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Resident-Disperser Differences and Genetic Variability Affect Communities in Microcosms

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ABSTRACT: Dispersal is a key process mediating ecological and evolutionary dynamics. Its effects on the dynamics of spatially structured systems, population genetics, and species range distribution can depend on phenotypic differences between dispersing and nondispersing individuals. However, scaling up the importance of resident-disperser differences to communities and ecosystems has rarely been considered, in spite of intraspecific phenotypic variability being an important factor mediating community structure and productivity. Here, we used the ciliate *Tetrahymena thermophila*, in which phenotypic traits are known to differ between residents and dispersers, to test (i) whether these resident-disperser differences affect biomass and composition in competitive communities composed of four other *Tetrahymena* species and (ii) whether these effects are genotype dependent. We found that dispersers led to a lower community biomass compared with residents. This effect was highly consistent across the 20 *T. thermophila* genotypes used, despite intraspecific variability in resident-disperser phenotypic differences. We also found a significant genotypic effect on biomass production, showing that intraspecific variability has consequences for communities. Our study suggests that individual dispersal strategy can scale up to community productivity in a predictable way, opening new perspectives to the functioning of spatially structured ecosystems.

Keywords: dispersal, intraspecific variability, community, ecosystem, *Tetrahymena*.

Introduction

Dispersal is a complex and key process mediating ecological and evolutionary dynamics in spatially structured landscapes (Mouquet and Loreau 2003; Bowler and Benton 2005; Ronce 2007; Edelaar et al. 2008; Clobert et al. 2012; Edelaar and Bolnick 2012). Spatially structured communities and ecosystems strongly rely on dispersal rates (i.e., the proportion of dispersing individuals; Loreau et al. 2003*b*) as dispersal mediates species interactions and nutrient fluxes, which in turn modify community composition and ecosystem functions (Loreau et al. 2003*a*; Harvey et al. 2016). Although metacommunity and metaecosystem theories generally assume dispersing and nondispersing individuals to be phenotypically similar, residents and dispersers are often found to strongly differ in multiple phenotypic traits (Bowler and Benton 2005; Clobert et al. 2009). The willingness and ability of organisms to disperse at each of the three dispersal phases (emigration, transience, and immigration) are indeed often associated with specific life histories, behaviors, morphologies, or physiologies (Clobert et al. 2009). Such phenotypic differences between dispersers and residents have been described in many taxa (Clobert et al. 2009; Le Galliard et al. 2012; Stevens et al. 2014; Legrand et al. 2015). For example, it has been shown that dispersers are generally larger than residents in freshwater fish (Comte and Olden 2018) and more active in rodents (Le Galliard et al. 2012).

Dispersal-related traits can vary between (Stevens et al. 2014; MacLean and Beissinger 2017) and within (Bowler and Benton 2005; Legrand et al. 2016; Cote et al. 2017*a*) species, and the origin of this variation can depend on both evolutionary and ecological factors. For instance, genetic covariances explain the link between dispersal and reproductive traits in wing-dimorphic crickets (reviewed in Zera and Brisson 2012; Saastamoinen et al. 2018). In toads, the interaction between landscape matrix composition and predation risk shapes the phenotypic differences between residents and colonizers of empty patches (Winandy et al. 2019). Therefore, variability in genetic composition and/or local environmental conditions (biotic or abiotic) can

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generate variability in resident-disperser differences among populations (Cote et al. 2017*a*). In turn, not only dispersal rate but also the above-mentioned dispersal-related traits can have consequences for ecological dynamics (Jacob et al. 2019). Some studies have shown that differences between residents and dispersers can affect metapopulation dynamics, species interactions, and phenotypic range distribution (Duckworth and Badyaev 2007; Phillips et al. 2010; Shine et al. 2011; Messager and Olden 2019). In ciliate microcosms, dispersal-related traits involving morphological and demographic traits affect metapopulation size and stability (Jacob et al. 2019). The consequences of intraspecific differences between residents and dispersers at the scale of communities and ecosystems have, however, rarely been studied, despite the fact that phenotypic variability within species can affect multiple ecological processes, including predator-prey interactions and interspecific competition (Harmon et al. 2009; Hart et al. 2016; Turcotte and Levine 2016; Hausch et al. 2018). For instance, increasing trait variability (e.g., resource preferences) in weevil species (*Callosobruschus* sp.) affects species coexistence because of resource partitioning (Hausch et al. 2018). Importantly, such intraspecific variability can affect ecological processes as much as species richness (Des Roches et al. 2018; Raffard et al. 2019).

Phenotypic differences between residents and dispersers (and intraspecific variability in the intensity of these differences) could affect species interactions within communities in different ways (Raffard et al. 2022). First, dispersers can differ from residents in their competitive abilities, for instance by displaying a higher aggressiveness (Duckworth and Badyaev 2007; Wolf and Weissing 2012), which may shape interspecific competition strength in colonized habitats, in turn modifying species coexistence (Hart et al. 2016; Turcotte and Levine 2016). Second, dispersing individuals can also differ in diet or trophic position (Cote et al. 2017*b*). For instance, in *Dikerogammarus villosus*—a freshwater amphipod decomposer—dispersers consume more detritus than residents, increasing the decomposition rate of organic material in colonized habitats (Little et al. 2019). Interestingly, the effects can differ between species (Little et al. 2019), suggesting that the effects of dispersal-related traits on community and ecosystem functioning might be species dependent. On top of these examples, differences between residents and dispersers involving functional traits may shape the spatial heterogeneity of communities and ecosystems across landscapes (Raffard et al. 2022).

