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► **To cite this version:**

Mélanie Thierry, Léonard Dupont, Delphine Legrand, Staffan Jacob. Phenotypic and dispersal plasticity are not alternative strategies for organisms to face thermal changes. *Proceedings of the Royal Society B: Biological Sciences*, 2025, 292 (2045), pp.20242796. <10.1098/rspb.2024.2796>. <hal-05391874>

HAL Id: hal-05391874

<https://hal.science/hal-05391874v1>

Submitted on 3 Dec 2025

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Journal:	<i>Proceedings B</i>
Manuscript ID	RSPB-2024-2796.R2
Article Type:	Research
Subject:	Behaviour < BIOLOGY, Ecology < BIOLOGY, Evolution < BIOLOGY
Keywords:	dispersal, phenotypic plasticity, movement, temperature, protists, emigration
Proceedings B category:	Evolution

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Phenotypic and dispersal plasticity are not alternative strategies for organisms to face thermal changes

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Running title: Local phenotypic plasticity and dispersal plasticity

Abstract

To buffer the effects of local environmental changes, organisms may modify their phenotypic traits (*i.e.*, phenotypic plasticity), or disperse toward other potential habitats (*i.e.*, dispersal plasticity). Despite extensive work studying either ‘local phenotypic plasticity’ or ‘dispersal plasticity’ independently, little is known about their potential covariation and interplay. These strategies are classically viewed as alternatives. However, this expectation has been challenged by theoretical work suggesting that they may instead evolve together under some environmental contexts. Here, we experimentally quantified morphological, movement, and dispersal plasticity in response to thermal changes in twelve strains of the ciliate *Tetrahymena thermophila*. We showed that phenotypic and dispersal plasticity are not alternative strategies, with half of the strains expressing simultaneously all dimensions of plasticity in response to thermal changes. Furthermore, the extent of morphological and movement plasticity weakly but significantly differed between residents and dispersers. Interestingly, we found no covariation between these different plasticity dimensions, suggesting that they may evolve independently, which pleads for studying which environmental contexts favour the evolution of each. The fact that phenotypic and dispersal

23 plasticity are not alternative strategies and may affect the expression of one another opens interesting
24 perspectives about their joint evolution and the potential consequences of their interplay.

25 **Key words:** dispersal, phenotypic plasticity, movement, emigration, temperature, protists

26 **Introduction**

27 Following an environmental change impacting their fitness, organisms may deal with the new local
28 conditions through a variety of strategies, including phenotypic plasticity, genetic adaptation, and
29 adjustment of the environment [1–3]. Local phenotypic plasticity, the ability of a genotype to produce
30 different phenotypes depending on the local environment, is expected to help organisms buffer the effects
31 of environmental changes [1,4]. This widespread mechanism is known as key for ecological and
32 evolutionary dynamics, allowing organisms to persist in changing or stressful environments [1,4–7]. For
33 instance, the western white butterfly (*Pontia occidentalis*) adaptively changes its colour pattern depending
34 on the season (*i.e.*, polyphenism) [8], and the microalga *Dunaliella salina* changes cell shape and content
35 to face temporal fluctuations of salinity [9].

36 Instead of dealing with new (unfavourable) local environmental conditions, organisms may avoid
37 them by dispersing toward another habitat [10–12]. Dispersal plasticity (also called context-dependent
38 dispersal) is a form of phenotypic plasticity in which the plastic trait is the decision of an organism to
39 emigrate from the local patch to disperse toward other potential habitats [13–16]. For instance, five ciliate
40 species of the genus *Tetrahymena* have been showed to change their emigration decisions across abiotic
41 gradients in microcosms, dispersal decisions that were correlated with the fitness sensitivity to these
42 environmental gradients [13]. Likewise, the Asteraceae *Crepis sancta* and *Carduus nutans* produce seed
43 dispersal morphs, hence plastically increasing emigration rates, both when nutrients are depleted [17] and
44 under drought conditions [18], respectively. Dispersal plasticity can strongly affect local adaptation,
45 metapopulation dynamics and meta-ecosystem functioning [19–23]. The first step of dispersal plasticity
46 consists in whether to stay in the local environment or leave it by initiating dispersal, *i.e.*, emigration
47 decision [14,21]. This first step has been shown to potentially have as strong consequences on
48 metapopulation dynamics and local adaptation as habitat choice at settlement can have [23,24].

49 Local phenotypic plasticity and dispersal plasticity may be considered as alternative mechanisms:
50 why change your phenotype if you can change your environment, and *vice versa* [25]? On the one hand,
51 adaptive dispersal plasticity allows organisms to leave unsuitable conditions to potentially find better ones
52 in a landscape. These plastic dispersal decisions should decrease the range of environments experienced by
53 individuals and may therefore mitigate the benefits of being locally phenotypically plastic. Dispersal
54 plasticity should thus favour the evolution of phenotypically non-plastic specialists [23,26–30]. On the other
55 hand, plastic changes in traits related to fitness in the local conditions should help organisms deal with local
56 environmental changes and thus allow high environmental generalism. As locally plastic organisms should
57 maintain their fitness across a wider range of environmental conditions, they should thus not need to adjust
58 their dispersal decisions compared to non-locally plastic organisms.

