1   Dispersal syndromes affect ecosystem functioning in ciliate microcosms

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8   **Abstract**

9   Dispersal is a key process mediating ecological and evolutionary dynamics. Its effects on

10   metapopulations dynamics, population genetics or species range distribution can depend on

11   phenotypic differences between dispersing and non-dispersing individuals (*i.e.*, dispersal

12   syndromes). However, scaling up to the importance of dispersal syndromes for meta-

13   ecosystems have rarely been considered, despite intraspecific phenotypic variability is now

14   recognised as an important factor mediating ecosystem functioning. In this study, we

15   characterised the intraspecific variability of dispersal syndromes in twenty isolated genotypes

16   of the ciliate *Tetrahymena thermophila* to test their consequences for biomass productivity in

17   communities composed of five *Tetrahymena* species. To do so, dispersers and residents of

18   each genotype were introduced, each separately, in ciliate communities composed of four

19   other competing species of the genus *Tetrahymena* to investigate the effects of dispersal

20   syndromes. We found that introducing dispersers led to a lower biomass compared to

21   introducing residents. This effect was highly consistent across the twenty *T. thermophila*

22   genotypes despite their marked differences of dispersal syndromes. Finally, we found a strong

23   genotypic effect on biomass production, confirming that intraspecific variability in general

24   affected ecosystem functions in our system. Our study shows that intraspecific variability and

25   the existence of dispersal syndromes can impact the functioning of spatially structured

26   ecosystems in a consistent and therefore predictable way.

27

28   **Introduction**

29   Dispersal is a complex and key process mediating ecological and evolutionary dynamics in

30   spatially structured landscapes (Mouquet and Loreau 2003, Bowler and Benton 2005, Ronce

31   2007, Edelaar et al. 2008, Clobert et al. 2012, Edelaar and Bolnick 2012). Spatially structured

32   ecosystems (*i.e.*, meta-ecosystems) strongly rely on dispersal rates (*i.e.*, the proportion of

33   dispersing individuals, Loreau et al. 2003b) as dispersal mediates species interactions and

34   nutrient fluxes in ecosystems, which in turn modifies ecosystem functions (Loreau et al.

35   2003b, Harvey et al. 2016). In meta-ecosystem modelling, dispersing individuals are mostly

36   considered as phenotypically similar to non-dispersing ones, although the dispersal status of

37   individuals (*i.e.*, being a disperser or a resident) is often associated with strong phenotypic

38   specializations (Bowler and Benton 2005, Clobert et al. 2009). Especially, the willingness and

39   ability of organisms to disperse at each of the three dispersal phases (*i.e.,* emigration,

40   transience, and immigration) is often associated with various phenotypic traits including

41   behaviours, morphology, life history or physiology (Clobert et al. 2009). Such suite of traits

42   differing between dispersers and residents, named dispersal syndromes, have been described

43   in many taxa (Clobert et al. 2009, Le Galliard et al. 2012, Stevens et al. 2014, Legrand et al.

44   2015). For instance, dispersers are often larger than residents in freshwater fish (Comte and

45   Olden 2018).

46   While often differing among species (Stevens et al. 2014, MacLean and Beissinger

47   2017), dispersal syndromes can also vary within species depending on both evolutionary and

48   ecological factors (Bowler and Benton 2005, Legrand et al. 2016, Cote et al. 2017a). For

49   instance, genetic covariances between dispersal and reproductive traits are found in wing-

50   dimorphic crickets (reviews in Zera and Brisson 2012, Saastamoinen et al. 2018). In toads,

51   interaction between landscape matrix composition and predation risk shapes movers

52   phenotype (Winandy et al. 2019). Therefore, variability in genetic composition and/or local

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53   environmental conditions (biotic or abiotic) can generate variability in dispersal syndromes

54   among populations (Cote et al. 2017a). In turn, not only dispersal rate itself, but also dispersal

55   syndromes (regardless of whether they differ within species or not) can have consequences on

56   ecological dynamics (Jacob et al. 2019). Some studies showed that phenotype-dependent

57   dispersal can be important in mediating metapopulation dynamics, species interaction, and

58   phenotypic range distribution (Duckworth and Badyaev 2007, Phillips et al. 2010, Shine et al.

59   2011, Messager and Olden 2019). In ciliate microcosms, dispersal syndromes involving

60   morphological and demographic traits can affect metapopulation size and stability (Jacob et

61   al. 2019). The consequences of dispersal syndromes at the scale of ecosystems have however

62   rarely been studied, despite the fact that phenotypic variability within species can affect

63   multiple ecosystem functions, including nutrient recycling, decomposition rate and primary

64   production (Harmon et al. 2009, Bassar et al. 2010). For instance, variability in sticklebacks

65   (*Gasterosteus aculeatus*) morphological traits (*e.g.*, mouth apparatus and body shape) can

66   affect primary production and carbon cycle through difference in diet among individuals

67   (Harmon et al. 2009, Schmid et al. 2019). Importantly, such intraspecific variability can affect

68   ecosystem functions as much as species richness (Des Roches et al. 2018, Raffard et al.

69   2019).

70   The impacts of dispersal syndromes and their intraspecific variability on ecosystem

71   functioning could be due to variability of interaction strengths in communities between

72   dispersers and residents. First, dispersers and residents could differ in their competitive

73   abilities, in turn modifying species coexistence (Hart et al. 2016, Turcotte and Levine 2016).

