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Mélanie Thierry, Julien Cote, Elvire Bestion, Delphine Legrand, Jean Clobert, et al.. The interplay between abiotic and biotic factors in dispersal decisions in metacommunities. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 2024, 379 (1907), 10.1098/rstb.2023.0137 . hal-04676422

HAL Id: hal-04676422

<https://hal.science/hal-04676422>

Submitted on 12 Sep 2024

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The interplay between abiotic and biotic factors on dispersal decisions in metacommunities

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Philosophical Transactions of the Royal Society B, 2024, 379(1907):20230137, doi:10.1098/rstb.2023.0137

Part of the Special Issue: “Diversity-dependence of dispersal interspecific interactions determine spatial dynamics”

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Key words: Habitat choice, plasticity, biotic context, *Tetrahymena*, competition.

Abstract

Suitable conditions for species to survive and reproduce constitute their ecological niche, which is built by abiotic conditions and interactions with conspecifics and heterospecifics. Organisms should ideally assess and use information about all these environmental dimensions to adjust their dispersal decisions depending on their own internal conditions. Dispersal plasticity is often considered through its dependence to abiotic conditions or conspecifics density, and to a lesser extent with the effects of interactions with heterospecifics, potentially leading to misinterpretation of dispersal drivers. Here, we first review the evidence for effects of, and the potential interplays between abiotic factors, biotic interactions with conspecifics and heterospecifics, and phenotype on dispersal decisions. We then present an experimental test of these potential interplays, investigating the effects of density and interactions with conspecifics and heterospecifics on temperature-dependent dispersal in microcosms of *Tetrahymena* ciliates. We found significant differences in dispersal rates depending on temperature, density, and presence of another strain or species. However, the presence and density of conspecifics and heterospecifics had no effects on the thermal-dependency of dispersal. We discuss the causes and consequences of the (lack of) interplay between the different environmental dimensions and the phenotype for metacommunity assembly and dynamics.

Introduction

Dispersal is a major ecological process consisting in the emigration of individuals from one patch, their transition between patches, and their immigration to another one. Dispersal can lead to gene flow between habitats and changes in population demography and meta-population dynamics [1–3]. It is thus essential for ecological and evolutionary dynamics of populations, communities and ecosystems [4–7]. To leave unsuitable conditions and try to settle in more suitable ones, individuals can adjust their dispersal by behavioral changes at any of its steps based on ecological cues (named context-dependent dispersal, habitat choice or dispersal plasticity) [2,8–10], which can be associated with phenotypic changes [11,12]. Dispersal plasticity is observed in many taxa [10,13], with variability within and between species [14–16].

In spatially and temporally fluctuating environments, dispersal plasticity should allow organisms to track environmental conditions within which their fitness is maximized (*i.e.*, their ecological niche) [9,10,17–19]. Benefits of such adaptive dispersal plasticity should exceed potential costs induced by both dispersal [20] and plasticity of associated traits [21] (but see [14,22]). Trait plasticity is expected to evolve to adaptively respond to fluctuating and somewhat predictable environmental conditions when cues are available and reliable [23–28]. How cues are used should depend on how organisms perceive and integrate information in their environment [8,29]. Adaptive plasticity cannot be viewed as a unidimensional response, as organisms are exposed to a multitude of environmental factors [8,9,30–32]. Indeed, species ecological niche is constrained by the suite of abiotic conditions within which organisms can survive and reproduce (*i.e.*, the fundamental niche), biotic interactions, and dispersal barriers [33–35]. All the elements composing organism's ecological niche and their interplay are therefore important for the expression and adaptiveness of dispersal plasticity, but which cues are prioritized in dispersal decisions remains poorly understood. Disentangling effects of abiotic conditions and biotic interactions on the evolution of dispersal plasticity requires an integrative approach [36] in a metacommunity context [37], which has been rarely investigated so far.

Biotic interactions modify the fitness landscape in which species live, influencing species' evolutionary responses to environmental changes [38–41]. Thus, organisms cannot track environmental changes based solely on their expected performance in given abiotic conditions [42,43], but should modify their dispersal decisions

accounting for the effects of conspecifics and heterospecifics and their interactions with abiotic conditions on their fitness. For instance, optimal abiotic conditions may increase species abundances and thus strengthen competitive interactions. In that case, an adaptive strategy could be to avoid such competitive habitats by choosing sub-optimal conditions, potentially resulting in niche partitioning [44]. For instance, in the ciliate *Tetrahymena thermophila*, an organism able to differentiate kin from non-kin [45], the most generalist genotypes have been found to disperse toward sub-optimal habitats, which has been hypothesized as a way to avoid competition with specialists [22]. Further, dispersal plasticity of one focal species can have cascading effects on the population dynamics of the other trophic levels [46] and strongly affects metacommunity diversity at both local and regional scales that depend on both consumer and resource dispersal [47].

To fully understand the causes and consequences of dispersal plasticity in metacommunities, we need to understand which cues are used for dispersal decisions, whether organisms change their use of abiotic cues depending on their biotic context (both intra- and interspecific), and what is the subsequent interplay between abiotic and biotic factors and the organism's phenotype on dispersal decisions. To address this knowledge gap, we first review existing evidence for the role of abiotic, intraspecific and interspecific contexts and their interplay on dispersal. We do not aim to be exhaustive but rather to highlight how the different dimensions of an organism's environment, and their interactions, may affect its dispersal decisions. We then experimentally explore these interplays in actively dispersing ciliates of the genus *Tetrahymena* [22]. Finally, we propose key perspectives for future research in metacommunity ecology, aiming to better understand the effects of the multidimensionality of the environment on dispersal decisions for metacommunity assembly and dynamics. We emphasize the importance of individual variation to gain insight into eco-evolutionary dynamics in metacommunities.

