Emerging predictable features of replicated biological invasion fronts

Andrea Giometto^{a,b}, Andrea Rinaldo^{a,c,1}, Francesco Carrara^a, and Florian Altermatt^b

^aLaboratory of Ecohydrology, School of Architecture, Civil and Environmental Engineering, École Polytechnique Fédérale de Lausanne, CH-1015 Lausanne, Switzerland; ^bDepartment of Aquatic Ecology, Eawag: Swiss Federal Institute of Aquatic Science and Technology, CH-8600 Dübendorf, Switzerland; and ^cDipartimento di Ingegneria Civile, Edile ed Ambientale, Università di Padova, I-35131 Padua, Italy

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Biological dispersal shapes species' distribution and affects their coexistence. The spread of organisms governs the dynamics of invasive species, the spread of pathogens, and the shifts in species ranges due to climate or environmental change. Despite its relevance for fundamental ecological processes, however, replicated experimentation on biological dispersal is lacking, and current assessments point at inherent limitations to predictability, even in the simplest ecological settings. In contrast, we show, by replicated experimentation on the spread of the ciliate Tetrahymena sp. in linear landscapes, that information on local unconstrained movement and reproduction allows us to predict reliably the existence and speed of traveling waves of invasion at the macroscopic scale. Furthermore, a theoretical approach introducing demographic stochasticity in the Fisher-Kolmogorov framework of reaction-diffusion processes captures the observed fluctuations in range expansions. Therefore, predictability of the key features of biological dispersal overcomes the inherent biological stochasticity. Our results establish a causal link from the short-term individual level to the long-term, broad-scale population patterns and may be generalized, possibly providing a general predictive framework for biological invasions in natural environments.

Fisher wave | microcosm | colonization | spatial | frontiers

What is the source of variance in the spread rates of bi-ological invasions? The search for processes that affect biological dispersal and sources of variability observed in ecological range expansions is fundamental to the study of invasive species dynamics (1-10), shifts in species ranges due to climate or environmental change (11-13), and, in general, the spatial distribution of species (3, 14–16). Dispersal is the key agent that brings favorable genotypes or highly competitive species into new ranges much faster than any other ecological or evolutionary process (1, 17). Understanding the potential and realized dispersal is thus key to ecology in general (18). When organisms' spread occurs on the timescale of multiple generations, it is the byproduct of processes that take place at finer spatial and temporal scales that are the local movement and reproduction of individuals (5, 10). The main difficulty in causally understanding dispersal is thus to upscale processes that happen at the shortterm individual level to long-term and broad-scale population patterns (5, 18–20). Furthermore, the large fluctuations observed in range expansions have been claimed to reflect an intrinsic lack of predictability of the phenomenon (21). Whether the variability observed in nature or in experimental ensembles might be accounted for by systematic differences between landscapes or by demographic stochasticity affecting basic vital rates of the organisms involved is an open research question (10, 18, 21, 22).

Modeling of biological dispersal established the theoretical framework of reaction-diffusion processes (1–3, 23–25), which now finds common application in dispersal ecology (5, 14, 22, 26–30) and in other fields (17, 23, 25, 31–36). Reaction-diffusion models have also been applied to model human colonization processes (31), such as the Neolithic transition in Europe (25, 37, 38). The classical prediction of reaction-diffusion models (1, 2, 24, 25) is the propagation of an invading wavefront traveling

undeformed at a constant speed (Fig. 1*E*). Such models have been widely adopted by ecologists to describe the spread of organisms in a variety of comparative studies (5, 10, 26) and to control the dynamics of invasive species (3, 4, 6). The extensive use of these models and the good fit to observational data favored their common endorsement as a paradigm for biological dispersal (6). However, current assessments (21) point at inherent limitations to the predictability of the phenomenon, due to its intrinsic stochasticity. Therefore, single realizations of a dispersal event (as those addressed in comparative studies) might deviate significantly from the mean of the process, making replicated experimentation necessary to allow hypothesis testing, identification of causal relationships, and to potentially falsify the models' assumptions (39).

Here, we provide replicated and controlled experimental support to the theory of reaction-diffusion processes for modeling biological dispersal (23-25) in a generalized context that reproduces the observed fluctuations. Firstly, we experimentally substantiate the Fisher–Kolmogorov prediction (1, 2) on the existence and the mean speed of traveling wavefronts by measuring the individual components of the process. Secondly, we manipulate the inclusion of demographic stochasticity in the model to reproduce the observed variability in range expansions. We move from the Fisher-Kolmogorov equation (Materials and Methods) to describe the spread of organisms in a linear landscape (1, 2, 24, 25). The equation couples a logistic term describing the reproduction of individuals with growth rate $r [T^{-1}]$ and carrying capacity $K[L^{-1}]$ and a diffusion term accounting for local movement, epitomized by the diffusion coefficient $D [L^2T^{-1}]$. These species' traits define the characteristic scales of the dispersal process. In this framework, a population initially located at one end of a linear landscape is predicted to form a wavefront of

Significance

Biological dispersal is a key driver of several fundamental processes in nature, crucially controlling the distribution of species and affecting their coexistence. Despite its relevance for important ecological processes, however, the subject suffers an acknowledged lack of experimentation, and current assessments point at inherent limitation to predictability even in the simplest ecological settings. We show, by combining replicated experimentation on the spread of the ciliate *Tetrahymena* sp. with a theoretical approach based on stochastic differential equations, that information on local unconstrained movement and reproduction of organisms (including demographic stochasticity) allows reliable prediction of both the propagation speed and range of variability of invasion fronts over multiple generations. PHYSICS

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¹To whom correspondence should be addressed. E-mail: andrea.rinaldo@epfl.ch.

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Fig. 1. Schematic representation of the experiment. (*A*) Linear landscape. (*B*) Individuals of the ciliate *Tetrahymena* sp. move and reproduce within the landscape. (*C*) Examples of reconstructed trajectories of individuals (Movie S1). (*D*) Individuals are introduced at one end of a linear landscape and are observed to reproduce and disperse within the landscape (not to scale). (*E*) Illustrative representation of density profiles along the landscape at subsequent times. A wavefront is argued to propagate undeformed at a constant speed v according to the Fisher–Kolmogorov equation.

colonization invading empty space at a constant speed $v = 2\sqrt{rD}$ (1, 2, 24, 25), which we measured in our dispersal experiment (Fig. 1D and *SI Text*).

Results

In the experiments, we used the freshwater ciliate *Tetrahymena* sp. (*Materials and Methods*) because of its short generation time (16) and its history as a model system in ecology (16, 40, 41). The

experimental setup consisted of linear landscapes, filled with a nutrient medium, kept in constant environmental conditions and of suitable size to meet the assumptions about the relevant dispersal timescales (*Materials and Methods*). Replicated dispersal events were conducted by introducing an ensemble of individuals at one end of the landscape and measuring density profiles throughout the system at different times, through image analysis (*Materials and Methods*). Density profiles are shown in



Fig. 2. Density profiles in the dispersal experiment and in the stochastic model. (A–F) Density profiles of six replicated experimentally measured dispersal events, at different times. Legends link each color to the corresponding measuring time. Black dots are the estimates of the front position at each time point. Organisms were introduced at the origin and subsequently colonized the whole landscape in 4 d (\sim 20 generations). (*G* and *H*) Two dispersal events simulated according to the generalized model equation, with initial conditions as at the second experimental time point. Data are binned in 5-cm intervals, typical length scale of the process.



Fig. 3. Range expansion in the dispersal experiment and in the stochastic model. (*A*) Front position of the expanding population in six replicated dispersal events; colors identify replicas as in Fig. 2. The dark and light gray shadings are, respectively, the 95% and 99% confidence intervals computed by numerically integrating the generalized model equation, with initial conditions as at the second experimental time point, in 1,020 iterations. The black curve is the mean front position in the stochastic integrations. (*B*) The increase in range variability between replicates in the dispersal experiment (blue diamonds) is well described by the stochastic model (red line). (*C*) Mean front speed for different choices of the reference density value at which we estimated the front position in the experiment; error bars are smaller than symbols.