Here, we tested whether differences between residents and dispersers, as well as intraspecific variability in these differences, affect the biomass production and composition of communities, as expected if residents and dispersers differ in traits of functional importance for communities and ecosystems. We used laboratory microcosms to quantify the effects of dispersers compared with residents, in multiple clonally reproducing isogenic strains (hereafter referred to as "genotypes") of the ciliated protist *Tetrahymena thermophila*, on the biomass production of communities composed of four competing species of the genus *Tetrahymena*. Miniaturized and simplified microcosms, including those using *Tetrahymena* ciliates, are classical model systems for the study of ecological and evolutionary dynamics at different temporal and spatial scales (Jessup et al. 2004; Benton et al. 2007; Pennekamp et al. 2014; Altermatt et al. 2015; Jacob et al. 2017; Larsen and Hargreaves 2020). As a prerequisite to this study, we quantified resident-disperser phenotypic differences and their variability among 20 genotypes of *T. thermophila* for multiple traits: for each genotype, we measured morphological traits (cell size and shape) and demographic parameters (population growth and maximal density) of resident and disperser individuals. Morphology and demography are often found to be correlated with dispersal in this species (Fjerdingstad et al. 2007; Pennekamp et al. 2014; Jacob et al. 2019). These traits are also generally important for species interactions in communities, determining, for instance, metabolic rate and resource uptake, with potential consequences for interspecific interactions and biomass productivity (Brown et al. 2004; Gibert et al. 2017; Tabi et al. 2020). Then, we tested whether residents and dispersers differently affect communities (composition and biomass) in which they were added, while experimentally controlling for initial density. We tested whether the effects of these resident-disperser differences on communities can depend on intraspecific variability by comparing 20 genotypes of *T. thermophila*.

Material and Methods

Study Species

Native of North America, *Tetrahymena thermophila* is a 30–50-μm unicellular eukaryote living in freshwater ponds and streams (Collins 2012; Doerder and Brunk 2012). Twenty isogenic genotypes (strains D1–D20; table S1) were used to assess variability in dispersal-related traits. *Tetrahymena thermophila* displays a particular genetic system where only the macronucleus is expressed and determines the phenotype variability among genotypes, with the micronucleus being perfectly silent and used only to form the new macronucleus during sexual reproduction. Such a particular genetic system makes genetic changes in the macronucleus akin to phenotypic plasticity by somatic selection during asexual phases (Verdonck et al. 2022). All genotypes displayed only clonal reproduction in our culture conditions, since sexual reproduction requires mixing cells with different mating types (i.e., from different genotypes) under strict starvation (Elliott and Hayes 1953; Bruns and Brussard 1974). Cells from different genotypes were kept isolated in standard conditions, propagating them approximately every 10 days by transferring a very small number of cells (~10–15 cells on average) to fresh medium. Cells were maintained in axenic rich liquid growth medium (0.5% Difco proteose peptone, 0.06% yeast extract) at 23°C, and all culture manipulations were performed in sterile conditions under a laminar flow hood.

Quantification of Differences between Residents and Dispersers in Multiple Traits

Dispersal-related traits, as well as their dependency to genotypes, have already been described in microcosms of *T. thermophila* (e.g., Fjerdingstad et al. 2007; Jacob et al. 2019, 2020). Dispersal rates and dispersal-related traits were quantified using standard two-patch systems (Schtickzelle et al. 2009; Pennekamp et al. 2014; Jacob et al. 2020). They consist of two habitats (1.5-mL microtubes) connected by a corridor (4-mm internal diameter, 2-cm-long silicone tube) filled with growth medium. Before the quantification of dispersal, each genotype was grown for 1 week in a 100-mL vial in order to obtain densities high enough to measure dispersal (Jacob et al. 2017, 2019, 2020). Cells from these cultures were used to inoculate five replicated dispersal systems for each genotype, in which we measured dispersal rate and characterized resident and disperser cells. To do so, cells were placed in one patch at a standardized density (40,000 cells/mL) during 30 min of acclimation, and the corridor was then opened to allow cells to disperse for 4 h toward the initially empty neighbor patch. Population growth rate is low enough during such a 4-h time frame in this species to avoid bias in the quantification of dispersal rates (Pennekamp et al. 2014; Jacob et al. 2018). Corridors were then closed to prevent further movements, and a series of traits were quantified for each genotype describing (i) their dispersal rate, (ii) their morphology, and (iii) the demography of both residents and dispersers.

Five samples of 10 μL were pipetted from each of the two patches (for resident and disperser cells) and pictured under dark-field microscopy (Axio Zoom V16, Zeiss) to assess cell density and morphology (averaged over the five samples) using a procedure developed with ImageJ software (Pennekamp and Schtickzelle 2013). First, the dispersal rate for each genotype was calculated as $N_{\mathrm{disp}}/(N_{\mathrm{resi}} + N_{\mathrm{disp}})$, where N_{disp} and N_{resi} are the abundance of dispersers and residents, respectively. Second, two morphological traits, cell size (cell surface area on pictures) and cell elongation (aspect ratio; i.e., ratio of cell major/minor axes), were estimated in both residents and dispersers of each genotype.

Third, demographic traits (i.e., growth rate and maximal population density) of residents and dispersers of each genotype were measured. To do so, ~150 cells (mean volume ± SE: 14.02 ± 1.25 μL) of both residents and dispersers of each dispersal system were separately transferred into 96-well plates (250-μL wells) filled with growth medium, with two technical replicates (averaged in subsequent analyses). Absorbance at 450 nm was recorded every 2 h for 2 weeks using a microplate reader (Infinite 200, Tecan) to quantify population growth. We used a general additive model (R package gam; R Core Team 2013; Hastie 2018) to smooth the observed absorbance measurements to avoid any bias due to slight variability in absorbance measures and fitted logistic growth curves using the package grofit (gcfit function with spline fit; Kahm et al. 2010). Growth rate was then assessed as the maximum slope of population growth, and maximal population density was assessed as the density reached at the plateau of the growth curve (Jacob et al. 2017).

