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Variability in Dispersal Syndromes Is a Key Driver of Metapopulation Dynamics in Experimental Microcosms

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ABSTRACT: Evolutionary ecology studies have increasingly focused on the impact of intraspecific variability on population processes. However, the role such variation plays in the dynamics of spatially structured populations and how it interacts with environmental changes remains unclear. Here we experimentally quantify the relative importance of intraspecific variability in dispersal-related traits and spatiotemporal variability of environmental conditions for the dynamics of two-patch metapopulations using clonal genotypes of a ciliate in connected microcosms. We demonstrate that in our simple two-patch microcosms, differences among genotypes are at least as important as spatiotemporal variability of resources for metapopulation dynamics. Furthermore, we show that an important proportion of this effect results from variability of dispersal syndromes. These syndromes can therefore be as important for metapopulation dynamics as spatiotemporal variability of environmental conditions. This study demonstrates that intraspecific variability in dispersal syndromes can be key in the functioning of metapopulations facing environmental changes.

Keywords: intraspecific variability, dispersal syndrome, eco-evolutionary dynamics, spatially structured populations, genetic diversity, environmental changes.

Introduction

Organisms live in a spatially and temporally structured world, meaning that populations are distributed in spatially structured habitats whose suitability changes through time (Hanski and Gaggiotti 2004). Since the environmental conditions encountered in a habitat govern an organisms' reproductive success and survival, the dynamics of local populations are affected by the extent of spatiotemporal variability in environmental conditions (Moran 1953; Levin 1976; Bascompte and Solé 1998; Hanski 1998). Such spatiotemporally variable selective pressures can drive changes in the distribution of phenotypic traits in populations (Kettlewell 1973; Endler 1980; Stearns 1983). Beyond being the target of selection, phenotypic traits can in turn influence ecological dynamics, such as population demography and community composition (Pimentel 1968; Thompson 1998; Urban et al. 2008; Pelletier et al. 2009; Hendry 2017; Legrand et al. 2017). Furthermore, although variability among species is of considerable importance, intraspecific variability can have an equivalent or even sometimes greater impact on ecological processes than interspecific variability (Des Roches et al. 2018; Raffard et al. 2019). Estimating the importance of genetic and phenotypic intraspecific variability relative to environmental variability for the dynamics of spatially structured populations is therefore one of the core current challenges in ecological and evolutionary research (Bolnick et al. 2003, 2011; Violle et al. 2012; Des Roches et al. 2018).

Dispersal is recognized as one of the central traits driving the dynamics of spatially structured populations (MacArthur and Wilson 1963; Hanski 1998; Lenormand 2002; Bowler and Benton 2005; Ronce 2007; Abbott 2011; Clobert et al. 2012). Since the establishment of metapopulation theory, a large body of theoretical studies has been dedicated to understanding and predicting the dynamics and persistence of spatially structured populations and the evolution of dispersal in fragmented landscapes (reviewed in Clobert et al. 2009, 2012; Duputié and Massol 2013). However, most of the theoretical framework on this topic assumes dispersal to be random with regard to the phenotype or the environmental context, and these simplifying assumptions contrast with increasing evidence from empirical studies for extensive variability in phenotypic and behavioral traits related to dispersal movements (reviewed in Bowler and Benton 2005; Ronce 2007; Clobert et al. 2012; Travis et al. 2012; Jacob et al. 2015*a*; Cote et al. 2017). Indeed, dispersal often depends on a variety of internal factors enabling or enhancing its

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success (e.g., orientation skills, energy reserves, fecundity, niche breadth) and external factors affecting individual fitness (e.g., population density, resources, temperature; Clobert et al. 2009; Stevens et al. 2014; Legrand et al. 2015; Cote et al. 2017). Multiple dispersal-related traits are most often assembled in dispersal syndromes, defined as the covariation between dispersal and other phenotypic traits (Fjerdingstad et al. 2007; Clobert et al. 2009; Stevens et al. 2014; Cote et al. 2017).

The existence of great variability in dispersal-related traits and strategies within species is a challenge for our ability to forecast ecological and evolutionary dynamics under environmental variability (Clobert et al. 2009). This is because the role of dispersal in the persistence of spatially structured populations may drastically differ depending on the dispersal-related traits involved and the environmental conditions encountered (reviewed in Bowler and Benton 2005; Clobert et al. 2009; Jacob et al. 2015*a*). For instance, theoretical models revealed that intraspecific variation, including colonizing strategies, might increase metapopulation persistence (Leimar and Norberg 1997). Furthermore, compared with random dispersal, phenotype-dependent dispersal decisions can favor local adaptation (Holt and Barfield 2015; Jacob et al. 2017), stabilize metapopulation dynamics (Mortier et al. 2019), or mediate specialist-generalist coexistence (Jacob et al. 2018). However, models also revealed that phenotypic variability can have either positive or negative effects on metapopulation stability depending on the mismatch between dispersal phenotypes and local conditions (Gibert 2016). Besides, the success of these different dispersal strategies should differ depending on the environmental context faced. Unfortunately, few theoretical predictions are available on this topic, because most models usually consider dispersal to be a random process (e.g., Wang et al. 2015). One notable exception for the interaction between dispersal strategies and environmental variability on metapopulation dynamics lies in a model from Rodrigues and Johnstone (2014), who showed that spatiotemporal variability of environmental conditions should favor positive density-dependent dispersal, while spatially variable but temporally stable environments should favor negative density-dependent dispersal.

However, experimental approaches quantifying the importance of different dispersal-related traits for the dynamics of spatially structured populations are still crucially lacking, especially under varying environmental conditions, as has been pointed out repeatedly (e.g., Travis et al. 2012; Jacob et al. 2015*a*; Cote et al. 2017; Hendry 2017; Legrand et al. 2017). This experimental gap mostly results from the constraints in handling the required replicated experiments of spatially structured populations followed over sufficient temporal scales. Experimental micro/mesocosms using short-generation-time species provide a valuable opportunity to fill this gap (Gause 1934; Jessup et al. 2004; Legrand et al. 2012; Altermatt et al. 2015; De Roissart et al. 2015), offering especially the possibility to quantify the importance of dispersal strategies for the dynamics of metapopulations facing different regimes of environmental variability.