74   Some traits often involved in dispersal syndromes, such as aggressiveness, may shape

75   competition strength in colonised habitat and affect species coexistence (Duckworth and

76   Badyaev 2007, Wolf and Weissing 2012), which could affect ecosystems. Dispersal

77   syndromes can also modulate ecosystem functioning through trophic interactions when

78   resource use differs between residents and dispersers (Cote et al. 2017b). Hence, primary

79   evidence emerged, showing that dispersers of *Dikerogammarus villosus* -a freshwater

80   amphipod decomposer- consume more detritus than residents, increasing the decomposition

81   rate of organic material in colonizing habitats (Little et al. 2019). Interestingly, effects

82   differed between the two related study species, suggesting that the effects of dispersal

83   syndromes on ecosystem functioning might be species-dependent. Since current rapid

84   environmental changes are shaping variability within species and notably in dispersal

85   syndromes (*e.g.*, habitat fragmentation; Cote et al. 2017a), unexpected effects going along

86   with alteration of the dispersal process could modify ecosystem functioning.

87   Here, we aimed at testing whether dispersal syndromes and their intraspecific

88   variability affect ecosystem functioning. We used microcosms to quantify the effects of

89   dispersal syndromes of multiple isogenic strains (hereafter referred to as *genotypes*) of the

90   ciliated protist *Tetrahymena thermophila* on biomass production of communities composed of

91   four competing species of the genus *Tetrahymena*. As a prerequisite to this study, we

92   quantified dispersal syndromes of *T. thermophila* and their variability among 20 genotypes:

93   for each genotype, we measured morphological traits (*i.e.*, cell size and shape) and

94   demographic parameters (*i.e.*, population growth and maximal density) of resident and

95   disperser individuals. We then tested whether residents and dispersers differently affect

96   biomass production, while controlling for density. We further tested whether intraspecific

97   variability in dispersal syndromes (*i.e.*, differences between genotypes in the measured

98   dispersal-related traits) mediates these ecosystem effects. We expected dispersal syndromes to

99   affect biomass production because of functional differences between dispersers and residents

100   (Little et al. 2019), and we expected that these effects might be genotype-dependent if the

101   traits associated with dispersal vary among genotypes.

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Material and methods

Study species

Native from North America, *Tetrahymena thermophila* is a 30–50μm unicellular eukaryote living in freshwater ponds and streams (Collins 2012, Doerder and Brunk 2012). Twenty isogenic genotypes (strains D1 to D20, characterised in Pennekamp et al. 2014, Table S1) were used to assess variability in dispersal syndromes. All genotypes displayed clonal reproduction in our culture conditions (Elliott and Hayes 1953, Bruns and Brussard 1974). Cells were maintained in axenic rich liquid growth medium (0.5% Difcoproteose peptone, 0.06% yeast extract) at 23°C (Schtickzelle et al. 2009, Altermatt et al. 2015) in sterile conditions under a laminar flow hood.

Quantification of dispersal syndromes

Dispersal syndromes, and their dependency to genotypes, have already been described in microcosms of *T. thermophila* (*e.g.*, Fjerdingstad et al. 2007, Jacob et al. 2019a, 2019b). We built on these previous studies to quantify them at a wider intraspecific level and test for their effect at the ecosystem level. Dispersal rates and syndromes were quantified using standard two-patch systems (*e.g.*, Schtickzelle et al. 2009, Pennekamp et al. 2014, Jacob et al. 2019b). They consist in two habitats (1.5 ml microtubes) connected by a corridor (4 mm internal diameter, 2 cm long silicone tube) filled with growth medium. We measured dispersal rate and characterised resident and disperser cells in five replicated systems for each genotype. To do so, cells from each genotype were placed in one patch at a standardised density (40,000 cells/ml) during 30 minutes of acclimation, and the corridor was then opened to allow cells to disperse for four hours towards the initially empty neighbour patch. Corridors were then closed to prevent further movements until measurement. Population growth rate is low

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127   enough during such a four hour time frame in this species to avoid bias in the quantification

128   of dispersal rates (Pennekamp et al. 2014, Jacob et al. 2018).

129   Five samples of 10µl were pipetted in each of the two patches (for resident and

130   disperser cells) and pictured under dark-field microscopy (Axio Zoom V16, Zeiss) to assess

131   cell density and morphology using a procedure developed within the ImageJ® software

132   (Pennekamp and Schtickzelle 2013). First, the dispersal rate for each genotype was calculated

133   as $\frac{D_{disp}}{D_{resi}+D_{disp}}$, where D_{disp}, D_{resi} are dispersers' and residents' abundances respectively.

134   Second, *cell size* (cell surface area on pictures) and *cell elongation* (aspect ratio, *i.e.*, ratio of

135   cell major/minor axes) were estimated in both residents and dispersers.

136   Then, demographic traits (*i.e.*, growth rate and maximal population density) of

137   residents and dispersers of each genotype were measured. To do so, ~150 cells of residents or

138   dispersers (mean volume ± SE: 14.02 ± 1.25 µl) from each patch of each dispersal system

139   were transferred into 96-well plates (250µl wells) filled with growth medium, with two

140   technical replicates (averaged in subsequent analyses). Absorbance at 450nm was recorded

141   every two hours for two weeks using a microplate reader (Infinite 200, TECAN) to quantify

142   population growth. We used a general additive model (R-package *gam*; R Core Team 2013,

143   Hastie 2018) to smooth the observed absorbance measurements to avoid any bias due to slight

144   variability in absorbance measures, and fitted logistic growth curves using the *grofit* package

145   (gcfit function with spline fit; Kahm et al. 2010). *Growth rate* was then assessed as the

146   maximum slope of population growth, and *maximal population density* as the density reached

147   at the plateau (Jacob et al. 2017).

