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Dispersal plasticity driven by variation in fitness across species and environmental gradients

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Abstract

Dispersal plasticity, when organisms adjust their dispersal decisions depending on their environment, can play a major role in ecological and evolutionary dynamics, but how it relates to fitness remains scarcely explored. Theory predicts that high dispersal plasticity should evolve when environmental gradients have a strong impact on fitness. Using microcosms, we tested in five species of the genus *Tetrahymena* whether dispersal plasticity relates to differences in fitness sensitivity along three environmental gradients. Dispersal plasticity was species- and environment-dependent. As expected, dispersal plasticity was generally related to fitness sensitivity, with higher dispersal plasticity when fitness is more affected by environmental gradients. Individuals often preferentially disperse out of low fitness environments, but leaving environments that should yield high fitness was also commonly observed. We provide empirical support for a fundamental, but largely untested, assumption in dispersal theory: the extent of dispersal plasticity correlates with fitness sensitivity to the environment.

KEYWORDS
adaptation, dispersal plasticity, environmental context, maladaptation, reaction norm, *Tetrahymena*

INTRODUCTION

Dispersal, the movement of individuals possibly leading to gene flow (Clobert et al., 2009, 2012; Ronce, 2007), plays an essential role in ecological and evolutionary dynamics, mediating metapopulation dynamics (Hanski, 1998), local adaptation (Bolnick & Nosil, 2007; Kawecki & Ebert, 2004) and response to environmental changes (Bellard et al., 2012; Kokko & Lopez-Sepulcre, 2006; Travis et al., 2013). Dispersal often depends not only on the individual phenotype, like body size (Hanski et al., 1991; O'Riain et al., 1996) or exploratory behaviour (Cote et al., 2010; Dingemanse et al., 2003), but also on the environmental context, like population density (Harman et al., 2020), temperature (Bonte et al., 2008), competition with kin (Cote & Clobert, 2010) or interspecific interactions (Fronhofer et al., 2015). Such dispersal plasticity, when organisms adjust their dispersal decisions depending on their environment (also called context-dependent dispersal or habitat choice, Edelaar et al., 2008; Clobert et al., 2009; Jacob, Bestion, et al., 2015), can affect eco-evolutionary dynamics differently than random movements (Arendt, 2015; Edelaar & Bolnick, 2012; Jacob, Bestion, et al., 2015). For instance, while random dispersal generally homogenises local gene pools, dispersal plasticity has been shown to favour local adaptation, since the resulting gene flow involves a non-random subset of genotypes that can be locally adapted (Jacob et al., 2017). Dispersal plasticity can furthermore stabilise metapopulation dynamics (Mortier et al., 2019) and increase spatial heterogeneity of functional traits in meta-communities and meta-ecosystems (Jacob, Bestion, et al., 2015; Raffard et al., 2022).

Like many examples of phenotypic plasticity (DeWitt & Scheiner, 2004; West-Eberhard, 2003), the form of dispersal reaction norms can differ within or among species. For instance, while the tendency to disperse increases with population density in many species (Bowler & Benton, 2005; Clobert et al., 2009; Cote et al., 2008; Matthysen, 2005), some birds and ciliates generally show negative density-dependent dispersal (Kim et al., 2009; Pennekamp et al., 2014). As environmental gradients often differ in their spatiotemporal variability and effects on organisms, organisms might use different environmental characteristics to adjust dispersal decisions (Clobert et al., 2012). In the ciliate *Tetrahymena thermophila*, genotypes differ in whether they perform resource and/or density-dependent dispersal (Jacob et al., 2019).

The accumulation of empirical studies on dispersal plasticity highlights that it often varies within or among species and across environmental gradients. Understanding why organisms differ in their dispersal plasticity requires digging into the key, but largely overlooked question of how dispersal plasticity is related to the differences in expected fitness between environments (Edelaar et al., 2008; Edelaar & Bolnick, 2019). Studies on the evolution of phenotypic plasticity, and by extension dispersal plasticity, have been largely focused on whether plasticity has consequences for fitness, and if so, whether it increases or decreases fitness (neutral, adaptive or maladaptive plasticity; reviewed in Ghalambor et al., 2007). To be adaptive, the expression of dispersal plasticity should provide fitness advantages compensating for the potential costs incurred during dispersal (Bonte et al., 2012; Clobert et al., 2009).

Beyond the potential costs and benefits of dispersal plasticity, a prerequisite for dispersal plasticity to be selected in theoretical models is that environmental conditions vary over time or space, and that this variability affects fitness (e.g. Bocedi et al., 2012; Edelaar et al., 2017; Holt, 1987; Scheiner, 2016). Differences in dispersal plasticity among organisms may indeed result from differences in fitness sensitivities to environmental conditions. For instance, ecological specialists, for which even small environmental changes have a strong effect on fitness, might show higher ability to plastically adjust their dispersal decisions than generalists, allowing them to find the restricted environmental conditions they are specialised for within landscapes (Edelaar et al., 2008; Holt, 1987; Holt & Barfield, 2008; Jacob et al., 2018; Jacob, Bestion, et al., 2015). Although considered a basic assumption in theoretical models (Holt, 1987; Bocedi et al., 2012; Scheiner, 2016; for phenotypic plasticity see also Gavrilets & Scheiner, 1993; Lande, 2009; Botero et al., 2015; Tufto, 2015), whether fitness sensitivity to the environment explains differences of dispersal reaction norms between species or environmental gradients has, to our knowledge, never been investigated empirically.

