Evolution of density-dependent movement during experimental range expansions

E. A. FRONHOFER*† (iD), S. GUT* & F. ALTERMATT*†

*Department of Aquatic Ecology, Eawag: Swiss Federal Institute of Aquatic Science and Technology, Dübendorf, Switzerland
†Department of Evolutionary Biology and Environmental Studies, University of Zürich, Zürich, Switzerland

Abstract

Range expansions and biological invasions are prime examples of transient processes that are likely impacted by rapid evolutionary changes. As a spatial process, range expansions are driven by dispersal and movement behaviour. Although it is widely accepted that dispersal and movement may be context-dependent, for instance density-dependent, and best represented by reaction norms, the evolution of density-dependent movement during range expansions has received little experimental attention. We therefore tested current theory predicting the evolution of increased movement at low densities at range margins using highly replicated and controlled range expansion experiments across multiple genotypes of the protist model system *Tetrahymena thermophila*. Although rare, we found evolutionary changes during range expansions even in the absence of initial standing genetic variation. Range expansions led to the evolution of negatively density-dependent movement at range margins. In addition, we report the evolution of increased intrastrain competitive ability and concurrently decreased population growth rates in range cores. Our findings highlight the importance of understanding movement and dispersal as evolving reaction norms and plastic life-history traits of central relevance for range expansions, biological invasions and the dynamics of spatially structured systems in general.

Introduction

Species' ranges and the distribution of taxa on earth have long been studied only from an ecological point of view and put in the context of local climatic and environmental conditions. Recent theoretical work and empirical case examples, however, have expanded upon this work by including an evolutionary perspective. Such an approach is needed because rapid evolutionary changes are thought to be especially relevant under transient and nonequilibrium conditions inherent to species range dynamics and population spread (Hanski, 2012; Kubisch *et al.*, 2014). Vice versa, range expansions can have serious consequences for the genetics of expanding populations (Excoffier *et al.*, 2009). For instance, deleterious mutations can accumulate at range fronts creating an expansion load (Peischl *et al.*, 2013) which may hamper further spread (Peischl *et al.*, 2015).

The importance of an evolutionary and eco-evolutionary perspective for understanding the dynamics of species ranges becomes evident when considering the main drivers of range dynamics: dispersal and reproduction. These life-history traits not only have a genetic basis (Bonte & Dahirel, 2017; Saastamoinen *et al.*, in press) and can be subject to evolutionary change, but ample theoretical evidence suggests that the evolution of dispersal and reproduction may also have important effects on the dynamics of species ranges (e.g. reviewed in Kubisch *et al.*, 2014). For instance, dispersal during range expansions is predicted to evolve to higher rates at range margins, a phenomenon called 'spatial selection' (Phillips *et al.*, 2010). Spatial selection relies on a simple ecological filter effect: if there is variation in dispersal ability, fast individuals will automatically be spreading more towards the range margin and colonize previously empty patches (see also Haag *et al.*, 2005).

Correspondence: Emanuel A. Fronhofer, Department of Aquatic Ecology, Eawag: Swiss Federal Institute of Aquatic Science and Technology, Überlandstrasse 133, CH-8600 Dübendorf, Switzerland.
Tel.: +41 58 765 5143; fax: +41 44 823 5028;
e-mail: emanuel.fronhofer@eawag.ch

As a consequence, populations at the range margin have a higher proportion of more dispersive individuals that will mate with each other. In combination with fitness advantages due to low intraspecific competition at the range margin, this spatial assortment can lead to the evolution of increased dispersal and movement abilities. These evolutionary changes have important consequences for (macro)ecological patterns: range expansions and biological invasions are predicted to proceed faster if dispersal evolves (Perkins *et al.*, 2013). Theoretical predictions regarding the evolution of reproduction have also been made, especially in the context of life-history trade-offs between dispersal, reproduction and competitive ability (Burton *et al.*, 2010; Fronhofer & Altermatt, 2015; Fronhofer *et al.*, 2017). As dispersal is costly (Bonte *et al.*, 2012), models generally assume that either reproduction or competitive ability has to decrease if dispersal increases.

Although there is accumulating comparative empirical evidence of spatial selection (e.g. Thomas *et al.*, 2001; Phillips *et al.*, 2006; Lombaert *et al.*, 2014), experimental confirmation is more scare. This scarcity is mainly due to the obvious challenges associated with studying how evolution impacts macroecological patterns experimentally. However, a recently increasing use of (small) model organisms has been spurring the study of experimental range expansions and population spread dynamics. As a consequence, range expansions are currently under intense scrutiny from an experimental ecological (e.g. Melbourne & Hastings, 2009; Giometto *et al.*, 2014, in press) and evolutionary point of view (e.g. Hallatschek *et al.*, 2007; Fronhofer & Altermatt, 2015; Gralka *et al.*, 2016; Williams *et al.*, 2016; Fronhofer *et al.*, 2017; Ochocki & Miller, 2017; Wagner *et al.*, 2017; Weiss-Lehman *et al.*, 2017). A result of these concerted efforts is the experimental demonstration that range expansions indeed may select for increased dispersal rates and distances at the range margin (in protists: Fronhofer & Altermatt, 2015; Fronhofer *et al.*, 2017; in insects: Ochocki & Miller, 2017; Weiss-Lehman *et al.*, 2017; and in plants: Williams *et al.*, 2016), which can lead to increased range expansion speeds.

We build on these studies and address in more detail two aspects that have received less attention so far: firstly, we explore evolutionary change during range expansions of populations initially harbouring no standing genetic variation. Understanding the consequences of depleted genetic variation may be especially relevant in the context of biological invasions, as genetic variation may be lost due to bottlenecks associated with the invasion process itself, which potentially constrains the success of invasions and evolutionary dynamics (for a critical discussion, see Roman & Darling, 2007; Dlugosch & Parker, 2008).

Secondly, we highlight that movement is context-dependent (Clobert *et al.*, 2009; Fronhofer *et al.*, 2017; Weiss-Lehman *et al.*, 2017) and should be represented by a reaction norm. The most well-known dispersal reaction norm captures dispersal as a function of conspecific density (e.g. Pennekamp *et al.*, 2014; Fronhofer *et al.*, 2015b), as the spatio-temporal distribution of densities is an important proximate and ultimate factor determining dispersal strategies (Bowler & Benton, 2005; Ronce, 2007). Current theory predicts that range expansions do select not only on the mean dispersal trait, but also on the shape of the reaction norm (Travis *et al.*, 2009). Dispersal is predicted to increase even at low densities which makes the reaction norm less positively density-dependent at the range margin (Travis *et al.*, 2009). Whereas density-dependent dispersal will optimize fitness in (quasi)equilibrium environments, such as the range core (Bowler & Benton, 2005), local conspecific density does not provide relevant information at the range margin: spatial selection makes dispersal highly advantageous even if local densities at the range margin are low. The evolution of increased dispersal at low densities at the range margin may have important consequences for range expansion dynamics: theory shows that density-dependent dispersal may slow down range expansions (Best *et al.*, 2007) but can ultimately lead to wider ranges (Kubisch *et al.*, 2011), to name but two examples.