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149   *Experimental communities and ecosystem functioning*

150   Competitive communities were assembled using four competing *Tetrahymena* species to

151   which residents or dispersers of each *T. thermophila* genotype from the first part of

152   experiment were added. A single strain of each competing species was used (*T. americanis*

153   A5, *T. borealis* B8, *T. pyriformis* P4, and *T. elliotti* E5; Table S1) to avoid potential

154   differences of competitive interactions due to genetic variability. To assemble communities,

155   we transferred ~150 cells of each of the four competing species (10 µl of cultures previously

156   diluted to 15,000 cells/ml) into 96-well plates (250 µl wells filled with growth medium) and

157   then introduced dispersers/residents from one specific *T. thermophila* genotype (~150 cells,

158   see above). In total, we assembled 200 communities with equal initial abundance of all

159   species: 20 *T. thermophila* genotypes × 2 dispersal status (resident and disperser) × 5

160   replicates. For each replicate of the dispersal experiment (see above), we additionally run two

161   technical replicates of community dynamics that were averaged for analyses. Absorbance at

162   450nm was recorded every two hours for two weeks to quantify the dynamics of ecosystem

163   functioning by measuring the biomass of the communities in the microcosms. As for

164   individual genotypes growth (see above), we fitted logistic growth curves to absorbance data

165   and computed *biomass production* as the maximum slope of community absorbance increase,

166   and the *maximal biomass* as the maximal absorbance reached by the community.

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168   *Statistical analyses*

169   We primarily aimed at confirming that morphological traits (*i.e.*, cell size and cell elongation)

170   and demographic parameters (*i.e.*, growth rate and maximal density) differed between

171   residents and dispersers in *T. thermophila* and that these differences vary among genotypes,

172   as observed in our previous studies. Firstly, population growth rate, maximal density, cell size

173   and elongation were summarised in a Principal Component Analysis (PCA, *ade4* R-package,

174   Chessel et al. 2007). Secondly, we fitted two linear models (lm function, *stats* R-package)

175   with the scores on the first two PCA axes (either PCA1 or PCA2) as dependent variables, and

176   the dispersal status (*i.e.*, disperser or resident), genotype identity and their interaction as

177   explanatory variables.

178   To test for the impact of dispersal syndromes and genotype identity on ecosystem

179   functioning, we fitted linear models with biomass production or maximal biomass as

180   dependent variables, and dispersal status (residents *vs* dispersers, two levels factor), genotype

181   identity, and their interaction as explanatory variables. Then, we fitted similar models by

182   replacing genotype identity and the dispersal status by the scores of PCA1 and PCA2 axes

183   summarising phenotypic traits, in order to test whether the dispersal syndrome (*i.e.*, the

184   measured phenotypic variability underlying differences between dispersers and residents) and

185   genotype identity affect biomass.

186

187   **Results**

188   The first two axes of the PCA on resident and disperser phenotypic traits explained 58% and

189   26% of phenotypic variation, respectively. The first axis (hereafter named *demographic axis*)

190   was positively associated with population growth rate (loading = 0.90) and maximal density

191   (0.92), with high values on this axis referring to cells with high growth capacities (Figure 1).

192   The second PCA axis (hereafter named *morphological axis*; Table S2) explained variance in

193   cell size (0.64) and elongation (-0.57), with high values describing larger and rounder cells.

194   The twenty genotypes of *T. thermophila* strongly differed in their position on both the

195   demographic and morphological axes (Table 1). Additionally, genotypes differed in the

196   intensity and direction of the resident-disperser differences, both in terms of demography and

197   morphology (significant genotype × dispersal status interactions; Table 1). This means that

198   the described dispersal syndrome varied among genotypes in this species. We also detected a

199   small difference of morphology between residents and dispersers independently of genotype

200   identity, residents being slightly smaller overall (Table 1).

201   *T. thermophila* dispersers and residents differed in their impacts on biomass (Figure

202   2). Specifically, introducing dispersers of any *T. thermophila* genotype led to communities

203   with lower biomass production and maximal biomass than introducing residents of the same

204   genotype at the same density (Figure 2). This effect of dispersal status on biomass production

205   and maximal biomass was highly consistent across genotypes (non-significant dispersal status

206   × genotype interactions; Table 2a). The genotype × dispersal status interaction still has a

207   marginal effect on biomass production (Table 2a), suggesting that some differences among

208   genotypes might mediate the effects of residents and dispersers on biomass production.

209   Additionally, independently of being a resident or a disperser, cells from different *T.*

210   *thermophila* genotypes affected biomass production and maximal biomass in communities,

211   suggesting an effect of intraspecific variability on ecosystem functioning (Figure 2 and Table

212   2a).

213   Then, we explored the mechanisms underlying the effects of dispersal status and

214   genotypes on biomass by quantifying the effects of phenotypic traits that we found to be

215   involved in dispersal syndromes summarised by the demographic and morphological PCA

216   axes. Overall, since the demographic and morphological traits were highly related to

217   genotypic identity, and slightly to the dispersal status (Table 1), they depicted mainly a

218   genotype effect on biomass and to a lesser extend a dispersal status effect. As expected, the

219   morphological axis was linked to maximal biomass, depicting a positive effect of cell size and

220   elongation on maximal biomass (Table 2b, Figure S1). More surprisingly, maximal biomass

221   and production were negatively affected by demographic traits of *T. thermophila* (Table 2b,

222   Figure S1). The higher the growth rate and maximal density of *T. thermophila* cells, the lower

223   the biomass in experimental communities.