We used ciliate microcosms to quantify dispersal plasticity across environmental gradients and species, and test whether differences in dispersal plasticity are associated with differences in fitness sensitivity to these environmental gradients. We independently quantified fitness and dispersal reaction norms along three environmental gradients (temperature, resources, salinity) in five genotypes from each of five species of the genus *Tetrahymena*. These species, which show high evolutionary divergence (~100 million years; Xiong et al., 2019), show high variability in their thermal niches and plasticity of cell morphology and movement (e.g. Jacob et al., 2019; Jacob & Legrand, 2021). Furthermore, this genus includes two model species used to test predictions about the ecology and evolution of dispersal in simple microcosms (e.g. Altermatt et al., 2015; Fronhofer & Altermatt, 2015; Jacob et al., 2017, 2019). Standard two-patch microcosms were used to quantify the plasticity of dispersal at emigration for each genotype along each environmental gradient. In parallel, we quantified fitness sensitivities along the same environmental gradients, without the possibility to disperse. We then used a meta-analytic approach to test whether dispersal plasticity correlates with fitness sensitivity across species and environmental gradients. We expected higher dispersal plasticity for organisms showing higher fitness sensitivity to the environment. Finally, we tested whether cells preferentially stayed in environments providing higher fitness, as would be expected under an adaptive plasticity scenario, by investigating whether and how dispersal rate correlates with expected fitness through a given environmental gradient.

MATERIAL AND METHODS

Culture conditions

Species from the *Tetrahymena* genus are 20–50 μm unicellular eukaryotes naturally living in freshwater ponds and streams (Collins, 2012; Doerder & Brunk, 2012). Five *Tetrahymena* species were used: *T. thermophila*, *T. pyriformis*, *T.americanis*, *T.elliotti* and *T.borealis*. The model species *T. thermophila* and *T. pyriformis* are commonly used in experimental ecology and evolution (e.g. Altermatt et al., 2015; Jacob et al., 2018; Ketola et al., 2004). Isogenic strains, hereafter called genotypes, were maintained in 24-well plates filled with axenic liquid growth media (0.6% Difco proteose peptone–0.06% yeast extract mix) at 23°C, and propagated every ~10 days into fresh media. Five genotypes from each of the five species were used (Table S1). All manipulations were performed under a sterile laminar flow hood.

Dispersal reaction norms along environmental gradients

Dispersal reaction norms were established from the quantification of dispersal rates in standard two-patch microcosms (Figure S1) consisting of Eppendorf microtubes (1.5 ml) linearly connected by a corridor (4 mm internal diameter silicon tube, 2.5 cm long) filled with 2.8 ml of growth media. These two-patch systems, in which environmental conditions are kept spatially homogeneous, are classically used to quantify emigration decisions (Cayuela et al., 2022; Fjerdingstad et al., 2007; Jacob, Chaine, et al., 2015; Junker et al., 2021; Pennekamp et al., 2014). One of the two patches was inoculated at 10% of a genotype's maximal density (150 μl of 1-week old culture). Cells were acclimatised during 30 min before opening the corridor, allowing dispersal over 5 h toward the second, initially empty patch (Jacob et al., 2016; Pennekamp et al., 2014). Corridors were then clamped to stop dispersal. The 5-h dispersal window is just below the mean asexual generation time in these species (Jacob et al., 2018; Jacob & Legrand, 2021; Pennekamp et al., 2014), and previous studies showed that population growth and survival are negligible during such 5-h dispersal window and do not affect estimates of dispersal rates (Jacob et al., 2018; Pennekamp et al., 2014). Two 10 μl samples were pipetted from each patch and placed into multi-chambered counting slides (Kima). We took from each sample a 15-s video under dark-field macroscopy (Axio Zoom V16, Zeiss) and quantified cell densities using the BEMOVI R-package (Pennekamp et al., 2015). This package tracks moving particles through an image processing workflow (Pennekamp et al., 2015) using IMAGEJ software (Schneider et al., 2012). Dispersal rate was estimated as the number of dispersers N_{disp} relative to the sum of residents N_{resi} and dispersers.

The three gradients were defined according to previous knowledge about the system to maximise fitness differences, but staying within the viable range of environmental conditions to avoid significant mortality that would prevent dispersal experiments (Juren et al., 2012; Morel-Journel et al., 2020). Each gradient consisted in three levels: 15, 23 and 31°C for temperature, 60%, 100% and 140% of growth media concentration for resources, and 0, 0.3 and 0.6% NaCl for salinity (Figure S2). Standard culture conditions were 23°C, 100% resources and 0% NaCl. Three replicates per genotype, environmental gradient and level within each environmental gradient were run, resulting in 675 dispersal systems. Due to low population sizes in some genotypes, data from a total of 639 out of 675 dispersal systems were available at the end of the experiment.