Fig. 2, in six replicated dispersal events (Fig. 2 A–F). Organisms introduced at one end of the landscape rapidly formed an advancing front that propagated at a remarkably constant speed (Fig. 3 and Table S1). The front position at each time was calculated as the first occurrence, starting from the end of the landscape, of a fixed value of the density (Fig. 2). As for traveling waves predicted by the Fisher–Kolmogorov equation, the mean front speed in our experiment is notably constant for different choices of the reference density value (Fig. 3C).

The species' traits r, K, and D were measured in independent experiments (Table 1). In the local-growth experiment, a lowdensity population of *Tetrahymena* sp. was introduced evenly across the landscape, and its density was measured locally at different times. Recorded density measurements were fitted to the logistic growth model, which gave the estimates for r and K (Table 1 and Table S2). In the local unimpeded movement experiment, we computed the mean-square displacement (*SI Text* and Fig. S1) of individuals' trajectories (42–44) to estimate the diffusion coefficient D in density-independent conditions (Table 1 and *Materials and Methods*). The growth and movement measurements were performed in the same linear landscape settings as in the dispersal experiment and therefore are assumed to accurately describe the dynamics at the front of the traveling wave in the dispersal events.

The comparison of the predicted front speed $v = 2\sqrt{rD}$ to the wavefront speed measured in the dispersal experiment, v_o , yields a compelling agreement. The observed speed in the dispersal experiment was $v_o = 52.0 \pm 1.8$ cm/d (mean \pm SE) (Table S1), which we compare with the predicted one $v = 51.9 \pm 1.1$ cm/d (mean \pm SE). The two velocities are compatible within one SE. A *t* test between the replicated observed speeds and bootstrap estimates of $v = 2\sqrt{rD}$ gives a *P* value of p = 0.96 (t = 0.05, df = 9). Thus, the null hypothesis that the mean difference is 0 is not rejected at the 5% level, and there is no indication that the two means are different. As the measurements of *r* and *D* were performed in independent experiments, at scales that were orders of magnitude smaller than in the dispersal events, the agreement between the two estimates of the front velocity is deemed remarkable.

Although the Fisher-Kolmogorov equation correctly predicts the mean speed of the experimentally observed invading wavefront, its deterministic formulation prevents it from reproducing the variability that is inherent to biological dispersal (21). In particular, it cannot reproduce the fluctuations in range expansion between different replicates of our dispersal experiment (Fig. 3A). We propose a generalization of the Fisher–Kolmogorov equation (Materials and Methods) accounting for demographic stochasticity that is able to capture the observed variability. The strength of demographic stochasticity is embedded in an additional species' trait σ [$T^{-1/2}$]. In this stochastic framework, the demographic parameters r, K, and σ were estimated from the local growth experiment with a maximum-likelihood approach (Table 1 and Materials and Methods) whereas the estimate of the diffusion coefficient D was left unchanged (SI Text). We then used these local independent estimates to numerically integrate the generalized model equation (45, 46), with initial conditions as in the dispersal experiment, and found that the measured front positions are in accordance with simulations (Fig. 3A and Fig. S2). In particular, most experimental data are within the 95% confidence interval for the simulated front position, and the observed range variability is well-captured by our stochastic model (Fig. 3B). Accordingly, the estimate for the front speed and its variability in the experiment are in good agreement with simulations (SI Text). Demographic stochasticity can therefore explain the observed variability in range expansions.

Discussion

To summarize, we suggest that measuring and suitably interpreting local processes allows us to accurately predict the main features of

Table 1. Experimentally measured species' traits (mean \pm SE)

Demogra	phic traits	Movement traits	
Deterministic model	Stochastic model		
$r = 4.9 \pm 0.5 \text{ d}^{-1}$ K = 901 ± 130 ind cm ⁻¹	$r = 6.1 \pm 0.8 \mathrm{d}^{-1}$ $K = 903 \pm 135 \mathrm{ind} \mathrm{cm}^{-1}$ $\sigma = 25 \pm 5 \mathrm{d}^{-\frac{1}{2}}$	$D = 0.17 \pm 0.01 \text{ mm}^2 \text{ s}^{-1}$ $\tau = 3.9 \pm 0.4 \text{ s}$	

Demographic traits were estimated both in the framework of the deterministic logistic equation and in the framework of the stochastic logistic Eq. **3**. Demographic stochasticity strongly affects the dynamics at low densities; thus, a different value for the growth rate r is obtained in the stochastic model, compared with the deterministic one. ind, individual.

global invasions. The deterministic Fisher-Kolmogorov equation is shown to correctly predict the mean speed of invasion but cannot capture the observed variability. Instead, characterizing the inherent stochasticity of the biological processes involved allows us to predict both the mean and the variability of range expansions, which is of interest for practical purposes, such as the delineation of worstcase scenarios for the spread of invasive species. Our phenomenological approach allows us to make predictions on the spread of organisms without the need to introduce all details on the movement behavior, biology, or any other information. Such details are synthesized in three parameters describing the density-independent vet stochastic behavior of individuals riding the invasion wave. The parsimony of the model allows generalization to organisms with different biology (e.g., growth rates and diffusion coefficients are available for several species in the literature) (6) and supports the view that our protocol may possibly provide a general predictive framework for biological invasions in natural environments.

In conclusion, we have shown that, at least in the simple ecological settings investigated here, predictability remains, notwithstanding biological fluctuations, owing to the stochastic treatment devised. We confirm that deterministic models can be applied to describe ecological processes and show that additional information on the stochasticity acting at the mesoscopic scale allows us to estimate fluctuations at the macroscopic scale. We believe that our results might have implications for the dynamics of phenomena other than species' invasions, such as morphogenesis (23, 47), tumor growth (23, 25, 36), and the spreading of epidemics (23, 30, 34, 35), which have been traditionally modeled with reaction–diffusion equations.

Materials and Methods

Study Species. The species used in this study is *Tetrahymena* sp. (Fig. 1*B*), a freshwater ciliate, purchased from Carolina Biological Supply. Individuals of *Tetrahymena* sp. have typical linear size (equivalent diameter) of 14 µm (41). Freshwater bacteria of the species *Serratia fonticola, Breviacillus brevis*, and *Bacillus subtilis* were used as a food resource for ciliates, which were kept in a medium made of sterilized spring water and protozoan pellets (Carolina Biological Supply) at a density of 0.45 gL^{-1} . The experimental units were kept under constant fluorescent light for the whole duration of the study, at a constant temperature of 22 °C. Overall, experimental protocols are wellestablished (16, 41, 48–50), and the contribution of laboratory experiments on protists to the understanding of population and metapopulation dynamics proved noteworthy (48).

Experimental Setup. Experiments were performed in linear landscapes (Fig. 1A) filled with a nutrient medium and bacteria of the three species above mentioned. The linear landscapes were 2 m long, 5 mm wide, and 3 mm deep, respectively, and 10⁵, 350, and 200 times the size of the study organism (41). Landscapes consisted of channels drilled on a Plexiglas sheet. A second sheet was used as lid, and a gasket was introduced to avoid water spillage (Fig. 1A). At one end of the landscapes, an opening was placed for the introduction of ciliates. The Plexiglas sheets were sterilized with a 70% (vol/vol) alcohol solution, and gaskets were autoclaved at 120 °C before filling the landscape with medium. As Plexiglas is transparent, the experimental units could be placed under the objective of a stereomicroscope, to record pictures (for counting of individuals) or videos (to track ciliates). Individuals were observed to distribute mainly at the bottom of the landscape, whose length was three orders of magnitude larger than its width (w) and depth and two orders of magnitude larger than the typical length scale of the process $(\sqrt{D/r} \simeq 5 \text{ cm})$. The population was thus assumed to be confidently well-mixed within the cross section after a time $\sim w^2/D$, which in our case is of the order of a minute after introduction of the ciliates in the landscape.