59 However, recent theoretical models [31,32] suggest that local phenotypic plasticity and dispersal
60 plasticity may sometimes evolve together. Especially, Scheiner's model [31] demonstrates that temporal
61 variations in environmental conditions can favour the evolution of phenotypic plasticity, even in the
62 presence of dispersal plasticity. Some empirical examples also challenged this view of phenotypic and
63 dispersal plasticity being alternatives, looking at dispersal plasticity at immigration (*i.e.*, habitat choice).
64 The ambush bug *Phymata americana* uses a combination of morphological and dispersal plasticity to match
65 its colour to the background in order to increase its prey capture success rate [33] while the chameleon
66 prawn *Hippolyte varians* uses the same mechanism of matching colour to improve its camouflage to the
67 perspective of predatory fishes [34]. The amphibious fish *Kryptolebias marmoratus* moves on land when
68 the water becomes hypoxic, and thus remodels its gill in order to survive out of the water [35]. Thermal
69 generalism is known to be associated with morphological plasticity in *T. thermophila* [36], and the more
70 generalist genotypes showed plastic immigration decisions in a habitat choice experiment [37]. Therefore,
71 whether local phenotypic plasticity and dispersal plasticity should be evolutionary alternatives or should
72 co-evolve likely depends on the characteristics of environmental changes, potential genetic covariation

73 between the two forms of plasticity, and the subsequent relative costs and benefits of these mechanisms
74 [25].

75 Further, plastic phenotypic changes may not only serve for local adaptation but can occur together
76 with the dispersal movement itself [14,38]. Phenotypic plasticity may indeed help organisms to perform
77 dispersal movements and deal with environmental conditions encountered during or after dispersal [33,35].
78 In these cases, we can expect local phenotypic plasticity and dispersal plasticity to be complementary rather
79 than alternative strategies, and to thus co-occur. Dispersal is often associated with a suite of other
80 phenotypic traits that enable dispersal or enhance dispersal success, also called dispersal syndrome
81 [14,38,39]. Across taxonomic groups, dispersers are often larger, with a marked locomotion-oriented
82 morphology, more active, and move faster than residents [40–42]. While these dispersal-traits associations
83 may result from genetic differences between residents and dispersers, phenotypic plasticity has also been
84 shown to play a key role in the establishment of resident-disperser phenotypic differences [38,43,44]. This
85 points out the possibility for important interplays between phenotypic and dispersal plasticity in driving
86 ecological and evolutionary dynamics when organisms evolve both strategies.

87 In this study, we investigated whether local phenotypic plasticity and dispersal plasticity at
88 emigration were alternative strategies, or on the contrary were both expressed in response to environmental
89 changes. We specifically investigated the first step of dispersal plasticity, namely the emigration decision
90 (*i.e.*, whether to stay in and deal with the local environment or leave it by initiating dispersal). To do so, we
91 quantified morphological, movement, and dispersal plasticity across twelve isogenic and clonally
92 reproducing strains of the ciliate *Tetrahymena thermophila* in response to thermal changes. This species
93 has been used as a model system in cellular and molecular biology for decades [45] and shows high
94 intraspecific variability in morphology, movement and dispersal rates [46,47]. Furthermore, the plasticity
95 of both phenotypic traits and dispersal show high intraspecific variability [13,37,48], which thus provides
96 the materials to investigate whether these two dimensions of plasticity covary. Morphology was
97 characterized as cell size, a trait known to be linked to resource acquisition and metabolic rate [49], and

98 cell shape that modifies surface area to volume ratio and thus sets protists energetic intake [50]. Linking
99 local phenotypic plasticity to fitness was not the aim of this study and could not be done with our
100 experimental design. However, in protists, cell size and shape are correlated with thermal performance
101 curve parameters and intrinsic growth rates [50]. Further, morphological plasticity in response to local
102 thermal fluctuations is associated with local performance in *T. thermophila* strains [36]. We therefore
103 predicted morphological plasticity to be mainly associated with strain adapting locally rather than
104 dispersing depending on environmental conditions. Movement was described as cell velocity, a trait often
105 linked to dispersal in this species [47,51], and trajectory linearity [47]. For dispersal plasticity, we quantified
106 temperature effects on emigration decisions [14,21]. Previous studies revealed a match between preference
107 at emigration and immigration in this species [37,52]. Under the hypothesis that local and dispersal
108 plasticity would be alternative strategies, we expected to see less dispersal plasticity in the most
109 morphologically plastic strains. However, theoretical and empirical evidence reviewed above suggest that
110 the two strategies may both be expressed in the same organisms exposed to the same environmental
111 conditions, thus leading to the expectation of a co-occurrence of local phenotypic and dispersal plasticity
112 within strains. Due to the expected link between movement traits and dispersal, we could expect movement
113 plasticity (*i.e.*, plastic changes in movement velocity and linearity) to be strongly associated with dispersal
114 plasticity. We also investigated whether the plasticity of morphological and movement traits covary.
115 Furthermore, we tested whether morphological and movement plasticity and their covariation differed
116 depending on dispersal decisions, as expected if dispersal itself or the associated changes of environmental
117 conditions encountered drive phenotypic plasticity or if phenotypic plasticity promotes dispersal. We
118 expected dispersers to show higher plasticity for traits related to movement and residents to show higher
119 plasticity for traits related to local adaptation. We further investigated the effects of the rate and amplitude
120 of the thermal change on local phenotypic plasticity and dispersal plasticity at emigration using a subset of
121 the strains.

122 **Materials and Methods**

123 ***Biological system***

124 We used twelve isogenic strains (D1, D2, D3, D6, D8, D9, D10, D12, D13, D16, D17, D19; Table S1) of
125 the ciliate *Tetrahymena thermophila*, a 20 to 50 μm micro-eukaryote naturally living in freshwater ponds
126 and streams in the Eastern United States [53,54]. The natural distribution of this species is restricted to the
127 Eastern United States where the strains were sampled, with a pattern of moderate endemism [54], in contrast
128 to other related species that show global distribution [55]. The strains were initially collected in the field
129 by Dr. Paul Doerder (Cleveland State University, USA) around 20 years ago (roughly representing $\sim 20,000$
130 clonal generations in the laboratory). They have been kept in the Station d'Ecologie Théorique et
131 Expérimentale of Moulis (France) since 2014 where they have been maintained in 24-wells culture plates
132 at 23 °C and axenic media (0.6 % Difco proteose peptone, 0.06 % yeast extract) with transfer every ~ 10
133 days. These twelve strains represent a large part of the phenotypic [56–58] and genomic [59] diversity in
134 the known natural isolates of *T. thermophila* (the strains differ from $\sim 1,000$ to more than 1,000,000 SNPs
135 from each other and are representative of six distinct genomic types [59]). These organisms are known to
136 be able to change their dispersal decisions depending on thermal conditions [13,23,37,52]. Prior to
137 experiments, strains were allowed to grow from 1 mL of stock culture into 10 mL of media in Falcon tubes
138 for seven days to obtain sufficient volumes for experiments. All manipulations were performed in sterile
139 conditions under a laminar flow hood.