224

225   **Discussion**

226   Dispersal is an important process affecting metacommunity and meta-ecosystem dynamics

227   (Loreau et al. 2003b, Massol et al. 2017, Gounand et al. 2018), but the role of dispersal

228   syndromes in these dynamics is poorly understood. In this study, we tested whether dispersal

229   syndromes and their intraspecific variability affect ecosystem functioning in ciliate

230   microcosms. As previously shown in *T. thermophila*, residents and dispersers differed in both

231   morphological and demographic traits, a dispersal syndrome that varied among genotypes

232   (Fjerdingstad et al. 2007, Jacob et al. 2019, 2020). Then using five ciliate species community

233   (*T. thermophila* with four competing species), we showed that introducing dispersers

234   consistently led to lower biomass production and maximal biomass irrespective of genotype-

235   specific dispersal syndromes.

236   Our results strikingly showed that the dispersal status of an individual leads to

237   consistent effects on ecosystem functioning across multiple genotypes, despite we measured

238   intraspecific variability in the phenotypic differences between residents and dispersers.

239   Specifically, dispersers lead to lower biomass than residents, suggesting that they may hence

240   be functionally dissimilar from residents, leading to different interspecific interactions

241   (Chesson 2000, Mitri and Foster 2013). Dispersal often incurs costs, for instance associated

242   with the development of specific phenotypic attributes or with energy and metabolic demands

243   required for moving among habitats (Bonte et al. 2012, Cayuela et al. 2019). We could

244   primarily expect that costs of dispersal would make dispersers less competitive for other

245   species in the communities, which would have probably increased biomass in microcosms

246   compared to residents (because of relaxed competition strength). At the opposite, we could

247   expect that a decrease of biomass production would come from higher competitive abilities of

248   dispersers resulting in an inhibition of biomass production (Mitri and Foster 2013).

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249   Competition may indeed lead to mutual inhibition among competing species (most of the

250   communities contained four species -including *T. thermophila*- at the end of the experiment,

251   and *T. elliotti* was always excluded, see Appendix S1), resulting in low growth rate of

252   individual species and eventually a low biomass production (Mitri and Foster 2013, Ghoul

253   and Mitri 2016). In microbial communities, competitive interactions might be caused

254   indirectly through resource exploitation or directly through cell damages (*e.g.*, chemical

255   toxin) (Ghoul and Mitri 2016). Hence, here, the dispersers of *T. thermophila* might increase

256   the strength of competitive interaction (direct and/or indirect), which may partly explain the

257   negative impact on total biomass in microcosms (Thompson et al. 2005, Sandau et al. 2019).

258   Further investigations might benefit the understanding of these results by assessing the

259   competitive strength of residents and dispersers against each one of the other species.

260   Additionally, investigating the mechanisms underlying the effects of *T. thermophila*

261   cells on ecosystem functioning, we found that demographic parameters and morphological

262   traits can impact biomass. These traits have been previously found to affect metapopulations

263   dynamics in *T. thermophila* (Jacob et al. 2019). Here, the higher the demographic parameters

264   (*i.e.*, growth rate and maximal biomass in isogenic conditions) of the introduced *T.*

265   *thermophila* cells, the lower maximal biomass and biomass production. While this might

266   seem contradictory, we could speculate on a trade-off between growth parameters of *T.*

267   *thermophila* (*i.e.*, proxies for fitness without competition) and competitive abilities

268   (Bohannan et al. 2002, Kneitel and Chase 2004, Mille-Lindblom et al. 2006). Competition is

269   associated with energetic costs, and for example the traits necessary for sustaining higher

270   growth (*e.g.*, efficiency of resource uptake) might come at the expense of other traits (*e.g.,*

271   toxin resistance) allowing to face other species competing for the same resource (Mille-

272   Lindblom et al. 2006). Interestingly, those effects were not due to density *per se* as

273   communities were made of species with equal densities. We rather measured *per capita*

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274   effects on biomass productivity. Including density effects, and determining the independent

275   effects of density, dispersal syndromes and phenotypic traits, might bring further insights into

276   the role of varying dispersal strategies in meta-ecosystems functioning.

277   Demography and morphology only partly explained differences between resident and

278   disperser individuals (up to 5% when cumulating simple and interactive effects, see Table 2),

279   while they differed mainly among *T. thermophila* genotypes. Therefore, they probably

280   account for a small amount of the variance explained by the dispersal status on biomass

281   metrics. This is confirmed by direct effects of dispersers and residents on maximal biomass

282   and biomass production, independently of their demography and morphology (see Table S3,

283   and Figure S2 for a conceptual diagram of our results). Dispersal is a complex process that

284   depends on many phenotypic traits (Clobert et al. 2012). It is then not surprising that we were

285   not able to capture much of the phenotypic variance explaining the disperser/resident

286   differences. It has been shown that swimming capacities have strong influence on *T.*

287   *thermophila* dispersal rates (Pennekamp et al. 2019) but other traits (*e.g.*, metabolism,

288   resource uptake, activity) should probably underline the general and consistent resident *vs.*

289   disperser effects on the measured ecosystem functions.