Experimental Communities

Competitive communities were assembled using four competing *Tetrahymena* species to which residents or dispersers of each *T. thermophila* genotype obtained from the first part of the experiment were added (from each dispersal system). A single strain of each competing species was used (*T. americanis* A5, *T. borealis* B8, *T. pyriformis* P4, and *T. elliotti* E5; table S1) to avoid potential differences in competitive interactions due to genetic variability. To assemble communities, we transferred ~150 cells of each of the four competing species (10 μL of cultures previously diluted to 15,000 cells/mL) into 96-well plates (250-μL wells filled with growth medium), and we introduced dispersers/residents from one specific *T. thermophila* genotype (~150 cells; see above). In total, we assembled 200 communities with equal initial abundance of all species: 20 *T. thermophila* genotypes × 2 dispersal statuses (resident and disperser) × 5 replicates (the five dispersal systems used for each genotype; see above). For each replicate, we ran two technical replicates of community dynamics that were averaged for analyses. Absorbance at 450 nm was recorded every 2 h for 2 weeks to quantify the biomass productivity of the communities in the microcosms. Similar to the quantification of the demographic growth of individual *T. thermophila* genotypes (see above), we fitted logistic growth curves to absorbance data and computed biomass production as the maximum slope of community absorbance increase (i.e., the maximal rate of biomass production) and maximal biomass as the maximal absorbance reached by the community.

To quantify the abundance of the five species at the end of the experiment, we performed a one-shot analysis of community composition (day 10, when communities reached the biomass plateau) using flow cytometry (FACS Canto 2, BD Sciences; Yi and Dean 2013; Bestion et al. 2018). Samples of each culture (10 μL) were analyzed with fast flux settings (66 μL/min) to quantify morphological (i.e., forward scatter and side scatter, respectively quantifying size and granularity of cells) and fluorescence parameters (i.e., fluorescein isothiocyanate [FITC], phycoerythrin [PE], PerCP.Cy5, PE.Cy7, allophycocyanin [APC], APC.H7, V450, and V500). Preliminary data (unpublished) showed that natural variability among species in phenotypic traits and autofluorescence allows differentiation of species (fig. S1). Based on this result, the 10 metrics were used in a random forest algorithm using the R package randomForest (Liaw and Wiener 2002) to determine species identity for each cell. The random forest algorithm was trained on data obtained from monocultures (i.e., isogenic cultures of each of the four competing species and of residents and dispersers of each *T. thermophila* genotype, all cultured under the same conditions) and then applied to assign species identity to each particle detected by the flow cytometer (species were discriminated with low error rate; mean ± SE: *T. thermophila*, 0.095 ± 0.030; *T. pyryformis*, 0.001 ± 0.000; *T. americanis*, 0.036 ± 0.006; *T. borealis*, 0.011 ± 0.001; *T. elliotti*, 0.018 ± 0.001). The important phenotypic differences that permit this discrimination are illustrated in figure S1. Importantly, the phenotypic characteristics of species might have changed in response to the inclusion in a community, which might affect the efficiency of species assignation. Although we cannot formally exclude this possibility, the distribution of traits in community samples is always contained within the distribution expected given the distribution of species traits under isogenic conditions, with a lower variance of traits in communities (fig. S2). Because of a technical issue during cytometry reading, data on 16 communities were not available for analyses. At the end of the experiment, we quantified species richness, S (the number of species present in the communities); Shannon diversity, H ($H = -\sum_i p_i \times \ln(p_i)$, where p_i is the relative abundance of species i in the community); and evenness of species ($H/(\log(S))$; Magurran 2004; Oksanen et al. 2005; Morris et al. 2014). While species richness quantifies the absolute number of species present, Shannon diversity is a measure of diversity weighted by the relative abundances of the species present in a community, and evenness represents the regularity of abundance distribution.

Statistical Analyses

We initially aimed at confirming that morphological traits (i.e., cell size and cell elongation) and demographic parameters (i.e., growth rate and maximal density) differed between residents and dispersers in *T. thermophila* and that these differences varied among genotypes, as observed in previous studies (e.g., Jacob et al. 2019, 2020). First, variability within and among genotypes in population growth rate, maximal density, cell size, and elongation were standardized and summarized in a principal component analysis (PCA; R package psych; Revelle 2011). The axes from the PCA were rotated using varimax rotation (using the function principal from the R package psych) to obtain axes with simple interpretation. Second, we fitted two linear models (lm function, R package stats) with the scores on the first two PCA axes (either PCA1 or PCA2) as dependent variables and with dispersal status (i.e., resident or disperser), genotype identity, and their interaction as explanatory variables.

To test for the impact of differences between residents and dispersers and their genotype identity on the biomass and composition of communities, we fitted linear models with biomass production, maximal biomass, Shannon diversity, and evenness as dependent variables and with dispersal status (residents vs. dispersers, two-level factor), genotype identity, and their interaction as explanatory variables. Then, to test to what extent the functional traits we measured could explain the effects of dispersal status and genotype on the communities, we fitted similar models by replacing genotype identity and dispersal status with the scores of the PCA1 and PCA2 axes summarizing the phenotypic traits of residents and dispersers of each genotype. Since species richness displayed only three modalities (three, four, or five species), the effects of genotype identity, dispersal status, and the subsequent scores of PCA1 and PCA2 were tested using ordered logistic regression (polr function in the R package MASS; Venables and Ripley 2002). Finally, we tested whether dispersal status and genotypic identity have an effect on the relative abundance of all five species using a multivariate analysis of variance with permutation (PERMANOVA; adonis2 function in the R package vegan; Oksanen et al. 2005). All statistical analyses were performed using R software (R Core Team 2013)

Results

The first two axes of the PCA on resident and disperser phenotypic traits explained 59% and 26% of phenotypic variation, respectively. The first axis (hereafter named the "demographic axis") was positively associated with population growth rate (loading $= 0.98$) and maximal density (0.97), with high values on this axis referring to cells with high growth capacities (fig. 1). The second PCA axis (hereafter named the "morphological axis"; table S2) explained variance in cell size (0.84) and elongation (-0.81), with high values describing larger and rounder cells. The 20 genotypes of *Tetrahymena thermophila* strongly differed in their position on the demographic axis, the morphological axis, or both (table 1). Additionally, genotypes differed in the intensity and direction of the resident-disperser differences, in terms of both demography and morphology (significant