Experimental Protocol. We performed three independent and complementing experiments, specifically: (*i*) a dispersal experiment was carried out to study the possible existence and the propagation of traveling invasion wavefronts in replicated dispersal events; (*ii*) a growth experiment was run to obtain estimates of the demographic species' traits, which are r and K in the deterministic framework of Eq. 1 and r, K, and σ in the stochastic framework of Eq. 2; (*iii*) a local movement experiment was performed to study the local

unimpeded movement of *Tetrahymena* sp. over a short timescale (in a time window $t \ll r^{-1}$), to estimate the diffusion coefficient *D* for our study species, independently from the dispersal and growth experiments.

Dispersal experiment. We performed six replicated dispersal events in the linear landscapes. After filling the landscapes with medium and bacteria, a small ensemble of *Tetrahymena* sp. was introduced at the origin. Subsequently, the density of *Tetrahymena* sp. was measured at 1-cm intervals, five times in the first 48 h and twice in the last 48 h. The whole experiment lasted for about 20 generations of the study species.

Local growth experiment. We performed five replicated growth measurements in the linear landscapes, to measure the demographic species' traits, in the same environmental conditions as in the dispersal experiment, but independently from it. A low-density culture of *Tetrahymena* sp. was introduced in the whole landscape, and its density was measured by taking pictures and counting individuals, covering a region of 7 cm along the landscape. Density measurements were performed at several time points for each of the five replicates, in a time window of 3 d.

Local movement experiment. We performed four additional, replicated dispersal events in the linear landscapes, initialized in the same way as in the dispersal experiment, to measure the diffusion coefficient of *Tetrahymena* sp. The diffusion coefficient *D* is the proportionality constant that links the mean square displacement of organisms' trajectories to time (42, 44) (5/*Text*). Macroscopically, it relates the local flux to the density of individuals, under the assumption of steady state (44). To estimate the diffusion coefficient, we recorded several videos of individuals moving at the front of the traveling wave (at low density), reconstructed their trajectories (42, 43), and computed their mean square displacement $\langle x^2(t) \rangle = \langle |x(t) - x(0)|^2 \rangle$.

Video recording. We recorded videos of *Tetrahymena* sp. at the front of the traveling wave in four replicated dispersal events, at various times over 4 d. The area covered in each video was of 24 mm in the direction of the land-scape and 5 mm orthogonal to it. Each video lasted for 12 min.

Trajectories reconstruction. For each recorded video, we extracted individuals' spatial coordinates in each frame and used the MOSAIC plugin for the software ImageJ to reconstruct trajectories (43). The goodness of the tracking was checked on several trajectories by direct comparison with the videos. Examples of reconstructed trajectories can be seen in Fig. 1C or in Movie S1.

Diffusion coefficient estimate. For each video, the square displacement of each trajectory in the direction parallel to the landscape was computed at all time points and then averaged across trajectories. Precisely, for each trajectory *i* we computed the quantity $x_i^2(t) = [X_i(t) - X_i(0)]^2$, where $X_i(t)$ is the 1-dimensional coordinate of organism *i* at time *t* in the direction parallel to the landscape and $X_i(0)$ is its initial position. The mean square displacement in a video was then computed as the mean of $x_i^2(t)$ across all trajectories. A typical measurement of $\langle x^2(t) \rangle$ is shown in Fig. S1. As shown in the figure, there exists an initial correlated phase, which we discuss in *SI Text*. To estimate the diffusion coefficient from the mean square displacement, we fitted the measured $\langle x^2(t) \rangle$ to the function $\langle x^2(t) \rangle = 2Dt - 2Dr[1 - e^{-t/r}]$ (*SI Text*) with the two parameters *D* (diffusion coefficient) and τ (correlation time). The total number of recorded videos was 28, that is, 7 for each replica.

Mathematical Models. *Deterministic framework*. The Fisher–Kolmogorov equation (1, 2). reads:

$$\frac{\partial \rho}{\partial t} = D \frac{\partial^2 \rho}{\partial x^2} + r \rho \left[1 - \frac{\rho}{K} \right],$$
[1]

where $\rho = \rho(x,t)$ is the density of organisms, r the species' growth rate, D the diffusion coefficient, and K the carrying capacity. Eq. **1** is known to foster the development of undeformed traveling waves of the density profile. Mathematically, the existence of traveling wave solutions implies that $\rho(x,t) = \rho(x - vt)$, where v is the speed of the advancing wave. Fisher (1) proved that traveling wave solutions can only exist with speed $v \ge 2\sqrt{rD}$, and Kolmogorov (2) demonstrated that, with suitable initial conditions, the speed of the wavefront is the lower bound.

The microscopic movement underlying the Fisher–Kolmogorov Eq. **1** is brownian motion (25, 51). Investigation of the movement behavior of *Tetrahymena* sp., instead, shows that individuals' trajectories are consistent with a persistent random walk with an autocorrelation time $\tau = 3.9 \pm 0.4$ s. The corresponding macroscopic equation for the persistent random walk should thus be the reaction–telegraph equation (25) (*SI Text*). Nonetheless, as the autocorrelation time for our study species is much smaller than the growth rate r ($\tau \sim 10^{-4}$), Eq. 1 provides an excellent approximation to the reaction–telegraph equation. See *SI Text* for a detailed discussion.

Stochastic framework. The stochastic model equation reads:

$$\frac{\partial \rho}{\partial t} = D \frac{\partial^2 \rho}{\partial x^2} + r \rho \left[1 - \frac{\rho}{K} \right] + \sigma \sqrt{\rho} \eta, \qquad [2]$$

where $\eta = \eta(x,t)$ is a Gaussian, zero-mean white noise (i.e., with correlations $\langle \eta(x,t)\eta(x',t')\rangle = \delta(x-x')\delta(t-t')$, where δ is the Dirac's delta distribution) and $\sigma > 0$ is constant. We adopt the Itô's stochastic calculus (51), as appropriate in this case. Note, in fact, that the choice of the Stratonovich framework would make no sense here, as the noise term would have a constant nonzero mean (22, 51), which would allow an extinct population to possibly escape the zero-density absorbing state. The square-root multiplicative noise term in Eq. 2 is commonly interpreted as describing demographic stochastici ular, standard stochastic integration schemes fail to preserve the positivity of ρ . We adopted a recently developed split-step method (45) to numerically integrate Eq. 2. This method allows us to perform the integration with relatively large spatial and temporal steps maintaining numerical accuracy.