140 ***Experimental design***

141 Firstly, we quantified the plasticity (*i.e.*, both the magnitude and the direction of the phenotypic change) of
142 cell morphology and movement in the absence of dispersal for each strain (Fig. 1A). We exposed the twelve
143 isolated strains to two temperatures: 23°C (the standard temperature at which strains are maintained in the
144 laboratory) and 35°C (a thermally stressful condition previously used for habitat choice experiments
145 [23,37,52]) for three hours. To make these results comparable with the dispersal assay regarding the
146 physical content in which cells are cultured, this quantification of phenotypic plasticity was performed

147 using standard dispersal systems as presented below, but preventing dispersal by keeping the corridors
148 closed.

149 In parallel, we quantified dispersal plasticity in response to the same thermal change using standard
150 1.5 mL two-patch systems connected by a corridor (4 mm internal diameter, 2.5 cm long silicone tube)
151 filled with growth medium (Fig. 1A). We inoculated one patch of these two-patch systems with 300 μ l of
152 the one-week-old culture (close to asymptotic density) and let cells disperse. After three hours we closed
153 the corridors to prevent further movements. This time is below the minimum generation time at the tested
154 temperatures but leaves sufficient time for cells to disperse [13] with negligible back and forth movement
155 between patches.

156 We performed five replicates per strain, temperature, and dispersal treatment ($N = 240$) in two
157 consecutive days (six strains with all treatments and replicates per block). To initiate the experiment, we
158 placed the inoculated systems in their corresponding temperature (incubator PolEko SmartPro) after a 30-
159 minute acclimation period at 23°C. For all systems, we quantified cell morphology, movement, and
160 dispersal rate after three hours by recording 15s videos of 10 μ l samples placed in counting slides (Kima
161 precision cell) under dark-field microscopy (Axio Zoom V16, Zeiss). We quantified cell abundance,
162 morphology and movement characteristics from the videos recorded using the BEMOVI R-package [60].
163 We calculated emigration rate as $\frac{N_{disp}}{N_{resi} + N_{disp}}$, where N_{disp} and N_{resi} are the abundance of dispersers and
164 residents, respectively. Dispersal plasticity at emigration were then quantified as the effect of local
165 temperature on dispersal rate (see below). We quantified cell morphology as cell size and cell shape (*i.e.*,
166 the ratio of cell major/minor axes). We characterized cell movement as velocity (*i.e.*, the total distance
167 travelled by cells divided by the duration of the trajectory) and trajectory linearity (ratio between the net
168 distance travelled and the total distance effectively moved through a more or less tortuous way) [47].
169 Because strains reproduce clonally in laboratory conditions, differences in trait values between replicated
170 environmental conditions for a given clonal strain result from the expression of phenotypic plasticity [48].

171 In a small complementary experiment, we investigated the co-occurrence and co-variation of
172 morphology, movement, and dispersal plasticity depending on the rate and the amplitude of thermal
173 changes. We used three of the twelve strains used in the main experiment (D2, D3, and D6). We exposed
174 them for three hours to three temperatures: 23°C, 35°C, and 31°C, an additional temperature corresponding
175 to the upper margin of 80% of the area under a Gaussian distribution representative of averaged thermal
176 tolerance curve in this species [23]. We quantified the influence of the rate of thermal changes on local
177 phenotypic plasticity and dispersal plasticity by setting up either a fast (*i.e.*, immediate thermal change with
178 thermic inertia from 23°C to either 31 or 35°C) or a gradual (*i.e.*, gradual increase every five minutes over
179 three hours from 23°C to either 31 or 35°C) increase in temperature. An immediate increase in temperature
180 correspond to the commonly used treatment to characterize phenotypic plasticity with reaction norms (*i.e.*,
181 the relationship between a given trait and an environmental gradient). The rest of the design was similar to
182 the one described above. We performed five replicates per strain, temperature, thermal change, and
183 dispersal treatment (N = 150).

184 ***Data analysis***

185 Firstly, we quantified morphology, movement, and dispersal plastic capacity for each strain along
186 the thermal axis and investigated if these plasticity types co-occurred and co-varied (Fig. 1B). To do so, we
187 modelled for the main experiment, morphology and movement without dispersal and dispersal rates
188 depending on temperature (two levels: 23 and 35°C), strains (twelve levels), and their two-way interactions.
189 All morphological and movement traits were standardized (*i.e.*, centred and scaled within traits) to allow
190 effect size comparison between traits. We included our block-day as a random effect to account for temporal
191 effect (two blocks). We verified model assumptions with the *DHARMA* package [61]. To correct for
192 heteroscedasticity of the residuals, dispersal rates were modelled using a beta-binomial error distribution
193 and a logit link function using the *glmTMB* function from the *TMB* package [62]. Morphological and
194 movement traits were modelled using a Gaussian error distribution and the *lme4* package. P-value were
195 adjusted with *holm* correction to account for multiple testing when appropriate. The significance of the

196 effects was tested using Wald type III analysis of deviance with Likelihood-ratio tests. Adjusted r^2 for the
197 whole model and each factor and interaction within were obtained with the *r.squaredLR* function of the
198 *MuMIn* package [63]. Factor levels were compared by Tukey's HSD *post hoc* comparisons of all means,
199 using the *emmeans* package [64], to extract the effect size of temperature on traits for each trait and each
200 strain quantifying plastic capacities. We tested for correlation between pairs of raw traits in each condition
201 (Table S1, Fig. S1), pairs of directional plasticity indices (effect sizes; hereafter, plasticities), and pairs of
202 plastic capacities (absolute effect size) with the Spearman's rank test (*cor.test* function). The relationship
203 between absolute values of plasticity allows to investigate whether the different dimensions of plasticity
204 are alternative or not, regardless of their direction, while the relationships between directional plasticity
205 indices allows to look at specific associations between these plastic strategies. All analyses were performed
206 using R 4.2.1 [65].