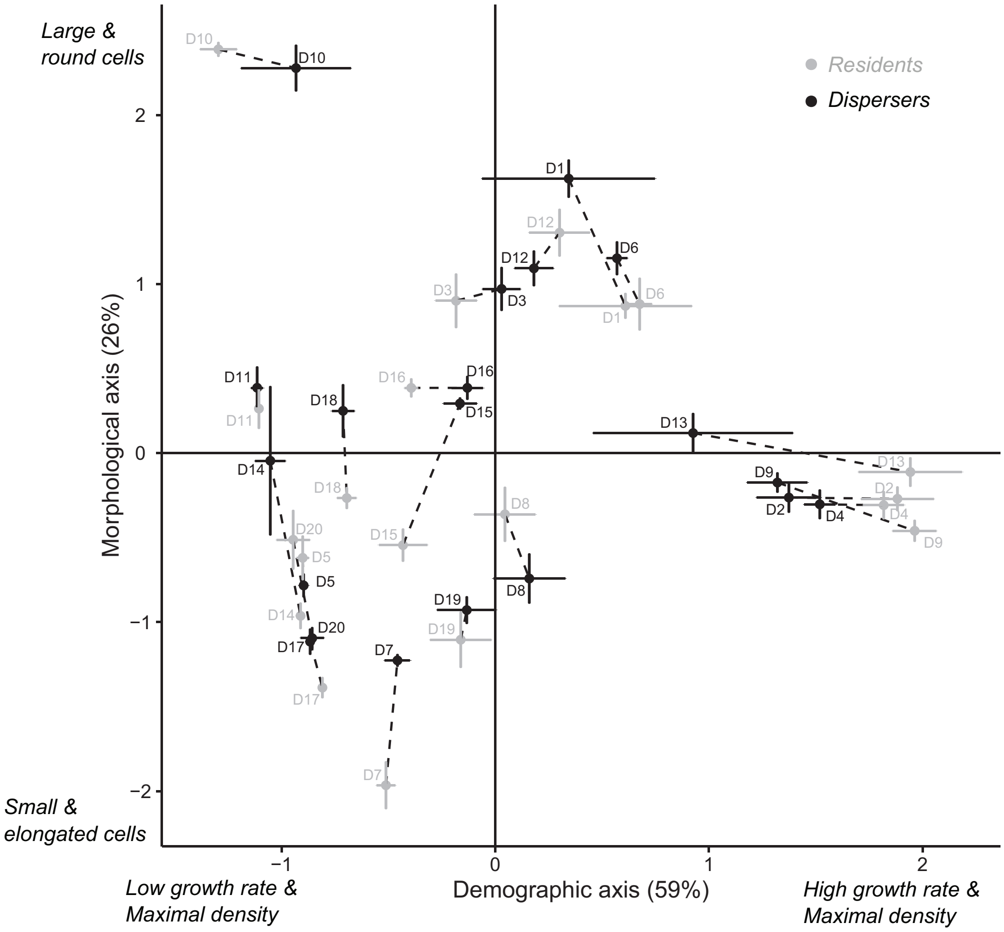

Figure 1: Variability of phenotypic traits among the 20 genotypes of *Tetrahymena thermophila* plotted on the first two axes of a varimax-rotated principal component analysis, expressing demography (population growth rate and maximal density; loadings: 0.98 and 0.97, respectively) and morphology (cell size and elongation; loadings: 0.84 and −0.81, respectively). Percentages are proportions of explained variance by each axis. Mean values (shown with standard errors among five replicates) for residents and dispersers for each genotype are displayed.

genotype × dispersal status interactions; table 1). We also detected a small ($R^2 = 1\%$) difference in morphology between residents and dispersers independently of genotype identity, with residents being slightly smaller overall (table 1).

Tetrahymena thermophila residents and dispersers differed in their impacts on the biomass of communities (fig. 2). Specifically, introducing dispersers led to communities with lower maximal biomass and usually lower maximal rates of biomass production than did introducing residents of the same genotype (fig. 2). This effect of dispersal status on maximal biomass was highly consistent regardless of the *T. thermophila* genotype added (dispersal status × genotype interaction: $F_{19,160} = 0.615$, $P = .891$). Regarding biomass production, the dispersal status × genotype interaction had a marginal effect (table 2), reflecting the fact that the differences between residents and dispersers in some genotypes were negligible (fig. 2). Additionally, independently of being a resident or a disperser, cells from different *T. thermophila* genotypes affected biomass production and maximal biomass differently in communities, showing an effect of intraspecific genetic variability on community dynamics (fig. 2; table 2).

Dispersal status further affected community diversity indicators. First, introducing dispersers led to slightly richer communities than introducing residents (mean richness ± SE: dispersers, 4.14 ± 0.048; residents, 4.00 ± 0.068; table 2). Second, we found that dispersal status further altered community evenness, with residents leading to higher evenness than dispersers (table 2; fig. 3). However, differences between dispersers and residents did not significantly affect Shannon diversity (table 2; fig. 3). Genotypic identity

Table 1: Effect of dispersal status (resident vs. disperser) and *Tetrahymena thermophila* genotype identity on the position in a varimax-rotated principal component analysis space defining a demographic axis and a morphological axis

	SS	df	F	P	R^2
Demographic axis					.90
Dispersal status	.4	1, 160	3.6	.061	.00
Genotype	**175.4**	**19, 160**	**82.2**	**<.001**	**.88**
Dispersal status × genotype	**5.2**	**19, 160**	**2.4**	**.001**	**.03**
Morphological axis					.93
Dispersal status	**1.7**	**1, 160**	**23.1**	**<.001**	**.01**
Genotype	**177.2**	**19, 160**	**122.03**	**<.001**	**.89**
Dispersal status × genotype	**7.8**	**19, 160**	**5.3**	**<.001**	**.04**

Note: Variables significant at the .05 level are shown in boldface type.

significantly affected species richness, Shannon diversity, and evenness (table 2). The dispersal status × genotype interaction did not significantly impact any of the three metrics describing community diversity (table 2; see table S3 for similar analyses while excluding *T. thermophila* from diversity estimations). Finally, the final relative abundances of the five species (including *T. thermophila*) did not differ between communities with residents compared with those with dispersers (PERMANOVA, $F_{1,163} = 1.704$, $P = .173$, $R^2 < 0.01$) but were strongly dependent on genotype identity (PERMANOVA, $F_{19,163} = 14.503$, $P = .001$, $R^2 = 0.63$).