Here we experimentally quantified the relative effects of intraspecific variability in dispersal-related traits and environmental variability for the dynamics of simple experimental metapopulations. Importantly, we aimed at expanding our understanding of the impact of dispersal syndromes on the dynamics of spatially structured populations. We thus did not compare the dynamics of metapopulations composed of different levels of intraspecific variability but separately quantified the effects of distinct genotypes and phenotypes for metapopulation dynamics. To do so, we used the ciliated protist *Tetrahymena thermophila* in simplified metapopulations consisting of replicated two-patch microcosms. We first characterized dispersal strategies and related phenotypic traits among six isogenic strains (hereafter called "genotypes"), including dispersal propensity, resource- and density-dependent dispersal, phenotypic specialization, and growth rate (fig. 1). Second, these characterized genotypes were separately introduced in experimental two-patch microcosms exposed to different regimes of spatial and temporal variability of resources and followed over 5 weeks (~200 generations). First, we expected that metapopulation dynamics would differ as a result of intraspecific variation in dispersal-related traits (Leimar and Norberg 1997; Gibert 2016). We also predicted that genotypes with traits enhancing dispersal would generate more homogeneous metapopulations than genotypes with reduced dispersal ability (Clobert et al. 2009; Cote et al. 2017). Second, we expected environmental variability to affect metapopulation dynamics as a result of differences in patch quality and therefore population growth. Temporal variability in environmental conditions, through its effect on population growth, should increase the temporal variability of metapopulation size compared with stable environmental conditions. In contrast, metapopulations should show higher spatial variability in local population sizes under spatially variable environmental conditions. Finally, we expected the dynamics of these simple experimental metapopulations to vary depending on the interaction between the characteristics of genotypes and the environmental context. In particular, specialized dispersal strategies (e.g., high dispersal rate, morphological specialization for dispersal) might buffer the effects of environmental variability on metapopulation dynamics.

Methods

Study Organism

The study organism *Tetrahymena thermophila* is a freshwater ciliate commonly used in experimental ecology and

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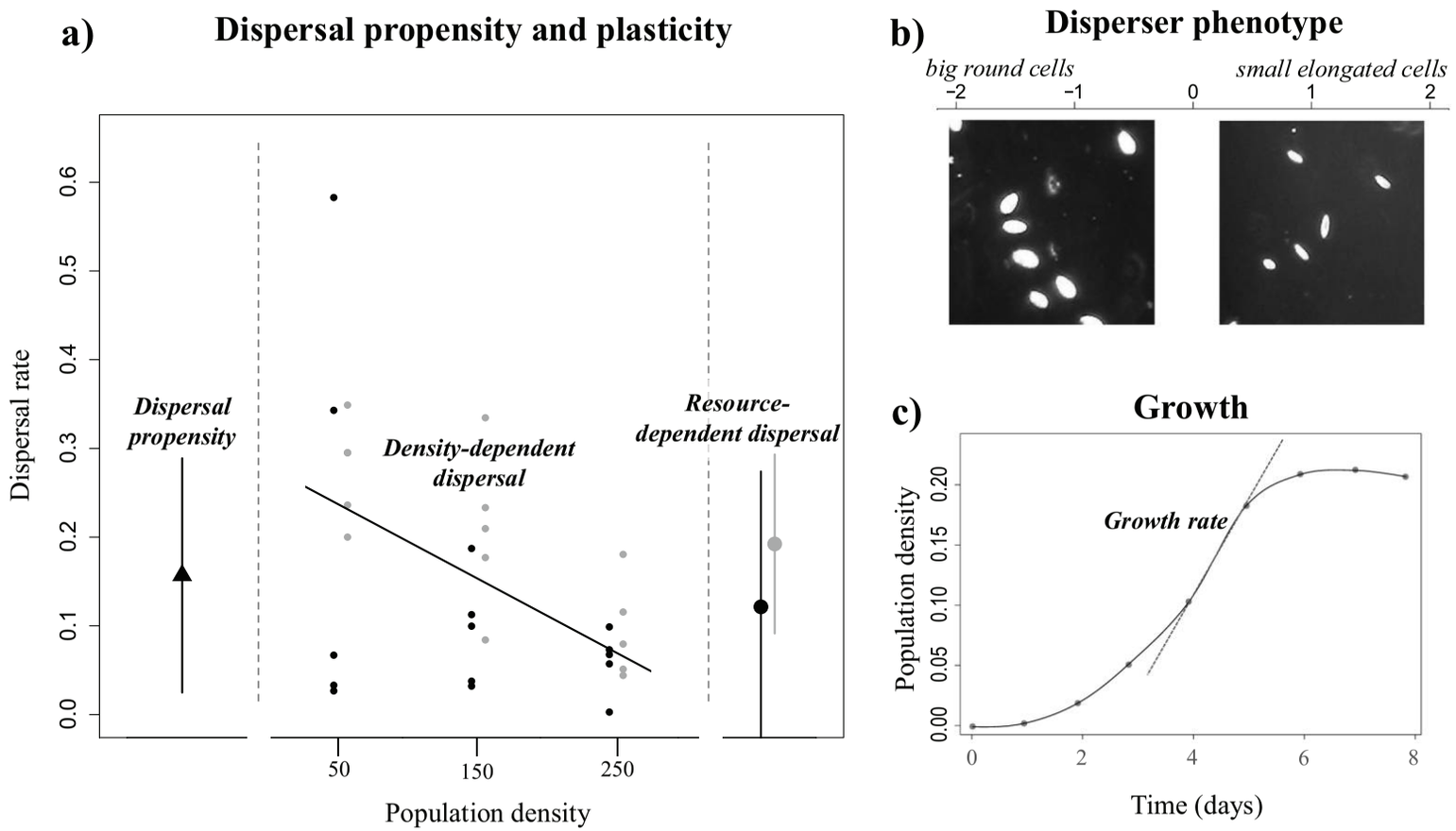

Figure 1: Quantification of dispersal propensity, resource- and density-dependent dispersal, phenotypic specialization, and growth rate of *Tetrahymena thermophila* genotypes. *a*, From a reaction norm experiment we quantified dispersal rate along two environmental factors in a full-factorial design (population density and resource concentration). For each genotype, we estimated dispersal propensity (mean dispersal rate over all densities and resource conditions), density-dependent dispersal (slope of the relationship between population density and dispersal rate, pooling together the two resource conditions), and resource-dependent dispersal (effect of resource availability on dispersal rate; i.e., dispersal rate under resource depletion [in gray] minus the dispersal rate at standard resource concentration [in black], pooling together the three population densities). Gray and black points respectively represent dispersal rates under low- and high-resource concentrations. For dispersal propensity and resource-dependent dispersal, mean ± SD are shown. *b*, The degree of phenotypic specialization of dispersers ("disperser phenotype") over all environmental conditions was quantified as cell elongation versus size following Jacob et al. (2016*b*) as scores on a principal component analysis of size and elongation of disperser cells. This metric increases when cells are small and elongated and decreases when cells are bigger and less elongated (Jacob et al. 2016*b*; picture adapted from Fjerdingstad et al. 2007). *c*, The growth rate of each genotype was quantified by monitoring population growth from a small number of cells. The tangent line illustrates population growth rate as computed using the gcFit function in the R package grofit.