290   The rate of dispersal is important for the functioning of meta-ecosystems,

291   metacommunities, and other ecological networks (Loreau et al. 2003b, Mouquet and Loreau

292   2003, Massol et al. 2011, Baguette et al. 2013, Thompson and Gonzalez 2017). Yet, resident

293   and disperser individuals are mostly considered as similar in those frameworks. We showed

294   that this is not the case, at least in a ciliate example as residents and dispersers differently

295   affected biomass production, with most probably *per capita* effects (*i.e.*, independent of

296   density). While dispersal is often seen to affect competition through changes in density

297   (Thompson et al. 2020), our study suggests that phenotypic differences are also at play. Such

298   a result might be important for theoretical predictions regarding meta-ecosystems dynamics.

299   For instance, in range expansion areas, we could speculate that differences in competitive

300   abilities between residents and dispersers might, independently of their growth capacities,

301   alter species coexistence in edge habitats. Subsequent diversity-ecosystem functioning

302   relationships might be altered (Thompson et al. 2020). Yet, these results might be species-

303   dependent, since dispersers can be stronger or weaker competitors than residents depending

304   on the species (Anholt 1990, Hanski et al. 1991, Bowler and Benton 2005, Cadotte et al.

305   2006, Duckworth and Badyaev 2007). Overall, our results need to be generalised to other

306   species in different ecological networks, which could ultimately benefit theories on meta-

307   ecosystem functioning by inferring finer predictive outputs.

308   To conclude, we found that dispersal syndromes, the differences between resident and

309   disperser individuals, affect ecosystem functioning with dispersers decreasing biomass

310   productivity compared to residents. This effect was not dependent upon the intraspecific

311   variability in dispersal syndromes we have measured in this experiment. These results suggest

312   that individual strategies linked to dispersal can affect the dynamics of meta-ecosystems,

313   potentially through variability in competitive abilities. Measuring other dispersal-related traits

314   than those related to morphology or growth (*e.g.*, behavioural and physiological) would allow

315   assessing more precisely the mechanisms explaining the described effects of dispersal

316   syndromes on ecosystems. An interesting perspective would be to integrate the ecological

317   differences between dispersers and residents in spatially explicit meta-ecosystem models to

318   test for the effects of dispersal syndromes on several aspects of meta-ecosystem dynamics.

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329   **References**

330   Altermatt, F. et al. 2015. Big answers from small worlds: a user's guide for protist
331   microcosms as a model system in ecology and evolution. - Methods Ecol. Evol. 6:
332   218–231.

333   Anholt, B. R. 1990. Size-biased dispersal prior to breeding in a damselfly. - Oecologia 83:
334   385–387.

335   Baguette, M. et al. 2013. Individual dispersal, landscape connectivity and ecological
336   networks. - Biol. Rev. 88: 310–326.

337   Bassar, R. D. et al. 2010. Local adaptation in Trinidadian guppies alters ecosystem processes.
338   - Proc. Natl. Acad. Sci. 107: 3616–3621.

339   Bohannan, B. J. M. et al. 2002. Trade-offs and coexistence in microbial microcosms.: 107–
340   115.

341   Bonte, D. et al. 2012. Costs of dispersal. - Biol. Rev. 87: 290–312.

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

344   Bruns, P. J. and Brussard, T. B. 1974. Pair formation inTetrahymena pyriformis, an inducible
345   developmental system. - J. Exp. Zool. 188: 337–344.

346   Cadotte, M. W. et al. 2006. On testing the competition-colonization trade-off in a multispecies
347   assemblage. - Am. Nat. 168: 704–709.

348   Cayuela, H. et al. 2019. Transgenerational dispersal plasticity and its fitness consequences are
349   under genetic control.

350   Chessel, D. et al. 2007. ade4: Analysis of ecological data: exploratory and euclidean methods
351   in multivariate data analysis and graphical display. R package version.: 1–4.

352   Chesson, P. 2000. Mechanisms of maintenance of species diversity. - Annu. Rev. Ecol. Syst.
353   31: 343–366.

354 Clobert, J. et al. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and
355   the dynamics of spatially structured populations. - Ecol. Lett. 12: 197–209.

356 Clobert, J. et al. 2012. Dispersal ecology and evolution. - Oxford University Press.

357 Collins, K. 2012. Tetrahymena thermophila. - Methods in Cell Biology - Elsevier.

358 Comte, L. and Olden, J. D. 2018. Evidence for dispersal syndromes in freshwater fishes. -
359   Proc. R. Soc. B Biol. Sci. 285: 20172214.

360 Cote, J. et al. 2017a. Evolution of dispersal strategies and dispersal syndromes in fragmented
361   landscapes. - Ecography 40: 56–73.

362 Cote, J. et al. 2017b. Non-random dispersal mediates invader impacts on the invertebrate
363   community. - J. Anim. Ecol. 86: 1298–1307.

364 Des Roches, S. et al. 2018. The ecological importance of intraspecific variation. - Nat. Ecol.
365   Evol. 2: 57–64.

366 Doerder, P. and Brunk, C. 2012. Chapter 9 - Natural populations and inbred strains of
367   tetrahymena. - In: Tetrahymena thermophila. Method in Cell Biology - Elsevier, in
368   press.

369 Duckworth, R. A. and Badyaev, A. V. 2007. Coupling of dispersal and aggression facilitates
370   the rapid range expansion of a passerine bird. - Proc. Natl. Acad. Sci. 104: 15017–
371   15022.

372 Edelaar, P. and Bolnick, D. I. 2012. Non-random gene flow: an underappreciated force in
373   evolution and ecology. - Trends Ecol. Evol. 27: 659–665.

374 Edelaar, P. et al. 2008. Matching habitat choice causes directed gene flow: a neglected
375   dimension in evolution and ecology. - Evolution 62: 2462–2472.

