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Information use shapes the dynamics of range expansions into environmental gradients

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ABSTRACT

Aim Globally, the geographical distributions of species are dynamic and strongly influenced by dispersal. At the same time, range dynamics feed back and may select for increased dispersal at expanding range fronts. This interplay between macroecological and evolutionary dynamics happens almost universally across environmental gradients and such gradients can have a direct impact on the fitness of organisms due to the match or mismatch between an individual's environmental optimum and the current conditions along the gradient. Importantly, gradients also provide individuals with information on environmental changes because dispersing individuals may sense whether environmental conditions improve or deteriorate. However, the ability of organisms to use this information on the environment and to subsequently adjust dispersal decisions plastically, that is, deciding to further disperse into the gradient or not, has been largely ignored and the macroecological consequences remain unclear. We here aim to demonstrate the impact of informed dispersal on the eco-evolutionary dynamics of ranges.

Location Laboratory and theoretical.

Methods We used individual-based simulations and controlled experiments in replicated microcosm landscapes. Range expansions of the protist model organism *Tetrahymena* were tracked using video recording and analysis.

Results We show that information on environmental gradients had a severe impact on range dynamics and inverted the spatial distribution of population densities in comparison with controls where this information was not provided. Additionally, the use of information on gradients prevented evolutionary changes in dispersal rates and an acceleration of range expansion.

Main conclusions We demonstrate the strong impact of informed dispersal and subsequent behavioural changes on range dynamics in environmental gradients. More generally, our findings highlight the importance of informed dispersal for spatial ecological and evolutionary dynamics.

Keywords

biological invasion, dispersal, environmental gradient, experimental evolution, information use, range expansion.

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INTRODUCTION

The capacity of organisms to spread in space and to expand their range into new habitats is crucial for their long-term fitness, especially in the context of current global

environmental and climatic changes (Hill *et al.*, 1999; Parmesan *et al.*, 1999; Parmesan & Yohe, 2003; Kelly & Goulden, 2008). The fundamental and applied relevance of range expansions and biological invasions has given rise to

extensive theoretical work predicting range dynamics (Hastings *et al.*, 2005; Holt *et al.*, 2005; Burton *et al.*, 2010; Dytham, 2009; Holt & Barfield, 2011; Perkins *et al.*, 2013; Williams *et al.*, 2016b). To date, however, our empirical understanding of range dynamics is mostly based on case studies of range shifts and invasions, with little experimental validation or manipulation (e.g. Thomas *et al.*, 2001; Phillips *et al.*, 2006; Lombaert *et al.*, 2014). The few studies that have experimentally tracked replicated range expansions are either limited by the short time frames considered (Melbourne & Hastings, 2009; Giometto *et al.*, 2014), preventing potentially important evolutionary changes from occurring, or by the unrealistic assumption that range expansions occur into uniform habitat (Fronhofer & Altermatt, 2015; Williams *et al.*, 2016a).

Realistically, all range expansions are limited by the heterogeneity of landscapes and universal gradients in environmental conditions, such as temperature or humidity. The importance of gradients as such for species ranges has been explored previously: gradients may, for instance, affect the evolution of dispersal (Kubisch *et al.*, 2014) and lead to stable range borders and even range contractions after the expansion phase (Kubisch *et al.*, 2010, 2016). Furthermore, gradients are often associated with the distribution of population densities throughout the range (Sagarin *et al.*, 2006; Sexton *et al.*, 2009) and the relevance of species interactions for range dynamics is hypothesized to be tightly linked to the harshness of environmental gradients (Louthan *et al.*, 2015). However, these works usually fail to consider that environmental gradients have a two-fold effect on organisms: Firstly, gradients have a direct, fitness-relevant effect due to the mismatch between local conditions and the environmental optimum of individuals. Secondly, gradients have indirect effects mediated by the information that the gradient conveys to dispersing organisms. Dispersers may be able to sample information on the environmental gradient, relate it to their level of (mal)adaptation to local conditions and finally make informed decisions on whether to disperse further into the gradient or not. If we take the example of a temperature gradient, dispersing individuals may be able to sense differences in temperature between patches as they move through the landscape and decide not to disperse further into the gradient, or even to disperse backwards. While the relevance of information use for making dispersal decisions and subsequent consequences for spatial dynamics has been recognized in general (Clobert *et al.*, 2009), the consequences of informed dispersal for macroecological dynamics remain under-appreciated.

Here, we theoretically and experimentally test the role of environmental gradients in the dynamics of range expansions considering the two-fold effect of environmental gradients discussed above. We use an individual-based model to predict ecological and evolutionary dynamics in three range expansion scenarios. Firstly ('control'), we model the range expansion of individuals into a previously empty linear

landscape of interconnected patches. Secondly, we include an analogous scenario, but where the landscape has a linearly increasing gradient of local mortality that affects the fitness of the spreading organisms without providing information on the spatial change in mortality ('gradient'). Finally, we contrast these two scenarios with a range expansion into a mortality gradient that provides information on the changes in mortality, and individuals use this information to plastically take optimal dispersal decisions ('gradient and information').

We tested our theoretical predictions using experimental evolution and replicated linear microcosm landscapes, which were invaded by the ciliate model organism *Tetrahymena pyriformis* (Altermatt *et al.*, 2015). The landscapes allowed for active dispersal and included the three scenarios detailed above (control, gradient, and gradient and information).

Our results show that range expansions in the control scenario led to the evolution of increased dispersal at the range front (see also Phillips *et al.*, 2006; Fronhofer & Altermatt, 2015; Williams *et al.*, 2016a). In our theoretical model, the mortality gradient in the second scenario led to a reduction in the speed of range expansion and, ultimately, to the establishment of a stable range border. Experimentally, we observed the evolution of increased reproductive rates at the range front which cancelled the effect of the mortality gradient to some degree. Finally, the availability of information allowed organisms to make informed and plastic dispersal decisions and thereby to avoid dispersal into areas characterized by local mortalities that were too high.