Then we explored the mechanisms underlying the effects of dispersal status and genotypes on communities by quantifying the effects of the phenotypic traits differing between residents and dispersers and among genotypes, as summarized by the demographic and morphological PCA axes. Overall, the demographic and morphological traits were highly related to genotypic identity and were slightly related to dispersal status (table 1). Therefore, they depicted mainly a genotype effect on communities (and to a lesser extent a dispersal status effect). Yet these demographic and morphological traits explained much less variance than the genotype effect (tables 2, 3). Moreover, the morphological axis was linked to maximal biomass, depicting a negative effect of cell size and elongation on maximal biomass (table 3; fig. S3). More surprisingly, maximal biomass and production were negatively affected by demographic traits of *T. thermophila* (table 3; fig. S3): the higher the growth rate and maximal density of *T. thermophila* cells, the lower the biomass in experimental communities. Demographic traits were also positively correlated with Shannon diversity and evenness (table 3; fig. S3). Finally, morphological traits were correlated with species richness and evenness: large and round cells slightly increased species richness and led to a less even distribution of species in the community (table 3; fig. S3).

Discussion

Dispersal is an important process affecting metacommunity and metaecosystem dynamics (Loreau et al. 2003*a*; Massol et al. 2017; Gounand et al. 2018), but the role of phenotypic and context-dependent dispersal in these dynamics is poorly understood (Edelaar et al. 2008; Jacob et al. 2015; Cote et al. 2017*a*; Raffard et al. 2022). In this study, we tested whether dispersers and residents from multiple genotypes affect competitive communities in ciliate microcosms. As previously shown in *Tetrahymena thermophila*, residents and dispersers differed in multiple morphological and demographic traits, and these differences varied among genotypes (Fjerdingstad et al. 2007; Jacob et al. 2019, 2020). Using communities of five ciliate species (*T. thermophila* with four competing species), we found that differences between residents and dispersers have important consequences for the overall biomass productivity of community ($R^2 = 21\%–26\%$), while the effects on community composition were weak when significant ($R^2 = 2\%$). Specifically, introducing dispersers consistently led to lower productivity and lower maximal biomass irrespective of genotypic differences in the measured morphological and demographic traits.

Differences in functional traits between residents and dispersers might have consequences for community biomass through altered interspecific interactions. Dispersal can indeed be associated with the development of specific phenotypic attributes and incur costs associated with energy and metabolic demands required for moving among habitats (Bonte et al. 2012; Cayuela et al. 2022). Potential costs of dispersal might make dispersers less competitive than individuals from other species in our communities where only *T. thermophila* was exposed to the dispersal treatment. On the contrary, the decreased biomass in the presence of dispersers suggests that dispersers might generate stronger competitive interactions in communities. Competition can indeed lead to mutual inhibition among competing species, resulting in low growth rate of individual species and eventually a low biomass production independently of the community composition (Mitri and Foster 2013; Ghoul and Mitri 2016). In microbial communities, competitive interactions can be caused indirectly through resource exploitation or directly through cell damage (e.g., chemical toxins; Ghoul and Mitri 2016). Here, we might, for instance, speculate that dispersers have higher efficiency of resource acquisition and assimilation, which evenly affects species in the community through decreased resource availability. This could be part of colonization strategies, where dispersers display features facilitating colonization success by overexploiting the environment and

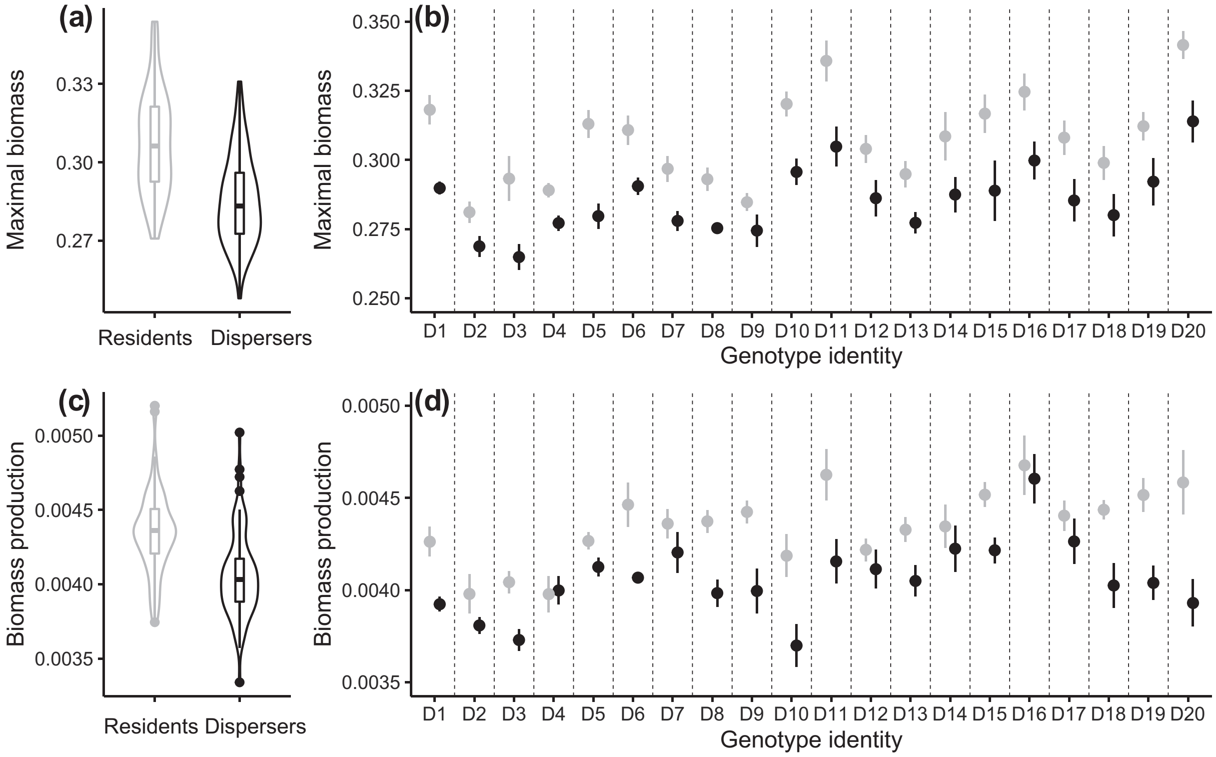

Figure 2: Impact of dispersers and residents on community biomass: effects of introducing *Tetrahymena thermophila* residents (gray) or dispersers (black) of each genotype into a ciliate community on its maximal biomass (i.e., maximal density reached by the community; *a*, *b*) and biomass production (i.e., maximal rate of biomass production; *c*, *d*). Left panels (*a*, *c*) are averaged effects over all 20 genotypes, whose individual results are presented in the right panels (*b*, *d*).