Here, we experimentally tested whether and how range expansions impact the evolution of density-dependent movement (as a proxy of dispersal) and potentially change the shape of the density-dependent movement reaction norm. We predicted movement to evolve towards higher values at low densities making the reaction norm less positively or even negatively density-dependent at the range margin (Travis *et al.*, 2009; Weiss-Lehman *et al.*, 2017). We tested this prediction using experimental evolution and a total of 48 replicate range expansions of 14 clonally reproducing *Tetrahymena thermophila* strains, as well as the mix of these strains. Due to the lack of initial standing genetic variation in the replicates with single clonal strains and the low population densities characteristic of expanding range margins, we expect consistent evolutionary differentiation between range core and margin populations to be rare and emerge only in a minority of our replicates. We recorded movement behaviour and changes in life-history traits, namely population growth rate and intrastrain competitive ability, to investigate potential concurrent evolutionary changes (Bonte & Dahirel, 2017).

Materials and methods

Model organism

We used the freshwater ciliate *Tetrahymena thermophila* (Cassidy-Hanley, 2012) as our model organism. It is, together with its sister species (*Tetrahymena pyriformis*), commonly and successfully employed in both ecological (e.g. Giometto *et al.*, 2014; Fronhofer *et al.*, 2015b) and evolutionary contexts (e.g. Fjerdingstad *et al.*, 2007;

Friman *et al.*, 2011; Hiltunen & Becks, 2014; Pennekamp *et al.*, 2014; Fronhofer & Altermatt, 2015) and is known to show density-dependent movement and dispersal (Pennekamp *et al.*, 2014; Fronhofer *et al.*, 2015b). *Tetrahymena thermophila* can reproduce both sexually (if a cell from another mating type is present and mating is induced, e.g., by starvation, which was not the case in our experiments) and clonally (Cassidy-Hanley, 2012). We used a total of 14 clonally reproducing strains that were isolated as single cells shortly prior to the experiment from seven mating types originally obtained from Cornell University's Tetrahymena Stock Center (Stock ID: MTP01). The 14 clonally reproducing strains used here differ in attributes ranging from population growth rates and equilibrium densities (Table S1) to morphology and movement characteristics (Table S2).

Tetrahymena thermophila was kept in filtered (cellulose paper filters, 4–7 μm; Whatman) and autoclaved protist pellet medium (0.46 g L^{-1}; Protozoan pellets, Carolina Biological Supply) under constant temperature (20 °C) and light conditions (Osram Biolux 30 W). Initially, we supplemented the medium with a mix of three bacterial species (*Serratia fonticola*, *Bacillus subtilis* and *Brevibacillus brevis*; obtained from Carolina Biological Supply) at approx. 5% of their equilibrium density as a food source. During the experiment, we replaced 2 mL of 15 mL medium in each microcosm with bacterial cultures at equilibrium density (approx. 1 week old) to prevent adaptation of the bacteria and co-evolutionary dynamics from occurring. For further methodological details, see Altermatt *et al.*, (2015).

Experimental set-up and microcosm landscapes

We set up microcosm landscapes to study range expansions into initially uninhabited habitat by propagating range core and range margin populations as described by Fronhofer & Altermatt (2015). In contrast to this study, Fronhofer & Altermatt (2015) investigated unconditional dispersal and used an other *Tetrahymena* species, *T. pyriformis*. The microcosm landscapes consisted of two vials (20 mL conical vials; Sarstedt) connected by silicone tubing (inside diameter: 4 mm, VWR) and a stopcock (Discofix, B.Braun) to control for dispersal (total length: 6 cm). For a graphical overview of the experimental procedure, see Fig. S1.

The first patch (start) was initially filled with the respective *T. thermophila* strain at equilibrium density, and dispersal into the empty target patch (filled with 15 mL protist pellet medium with bacteria) was allowed for 4 h. Thereafter, the populations in the start and target patches were propagated to start patches in respectively new two-patch systems. The population from the original start patch was subsequently taken as the range core. Dispersal was allowed for 4 h, and only the individuals remaining in the start patch were further propagated. By contrast, the population from the original target patch represented the range margin. Dispersal was also allowed for 4 h. Thereafter, the population in the target patch was propagated to a new two-patch system. This procedure, effectively tracking range core and expanding range margin populations, was repeated three times per week for 1 month.

During transfer to new two-patch systems, only 13 of the 15 mL of the range core was transferred and the remaining 2 mL was filled with bacterial cultures at equilibrium (approx. 1 week old) to avoid evolutionary changes in the bacterial populations. This procedure was not necessary for the range margin, as the individuals of the range margin had always just dispersed into medium with bacteria from the stock population.

We chose this experimental approach that tracks only range core and range margin for convenience and feasibility. Firstly, we can easily control resource levels and avoid loss of control and contaminations due to ageing medium in long landscapes. Secondly, we have shown that although the experimental procedure obviously prevents feedbacks between core and margin populations, our results are not altered if we indeed use long interconnected linear landscapes (Fronhofer *et al.*, 2017). It is important to note that our approach reduces the likelihood of mutations occurring towards the range margin, as there is no possibility for dispersal, that is gene flow, from the core towards the margin, which effectively reduces the relevant population size. Our results will therefore be conservative and underestimate the potential occurrence of evolutionary change and subsequent range expansion success.

We followed a total of 48 range expansions, that is pairs of range cores and margins. We replicated the range expansion of each of the 14 strain three times and additionally included six replicates of a mix (in equal proportions) of all strains. The latter range expansions using the mix of strains thus differ from the range expansions of the single clones in that they were started with standing genetic variation.

Recording of population densities and movement data

During the experiment, all microcosms were sampled at every transfer, that is three times per week. We used video recording and automated analysis to collect data on population densities (number of cells) as well as movement metrics (e.g. velocity of the cells). More specifically, using a Leica M205C stereomicroscope at a 16-fold magnification and an Orca Flash 4 camera (Hamamatsu), we recorded 20 s videos (25 frames per second) of an effective volume of 34.4 μL (sample height: 0.5 mm). Videos were subsequently analysed using the ʀ environment for statistical computing (version 3.2.3) and a customized version of the 'ʙᴇᴍᴏᴠɪ' package (available on GitHub: https://github.com/efronhofer/bemovi; originally developed by Pennekamp *et al.*,

2015). The 'bemovi' package uses the image processing software imagej to locate moving particles in the videos and to calculate population densities as well as movement metrics. Data are automatically filtered to exclude artefacts such as debris that are outside the size or movement range of the study species (detailed settings available on GitHub: https://github.com/efronhofer/analysis_script_bemovi). As movement velocity has been shown to correlate well with dispersal rates in this system (Fronhofer & Altermatt, 2015; Fronhofer *et al.*, 2015a) we will focus on velocity as a proxy for dispersal.

Common garden phase

To separate evolutionary from potential plastic intergenerational and environmental effects, movement behaviour of individuals from range core and range margin populations was measured not only during the evolution experiment, but also after the end of the experiment and an additional 3-day common garden phase (doubling time for the strains of *T. thermophila* used here: approx. 3–12 h; see Table S1). The common garden was initiated with 1.5 mL samples obtained from the respective core and margin populations from the last day of the evolution experiment that were added to 13.5 mL medium with bacteria from the stock population to homogenize environmental conditions.

In addition, we kept a subset of the individuals analysed in this first common garden for an extended period in a common environment (a total of 38 days). This allowed us to explore the long-term stability of potential evolutionary changes. Resources were not refreshed to create strong competition similar to stable range core populations.