For each genotype along each environmental gradient, we computed dispersal plasticity as the standardised slopes of dispersal rate along the environmental gradient. Dispersal rates were logit transformed and scaled within each genotype, and environmental levels were scaled within each environmental gradient (i.e. centred on the mean, and scaled by the standard deviation using the *scale* function in R). Dispersal plasticity was thus comparable across environmental gradients. We used slopes from linear models calculated for each genotype and environmental gradient separately to capture the potential for increasing or decreasing reaction norms along environments (positive and negative slopes, respectively). Before computing dispersal plasticity, we checked that the assumption of linear slopes was valid and found that a quadratic effect did not better explain dispersal rate than a linear model (comparison of linear vs. quadratic models, including interactions with species and environmental gradients: $F_{7,578} = 1.302$; $p = 0.247$). Furthermore, relaxing the linear assumption and quantifying plasticity as overall differences between the three levels of each environmental gradient (i.e. effect sizes based on F-statistics from ANOVAs with environment defined as a factor) did not change the conclusions of this study (Supplementary Materials). Estimates of slopes of dispersal along each environmental gradient (β) for each genotype obtained from linear models (*lm* function; 'stats' R-package) were transformed into correlation coefficients (r) as $r = \frac{\beta \times \sqrt{R^2}}{|\beta|}$ (R^2 is the coefficient of determination of each linear regression; Koricheva et al., 2013), then converted into standardised effect size Z-scores (Z_r), where $Z_r = 0.5\ln\left(\frac{1+r}{1-r}\right)$ with standard error $se_{Z_r} = \frac{1}{\sqrt{n-3}}$ (mean number of points used to build dispersal reaction norm ± SE = 8 ± 0.13; Nakagawa & Cuthill, 2007). This standardised effect size was used as the metric of dispersal plasticity in the analyses, following a meta-analytic framework. Dispersal plasticity estimates close to zero indicate flat reaction norms, while positive or negative values, respectively, denote increase and decrease in dispersal rate along environmental gradients. We restricted estimations of dispersal plasticity for genotypes where at least one replicate for each of the three environmental ordered values were available, resulting in 71 dispersal plasticity values over the 75 initially planned (5 genotypes × 5 species × 3 environmental gradients).

Fitness along environmental gradients

Population growth without possibility to disperse was quantified as a proxy of fitness for each genotype in each environmental condition (Figure S1). As for dispersal plasticity, three replicates per genotype and environmental level within each gradient were performed. A small number of cells (10 μl, ~100 cells) of each isolated genotype was inoculated in 96-well plates, each well filled with 240 μl of growth media at the required nutrient and salt concentration, and placed in incubators at the required temperature. Population growth was measured through absorbance at 450 nm twice a day until populations reached their maximal density (10 days to 3 weeks) using a microplate reader (Tecan Infinite Spectrophotometer). Absorbance is linearly and positively correlated with cell density within the range of densities observed under our laboratory conditions (Jacob et al., 2017; Pennekamp, 2014). Spline-based growth curves were fitted using the *grofit* R-package (*gcfit* function; Kahm et al., 2010) and growth rates were computed as the maximum slopes of population growth as in previous studies (Jacob et al., 2017, 2018; Jacob & Legrand, 2021).

We quantified for each genotype along each environmental gradient one value of fitness sensitivity. As with dispersal plasticity, we checked the validity of a linear relationship between fitness and environmental gradients. We found significant quadratic relationships for two out of the three environmental gradients (linear relationship with salt concentration, species × salt^2: $F_{4,219} = 0.37$, $p = 0.83$; quadratic relationships with temperature, species × temperature^2: $F_{4,219} = 18.21$, $p < 0.001$, and resources, species × resources^2: $F_{4,219} = 8.01$, $p < 0.001$). We therefore quantified fitness sensitivity as overall differences of fitness among environmental levels using the F-statistic (F) from an ANOVA. As for the effect sizes based on slopes, F-statistics from ANOVA (*lm* function; 'stats' R-package) were transformed into r coefficients as $r = \sqrt{\frac{df_n F}{df_n F + df_d}}$, where df_n is the number of degrees of freedom and df_d is the residual number of degrees of freedom (Koricheva et al., 2013). These r coefficients were then converted into Z-scores ($Z_r \pm se_{Z_r}$) as detailed above. Fitness sensitivity close to zero indicates low effects of environmental variation on fitness, while high values denote a high impact of environmental variation on fitness.

Dispersal along expected fitness

We characterised the variation of dispersal rate as a function of expected fitness (i.e. maximal population growth rate measured independently from dispersal, see above) along each environmental gradient using the same method as for dispersal plasticity: for each genotype along each environmental gradient, we computed slopes from linear models to capture the potential for increasing or decreasing reaction norms along expected fitness. Relaxing the linear assumption by quantifying dispersal along fitness defined as a factor (i.e. effect sizes based on F-statistics from ANOVAs) did not change the conclusions of this study (Supplementary Materials). Slopes of dispersal along expected fitness across environmental gradients were converted into standardised effect sizes as explained above. Values close to zero represent no effect of expected fitness on dispersal rate, while positive or negative values respectively denote increase and decrease of dispersal rate along expected fitness.

Statistical analysis

We first tested whether dispersal plasticity differed among environmental gradients and species using linear models (*lm* function, on R version 4.0.3, R Core Team, 2020). Dispersal plasticity was the response variable, environmental gradient identities, species and their two-way interaction were explanatory factors. We attributed lower weight to dispersal plasticity estimates based on reduced dispersal rate data points by using $\frac{1}{se_{Z_r}}$ as weights in the models. Post hoc contrasts to compare the relative effects of each environmental gradient on dispersal plasticity were performed using *emmeans* (*lsmeans* function; Lenth, 2016).