376 Elliott, A. M. and Hayes, R. E. 1953. Mating types in Tetrahymena. - Biol. Bull. 105: 269–
377   284.

378 Fjerdingstad, E. J. et al. 2007. Evolution of dispersal and life history strategies – Tetrahymena
379   ciliates. - BMC Evol. Biol. 7: 133.

380 Ghoul, M. and Mitri, S. 2016. The ecology and evolution of microbial competition. - Trends
381   Microbiol. 24: 833–845.

382 Gounand, I. et al. 2018. Meta-ecosystems 2.0: rooting the theory into the field. - Trends Ecol.
383   Evol. 33: 36–46.

384 Hanski, I. et al. 1991. Natal Dispersal and Social Dominance in the Common Shrew Sorex
385   araneus. - Oikos 62: 48.

386 Harmon, L. J. et al. 2009. Evolutionary diversification in stickleback affects ecosystem
387   functioning. - Nature 458: 1167–1170.

388 Hart, S. P. et al. 2016. How variation between individuals affects species coexistence (T
389   Coulson, Ed.). - Ecol. Lett. 19: 825–838.

390 Harvey, E. et al. 2016. Spatially cascading effect of perturbations in experimental meta-
391   ecosystems. - Proc. R. Soc. B Biol. Sci. 283: 20161496.

392 Hastie, T. 2018. gam: generalized additive models. – R package ver. 1.16. in press.

393 Jacob, S. et al. 2017. Gene flow favours local adaptation under habitat choice in ciliate
394   microcosms. - Nat. Ecol. Evol. 1: 1407–1410.

395 Jacob, S. et al. 2018. Habitat choice meets thermal specialization: Competition with
396   specialists may drive suboptimal habitat preferences in generalists. - Proc. Natl. Acad.
397   Sci. 115: 11988–11993.

398 Jacob, S. et al. 2019. Variability in Dispersal Syndromes Is a Key Driver of Metapopulation
399   Dynamics in Experimental Microcosms. - Am. Nat. 194: 613–626.

400 Jacob, S. et al. 2020. Fragmentation and the context-dependence of dispersal syndromes:
401   matrix harshness modifies resident-disperser phenotypic differences in microcosms. -
402   Oikos: oik.06857.

403 Kahm, M. et al. 2010. Grofit: Fitting biological growth curves. - Nat. Preced. in press.

404 Kneitel, J. M. and Chase, J. M. 2004. Trade-offs in community ecology: linking spatial scales
405   and species coexistence. - Ecol. Lett. 7: 69–80.

406 Le Galliard, J.-F. et al. 2012. Patterns and processes of dispersal behaviour in arvicoline
407   rodents: dispersal mechanisms in microtine rodents. - Mol. Ecol. 21: 505–523.

408 Legrand, D. et al. 2015. Ranking the ecological causes of dispersal in a butterfly. - Ecography
409   38: 822–831.

410 Legrand, D. et al. 2016. Evolution of a butterfly dispersal syndrome. - Proc. R. Soc. B Biol.
411   Sci. 283: 20161533.

412 Little, C. J. et al. 2019. Dispersal syndromes can impact ecosystem functioning in spatially
413   structured freshwater populations. - Biol. Lett. 15: 20180865.

414 Loreau, M. et al. 2003a. Meta-ecosystems: a theoretical framework for a spatial ecosystem
415   ecology. - Ecol. Lett. 6: 673–679.

416 Loreau, M. et al. 2003b. Biodiversity as spatial insurance in heterogeneous landscapes. - Proc.
417   Natl. Acad. Sci. 100: 12765–12770.

418 MacLean, S. A. and Beissinger, S. R. 2017. Species' traits as predictors of range shifts under
419   contemporary climate change: A review and meta-analysis. - Glob. Change Biol. 23:
420   4094–4105.

421 Massol, F. et al. 2011. Linking community and ecosystem dynamics through spatial ecology:
422   An integrative approach to spatial food webs. - Ecol. Lett. 14: 313–323.

423 Massol, F. et al. 2017. How life-history traits affect ecosystem properties: effects of dispersal
424   in meta-ecosystems. - Oikos 126: 532–546.

425 Messager, M. L. and Olden, J. D. 2019. Phenotypic variability of rusty crayfish (*Faxonius*
426   *rusticus*) at the leading edge of its riverine invasion. - Freshw. Biol. 64: 1196–1209.

427 Mille-Lindblom, C. et al. 2006. Antagonism between bacteria and fungi: substrate
428   competition and a possible tradeoff between fungal growth and tolerance towards
429   bacteria. - Oikos 113: 233–242.

430 Mitri, S. and Foster, K. R. 2013. The genotypic view of social interactions in microbial
431   communities. - Annu. Rev. Genet. 47: 247–273.

432 Mouquet, N. and Loreau, M. 2003. Community patterns in source-sink metacommunities. -
433   Am. Nat. 162: 544–557.

434 Pennekamp, F. and Schtickzelle, N. 2013. Implementing image analysis in laboratory-based
435   experimental systems for ecology and evolution: a hands-on guide. - Methods Ecol.
436   Evol. 4: 483–492.

437 Pennekamp, F. et al. 2014. Dispersal propensity in *Tetrahymena thermophila* ciliates - a
438   reaction nom perspective. - Evolution 68: 2319–2330.

439 Pennekamp, F. et al. 2019. The interplay between movement, morphology and dispersal in
440   *Tetrahymena* ciliates. - PeerJ 7: e8197.