207 For the complementary experiment, we modelled morphology and movement without dispersal,
208 and dispersal rates depending on temperature (three levels: 23, 31 and 35°C), strains (three levels), and their
209 two-way interactions for each rate of thermal change. We then tested whether morphological, movement,
210 and dispersal plasticity (*i.e.*, differences between standard and warmer temperatures) differed depending on
211 the rate of thermal change (two levels: immediate and gradual), the amplitude of thermal change (two levels:
212 31 and 35°C), the strains (three levels: D2, D3, and D6), and their two- and three-way interactions. We
213 investigated whether correlations between the different plasticities changed when the thermal change was
214 gradual compared to immediate change using a Spearman's rank correlation.

215 Secondly, we tested whether the opportunity to disperse changed how strains performed morphological
216 and movement plasticity compared to when dispersal was not allowed. To do so, we included dispersal
217 status (three levels: without dispersal, residents in treatment with dispersal, and dispersers) in our models,
218 and the two- and three-way interactions with temperature and strain. The dispersal system identity was
219 included as a random effect to account for biological non-independence. Effect sizes of temperature were
220 computed within each level of dispersal status as explained above.

221 **Results**

222 ***Local phenotypic plasticity and dispersal plasticity are not alternative strategies***

223 Plasticity varied between strains for all five tested variables (two-way interaction between temperature and
224 strains for cell size: $\eta^2_{(11)} = 134.0$, P-value < 0.0001, $r^2 = 0.084$; for cell shape: $\eta^2_{(11)} = 117.6$, P-value <
225 0.0001, $r^2 = 0.169$; for velocity: $\eta^2_{(11)} = 163.8$, P-value < 0.001, $r^2 = 0.242$; for linearity: $\eta^2_{(11)} = 149.3$, P-
226 value < 0.001, $r^2 = 0.236$; for dispersal rate: $\chi^2_{(11)} = 30.2$, P-value = 0.0002, $r^2 = 0.109$; Table S3, Fig. S2).
227 Half of the strains (6 out of 12) significantly expressed the five types of plasticity measured (all four local
228 phenotypic plasticity and dispersal plasticity) (Fig. 2, Fig. S3, Table S4). Five strains did not express
229 significant dispersal plasticity, among which two were plastic for all the local phenotypic traits measured
230 (D8 and D17), and the three others for traits related to morphology, but not to movement (D13, D16, D19)
231 (Fig. 2, Fig. S3, Table S4).

232 Despite co-occurrence of the different types of plasticity, there were no significant correlations
233 between local phenotypic (morphology and movement) and dispersal plasticities (*i.e.*, effect size of
234 temperature on traits for each strain; Table S5, Fig. S3) nor plastic capacities (*i.e.*, absolute effect size;
235 Table S6, Fig. 2). Similarly, we found no significant correlation between size and movement plasticity, but
236 we did find a positive correlation between velocity and linearity plasticity (Fig. S3, Tables S5&S6) and a
237 negative correlation between shape and linearity plastic capacities (Fig. 2, Table S6).

238 ***Differences in morphological and movement plasticity between residents and dispersers***

239 When dispersal was allowed, morphological and movement plasticity significantly differed compared to
240 without dispersal, with effects that varied across strains and dispersal status (residents or dispersers in the
241 dispersal treatment and individuals in the no-dispersal treatment; three-way interaction between
242 temperature, strains and dispersal status for cell size: $\eta^2_{(22)} = 47.2$, P-value = 0.001; for cell shape: $\eta^2_{(22)} =$
243 57.6, P-value < 0.0001; for velocity: $\eta^2_{(22)} = 70.8$, P-value < 0.0001; for linearity: $\eta^2_{(22)} = 45.6$, P-value =
244 0.002; Table S7, Table S8). Dispersers tended to become smaller in response to increased temperature than

245 individuals in the no-dispersal treatment while size plasticity of residents was in most cases similar (Fig.
246 3). Mean plastic changes for the other traits were similar between residents, dispersers and individuals in
247 the no-dispersal treatment due to high intraspecific variations in these plastic responses (Fig. 3).
248 Morphological and movement plasticity significantly changed compared to the treatments without dispersal
249 in 48% of the cases (23 out of 48 [12 strains * four traits]) for dispersers and 29% of the cases (14 out of
250 48) for residents (Fig. 3). These differences tended to lead to new correlations between the different local
251 phenotypic plasticities but no association was observed with dispersal plasticity (Tables S5&S6).

252 *Effects of the rate and the amplitude of thermal change on morphological, movement, and dispersal* 253 *plasticity*

254 Morphological plasticity was higher in case of a fast change in comparison with a gradual thermal increase
255 and a higher thermal change (Fig. S4&S5; Table S9). These differences led to some changes in correlation
256 between the different types of plasticity (Tables S10 and S11). As in the results above, marked differences
257 in the response to thermal changes were observed between residents and dispersers (Fig. S6; Table S12).