MATERIALS AND METHODS

Numerical analyses

General overview

We developed a stochastic, individual-based simulation model (Burton *et al.*, 2010; Kubisch *et al.*, 2014; Fronhofer & Altermatt, 2015) that tracks (1) ecological dynamics, such as spatial spread in a linear landscape, population densities and dispersal events, and (2) evolutionary changes, more specifically the evolution of dispersal and the concurrent evolution of reproductive and competitive ability. In each replicate linear landscape, populations are initialized at one end of the landscape and individuals may subsequently spread following a stepping-stone model (nearest-neighbour dispersal).

We assume local competition for resources and, for simplicity, non-overlapping generations. As a result of standing genetic variation present at the beginning and of subsequent mutations, the distribution of traits in a population may shift, leading to evolutionary changes in dispersal. Since it is well known that dispersal is costly (Bonte *et al.*, 2012), we assume that more dispersive individuals reproduce less due to their investment of energy in dispersal (Fronhofer & Altermatt, 2015; dispersal–fecundity trade-off; equation (3)). Furthermore, reproduction and competitive ability are positively correlated (equation (2)) due to underlying consumer–

resource dynamics (Matessi & Gatto, 1984; a detailed derivation is given in Appendix S1 in the Supporting Information).

In addition to a control scenario (scenario 1), in which a range expansion occurs into a previously empty landscape, we implemented scenarios that include linearly increasing spatial gradients in local mortality (scenarios 2 and 3). We contrast a setting in which dispersal propensity may evolve and the organisms do not have the capacity to sense the environmental change in such a gradient (scenario 2) and a scenario in which we assume that individuals have perfect information to make an optimal dispersal decision plastically and therefore evolutionary changes become irrelevant (scenario 3). Informed dispersal is based on a cost–benefit analysis, which takes into account population densities (i.e. competition) in the patch of origin and in all potential target patches, as well as the effect of the mortality gradient.

The model was designed to be as simple as possible and to provide qualitative predictions on the impact of environmental gradients and information use on the ecological and evolutionary dynamics of range expansions. We therefore ran an extensive sensitivity analysis (Figs. S6–S10). We neither parameterize nor fit the model to the experimental data.

Landscape and the environmental gradient

For simplicity, we assume a linear landscape of 100 interconnected patches. At the start of each replicate simulation only the first five patches are populated. The landscape allows individuals to disperse following a stepping-stone model, that is, we assume nearest-neighbour dispersal with reflecting boundary conditions at both ends of the landscape. In scenarios 2 and 3, which include an environmental mortality gradient, we assume that this additional source of local mortality (μ_x) acts after reproduction and density regulation (see below) and before dispersal. The mortality gradient is linear and increases from $\mu_1 = 0$ in the first patch to $\mu_{100} = 1$ in the last patch.

Dispersal

Besides being governed by the landscape setting as described above, dispersal of individuals is assumed to be either genetically controlled (scenarios 1 and 2) or fully plastic and informed (scenario 3). Here we only describe the former two scenarios, the latter will be dealt with in detail below. The probability of dispersing, more specifically emigrating from a natal patch, is genetically controlled by a haploid locus that codes for the dispersal rate (d_i). When an individual (i) disperses according to its specific dispersal rate, the direction in the linear landscape (i.e. towards the range core or towards the range front) is drawn randomly.

We do not assume explicit dispersal costs (Bonte *et al.*, 2012). However, dispersal is implicitly costly, as we assume that dispersal trades off with reproduction and competitive ability as described below.

Reproduction and density regulation

Reproduction occurs after dispersal and follows a modified logistic, density-dependent growth model based on Beverton & Holt (1957). As reproductive (λ_i) and competitive ability (α_i) are individual-based traits, the mean number of offspring (Λ_i) an individual produces in patch x at time t with a population of size $N_{x,t}$ is

$$\Lambda_i = \lambda_i \frac{1}{1 + \sum_{j=1}^{j=N_{x,t}} \alpha_j} \quad (1)$$

We include demographic stochasticity by assuming that reproduction follows a Poisson process and drawing the realized number of offspring for individual i from a Poisson distribution with mean Λ_i . After reproduction all individuals of the previous generation die.

Trait correlations and trade-offs

As outlined in Appendix S1, we assume that reproductive and competitive ability (λ_i and α_i , respectively) are individual-based traits that are positively correlated:

$$\alpha_i = \alpha_0 \lambda_i^\rho \quad (2)$$

with α_0 the baseline competitive ability and ρ the correlation exponent between competitive and reproductive ability. As Fronhofer & Altermatt (2015) showed previously, to a large part the changes in competitive ability seem driven by changing feeding rates and not by changing assimilation coefficients. We therefore assume $\rho = 2$ as a standard scenario following the logic outlined in Appendix S1. For a summary of parameters and tested values see Table S1.

Furthermore, we assume that dispersal is costly (Bonte *et al.*, 2012) and trades off with reproduction, and, therefore, also with competitive ability:

$$\lambda_i = \lambda_0 e^{d_i \tau} \quad (3)$$

where λ_0 is the baseline fecundity, d_i the dispersal rate of individual i and τ the strength of the trade-off between dispersal and fecundity.

Information use

In scenario 3 we assume that dispersal is plastic, in the sense that individuals make informed dispersal decisions. The decision of whether to disperse to one of the two neighbouring patches in the linear landscape or to stay in the natal patch is based on a cost–benefit calculation. We assume that individuals have perfect knowledge on the population densities in their natal patch ($N_{x,t}$) and in the potential target patches, as well as information on local mortality (μ_x) due to the mortality gradient. Individuals disperse to the patch x that maximizes their fitness according to equation (1):

$$\Lambda_{i,x} = \lambda_i \frac{1}{1 + \sum_{j=1}^{j=N_{x,t}} \alpha_j} (1 - \mu_x) \quad (4)$$

This approach only accounts for direct fitness benefits and ignores inclusive fitness (Hamilton & May, 1977). Our simulations therefore underestimate rates of dispersal and spatial spread in the informed scenario. For a detailed treatment of the effect of kin competition on range dynamics see Kubisch *et al.* (2013).