The evidence for the role of abiotic, intraspecific and interspecific contexts, and their interplay on dispersal

Use of information in dispersal decisions

In the case of informed dispersal, organisms need to perceive and process information about their environment to decide whether or not to disperse and to settle in another habitat [29,48,49], potentially in relation with their

phenotype (physiology, behavior, morphology and life-history traits) [9,50,51]. The external information acquired can be abiotic (*e.g.*, temperature, humidity, light), or biotic (*e.g.*, conspecifics density, presence and density of heterospecifics like competitors, resource/prey or predators/parasites) [52], and can be acquired via visual, auditory, olfactory, chemical, or haptic cues. Information can also be transmitted by ascendants [53,54], or other (unrelated) individuals. Abiotic conditions can drastically influence organism's fitness. Adaptive dispersal plasticity following changes in abiotic conditions should allow organisms to track abiotic conditions in which they live and thrive (*i.e.*, their fundamental niche) [14]. Population density, involving either kin or non-kin, is an important biotic factor for ecological processes, including dispersal [55]. Conspecific density-dependent dispersal has been observed in many taxa including plants [56], birds [57], lizards [58], mammals [59,60], and ciliates [16]. For the information coming from heterospecific presence and density, how organisms perceive and use it likely depends on the type and strength of biotic interactions [37,61]. In the case of mutualistic interactions, dispersers may prefer to join an occupied patch rather than to disperse toward an empty habitat [62]. In the case of competitive or trophic interactions, dispersers may avoid strong levels of competition or predation. Trophic interactions lead to fluctuations between prey and predator densities [63], making disentangling density-dependent dispersal from direct effects of interactions with heterospecifics on dispersal decisions difficult [64]. We highlight in Table 1 a few empirical evidences of dispersal plasticity along these three key environmental dimensions: abiotic and biotic context, both intra- and interspecific. We did not aim to review the literature exhaustively here, as it has previously been done [8,60]. We however aimed to illustrate the environmental dimensions experienced by an organism that can modify dispersal, thus presenting effect of the different types of biotic interactions with very different underlying mechanisms.

The relative importance and interplay between abiotic and biotic dimensions of the environment

Organisms likely integrate multiple cues to fine-tune their dispersal decisions in temporally and spatially fluctuating environment [65]. However, little is known on how they process these multiple information sources, whether, some cues are prioritized, and under which conditions they have or not interactive effects on dispersal decisions [66,67]. Whether effects of abiotic conditions and interactions with conspecifics and heterospecifics on dispersal decisions have interactive, additive or compensatory effects thus remains an open question.

Optimality in information use should result from a trade-off between the cost of information acquisition and the benefits resulting from informed dispersal [5,68,69]. Cues do not have to be the direct environmental conditions selecting for adaptive dispersal plasticity, but should correlate with the selective environment [70], at least partially [71]. Expressed dispersal plasticity may not be seen as adaptive when considering one dimension of the environment if the fitness responses to abiotic context and biotic interactions go in different directions. For instance, the presence of competitors constrained the adaptive response of the algae *Chlamydomonas reinhardtii* to an increase in CO₂ level [72], changed both the plastic and evolutionary responses of *Arabidopsis thaliana* to drought [40], and hindered evolutionary changes in cell shape and velocity of the protist *Paramecium aurelia* – two traits linked to dispersal propensity – in response to change in salinity [73]. While these studies looked at the plasticity of other traits than dispersal, they show that an integration of the different abiotic and biotic elements of the environment in studies of dispersal plasticity may be essential.

Densities of prey, predators and competitors are not independent. Hence, effects of intra- and interspecific contexts on dispersal decisions likely interact [74]. However, this topic still requires experimental validation. After detailed literature searching, among the studies investigating interspecific effect on dispersal decisions, 5 out of 95 for host-parasite, 22 out of 208 for prey-predator, 4 out of 91 for resource-consumer, and 20 out of 108 investigated the interplay between intra- and interspecific interactions (Bestion *et al.* this issue). The relative proportion of their effects, when additive, may also be crucial to understand metacommunity dynamics. Indeed, the balance between competitive intra- and interspecific interactions is important for species coexistence in community [75] but less considered in the metacommunity framework (but see [76]). We could expect stronger positive density-dependence of dispersal with conspecifics than heterospecifics because intraspecific competition may be stronger than interspecific competition for species to coexist [75]. However, the reverse could also hold if the competitive species is a better competitor, with high heterospecific densities, or if the niche overlap between heterospecifics is strong. We may predict that the relative importance of intra- vs. interspecific interactions and the sign of their relationship with dispersal depend of niche overlap.

Effects of interactions with conspecifics and heterospecifics on dispersal decisions should be tightly coupled with abiotic conditions. Indeed, the abiotic context can change species carrying capacity [77], the way species interact within a habitat because it changes their niche [78,79], and the outcome of species interactions

[80–82]. The abiotic context may thus change the effect of conspecifics and heterospecifics presence and density on dispersal decisions, and *vice versa*. For instance, inferior competitors may avoid species with whom they would strongly compete (*i.e.*, with a strong niche overlap) by choosing a sub-optimal habitat that would maximize their fitness when considering both the abiotic and biotic dimensions of the habitat [22]. As conspecific density can be used as proxy for abiotic conditions, disentangling density- and abiotic-dependency of dispersal and which cues may be prioritized can be challenging. Moreover, the dispersal decisions resulting from the interplay between one biotic and one abiotic factor could change depending on the variation of another factor [83–86].