thus lowering the performance of other individuals, regardless of whether they belong to the same or a different species. For instance, higher aggressiveness of dispersers in passerine birds can give a competitive advantage and may help colonization, but it entails reproductive costs for dispersers (Duckworth and Badyaev 2007). Importantly, these effects were detected after several generations. Although we cannot conclude on their origin, they were possibly due to two different mechanisms. First, the nongenetic inheritance of phenotypic differences between residents and dispersers across several generations, a pattern that has recently been shown for cell velocity and shape in some genotypes of *T. thermophila* (Cayuela et al. 2022), could induce long-term community consequences. Second, a founder effect of residents and dispersers might have occurred where initial conditions determine the fate of the community (Chase 2003). Interestingly, despite the relatively strong effect of resident-disperser differences on community biomass, the composition of the ciliate community was weakly affected by the dispersal status of *T. thermophila*. Importantly, assessments of community composition through flow cytometry as performed in this study might be sensitive to potential changes in phenotypic characteristics of species when included in communities. The five *Tetrahymena* species, however, strongly differ phenotypically (fig. S1), and we found lower variance of traits in communities compared with isogenic conditions, as expected if not all species survive in the communities (fig. S2), making this method a good candidate to describe ciliate communities. Although it is important to keep this limit in mind, the weak effects of dispersal for community composition suggests that *T. thermophila* residents and dispersers did not overgrow or exclude other species, and competitive hierarchy among species was conserved regardless of the dispersal status of *T. thermophila* individuals. Importantly, it is likely that phenotypic variability within *T. thermophila* does impact community structure, since genotypic variability (which at least in part determines phenotypic variability) had a significant effect on each component of community composition that we measured. Further investigations are, however, required to assess the competitive strength of residents and dispersers against each one of the other species.

Morphological and demographic traits quantified here differed markedly both among *T. thermophila* genotypes

Table 2: Effect of intraspecific variability and resident-disperser differences on maximal community biomass, biomass production, Shannon diversity, community evenness, and species richness

	SS	df	*F*	*P*	R^2
Maximal biomass					.69
Dispersal status	**.024**	**1, 160**	**140.8**	**<.001**	**.26**
Genotype	**.037**	**19, 160**	**11.6**	**<.001**	**.41**
Dispersal status × genotype	.002	19, 160	.615	.891	.02
Biomass production					.60
Dispersal status	$\mathbf{4.2 \times 10^{-6}}$	**1, 160**	**88.8**	**<.001**	**.21**
Genotype	$\mathbf{6.2 \times 10^{-6}}$	**19, 160**	**6.8**	**<.001**	**.31**
Dispersal status × genotype	1.4×10^{-6}	19, 160	1.6	.063	.07
Shannon diversity					.54
Dispersal status	.019	1, 144	1.1	.308	<.01
Genotype	**2.916**	**19, 144**	**8.4**	**<.001**	**.50**
Dispersal status × genotype	.171	19, 144	.5	.963	.03
Evenness					.45
Dispersal status	**.050**	**1, 144**	**4.7**	**.031**	**.02**
Genotype	**1.051**	**19, 144**	**5.2**	**<.001**	**.38**
Dispersal status × genotype	.145	19, 144	.7	.797	.05
Species richness					.26
Dispersal status	...	**1**	$\boldsymbol{\chi^2 = 4.77}$	**.028**	**.02**
Genotype	...	**19**	$\boldsymbol{\chi^2 = 39.96}$	**.003**	**.15**
Dispersal status × genotype	...	19	$\chi^2 = 22.44$	.262	.09

Note: Ordered logistic regression was run on species richness, and McFadden pseudo-R^2 values are reported. Variables significant at the .05 level are shown in boldface type.

and between residents and dispersers. Moreover, whether dispersers display a phenotype specialized for long-distance movement (small and elongated) or, on the contrary, short distance (large and round cells) varies across genotypes, as previously found (Jacob et al. 2016). However, these traits poorly explained the differential effects that residents and dispersers have on community biomass (up to 5% when cumulating simple and interactive effects; see table 1). Therefore, the investigated traits probably solely account for a small amount of the variance in community biomass explained by the dispersal status. Dispersal is a complex process that depends on many phenotypic traits (Clobert et al. 2012). It would then not be surprising that the four traits quantified in this study do not capture much of the phenotypic variance explaining the disperser-resident differences. For instance, behavioral traits, such as activity and exploration, are important in shaping ecological interactions (Wolf and Weissing 2012) as well as in determining individual dispersal (e.g., swimming capacities or ciliate numbers in *T. thermophila*; Nelsen and Debault 1978; Pennekamp et al. 2019; Junker et al. 2021). Also, cell metabolism and resource uptake could probably underline the general and consistent resident versus disperser effects on the measured community. Alternatively, the phenotypic differentiation between residents and dispersers in a genotype is a plastic process (Jacob et al. 2020), which can involve energetic investment in movement or in changing morphology. Therefore, these energetic costs could also modify interactions among species in the communities, altering subsequent biomass production. As many traits can be correlated to the dispersal capacities of individuals, traits other than those quantified here should explain the consistent effects of dispersal for community biomass we found in this study.