Evolution and the genetic algorithm

Evolutionary dynamics are an emergent phenomenon of any individual-based model that allows for variation in heritable, individual-based traits. The specific simulation scenario leads to selection pressures, such as spatial selection (Phillips *et al.*, 2010; Shine *et al.*, 2011) in range expansion scenarios for instance. We here assume that the dispersal rate (d_i) is heritable and passed on from parent to offspring with a mutation rate $m = 0.001$ that leads to a random change of the trait value drawn from a Gaussian distribution with mean zero and standard deviation $\Delta m = 0.1$. Only the dispersal trait is inherited since both other traits, fecundity (λ_i) and competitive ability (α_i), depend on dispersal via the trade-off and correlation structures explained above (equations (2) and (3)).

At the genotype level we do not implement any boundary conditions on the dispersal trait, that is, depending on mutations d_i may be negative or greater than one. At the phenotype level values of less than zero are set to zero and values of greater than one are set to one. These phenotypic values are also used to calculate fecundity according to equation (3).

Simulation experiments

All simulations were initialized with populations at a baseline equilibrium density, $(\lambda_0 - 1)/\alpha_0$, in the first five patches in order to allow the individuals to subsequently spread through the landscape. Individuals in these populations were initialized with random dispersal rates ($0 \leq d_i \leq 1$) as standing genetic variation. All simulations were allowed to proceed for 95 generations which, given the stepping-stone dispersal model, is the minimum time span needed to reach the opposite end of the landscape. In general, simulations were replicated 20 times. The sensitivity analysis of scenario 3 (gradient and information) was performed on fewer replicates (between one and ten) as these simulations show only very little variation between replicates (see Fig. 1e) and take an excessive amount of time to run (See Table S1 for the parameter combinations tested and Figs. S6–S10 for a sensitivity analysis).

Microcosm experiments

Study organism

We used *T. pyriformis*, a unicellular freshwater ciliate, as a model organism (Altermatt *et al.*, 2015; Fronhofer &

Altermatt, 2015). *Tetrahymena pyriformis* is small (c. 40–50 μm along the major axis), has a relatively short doubling time (c. 4–5 h) and reaches high densities (equilibrium densities of 5000–15,000 individuals ml^{-1}) which makes it well suited for ecological and evolutionary experiments (Altermatt *et al.*, 2015). We kept *T. pyriformis* under controlled environmental conditions at 20 °C in protist pellet medium (0.46 g l^{-1} ; Carolina Biological Supply) with bacteria (5 vol% of standardized 7-day-old cultures of *Serratia fonticola*, *Brevibacillus brevis* and *Bacillus subtilis*) as food resources. We used the same protist cultures as Fronhofer & Altermatt (2015) and therefore started evolution experiments with standing genetic variation. The cultures were originally obtained from Carolina Biological Supply and regularly restocked to conserve genetic variation (Cadotte, 2007).

Microcosm landscapes

The range expansion experiments were performed in linear landscapes consisting of 14 interconnected microcosms (patches). We used 20-ml vials (Sarstedt), connected them with silicone tubing (VWR; 4 mm inside diameter) and a stopcock (B. Braun, Discifix) to regulate dispersal (the length of the tubing and stopcock was 6 cm). All experiments were replicated six times in two experimental blocks of three replicates each separated by 1 day.

Scenarios and experimental procedure

At the beginning of each experiment, the first patch of a landscape was filled with a 1-week-old *T. pyriformis* culture that had reached its equilibrium density. Subsequently, the stopcocks were opened and dispersal was allowed for 4 h. In order to avoid aging of the medium and to limit contamination, the landscape was not completely filled with medium from the start of the experiment but empty patches were added subsequently to the landscape front. At the beginning of the experiment, 3 of the 14 patches were filled. At each day of the experiment, one additional patch filled with freshly bacterized medium (5 vol%) was added at the front. Since all patches between the range core and range front were connected, dispersal could potentially occur across multiple patches and towards the range front as well as towards the range core.

To analyse the influence of information use on the eco-evolutionary dynamics of range expansions into environmental gradients, we designed two experimental treatments in addition to the control treatment (scenario 1) described above. For both uninformed (scenario 2) and informed scenarios (scenario 3), a linear mortality gradient was applied, ranging from 0% mortality in the first patch to 100% mortality in the last patch. In the uninformed scenario (scenario 2), depending on the mortality gradient, a certain volume of the microcosm was removed, discarded and replaced with bacterized medium. In the informed scenario (scenario 3), we followed the same procedure but replaced the volume with dead *T. pyriformis* from a 4-day-old culture that was killed by ultrasonication (duration 4 min, amplitude 40%,