258 **Discussion**

259 Although local phenotypic plasticity and dispersal plasticity may be considered as alternative mechanisms
260 [2,25], theoretical and empirical studies pointed out that they can instead both be expressed in the same
261 organisms [31,33–35,66,67]. Accordingly, our experiment demonstrated that local phenotypic plasticity
262 and dispersal plasticity were not alternative strategies in our study system: half of the twelve *T. thermophila*
263 strains tested here expressed simultaneously morphological, movement, and dispersal plasticity. This result
264 highlights that these two dimensions of plasticity, instead of alternatives, may sometimes evolve together.
265 For instance, dispersal plasticity may benefit from the expression of phenotypic plasticity to deal with
266 environmental conditions encountered during or after dispersal [35]. Even though it can be conceptually
267 helpful to separate dispersal and phenotypic plasticity, dispersal plasticity is a form of phenotypic plasticity
268 where dispersal is the plastic trait. Both phenotypic and dispersal plasticity require environmental

269 variability with somehow reliable environmental cues to evolve [25,31]. Future studies should investigate
270 whether they may, in some organisms, share specific underlying mechanisms such as sensory structures,
271 explaining why they could co-occur.

272 In spite of both phenotypic and dispersal plasticity being expressed in most of the strains tested, we
273 did not find significant correlations between the plastic capacities of morphological, movement, and
274 dispersal. This suggests that these plasticity dimensions, despite co-occurring, might have evolved
275 independently and be favoured by different environmental contexts. Indeed, although cell morphology,
276 movement and dispersal were previously found to be correlated in *T. thermophila* [43,44,47,51,56], we did
277 not find correlation between their plasticity nor their plastic capacity. Especially, the absence of correlation
278 between thermal plasticity of cell movement and that of dispersal shows that these two dimensions of
279 plasticity are not necessarily two sides of the same mechanisms. Cell movement plasticity could enhance
280 dispersal plasticity but did not explain the changes in dispersal induced by thermal change. Indeed, strains
281 with the highest dispersal plasticity also showed relatively weak movement plasticity. Dispersal and
282 movement plasticity may represent different, partly independent responses to thermal change.

283 Further, some theoretical work predicts that the evolution of adaptive phenotypic plasticity should
284 be more common than the evolution of adaptive dispersal plasticity because the mismatch between the
285 phenotype and the new environment can be more easily resolved with changes in the local phenotype rather
286 than by finding the right environment [25,31]. However, in our experiment some strains showed weak
287 dispersal plasticity and high plasticity for other traits, other strains showed the opposite, and others had
288 more intermediate values for all types of plasticity. These results suggest that some strains may be more
289 specialized to deal with local conditions through plasticity, others might be more specialized to adjust their
290 emigration decisions, and the rest might perform both strategies. Hence, we did not find evidence for the
291 evolution of one of these strategies over the others.

292 Interestingly, we observed that the correlation between morphological and movement traits at 23°C
293 disappeared under warmer thermal condition (35°C). The loss of phenotypic integration – the pattern of

294 functional, developmental and/or genetic correlation among phenotypic traits [68] – under stressful
295 conditions was also observed in the perennial shrub *Lepidium subulatum* (Brassicaceae) [69]. Whether such
296 differences in patterns of covariation between traits depending on environmental conditions [70] may
297 constrain or on the contrary favour plasticity [69], and whether the resulting different dimensions of
298 plasticity should correlate altogether or not are open questions. In addition, phenotypic traits tended to
299 homogenize at the intraspecific level under warmer conditions while intraspecific variability was important
300 at ambient temperature, and the direction of plastic phenotypic changes differed across strains (Fig. S1).
301 This trait homogenization at warmer temperatures could be a result of adaptive plasticity, whereby traits
302 would converge towards specific values that may enhance thermal tolerance or of shared physiological
303 effects at high temperatures. Such changes in intraspecific variability may have important consequences for
304 ecological and evolutionary dynamics [71,72], especially if phenotypic plasticity leads to rapid trait changes
305 that may help organisms to deal with environmental change. Here, we looked at morphological, movement
306 and dispersal plasticity but many other traits could have responded to thermal change and covaried with the
307 plastic traits studied. For instance, the expression of heat-shock proteins (HSPs) is an important part of most
308 organisms' response to thermal change [73,74] and could be coupled with other adaptive mechanisms such
309 as changes in morphology if linked to fitness.

310 We furthermore showed that the extent of phenotypic plasticity in morphological and movement
311 traits significantly changed when strains were allowed to disperse compared to the no dispersal setup, and
312 between dispersers and residents within the dispersal treatment. These results raise the question of a
313 potential role of phenotypic plasticity in helping organisms to disperse and to improve settlement
314 probability [75,76]. One striking example found in the literature is the expression of a caudal cilium, thought
315 to help swimming movement, in 10% of *T. thermophila* cells of the same strain under starvation, an
316 environmental condition known to induce dispersal behavior [77]. Further, dispersers tended to be more
317 morphologically plastic than residents (*i.e.*, steeper reaction norms; Fig. S2). Especially, dispersers tended
318 to become smaller in response to increased temperature compared to residents and individuals in the no-