Data from the growth experiment were fitted to the equation:

$$\frac{d\rho}{dt} = r\rho \left[1 - \frac{\rho}{\kappa} \right] + \frac{\sigma}{\sqrt{I}} \sqrt{\rho} \ \eta,$$
[3]

where $\rho = \rho(t)$ is the local density, $\eta = \eta(t)$ is a Gaussian, zero-mean white noise (i.e., with correlations $\langle \eta(t)\eta(t')\rangle = \delta(t-t')$), $\sigma > 0$ is constant, and *I* is the

- 1. Fisher RA (1937) The wave of advance of advantageous genes. Ann Eugen 7:355-369.
- Kolmogorov AN, Petrovskii IG, Piskunov NS (1937) A study of the diffusion equation with increase in the amount of substance, and its application to a biological problem. Bull. Moscow Univ. Math. Mech. 1(1):1–25.
- Skellam JG (1951) Random dispersal in theoretical populations. *Biometrika* 38(1-2): 196–218.
- 4. Elton CS (1958) The Ecology of Invasions by Animals and Plants (Methuen, London).
- Andow DA, Kareiva PM, Levin SA, Okubo A (1990) Spread of invading organisms. Landscape Ecol 4(2/3):177–188.
- Grosholz ED (1996) Contrasting rates of spread for introduced species in terrestrial and marine systems. *Ecology* 77(6):1680–1686.
- 7. Shigesada N, Kawasaki K (1997) *Biological Invasions: Theory and Practice* (Oxford University Press, Oxford).
- Clobert J, Danchin E, Dhondt AA, Nichols JD, eds (2001) Dispersal (Oxford University Press, Oxford).
- 9. Okubo A, Levin SA (2002) Diffusion and Ecological Problems: Modern Perspectives (Springer, Berlin), 2nd Ed.
- Hastings A, et al. (2005) The spatial spread of invasions: New developments in theory and evidence. *Ecol Lett* 8(1):91–101.
- 11. Parmesan C, et al. (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399(6736):579–583.
- 12. Bell G, Gonzalez A (2011) Adaptation and evolutionary rescue in metapopulations experiencing environmental deterioration. *Science* 332(6035):1327–1330.
- 13. Leroux SJ, et al. (2013) Mechanistic models for the spatial spread of species under climate change. *Ecol Appl* 23(4):815–828.
- Bertuzzo E, Maritan A, Gatto M, Rodriguez-Iturbe I, Rinaldo A (2007) River networks and ecological corridors: Reactive transport on fractals, migration fronts, hydrochory. Water Resour Res 43(4):W04419.
- Muneepeerakul R, et al. (2008) Neutral metacommunity models predict fish diversity patterns in Mississippi-Missouri basin. Nature 453(7192):220–222.
- Carrara F, Altermatt F, Rodriguez-Iturbe I, Rinaldo A (2012) Dendritic connectivity controls biodiversity patterns in experimental metacommunities. Proc Natl Acad Sci USA 109(15):5761–5766.
- Hallatschek O, Nelson DR (2008) Gene surfing in expanding populations. *Theor Popul Biol* 73(1):158–170.
- Sutherland WJ, et al. (2013) Identification of 100 fundamental ecological questions. J Ecol 101(1):58–67.
- 19. Levin SA (1992) The problem of pattern and scale in ecology. *Ecology* 73(6):1943–1967.
- Bascompte J, Solé RV (1995) Rethinking complexity: Modelling spatiotemporal dynamics in ecology. Trends Ecol Evol 10(9):361–366.
- Melbourne BA, Hastings A (2009) Highly variable spread rates in replicated biological invasions: Fundamental limits to predictability. Science 325(5947):1536–1539.
- Méndez V, Llopis I, Campos D, Horsthemke W (2011) Effect of environmental fluctuations on invasion fronts. J Theor Biol 281(1):31–38.
- 23. Murray JD (2004) Mathematical Biology I: An Introduction (Springer, Berlin), 3rd Ed. 24. Volpert V, Petrovskii S (2009) Reaction-diffusion waves in biology. Phys Life Rev 6(4):
- 267–310.
 Méndez V, Fedotov S, Horsthemke W (2010) *Reaction-Transport Systems* (Springer, Berlin).
- Lubina JA, Levin SA (1988) The spread of a reinvading species: Range expansion in the California sea otter. Am Nat 131(4):526–543.
- Holmes EE (1993) Are diffusion models too simple? A comparison with telegraph models of invasion. Am Nat 142(5):779–795.

size of the region over which densities were measured (*SI Text*). Eq. **3** describes the time-evolution of the density in a well-mixed patch of length *I* (*SI Text*). The likelihood function for Eq. **3** can be written as:

$$L(\theta) = \prod_{j=2}^{n} P[\rho(t_j), t_j | \rho(t_{j-1}), t_{j-1}; \theta],$$
[4]

where *n* is the total number of observations in the growth time series, $\theta = (r, K, \sigma)$ is the vector of demographic parameters, and $P(\rho, t|\rho_0, t_0; \theta)$ is the transitional probability density of having a density of individuals ρ at time *t*, given that the density at time t_0 was ρ_0 (for a given θ). The transitional probability density $P(\rho, t|\rho_0, t_0; \theta)$ satisfies the Fokker–Planck equation associated to Eq. **3** (*SI Text*), which was solved numerically for all observed transitions and choices of parameters (*SI Text*), adopting the implicit Crank– Nicholson scheme. The best fit parameters were those that maximized the likelihood function Eq. **4** (Table 1 and *SI Text*).

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- Solé RV, Bascompte J (2006) Self-Organization in Complex Ecosystems (Princeton Univ Press, Princeton).
- Roques L, Garnier J, Hamel F, Klein EK (2012) Allee effect promotes diversity in traveling waves of colonization. Proc Natl Acad Sci USA 109(23):8828–8833.
- 30. Pybus OG, et al. (2012) Unifying the spatial epidemiology and molecular evolution of emerging epidemics. *Proc Natl Acad Sci USA* 109(37):15066–15071.
- Campos D, Fort J, Méndez V (2006) Transport on fractal river networks: application to migration fronts. *Theor Popul Biol* 69(1):88–93.
- Hallatschek O, Hersen P, Ramanathan S, Nelson DR (2007) Genetic drift at expanding frontiers promotes gene segregation. *Proc Natl Acad Sci USA* 104(50):19926–19930.
 Fort J, Pujol T (2008) Progress in front propagation research. *Rep Prog Phys* 71(8):
- Sorte Z, Hoje Hessel, Hogers in Hole propagation research. Rep Frog Frigs Frigs. 086001.
 Bertuzzo E, Casagrandi R, Gatto M, Rodriguez-Iturbe I, Rinaldo A (2010) On spatially
- explicit models of cholera epidemics. *J R Soc Interface* 7(43):321–333. 35. Righetto L, et al. (2010) Modelling human movement in cholera spreading along
- fluvial systems. *Ecohydrology* 4(1):49–55.
- Fort J, Solé RV (2013) Accelerated tumor invasion under non-isotropic cell dispersal in glioblastomas. New J Phys 15(5):055001.
- 37. Ammerman AJ, Cavalli-Sforza LL (1984) The Neolithic Transition and the Genetics of Populations in Europe (Princeton Univ Press, Princeton).
- Fort J (2012) Synthesis between demic and cultural diffusion in the Neolithic transition in Europe. Proc Natl Acad Sci USA 109(46):18669–18673.
- Hekstra DR, Leibler S (2012) Contingency and statistical laws in replicate microbial closed ecosystems. Cell 149(5):1164–1173.
- Schtickzelle N, Fjerdingstad EJ, Chaine A, Clobert J (2009) Cooperative social clusters are not destroyed by dispersal in a ciliate. *BMC Evol Biol* 9(251):251, 10.1186/1471-2148-9-251.
- Giometto A, Altermatt F, Carrara F, Maritan A, Rinaldo A (2013) Scaling body size fluctuations. Proc Natl Acad Sci USA 110(12):4646–4650.
- 42. Berg HC (1993) Random Walks in Biology (Princeton Univ Press, Princeton).
- Sbalzarini IF, Koumoutsakos P (2005) Feature point tracking and trajectory analysis for video imaging in cell biology. J Struct Biol 151(2):182–195.
- Polin M, Tuval I, Drescher K, Gollub JP, Goldstein RE (2009) Chlamydomonas swims with two "gears" in a eukaryotic version of run-and-tumble locomotion. Science 325(5939): 487–490.
- Dornic I, Chaté H, Muñoz MA (2005) Integration of Langevin equations with multiplicative noise and the viability of field theories for absorbing phase transitions. *Phys Rev Lett* 94(10):100601.
- Bonachela J, Muñoz MA, Levin SA (2012) Patchiness and demographic noise in three ecological examples. J Stat Phys 148(4):723–739.
- Turing AM (1952) The chemical basis of morphogenesis. Philos Trans R Soc Lond, B 237(641):37–72.
- Holyoak M, Lawler SP (2005) Population dynamics and laboratory ecology. Advances in Ecological Research (Academic, London), Vol 37, pp 245–271.
- Altermatt F, Bieger A, Carrara F, Rinaldo A, Holyoak M (2011) Effects of connectivity and recurrent local disturbances on community structure and population density in experimental metacommunities. *PLoS ONE* 6(4):e19525.
- Altermatt F, Schreiber S, Holyoak M (2011) Interactive effects of disturbance and dispersal directionality on species richness and composition in metacommunities. *Ecology* 92(4):859–870.
- 51. Gardiner C (2006) Stochastic Methods (Springer, Berlin), 4th Ed.
- Moro E (2004) Numerical schemes for continuum models of reaction-diffusion systems subject to internal noise. *Phys Rev E Stat Nonlin Soft Matter Phys* 70(4 Pt 2): 045102.