Some phenotypes influence the competitiveness and optimality of organisms in a given environment. Therefore, in addition to interactive effects of abiotic and biotic factors on dispersal decisions, the environment and the phenotype can also interact [87] (Fig.1). An individual's phenotype likely plays a major role in how it uses information of its environment, both biotic and abiotic [9,50,51]. Further, phenotypic differences between dispersers and residents are widespread across taxa [8], and can be affected by environmental factors depending on the associated costs of dispersal [88].

We illustrate the different interplays between these three axes of external conditions (abiotic, conspecifics, and heterospecifics) and the internal conditions with selected evidence in Table 1.

The interplay between all dimensions of the environment

Studies integrating the interplay of two or more dimensions of the environment on dispersal plasticity are scarce although interactive effects between all dimensions of the environment and the phenotype is probably the rule rather than the exception. It would require very large experimental designs to have enough statistic power to test more than two-way interactions between environmental factors. Short-distance dispersal of the predator *Orius minutus* was affected by both weather conditions and intra- and inter-trophic densities in the field, but the interactive effects between abiotic and biotic factors were not tested [89]. Emigration of the stream fish *Rivulus hartii* was positively correlated to water level and body size, but only when the predator *Hoplias malabaricus* was present [90]. The mesocosm experiment using butterflies mentioned above [67] presents ten dimensions including weather conditions, conspecifics density, habitat quality, and several phenotypic traits. However, they only tested two-way interactions between the most significant environmental factors and phenotypic factors as higher order interactions require statistical power that even this highly controlled mesocosm experiment was not able to meet.

We can expect, for two hypothetical co-occurring species having partial niche overlap in a two-dimensional space (Fig. 2a), that their dispersal decisions along these environmental axes would depend on their optimum and performance relative to the other species (Fig. 2b) [22]. This would translate into an interactive effect between the abiotic factors and the biotic context on dispersal (Fig. 2c). An organism's dispersal decision should thus depend on its niche and its competitive abilities compared to other organisms with whom it shares its habitat.

Case study: interplay of abiotic and biotic conditions on dispersal in *Tetrahymena*

To illustrate such dependency of dispersal decisions to an organism's performance and biotic interactions, we present below a case study using microcosm with *Tetrahymena* species. We investigated the dependence of dispersal decisions to thermal conditions, biotic context, and their potential interplay in light of their thermal niche and competitive abilities. We manipulated the biotic context as conspecific population density and presence/absence of conspecifics or heterospecifics, and quantified the consequences for the decision to leave a habitat (emigration step of dispersal) depending on thermal local conditions.

We used two strains for three *Tetrahymena* species (D2 and D3 for *T. thermophila*, A3 and A5 for *T. americanis*, P2 and P3 for *T. pyriformis*; Table S1), 20 to 50 μm ciliates naturally living in freshwater ponds and streams [91]. Evidence for thermal-dependent dispersal and important intra- and interspecific variations in the direction and magnitude of the response has been provided in previous studies [14,22,92,93]. We created a design comprising in total six monocultures, three intraspecific cocultures (D2/D3, A3/A5, P2/P3) and three interspecific cocultures (D3/A5, D3/P3 and A5/P3, *i.e.*, one focal strain per species for logistical reasons). Cells were maintained in the laboratory in 24-wells plates in 2mL of axenic liquid growth media (0.6% Difco proteose peptone, 0.03% yeast extract, 0.006% glucose, 0.0009% sequestrene Fe-EDTA) at 23°C. All manipulations were performed in sterile conditions under a laminar flow hood. We prepared cultures in Erlenmeyer flasks with 0.5 mL of the stock culture in 50 mL of media five days before the start of the experiments to reach densities close to asymptotic density.

We first measured the thermal niche of each strain by following their growth at eight temperatures (11, 15, 19, 23, 27, 31, 35 and 39°C) for eleven days, with six replicates per strain and temperature. The thermal optimum corresponds to the temperature for which population growth is maximal (Fig. S1). *T. americanis* strains

(A3 and A5) have their thermal optimum close to 23°C (22.7 and 22.2°C respectively), *T. pyriformis* strains (P2 and P3) have their optimum slightly below it (21.6 and 21.2 respectively), and *T. thermophila* strains (D2 and D3) above 23°C (27.6 and 25°C respectively). For all of them, 31°C is above their thermal optimum, but either within (D2, D3) or outside (A3, A5, P2, P3) the 80% performance zone (Fig. S1). Based solely on their thermal niche, we could therefore expect *T. americanis* and *pyriformis* strains to avoid 31°C, a temperature that negatively impact their fitness, while *T. thermophila* strains should be less impacted by an increase in temperature from 23 to 31°C.

