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LETTER

Condition-dependent movement and dispersal in experimental metacommunities

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Abstract

Dispersal and the underlying movement behaviour are processes of pivotal importance for understanding and predicting metapopulation and metacommunity dynamics. Generally, dispersal decisions are condition-dependent and rely on information in the broad sense, like the presence of conspecifics. However, studies on metacommunities that include interspecific interactions generally disregard condition-dependence. Therefore, it remains unclear whether and how dispersal in metacommunities is condition-dependent and whether rules derived from single-species contexts can be scaled up to (meta)communities. Using experimental protist metacommunities, we show how dispersal and movement depend on and are adjusted by the strength of interspecific interactions. We found that the predicting movement and dispersal in metacommunities requires knowledge on behavioural responses to intra- and interspecific interaction strengths. Consequently, metacommunity dynamics inferred directly from single-species metapopulations without taking interspecific interactions into account are likely flawed. Our work identifies the significance of condition-dependence for understanding metacommunity dynamics, stability and the coexistence and distribution of species.

Keywords

Allee effect, density-dependent dispersal, density-dependent movement, interspecific competition, microcosms, plasticity, protists, reaction norm.

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INTRODUCTION

Local populations and communities are usually not isolated entities, but rather part of larger spatially structured systems, like metapopulations and metacommunities (Hanski 1999; Leibold *et al.* 2004) where dispersal is by definition a process of central relevance for both local and global ecological and evolutionary dynamics (Clobert *et al.* 2012). It is now clear that dispersal and movement can be highly complex behaviours (Nathan *et al.* 2008; Clobert *et al.* 2012) with important consequences, even for large-scale patterns such as metapopulation dynamics (Fronhofer *et al.* 2012), species coexistence (Salomon *et al.* 2010), or the distribution of biological diversity (Seymour *et al.* 2015).

Both empirical and theoretical studies show that dispersal as well as the underlying movement behaviour are condition-dependent and, in the broad sense, informed processes (Nathan *et al.* 2008; Clobert *et al.* 2009). Condition-dependence and information use is highly advantageous during all three stages of dispersal (emigration, transition, immigration) and a variety of cues, such as local population density (De Meester & Bonte 2010; Bitume *et al.* 2013; Fronhofer *et al.* 2015), food availability (Kuefler *et al.* 2012), relatedness (Bitume *et al.* 2013), body condition (Bonte & de la Peña

2009) or abiotic conditions (Altermatt & Ebert 2010) can be used to trigger dispersal and movement decisions. Furthermore, it has been shown that emigrants can not only use information on local conditions but also utilise information on potential target patches conveyed by arriving immigrants (Cote & Clobert 2007; Jacob *et al.* 2015) and that settlement decisions can be informed with regard to population density, for example (Doligez *et al.* 2002). Therefore, dispersal and movement are generally condition-dependent or informed and not fixed traits. In the following, we will focus on the use of intra- and interspecific densities for condition-dependent dispersal and movement strategies.

Condition-dependent dispersal and movement can have far-reaching consequences such as altered (macro)ecological and evolutionary dynamics. For instance, source-sink dynamics were shown theoretically to be impacted by density-dependent dispersal (Amarasekare 2004) and species ranges are predicted to be larger (Kubisch *et al.* 2011) and invasions slower (Altwegg *et al.* 2013) when dispersal is positively density-dependent. By contrast, negatively density-dependent dispersal may increase invasion speeds (Altwegg *et al.* 2013). Finally, evolutionarily stable dispersal rates are usually higher for non-conditional dispersers implying higher costs (Enfjäll & Leimar 2009), to name just a few consequences.

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Most studies on density-dependent dispersal have focused on the effects of intraspecific density (De Meester & Bonte 2010; Bitume *et al.* 2013; Fronhofer *et al.* 2015), largely ignoring effects of species interactions and interspecific densities. However, species rarely exist in isolation and the use of social information from heterospecifics is known to be relevant, for example in mixed-species groups (Goodale *et al.* 2010). Therefore, in a metacommunity context, both dispersal and movement should also depend on interspecific interactions. However, metacommunity studies usually assume that dispersal is a random process in the sense that it does not depend on metacommunity composition (but see Amarasekare 2010 for a theoretical model and De Meester *et al.* 2015 for empirical evidence). Clearly, this is a relatively unlikely assumption, and for the specific cases of host-parasitoid (e.g. French & Travis 2001; Fellous *et al.* 2010) and predator-prey systems (e.g. Hauzy *et al.* 2007; Poethke *et al.* 2010; Kuefler *et al.* 2012; Cote *et al.* 2013) it has been shown that movement and dispersal are condition-dependent and modulated by the abundance of the antagonist. Surprisingly, the effect of omnipresent competitive interactions on movement and dispersal has been ignored in communities with more than two species. Therefore, we are lacking an understanding of the effects of competition among species of the same trophic level on dispersal and movement and it remains unclear whether one can simply infer these effects from intraspecific density-dependence or if interspecific interactions modulate movement and dispersal dynamics. Such knowledge, however, is crucial and a prerequisite for building a reliable, predictive science of ecological dynamics in space.

