward (9). Although some theory has been developed for this case (10), there is no simple replacement formula for the spreading speed. To compound the issue, the demographic details needed to predict the spreading speed of a population with an Allee effect are, by definition, difficult to measure because they require observations of declining populations at low densities. Thus, predictions and subsequent comparisons with geographical case studies have been few and far between (but see ref. 11).

In the paper by Gandhi et al. (4), the Allee effect was induced by the cooperative growth dynamics arising from sucrose versus glucose consumption in yeast (Table 1). Thus, the set of laboratory experiments allowed for replication and modulation of the Allee dynamics based on known underlying causes, thereby providing a perfect mechanism for predicting outcomes from specific experimental manipulations on the spreading speed. In summary, the work overcame the three major shortcomings in testing invasions outlined in the previous paragraph, and thus constitutes a breakthrough in connecting experiment to theory.

Furthermore the experimental set-up allows for additional detailed comparisons between other theoretical predictions and experimental observations. As noted above, the theoretical prediction for pulled waves is that the spreading speed is independent of carrying capacity. This was tested using glucose versus galactose sugars, the former having a lower carrying capacity than the latter (Table 1). It was also possible to test the steepness of the wave in pushed versus pulled dynamics. The theoretical prediction is that pushed waves have the steeper profile. Both theoretical predictions were tested experimentally and held true.

The Gandhi et al. (4) paper illuminates the role of controlled small-scale experiments in connecting theory to experiment in mathematical ecology. Other notable examples include the search for chaos in biological populations via the manipulation of flour beetle populations (12), and the analysis of founder effects in spread rates, again using flour beetles (13). Ecologists may claim that these experimental systems are manipulated to the point where conclusions are no longer ecologically relevant. However, a strong argument can be made that the systems actually become crucial stepping-stones that lie between the abstract mathematical theory and the highly complex natural ecological systems that we ultimately wish to understand.

It is sobering to contemplate that, as with many subjects in mathematical ecology, the theory of pulled versus pushed waves preceded experiment by a long shot: the Gandhi et al. (4) paper comes approximately 40 y after the pioneering mathematical work in the subject (9). Although belated, the connectivity speaks to the value of deep mathematical analysis of biological phenomena, even long before experimental testing is possible.

1 Pimentel D, ed (2011) *Biological Invasions: Economic and Environmental Costs of Alien Plant, Animal, and Microbe Species* (CRC, Boca Raton, FL).
2 Elton CS (1958) *The Ecology of Invasions by Animals and Plants* (Methuen, London).
3 Davis MA (2009) *Invasion Biology* (Oxford Univ Press, Oxford).
4 Gandhi SB, Yurtsev EA, Kirill SK, Gore J (2016) Range expansions transition from pulled to pushed waves as growth becomes more cooperative in an experimental microbial population. *Proc Natl Acad Sci USA* 113:6922–6927.
5 Fisher RA (1937) The wave of advance of advantageous genes. *Ann Eugen* 7(4):355–369.
6 Kolmogorov AN, Petrovsky IG, Piskunov NS (1937) Etude de l'équation de la diffusion avec croissance de la quantité de matiere et son applicationa un probleme biologique. *Moscow Univ Math Bull* 1:1–25.
7 Skellam JG (1951) Random dispersal in theoretical populations. *Biometrika* 38(1-2):196–218.
8 Andow DA, Kareiva PM, Levin SA, Okubo A (1990) Spread of invading organisms. *Landsc Ecol* 4(2):177–188.
9 Stokes AN (1976) On two types of moving front in quasilinear diffusion. *Math Biosci* 31(3-4):307–315.
10 Lewis MA, Kareiva P (1993) Allee dynamics and the spread of invading organisms. *Theor Popul Biol* 43(2):141–158.
11 Veit RR, Lewis MA (1996) Dispersal, population growth, and the Allee effect: Dynamics of the house finch invasion of eastern North America. *Am Nat* 148(2):255–274.
12 Costantino RF, Desharnais RA, Cushing JM, Dennis B (1997) Chaotic dynamics in an insect population. *Science* 275(5298):389–391.
13 Melbourne BA, Hastings A (2009) Highly variable spread rates in replicated biological invasions: fundamental limits to predictability. *Science* 325(5947):1536–1539.