The rate of dispersal is important for the functioning of metaecosystems, metacommunities, and other ecological networks (Loreau et al. 2003*a*; Mouquet and Loreau 2003; Massol et al. 2011; Baguette et al. 2013; Thompson and Gonzalez 2017). Yet resident and disperser individuals are often considered as (phenotypically) similar in those frameworks. We showed that this is not the case in our experiment, where residents and dispersers differently affected biomass production independently of density. While dispersal is often seen to affect competition through changes in density (Thompson et al. 2020), our study suggests that differences of phenotypic traits or dispersal strategies are also at play. Such a result might be important for theoretical predictions regarding metacommunities and metaecosystems dynamics, as recently highlighted (Raffard et al. 2022). Especially, spatial and temporal heterogeneity of environmental conditions (e.g., source-sink dynamics, environmental gradients) can favor asymmetric trait fluxes. Hence, spatial heterogeneity of ecosystem functioning might be altered (Raffard

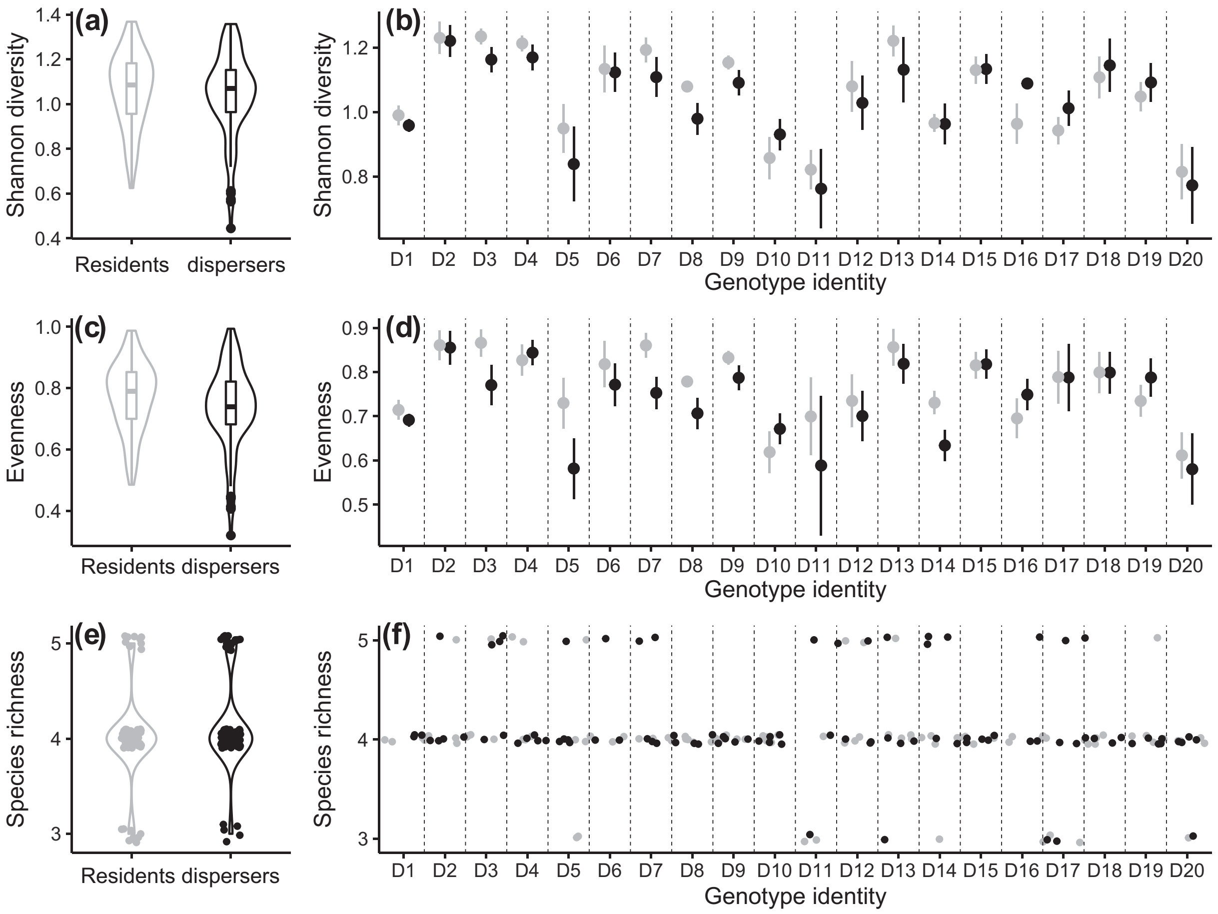

Figure 3: Impact of dispersers and residents on community composition: effects of introducing *Tetrahymena thermophila* residents (gray) or dispersers (black) of each genotype into a ciliate community on Shannon diversity (*a*, *b*), evenness (*c*, *d*), and species richness (*e*, *f*). Left panels (*a*, *c*, *e*) are averaged effects over all 20 genotypes, whose individual results are presented in the right panels (*b*, *d*, *f*). Since species richness (*e*, *f*) presents only three modalities, the position of points was slightly shifted to allow their distinction.

et al. 2022). For instance, in range expansion areas we could speculate that differences in competitive abilities between residents and dispersers might, independently of their growth capacities, alter species productivity in edge habitats. Subsequent diversity-productivity relationships might be altered (Thompson et al. 2020). Yet these results might be species dependent, since dispersers can be stronger or weaker competitors than residents depending on the species (Anholt 1990; Hanski et al. 1991; Bowler and Benton 2005; Cadotte et al. 2006; Duckworth and Badyaev 2007). Overall, further investigations of other species in different ecological networks are required, since understanding which species characteristics and dispersal-related traits (e.g., trophic level, mode of dispersal) influence the effects of residents and dispersers on communities should ultimately benefit theories on metasystem functioning (Massol et al. 2017; Raffard et al. 2022).