441 Phillips, B. L. et al. 2010. Life-history evolution in range-shifting populations. - Ecology 91:
442   1617–1627.

443 R Core Team 2013. R: a language and environment for statistical computing. in press.

444 Raffard, A. et al. 2019. The community and ecosystem consequences of intraspecific
445   diversity: a meta-analysis. - Biol. Rev. 94: 648–661.

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

448 Saastamoinen, M. et al. 2018. Genetics of dispersal: Genetic of dispersal. - Biol. Rev. 93:
449   574–599.

450 Sandau, N. et al. 2019. Understanding negative biodiversity–ecosystem functioning
451   relationship in semi-natural wildflower strips. - Oecologia 189: 185–197.

452 Schmid, D. W. et al. 2019. Rapid divergence of predator functional traits affects prey
453   composition in aquatic communities. - Am. Nat. 193: 331–345.

454 Schtickzelle, N. et al. 2009. Cooperative social clusters are not destroyed by dispersal in a
455   ciliate. - BMC Evol. Biol. 9: 251.

456 Shine, R. et al. 2011. An evolutionary process that assembles phenotypes through space rather
457   than through time. - Proc. Natl. Acad. Sci. 108: 5708–5711.

458 Stevens, V. M. et al. 2014. A comparative analysis of dispersal syndromes in terrestrial and
459   semi-terrestrial animals. - Ecol. Lett. 17: 1039–1052.

460 Thompson, P. L. and Gonzalez, A. 2017. Dispersal governs the reorganization of ecological
461   networks under environmental change. - Nat. Ecol. Evol. 1: 0162.

462 Thompson, K. et al. 2005. Biodiversity, ecosystem function and plant traits in mature and
463   immature plant communities. - Funct. Ecol. 19: 355–358.

464 Thompson, P. L. et al. 2020. A process-based metacommunity framework linking local and
465   regional scale community ecology. - Ecol. Lett. 23: 1314–1329.

466 Turcotte, M. M. and Levine, J. M. 2016. Phenotypic plasticity and species coexistence. -
467   Trends Ecol. Evol. 31: 803–813.

468 Winandy, L. et al. 2019. Local predation risk and matrix permeability interact to shape
469   movement strategy. - Oikos 128: 1402–1412.

470 Wolf, M. and Weissing, F. J. 2012. Animal personalities: consequences for ecology and
471   evolution. - Trends Ecol. Evol. 27: 452–461.

472 Zera, A. J. and Brisson, J. A. 2012. Quantitative, physiological, and molecular genetics of
473   dispersal/migration. - In: Dispersal: causes and consequences. Oxford Univ. Press, pp.
474   63–82.

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477 **Figure captions**

478 **Figure 1.** Variability of phenotypic traits (extracted from PCA) among twenty genotypes of

479 *Tetrahymena thermophila*. The first axis expresses demography (population growth rate and

480 maximal density), and the second axis expresses morphology (cell size and elongation). Mean

481 values (±SE among 5 replicates) for residents and dispersers for each genotype are displayed.

482

483 **Figure 2.** Impact of dispersers and residents on community biomass: effects of introducing *T.*

484 *thermophila* residents or dispersers of each genotype in a ciliate community on its maximal

485 biomass **(a & b)** and biomass production **(c & d)**. Left panels **(a & c)** are averaged effects

486 over all 20 genotypes, whose individual results are presented on right panels **(b & d)**, sorted

487 from small to high mean.