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evolution (Pennekamp et al. 2014; Altermatt et al. 2015; Fronhofer and Altermatt 2015; Jacob et al. 2015*b*, 2016*a*, 2016*b*, 2017). Clonally reproducing isogenic strains are typically maintained at 23°C in synthetic liquid growth medium (2% Difco proteose peptone, 0.2% yeast extract) and propagated once a week by transferring 10 μL (i.e., ~100 cells) into fresh medium. Here we used six genotypes originally sampled in North America by P. Doerder that are available at the Tetrahymena Stock Center (table S1; tables S1–S3 are available online; see Pennekamp et al. 2014; Jacob et al. 2017).

Experiments

The experimental procedure consisted of two steps, as described below. First, we quantified dispersal-related phenotypic variability among six genotypes of *T. thermophila*. Second, we submitted those characterized genotypes to four environmental variability regimes in two-patch microcosms, allowing us to quantify the relative importance of among-genotype differences and environmental variability for the dynamics of simple experimental metapopulations.

Experiment 1: Quantification of Genotype-Specific Dispersal Strategies and Related Phenotypic Traits. Our available stock of isogenic lines strongly differ in their phenotypic and life-history traits as previously measured in standard resource conditions (Fjerdingstad et al. 2007; Pennekamp et al. 2014; Jacob et al. 2015*b*, 2016*a*, 2016*b*, 2018). We extended this characterization by quantifying dispersal decisions and related phenotypic traits using a standard reaction norm approach on six genotypes (table S1; see Pennekamp et al. 2014; Jacob et al. 2017). We used connected microcosms consisting of two habitat patches (1.5-mL microtubes) connected by a corridor (silicone tube, 4 mm internal diameter, 2.5 cm long, meaning 10% of the total volume of the two-patch microcosms; Chaine et al. 2010; Pennekamp et al. 2014; Jacob et al. 2015*b*, 2016*b*). We quantified dispersal strategies along two environmental factors in a replicated full-factorial design: population density (three levels: 50,000, 150,000 and 250,000 cells/mL; see Pennekamp et al. 2014; Jacob et al. 2016*b*) and habitat quality (two conditions: a standard concentration and a low-resource treatment with nine times fewer resources, resulting in growth rates 22.68 ± 10.83 (mean $\pm$ SE) times lower compared with the standard condition).

Both this initial quantification of dispersal strategies and the metapopulation dynamics experiment (see below) were performed using an agar-based nutrient system. Different concentrations of resources were initially placed in 100 μL of 1.5% agar at the bottom of the microtubes. Once the agar solutions solidified, tubes were filled with water. This method limits the homogenization of nutrients between patches observed in water-based nutrient solutions and thus allowed us to generate spatial heterogeneity of resources that is still visible after 4 days (nutrients are naturally colored).

To quantify dispersal strategies, five replicates of each genotype were placed in the "start patch" of standard two-patch systems for each combination of cell density and resource treatments (three densities × two levels of resources; see above), while the other patch (hereafter called the "target patch") was initially free of cells and filled with standard resource concentration. Dispersal was allowed for 5 h (Pennekamp et al. 2014; Jacob et al. 2016*a*), and we used automatic analysis of digital pictures taken under dark-field microscopy (Axio Zoom V16; Zeiss) to quantify population sizes and cell morphology in the start (residents) and target (dispersers) patches (Pennekamp and Schtickzelle 2013; Pennekamp et al. 2014; Jacob et al. 2015*b*, 2016*b*). As illustrated in figure 1, for each genotype we quantified dispersal propensity, density-dependent dispersal, resource-dependent dispersal, disperser phenotype, and growth rate. Dispersal propensity is defined as the mean dispersal rate over all environmental conditions (i.e., three densities × two resources conditions), indicative of the genotype's general tendency to disperse. Density-dependent dispersal is the slope of the relationship between population density and dispersal rate, pooling together the two resource concentrations, meaning, for instance, that negative values denote a tendency to preferentially leave low-density patches. Resource-dependent dispersal is the effect of resource availability on dispersal rate, quantified as the dispersal rate under resource depletion minus the dispersal rate at standard resource concentration (pooling the three population densities). Genotypes increasing their dispersal rate when resources are depleted are characterized by positive values of resource-dependent dispersal, while those decreasing dispersal rate when resources are depleted show negative resource-dependent dispersal. Disperser phenotype is cell elongation versus size following Jacob et al. (2016*b*), as scores of a principal component analysis (PCA) on size and elongation of disperser cells. This metric increases when cells are small and elongated and decreases when cells are bigger and less elongated (Jacob et al. 2016*b*). We calculated this metric because in *T. thermophila*, small and elongated cells are usually specialized for long-distance movements and show greater swim speed and straighter movements (Nelsen 1978; Fjerdingstad et al. 2007; Schtickzelle et al. 2009; Pennekamp et al. 2014; Jacob et al. 2016*b*). Finally, growth rate was quantified by monitoring population growth from a small number of cells in single unconnected microtubes (absorbance measurements at 550 nm every day for 1 week; growth rate computed using the gcFit function in the R package grofit). Preliminary tests revealed that growth rate differed among genotypes ($F_{5,42} = 7.59$, $P < .001$) and along resource concentration ($F_{1,42} = 5.65$, $P = .02$) but that genotypes did not significantly differ in their response to

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resource concentration (genotype × resource interaction: $F_{5,42} = 0.17$, $P = .97$). We therefore used growth at standard resource concentration as our measure of genotypes' growth rate in all analyses.