Second, we tested whether variability of dispersal plasticity correlated with fitness sensitivity using linear models. Dispersal plasticity was the response variable, and fitness sensitivity, environmental gradient identity, species and their three-way interaction were explanatory factors, with $\frac{1}{se_{Z_r}}$ as weights.

Finally, we explored how dispersal rate varied along expected fitness, and whether this relationship differed between environmental gradients and species using linear models. Indices of how dispersal varies along local expected fitness were the dependent variables, and environmental gradient identity, species and their two-way interaction were explanatory factors, with $\frac{1}{se_{Z_r}}$ as weights. We furthermore explored whether dispersal plasticity and fitness sensitivity across one environmental gradient correlated with plasticity or sensitivity across the other gradients using Pearson correlation coefficients.

RESULTS

Dispersal plasticity differed between species ($F_{4,55} = 5.189$; $p = 0.001$) and between environmental gradients ($F_{2,55} = 26.986$; $p < 0.001$; non-significant species × environmental gradient interaction: $F_{8,55} = 0.918$; $p = 0.509$; Figure 1a; Table S2). Warmer temperatures generally led to an increased dispersal rate (mean dispersal plasticity ± SE = 0.64 ± 0.14), since most genotypes had positive values of dispersal plasticity, while an increase in salinity had a global negative effect on dispersal rates (i.e. mostly negative values of dispersal plasticity: −0.53 ± 0.11). Resources showed the weakest global effect on dispersal rate (−0.08 ± 0.11), but with variability among species in the degree and direction of resource-dependent dispersal. The degree of dispersal plasticity (absolute value ignoring whether dispersal increases or decreases along the environment) did not significantly differ between temperature and salinity (estimates ± SE = 0.175 ± 0.120, df = 63, $p = 0.318$) nor between resources and salinity

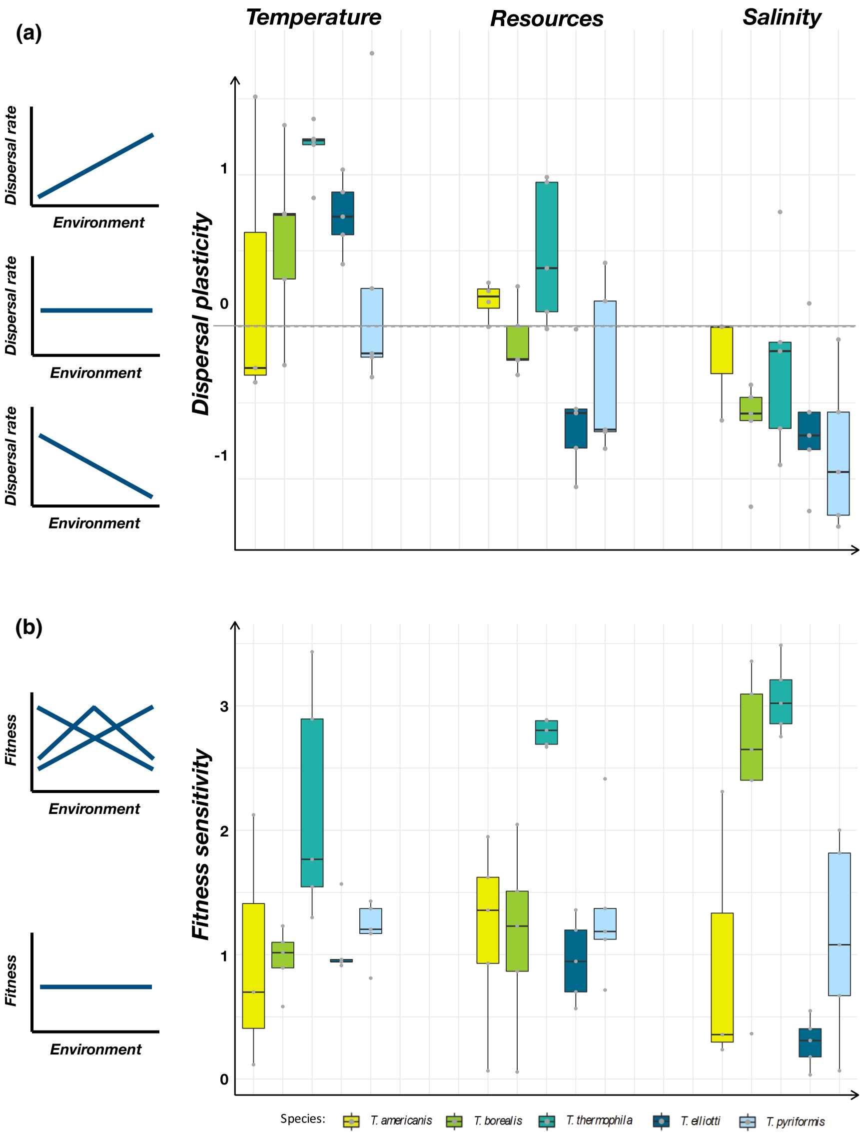

FIGURE 1 Dispersal plasticity (a) and fitness sensitivity to the environment (b) across species and environmental gradients. Reaction norms are provided on the left to illustrate the meaning of dispersal plasticity (a) and fitness sensitivity (b) values along the y-axes. (a) Dispersal plasticity estimates close to zero indicate flat reaction norms, while positive or negative values respectively denote increase and decrease of dispersal rate along environmental gradients. (b) Fitness sensitivity close to zero indicates low effects of environmental variation on fitness, while high values denote a high impact of environmental variation on fitness. Variability of dispersal plasticity and fitness sensitivity to environment between species are shown along the gradients of temperature, resources and salinity (blocs of five coloured boxplots from left to right). Boxplots show the distribution of dispersal plasticity and fitness sensitivity of the five genotypes (grey dots) of each species.