Then, we assessed potential intra- and interspecific interactions (either competition or facilitation) for each pair of strains. To do so, we inoculated 24-well plates by diluting the five-days old cultures to constitute monocultures of each strain with ~10,000 cells/mL, and co-cultures of each of the six pairs with ~10,000 cells/ml of each strain (~20,000 cells/mL in total). We placed these 24-well plates at two temperatures: 23°C, the standard temperature at which strains are maintained at the laboratory, and 31°C, resulting in 24 experimental conditions, each replicated six times (N = 144). We assessed biotic interactions for each pair in each temperature by comparing the sum of the monocultures with the abundance of cells in cocultures measured with flow cytometry (Supplement Text 1) after five days following [94]. If the abundance of cells in coculture is inferior to the sum of the monocultures this indicates competitive interaction, if it is superior facilitation, and if it is equal neutral interaction. Error rates to discriminate between strains and species are presented in Table S2. Despite intra- and interspecific differences in performance at 23 and 31°C (Fig. S1), all strains decreased in abundance when in co-culture (Fig. S2). Biotic interactions at 23°C were always competitive while biotic interactions at 31°C were either competitive or neutral (Fig. S2). There were no marked differences between intra- and interspecific competition, reflecting an overall similar effect on fitness. The type of biotic interaction is thus expected to have no significant effect on dispersal. D3 and P3 strains had significant lower abundances in cocultures of conspecifics than in monocultures at 23°C while their conspecific strain had no significant decrease in abundance. We could therefore expect dispersal of these strains to be affected by presence of their conspecific strain (D2 and P2 respectively). A5 and D3 paired with P2 had significant lower abundances in cocultures of heterospecifics than in monocultures at 23°C, meaning that P2 strain seems to be a stronger heterospecific competitor than these two strains at 23°C. We could therefore expect this decrease in fitness of A5 and D3 to be reflected on their dispersal decisions when paired with P2. However, these declines in abundance of D3 and P3 with conspecific strains and of A5 and D3 paired with P2

became non-significant at 31°C. At 31°C, the effect of biotic interaction on dispersal may thus become non-significant if dispersal decisions depend on the fitness consequences of biotic interactions.

Finally, we tested the effect of density and the presence of conspecifics *vs.* heterospecifics on thermal dispersal plasticity. We used standard 1.5 mL two-patches systems where two 1.5mL Eppendorf tubes are connected by a corridor (4 mm internal diameter, 2.5 cm long silicone tube), the whole system being filled with growth medium [16]. As for to the biotic interaction assessment experiment, we inoculated the start patches of the systems with monocultures of each strain with either 10,000 cells (low density) or 20,000 cells (high density) and co-cultures of the six pairs with 10,000 cells of each strain (20,000 cells in total). Each combination of strains and density was placed at either 23 or 31°C. We replicated each of the resulting 36 conditions six times in three block days (N = 216). After a 30 min acclimation at the corresponding temperature, we allowed cells to disperse for three hours to remain below the minimum generation time at the tested temperatures, but still letting sufficient time for cells to disperse. We then closed the corridors to prevent further movements and sampled residents (start patch) and dispersers (immigration patch). We estimated total and relative abundance of each strain in samples with flow cytometry (Supplement Text 1). Error rates to discriminate between strains and species are presented in Table S3. They were low enough to not change the estimated abundances. We calculated dispersal rate as $\frac{N_{disp}}{N_{resi} + N_{disp}}$, where N_{disp} and N_{resi} are the abundance of dispersers and residents, respectively. Statistical analyses are described in Supplement Text 2.

In monocultures, we found evidence for thermal dispersal plasticity ($\chi^2_{(1)} = 6.30$, p-value = 0.012; Fig. 3a&d) and density-dependent dispersal ($\chi^2_{(1)} = 5.86$, p-value = 0.016; Fig. 3a&d), as previously described [14,16,22,92,93,95]. Thermal dispersal plasticity varied between strains in terms of magnitude and direction (temperature x strain: $\chi^2_{(5)} = 27.46$, p-value < 0.0001; Fig. 3d; Table S4&5), but the direction of the effect did not follow what we could have expected according to their thermal niche. Indeed, strains of a same species have very similar thermal niche (Fig. S1) while their dispersal response to temperature were in opposite direction (Fig. 3a&d). Density-dependent dispersal was always positive when significant (density x strain: $\chi^2_{(5)} = 5.51$, p-value = 0.36; Fig. 3d; Table S5). However, we found no significant interactive effect between temperature and

monoculture density ($\chi^2_{(1)} = 0.90$, p-value = 0.342; Table S4), meaning that the density dimension of the biotic context had no significant effect on thermal dispersal plasticity (Fig. 3a&g).

Looking at dispersal response in monocultures at high density and cocultures, we found that the effects for both temperature and the presence of another strain (either conspecific or heterospecific) varied depending on the strain (temperature x strain: $\chi^2_{(5)} = 20.38$, p-value = 0.0011; presence/absence of another strain x strain: $\chi^2_{(5)} = 39.33$, p-value < 0.0001; Fig. 3b&e; Table S6&7). Three out of the six strains tested showed a decrease in dispersal rate with presence of another strain (A3, D3 and P2), two showed an increase in dispersal with presence of another strain (D2 and P3), and one strain was not significantly affected by the presence of another strain nor by temperature (A5) (Fig. 3e). Interestingly, the strain P3, that showed no dispersal plasticity to temperature despite very low performance at 31°C compared to 23°C (Fig. S1), had significant changes in its dispersal rate between monoculture and coculture (Fig. 3e; Table S7). Further, despite change in biotic interactions with temperature (Fig. S2), temperature did not modify the effect of presence or absence of another strain on dispersal ($\chi^2_{(1)} = 0.08$, p-value = 0.781; Fig. 3h; Table S6).