Estimating population growth rates and intrastrain competition coefficients

Both at the beginning of the experiment and after the common garden, we used population growth experiments to estimate population growth rates (r_0) as well as intrastrain competition coefficients (α_{ii}). These experiments were always started with 1 mL of the respective strain (1 week old for the beginning; from the common garden for the end) and 14 mL medium with bacteria from the stock population. We then followed population densities and movement over the course of 9 days, measuring twice in the first 2 days and then once on days 2, 3, 4, 7 and 9.

Population growth rates (r_0) and intrastrain competition coefficients (α_{ii}) were estimated by fitting the logistic growth model according to Verhulst (1838)

$$\frac{dN}{dt} = (r_0 - \alpha_{ii}N)N \qquad (1)$$

where N is the population size, to the data obtained from the growth experiments. The equilibrium density

is obtained as $\hat{N} = \frac{r_0}{\alpha_{ii}}$. We used the r environment for statistical computing (version 3.3.2) to solve (function 'ode'; 'desolve' package) and subsequently fit eqn 1 by minimizing residuals using the Levenberg–Marquardt algorithm (function 'nls.lm'; 'minpack.lm').

In the context of competition for shared resources (Mallet, 2012), α_{ii}, which is the slope of the function relating population growth to population size, can be easily interpreted as intrastrain competitive ability, where a higher value of α_{ii}, that is a steeper slope of the density-regulation function, corresponds to a higher (intrastrain) competitive ability. We explicitly do not use the equilibrium density as a proxy for competition, as the equilibrium density cannot always be assumed to be maximized by density-dependent selection (e.g. Matessi & Gatto, 1984). Intrastrain competitive ability, α_{ii}, can only be understood as a proxy for between-strain competition, if the same mechanisms of competition act within and between strains.

Density-dependent movement

The data obtained from the growth experiments were also used to assess potential evolutionary changes in density-dependent movement (see also Fronhofer *et al.*, 2015b), that is velocity as a function of relative population density ($\frac{N}{\hat{N}}$). Correlating population densities and movement may be challenging: for instance, low densities due to declining or growing populations may lead to very different movement decisions, as protists likely base movement decisions on chemical cues (Fronhofer *et al.*, 2015b). We therefore determined whether there was an indication for a decay phase towards the end of the growth experiments by additionally fitting a logistic model that allows for decaying population densities. This growth model follows eqn 1; however, it assumes that $\alpha_{ii} = \alpha_0(1 + \beta(t - t_{crit}))$ if $t > t_{crit}$, where α_0 is a baseline intrastrain competitive ability, β the rate at which intrastrain competition increases over time (t) and t_{crit} the critical time point from which on the increase in intrastrain competition (respectively decrease in equilibrium density) occurs. Based on these analyses, we excluded all movement data of day 7 of the growth experiment onwards as both mean and median values of t_{crit} estimates were approx. 7 days.

Statistical analyses

All data were analysed statistically using the r environment for statistical computing (version 3.3.2) and linear mixed models (function 'lme'; 'nlme' package). Response variables were appropriately transformed to satisfy model assumptions. Statistical analyses were performed across all strains simultaneously as the different genetic backgrounds represent the biologically relevant replicates in contrast to the technical replicates within each strain. This nested replication structure was accounted

for in the random effects. The data are available at Dryad (https://doi.org/10.5061/dryad.36q03).

More specifically, movement velocity (log-transformed) change during the experiment was analysed using individual-based velocity data with 'time' as a random slope and 'replicate' within 'strain ID' as a random effect structure to account for the nonindependence of individuals measured in one sample as well as the temporal nonindependence of the repeated measures through time (see Crawley, 2013). Following (Crawley, 2013), we started with the full model including an interaction between the two explanatory variables 'time' and 'range position' and subsequently simplified the model by removing explanatory variables to obtain the minimal adequate model. We used the 'ANOVA' function and maximum-likelihood (ML) estimates obtained with the 'optim' optimizer for model simplification. Subsequently, the minimal adequate model was refit using REML to obtain model estimates.

For the analysis of movement velocity (nontransformed) after the common garden phase, the full model included 'time' (end of evolution experiment, common garden 1, common garden 2) and 'range border position' as interacting fixed effects as well as 'time' within 'replicate' within 'strain ID' as random effects. Model simplification was carried out as described above.

Density-dependent movement (log-transformed) was analysed analogously using 'population density' and 'population history' (range border position and starting populations) as interacting fixed effects in the full model and 'replicate' within 'strain ID' as random effects with 'population density' as a random slope. The analysis of population growth rates (r_0; log-transformed) and intrastrain competition coefficients (α_{ii}; inverse-transformed) included only 'population history' (range border position and starting populations) as a fixed effect as well as 'strain ID' as a random effect.

Finally, potential differences between failed and successful range expansions, that is experimental replicates in which the range margin failed to expand and went extinct versus those that kept up with our experimental treatment, were explored by relating growth rates (r_0; inverse-transformed), intrastrain competition coefficients (α_{ii}; inverse-transformed) and median and standard deviation of movement velocity of the starting populations (respectively log- and inverse-transformed) with invasion success (yes/no). As a random effect, we included 'strain ID'.

Quantification of plasticity and evolutionary change in density-dependent movement

To quantify the different components of plasticity and evolutionary change in density-dependent movement, we used a reaction norm (RN) approach (e.g. Stoks *et al.*, 2015; Govaert *et al.*, 2016). Whereas the classical RN approach includes changes in the trait of interest

(here, movement) only between one control setting and one treatment setting, we here expanded this idea to RNs of continuously changing environmental conditions (here, relative density). Our analysis was based on the density-dependent movement RNs estimated using the mixed models described above. To avoid artefacts due to extrapolation, we restricted our analyses to the relative density interval that includes estimated RNs for ancestor, range core and range margin. For a graphical representation of our approach, see Fig. S2.

In analogy to the original RN approach, we quantified ancestral plasticity (AP), that is the plasticity in movement exhibited by the ancestor, as the difference between the ancestor's RN and a density-independent RN that has the same reference point as the ancestor RN. In the classical approach, the reference point is the intercept of the RN. To avoid bias due to extrapolation, we here did not use the estimated intercept, but the trait value at the lowest relative density in the relative density interval of interest. We quantified constitutive evolution (CE), that is the overall shift of the RN, as the difference between a density-independent RN at the reference point of the ancestor and a density-independent RN at the equivalent reference point of the range core, respectively range margin RN. Finally, evolution of plasticity (EP) was quantified as the difference between the ancestral RN shifted by the difference in reference points and the RN of the range core, respectively range margin. The three eco-evolutionary contributions were approximated by summing differences between the RNs.

We estimated the uncertainty of the relative contributions of AP, CE and EP using bootstrapping. We obtained a distribution of relative contributions by calculating the contributions of 10 000 randomly drawn RN sets based on estimates and standard errors extracted from the mixed model estimating the RNs. The individual RNs were first obtained in log-transformed space assuming normal distributions for the parameters as in the statistical model and were subsequently back-transformed. Subsequently, contributions were calculated in nontransformed space and normalized to sum to 1.