(−0.190±0.119, df = 63, p = 0.254), but significantly differed between temperature and resources (0.365±0.118, df = 63, p = 0.008). Interestingly, measures of dispersal plasticity induced by the three environmental gradients were not correlated among each other (temperature vs. resources: Pearson correlation $\rho = 0.314$, $t_{1,21} = 1.516$, $p = 0.144$; temperature vs. salinity: $\rho = 0.146$, $t_{1,21} = 0.676$, $p = 0.506$; resources vs. salinity: $\rho = 0.248$, $t_{1,21} = 1.172$, $p = 0.254$).

We found a significant effect of species × environmental gradient interaction on fitness sensitivity ($F_{8,55} = 2.404$, $p = 0.027$;Table S2), denoting that species differed in how much they were affected by environmental gradients (Figure 1b). *T. thermophila* showed the highest fitness sensitivity to the environment among the five species (Figure 1b). Contrary to dispersal plasticity, fitness sensitivity was positively correlated among environmental gradients (temperature *vs.* resources: Pearson correlation $\rho = 0.650$, $t_{1,21} = 3.917$, $p < 0.001$; temperature vs. salinity: $\rho = 0.563$, $t_{1,21} = 3.123$, $p = 0.005$; resources vs. salinity: $\rho = 0.493$, $t_{1,21} = 2.595$, $p = 0.017$). Although fitness sensitivity differed between species and environmental gradients, the range of environmental conditions experimentally manipulated within each gradient had comparable global effects on fitness (temperature effect: mean ± SE = 1.30 ± 0.15; resource effect: 1.49 ± 0.17; salinity effect: 1.62 ± 0.27).

Dispersal plasticity was positively correlated to fitness sensitivity (Figure 2), and this relationship differed between species and environmental gradients (environmental sensitivity × species × environmental gradient interaction: $F_{8,40} = 2.822$; $p = 0.014$; Figure S3; Table S3). Specifically, dispersal plasticity was positively correlated with fitness sensitivity along thermal (estimate ± SE = 0.503 ± 0.163, $t_{1,21} = 3.078$, $p = 0.006$) and resource (0.377 ± 0.105, $t_{1,22} = 3.588$, $p = 0.002$) gradients across species (no significant interaction with species respectively: $F_{4,13} = 1.222$, $p = 0.349$ and $F_{4,14} = 0.809$, $p = 0.540$; Figure S3). Along the thermal gradient, for which almost all genotypes had positive values of dispersal plasticity, this positive correlation means that genotypes with higher fitness sensitivity showed greater dispersal plasticity (Figure 2). Along resource gradients, for which genotypes had either negative or positive values of dispersal plasticity, this correlation means that genotypes with lower fitness sensitivity decreased their dispersal rate when resources increased (i.e. negative resource-dependent dispersal), while those with high fitness sensitivity increased their dispersal rate when resources increased (i.e. positive resource-dependent dispersal, Figure 2). Importantly, the relationship between dispersal plasticity and fitness sensitivity along the thermal gradient resulted primarily from differences in the absolute degree of plasticity rather than the direction of plasticity (i.e. results using directional slopes vs. degree of change via ANOVA showed the same pattern; Supplementary Materials). In contrast, the same relationship along the resource gradient appeared mostly driven by the direction of dispersal plasticity (i.e. sign of the slope of reaction norms associated with fitness, but not when using effect sizes from ANOVA; Supplementary Materials). Along the salinity gradient, the relationship between dispersal plasticity and fitness sensitivity significantly differed between species, meaning that we cannot describe a general pattern of salinity-dependent dispersal as a function of fitness sensitivity ($F_{4,13} = 6.853$; $p = 0.003$; Figure 2, Figure S3).

Finally, reconstructing dispersal reaction norms along expected fitness revealed differences between species and environmental gradients in both intensity and direction of the variation of dispersal rate as a function of fitness (species × environmental gradient: $F_{8,55} = 3.255$; $p = 0.004$; Table S4). As expected, in some species such as *T. elliotti*, cells tended to preferentially stay in patches with high expected fitness (i.e. negative correlation between dispersal rate and expected fitness, Figure 3). Nonetheless, we also found the opposite pattern, such as in *T. thermophila* where cells left patches with high expected fitness (i.e. positive correlation between dispersal rate and expected fitness, Figure 3).