319 dispersal treatment. This hints toward local phenotypic plasticity helping dispersal, and especially size
320 plasticity. These plastic changes could be due to the dispersal movement itself, for instance because of
321 dispersal costs or the expression of specific phenotypic attributes favouring dispersal, or indirectly due to
322 differences in environmental conditions induced by dispersal [38,43,78]. Indeed, when organisms disperse
323 depending on conditions along an environmental axis, variations along other environmental axes are often
324 associated. In such case, the phenotypic changes observed may not be due to the environmental factor
325 inducing dispersal plasticity but to other associated environmental changes. For instance, dispersal can lead
326 to changes in local population densities, a biotic gradient along which traits may change [79], including
327 dispersal decisions [80,81]. In addition to local/temporal changes in environmental conditions, phenotypic
328 differences between dispersers and residents within an isogenic strain, hence without genetic variance,
329 could also be due to non-genetic mechanisms (*e.g.*, differences in gene expression, methylation, small RNA
330 contents and other molecules transmitted by the cytoplasm between cells), to developmental noise, to
331 residual phenotypic variance [82], or to the unique genome organization of ciliates. Indeed, ciliates possess
332 two nuclei, one hosting their germline that is silent except during sexual reproduction, the other hosting
333 their highly polyploid and fragmented somatic genome (about 45 copies of 181 chromosomes in *T.*
334 *thermophila*), responsible for phenotypic expression. This somatic nucleus divides amitotically during the
335 clonal phase, meaning that the chromosomes are not equally segregated and that cells do not receive the
336 exact same number of copies [45,83]. This means that while the genomic sequence does not vary (at the
337 exception of a few *de novo* mutations that should remain negligible within the short timeframe of the present
338 experiment), the chromosomal copy number does, albeit some unknown regulatory mechanisms seems to
339 avoid chromosomal loss [84]. Environmental variation, non-genetic mechanisms, developmental noise and
340 chromosomal content can all induce phenotypic variance within isogenic strain potentially influencing
341 dispersal, and/or creating differences in phenotypes between residents and dispersers as observed here and
342 in other studies. However, this should be considered cautiously because the effect of dispersal status on
343 phenotypic changes remained weak, with important differences between strains. Strain identity explained
344 the most part of the phenotypic response observed, as in [56,85].

345 Here, we cannot determine whether the phenotypic changes occurred before the initiation of
346 dispersal movements, at the transience phase, or after dispersal during the colonization of the initially empty
347 patch. This pleads for the development of studies capturing the plastic changes occurring at each dispersal
348 step through individual tracking. Indeed, one key element to understand what drives the co-occurrence
349 between phenotypic and dispersal plasticity may lay in the relative timing of such plastic changes. One
350 crucial aspect of plasticity that should be considered when investigating the relationships between
351 phenotypic and dispersal plasticity is their timings [6,34,86]. If the environment changes faster than the
352 time needed for phenotypic changes to take place (*i.e.*, plasticity rate) [6,34,86] or at an amplitude higher
353 than the capacity for plasticity, phenotypic plasticity may be insufficient for organisms to locally deal with
354 new environmental conditions [6,67,86] and dispersal may be favoured. With thermal changes for example,
355 we can expect high amplitude of thermal change compared to the organism's thermal limits [87] and fast
356 thermal changes to favour dispersal plasticity at the expense of local phenotypic plasticity. In the
357 complementary experiment, we showed that the rate and amplitude of thermal changes had a stronger effect
358 on the expression of morphological plasticity than movement and dispersal plasticity. Indeed, the results
359 hint at a latency time for morphological plasticity to be mounted in response to thermal change while
360 plasticity in movement and dispersal were almost immediate. We also observed that immediate *vs.* gradual
361 changes in thermal regimes modified the covariation between some types of local plasticity but not between
362 local phenotypic and dispersal plasticity. These complementary results suggest that, in our system, the rate
363 and the amplitude of environmental changes might have limited impact on the interplay between local
364 phenotypic and dispersal plasticity, but a deeper exploration of the rate and amplitude of environmental
365 changes is necessary.

366 ***Conclusion***

367 Our study demonstrated that local phenotypic plasticity and dispersal plasticity were not alternative
368 mechanisms, and that how they associated with each other varied intraspecifically. Considering the
369 potential interactions between local phenotypic and dispersal plasticity is therefore crucial for our

370 understanding of ecological and evolutionary dynamics. For instance, phenotypic plasticity associated with
371 adaptive dispersal plasticity may allow adaptive divergence by creating reproductive barriers between
372 alternative phenotypes and reinforcing mate choice [32]. Initial plastic divergence could be followed by the
373 evolution of reduced phenotypic plasticity with genetic differences between phenotypes (*i.e.*, genetic
374 assimilation) [32]. This reinforcement by morphological plasticity of phenotypic divergence caused by
375 adaptive dispersal plasticity has been observed in salamanders (*Gyrinophilus porphyriticus*) [66].
376 Experimental evolution will be key to understand the relationships between these two processes and to
377 assess whether phenotypic and dispersal plastic changes are adaptive or not [13,48]. In addition, further
378 investigating the environmental scenarios under which either or both local and spatial strategies are selected
379 for [31], especially focusing on the frequency and predictability of environmental changes [9,88–90] and
380 the landscape composition [25], will be key to understand their evolution. Here we focused on dispersal
381 plasticity at emigration, a key first step of the dispersal process that have been shown to have important
382 consequences on metapopulation dynamics and local adaptation [23,24]. Extending this investigation to
383 dispersal plasticity at immigration, namely the choice of where to settle in a heterogeneous landscape, is a
384 key future step to understand the relationship between phenotypic and dispersal plasticity and their
385 ecological and evolutionary consequences [91]. Further, changes in population and community contexts
386 may modify how a focal species respond to environmental changes [92], and thus the relationship between
387 phenotypic and dispersal plasticity [93].

388 **Data accessibility.** All raw data and R scripts used for this study are available on the Zenodo repository
389 [10.5281/zenodo.15017236](https://doi.org/10.5281/zenodo.15017236).

390 **Authors' contributions.** MT and SJ conceived the project; MT, LD, DL and SJ performed the
391 experiments; MT analyzed the data and led the writing of the manuscript. All authors contributed critically
392 to the drafts and gave final approval for publication.

393 **Competing Interest.** The authors declare no competing interests.

394 **Acknowledgments.** We thank Michèle Huet for the maintenance of cell cultures and technical support.

395 **Funding.** This work benefitted from financial support by the Agence Nationale de la Recherche for the
 396 project CHOOSE (ANR-19-CE02-0016), and is part of TULIP (Laboratory of Excellence Grant ANR-10
 397 LABX-41).