Results

Range expansion success

As expected, successful range expansions were rare: of 48 replicated range expansions, only four replicates belonging to three clonal strains (Fig. 1, upper panel) successfully tracked our experimental treatment and expanded their range over the entire duration of the experiment. All other replicates of both clonal strains and the genetically mixed populations only tracked the range expansion over part of the experimental duration and subsequently went extinct at the range margin.
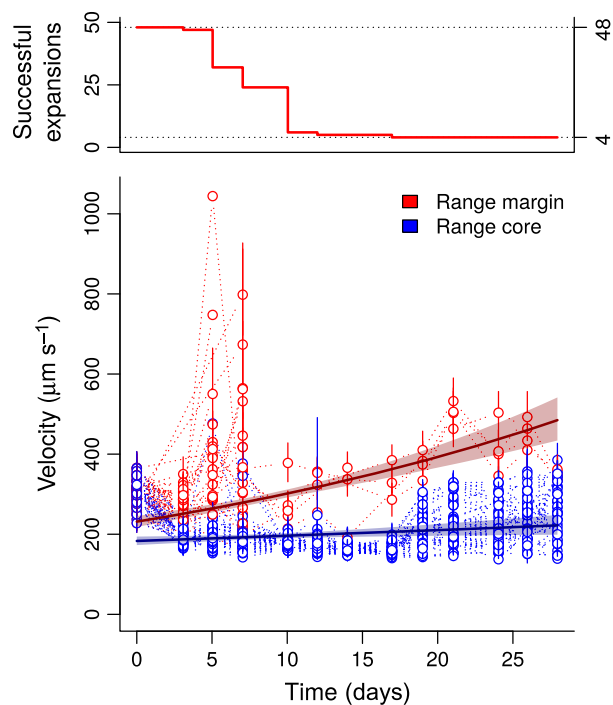
Fig. 1 Temporal dynamics of movement velocity during range expansions. Whereas most replicates did not expand their range and went extinct (upper panel), four replicates belonging to three different strains successfully expanded and increased in movement velocity (lower panel). Points and error lines show medians and interquartile ranges of the individual-based velocity data for each replicate separately. We additionally show estimates (solid lines) and confidence intervals (shaded area) obtained from the minimal adequate models relating velocity and time for range cores (blue) and margins (red).

The four successfully expanding replicates did, at the start of the experiment, not statistically differ from all other stains based on their initial properties (Fig. S3).

Evolution of movement

All four successfully expanding replicates showed increased movement velocity during the experimental evolution phase at the range margin (Fig. 1; LMM; minimal adequate model: time × position; intercept difference core-margin: $t_{199403} = -63.65$, $P < 0.001$; slope margin: $t_{199403} = 183.11$, $P < 0.001$; slope difference core – margin: $t_{199403} = -72.38$, $P < 0.001$). Individuals in populations at the range margin were on average 1.29 times faster than individuals in the range core (comparison of estimates; Fig. 2). Overall, these differences could be shown to be stable both after a 3-day common garden (approx. 10–20 doubling time periods based on the estimates of r_0 in Table S1) and after an additional month of selection for competitive ability in a common garden setting, thus indicating evolutionary change
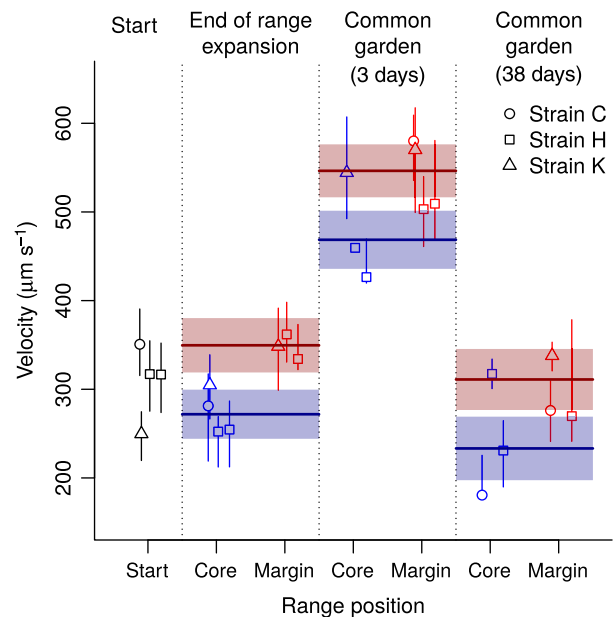

Fig. 2 Evolutionary differences in movement velocity between range cores and range margins for the replicates that successfully expanded their range. The increased movement velocity at the range margin at the end of the range expansion (see also Fig. 1) was stable after both the 3-day common garden and the 1-month common garden. Points and error lines show medians and interquartile ranges of the individual-based velocity data for each replicate separately. Strain ID (see Tables S1 and S2) is represented by different point symbols. We additionally show estimates (solid lines) and confidence intervals (shaded area) obtained from the minimal adequate model comparing velocity in range cores and margins at the three represented time points. Note that velocity at the start of the experiment (black points) is only shown as a visual reference and not included in the statistical analysis. Missing data points are due to low population densities in some replicates that prevented data collection. For results across all densities, see Fig. 3.

(Fig. 2; LMM; minimal adequate model: time + position; difference margin – core: $t_{934} = -10.28$, $P < 0.001$; difference end of evolution experiment – common garden 1: $t_6 = -14.23$, $P < 0.001$; difference common garden 1 – common garden 2: $t_6 = -14.54$, $P < 0.001$).

The successfully expanding replicates did not only show differences in movement after the two common garden periods, which captures evolutionary change only under one specific environmental condition (low densities). In line with our predictions, we also found differences in movement between range core and range margin populations across a large spectrum of population densities (up to two-fold equilibrium density; Fig. 3). The slope of the density-dependent movement reaction norm for range margin populations was negative in comparison with the density-dependent movement reaction norm for range core populations which tended to be slightly positively density-dependent (Fig. 3; LMM on log-transformed data; minimal
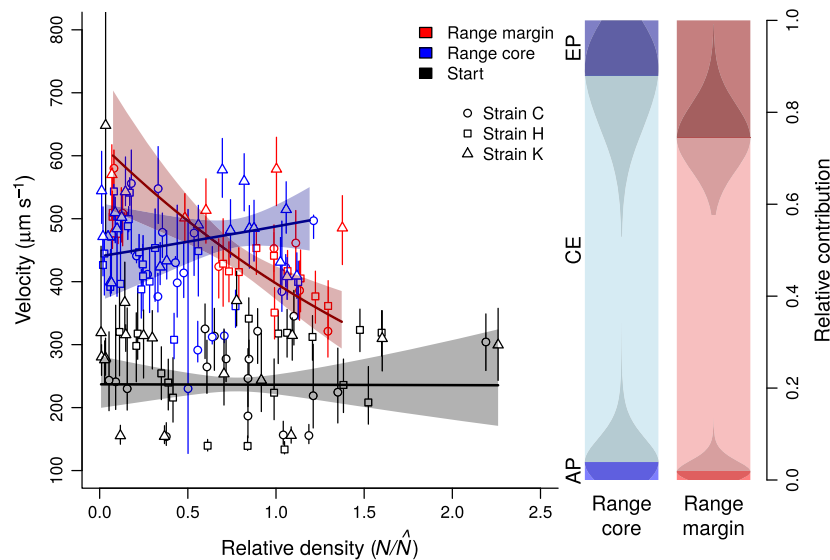
Fig. 3 Evolution of density-dependent movement in range cores and at range margins for the replicates that successfully expanded their range. The shifts in intercept, that is movement at low densities, recapture the results depicted in Fig. 2, and the slope of the density-dependent movement reaction norm was clearly negative at the range margin, whereas it was not significantly different from zero for both range core and starting populations. Points and error lines show medians and interquartile ranges of the individual-based velocity data recorded after the 3-day common garden phase. Strain ID (see Tables S1 and S2) is represented by different point symbols. We additionally show estimates (solid lines) and confidence intervals (shaded area) obtained from the minimal adequate model of the density-dependent movement reaction norm. The x-axis captures the relative density, that is population size (N) divided by the equilibrium population size ($\hat{N}$) estimated by fitting eqn 1 (for the same analysis based on absolute densities, see Fig. S4). The right panels summarize these results using the modified reaction norm (RN) approach. Clearly, there was very little ancestral plasticity (AP) and a large contribution of constitutive evolution (CE) for both range core and margin. Whereas the contribution of evolution of plasticity (EP) had a very wide distribution for the range core (grey shading), the distribution for the range margin did not include zero and had a median of 25%.