We found that conspecific vs. heterospecific biotic interactions had no significant effect on dispersal rate and its thermal plasticity (interaction type: $\chi^2_{(1)} = 0.36$, p-value = 0.55; strain x interaction type: $\chi^2_{(2)} = 0.51$, p-value = 0.77; Fig. 3c&f&i; Table S8&9). This was in line with the similar overall effect of interaction type observed on fitness (Fig. S2). However, effect of competitors on dispersal rates varied depending on their identity for A5 and D3 (but not for P2; Fig. S3; Table S10), without an interactive effect with temperature (Table S10). Surprisingly, effects of P2 strain compared to the other heterospecific strain and conspecifics on dispersal were opposite between A5 and D3 despite that both had a decrease in fitness in coculture of P2 compared to monocultures (Fig. S2).

Overall, our results show that temperature and the biotic context independently affect dispersal decisions in *Tetrahymena*, with both intra- and interspecific variations in their effect. Further, the direction of the effects of temperature and the biotic context could not have been predicted by effect on fitness from their thermal niche and the biotic interaction assessment.

Discussion

Our literature overview and case study highlight that, to understand how environmental changes affect dispersal decisions, we need a deeper consideration of both biotic and abiotic environmental factors and their incorporation in the context of metacommunities. In the literature, we found several studies investigating the additive and interactive effects of the multiple dimensions of the environment on dispersal decisions. Integrating effects of more than two environmental axes is however technically challenging, which explains the scarcity of evidence. In our study case using microcosms of *Tetrahymena* species, effects of temperature and the biotic context on dispersal did not interact significantly. Further, we observed important intra- and interspecific variations in terms of magnitude and direction of dispersal response to temperature and the biotic context despite similar direction in their effect on fitness. Below, we propose perspectives on the causes and consequences of presence or absence of interplay between the multiple dimensions of the environment and the phenotype on dispersal plasticity expression and evolution for metacommunity dynamics.

Dispersal plasticity evolution and expression along multiple environmental axes

We highlighted in the first sections the importance of considering interactions between multiple environmental factors to understand the evolution and expression of dispersal plasticity by reviewing the different interplays possible between the three external environmental context types (abiotic, conspecifics, heterospecifics). Based on our literature survey, we expected in our case study that the biotic factors (conspecific density, presence of another strain, and biotic interaction type) would interact with thermal effect on dispersal. This was not the case. Both temperature and biotic interactions (presence of another strain) significantly changed dispersal decisions, but their effects were additive. This was surprising considering the decrease in competition observed with an increase in temperature. The expected interaction between the abiotic and biotic context on dispersal decisions may simply not hold in all cases and/or for all organisms, and likely depends on the degree of niche overlap between organisms. A large experimental study on 21 species ranging from protozoa to vertebrates found general effects of resource availability and predation risk on emigration decisions [46]. Effects of resource availability in this study could be similar than effects of density or competition. We could hope for similar generality of the abiotic- and biotic-dependency of dispersal, which may help forecasting metacommunity dynamics in a changing world. Expanding our comprehension of the interplay (or lack of) between abiotic conditions and interactions with conspecific and

heterospecifics (both within and between trophic levels) on dispersal plasticity, and the consequences for metacommunities, will require further systematic investigation across environmental contexts and taxa.

Here, we investigated effects and interplay of abiotic and biotic factors over a single generation. The interplay between different environmental dimensions may not act on dispersal plasticity, but on its evolution. Indeed, organisms may have previously adapted their dispersal decisions based on the fitness landscape combining both abiotic and biotic conditions, and what is observed may be the result of niche partitioning [44]. We may expect organisms free of competition or predation (*e.g.*, during range expansion or invasion) to evolve their dispersal decisions without the biotic pressure exerted by other species (illustrated by the differences in dispersal reaction norms on Fig. 2c&d). This is often observed in the realized niche shifts of invasive species free of their native competitors [96] and natural enemies [97]. Experimental evolution integrating dispersal with a factorial design combining effects of abiotic factors and biotic context could tell us under which conditions interactive effects could emerge as drivers of dispersal plasticity evolution [36].

High intra- and interspecific variations in dispersal response

Dispersal rates were always positively correlated with conspecific density independently of the abiotic conditions. Another study found a similar positive effect of density of conspecifics or heterospecifics on nematodes' dispersal in laboratory independent of the level of salinity [98]. However, dispersal response to the other external factors studied (temperature, presence of another strain, and competitor identity) varied significantly in terms of both magnitude and direction across strains and species despite a same direction of their effect on fitness. Therefore, even with a lack of interplay between the abiotic and biotic contexts, it might be difficult to predict how organisms would disperse depending on the fitness landscape. These variations in dispersal response may be linked to high intra- and interspecific variations observed in phenotypic traits and depending on the dispersal status (morphological and movement traits; Fig. S4). This highlights the importance of the interplay between external factors and the phenotype for dispersal decisions. The studies discussed in the previous section about the interplay between external and internal conditions found generalities in this interplay when considering personality (*e.g.*, for boldness [99,100]), starvation [101], and life stage [102]. These generalities become harder to make when talking about phenotypic traits that are also plastic to these external factors as in our case study.