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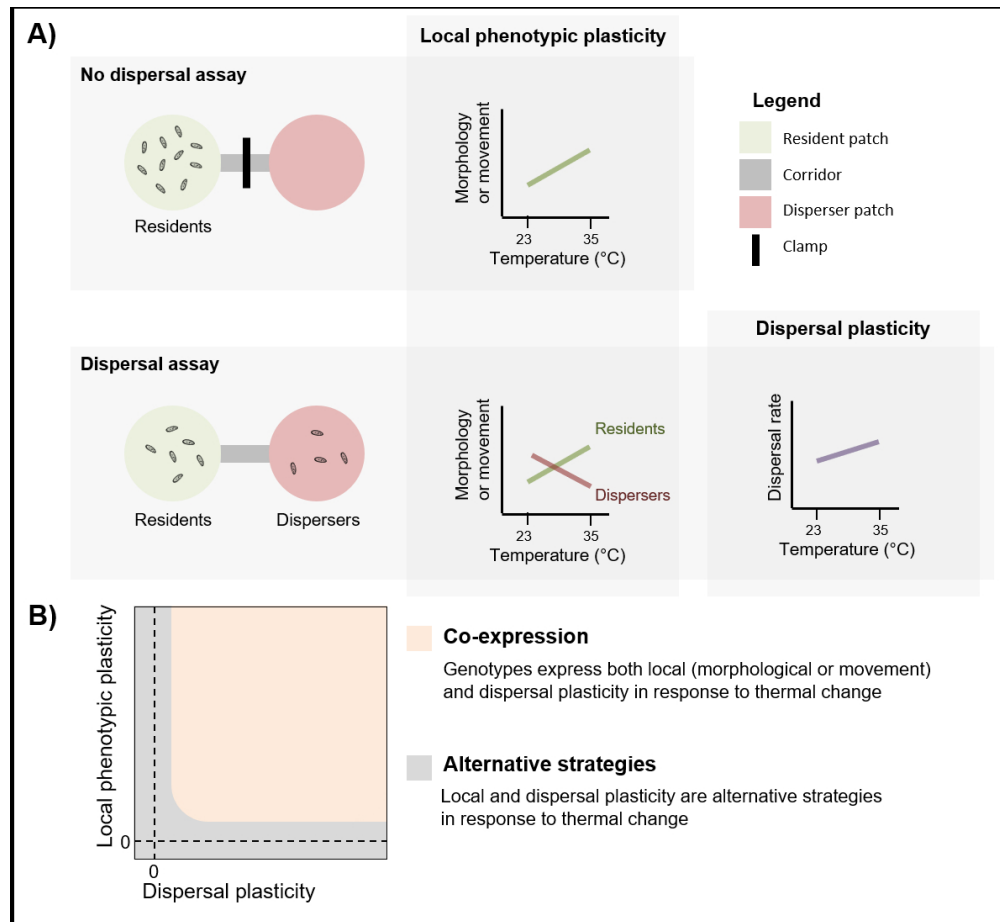
618 **Figure legends**

619 **Figure 1. (A) Experimental set up to quantify local phenotypic plasticity (cell morphology and**
620 **movement) and dispersal plasticity.** We inoculated the two-patch systems with a culture of one of the
621 twelve strains and placed them at either 23°C or 35°C. We measured morphological and movement traits
622 in systems without dispersal (no dispersal assay; N = 120) and for residents and dispersers (dispersal assay;
623 N = 120), and reconstructed reaction norms of cell morphology, movement and dispersal rate along the
624 temperature axis. The reaction norms presented here are for illustration only (random slopes attributed for
625 residents, dispersers, and dispersal rate). **(B) Predictions for the relationship between local plasticity**
626 **(morphological and movement) and dispersal plasticity in response to thermal change.** Genotypes
627 expressing both local plasticity (morphological and/or movement) and dispersal plasticity would be in the
628 orange zone of the plot (co-expression) while genotypes expressing either local or dispersal plasticity would
629 be in the grey zone (alternatives). On zero the genotypes are not plastic at all.

630 **Figure 2. Co-occurrence of morphological (cell size and shape), movement (velocity and linearity)**
631 **and dispersal plastic capacity.** Points represent the absolute effect size of thermal change for each strain
632 (absolute estimates \pm 95% CIs). Horizontal and vertical dotted lines situate the effect size values

633 corresponding to no plasticity. Points with errors non-overlapping these lines represent significant
634 plasticity.