adequate model: density x history; intercept difference core − margin: $t_{29608} = -16.39$, $P < 0.001$; intercept difference start − margin: $t_{29608} = -66.96$, $P < 0.001$; slope margin: $t_{29608} = -4.07$, $P < 0.001$; slope difference core − margin: $t_{29608} = 24.09$, $P < 0.001$; slope difference start − margin: $t_{29608} = 32.67$, $P < 0.001$).

Whereas the differences in intercept observed here recapture the results depicted in Fig. 2, the estimated slopes suggest that density dependence of movement only evolved at the range margin and did not change in the range core in comparison with the ancestral populations. The estimated slopes for range core and start populations both had confidence intervals that strongly overlap with zero [slope range core: 0.10 (−0.12, 0.32); slope start population: −0.0028 (−0.2166, 0.2113); values represent estimates as well as lower and upper CI for log-transformed data extracted from the minimal adequate model], suggesting no density dependence. By contrast, the slope of the density-dependent movement reaction norm for the range margin populations was clearly negative [slope range margin: −0.45 (−0.47, −0.42)]. These results were not qualitatively changed if we considered absolute instead of relative densities as an explanatory variable, except for the slope of the range core which became positive (see Fig. S4).

These results are corroborated by the analysis of eco-evolutionary contributions using the density-dependent movement reaction norms (Fig. 3, right panel). Whereas the relative contribution of ancestral plasticity (AP), that is the slope of the ancestral reaction norm, was overall small (between 2 and 4%) and its distribution overlapped strongly with zero, the contribution of constitutive evolution (CE), that is the overall shift of the reaction norms compared to the ancestor, was large (83% for range core and 73% for range margin). As in the analyses reported above, the contribution of evolution of plasticity (EP) was smaller for the range core (12%) and the distribution was wide, suggesting only a weak tendency. By contrast, the effect of EP was stronger for the range margin (25%) and the distribution did not overlap with zero.

Evolution of population growth rate and intrastrain competitive ability

Besides evolutionary changes in density-dependent movement, we could find clear differences in population growth rates after the common garden phase between range core and range margin (Fig. 4). Range margin populations exhibited population growth rates
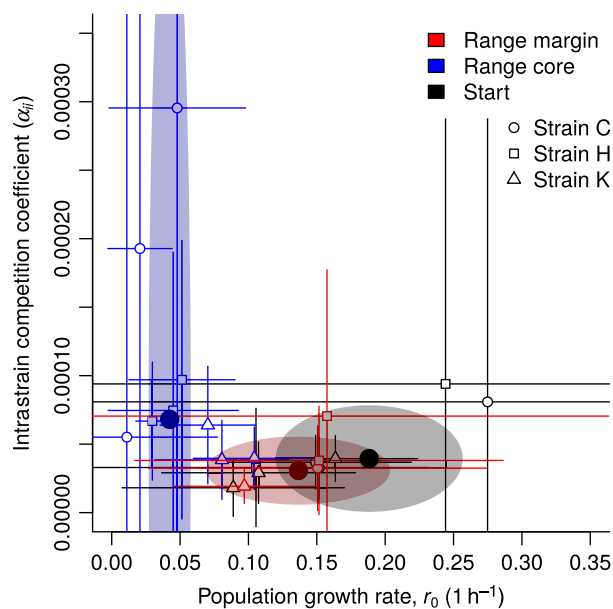
Fig. 4 Concurrent evolution of population growth rates (r_0) and intrastrain competition coefficients (α_{ii}) in range cores and at range margins for the replicates that successfully expanded their range. Range core population showed increased intrastrain competitive abilities and concurrently decreased population growth rate in comparison with range margins and the starting population. Points and error lines show estimates and confidence intervals of growth rates (r_0) and intrastrain competition coefficients (α_{ii}) obtained from fitting the logistic growth model (eqn 1) to data of population growth experiments performed after the 3-day common garden phase. Strain ID (see Tables S1 and S2) is represented by different point symbols. We additionally show estimates (large filled points) and confidence intervals (shaded area) obtained from the minimal adequate model comparing population growth rate and intrastrain competition coefficient between range cores, margins and the starting populations.

that were on average 3.2 times higher than range core populations (Tukey post hoc test after LMM on log-transformed data; core – margin: $z = -2.82$, $N = 22$, $P = 0.013$). Interestingly, whereas the difference between population growth rates at the range margin and in the starting populations was not significant (Tukey post hoc test after LMM on log-transformed data; core – margin: $z = 0.77$, $N = 22$, $P = 0.72$), the difference between range core and start was (Tukey host hoc test after LMM on log-transformed data; core – margin: $z = -2.82$, $N = 22$, $P = 0.013$).

Contrary to population growth rate patterns, range core populations showed a tendency for increased intrastrain competitive ability in comparison with range margin populations (average increase of 2.2-fold, however with strongly overlapping confidence intervals; Tukey post hoc test after LMM on inverse-transformed data; core – margin: $z = -2.98$, $N = 22$, $P = 0.008$). Again, range core populations tended to differ from the

starting populations (Tukey post hoc test after LMM on inverse-transformed data; core – margin: $z = 2.28$, $N = 22$, $P = 0.058$), whereas range margin populations did clearly not (Tukey post hoc test after LMM on inverse-transformed data; start – margin: $z = -1.20$, $N = 22$, $P = 0.45$).

Discussion

We investigated evolutionary differentiation between range core and range margin populations using highly controlled and replicated range expansions of both clonal *Tetrahymena thermophila* strains without initial standing genetic variation and a mix of all strains. Our experimental results provide evidence of rapidly emerging evolutionary differences in movement reaction norms, population growth rates and intrastrain competitive ability during range expansions.

As expected, successful range expansions (Fig. 1) occurred relatively rarely (four of 48 replicates). All other range margin populations went extinct at some point during the temporally advancing range propagation and ultimately failed to expand their range (Fig. 1). It is interesting to note that we did not observe successful range expansions in the replicates that harboured initial standing genetic variation. Furthermore, we could not identify any common attributes of the strains that successfully expanded their range, which is in good accordance with previous findings highlighting the intrinsically stochastic and variable nature of range expansions, in both an ecological (Melbourne & Hastings, 2009; Giometto *et al.*, 2013) and evolutionary context (Ochocki & Miller, 2017; Weiss-Lehman *et al.*, 2017). The lack of attributes that favour successful range expansions across the ancestors may also explain why replicates that started with mixes of clones did not stand out in terms of range expansion success, simply because advantageous genotypes were not present in the mix. Of course, a direct comparison in terms of expansion success between replicates with and without standing genetic variation is difficult due to the comparatively low number of mixed replicates.