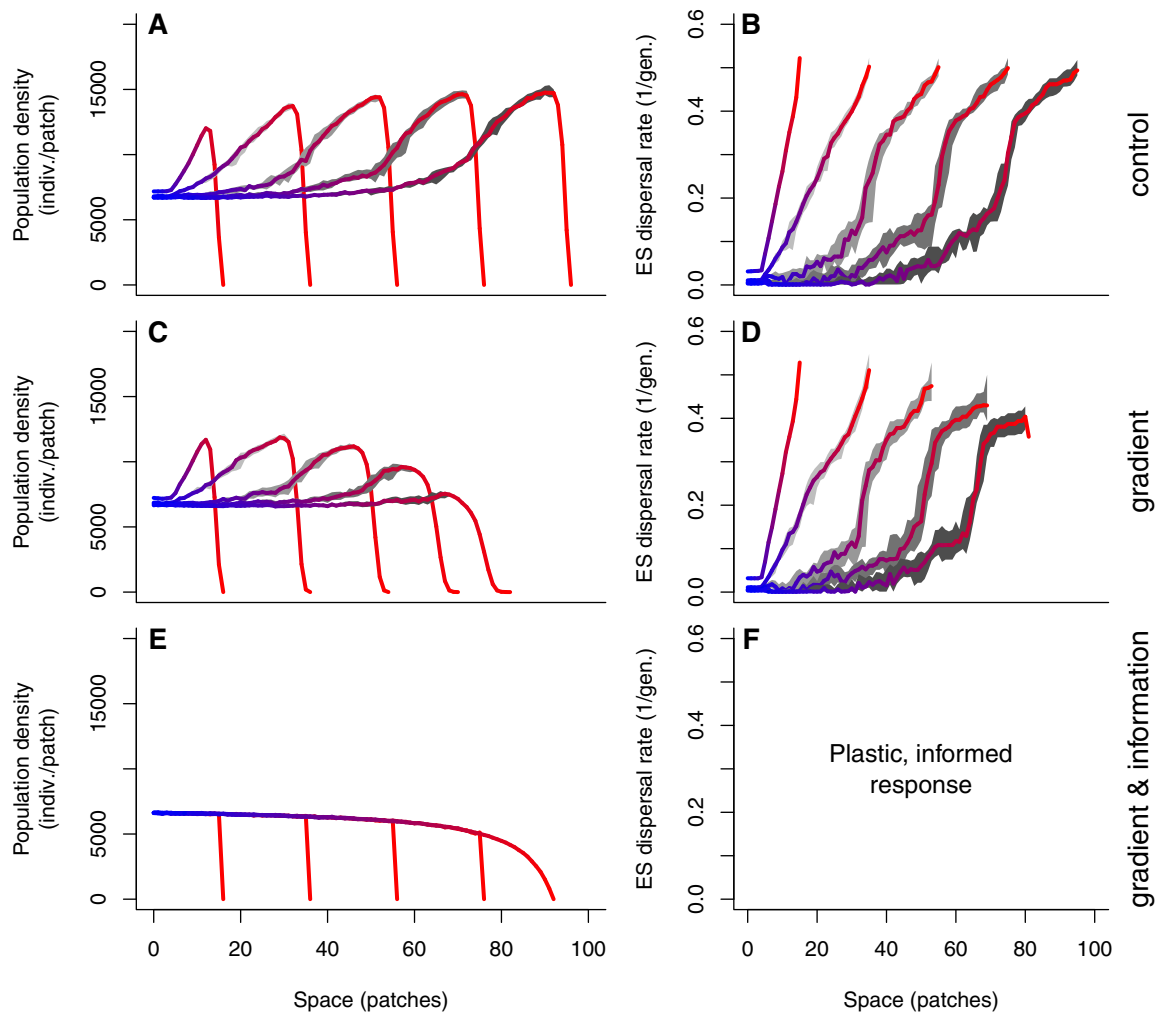


Figure 1 Range dynamics – theoretical predictions. (a), (b) Expansion into a homogeneous environment (control). Population densities increase from the range core to the range front due to dispersal–fecundity trade-offs (equation (3)) and fecundity–competition correlations (equation (2)). Spatial selection leads to increased dispersal at range fronts. (c), (d) Expansion into a mortality gradient. Density patterns are not fundamentally altered during a major part of the expansion (see also Fig. S3). However, increasing mortality locally reduces population densities and selects against dispersal. (e), (f) Expansion in a mortality gradient and information use. Dispersal is plastic and individuals are fully informed about the mortality gradient, population densities in their natal and potential target patches (equation (4)). The distribution of population densities over space is inverted (Fig. S3). Dispersal does not evolve, but it is predicted to be plastically higher at the range front during the expansion due to the decision rule. Temporal snapshots: $t = [10, 30, 50, 70, 90]$. Parameter settings: $\lambda_0 = 14$, $\alpha_0 = 0.00001$, $\rho = 2$, $\tau = 2$. We report medians over 20 replicate simulations [solid line; blue (range core) to red (range front)] and the 25th and 75th percentiles (grey shading; darker with time).

pulse on 2 s, pulse off 1 s; all in an ice bath to avoid heating). We therefore used dead *T. pyriformis* and their chemical cues to inform the protists in the experiments about the increasing mortality in the landscape. Prior to the experimental evolution assays we performed chemical orientation assays to confirm that dead conspecifics are indeed used as a negative tactic cue (see Appendix S2).

The general experimental procedure was as follows: we first applied the respective treatments (scenario 1, control; scenario 2, mortality gradient; scenario 3, mortality gradient and information) and allowed for dispersal (4 h) on one day. The following day we allowed for regrowth. We therefore had

discrete dispersal and growth phases in analogy to the individual-based model described above. In total, the evolution experiment took 26 days with 13 dispersal events and subsequently 2 days of common garden. Each scenario was replicated six times and the experimental units were arranged in two blocks of three replicates each shifted by one day due to the large number of samples that had to be processed.

Common garden, growth curves and fitness estimation

In order to tease apart plastic changes, due to environmental or parental effects, in dispersal (respectively, movement strategies), growth rates and competitive abilities from genetically

or non-genetically inherited evolutionary changes, we transferred range core and range front populations to a common environment after the experimental evolution phase. We transferred all core and front populations from the end of the experiment to 200-ml Erlenmeyer flasks and added 100 ml of freshly bacterized medium to the 15 ml from the experimental microcosms. This transfer reset all populations to roughly the same environmental conditions in terms of resource availability and chemical composition of the medium. After 2 days in this common environment, all populations were assessed for divergence in movement behaviour, growth rates and competitive abilities.

Growth rates and competitive abilities were estimated by performing growth curve experiments and subsequently fitting logistic growth curves (equation (S2)) to the time-series data. All growth curves were started with *c.* 500 individuals ml^{-1} by diluting the populations from the common garden. As resources, 5 vol% bacteria from a standardized 7-day-old culture were added. The growth of each population was followed for 10 days using video recording and analysis as described below.

Logistic growth curves were fitted to the individual replicates using a least-squares approach. Equation (S2) was solved (function 'ode' of the 'deSolve' package in R version 3.2.3) and the model was fitted using the Levenberg–Marquardt algorithm (function 'nls.lm' of the 'minpack.lm' package) which minimizes the sum of squared residuals.

Data collection

Before a treatment was performed, a 0.5-ml sample of each patch was collected. In the control and uninformed scenario, the sampling volume was replaced with fresh, bacterized medium. In the informed scenario, the sampling volume was replaced with dead *T. pyriformis* and fresh, bacterized medium for the first patch, respectively.