Importance of intra- vs. interspecific interactions in metacommunities

We did not find differences between the effect of conspecifics and heterospecifics presence and density on dispersal rates nor on thermal dispersal plasticity in our case study. They are however able to differentiate themselves from other clonal lineages [45], and another study found that *T. thermophila* is able to change its dispersal decisions based on biotic cues coming from kin or non-kin [103]. Therefore, in our experiment, cells likely differentiate cues coming from conspecifics and heterospecifics, but they translated into a similar dispersal response because intra- and interspecific interactions had similar effects on fitness. Such generic response to potential competitors has been observed in the propensity to move in flour beetles [104]. We tested the effects of biotic interactions during the emigration phase only. Effects in the settlement phase may be different because of different associated costs [106] or different cues potentially prioritized [62].

Conclusion and perspectives

We have discussed the causes and consequences of the interplay (or lack of) between the environmental dimensions and the phenotype in metacommunities. Comparative and integrative approaches are essential to build our knowledge on the multi-cause and consequences of dispersal decisions. How and why organisms decide to disperse based on the interplay between the different dimensions of the environment and their internal conditions is particularly important to forecast the impact of ongoing climate change, and to advance our understanding on biological invasions and disease biogeography. In this section, we discuss timely questions considering dispersal decisions that integrate the multiple dimensions of the environment.

How important individual variations are in dispersal plasticity for metacommunity dynamics?

Ecological and evolutionary processes such as dispersal and niche partitioning are often looked at the population or community scales, but looking at the individual scale allows to merge ecological and evolutionary processes [107]. The ecological niche an individual occupies can be mediated by its phenotype and makes explicit the intraspecific context as a whole dimension of the niche [108]. Each individual can thus occupy a specific niche space that can be different from another individual of a same species, leading to intra-specific variations in performance along environmental axes, and therefore differences in dispersal decisions [109]. Individual variations can be determinant in metacommunity dynamics because they impact both dispersal decisions [110]

and the strength and outcome of biotic interactions [111]. If individuals adaptively disperse depending on their fitness landscape, we could expect a spatial sorting of the metacommunity that would maximize niche partitioning. At the landscape scale, this would translate into a spatial homogenization of fitness among individuals and of trophic and competitive impacts on other species, which should stabilize the metacommunity [112]. Although not possible with our experimental design, methods exist to individually track dispersers for our biological system and others [113], both in the laboratory and in the field. This would allow for a deeper understanding of the link between phenotype and dispersal decisions and its consequences for populations and communities. Such methodological and conceptual advances could bring a deeper understanding on how individual variations in dispersal decisions would scale up to metacommunity dynamics and ecosystem functioning [87].

Dispersal syndromes: a key driver of the interplay between abiotic conditions and biotic interactions on dispersal decisions?

Dispersal is often associated with a suite of traits (*i.e.*, dispersal syndrome) [9,114]. Dispersers are generally larger than residents [11,12], which may be linked to the level of energy reserves required to overcome costs of dispersal [20]. Dispersers also often have a more locomotion-oriented morphology than residents to move faster and farther (*e.g.*, bigger wings, longer legs, elongated body shape). This dispersal syndrome was observed to be stronger under predation risk across taxa [12]. Dispersal decisions likely depend on the balance between dispersal costs and local predation and competition strength [12]. This balance could be dictated for instance by the relationship between dispersal and body size. Indeed, both dispersal propensity and interaction strengths can be mediated by body size [115]. In our dispersal experiment, we could not characterize phenotypic traits at the strain level in competitive treatments with two strains. However, the relationship between dispersal status and cell size was either positive, negative or null depending on the strains and thermal conditions at the community scale and in monocultures (Figure S4). These intra- and inter-specific variations were found in previous studies on *Tetrahymena* species [14,95] and other species [11]. This variability in dispersal syndromes can have important implications for metapopulation dynamics [95]. The lack of a univocal relationship between dispersal and phenotypes suggests the existence of a range of dispersal strategies (*e.g.*, [116]) and would require further investigation.

What would be the consequences of dispersal plasticity for metacommunities under global change?

With the ongoing global change, abiotic conditions are changing and induce numerous phenotypic changes including life-history traits. These individual changes alter community composition and biotic interactions, with range shifts, reshufflings of entire species communities [117–119] and desynchronization of previously interacting species [120–122], which feedback to individual evolutionary responses [123]. These abiotic and biotic changes modify the fitness landscape in which dispersal plasticity has evolved. By overlooking unpredictable novel biotic interactions and differences in dispersal response among individuals we are at risk of underestimating the impact of climate change on biodiversity and ecosystem functioning [41,118,124,125]. Moreover, environmental factors impacting organisms' fitness (*e.g.*, temperature) are increasingly variable and fluctuate in an unpredictable manner [126]. Future climate variability may therefore prevent organisms to adaptively track favorable conditions through dispersal plasticity, which would lead to a destabilization of the whole meta-community. Landscape fragmentation is also increasing [127], preventing free movement between habitats [128], and therefore limiting the potential for spatial sorting through adaptive dispersal and so its potential stabilizing effects. Further, dispersal plasticity could become maladaptive with changing climate if the cues used for adaptive dispersal behavior became decoupled with the selective conditions [129]. This is especially true when plastic capacity depends on developmental conditions [130], which would induce a mismatch between adult dispersal and environmental conditions [131]. With climate change, cues to detect environmental changes may not be reliable anymore, and bet-hedging (or other unconditional strategies) may be better evolutionary strategy than plasticity in some cases [132].

Data accessibility. All raw data used for this study are available from the Zenodo database: [10.5281/zenodo.8406074](https://doi.org/10.5281/zenodo.8406074).