Experiment 2: Metapopulation Dynamics under Environmental Variability. The experimental system of simplified metapopulations consisted of the same two-patch microcosms as used in experiment 1 (see above). For each of the six genotypes and four environmental variability regimes we constructed five experimental systems, resulting in a total of 120 two-patch microcosms (six genotypes × four environmental variability regimes × five replicates; initial density, 50,000 cells/mL). Twice a week for 5 weeks (~200 generations) the size of local populations was quantified through picture analysis, and 10% of each local population was transferred into the corresponding patch of a new two-patch microcosm with fresh agar-based nutrients (see above). The spatial/temporal variability of resources was manipulated under four environmental variability regimes, which were set up in order to maintain equal quantities of resources among treatments at the two-patch microcosm level over time. The homogeneous regime consisted of metapopulations with half of standard resource concentration in each patch. Temporal variability was set up with an alternation of depleted and standard resource concentration in the two patches twice a week (i.e., ~20 generations), with the two patches containing equal resource conditions. Spatial variability consisted of one patch with low-resource concentration and the other at standard concentration, with fixed spatial distribution of resources over time. Finally, spatiotemporal variability was similar to spatial variability but inverting the patch resources twice a week, leading to regular and predictable spatiotemporal variability of resources.

From local population sizes estimated twice a week we computed three descriptors of the dynamics of these two-patch microcosms: metapopulation size (sum of local population sizes at each time), spatial variability in population size (coefficient of variation of local population sizes at each time; R packages cvar and BioStatR; Bertrand and Maumy-Bertrand 2010), and temporal variability in metapopulation size (coefficient of variation of metapopulation size through time).

Finally, we reiterated the quantification of dispersal traits at the end of the experiment to test for evolution of genotypes' traits. As we found no effect of environmental variability regimes on the dispersal traits of genotypes after ~200 generations in the two-patch microcosms (table S2), we used initial phenotypic values in all analyses.

Statistical Analyses. The architecture of genotypes' traits measured in experiment 1 was explored using Pearson correlation coefficients, and their organization in dispersal syndromes was quantified using PCA (dudi.pca function, R package ade4). The contribution of variables to each principal component (fig. 2) was determined by comparing the observed contributions to a uniform distribution using the fviz_contrib function (R package factoextra). Since growth rate is expected to be an important driver of ecological dynamics, we included it as a separate trait in the analyses (see below) and thus excluded it from the PCA of dispersal-related traits.

We tested for the influence of genotype identity and environmental variability on metapopulation dynamics using linear models (lm function, R package stats). Following De Roissart et al. (2015), we used the mean of metapopulation dynamic descriptors over time as dependent variables in models (i.e., metapopulation size and spatial variability in population size; temporal variability in metapopulation size being already computed over time; see above) over time as dependent variables in models, and explanatory factors were environmental variability treatments, genotype identity, and their interaction. Following a backward-selection procedure, we removed explanatory factors and their interaction from the models when nonsignificant at the $P \leq .05$ level. Conducting analyses separately through time step led to qualitatively similar conclusions (fig. S1, available online; table S3). To estimate the relative contribution of each explanatory factor to metapopulation dynamics, we conducted variance partitioning analyses using calc.relimp with the lmg metric (R package relaimpo; Lindeman et al. 1980; Groemping 2006).

Following the above-described analyses that aimed at quantifying the importance of intraspecific variability and environmental variability for metapopulation dynamics, we more specifically tested the importance of variability in dispersal-related traits among genotypes compared with environmental variability for ecological dynamics. To do so, we used linear models followed by variance partitioning, as described above, to test the effect of environmental variability treatments, dispersal syndromes (summarized in PCA axes; see fig. 2), genotype-specific growth rates, and their interaction for metapopulation size and variability. Quadratic effects were initially included but not presented in the table because they were not significant.

Results

Architecture of Dispersal Strategies

From the multiple traits we quantified in this study, we first examined the patterns of covariation between traits using Pearson correlations. We found that dispersal propensity was correlated to dispersal phenotype and resource-dependent dispersal (fig. 2*a*), meaning that the more dispersive genotypes showed specialized dispersal phenotypes and increased

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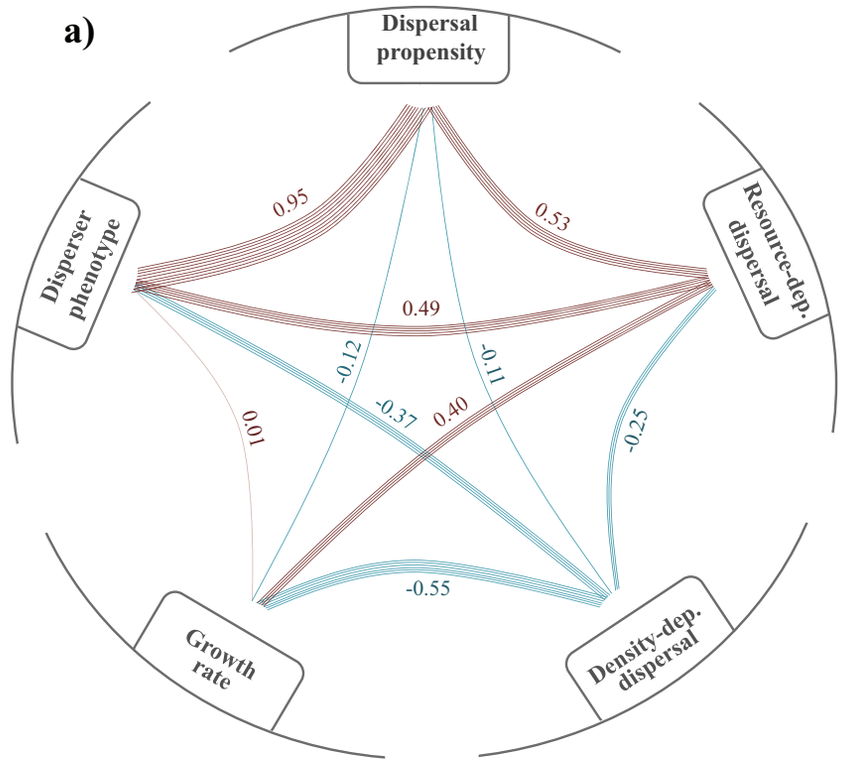

b) Components of dispersal syndromes

	PC 1 Dispersal specialization and resource-dependency	PC 2 Density-dependent dispersal
Dispersal propensity	**0.91**	0.35
Disperser phenotype	**0.95**	0.08
Resource-dependent dispersal	**0.73**	-0.01
Density-dependent dispersal	-0.44	**0.89**

Figure 2: Architecture of traits in *Tetrahymena thermophila* in the six genotypes used in this study. *a*, Correlations among pairs of traits. Pearson correlation coefficients are shown, with the width of the lines connecting traits proportional to the strength of correlations (red for positive correlation, blue for negative correlations). *b*, Organization of dispersal-related traits in dispersal syndromes. The contributions of variables to each principal component (highlighted in bold) were defined compared with uniform distribution of contributions using the fviz_contrib function in the R package factoextra. The first axis comprises 61.4% of original variance, and the second 23.1%. Since growth rate is expected to be an important driver of population dynamics, it was excluded from the principal component analysis and included as a separate trait in the analyses (see "Methods").