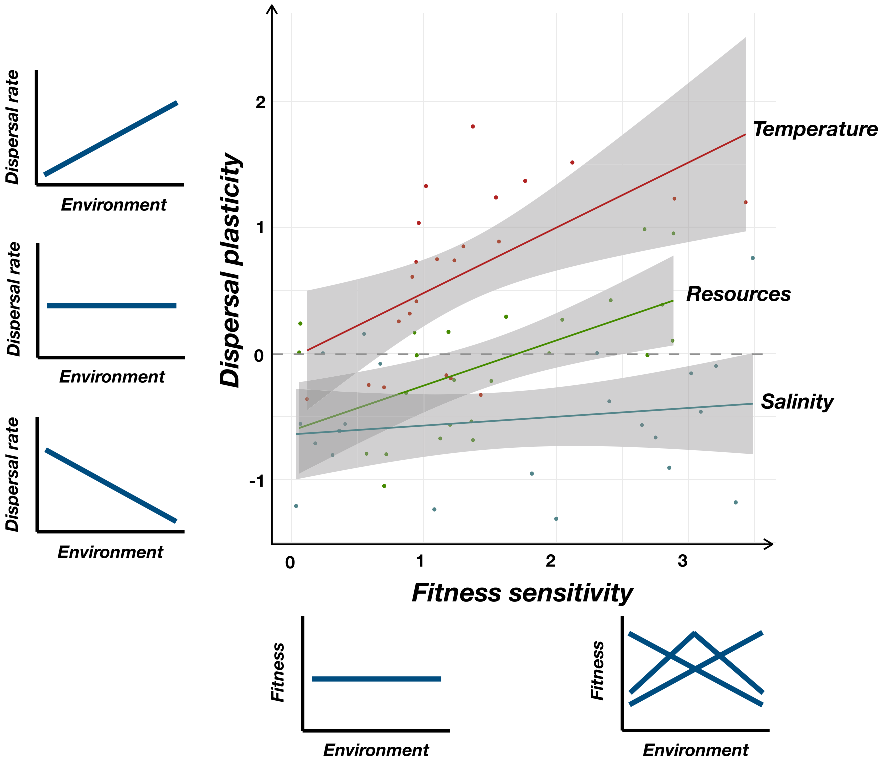

FIGURE 2 Dispersal plasticity depends on fitness sensitivity to the environment. Coloured lines and grey shaded areas represent linear regressions of dispersal plasticity function of fitness sensitivity along each environmental gradient (red: temperature; green: resources; blue: salinity). As in Figure 1, reaction norms are provided along the y and x-axes to illustrate the meaning of dispersal plasticity and fitness sensitivity. Detailed relationships per species are provided in Figure S3.

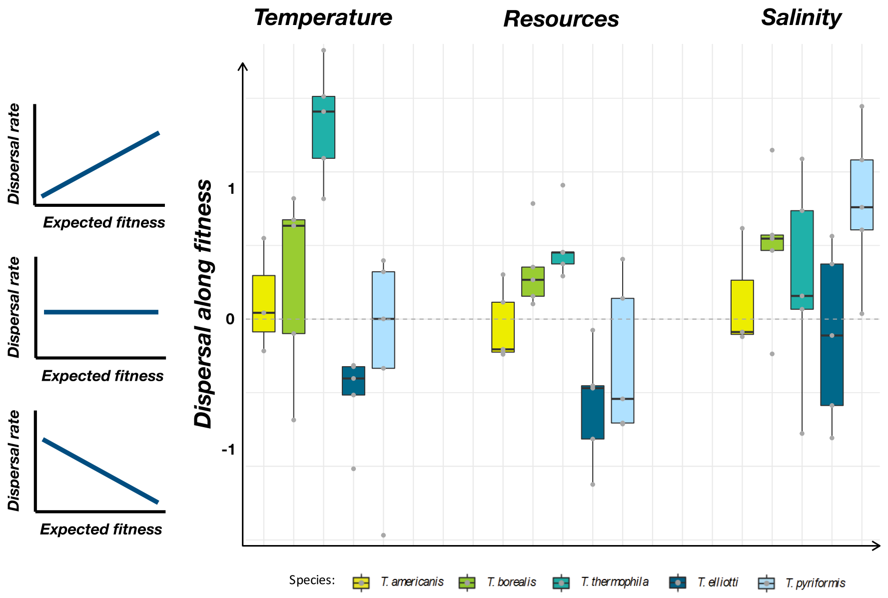

FIGURE 3 Relationship between dispersal rate and expected fitness across species and environmental gradients. Reaction norms along the y-axis illustrate the meaning of dispersal along fitness: estimates close to zero indicate flat reaction norms, while positive or negative values respectively denote increase and decrease of dispersal rate along expected fitness. Variability of dispersal along fitness between species are showed along the gradients of temperature, resources and salinity (blocs of five coloured boxplots from left to right). Boxplots show the distribution of dispersal along fitness of the five genotypes (grey dots) of each species.

DISCUSSION

Dispersal plasticity is classically considered as a way for organisms to track optimal habitats across landscapes (i.e. adaptive dispersal plasticity). Following this reasoning, organisms whose fitness is highly impacted by variation in the environment should show higher dispersal plasticity—yet this predicted link has not been evaluated empirically. Here, we experimentally confirmed that dispersal plasticity differed between species and across three environmental gradients, and is positively correlated to fitness sensitivity to the environment across species. Interestingly, the link between dispersal and expected fitness often differed from classic expectations that organisms preferentially stay in environments providing higher fitness. Our results provide important insights for understanding how dispersal plasticity varies across species and environmental gradients and how expected fitness associated with different environments could shape plasticity.