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

Competing Interest. The authors declare no competing interests.

Acknowledgments. We thank Michèle Huet for the maintenance of cell cultures and technical support, Pablo Molina Vila for technical support, Amélie Cocchiara for her help in the lab to perform the experiments, and Léonard Dupont for fruitful discussions and his help to fit the thermal niche.

Funding. This work benefitted from financial support by the Agence Nationale de la Recherche for the project CHOOSE (ANR-19-CE02-0016), and is part of TULIP (Laboratory of Excellence Grant ANR-10 LABX-41). JCo is supported by a funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation program (grant agreement no. 817779).

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Figure captions

Figure 1. Overview of the cause of dispersal decisions depending on the different dimensions of the environment and their interplay. Dispersal decisions can depend on the abiotic and biotic (both intra- and interspecific) conditions and are influenced by the individual internal conditions (plain arrows). However, abiotic and biotic factors are not independent (dashed arrows) and can thus have interactive effects on dispersal decisions.

Figure 2. Predictions about dispersal decisions along two environmental gradients depending on ecological niche and biotic interactions. a) Hypothetical ecological niche of individuals of two species (species A in orange and species B in blue) along two environmental gradients with their performance curves. Along the environmental gradient 1, species A is a specialist while species B is a generalist. Their optimum along the gradient do not overlap. Along the environmental gradient 2, species A is a generalist while species B is a specialist and they have the same optimum. b) Dispersal reaction norms of the two species in isolation along each environmental gradient following their performance curves. We hypothesize that, for a given environmental axis, the generalist species has never a null dispersal rate while the specialist species does not disperse at its optimum. c) In presence of the other species, dispersal decisions of species B along the environmental gradient 1 change slightly due to the small niche overlap with the superior competitor at the beginning of the gradient. Along the environmental gradient 2, species A avoids the superior competitor species B by dispersing toward sub-optimal habitats [22]. More complex dispersal decisions would appear in a three-dimensional space combining environmental gradients 1 and 2 and biotic interactions.

Figure 3. a-c) Reactions norms of dispersal rates along the thermal axis depending on a) monoculture density, b) presence of another strain in cultures at high density and c) biotic interaction type in cocultures. Small points represent raw data and big point the means with their standard errors for each strain (color) and species (shape). Lines between factor levels of the x-axis represent the reaction norms. **d-f) Dispersal plasticity along the abiotic (x axis) and biotic (y axis) axes in d) monocultures, e) cultures at high density, and f) cocultures. g-i) Thermal effect on dispersal depending on g) monoculture density, h) presence of another strain in cultures at high density and i) biotic interaction type in cocultures.** Points represent the effects size on dispersal rates (contrasts \pm 95% CIs) recovered from the models for each strain (color) and species (shape). Horizontal and vertical dot lines situate the effect size values corresponding to no plasticity.

Table 1. Evidence of the effects and interplays between abiotic conditions, biotic context (decomposed in conspecifics and heterospecifics), and the phenotype on dispersal decisions (presented with the biological system, the observed effects, the type of study, and references).

FACTORS	Species	EFFECTS ON DISPERSAL DECISIONS	TYPE OF STUDY	REFERE NCES
Abiotic	Five <i>Tetrahymena</i> species	Dispersal plasticity correlates with fitness sensitivity to the environment along three abiotic gradients (temperature, salinity and nutrients)	Microcosm experiment	[14]
	Money spiders (<i>Erigone atra</i>)	Thermal conditions during the development determine adult dispersal strategy	Microcosm experiment	[131]
	<i>Crepis sancta</i> (Asteraceae)	A greater proportion of seed dispersal morphs are produced when nutrients are depleted	Mesocosm experiment	[133]
Conspecifics	Various	High conspecific densities can reflect a good habitat quality or a crowded competitive habitat and lead to negative or positive density-dependent dispersal respectively	Various	[60,134,135]
	Glanville Fritillary butterfly (<i>Melitaea cinxia</i>)	Low conspecific densities can lead to a scarcity of mates and thus enhance dispersal	Mesocosm experiment	[136]
	Wood pigeons (<i>Columba palumbus</i>)	Low conspecific densities can reduce the effectiveness of antipredator strategies such as flocking	Field experiment	[137]
	Collared flycatcher (<i>Ficedula albicollis</i>)	Fitness of conspecifics is used as information sources about habitat quality	Field experiment	[138]
	Common lizard (<i>Zootoca vivipara</i>)	Informed emigration decisions with the intra-specific competitive level that immigrants experienced (probably cued by differences in behavior or physiology)	Mesocosm experiment	[139]
Heterospecifics of a same trophic level	Various	Densities of competitive heterospecifics can be cues for either habitat quality or competitive habitats	Various	[140–145]
	Blue Tits (<i>Cyanistes caeruleus</i>)	Condition and reproductive success of heterospecifics represent cues about habitat quality	Field experiment	[146]
Heterospecifics	21 species ranging from protozoa to	Cues about the presence of	Microcosm	[46]