their tendency to disperse when local resources are depleted. On the other side, genotypes' growth rate and density-dependent dispersal were weakly correlated with the three other traits and correlated negatively with each other (fig. 2*a*). This means that genotypes with the highest growth rate exhibited negative density-dependent dispersal. Then we summarized the variance in these dispersal-related traits using PCA, while excluding growth rate from the PCA to include it as a separate trait in the analyses (see "Methods"). The PCA provided evidence for two dimensions of dispersal syndromes (fig. 2*b*; 84.5% of total variance explained by the first two axes; 61.4% on the first axis and 23.1% on the second). The first axis comprised dispersal propensity, disperser phenotype, and resource-dependent dispersal, which generally

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describe a genotype's dispersal specialization and resource dependency (fig. 2*b*). When increasing values on this first axis, genotypes show higher dispersal propensity, display more specialized dispersal phenotype (small and elongated cells), and preferentially leave poor patches compared with rich ones. The second axis includes density-dependent dispersal, with higher axis values for genotypes that have a positive density-dependent dispersal (meaning that dispersal increases when density increases).

Drivers of Metapopulation Dynamics

As expected, environmental variability was an important driver of the dynamics of experimental two-patch microcosms (fig. 3; table 1, pt. A). Metapopulation size was on average the highest in a homogeneous environment, followed by spatiotemporally and spatially variable environments, and the lowest under temporally variable environments (fig. 3). Spatial variability in population sizes was higher under spatial and spatiotemporal environmental variability than under temporally variable and homogeneous environments (fig. 3). Finally, we found higher temporal variability in population size under temporal environmental variability compared with a homogeneous environment, with intermediate values under spatial and spatiotemporal environmental variability (fig. 3).

Although the environmental variability regimes were of great importance as developed above, their effects on the dynamics of experimental two-patch microcosms differed among genotypes. Furthermore, differences among genotypes were overall more important for these dynamics than environmental variability treatments in our experiment (table 1, pt. A). In particular, we found 73% of variance in metapopulation size explained by genotype and 4% by the interaction between environmental variability and genotype, while 19% was attributed to environmental variability (total variance explained, 96%; table 1, pt. A). Regarding spatial variability of population size, environmental variability and genotype identity appeared to be of similar importance: 24% of spatial variability in population size was attributed to genotype, 34% to environmental variability, and 22% to the genotype × environmental variability interaction (total variance explained, 80%; table 1, pt. A). Finally, 39% of temporal variability in metapopulation size was explained by environmental variability per se, and respectively 52% and 3% was attributed to genotype and the genotype × environmental variability interaction (total variance explained, 94%; table 1, pt. A).

We then tested to what extent the effects of genotype on metapopulation dynamics result from variability in dispersal-related traits. We found that dispersal-related traits (summarized in PCA axes as described above; see fig. 2) play an important role for the dynamics of two-patch microcosms, affecting metapopulation size and the spatial and temporal variability in metapopulation size (fig. 3; table 1, pt. B). Metapopulation size increased with dispersal specialization and resource dependency (PC1; 6% of variance explained) and density-dependent dispersal (PC2; 12% of variance explained; fig. 3; table 1, pt. B), while growth rate explained 32% of metapopulation size. Interestingly, both the dispersal strategies of genotypes and environmental variability regimes affected metapopulation size, but the interactions between environmental variability and dispersal-related traits appeared nonsignificant (table 1, pt. B).

In contrast to metapopulation size, we found significant interactions between environmental variability regime and dispersal strategies on spatial variability in population size (fig. 3; table 1, pt. B). When resources varied spatially (i.e., spatial and spatiotemporal variability regimes), an increase in dispersal specialization and resource dependency (PC1) was associated with a reduced spatial variability of population size (fig. 3). We also found a significant interaction between environmental variability and density-dependent dispersal (PC2) on population spatial variability (table 1, pt. B): positive density-dependent dispersal was associated with amplified effects of spatiotemporal environmental variability for population spatial variability, while negative density-dependent dispersal was associated with reduced population spatial variability.

Finally, temporal variability in metapopulation size appeared to be mostly driven by genotype growth rate, with 26% of total variance attributed to growth rate and 39% to environmental variability regimes (table 1, pt. B).

Discussion

Intraspecific variability can be considerable, often equaling or even exceeding interspecific variability (Des Roches et al. 2018; Raffard et al. 2019). Since phenotypic traits not only are the target of selection but can influence ecological dynamics (Hendry 2017), assessing whether and to what extent phenotypic variability matters for ecological and evolutionary dynamics compared with environmental variability is crucial (Des Roches et al. 2018; Raffard et al. 2019). Here we experimentally demonstrated for the first time that differences among genotypes within a species may be at least as important as spatial and temporal variability in habitat quality for metapopulation dynamics in simple two-patch microcosms. Furthermore, we showed that a great proportion of this intraspecific variability effect results from differences among genotypes in dispersal syndromes.

Architecture of Dispersal Syndromes

Dispersal-related traits organize into two strategies in *Tetrahymena thermophila*. A first dimension reflects dispersal