Finally, in addition to a consistent effect of disperser-resident differences across genotypes, we found evidence for an effect of intraspecific genetic variability in *T. thermophila* on community biomass and composition. This confirms the key role of intraspecific variability on ecological processes (Raffard et al. 2019). Importantly, while overall phenotypic differences between genotypes result from genetic effects, the differences between residents and dispersers we found here occur through phenotypic plasticity (Jacob et al. 2020). The combined effects of genotype and dispersal status on community biomass we demonstrated here are therefore the outcome of a combination of both genetic and plastic effects occurring during the dispersal process. Competition was likely a determinant process in the experimental communities we used, and our results suggest that genotypic differences within *T. thermophila* might modulate these competitive interactions. This result supports previous studies

Table 3: Effect of morphological and demographic traits (principal component analysis axes) characterizing resident-disperser differences and intraspecific variability on maximal community biomass, biomass production, Shannon diversity, community evenness, and species richness

	Estimate (SE)	SS	df	F	P	R^2
Maximal biomass						.15
Demographic axis	**−.008 (.001)**	**.012**	**1, 197**	**32.93**	**<.001**	**.14**
Morphological axis	.001 (.001)	<.001	1, 197	.52	.469	<.01
Biomass production						.07
Demographic axis	**-5.3×10^{-5} (2.1×10^{-5})**	**6×10^{-7}**	**1, 197**	**6.06**	**.014**	**.03**
Morphological axis	**-6.4×10^{-5} (2.1×10^{-5})**	**8×10^{-7}**	**1, 197**	**9.11**	**.002**	**.04**
Shannon diversity						.22
Demographic axis	**.082** (.011)	**1.265**	**1, 181**	**51.06**	**<.001**	**.22**
Morphological axis	−.007 (.012)	.010	1, 181	.38	.534	<.01
Evenness						.17
Demographic axis	**.048** (.008)	**.437**	**1, 181**	**34.38**	**<.001**	**.15**
Morphological axis	**−.017** (.008)	**.053**	**1, 181**	**4.21**	**.041**	**.02**
Species richness						.04
Demographic axis	.321 (.177)	...	1	$\chi^2 = 3.329$	.068	.01
Morphological axis	**.431 (.180)**	...	1	**$\chi^2 = 5.815$**	**.016**	**.02**

Note: Ordered logistic regression was run on species richness, and McFadden pseudo-R^2 values are reported. Variables significant at the .05 level are shown in boldface type.

suggesting that genetic diversity is important for the assembly of communities (Hughes et al. 2008). Especially, some genotypes may be more efficient in outcompeting other species, modifying the competitive network of a whole community (Hart et al. 2016). The effects of genotypic variability were partly underlined by morphological and demographic traits, since 91% and 85% of their variance (table 1), respectively, were explained by differences among genotypes. Accordingly, genetic variability in morphological and demographic traits have been previously found to affect metapopulation dynamics in *T. thermophila* (Jacob et al. 2019). Here, the higher the demographic parameters (i.e., growth rate and maximal biomass in isogenic conditions) of the introduced *T. thermophila* cells, the lower the productivity (maximal biomass and biomass production) and the higher the diversity (Shannon, evenness) in the communities. While this might seem contradictory, we speculate on a trade-off between growth parameters (i.e., proxies of fitness without interspecific competition) and competitive abilities (Bohannan et al. 2002; Kneitel and Chase 2004; Mille-Lindblom et al. 2006). For instance, traits associated with competitive abilities, such as toxin resistance, could allow facing other species competing for the same resource (Mille-Lindblom et al. 2006). Interestingly, those effects were not due to density per se in the first stage of communities' growth, as they were made of species with equal initial densities. We rather measured per capita effects on biomass productivity and community composition. Manipulating density in similar experiments will be a key step forward, to investigate whether density and phenotypic traits have additive or interactive effects on communities.

To conclude, we found that the differences between resident and disperser individuals affect communities' biomass, with dispersers decreasing productivity compared with residents. This effect was highly consistent across the 20 genotypes we used in this study. Differences between resident and disperser effects on community biomass productivity may have important repercussions for ecosystem dynamics (Raffard et al. 2022), since biomass is classically considered as a main component of ecosystem functioning (Loreau 2001; Loreau et al. 2003*a*; Harvey et al. 2016). Measuring dispersal-related traits other than those related to morphology and growth (e.g., behavioral, physiological, structural) should help to assess more precisely the mechanisms explaining the described effects of resident-disperser differences on community outcomes. An interesting perspective would be to integrate the ecological differences between residents and dispersers in spatially explicit metaecosystem models to test for the effects of dispersal-related traits on metaecosystem dynamics.

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Statement of Authorship

A.R., D.L., N.S., and S.J. designed the study. S.J. and J.L.M.C. performed the experiment. A.R. performed statistical analyses with contributions from S.J. and N.S. A.R., D.L., N.S., and S.J. interpreted and discussed the results. A.R. wrote the first draft of the manuscript. All authors corrected and improved the manuscript and approved the final version.

Data and Code Availability

Data and code are available via the Dryad Digital Repository (https://doi.org/10.5061/dryad.mpg4f4r34; Raffard 2022).

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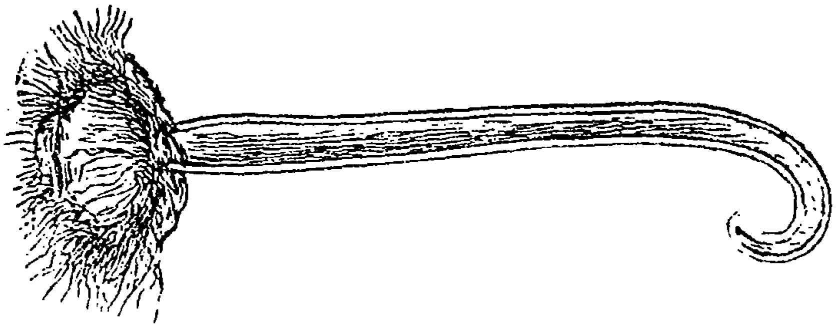

“The fruit of *Circæa lutetiana*, enchanter’s nightshade, is covered with rather stout one-celled hairs which have a hook at the extremity [figured]. The stems of the common butter bean of our gardens have a few scattering hairs of similar structure, though they are smaller and much more delicate.” From “Hairs and Glandular Hairs of Plants, Their Forms and Uses” by W. J. Beal (*The American Naturalist*, 1878, 12:271–282).