Dispersal plasticity across species and environmental gradients

Organisms often modify their decision to disperse depending on diverse environmental characteristics such as population density, food availability, temperature, relatedness among individuals or interactions with other species (Bowler & Benton, 2005; Clobert et al., 2009). Although evidence for such plasticity of dispersal is common (Bowler & Benton, 2005; Clobert et al., 2009, 2012), studies to date have mostly investigated one species at a time, or focused on single environmental factors (but see Fronhofer et al., 2018 for a notable exception). A better understanding of when and how dispersal plasticity occurs, requires quantifying dispersal plasticity in standardised conditions across different species and along multiple environmental gradients. Based on an experimental design including intraspecific replication (i.e. five genotypes per species), we showed that dispersal plasticity can differ considerably between species of the genus *Tetrahymena*, as expected since the evolution of phenotypic plasticity should depend on the costs and benefits associated with the environmental variability a species has experienced during its own evolutionary history. For instance, *T. americanis*, which has been previously found to show low plasticity in cell morphology (Jacob & Legrand, 2021), also showed weak dispersal plasticity here. On the contrary, *T. thermophila* or *T. elliotti* known to be highly plastic species (Jacob & Legrand, 2021; Morel-Journel et al., 2020), also showed high dispersal plasticity along all three environmental gradients. Whether these differences within and across species result from differences in evolutionary history, and whether plasticity of phenotypic traits such as cell morphology enable dispersal plasticity, or on the contrary trade-off against it, representing alternative strategies (Edelaar & Bolnick, 2019; Scheiner, 2016), are key questions for future investigations. Comparing reaction norms of dispersal rate as performed in this study to reaction norms of morphological traits along the same gradients, but without the possibility to disperse, would be key to identify the degree of covariation and potential trade-offs between these strategies.

In addition to differences among species, we showed that dispersal plasticity differed between environmental gradients for a given species. Dispersal rate generally increased with temperature, while it decreased with salinity and was only weakly affected by resources (Figure 1a). These three environmental gradients are important components of organisms' habitat quality known to affect dispersal and phenotypic reaction norms in many species (Bowler & Benton, 2005; Clobert et al., 2009; Dell et al., 2011; Leung et al., 2020) including *Tetrahymena* (Jacob et al., 2018, 2019; Laurent et al., 2020; Morel-Journel et al., 2020). We further showed that the genotypes studied differed in how much they were affected by changes of conditions along environmental gradients depending on both the species they belong to and the environmental gradient considered. A recent study showed that both the shape and intensity of phenotypic reaction norms can differ strongly between thermal and resource gradients (Morel-Journel et al., 2020). Accordingly, we found that dispersal plasticity on one environmental gradient did not correlate with dispersal plasticity along the other gradients investigated, although fitness sensitivity was correlated across environmental gradients. Importantly, environmental gradients differ in many ways, such as their level of spatiotemporal variability in nature or the mechanisms potentially underlying their effects on organisms. For instance, thermal stress might result in increased cell metabolism and motility (Jacob & Legrand, 2021; Luan et al., 2012), which might increase dispersal rate. On the contrary, response to osmotic stress involves mechanisms such as glycerol production or regulation of intracellular sodium concentration (Dunham, 1964; Rifkin, 1973) that might trade-off against dispersal ability.

Organisms might also respond similarly to different environmental gradients through general stress response mechanisms, such as the production of heat shock proteins in response to thermal as well as other physical or chemical stressors (Feder & Hofmann, 1999). Indeed, *Tetrahymena* species are known to use a general hormonal regulation mechanism to deal with both saline and thermal stresses (Csaba & Pállinger, 2008). Likewise, the degree to which increasing or decreasing environmental conditions relative to average conditions could have important effects on plasticity and fitness. In our experiment, how environmental levels differed from the standard culture conditions was not the same between gradients since standard conditions were intermediate in both temperature and resource gradients but the standard was the low condition in the salinity gradient. Determining the relative importance of mechanisms underlying plastic responses, history of environmental fluctuations and potential differences in response to increasing or decreasing environmental values for dispersal plasticity and fitness are important future questions. Overall, these results highlight that dispersal reaction norms can greatly vary depending on the environmental dimensions considered, pointing out the need to explore more systematically plasticity along multiple environmental dimensions to improve our understanding of the evolution and consequences of dispersal plasticity in multidimensional landscapes (Laughlin & Messier, 2015; Morel-Journel et al., 2020).

Dispersal plasticity and fitness

Tetrahymena genotypes differed in how sensitive they are to environmental gradients, and this variability in fitness sensitivity might have resulted in the evolution of different degrees of dispersal plasticity. Indeed, if environmental changes have a strong effect on fitness, organisms are expected to show a higher ability to plastically adjust their dispersal decisions, allowing them to find the restricted environmental conditions they are specialised for within landscapes. Accordingly, dispersal plasticity was positively correlated with fitness sensitivity to the environment (Figure 2). Genotypes with higher sensitivity to temperature and resources were more plastic in their dispersal decisions regardless of species, while this relationship differed between species along the salinity gradient (Figure S3). This result matches with an intuitive theoretical assumption: there is a higher probability of selection for plasticity when shifts in the environment have a stronger effect on fitness (e.g. Bocedi et al., 2012; Holt, 1987; Scheiner, 2016). Our study therefore provides empirical support for the fundamental expectation that organisms with higher fitness sensitivity to the environment should evolve higher dispersal plasticity. This relationship might have resulted from higher fitness sensitivity generating strong selective pressure toward the evolution of dispersal plasticity. Furthermore, dispersal plasticity can enable ecological specialisation: individuals either staying in, or dispersing towards habitats that maximise their performance should bias the gene flow toward locally-adapted genotypes (Edelaar et al., 2008, 2012; Holt, 1987; Jacob et al., 2017, 2018; Kawecki & Ebert, 2004; Rosenzweig, 1987). Exploring the dispersal–fitness covariations in real landscapes is a key future challenge that might help understand the evolutionary drivers and covariations between ecological specialisation and dispersal.