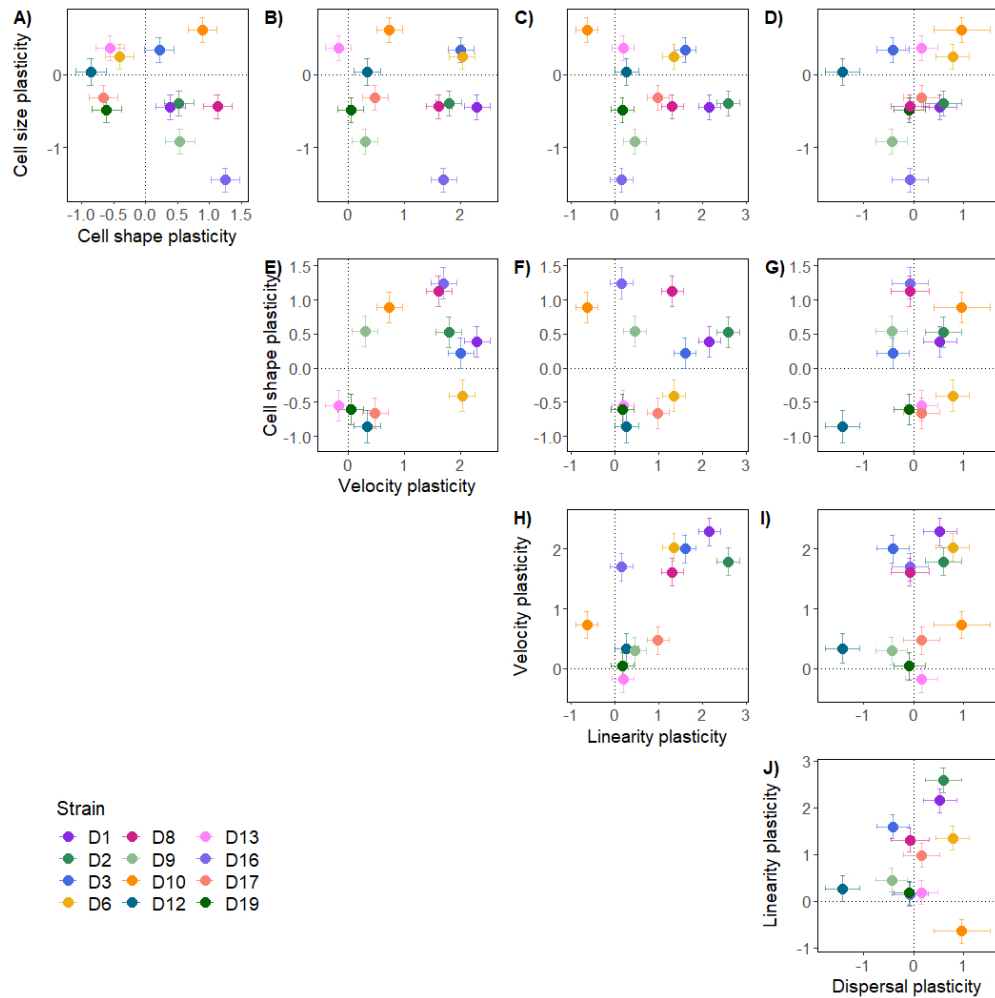
635 **Figure 3. Changes of cell A) size, B) shape, C) velocity and D) linearity plasticity between residents**
636 **and dispersers compared to when dispersal was not allowed.** Points represent the effect size of thermal
637 change for each strain (colours) and dispersal status (circles for residents, triangles for dispersers) recovered
638 from the models (contrasts \pm 95% CIs) and centred around the thermal plasticity without dispersal
639 (horizontal dash line \pm 95% CIs). Big black points represent the mean effects across strains. Points outside
640 the range represent significant differences of plasticity for residents or dispersers compared to without
641 dispersal, while deviation between circles and triangles illustrates differences of phenotypic plasticity
642 between residents and dispersers within each strain.



(A) Experimental set up to quantify local phenotypic plasticity (cell morphology and movement) and dispersal plasticity. We inoculated the two-patch systems with a culture of one of the twelve strains and placed them at either 23°C or 35°C. We measured morphological and movement traits in systems without dispersal (no dispersal assay; N = 120) and for residents and dispersers (dispersal assay; N = 120), and reconstructed reaction norms of cell morphology, movement and dispersal rate along the temperature axis.

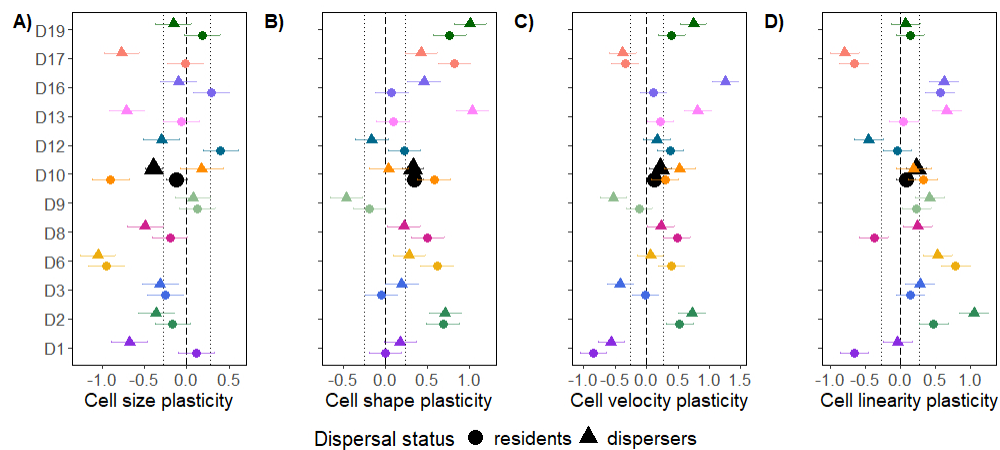
The reaction norms presented here are for illustration only (random slopes attributed for residents, dispersers, and dispersal rate). (B) Predictions for the relationship between local plasticity (morphological and movement) and dispersal plasticity in response to thermal change. Genotypes expressing both local plasticity (morphological and/or movement) and dispersal plasticity would be in the orange zone of the plot (co-expression) while genotypes expressing either local or dispersal plasticity would be in the grey zone (alternatives). On zero the genotypes are not plastic at all.

512x470mm (59 x 59 DPI)



Co-occurrence of morphological (cell size and shape), movement (velocity and linearity) and dispersal plastic capacity. Points represent the absolute effect size of thermal change for each strain (absolute estimates \pm 95% CIs). Horizontal and vertical dotted lines situate the effect size values corresponding to no plasticity. Points with errors non-overlapping these lines represent significant plasticity.

701x701mm (38 x 38 DPI)



Changes of cell A) size, B) shape, C) velocity and D) linearity plasticity between residents and dispersers compared to when dispersal was not allowed. Points represent the effect size of thermal change for each strain (colours) and dispersal status (circles for residents, triangles for dispersers) recovered from the models (contrasts \pm 95% CIs) and centred around the thermal plasticity without dispersal (horizontal dash line \pm 95% CIs). Big black points represent the mean effects across strains. Points outside the range represent significant differences of plasticity for residents or dispersers compared to without dispersal, while deviation between circles and triangles illustrates differences of phenotypic plasticity between residents and dispersers within each strain.

668x300mm (38 x 38 DPI)