of a different trophic level	vertebrates	resources and predators affect dispersal decisions	and mesocosm experiments	
	<i>Tetrahymena pyriformis</i> and its prey <i>Dileptus</i> sp.	A decrease in the prey density led to an increase in predator dispersal while an increase in the predator density led to an increase in prey dispersal	Microcosm experiment	[64]
	Pea aphid (<i>Acyrtosiphon pisum</i>)	Specialized dispersal morphs production in the presence of natural enemies	Mesocosm experiment	[147]
	Parasitoids (<i>Diadegma semiclausum</i> and <i>D. fenestrata</i>) and their host caterpillars of the diamondback moth (<i>Plutella xylostella</i>)	Natural enemies locate and disperse toward herbivores via the volatile organic compounds produced by the plant due to herbivory	Mesocosm experiment	[148]
Abiotic x conspecifics	Cliff swallows (<i>Petrochelidon pyrrhonota</i>)	Natal dispersal induced by ectoparasitism	Field observations	[149]
	Common lizard (<i>Zootoca vivipara</i>)	Biotic information about kin competition prioritized over cues about suitable habitats	Mesocosm experiment	[150]
	Large white butterfly (<i>Pieris brassicae</i>)	Weather conditions and habitat quality prioritized over population density and sex ratio	Mesocosm experiment	[67]
Abiotic x heterospecifics	House sparrow (<i>Passer domesticus</i>)	Temperature- and density-dependent dispersal vary depending on resource availability	Field observations	[83]
	Larval hydroptychid caddisflies	Interactive effects of predator presence, algal cover and substrate size	Experiments in real and artificial streams	[84]
	Parasitoid (<i>Eupelmus vuilleti</i>)	Independent effect of host detection via olfactory cues and interactive effect of light and gravity	Microcosm experiment	[85]
Conspecifics x heterospecifics	Predatory spider (<i>Neoseiulus fallacis</i>)	Negative effect of prey density, but only for temperatures above 23°C	Microcosm experiment	[86]
	Ciliate (<i>Paramecium aurelia</i>) and its predator (<i>Stenostomum virginianum</i>)	Positive effect of predation risk at low conspecific density and negative effect at high conspecific density	Microcosm experiment	[151]
	Cowpea bruchid (<i>Callosobruchus chinensis</i>) and its parasitoid (<i>Anisopteromalus calandrae</i>)	Negative effect of parasitoid:host ratio, potentially due to increase in intraspecific competition	Microcosm experiment	[152]
	Backswimmers (<i>Notonecta undulata</i>)	Positive effect of predation risk at intermediate conspecific density but almost no effects of predation at high and low conspecific densities	Mesocosm experiment	[153]
	Predatory bug (<i>Orius minutes</i>) and its prey	Importance of the ratio between prey and predator	Field experiment	[89]

		densities		
	Nematods (<i>Litoditis marina</i>)	Positive effect of density, either with conspecifics or heterospecifics	Microcosm experiment	[98]
	Wing-dimorphic planthoppers (<i>Sogatella furcifera</i> and <i>Nilaparvata lugens</i>)	Intraspecific effects stronger for <i>S. furcifera</i> and interspecific stronger for <i>N. lugens</i>	Microcosm experiment	[154]
	Diving beetles (<i>Laccophilus fasciatus rufus</i> and <i>Laccophilus Proximus</i>)	Effect of unknown intraspecific interactions rather than interspecific interactions	Field and microcosm experiments	[155]
	Nematode (<i>Caenorhabditis elegans</i>)	Increase in conspecifics competition (with decreasing food availability and increasing population density) increases dispersal. The effect was amplified by the presence of a predator for certain food-supply levels	Microcosm experiment	[74]
Environment x phenotype	Poultryhouse pill beetle (<i>Carcinops pumilio</i>)	Effect of temperature but only when individuals were starved	Microcosm experiment	[101]
	Mosquitofish (<i>Gambusia affinis</i>)	Bold and social mosquitofish dispersed more than shy and less social ones without predation risk but no differences under predation risk	Mesocosm experiment	[99]
	Common toad (<i>Bufo bufo</i>)	Interactive effect of matrix permeability and predation risk on movement syndrome	Mesocosm experiment	[88]
	Common lizard (<i>Zootoca vivipara</i>)	Individuals with low preferred temperatures dispersed more from warmer habitats, whereas individuals with higher preferred temperatures dispersed more from cooler habitats.	Mesocosm experiment	[109]
	Salt marsh snails (<i>Cerithidea californica</i> Haldeman and <i>Batillaria attramentaria</i> Sowerby)	Dispersal of large snails for both species increased as resource levels decreased, supporting that competition influences dispersal rates. However, small snails always dispersed at relatively higher rates than larger individuals and were not influenced by variation in resource levels because competition reduces with body size.	Field experiment	[156]
	Backswimmers (<i>Notonecta undulata</i>)	Additive effects between body condition and	Field experiment	[157,158]

		predation risk but interactive effect between sex, body mass and population density		
	Stream fish (<i>Rivulus hartii</i>)	Emigration positively correlated to water level and body size, but only when presence of the predator <i>Hoplias malabaricus</i>	Field observations	[90]
	Roe deer (<i>Capreolus capreolus</i>)	Natal dispersal propensity depends on both endoparasite abundance and body mass	Field observations	[159]
	Salmonid fish (<i>Oncorhynchus masou masou</i>)	Large fish infested by larval parasites of the freshwater mussel <i>Margaritifera laevis</i> become dispersed more, whereas small infested fish tended to stay in the patch	Field observations	[160]
	Wild guppies (<i>Poecilia reticulata</i>)	Natal dispersal is positively influenced by conspecific density at both the local and landscape scale because of intra-specific competition for resources while adult dispersal switched from conspecific attraction to conspecific avoidance along a predation-risk gradient (from high to low) at the local scale	Field observations	[161]