A subsample was then used for video recording with a Leica M205 C stereomicroscope (16-fold magnification) and a Hamamatsu Orca Flash 4 video camera (imaged volume 34.4 μl ; sample height: 0.5 mm). Videos of 20-s duration were recorded with a total of 500 grey-scale images with a resolution of 2024×2024 pixels.

The general method of automated image analysis was introduced by Pennekamp & Schtickzelle (2013) and Pennekamp *et al.* (2015) and has been successfully used in previous experiments (Giometto *et al.*, 2014; Fronhofer *et al.*, 2015a,b; Fronhofer & Altermatt, 2015). The aim is to collect abundance data as well as morphological and behavioural data simultaneously and provide information at the individual level. The principle of automated image analysis first includes a cleaning step followed by different analytical steps to determine morphological traits (length, size), abundance and movement data (velocity, turning angle, Euclidean distance). The first step of the image analysis consists in identifying the objects of interest by segmenting the moving foreground from the static background. Therefore the difference between picture t and $t+1$ was analysed. In general, only particles

with a size between 20 and 200 pixels and a minimal path length of 100 frames were included in the analysis. Trajectories of each individual were analysed with the ImageJ MOSAIC plugin (Sbalzarini & Koumoutsakos, 2005). Data for each sample (abundance, velocity, body size, turning angle) were saved as mean values. As previous work consistently showed that dispersal rates and movement behaviour correlate highly in these protist microcosms (Fronhofer & Altermatt, 2015; Fronhofer *et al.*, 2015a), we here use movement as a proxy for dispersal. Data can be downloaded from Dryad doi: 10.5061/dryad.113v9.

Statistical analysis

Differences in velocity were analysed using linear mixed models (LMMs). We included the experimental block (replicates 1–3 and 4–6) as a random effect in our analyses. We used a Gaussian error structure because the Q–Q plots indicated that this assumption was not heavily violated. All analyses were performed at the population level, i.e. on mean parameters over all individuals in a sample. This approach is very conservative, since it significantly reduces the sample size given the high population densities and the individual-based data collected by video recording and analysis. These analyses were performed using R version 3.2.3 and the 'lmerTest' package.

The distribution of population densities over space was compared between treatments using the empirical cumulative population density distributions (see Fig. S3d–f). Again, we chose a very conservative approach and only compared the median cumulative density distributions of the treatments using the Cramer–von Mises (CvM) statistic (ω^2) for two samples. We therefore calculated the sum of the squared differences between two empirical cumulative density distributions (ω^2). We subsequently analysed significance levels by resampling (one-sided tests) and additionally provide probability–probability plots for visual analysis (Fig. S4). As we performed all pairwise comparisons (two comparisons per treatment), we corrected the obtained significance thresholds using the Bonferroni method, which consists of multiplying the initially obtained significance thresholds with the number of comparisons.

The chemical orientation assay was analysed using generalized linear mixed models (GLMMs) with binomial error distributions and counts of individuals choosing either the treatment or the control patch. We included 'replicate' as a random effect to take into account the pairing between dispersal to control and to treatment patches within one replicate. We further included a sample-level random effect to account for overdispersion.

The empirical correlation between competition coefficients (α) and growth rates (r_0) for populations from the range core and the range margin was analysed using nonlinear regressions (following equation (2)) for grouped data with the function 'nlsList' of the 'nlme' package in R version 3.2.3. For this analysis, we only used data from scenarios 1 and 2 as we did not observe evolutionary dynamics in scenario 3 so

that the classification into core and front populations is not meaningful. We nevertheless report data from scenario 3 in Fig. 3b. Note that while the parameter estimates differ slightly if we nevertheless include scenario 3 in the analysis, the confidence intervals clearly overlap for the parameter of interest (ρ) implying no significant differences ($CI_{\text{core}(1,2)}^{\rho}$ 1.80, 2.11; $CI_{\text{core}(1,2,3)}^{\rho}$ 1.80, 2.91; $CI_{\text{front}(1,2)}^{\rho}$ 4.31, 7.86; $CI_{\text{front}(1,2,3)}^{\rho}$ 1.48, 10.47).

RESULTS

Theoretical predictions

In the control and gradient scenarios our theoretical analyses (Fig. 1) predict evolutionarily increased dispersal at the range front compared with the range core (Fig. 1b, d). In the gradient scenario, the difference in evolved dispersal propensities between range core and front populations is reduced. Furthermore, we predict higher population densities at range fronts in the control scenario and, to a lesser extent, also in the gradient scenario (Figs. 1a, c & S3a, b). The invasion does not proceed as far in the gradient scenario as in the control, suggesting the formation of a stable range border (Figs. 1a, c & S3a, b).

In the informed dispersal scenario, the density profile of populations across the range is inverted in comparison with the evolutionary scenarios, implying lower densities at range fronts in comparison with range cores (Figs. 1e & S3c). These predictions qualitatively hold true across a large range of tested parameter values (Table S1, Figs. S6–S10), especially for weak dispersal–fecundity trade-offs and fecundity–competition correlation coefficients greater than one.

Experimental range dynamics

Our experimental results corroborate our theoretical predictions (Fig. 2). At the end of the range expansion phase we found increased movement velocities (which correlate strongly with dispersal; Fronhofer & Altermatt, 2015; Fronhofer *et al.*, 2015a) at range fronts (Fig. 2b, e, h), although the effect was weak in the informed scenario (control: LMM space $n = 74(6)$, d.f. = 72, $t = 11.79$, $P < 0.001$; gradient: LMM space $n = 77(6)$, d.f. = 74, $t = 13.24$, $P < 0.001$; information and gradient: LMM space, $n = 64(6)$, d.f. = 62, $t = 4.69$, $P < 0.001$). After the common garden, the velocities in the range core, respectively range front, populations, were still significantly different in the control (Fig. 2c; LMM range position, $n = 12$, d.f. = 9, $t = 3.94$, $P = 0.0034$) and in the gradient scenario (Fig. 2f; LMM range position, $n = 12$, d.f. = 10, $t = 7.23$, $P < 0.001$). No differences were observed in the informed scenario (Fig. 2i; LMM range position, $n = 12$, d.f. = 10, $t = -0.045$, $P = 0.965$).

