

# Emerging predictable features of replicated biological invasion fronts

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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

**W**hat is the source of variance in the spread rates of biological 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 short-term 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. 1E). 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.**

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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 worst-case 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 yet 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. 1B), a freshwater ciliate, purchased from Carolina Biological Supply. Individuals of *Tetrahymena* sp. have typical linear size (equivalent diameter) of 14  $\mu\text{m}$  (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  $\text{g}\cdot\text{L}^{-1}$ . The experimental units were kept under constant fluorescent light for the whole duration of the study, at a constant temperature of 22  $^{\circ}\text{C}$ . Overall, experimental protocols are well-established (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  $10^5$ , 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  $^{\circ}\text{C}$  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 ( $\sqrt{D/r} \approx 5$  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  $\sigma$  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) (SI 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 landscape 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, that is,  $\langle x^2(t) \rangle = \frac{1}{N} \sum_i x_i^2(t)$  (where  $N$  is the total number of 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  $\langle x^2(t) \rangle = 2Dt - 2D\tau[1 - e^{-t/\tau}]$  (SI Text) with the two parameters  $D$  (diffusion coefficient) and  $\tau$  (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:

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

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  $v \geq 2\sqrt{rD}$ , 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  $r$  ( $r\tau \sim 10^{-4}$ ), 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:

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

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  $\delta$  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 stochasticity in a population (46) and needs extra care in simulations (45, 52). In particular, standard stochastic integration schemes fail to preserve the positivity of  $\rho$ . 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:

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

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  $l$  is the

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  $l$  (*SI Text*). The likelihood function for Eq. 3 can be written as:

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

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  $\rho$  at time  $t$ , given that the density at time  $t_0$  was  $\rho_0$  (for a given  $\theta$ ). 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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