ECOLOGY

Supporting Information

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Experiments

1.1. Dispersal Experiment. Density profiles in the six replicated dispersal events, at successive times, are shown in Fig. 2 A-F. Collected data were binned in 5-cm bins, which corresponds to the typical length scale of the dispersal process $(\sqrt{D/r} \simeq 5 \text{ cm})$. Individuals of Tetrahymena sp., initially localized at one end of the landscape, colonized the whole system in 4 d. The position of the wavefront at each time was estimated by looking for the first occurrence, starting from the end of the landscape, of a fixed value of the density (more precisely, we linearly interpolated the density profile between the first occurrence of a density value above threshold and the following spatial point), which we set at $\rho^{\star} = 200$ ind/cm (results are not affected by different choices of this reference value) (Fig. 3C). The position of the wavefront at different times is shown in Fig. 3A. As noticeable, there is an initial growth phase followed by a linear increase in the front's coordinate with time. We fitted a linear model (least-squares fit) to each replica in the linear region (1-4 d) and found a mean speed of $v_o = 52.0 \pm 1.8 \text{ cm/d}$ (mean \pm SE). Note that the existence of an initial nonlinear spread has been documented in several case studies (1-3). Shown in Table S1 are the observed velocities in the six replicas (Fig. 3).

1.2. Local Growth Experiment. We discuss here the analysis of growth measurements according to the deterministic framework of the Fisher–Kolmogorov equation. For the analysis of these data in the stochastic framework, see section 2.2.

We report in Table S2 the best-fit parameters of the deterministic logistic model $d\rho/dt = r\rho[1-\rho/K]$ to the growth measurements data. Note that the variability in the carrying capacity among replicas resembles the variability in the mean density observed in the dispersal experiment in the region behind the wavefront (Fig. 2).

1.3. Local Movement Experiment. We ran four additional dispersal events, independent from the dispersal experiment, and recorded videos of individuals moving ahead of the advancing wavefront, where the density was low. To obtain experimental estimates of the diffusion coefficient, we fitted the measured values of $\langle x^2(t) \rangle$ to the equation $\langle x^2(t) \rangle = 2Dt - 2D\tau [1 - e^{-t/\tau}]$, for all videos of each replica (see section 4.2.1 for a derivation of this equation in the context of persistent random walks). The mean value of the diffusion coefficient is $D = 0.17 \pm 0.01 \text{ mm}^2/\text{s} = 140 \pm 10 \text{ cm}^2/\text{d}$; the mean autocorrelation time is $\tau = 3.9 \pm 0.4$ s.

Note that we have measured the diffusion coefficient by looking at individuals at the front of the traveling wave, as these are the individuals responsible for the colonization of empty space. During the dispersal experiment, we also measured the diffusion coefficient of *Tetrahymena* sp. in the bulk of the wave, that is, where the population was at high density. We observed that trajectories differ qualitatively between the bulk and the front of the wave, and this difference reflects in a much smaller diffusion coefficient estimate where the population is at carrying capacity. In fact, in the bulk of the wave, we measured a mean diffusion coefficient of $D_{bulk} = 0.003 \pm 0.001 \text{ mm}^2/\text{s}$, much smaller than at the wavefront. Such density-dependent effects, however, are not assumed to be operating at the low densities that determine the speed of the front, and the results support our assumption.

1.4. Speed of the Wavefront: Deterministic Prediction and Observations. Here, we compare the wavefront speeds observed in the dispersal experiment to predictions of the theory (deterministic Fisher-Kolmogorov Eq. 1) (Materials and Methods), for which we use the independent estimates of r and D (as in sections 1.2 and 1.3). Use of the mean value of $r = 4.9 \pm 0.5$ d⁻¹ (mean \pm SE) and $D = 140 \pm 10 \text{ cm}^2/\text{d}$ (mean \pm SE) gives a predicted speed of $v_{FK} = 2\sqrt{rD} = 52.4 \pm 3.3$ cm/d. In the main text, we adopted a bootstrap approach and computed the quantity $2\sqrt{rD}$ for all possible combinations of the r and D values measured in the growth and movement experiments. The mean speed computed with this approach is $v = 51.9 \pm 1.1$ cm/d (mean \pm SE). Both v_{FK} and v are very close and compatible with the mean observed speed in the dispersal experiment, $v_o = 52.0 \pm 1.8 \text{ cm/d} (\text{mean} \pm \text{SE})$. To further compare the predicted values for the speed in the bootstrap approach to the observed speed in the dispersal experiment, we performed a t test between the two sets. The t test gives a P value p = 0.96 (t = 0.05, df = 9); thus, the null hypothesis that the mean difference is 0 is not rejected at the 5% level. Therefore, there is no indication that the two means are different.

Stochastic Model

The Fisher–Kolmogorov Eq. 1 (*Materials and Methods*) is deterministic and therefore cannot reproduce the variability observed in biological dispersal (4) (Fig. 3). To address fluctuations in the range expansion of invading species, we propose a stochastic partial differential equation (SPDE), that is, a generalization of Eq. 1, accounting for demographic stochasticity. The SPDE reads:

$$\frac{\partial \rho}{\partial t} = D \frac{\partial^2 \rho}{\partial x^2} + r\rho \left[1 - \frac{\rho}{K} \right] + \sigma \sqrt{\rho} \eta, \qquad [S1]$$

where η is a Gaussian, zero-mean white noise [i.e., $\langle \eta(x,t) \rangle$ $\eta(x',t') = \delta(x-x')\delta(t-t')$, with δ the Dirac's delta function] and $\sigma > 0$ measures the noise strength. We adopt the Itô's stochastic calculus (5), as appropriate in this case. Note, in fact, that the choice of the Stratonovich framework would make no sense here, as the noise term would have a constant nonzero mean (5, 6), which would allow an extinct population to possibly escape the zero-density absorbing state. We simulated Eq. S1 using the estimates for r, K, and σ obtained with a maximum likelihood approach applied to the growth experiment data (section 2.2) and D as estimated in the local movement experiment (section 1.3). The square-root multiplicative noise term in Eq. S1 is commonly interpreted as describing demographic stochasticity in a population (7) and needs extra care in simulations (8, 9). In particular, standard stochastic integration schemes fail to preserve the positivity of ρ . We adopted a recently developed split-step method (9) (see also section 2.1) to numerically integrate Eq. S1. This method allows us to perform the integration with relatively large spatial and temporal steps maintaining numerical accuracy. Fig. 2 G and H shows two integrations of Eq. 1 with initial conditions as in Fig. 2 A and B at the second experimental time point. Simulations were performed with reflective boundary conditions at x=0 cm and x=220 cm and with the parameters $r = 6.1 \text{ d}^{-1}$, K = 903 ind/cm, $\sigma = 25 \text{ d}^{-\frac{1}{2}}$ (results of the maximum likelihood estimation) (see section 2.2) and $D=140 \text{ cm}^2/\text{d}$. The integration steps were $\Delta x=5 \text{ cm}$ and $\Delta t = 0.002$ d, which were able to reproduce the deterministic behavior and speed for very small values of the noise strength σ . It should be noted that the mathematical structure of Eq. S1 allows the formation of traveling waves, although endowed with a speed slower than $2\sqrt{rD}$. The reader is referred to the literature for a detailed account of the mathematical details (6, 10, 11). Suffice it here to note that the parameter identification of the

demographic traits r, K, and σ on the growth experiment data accounts for the relative balance of the processes and results in a reliable prediction of both the mean speed and the range variability (section 2.3).