Furthermore, we observed the predicted spatial distribution of population densities with high densities at range fronts and low densities in range cores in the control and gradient scenario (Figs. 2a, c & S3d, e). Information use completely inverted this pattern, leading to significantly

different distributions of population densities between informed and uninformed scenarios (Figs. 2, S3d–f & S4) as well as to lower population densities overall.

Concurrent changes in reproduction and competition

At the end of the experiment, we measured population growth rates and competitive abilities after a common garden phase to separate genetic from plastic effects. We observed a positive correlation between growth rate and competitive ability (Fig. 3b), corroborating our assumption about this correlation (Fig. 3a; for details see equation (2) and Appendix S1). While individuals from range cores followed the theoretically predicted correlation quantitatively, individuals from range fronts shifted the predicted correlation curve towards increased growth rates (Fig. 3b).

DISCUSSION

Research on range dynamics has often assumed homogeneous environments and consistently ignored that universally occurring environmental gradients provide information to spreading organisms about local conditions. Such information may allow organisms to plastically adapt their dispersal decisions (Clobert *et al.*, 2009) and can potentially alter macroecological patterns. Consequences of behavioural changes for range dynamics have been discussed in the context of density-dependent dispersal (Kubisch *et al.*, 2011), resulting in wider ranges, and in the context of social learning (Keith & Bull, 2016), to name but two examples. We here theoretically and experimentally show that the ecological and evolutionary dynamics of species ranges are not only driven by the direct, fitness-relevant effect of environmental gradients but, most importantly, by the information content of such gradients.

We find that range expansions lead to increased dispersal at the range front in the control and gradient scenarios (Fig. 2c, f), which is consistent with previous theoretical (reviewed in Kubisch *et al.*, 2014), comparative (e.g. Thomas *et al.*, 2001; Phillips *et al.*, 2006; Lombaert *et al.*, 2014) and experimental results (Fronhofer & Altermatt, 2015; Williams *et al.*, 2016a). Importantly, however, the latter has hitherto only been studied in unrealistic environmentally homogeneous landscapes. The evolutionary increase in dispersal is due to spatial assortment and the fitness advantages of dispersers colonizing empty habitat at the range front and therefore being released from competition ('spatial selection'; Phillips *et al.*, 2010; Shine *et al.*, 2011). As ecological and evolutionary dynamics were shown to occur at similar time-scales across a large number of taxa (from protists to vertebrates; DeLong *et al.*, 2016), we expect spatial selection to be a widespread phenomenon. Accordingly, we observe the evolution of increased dispersal at the range front in the gradient scenario as well. However, spatial selection is counteracted by the increasing mortality. From a macroecological point of view, the evolution of increased dispersal at range fronts accelerates range expansions, as empirically found in cane