We tested experimentally whether and how one can generalise models of density-dependent dispersal and movement,

which have been developed for single-species metapopulations, to be applicable to a multi-species, metacommunity context. Intraspecific density-dependent dispersal has been shown theoretically to be generally positive as a means to escape from competition, with the exact shape of the function depending on model assumptions (Metz & Gyllenberg 2001; Poethke & Hovestadt 2002). For continuous-time models, Metz & Gyllenberg (2001) could show that the relationship follows a step function (as assumed in Fig. 1). Negative density-dependence (e.g. Baguette *et al.* 2011; Fellous *et al.* 2012) may arise for example at low population densities due to Allee effects (Kim *et al.* 2009; Fronhofer *et al.* 2015), which, in a single-species framework, is predicted to lead to a U-shaped density-dependent dispersal and movement reaction norm (Fig. 1). In a multi-species context, we predict that dispersal and movement fundamentally follow the same U-shaped relationship, but that conspecific and all heterospecific densities weighted by their respective interaction strength have to be taken into account to explain and predict dispersal and movement behaviour correctly (see Fig. 1 and below for details). To test our prediction in a multi-species context, we focused on metacommunities of competitors, that is, species of the same trophic level, reflecting some of the most studied and most relevant interactions found in nature (e.g. Chesson 2000; Hubbell 2001). Based on experimentally assessed differences in competition strength, we identified the effects of competition on movement and dispersal across levels of community diversity from single-species to all two- and three-species metacommunities of three protist model organisms (Altermatt *et al.* 2015).

Using the general model depicted in Fig. 1 as a framework, one can predict the following plastic adjustments of move-

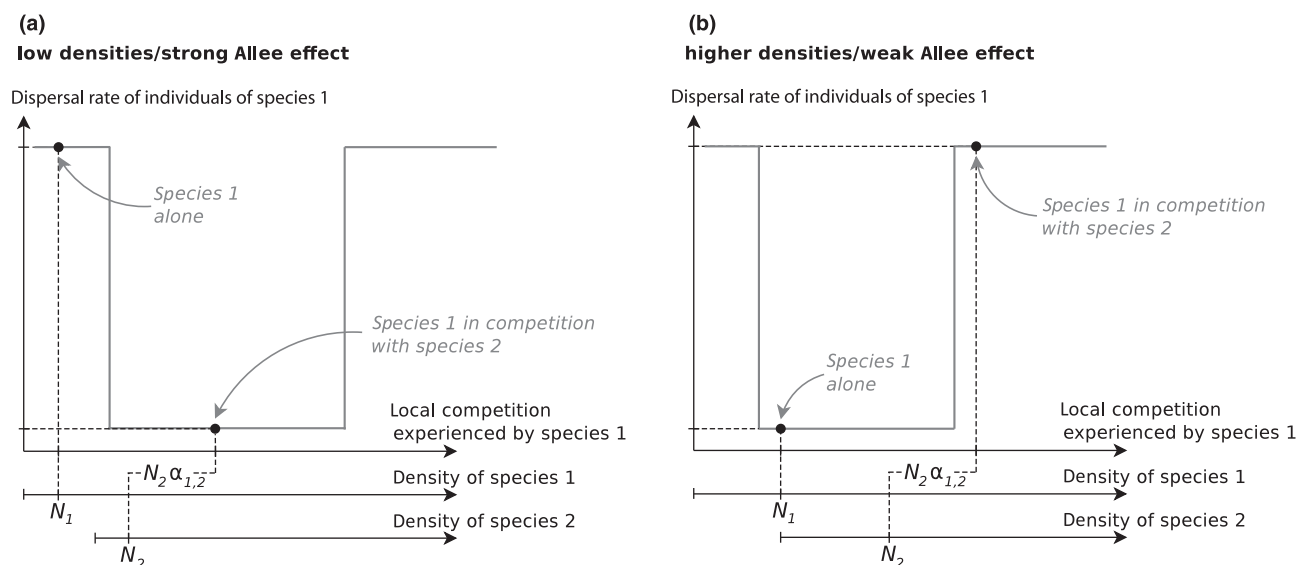


Figure 1 Predicted impact of interspecific competition on conditional dispersal and movement of individuals in a metacommunity of species experiencing Allee effects. Single species with Allee effects are expected to exhibit roughly U-shaped density-dependent dispersal/ movement functions (reaction norm; grey line; for example, for a continuous time model; the lower threshold should always be step-like, as all individuals should disperse if fitness is reduced by Allee effects). Conspecific density then determines dispersal and movement strategies ('species 1 alone'). If this model holds for metacommunities, the dispersal rate/ movement strategy of the focal species (species 1) should be determined by its own density (N_1) and the density of competitors weighted by the respective competition coefficient ($N_2 \alpha_{1,2}$) and result in an altered dispersal/ movement strategy ('species 1 in competition with species 2'). Whether dispersal/ movement is decreased (a) or increased (b) due to interspecific competition depends on population densities and the Allee effect strength.