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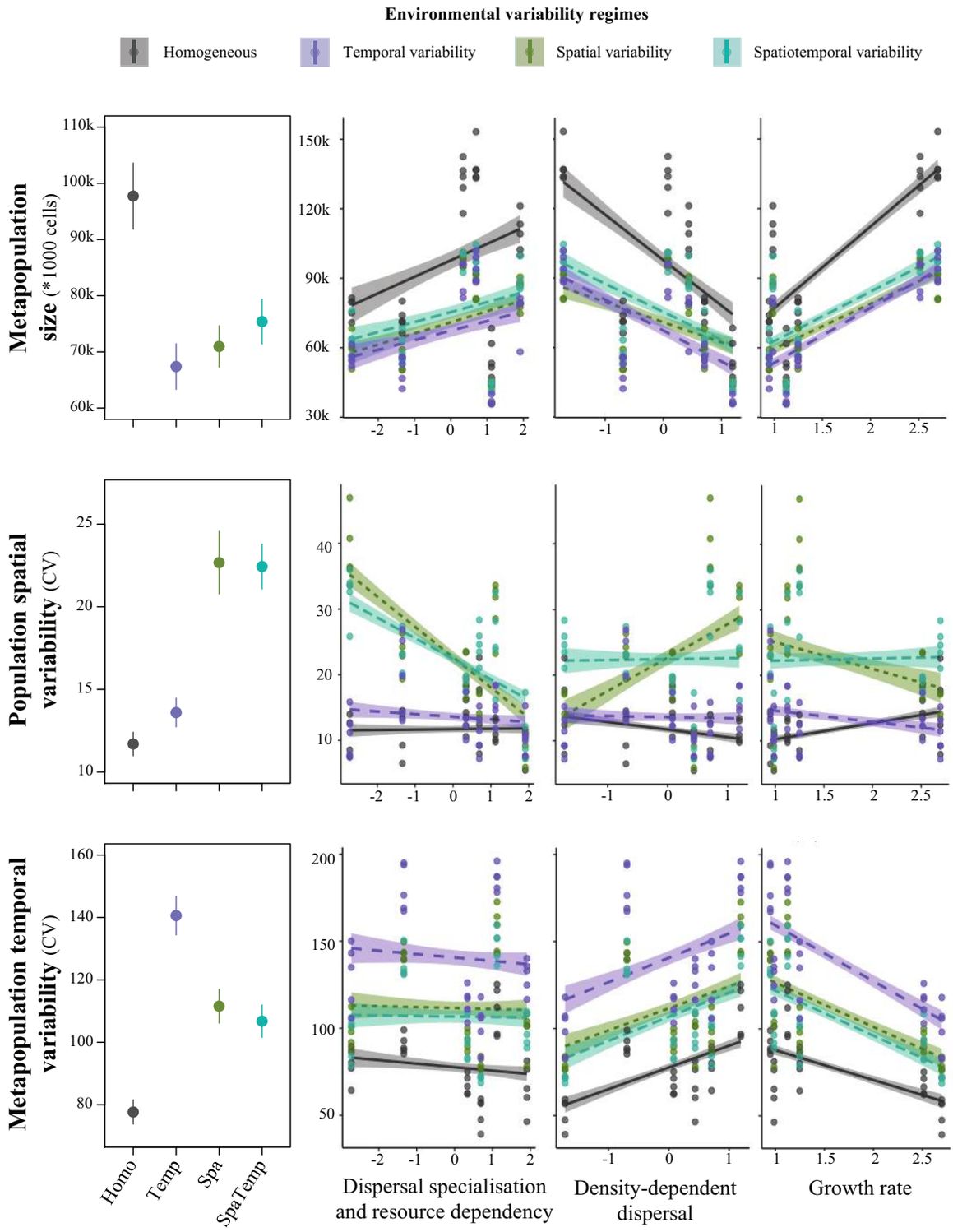

Figure 3: Dispersal syndromes and environmental variability affect metapopulation dynamics. Colors correspond to environmental variability regimes. Left panels show the effects of environmental variability regimes on average values of the dynamics of two-patch microcosms (i.e., all genotypes; mean ± SE). In right panels, lines show predicted values from linear regressions of metapopulation variables in the function of genotypes' dispersal strategies and growth rate. Colored areas represent the 50% confidence interval of the regressions. CV = coefficient of variation.

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Table 1: Statistics of the drivers of the dynamics of simple experimental metapopulations

	Metapopulation size			Spatial variability			Temporal variability		
	F (df)	*P*	R^2	*F* (df)	*P*	R^2	*F* (df)	*P*	R^2
Part A:									
Genotype	152.63 (5, 96)	<.001	.73	3.28 (5, 96)	.009	.24	20.68 (5, 96)	<.001	.52
Environmental variability regime	11.99 (3, 96)	<.001	.19	43.94 (3, 96)	<.001	.34	21.87 (3, 96)	<.001	.39
Genotype × environmental variability	5.90 (15, 96)	<.001	.04	6.65 (15, 96)	<.001	.22	2.77 (15, 96)	.001	.03
Part B:									
PC1: dispersal specialization and resource dependency	14.47 (1, 113)	<.001	.06	.05 (1, 104)	.817	.13			
PC2: density-dependent dispersal	6.65 (1, 113)	.011	.12	.01 (1, 104)	.948	.01			
Growth rate	70.57 (1, 113)	<.001	.32	2.75 (1, 104)	.114	.01	84.00 (1, 115)	<.001	.26
Environmental variability regime	24.22 (3, 113)	<.001	.19	4.13 (3, 104)	.008	.34	41.69 (3, 115)	<.001	.39
Environmental variability × PC1				16.13 (3, 104)	<.001	.12			
Environmental variability × PC2				8.27 (3, 104)	<.001	.07			
Environmental variability × growth rate				2.83 (3, 104)	.042	.03			

Note: Part A shows the quantification of the importance of genotype (intraspecific variability), environmental variability regime, and their interaction on metapopulation dynamics descriptors. Part B shows the contribution of dispersal syndromes, growth rate, and environmental variability regimes to variability in the dynamics of two-patch microcosms. Nonsignificant interactions were removed from the models following a backward-selection procedure. PC = principal component.

specialization comprising multiple correlated traits (i.e., dispersal propensity, phenotypic specialization for dispersal, and the ability to preferentially leave poor patches compared with rich ones), in agreement with previous studies that defined dispersal specialization as the combination of multiple traits organized in a syndrome, beyond simply an increased tendency to disperse (Clobert et al. 2009; Stevens et al. 2014; Cote et al. 2017). The second dimension includes density-dependent dispersal, a component of dispersal strategies that appears to covary with growth rate (fig. 2*a*). High growth rate is associated with a tendency to decrease dispersal rate when density increases (i.e., they preferentially stay in more crowded patches), while low-growth-rate genotypes show positive density-dependent dispersal, preferentially leaving high-density patches. This suggests that high-growth-rate genotypes might use density as a cue of habitat quality, as suggested in previous studies (McPeek and Holt 1992; Poethke et al. 2011; Pennekamp et al. 2014; Jacob et al. 2016*b*), preferentially staying in large and dense populations. Furthermore, we found that growth rate was decoupled from dispersal specialization (fig. 2*a*). Although dispersal has been repeatedly found to correlate with traits linked to reproduction (e.g., Duckworth and Badyaev 2007; Stevens et al. 2014; Bonte and Dahirel 2017; reviewed in Ronce and Clobert 2012), the way dispersal-related traits covary and the form of the resulting dispersal syndromes can be shaped by the environmental context and may thus differ among populations and species (Legrand et al. 2016; Cote et al. 2017). This points out the importance of investigating the occurrence and drivers of variability in dispersal syndromes for our understanding of dispersal evolution.