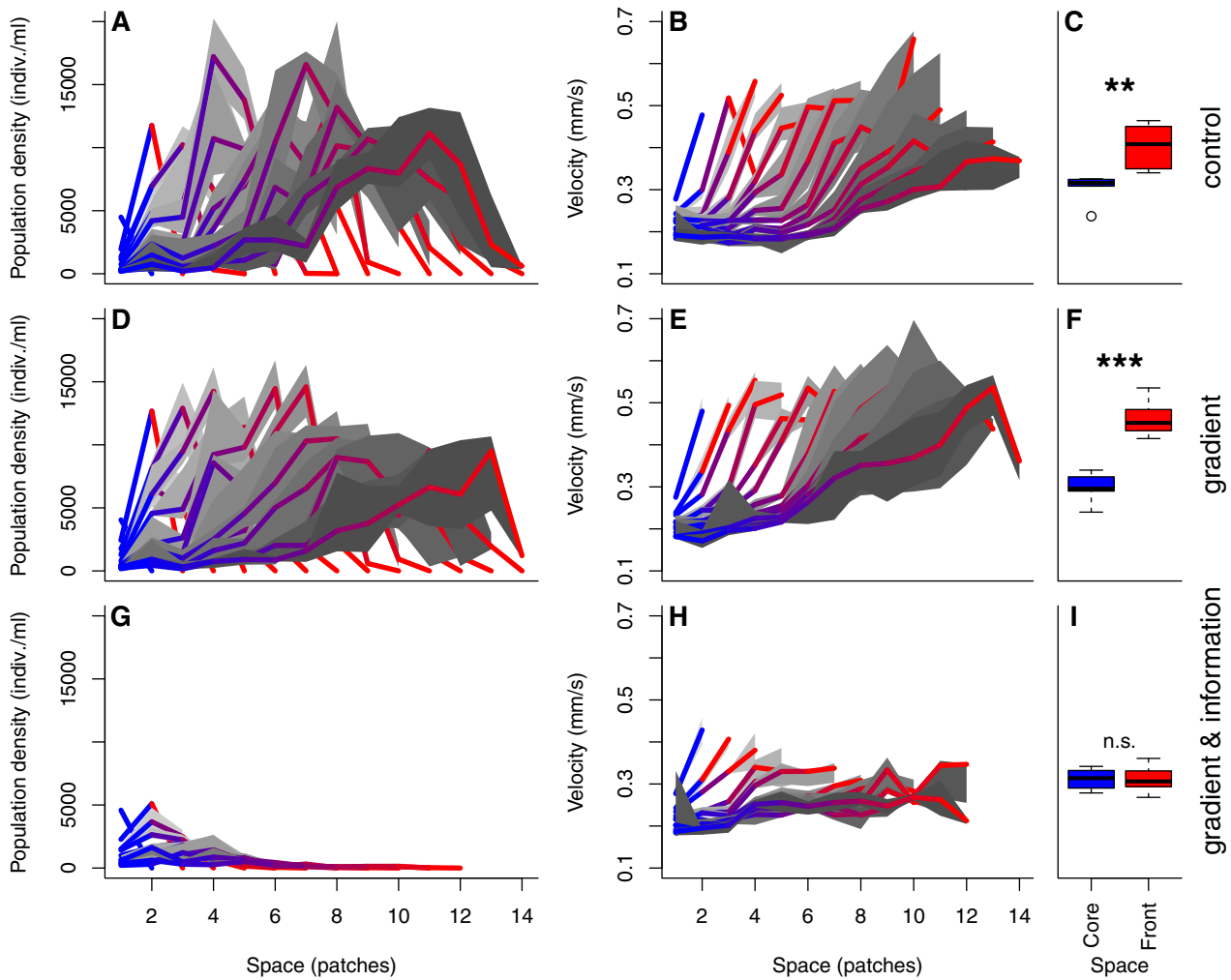


Figure 2 Range dynamics – experimental results. As predicted, the spatial distribution of population densities (a, d, g) showed an increase in density towards the range front in the control (a) and gradient (d) scenarios. Information use (g) inverted this pattern (see Fig. S3d–f; the distribution is statistically different from the other two; Fig. S4). On the last day of the evolution phase clear differences in movement over space were found in all scenarios (b, e, h), although the effect was weak in the informed scenario. After the common garden phase, the velocities in range core, respectively range front, populations were still significantly different in the control (c) and in the gradient scenario (f). No differences were observed in the informed scenario (i). We report medians over six experimental replicates [solid line; blue (range core) to red (range front)] and the 25th and 75th percentiles (grey shading; darker with time). Asterisks indicate statistical significance (see text for details).

toad invasions (Perkins *et al.*, 2013) or in experimental plant invasions (Williams *et al.*, 2016a).

In the informed scenario, however, we find that dispersal differences present at early stages of the expansion vanish after a common garden phase (Fig. 2h, i), confirming our model assumption regarding complete plasticity of dispersal in this scenario. The significance of dispersal cues and subsequent informed decisions is in good accordance with the movement ecology paradigm (Nathan *et al.*, 2008) which stresses the non-random nature of movement and, by extension, dispersal (Clobert *et al.*, 2009).

Both our theoretical predictions and our experimental results show a spatial density pattern of increasing population sizes towards the range front in the absence of information (Figs. 1 & 2). These density patterns emerge in the

theoretical results because resources are less depleted by more dispersive individuals at range fronts due to the trade-off between dispersal and reproduction (Eq. (3)) and concurrent changes in competitive abilities (Eq. (2)). Consequently, patches at the range front can support higher equilibrium population densities (Fronhofer & Altermatt, 2015). Our empirical results, especially the observed correlation between reproduction and competition (Fig. 3), support our model assumptions and the relationship between growth rate and competitive ability derived in Appendix S1. In the informed scenario we do not find increased densities at the range front, because dispersal was completely plastic (Fig. 2h, i) and the density differences are due to evolutionary dynamics. Thus, information use inverts the spatial distribution of population densities across a species' range.

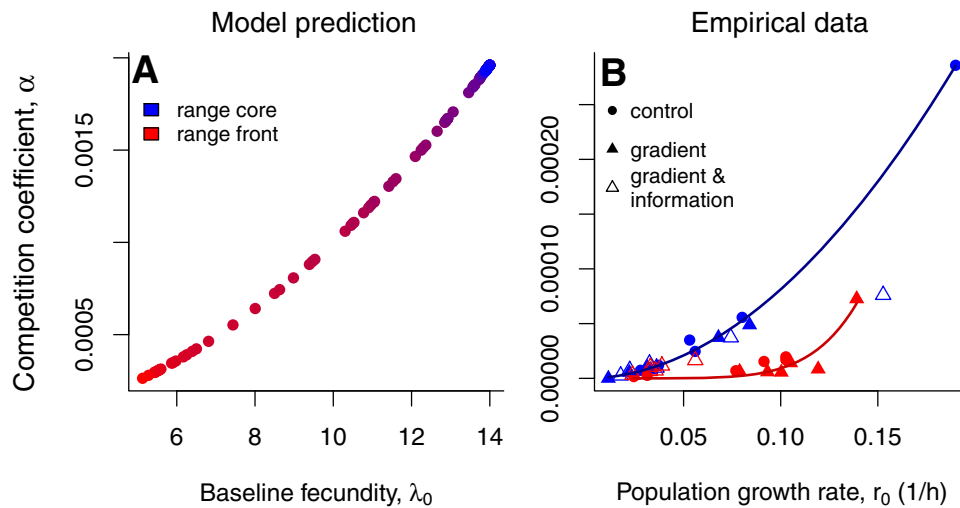


Figure 3 Concurrent evolution of reproduction and competition. (a) As derived in Appendix S1, our model assumes a correlation between competitive ability (α) and fecundity (λ ; equation (2)). Given a linear functional response we predict a quadratic relationship (λ – α correlation coefficient $\rho = 2$). Due to the trade-off between dispersal and fecundity, high fecundities and competitive abilities are predicted in the range core, where individuals are less dispersive (blue colour tones indicate the range core and red colour tones the range front; data from the control scenario; see Fig. 1). (b) Empirically measured competition coefficients (α) and growth rates (r_0) after the common garden phase. The theoretically predicted relationship between competition and reproduction was found for core populations [blue; empirically measured $\alpha_0 = 0.0074$ (CI 0.0053, 0.0094); $\rho = 1.96$ (CI 1.80, 2.11); only data from scenarios 1 and 2]. However, selection acting during the range expansion altered this relationship [red; $\alpha_0 = 11.24$ (CI $-29.11, 51.60$); $\rho = 6.09$ (CI: 4.31, 7.86); only data from scenarios 1 and 2] allowing individuals at the range front to have higher reproductive rates than theoretically predicted. Increased reproduction is highly advantageous as populations at the range front experience strong selection for both dispersal and reproductive ability.