2.1. Spatial Discretization. Eq. **S1** is interpreted as the continuum limit of a set of coupled Itô equations resulting from a discretization of space (9). Let Δx be the step of spatial discretization on a 1*D* lattice. The discretization reads:

$$\begin{aligned} \frac{d\rho_i}{dt}(t) &= \frac{D}{\left(\Delta x\right)^2} \left[\rho_{i+1}(t) + \rho_{i-1}(t) - 2\rho_i(t)\right] + \\ &+ r\rho_i(t) \left(1 - \frac{\rho_i(t)}{K}\right) + \frac{\sigma}{\sqrt{\Delta x}} \sqrt{\rho_i(t)} \eta(t), \end{aligned}$$
[S2]

where *i* identifies the lattice site and the term $\sqrt{\Delta x}$ ensures proper normalization in the continuum limit (12). This spatial discretization allows us to compare the noise term in Eq. **S1** to the local noise acting at a lattice site of size Δx . In particular, it allows us to estimate the noise strength σ by parameter identification on the growth experiment data, where we looked at the density of a single site *i* of size l=7 cm (a length comparable with the step size adopted in the numerical integration, that is $\Delta x = 5$ cm). The equation governing the density of the single site *i* in the growth experiment is thus:

$$\frac{d\rho}{dt}(t) = r\rho(t)\left(1 - \frac{\rho(t)}{K}\right) + \frac{\sigma}{\sqrt{l}}\sqrt{\rho(t)}\eta(t),$$
[S3]

where the diffusion term is neglected as we are in a well-mixed setting and we dropped the *i* subscript as we only have one site. The maximum likelihood approach described in the following section allows us to estimate *r*, *K*, and σ from the experimental growth data.

2.2. Parametric Inference in the Stochastic Framework. We fit Eq. S3 to the growth data (local growth experiment), with fitting parameters r, K, and σ . The likelihood function for Eq. S3 can be written as:

$$L(\theta) = \prod_{j=2}^{n} P[\rho(t_j), t_j | \rho(t_{j-1}), t_{j-1}; \theta], \qquad [S4]$$

where *n* is the total number of observations in the growth time series, $\theta = (r, K, \sigma)$ is the vector of demographic parameters, and $P(\rho, t|\rho_0, t_0; \theta)$ is the transitional probability density of having a density of individuals ρ at time *t*, given that the density at time t_0 was ρ_0 (for a given θ). The transitional probability density $P(\rho, t|\rho_0, t_0; \theta)$ satisfies the Fokker–Planck equation associated with Eq. **S3**, that is:

$$\begin{aligned} \frac{\partial}{\partial t} P(\rho, t|\rho_0, t_0; \theta) &= -\frac{\partial}{\partial \rho} \left[r\rho \left(1 - \frac{\rho}{K} \right) P(\rho, t|\rho_0, t_0; \theta) \right] + \\ &+ \frac{\sigma^2}{2t} \frac{\partial^2}{\partial \rho^2} \left[\rho P(\rho, t|\rho_0, t_0; \theta) \right]. \end{aligned}$$
[S5]

Maximization of the likelihood is equivalent to the minimization of the negative log-likelihood $-\log L(\theta)$, which is computationally less expensive. To compute the likelihood for a fixed set of parameters θ , one has to solve numerically the Fokker–Planck Eq. S5 for all observed transitions, with the $[t_j, \rho(t_j)]$ as measured in the experiment. It is computationally more accurate to solve Eq. S5 in terms of the cumulative distribution function (CDF), as its initial condition in the transition $[t_{j-1}, \rho(t_{j-1})] \rightarrow [t_j, \rho(t_j)]$ can be expressed as a step function instead of a delta function, the first one being more accurate in the numerical approximation (13). The transitional probability densities (solutions of Eq. S5) can then be recovered by numerical differentiation. The numerical

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integration was performed adopting the implicit Crank–Nicolson scheme (13); the minimization was performed with the software *MATLAB*, adopting the active-set algorithm in a large domain. We verified that different initial conditions for the parameters led to the same estimate for the minimum, which is thus interpreted as the global minimum of the negative log-likelihood function, that is, the global maximum for the likelihood function. The set of demographic parameters that maximized the likelihood function is $r = 6.1 \pm 0.8 \text{ d}^{-1}$, $K = 903 \pm 135 \text{ ind/cm}$, $\sigma = 25 \pm 5 \text{ d}^{-\frac{1}{2}}$ (mean \pm SE).

2.3. Comparison with Experimental Data. *Wavefront.* The black curve in Fig. 3*A* is the mean position of the front over 1,020 integrations of Eq. **S1**, with 170 iterations starting from each experimental density profile at the second measurement time point (Fig. 3*A* and *Materials and Methods*). The dark and light gray shadings in Fig. 3*A* represent, respectively, the 95% and 99% intervals for the front's position. The increase in width for the front's position is captured by the red curve in Fig. 3*B*, which represents the 95% interval width for the front's position at each time step. Simulations are in quantitative agreement with data (Fig. 3*B*). Examples of the front's position in different simulations of the stochastic equation are shown in Fig. S2.

Speed of the front. We measured the speed of the front in the stochastic simulations by fitting the front's position at eight equally spaced time points in the time interval [1-4] d, over 1,020 integrations of Eq. S1. The resulting mean speed of the front was 52.1 cm/d; the SD was 4.2 cm/d. The mean speed in the dispersal experiment was 52.0 cm/d, and the measured SD was 4.3 cm/d.

On the Diffusion Coefficient Estimates in Field Studies

In the literature, reaction-diffusion processes applied to ecological processes were sometimes criticized because of unsatisfactory fits to some empirical observations. For instance, reaction-diffusion models have been questioned for neglecting the fact that organisms move at a finite speed (3, 14) or for predicting slower spreads with respect to observations (3). The presence of rare long-distance dispersers has been invoked by some authors (1, 3) to account for the observation of faster-than-predicted spreads. We argue that the origins of some mismatches between empirical observations and reaction-diffusion models could be due to imprecise estimates of the diffusion coefficient, which proved to be the most delicate measurement also in our experiment. In fact, the diffusion coefficient is traditionally measured through the mean square displacement (MSD) of individuals or collective movement, computed with the available data. These data might refer to a timescale that is too short to be in the region of linear increase of MSD with time; that is, one might be still observing the autocorrelated phase that is shown in Fig. S1 for small times. Computing the MSD in the auto-correlated region leads to a lower estimate of the diffusion coefficient, which in turn leads to a smaller predicted speed for the advancing wavefront. When computing the MSD, therefore, one should compute it at different time points until the autocorrelated and linear regimes are discernible. Notably, the duration of the autocorrelated phase is expected to vary significantly from species to species (15). Additionally, our experiment supports that the diffusion coefficient estimate should be performed in density-independent conditions.

Theoretical Background

Reaction-diffusion models have been shown to accurately describe the spread of organisms in many comparative studies (1, 16, 17) and are here experimentally confirmed. We acknowledge that models other than reaction-diffusion equations, such as integro-difference equations involving dispersal kernels, are best suited to describe dispersal of organisms that exhibit distinct reproductive and dispersive phases (3, 4). However, for many organisms, especially those with continuous, nonoverlapping generations and temporally unstructured dispersal-reproductive dynamics, the reaction-diffusion approach is highly appropriate (16–18). Refinements of reaction-diffusion models have also been put forward in the literature. For instance, reaction-telegraph models were introduced to account for the finite movement speed of individuals, resulting in a correction to the wavefront speed (14), which is, however, negligible for our study species, as we show in the following sections. Here, we briefly review the theoretical framework of reaction-diffusion processes and discuss the relationship to reaction-telegraph processes, with reference to our experiment. The interested reader can refer to specialized texts for further investigation and generalizations (5, 19, 20).