Genotype-Dependent Metapopulation Dynamics

As expected since resources affect growth rate, the environmental variability treatments consisting of spatial and spatiotemporal variability of resources increased spatial variability in population size (fig. 3). Beyond these environmental variability effects on metapopulation dynamics, a major finding of this experimental study is that variability among genotypes may explain as much variation in the dynamics of experimental two-patch microcosms as environmental variability (fig. 4*a*). Furthermore, these differences among genotypes interact with environmental variability in driving these dynamics (fig. 4*a*). While environmental variability is probably the most intuitive driver of metapopulation dynamics, our results provide experimental evidence for a potential great importance of intraspecific variability for ecological dynamics. Furthermore, the effects of environmental variability for metapopulation dynamics differ among genotypes. The large intraspecific variability found in numerous organisms (Albert et al. 2010; Violle et al. 2012) may therefore also be an important factor driving metapopulation dynamics (Bolnick et al. 2003; Cote et al. 2017).

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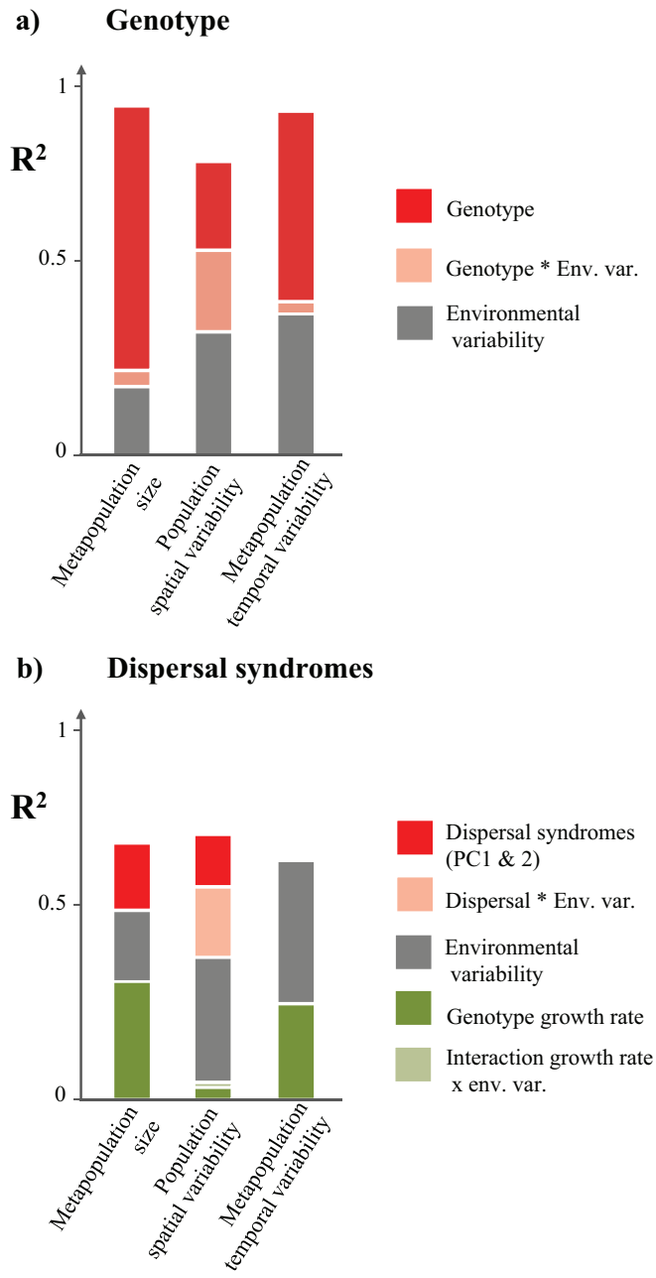

Figure 4: Relative contribution of the drivers of the dynamics of simple experimental metapopulations. *a*, Contribution of intraspecific variability (i.e., genotype), environmental variability regime, and their interaction on metapopulation dynamics descriptors. *b*, Contribution of dispersal syndromes, growth rate, and environmental variability regimes to variability in the dynamics of two-patch microcosms. The size of colored bars is proportional to the R^2 of the different potential drivers. Associated statistics are provided in table 1.

Homogeneous environments result in larger metapopulation sizes compared with spatially and/or temporally variable environments for all genotypes. Although our experiment was designed to ensure that all two-patch microcosms would contain an identical total quantity of resources over time, the relationship between resources and growth rate in single nonconnected tubes was nonlinear: increasing resources from low resources to half of standard significantly increased growth rate ($F_{1,34} = 9.93$, $P = .003$), but further increasing to standard resource concentration did not significantly increase growth rate ($F_{1,34} = 0.005$, $P = .95$). Consequently, although all environmental variability treatments contained the same quantity of resources at the two-patch microcosm level, such a nonlinear relationship

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may lead to higher growth in homogeneous microcosms compared with other regimes and thus likely explains the higher metapopulation size found in homogeneous environments (fig. 2). However, since the effects of resource concentration on growth rate did not significantly differ among genotypes (see "Methods"), this nonlinear relationship would not affect our conclusions regarding genotype and genotype × environmental variability interaction effects on metapopulation dynamics.

Dispersal Syndromes and Environmental Variability Drive Metapopulation Dynamics

The consequences of dispersal for spatially structured populations are predicted to differ depending on the dispersal-related traits involved (Bowler and Benton 2005; Clobert et al. 2009; Jacob et al. 2015*a*). Here we found that variability in dispersal syndromes accounted for one-fifth to one-third of variability in the dynamics of experimental metapopulations (fig. 4*b*). As anticipated, given the importance of the dispersal process in metapopulation dynamics (Ronce 2007; Clobert et al. 2012), this study demonstrates that variability in dispersal syndromes may be responsible for more than one-third of the variability in simple experimental metapopulations. Interestingly, however, dispersal syndromes and growth rate explained a lower percentage of variance in metapopulation dynamics than genotypes did (fig. 4). This result highlights that other phenotypic traits not measured in this study might play a significant role in driving metapopulation dynamics, such as cooperation strategy (Schtickzelle et al. 2009; Chaine et al. 2010; Jacob et al. 2016*b*), information use abilities (Jacob et al. 2015*b*, 2017, 2018), resistance to starvation (Fjerdingstad et al. 2007), or ecological specialization (Jacob et al. 2018).