The distribution of densities across a range, especially in the context of environmental gradients, has important consequences for range dynamics. It has been argued that range expansions could be halted due to migration load, that is, the influx of a large number of maladapted individuals from the range core to the range front (Kirkpatrick & Barton, 1997). This prediction heavily relies on range cores exhibiting larger densities than range margins. If the density pattern is inverted, as in our control and gradient scenarios, or if informed dispersal is the rule, the influx of maladapted genotypes from range core to margin will be very limited and will probably not affect range dynamics. Increased densities at range fronts could also alter genetic patterns related to drift and the resulting gene surfing of deleterious alleles in expanding populations (Excoffier & Ray, 2008).

Remarkably, in our experiments the impact of the mortality gradient on the spatial distribution of densities was relatively weak, while information use strongly inverted the spatial pattern of population densities (Figs. 2d, g & S3d–f). This indicates that it is not the direct fitness effect of the environmental gradient itself but rather altered dispersal behaviour based on the information content of the gradient that drives range expansion dynamics into our experimental environmental gradients. Our finding underlines the importance of information use and behavioural plasticity for dispersal and spatial dynamics under changing environmental conditions (Clobert *et al.*, 2009; O'Connor *et al.*, 2011;

Ponchon *et al.*, 2015), as well as for ecological and evolutionary dynamics in general (Dall *et al.*, 2005; Schmidt *et al.*, 2010).

In our experiments, the mortality gradient selected for increased reproduction (Fig. 3b). The quantitative difference between theoretical prediction and experimental results (Fig. S3) regarding the impact of information use can be linked to the observed shift in the structure of trait correlation (Fig. 3). This shift can be interpreted as the result of strong selection for high reproduction at range fronts, explaining the relatively small effect of the mortality gradient (Fig. 2d): populations compensated for increased mortality with increasing reproduction. The shift in the trait correlation structure is probably due to a change in foraging behaviour from a linear to a saturating functional response (see Appendix S1 and Fronhofer & Altermatt, 2015). While increased reproduction can thus be interpreted as an adaptation to the gradient, our data suggest that the informed strategy still achieves higher fitness at the range front (see Appendix S3).

We explored the ecological and evolutionary consequences of an environmental gradient acting on mortality. Evidently, changes in local conditions can also act by reducing fecundity, and the nature of the gradient may impact eco-evolutionary dynamics of ranges in general (see, e.g., Kubisch *et al.*, 2010, 2016). Nevertheless, here we theoretically show that a combined gradient, simultaneously increasing mortality and decreasing fecundity, does not alter our results

qualitatively (Fig. S5). A pure fecundity gradient may reduce or even cancel the increase in population sizes across the range. Nevertheless, information on environmental changes along the gradient will be highly relevant to fitness and therefore readily used by organisms capable of plastically adjusting their dispersal strategy.

Our theoretical and experimental findings highlight the need to include environmental heterogeneity and the capacity of organisms to process information thereon into more realistic predictions of invasion dynamics and range expansions. This is especially true in the context of changing environments and climatic conditions, as has been discussed by O'Connor *et al.* (2011), who highlight that dispersal and navigation behaviour are plastic traits which will affect local adaptation, colonization and acclimatization. Urban *et al.* (2016) also argue for more realism in biological models forecasting biodiversity dynamics under changing climates, and stress the complexities of the dispersal process. It is especially important to improve models, because more mechanistic and dynamic process-based approaches have been shown to outperform the predictive ability of correlative models (Pagel & Schurr, 2012; Zurell *et al.*, 2016).

In conclusion, we show that environmental gradients have a two-fold effect consisting of (1) a direct fitness-relevant effect of the gradient itself and (2) the information the gradient conveys on the environmental change. This information can steer dispersal decisions which affects macroecological patterns of range expansions along environmental gradients. Informed dispersal does not only affect expansion dynamics but can completely invert the spatial distribution of population densities.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site:

Appendix S1 Linking consumer–resource dynamics to logistic growth.

Appendix S2 Effects of chemical cues provided by dead conspecifics.

Appendix S3 Fitness expectations in the gradient scenarios at the range front.

Figure S1 *Tetrahymena pyriformis* — chemical cues of dead conspecifics used for negative chemotaxis.

Figure S2 *Tetrahymena pyriformis* — chemical cues of dead conspecifics impact population growth and intraspecific competition.

Figure S3 Cumulative density distributions of population densities over space during the range expansion — theoretical predictions and empirical results.

Figure S4 Statistical analysis of the empirical cumulative density distributions of population densities over space during the range expansion.

Figure S5 Predicted range dynamics into a combined mortality and decreasing fecundity gradient without information use.

Figure S6 Sensitivity analysis: control. Convexity (concavity) of the relative cumulative population density distribution.

Figure S7 Sensitivity analysis: control. Difference between evolutionarily stable dispersal strategies in range cores and range fronts.

Figure S8 Sensitivity analysis: gradient. Convexity (concavity) of the relative cumulative population density distribution.

Figure S9 Sensitivity analysis: gradient. Difference between evolutionarily stable dispersal strategies in range cores and range fronts.

Figure S10 Sensitivity analysis: gradient and information. Convexity (concavity) of the relative cumulative population density distribution.

Figure S11 Fitness expectations at the range front in scenarios 2 and 3 in comparison to a recalculated ‘no evolution’ scenario using growth rates and competitive abilities from the range core of scenario 2.

Table S1 Important parameters of the evolutionary individual-based model, their meaning and tested values. Standard values are underlined.

DATA ACCESSIBILITY

All data and computer code are archived in Dryad (doi: 10.5061/dryad.113v9).

BIOSKETCH

Emanuel A. Fronhofer is a research assistant in the Altermatt Lab. He combines theory and experiments in order to understand spatial eco-evolutionary dynamics.

The Altermatt Lab is part of the Department of Evolutionary Biology and Environmental Studies at the University of Zurich as well as the Department of Aquatic Ecology at Eawag. With our work we want to understand how species occur in space and time, how they interact, and how processes such as species invasions, dispersal or climate change affect natural communities.

Author contributions: E.A.F., N.N. and F.A. designed the research; N.N. performed the experiments; N.N. and E.A.F. analysed the data; E.A.F. developed the stochastic modelling framework; E.A.F. and F.A. wrote the paper.

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