Range expansions can lead to trait evolution even in the absence of initial standing genetic variation

Evolution of increased dispersal at range margins due to spatial selection (Phillips *et al.*, 2010) and potentially kin competition (Kubisch *et al.*, 2013) has been recognized to impact range expansion dynamics theoretically (Kubisch *et al.*, 2014) as well as in empirical studies (Fronhofer & Altermatt, 2015; Williams *et al.*, 2016; Fronhofer *et al.*, 2017; Ochocki & Miller, 2017; Wagner *et al.*, 2017; Weiss-Lehman *et al.*, 2017). We here explored the relevance of spatial selection for systems that do not initially harbour high amounts of standing genetic variation. Our results may therefore be relevant

in the context of invasions of non-native organisms, which, in contrast to expansions of species' ranges starting from a large and potentially diverse core habitat, may often start with a colonization event involving one or very few individuals and therefore may exhibit very little standing genetic variation (e.g. Tsutsui *et al.*, 2000; but see also Roman & Darling, 2007 and Dlugosch & Parker, 2008). Given the ecological and economical relevance of invasive species (Pimentel *et al.*, 2000), a better understanding of the underlying evolutionary dynamics is highly valuable.

We show that differentiation between range cores and range margins in movement and other life-history traits (population growth rate and intrastrain competitive ability) is possible in a relatively short time (13 discrete dispersal and population growth phases; the growth phases correspond to approx. 10–20 doubling time periods based on the estimates of r_0 in Table S1) even without initial standing genetic variation and despite our experimental setting that additionally limits gene flow towards the range margin population (Figs 2–4). Nevertheless, in our study system rapid evolution in asexually reproducing lines does not seem fundamentally surprising, as mutation rates are relatively high in *T. thermophila*: Brito *et al.* (2010) performed mutation accumulation experiments and report that the observed extinction rate is two to three orders of magnitude higher than in comparable experiments with yeast and bacteria. These high rates are likely due to gain and loss of chromosomes that typically occur during the amitotic division of the macronucleus (Brito *et al.*, 2010).

More generally, our findings fit well into the current invasion literature: for instance, Dlugosch & Parker (2008) discuss the invasive plant *Hypericum canariense* which shows evidence for the evolution of increased growth rates (survival and reproduction) and local adaptation in flowering time in invasive populations despite bottleneck events. Furthermore, genetic diversity does not seem to consistently predict invasion success in nature (Roman & Darling, 2007; Dlugosch & Parker, 2008), which is also consistent with our findings, especially with the failure to expand in the replicates that exhibited standing genetic variation. As Roman & Darling (2007) note, those species that do become invasive may not exhibit a general loss of diversity, which is well captured by our results, as those replicates that did expand their range overall showed diversification in life-history traits between core and margin (Figs 2 and 4). However, a direct comparison of the range expansion success in our study and natural invasion success is not readily possible, as our experimental approach is conservative and underestimates expansion success. On a more speculative note, failures of range expansions in our study may, of course, also be due to the accumulation of deleterious mutations leading to expansion load (e.g. Peischl *et al.*, 2015).

Besides being applicable to biological invasions, our results and conclusions are potentially relevant to climate-driven or generally environmental change-driven range expansions. Our experimental procedure basically simulates a shifting window of suitable habitat for the range margin as is often done in theoretical studies (e.g. Henry *et al.*, 2013). Figure 1 highlights that, despite often leading to extinction, evolutionary change (Figs 2 and 3) can potentially prevent these marginal populations from going extinct (evolutionary rescue; Gonzalez *et al.*, 2013; Carlson *et al.*, 2014). Empirical work has shown that evolutionary rescue may be promoted by dispersal (e.g. Bell & Gonzalez, 2011; Low-Décarie *et al.*, 2015) which suggests the possibility of selection for increased dispersal in such contexts. Theoretical work indicates that, especially in the context of rapidly shifting windows of climatic suitability, evolutionary rescue can occur by selecting for increased dispersal distances which allows populations to track climate change and even cope with severely fragmented landscapes (Boeye *et al.*, 2013). However, if one takes into account more complex scenarios and includes local adaptation (Schiffers *et al.*, 2013), evolutionary rescue may only be partial and species ranges are predicted to be severely narrowed after climate change. Interpreting our results in the context of evolutionary rescue is of course speculative, as we cannot determine whether evolutionary change happened because of the range expansions (spatial selection) or if evolutionary change allowed for the range expansion to happen in the first place.

Evolution during range expansions changes the density-dependent movement reaction norm

Our work shows that movement and dispersal evolution at expanding range margins does not only impact average movement strategies and dispersal probabilities, but changes the slope of the density-dependent movement reaction norm (Fig. 3). Theory predicts that dispersal should increase even at low densities at expanding range margins, that is become less positively density-dependent (Travis *et al.*, 2009) because conspecific density looses its value as a cue for context-dependent dispersal. As potential target patches for range margin populations tend to be empty, dispersal is advantageous already at low densities and an unconditional dispersal strategy will be less costly (Bonte *et al.*, 2012) as energy and time do not have to be invested in information collection and processing.

We find that the starting populations showed weak or no density-dependent movement (Fig. 3). Subsequently, individuals in the range core conserved this density-independent movement strategy, whereas individuals at the range margin exhibited evolution of plasticity and evolved increased movement at low densities (Fig. 3) thereby changing the slope from slightly

positive or neutral to negative. Our experimental results therefore substantiate the theoretical predictions of Travis *et al.* (2009) and are in accordance with recent empirical work that suggested a weakening of the slope of the density-dependent dispersal function in an insect system (Weiss-Lehman *et al.*, 2017). We can only speculate what led to the overall increase in movement (intercepts; constitutive evolution) when comparing starting populations and populations after the first common garden (Figs 2 and 3). This intercept shift, which is reversed in the second common garden (Fig. 2), may be due to increased resource availability during the experimental evolution phase as a consequence of the high rates of resource replenishment we chose to avoid evolution in the resources.

Range expansions lead to the evolution of increased intrastrain competitive ability and decreased population growth rates in range cores

Whereas dispersal is a central and potentially independent life-history trait of major importance for spatial dynamics (Bonte & Dahirel, 2017), other life-history traits, such as reproduction, may evolve concurrently or even trade off with dispersal (e.g. Burton *et al.*, 2010; Fronhofer *et al.*, 2011; Stevens *et al.*, 2014; Fronhofer & Altermatt, 2015). Our results show that not only movement capacities but also reproductive rates and intrastrain competitive abilities can evolve during range expansions and biological invasions (Fig. 4). Substantiating theoretical predictions (e.g. Burton *et al.*, 2010), we experimentally find higher population growth rates at the range margin in comparison with range core populations. Whereas the slope of the movement reaction norm showed evolutionary change in comparison with the starting population only at the range margin, it is populations in the range core that exhibited lower population growth rates in comparison with populations at the range margin and the starting population and not vice versa. At the same time, we observe higher intrastrain competitive abilities in range core populations, which hints at a trade-off between intrastrain competitive ability and population growth rates.