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490 **Figure 1**
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494 **Figure 2**
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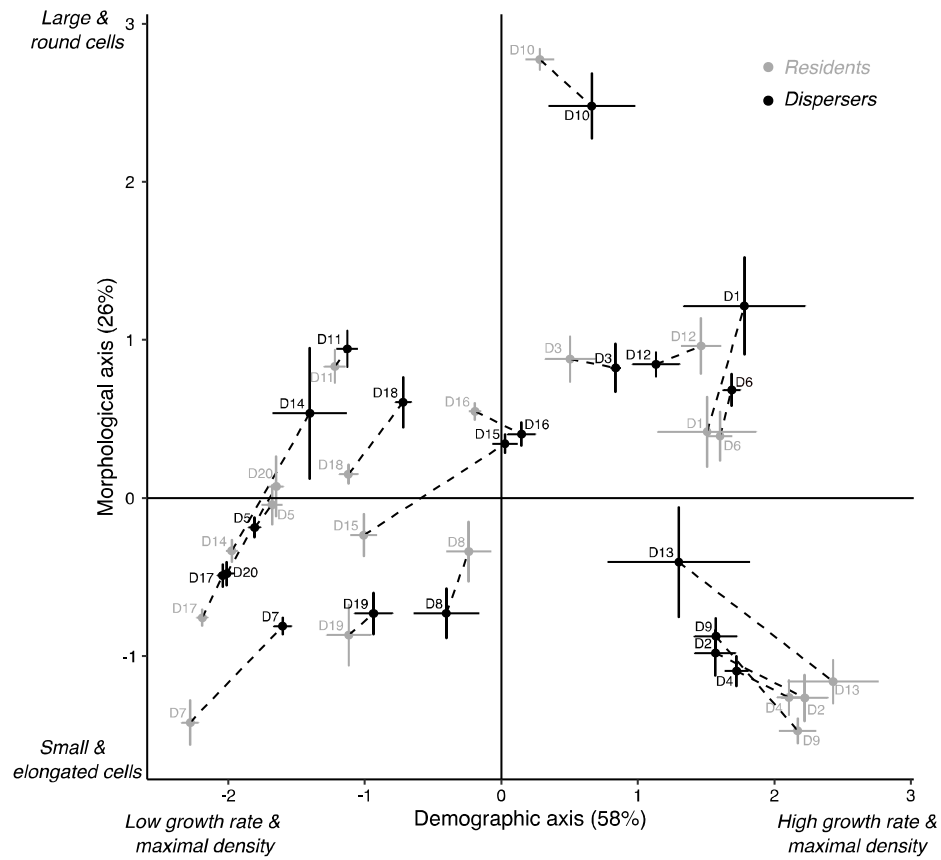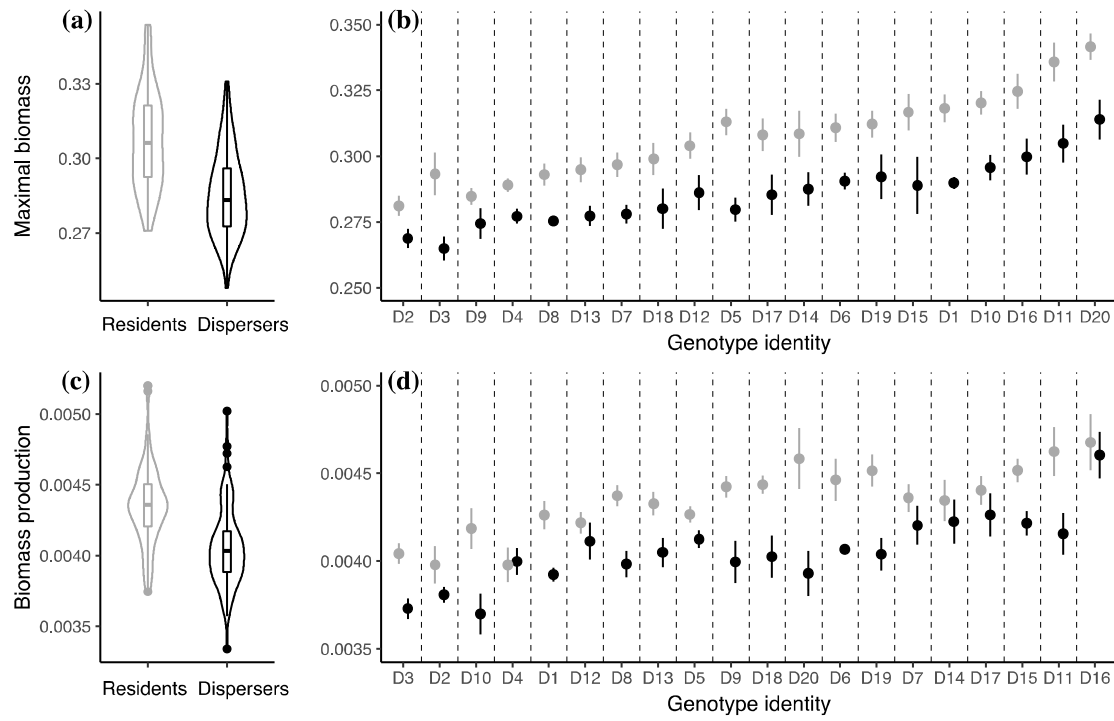
496 **Table 1.** Effect of dispersal status (dispersers vs residents) and *T. thermophila* genotype on

497 the position in the PCA space defined by a demographic axis and a morphological axis.

	Sum sq	df	F	*p*-value	R^2
Demographic axis					0.94
Dispersal status	0.07	1, 160	0.448	0.504	0.00
Genotype	431.16	19, 160	138.025	<0.001	0.91
Dispersal status × Genotype	12.50	19, 160	4.003	<0.001	0.03
Morphological axis					0.90
Dispersal status	2.23	1, 160	17.903	<0.001	0.01
Genotype	178.05	19, 160	75.180	<0.001	0.85
Dispersal status × Genotype	8.09	19, 160	3.419	<0.001	0.04

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23

499 **Table 2.** Effect on maximal biomass and biomass production of the 40 types of *T.*

500 *thermophila* cells that were introduced (20 genotypes × 2 residents/dispersers status)

501 considered either as combinations of the dispersal status and genotype identity **(a)** or as

502 positions that they occupy along the demographic and morphological PCA axes **(b).**

503 Significant variables are in bold.

	Sum sq	df	F	*p*-value	R^2
(a)					
Maximal biomass					0.69
Dispersal status	**0.023**	**1, 160**	**140.766**	**< 0.001**	**0.26**
Genotype	**0.036**	**19, 160**	**11.567**	**< 0.001**	**0.41**
Dispersal status × Genotype	0.002	19, 160	0.615	0.891	0.02
Biomass production					0.60
Dispersal status	**4.2×10^{-6}**	**1, 160**	**88.839**	**< 0.001**	**0.21**
Genotype	**6.2×10^{-6}**	**19, 160**	**6.831**	**< 0.001**	**0.31**
Dispersal status × Genotype	1.4×10^{-6}	19, 160	1.593	0.063	0.07
(b)					
Maximal biomass					0.15
Demographic axis	**0.007**	**1, 197**	**19.898**	**< 0.001**	**0.09**
Morphological axis	**0.005**	**1, 197**	**29.909**	**< 0.001**	**0.06**
Biomass production					0.07
Demographic axis	**1.3×10^{-6}**	**1, 197**	**13.661**	**< 0.001**	**0.06**
Morphological axis	1.4×10^{-8}	1, 197	1.521	0.219	< 0.01

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