Although dispersal plasticity correlates with fitness sensitivity to the environment, the shape of this plasticity greatly varies among species and environmental gradients (Figure 3). Half of the genotypes showed increased dispersal rate when local expected fitness decreases, regardless of the environmental gradient (Figure 3), as expected if increasing dispersal rate is a strategy to escape locally unsuitable conditions (i.e. adaptive plasticity; Ronce, 2007). However, the other half showed an increased dispersal rate when expected fitness increases. This variability of dispersal plasticity, including this apparently maladaptive dispersal strategy, has previously been found in *T. thermophila* (Jacob et al., 2018) and now appears to be a more general pattern. One hypothesis to explain this pattern is that competition among genotypes might select for a preference for suboptimal habitats if fundamentally optimal habitats provide lower realised fitness as a consequence of competition with specialists (Jacob et al., 2018). This variability in the adaptiveness of dispersal plasticity might also result from differences of spatiotemporal variability of the environment: although unpredictable temporal fluctuations can select for higher dispersal rates (Travis, 2001), reliability of cues about environmental conditions and predictability of environmental changes generally promote the evolution of plasticity (e.g. Botero et al., 2015; Hendry, 2016; Leung et al., 2020). Dispersal plasticity is therefore expected to evolve when the environment fluctuates in space and time in a predictable way, making informed dispersal decisions more beneficial than random movements (Edelaar et al., 2008; Jacob, Bestion, et al., 2015; Lande, 2014; Leung et al., 2020; Tufto, 2015). Organisms should furthermore acquire reliable information about their environment to perform dispersal plasticity, which requires the evolution of information use abilities (Chaine & Clobert, 2012; Edelaar et al., 2008; Jacob, Bestion, et al., 2015), and depends on the predictability of fluctuations and the reliability of cues organisms can obtain about their environment (Botero et al., 2015). As a result, any reduction of cue reliability resulting from changes in the temporal variability of environmental variations (Ruokolainen et al., 2009) or changes in organism information use abilities might potentially make plasticity become maladaptive (Lyon et al., 2008). For instance, Singer (2015) showed that reduced cue reliability in a butterfly can cause habitat choice to result in local reductions in fitness. The selective pressures on the evolution of dispersal plasticity might therefore differ among species and environmental gradients, and might potentially lead to maladaptive use of potentially unreliable cues about environmental conditions encountered.

CONCLUSION

Although empirical evidence for dispersal plasticity is strong, whether it links to fitness, and how much it varies among species and environmental gradients are poorly resolved questions. Here, we provide experimental support for a basic and fundamental, but largely untested, assumption in theoretical models: the extent of dispersal plasticity correlates with fitness sensitivity to the environment. This suggests that, despite important variability in life-history traits and potentially environmental history, a link between fitness sensitivity to the environment and dispersal plasticity may be common. Future work using a broader array of phylogenetic groups and biomes would help evaluate this contention. If this link between fitness sensitivity and dispersal plasticity is general, experiments like ours might provide essential parameters to calibrate theoretical metapopulation, community and ecosystem frameworks.

We show that dispersal decisions do not always consist of preferring fundamentally optimal habitats, echoing a recent increased consideration for maladaptation being probably more frequent than generally thought (Brady et al., 2019). Why organisms might target fundamentally suboptimal habitats is a timely question that requires further investigation of the behavioural rules underlying dispersal. Specifically, which cues about the environment are used to adjust dispersal decisions and whether they link to fundamental or realised fitness in a given context are crucial questions to tackle (Jacob et al., 2018). Additionally, the variability of dispersal plasticity and its links with fitness we showed at emigration might differ from the cues involved and preferences at immigration (i.e. decision of where to settle). For example, immigration decisions relying on prospection or social information use may include higher costs or result in less reliable information than simply assessing the local environmental context for an emigration decision (Cote & Clobert, 2007; Doligez et al., 2004; Jacob, Bestion, et al., 2015; Jacob, Chaine, et al., 2015; Schmidt et al., 2010). Further systematic investigation of dispersal plasticity across dispersal phases, species and environmental gradients as well as their fitness correlates in both fundamental and realised scenarios will be key for our understanding of dispersal plasticity evolution and its importance for eco-evolutionary dynamics.

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AUTHORSHIP

JLMC, DL, ASC and SJ conceived and designed research. JLMC and SJ performed experiments. MH maintained cell cultures and provided technical assistance during experiments. JLMC, AR and SJ analysed the data. JLMC and SJ wrote the manuscript, with major contributions from all authors.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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