Our results regarding the evolution of population growth and intrastrain competitive ability, as well as previous findings in a similar system (Fronhofer *et al.*, 2017), are opposed to some recent experimental investigations reporting lower reproduction, respectively investment in population growth at the range margin (Fronhofer & Altermatt, 2015; Weiss-Lehman *et al.*, 2017) or no effect on reproduction (Ochocki & Miller, 2017). Whereas this heterogeneity in results may be linked to differences in resource dynamics in the experiments (Fronhofer & Altermatt, 2015; Fronhofer *et al.*, 2017), it also hints at the potential evolutionary independence of dispersal from other life-history traits

(Bonte & Dahirel, 2017). Clearly, more conceptual and experimental research is needed to provide synthesis on these questions.

Conclusions

We present experimental evidence showing that range expansions can lead to the evolution of increased movement at low densities at range margins in comparison with range cores due to evolutionary changes in plasticity, specifically in the density-dependent movement reaction norm. Movement evolved to be negatively density-dependent at the range margin. Additionally, we observed concurrent changes in life-history traits towards lower population growth rates and higher intrastrain competitive abilities in the range core. Importantly, these evolutionary changes emerged *de novo* in our experiments and did not require initial standing genetic variation. Our findings suggest that evolution can favour the spread of invasive species, even if standing genetic variation is initially low. In the context of climate change, evolution of increased movement at range margins may allow individuals to track their climatic niche by adapted dispersal and growth strategies.

Acknowledgments

Data accessibility

The data are available at Dryad (https://doi.org/10.5061/dryad.36q03). Video analysis scripts can be found on GitHub (https://github.com/efronhofer/analysis_script_bemovi).

References

Altermatt, F., Fronhofer, E.A., Garnier, A., Giometto, A., Hammes, F., Klecka, J. *et al.* 2015. Big answers from small worlds: a user's guide for protist microcosms as a model system in ecology and evolution. *Methods Ecol. Evol.* **6**: 218–231.

Bell, G. & Gonzalez, A. 2011. Adaptation and evolutionary rescue in metapopulations experiencing environmental deterioration. *Science* **332**: 1327–1330.

Best, A.S., Johst, K., Munkemuller, T. & Travis, J.M.J. 2007. Which species will succesfully track climate change? the influence of intraspecific competition and density dependent dispersal on range shifting dynamics. *Oikos* **116**: 1531–1539.

Boeye, J., Travis, J.M.J., Stoks, R. & Bonte, D. 2013. More rapid climate change promotes evolutionary rescue through selection for increased dispersal distance. *Evol. Appl.* **6**: 353–364.

Bonte, D. & Dahirel, M. 2017. Dispersal: a central and independent trait in life history. *Oikos* **126**: 472–479.

Bonte, D., Van Dyck, H., Bullock, J.M., Coulon, A., Delgado, M., Gibbs, M. *et al.* 2012. Costs of dispersal. *Biol. Rev.* **87**: 290–312.

Bowler, D.E. & Benton, T.G. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biol. Rev.* **80**: 205–225.

Brito, P., Guilherme, E., Soares, H. & Gordo, I. 2010. Mutation accumulation in *Tetrahymena*. *BMC Evol. Biol.* **10**: 354.

Burton, O.J., Pillips, B.L. & Travis, J.M.J. 2010. Trade-offs and the evolution of life-histories during range expansion. *Ecol. Lett.* **13**: 1210–1220.

Carlson, S.M., Cunningham, C.J. & Westley, P.A. 2014. Evolutionary rescue in a changing world. *Trends Ecol. Evol.* **29**: 521–530.

Cassidy-Hanley, D.M. 2012. *Tetrahymena* in the laboratory: strain resources, methods for culture, maintenance, and storage. *Methods Cell Biol.* **109**: 237–276.

Clobert, J., Le Galliard, J.F., Cote, J., Meylan, S. & Massot, M. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecol. Lett.* **12**: 197–209.

Crawley, M.J. 2013. *The R Book*. John Wiley & Sons Inc, Southern Gate, Chichester, UK.

Dlugosch, K. & Parker, I. 2008. Founding events in species invasions: genetic variation, adaptive evolution, and the role of multiple introductions. *Mol. Ecol.* **17**: 431–449.

Excoffier, L., Foll, M. & Petit, R.J. 2009. Genetic consequences of range expansions. *Annu. Rev. Ecol. Evol. Syst.* **40**: 481–501.

Fjerdingstad, E., Schtickzelle, N., Manhes, P., Gutierrez, A. & Clobert, J. 2007. Evolution of dispersal and life history strategies — *Tetrahymena* ciliates. *BMC Evol. Biol.* **7**: 133.

Friman, V.P., Laakso, J., Koivu-Orava, M. & Hiltunen, T. 2011. Pulsed-resource dynamics increase the asymmetry of antagonistic coevolution between a predatory protist and a prey bacterium. *J. Evol. Biol.* **24**: 2563–2573.

Fronhofer, E.A. & Altermatt, F. 2015. Eco-evolutionary feedbacks during experimental range expansions. *Nat. Commun.* **6**: 6844.

Fronhofer, E.A., Kubisch, A., Hovestadt, T. & Poethke, H.J. 2011. Assortative mating counteracts the evolution of dispersal polymorphisms. *Evolution* **65**: 2461–2469.

Fronhofer, E.A., Klecka, J., Melián, C. & Altermatt, F. 2015a. Condition-dependent movement and dispersal in experimental metacommunities. *Ecol. Lett.* **18**: 954–963.

Fronhofer, E.A., Kropf, T. & Altermatt, F. 2015b. Density-dependent movement and the consequences of the Allee effect in the model organism *Tetrahymena*. *J. Anim. Ecol.* **84**: 712–722.

Fronhofer, E.A., Nitsche, N. & Altermatt, F. 2017. Information use shapes the dynamics of range expansions into environmental gradients. *Glob. Ecol. Biogeogr.* **26**: 400–411.

Giometto, A., Altermatt, F., Carrara, F., Maritan, A. & Rinaldo, A. 2013. Scaling body size fluctuations. *Proc. Natl. Acad. Sci. USA* **110**: 4646–4650.

Giometto, A., Rinaldo, A., Carrara, F. & Altermatt, F. 2014. Emerging predictable features of replicated biological invasion fronts. *Proc. Natl. Acad. Sci. USA* **111**: 297–301.

Giometto, A., Altermatt, F. & Rinaldo, A. in press. Demographic stochasticity and resource autocorrelation control biological invasions in heterogeneous landscapes. *Oikos*. https://doi.org/10.1111/oik.04330.

Gonzalez, A., Ronce, O., Ferriere, R. & Hochberg, M.E. 2013. Evolutionary rescue: an emerging focus at the intersection between ecology and evolution. *Philos. Trans. R. Soc. B. Biol. Sci.* **368**: 20120404.

Govaert, L., Pantel, J.H. & Meester, L.D. 2016. Eco-evolutionary partitioning metrics: assessing the importance of ecological and evolutionary contributions to population and community change. *Ecol. Lett.* **19**: 839–853.

Gralka, M., Stiewe, F., Farrell, F., Möbius, W., Waclaw, B. & Hallatschek, O. 2016. Allele surfing promotes microbial adaptation from standing variation. *Ecol. Lett.* **19**: 889–898.

Haag, C.R., Saastamoinen, M., Marden, J.H. & Hanski, I. 2005. A candidate locus for variation in dispersal rate in a butterfly metapopulation. *Proc. Biol. Sci.* **272**: 2449–2456.

Hallatschek, O., Hersen, P., Ramanathan, S. & Nelson, D.R. 2007. Genetic drift at expanding frontiers promotes gene segregation. *Proc. Natl. Acad. Sci. USA* **104**: 19926–19930.