Increased dispersal movements are predicted to homogenize metapopulations, thus reducing spatial variability in population size (Briggs and Hoopes 2004; Vogwill et al. 2009; Abbott 2011; Wang et al. 2015). Accordingly, we found that increased dispersal propensity coupled with phenotypic specialization and the ability to preferentially leave poor patches reduces spatial variability in population size (fig. 3). Interestingly, dispersal generally incurs costs arising from increased movements toward poor habitats in source-sink contexts or mortality rates during movement (Abbott 2011; Bonte et al. 2012). Consequently, we would expect increased dispersal propensity alone without phenotypic specialization or plasticity in dispersal decisions to have negative effects on metapopulation size. On the contrary, here we found that increasing dispersal specialization and resource dependency led to increased metapopulation size (fig. 2). This pattern might result from this coupling of phenotypic specialization for dispersal and context-dependent dispersal, which is expected to increase the success of movements between patches and thus improve metapopulation persistence (Edelaar et al. 2008; Clobert et al. 2009; Jacob et al. 2015*a*). Furthermore, we found that positive density-dependent dispersal was associated with decreased metapopulation size and increased spatial variability of population size under spatiotemporal environmental variability (fig. 3; table 1, pt. B). Theoretical work predicts negative density-dependent dispersal to be selected in spatially heterogeneous environments that are temporally stable, while spatiotemporal variability should favor positive density-dependent dispersal (Rodrigues and Johnstone 2014). Overall, these results highlight the importance of experimentally quantifying the consequences of different architectures of dispersal syndromes for metapopulation dynamics under different degrees and directions of environmental changes.

Conclusion

Dispersal is a core process driving population dynamics in spatially structured environments (Clobert et al. 2012). Improving our ability to predict the dynamics and persistence of populations facing environmental changes crucially requires accounting for the complexity of the dispersal process (Clobert et al. 2009; Travis et al. 2012; Cote et al. 2017). Considering not only mean values of phenotypic traits but variance and covariance between the multiple phenotypic and life-history traits related to dispersal is an important challenge (Laughlin and Messier 2015; Cote et al. 2017). Here we provide the first experimental evidence for the role played by intraspecific variability in dispersal syndromes in driving metapopulation dynamics. Variability in dispersal decisions, related phenotypic traits, and their organization in strategies might indeed profoundly modify how organisms respond to environmental changes. Investigating the conditions favoring the evolution of different dispersal syndromes, their coexistence, and the metapopulation consequences of a diversity of competing dispersal strategies thus represent a central future step. Intraspecific variability of dispersal syndromes furthermore appeared to be important for metapopulation dynamics as a central aspect of the environment that is resource availability in our simple experimental metapopulations.

To reach this conclusion, we used simple laboratory microcosms, that is, highly controlled and replicated experimental systems providing a unique opportunity to study the causality of tested factors (Jessup et al. 2004; Benton et al. 2007), especially in the context of dispersal (Haddad 2012). These simplified worlds often lack the necessary realism to fully explain natural patterns (Srivastava et al. 2004), being by definition of extreme simplicity compared with the plethora of environmental factors that play in nature. The degree to which intraspecific variability influences metapopulation dynamics is consequently expected to change

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between our specific experimental situation and a natural system, the challenge being to know how much. Furthermore, here we separately quantified the effects of isolated genotypes and phenotypes for metapopulation dynamics, a scenario that contrasts with many natural populations that are genetically diversified (with the notable exception of habitats recently colonized by a few individuals). Future experiments are now required to determine how genetic diversity affects ecological dynamics and to identify the environmental conditions that are required to maintain local polymorphism in dispersal syndromes. Nonetheless, by highlighting the high importance of intraspecific variability in metapopulation dynamics in simple microcosms, our study should help build and calibrate complementary theoretical models (Cote et al. 2017; Jacob et al. 2018). It should also stimulate future research effort required to assess the degree of generality of our results in more complex environments and landscape configurations. Finally, the present experiment provides evidence that the integration of variability in dispersal syndromes would improve models forecasting population and species response to environmental changes (Travis et al. 2013; Urban et al. 2013).

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Data and Code Availability

The data supporting the findings of this study are available in the Dryad Digital Repository (https://doi.org/10.5061/dryad.r63jf31; Jacob et al. 2019).

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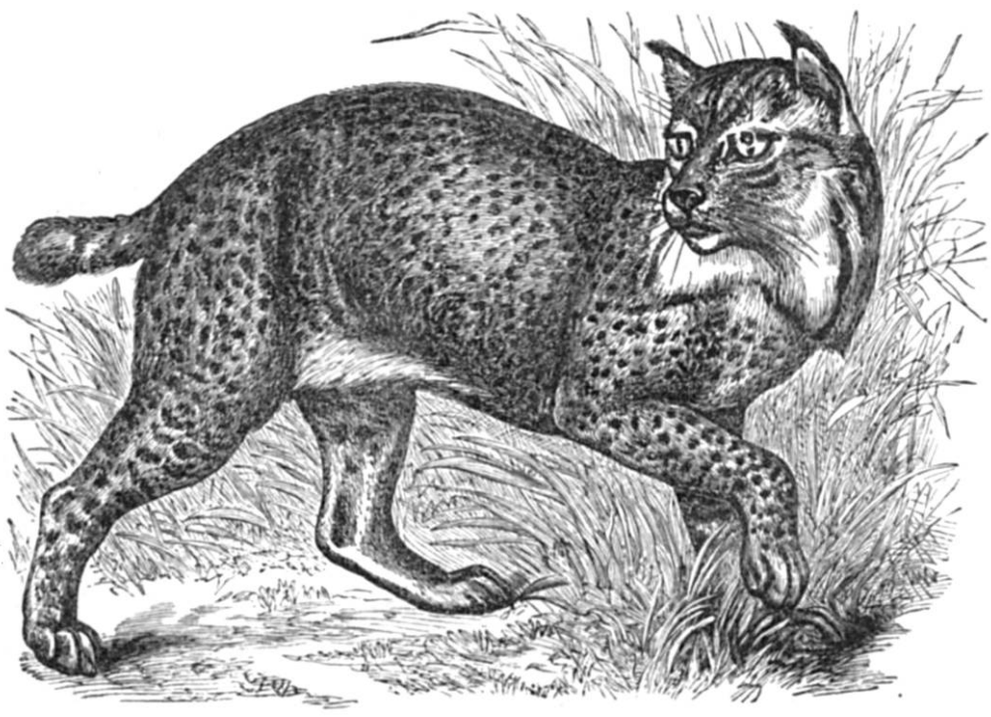

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