4.1. The Fisher–Kolmogorov Equation. *4.1.1. Brownian motion and the mean square displacement of particles.* The diffusion equation

$$\frac{\partial \rho}{\partial t}(x,t) = D \frac{\partial^2 \rho}{\partial x^2}(x,t)$$
 [S6]

describes the evolution of the density of an ensemble of independent random walkers (5). The diffusion coefficient D can be measured as the proportionality constant that links the mean square displacement to time as (5):

$$\langle x_t^2 \rangle = 2Dt, \qquad [S7]$$

with D as in Eq. S6.

4.1.2. *Reaction–diffusion equations and the Fisher–Kolmogorov equation.* Macroscopically, or phenomenologically, the continuity equation in the presence of a reaction term reads:

$$\frac{\partial \rho}{\partial t} = -\frac{\partial J}{\partial x} + F(\rho).$$
 [S8]

Assuming proportionality between the flux J and the density gradient $\partial \rho / \partial x$ via the diffusion coefficient, one finds the so-called reaction-diffusion equation (18, 20–22):

$$\frac{\partial \rho}{\partial t} = D \frac{\partial^2 \rho}{\partial x^2} + F(\rho).$$
 [S9]

If the reaction term $F(\rho)$ is logistic, one finds the Fisher–Kolmogorov equation:

$$\frac{\partial \rho}{\partial t} = D \frac{\partial^2 \rho}{\partial x^2} + r \rho \left[1 - \frac{\rho}{K} \right],$$
[S10]

where ρ is the density of organisms, *D* is the diffusion coefficient of the species, *r* is its growth rate, and *K* its carrying capacity.

4.1.3. Traveling waves in the Fisher–Kolmogorov equation. The Fisher–Kolmogorov Eq. **S10** is probably the best known example of an equation that accepts traveling wave solutions. A traveling wave is a wave that travels without change of shape; that is, the density profile along a line moves rigidly in time without deformation (Fig. 1*E*). Mathematically, these dynamics of propagation mean that, if u(x,t) is a traveling wave solution of a reaction–diffusion equation, then u(x,t) is a function of x - vt, where v is the speed of the wave; that is, u(x,t) = u(x - vt).

Dimensional analysis of Eq. **S10** shows that the speed is $v \propto \sqrt{rD}$. Fisher (21) proved that traveling wave solutions can only exist with speed $v \ge 2\sqrt{rD}$ and Kolmogorov (22) demonstrated that, with suitable and reasonable initial conditions, the verified speed of the wavefront is equal to the lower bound; that is,

$$v = v_{FK} = 2\sqrt{rD}.$$
 [S11]

For any concave $F(\rho)$ in Eq. **S9**, that is, $F(\rho) \le \rho F'(0)$, the front velocity has been shown to be equal to $v_{RD} = 2\sqrt{DF'(0)}$ (20). The interested reader can refer to the original works by Fisher

(21) and Kolmogorov (22) or read one of the many good books on the topic (18, 20).

4.2. The Reaction–Telegraph Equation. The diffusion equation has been widely used to describe the movement of organisms (2, 18). It is clear, however, that individuals do not perform exact random walks at the microscopic scale (where "microscopic" here is used to refer to the typical length scale of an organism). What is implied when adopting diffusion equations to describe movement behaviors is that there exists an appropriate mesoscopic scale in which the collective behavior of organisms is indistinguishable from that of an ensemble of random walkers (1). In this section, we justify why the adoption of a reaction–diffusion equation is appropriate for our system, which follows from the fact that the correlation time in the trajectories performed by individuals of the species *Tetrahymena* sp. is much smaller than the typical timescale of the dispersal process or, more precisely, the growth rate of the species (Eq. **S19**).

4.2.1. Persistent random walk. One can describe the movement of an individual (particle) as a sequence of jumps of length Δx and duration Δt . A model for a correlated random walk was introduced by R. Fürth (23) and assumes that particles move along an infinite line at a constant speed γ , with a probability μ per unit time to reverse its direction of motion. Precisely, the probability for the particle to continue in the direction of motion is given by $1 - \mu \Delta t$ and the probability to reverse its direction is $\mu \Delta t$, in such a way that the speed $\lim_{\Delta x, \Delta t \to 0} \Delta x / \Delta t = \gamma$ is constant.

With these assumptions (20) one obtains the telegraph equation for the density of particles:

$$\frac{1}{2\mu}\frac{\partial^2 \rho}{\partial t^2} + \frac{\partial \rho}{\partial t} = \frac{\gamma^2}{2\mu}\frac{\partial^2 \rho}{\partial x^2},$$
 [S12]

which we rewrite as

$$\frac{\partial^2 \rho}{\partial t^2} + \frac{\partial \rho}{\partial t} = D \frac{\partial^2 \rho}{\partial x^2},$$
 [S13]

where $\tau^{-1} = 2\mu$ is the correlation time of the turning process and $D = \gamma^2/(2\mu)$. Note that Eq. **S13** differs from the diffusion equation for the additional term $\tau \frac{d^2 \mu}{dt^2}$. Eq. **S13** is a hyperbolic equation, and therefore information cannot travel faster than the speed of particles γ . In a way, then, the telegraph equation is physically more appropriate than the diffusion equation, as for the diffusion equation the probability density of finding a particle in an infinitesimal interval around (x, t) is larger then zero for all x and t > 0; that is, signals can travel at infinite speed. In our specific case, the correlation time τ is very small, so we argue that the term $\tau \frac{d^2 \mu}{dt^2}$ is negligible compared with the other terms in the equation, and thus the system is well-described by the diffusion equation. To estimate the parameters τ and *D* from experimental data, one can compute the value for the mean square displacement along the line, that is,

$$\langle x^2 \rangle = \int_{-\infty}^{+\infty} dx \, x^2 \rho(x,t).$$
 [S14]

Multiplying Eq. **S13** by x^2 and integrating one has

$$\tau \int_{-\infty}^{+\infty} dx \, x^2 \frac{\partial^2 \rho}{\partial t^2}(x,t) + \int_{-\infty}^{+\infty} dx \, x^2 \frac{\partial \rho}{\partial t}(x,t) =$$

$$= D \int_{-\infty}^{+\infty} dx \, x^2 \frac{\partial^2 \rho}{\partial x^2}(x,t),$$
[S15]

which reads

$$\tau \frac{d^2 \langle x^2 \rangle}{dt^2} + \frac{d \langle x^2 \rangle}{dt} = 2D,$$
 [S16]

assuming that $\rho(x,t)$, $\frac{\partial \rho}{\partial t}(x,t)$ and $\frac{\partial^2 \rho}{\partial t^2}(x,t)$ go to zero sufficiently fast for $x \to \pm \infty$. Assuming further that $\rho(x,0) = \delta(x)$ (where δ is the delta function) and $\frac{\partial \rho}{\partial t}(x,t)|_{t=0} = 0$, one has $\langle x^2 \rangle|_{t=0} = d \langle x^2 \rangle / dt|_{t=0} = 0$ and

$$\langle x^2(t) \rangle = 2Dt - 2D\tau \left[1 - e^{-t/\tau} \right].$$
 [S17]

Fig. S1 shows that Eq. **S17** provides a very good fit to the experimentally measured mean square displacement for individuals of *Tetrahymena* sp.