Hanski, I. 2012. Eco-evolutionary dynamics in a changing world. *Ann. N. Y. Acad. Sci.* **1249**: 1–17.

Henry, R.C., Bocedi, G. & Travis, J.M. 2013. Eco-evolutionary dynamics of range shifts: elastic margins and critical thresholds. *J. Theor. Biol.* **321**: 1–7.

Hiltunen, T. & Becks, L. 2014. Consumer co-evolution as an important component of the eco-evolutionary feedback. *Nat. Commun.* **5**: 5226.

Kubisch, A., Poethke, H.J. & Hovestadt, T. 2011. Density-dependent dispersal and the formation of range borders. *Ecography* **34**: 1002–1008.

Kubisch, A., Fronhofer, E.A., Poethke, H.J. & Hovestadt, T. 2013. Kin competition as a major driving force for invasions. *Am. Nat.* **181**: 700–706.

Kubisch, A., Holt, R.D., Poethke, H.J. & Fronhofer, E.A. 2014. Where am I and why? Synthesising range biology and the eco-evolutionary dynamics of dispersal. *Oikos* **123**: 5–22.

Lombaert, E., Estoup, A., Facon, B., Joubard, B., Grégoire, J.C., Jannin, A. *et al.* 2014. Rapid increase in dispersal during range expansion in the invasive ladybird *Harmonia axyridis*. *J. Evol. Biol.* **27**: 508–517.

Low-Décarie, E., Kolber, M., Homme, P., Lofano, A., Dumbrell, A., Gonzalez, A. *et al.* 2015. Community rescue in experimental metacommunities. *Proc. Natl. Acad. Sci. USA* **112**: 14307–14312.

Mallet, J. 2012. The struggle for existence: how the notion of carrying capacity, K, obscures the links between demography, darwinian evolution, and speciation. *Evol. Ecol. Res.* **14**: 627–665.

Matessi, C. & Gatto, M. 1984. Does k-selection imply prudent predation? *Theor. Popul. Biol.* **25**: 347–363.

Melbourne, B.A. & Hastings, A. 2009. Highly variable spread rates in replicated biological invasions: fundamental limits to predictability. *Science* **325**: 1536–1539.

Ochocki, B.M. & Miller, T.E.X. 2017. Rapid evolution of dispersal ability makes biological invasions faster and more variable. *Nat. Commun.* **8**: 14315.

Peischl, S., Dupanloup, I., Kirkpatrick, M. & Excoffier, L. 2013. On the accumulation of deleterious mutations during range expansions. *Mol. Ecol.* **22**: 5972–5982.

Peischl, S., Kirkpatrick, M. & Excoffier, L. 2015. Expansion load and the evolutionary dynamics of a species range. *Am. Nat.* **185**: E81–E93.

Pennekamp, F., Mitchell, K.A., Chaine, A.S. & Schtickzelle, N. 2014. Dispersal propensity in *Tetrahymena thermophila* ciliates — a reaction norm perspective. *Evolution* **68**: 2319–2330.

Pennekamp, F., Schtickzelle, N. & Petchey, O.L. 2015. Bemovi, software for extracting behavior and morphology from videos, illustrated with analyses of microbes. *Ecol. Evol.* **5**: 2584–2595.

Perkins, A.T., Phillips, B.L., Baskett, M.L. & Hastings, A. 2013. Evolution of dispersal and life history interact to drive accelerating spread of an invasive species. *Ecol. Lett.* **16**: 1079–1087.

Phillips, B.L., Brown, G.P., Webb, J.K. & Shine, R. 2006. Invasion and the evolution of speed in toads. *Nature* **439**: 803.

Phillips, B.L., Brown, G.P. & Shine, R. 2010. Life-history evolution in range-shifting populations. *Ecology* **91**: 1617–1627.

Pimentel, D., Lach, L., Zuniga, R. & Morrison, D. 2000. Environmental and economic costs of nonindigenous species in the united states. *Bioscience* **50**: 53–65.

Roman, J. & Darling, J.A. 2007. Paradox lost: genetic diversity and the success of aquatic invasions. *Trends Ecol. Evol.* **22**: 454–464.

Ronce, O. 2007. How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annu. Rev. Ecol. Evol. Syst.* **38**: 231–253.

Saastamoinen, M., Bocedi, G., Cote, J., Legrand, D., Guillaume, F., Wheat, C. *et al.* in press. Genetics of dispersal. *Biol. Rev.* https://doi.org/10.1111/brv.12356.

Schiffers, K., Bourne, E.C., Lavergne, S., Thuiller, W. & Travis, J.M. 2013. Limited evolutionary rescue of locally adapted populations facing climate change. *Philos. Trans. R. Soc. B. Biol. Sci.* **368**: 20120083.

Stevens, V.M., Whitmee, S., Le Galliard, J.F., Clobert, J., Böhning-Gaese, K., Bonte, D. *et al.* 2014. A comparative analysis of dispersal syndromes in terrestrial and semi-terrestrial animals. *Ecol. Lett.* **17**: 1039–1052.

Stoks, R., Govaert, L., Pauwels, K., Jansen, B. & De Meester, L. 2015. Resurrecting complexity: the interplay of plasticity and rapid evolution in the multiple trait response to strong changes in predation pressure in the water flea daphnia magna. *Ecol. Lett.* **19**: 180–190.

Thomas, C.D., Bodsworth, E.J., Wilson, R.J., Simmons, A.D., Davies, Z.G., Musche, M. *et al.* 2001. Ecological and evolutionary processes at expanding range margins. *Nature* **411**: 577–581.

Travis, J.M.J., Mustin, K., Benton, T.G. & Dytham, C. 2009. Accelerating invasion rates result from the evolution of density-dependent dispersal. *J. Theor. Biol.* **259**: 151–158.

Tsutsui, N.D., Suarez, A.V., Holway, D.A. & Case, T.J. 2000. Reduced genetic variation and the success of an invasive species. *Proc. Natl. Acad. Sci. USA* **97**: 5948–5953.

Verhulst, P.F. 1838. Notice sur la loi que la population suit dans son accroissement. *Correspondance Mathématique et Physique* **10**: 113–121.

Wagner, N.K., Ochocki, B.M., Crawford, K.M., Compagnoni, A. & Miller, T.E. 2017. Genetic mixture of multiple source populations accelerates invasive range expansion. *J. Anim. Ecol.* **86**: 21–34.

Weiss-Lehman, C., Hufbauer, R.A. & Melbourne, B.A. 2017. Rapid trait evolution drives increased speed and variance in experimental range expansions. *Nat. Commun.* **8**: 14303.

Williams, J.L., Kendall, B.E. & Levine, J.M. 2016. Rapid evolution accelerates plant population spread in fragmented experimental landscapes. *Science* **353**: 482–485.

Supporting information

Additional Supporting Information may be found online in the supporting information tab for this article:
Figure S1 Experimental set-up as used here and in Fronhofer & Altermatt (2015).
Figure S2 Eco-evolutionary partitioning using a modified reaction norm (RN) approach (Stoks *et al.*, 2015; Govaert *et al.*, 2016).
Figure S3 Differences between successful and failed range expansions.
Figure S4 Evolution of density-dependent movement in range cores and at range margins margins for the replicates that successfully expanded their range.
Table S1 Strain characteristics: population dynamics.
Table S2 Strain characteristics: morphology and movement.