4.2.2. The reaction-telegraph equation. One can amend the instantaneous adjustment of the flux to the density gradient implied by Fick's first law with the introduction of a relaxation time τ , which leads to the reaction-telegraph equation (14, 20)

$$\tau \frac{\partial^2 \rho}{\partial t^2} + \left[1 - \tau F'(\rho)\right] \frac{\partial \rho}{\partial t} = D \frac{\partial^2 \rho}{\partial x^2} + F(\rho).$$
 [S18]

Eq. S18 can be obtained combining the telegraph Eq. S13 with kinetics (20). Eq. S18 differs from the reaction-diffusion Eq. S9 for the additional term $\tau \frac{\partial^2 \rho}{\partial t^2} - \tau F'(\rho) \frac{\partial \rho}{\partial t}$. Solutions of Eq. S18

- Andow DA, Kareiva PM, Levin SA, Okubo A (1990) Spread of invading organisms. Landscape Ecol 4(2/3):177–188.
- Okubo A, Levin SA (2002) Diffusion and Ecological Problems: Modern Perspectives (Springer, Berlin), 2nd Ed.
- Hastings A, et al. (2005) The spatial spread of invasions: New developments in theory and evidence. *Ecol Lett* 8(1):91–101.
- Melbourne BA, Hastings A (2009) Highly variable spread rates in replicated biological invasions: fundamental limits to predictability. *Science* 325(5947):1536–1539.
- 5. Gardiner C (2006) Stochastic Methods (Springer, Berlin), 4th Ed.
- Méndez V, Llopis I, Campos D, Horsthemke W (2011) Effect of environmental fluctuations on invasion fronts. J Theor Biol 281(1):31–38.
- Bonachela J, Muñoz MA, Levin SA (2012) Patchiness and demographic noise in three ecological examples. J Stat Phys 148(4):723–739.
- Moro E (2004) Numerical schemes for continuum models of reaction-diffusion systems subject to internal noise. *Phys Rev E Stat Nonlin Soft Matter Phys* 70(4 Pt 2): 045102.
- Dornic I, Chaté H, Muñoz MA (2005) Integration of Langevin equations with multiplicative noise and the viability of field theories for absorbing phase transitions. *Phys Rev Lett* 94(10):100601.
- Moro E (2001) Internal fluctuations effects on Fisher waves. Phys Rev Lett 87(23): 238303.
- Hallatschek O, Korolev KS (2009) Fisher waves in the strong noise limit. Phys Rev Lett 103(10):108103.
- Doering CR, Sargsyan KV, Smereka P (2005) A numerical method for some stochastic differential equations with multiplicative noise. *Phys Lett A* 344(2/4):149–155.

converge to solutions of the reaction–diffusion equation as $\tau \to 0$ (20, 24). In our case, we argue that the correlation time τ is sufficiently small to consider the process as well described by the reaction–diffusion equation. We will give quantitative support to this statement in the next section. One can also show that the introduction of reactions in the persistent random-walk equations leads to the reaction–telegraph Eq. **S18** (20) with $\tau^{-1} = 2\mu$ and $D = \gamma^2/(2\mu)$ as in Eq. **S13**.

4.2.3. Traveling waves in the reaction-telegraph equation. E. E. Holmes (14) studied the propagation of traveling wavefronts in the reaction-telegraph equation with logistic reaction F, estimating model parameters for several case studies. The reaction-telegraph Eq. **S18** with logistic growth was shown (25) to accept traveling wave solutions with speed:

$$v_{RT} = \frac{2\sqrt{rD}}{1+\tau r} = \frac{v_{FK}}{1+\tau r}$$
[S19]

if $r\tau < 1$; otherwise $v_{RT} = (D/\tau)^{\frac{1}{2}}$. In this perspective, we claim that, in our specific case, the ratio between the speed of a reaction– telegraph and that of a reaction–diffusion equation is practically one. In fact, we find $r\tau = (2.2 \pm 0.3) \cdot 10^{-4}$ so that $v_{RT}/v_{RD} > 0.999$, which makes the two processes experimentally undistinguishable. Therefore, we conclude that our system is well-described by Eq. **1** (*Materials and Methods*), and this agreement with the Fisher–Kolmogorov equation is due to the very small value of the correlation time τ with respect to the growth rate *r*.

- Hurn AS, Jeisman JI, Lindsday KA (2007) Transitional densities of diffusion processes: A new approach to solving the Fokker-Planck equation. J Deriv 14(4):86–94.
- Holmes EE (1993) Are diffusion models too simple? A comparison with telegraph models of invasion. Am Nat 142(5):779–795
- Li L, Nørrelykke SF, Cox EC (2008) Persistent cell motion in the absence of external signals: A search strategy for eukaryotic cells. *PLoS ONE* 3(5):e2093.
- Lubina JA, Levin SA (1988) The spread of a reinvading species: Range expansion in the California sea otter. Am Nat 131(4):526–543.
- Grosholz ED (1996) Contrasting rates of spread for introduced species in terrestrial and marine systems. *Ecology* 77(6):1680–1686.
- 18. Murray JD (2004) Mathematical Biology I: An Introduction (Springer, Berlin), 3rd Ed.
- 19. Berg HC (1993) Random Walks in Biology (Princeton Univ Press, Princeton).
- Méndez V, Fedotov S, Horsthemke W (2010) Reaction-Transport Systems (Springer, Berlin).
- 21. Fisher RA (1937) The wave of advance of advantageous genes. Ann Eugen 7:355-369.
- Kolmogorov AN, Petrovskii IG, Piskunov NS (1937) A study of the diffusion equation with increase in the amount of substance, and its application to a biological problem. Bull. Moscow Univ. Math. Mech. 1(1):1–25.
- Fürth R (1920) Die Brownsche Bewegung bei Berücksichtigung einer Persistenz der Bewegungsrichtung. Mit Anwendungen auf die Bewegung lebender Infusorien. Z Phys 2(3):244–256.
- 24. Zauderer E (1989) Partial Differential Equations of Applied Mathematics (Wiley, New York), 2nd Ed.
- Méndez V, Camacho J (1997) Dynamics and thermodynamics of delayed population growth. Phys Rev E Stat Phys Plasmas Fluids Relat Interdiscip Topics 55(6):6476–6482.



Fig. S1. Mean square displacement $\langle x^2 \rangle$ of individuals' trajectories versus time, for a representative video. The red curve is the best fit of the data to the equation $\langle x^2(t) \rangle = 2Dt - 2D\tau [1 - e^{-t/\tau}]$. After an initial auto-correlated phase, the mean square displacement increases linearly with time. Error bars are \pm SE.



Fig. S2. Front's position in six integrations of the stochastic model Eq. S1 (compare with experimental positions in Fig. 3A). Each simulation was initialized from each of the measured density profiles at the second experimental time point.

Replica	Speed, cm/d		
1	54.6±1.9		
2	51.7±2.8		
3	48.0±1.5		
4	58.0 ± 4.0		
5	53.4±1.8		
6	46.3 ± 1.0		

Table S1.	Best-fit estimate	es of the	e wavef	ront speed	in	six
replicated	dispersal events					

Errors are \pm SE.

 Table S2. Best-fit estimates of the growth rate r and the carrying capacity K for Tetrahymena sp.

Replica	<i>r</i> , d ⁻¹	K, ind/cm
1	6.0 ± 0.2	1020 ± 20
2	3.7 ± 0.2	680 ± 30
3	3.8 ± 0.5	950 ± 80
4	5.2 ± 0.7	550 ± 30
5	5.8 ± 0.5	1300 ± 92

Estimates of growth rate r and carrying capacity K obtained in five independent growth measurements. The fit is performed in the framework of the deterministic logistic equation. ind, individuals. Errors are \pm SE.



Movie S1. Reconstructed trajectories of individuals of *Tetrahymena* sp. swimming in density-independent conditions at the front of a traveling wave. Different colors identify different individuals.

Movie S1

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