ment and dispersal in our experimental two-species metacommunities and differentiate two main scenarios: (a) Species 1 has a high dispersal/ movement rate when alone due to low densities and/or strong Allee effects. In competition with species 2, it should then decrease its dispersal/ movement rate as shown in Fig. 1a. (b) Species 1 experiences a weak Allee effect or is at higher densities and thus exhibits a low dispersal/ movement rate when alone. Competition with species 2 can then lead to an increase in dispersal and movement as depicted in Fig. 1b. Evidently, the observed effect size may be small when interspecific competitive interactions are very weak and we do not depict the cases in which the effect of species 2 on species 1 does not impact dispersal and movement behaviour. Species 2 in principle follows the same rules as species 1 (Fig. 1). This allows us, on a more speculative note, to predict the behavioural response of species 2 to the elicited changes in behaviour of species 1. In principle, local density and therefore competition will be increased or decreased as a consequence of species 1 decreasing, respectively increasing its dispersal/ movement rate. Depending on the Allee effect strength and initial densities, species 2 may then in turn alter and adjust its behaviour to the changed local conditions following the logic outlined above and in Fig. 1.

Our experimental results show that movement and dispersal are condition-dependent with regard to interspecific competition. Specifically, interspecific interaction strength and U-shaped density-dependent dispersal and movement reaction norms (Fig. 1) in combination with knowledge about the behavioural response of competing species can be used to explain dispersal and movement behaviour across metacommunities as outlined in the paragraph above. The ability to predict dispersal is a prerequisite for successfully scaling from simple, single-species to diverse and potentially complex multi-species systems and for understanding and predicting multi-species metacommunity dynamics and thus spatial dynamics in general.

MATERIALS AND METHODS

Study organisms

We used a set of three freshwater protist species that are commonly used in experimental metacommunity studies: *Tetrahymena pyriformis* (Tet), *Colpidium* sp. (Col) and *Paramecium aurelia* (Pau). These ciliate species cover a wide range of growth rates (Pau \sim Col < Tet; Altermatt *et al.* 2015), equilibrium densities (Pau < Col < Tet; Altermatt *et al.* 2015; see also Fig. S1 and Table S1) and body sizes (Tet < Col < Pau; Giometto *et al.* 2013; see also Fig. S2). Importantly, the three species differ in competitive abilities (Carrara *et al.* 2015; see also Table 1; Fig. S3 and Table S3). *T. pyriformis* is known to suffer from an Allee effect (Chaine *et al.* 2010; Fronhofer *et al.* 2015), which implies reduced growth at low population densities. The underlying chemical mechanisms are general enough to allow the conclusion that both other species likely also have Allee effects which has been suggested for *Colpidium* and *Paramecium caudatum* (e.g. Odum & Allee 1954; Duncan *et al.*

Table 1 Interaction coefficients (α_{ij}) of a Lotka-Volterra model of inter-specific competition

	Tet	Col	Pau
Tet	1	0.32	0.06
Col	2.85	1	0.01
Pau	18	2.53	1

α_{ij} represents the relative effect of species j on i . For example, if $\alpha_{ij} = 2$ species j has twice the competitive effect on species i as species i has on itself, $\alpha_{ij} = 1$ implies that inter- and intraspecific competition are equivalently strong and $\alpha_{ij} = 0$ suggests that species j does not compete with species i . Species i can be found in the columns and species j in the rows, so that $\alpha_{Tet,Col} = 2.85$, for example. Reported values are median values of eight independently fitted replicates. See Fig. S3 for community dynamics and model fits and Table S3 for information on variation.

2011). The presence of Allee effects in all three species studied is also supported by our data (see Table S2).

Protist (meta)communities and single species (meta)populations were kept in protist medium (Protozoan pellets; Carolina Biological Supply, Burlington, USA; 0.46 g/L) at a constant temperature of 22 °C (for detailed protocols see Altermatt *et al.* 2015). Resources were supplied as 5% equilibrium density bacterial culture (*c.* 1 week old; *Serratia fonticola*, *Bacillus subtilis* and *Brevibacillus brevis*) per litre of medium.

Microcosm experimental design

We used two-patch microcosms for all experiments. In order to investigate the dependence of dispersal and movement on the presence of competing species, we manipulated community composition in one patch (the start patch) and measured dispersal and movement to the second, initially empty patch (the target patch). These experimental, spatially structured systems consisted of two 20 mL vials (Sarstedt, Nümbrecht, Germany; distance between vials: 4 cm) which were connected by silicone tubes (inside diameter: 4 mm; VWR, Radnor, USA). Using clamps, we controlled whether the connecting tubes were open or closed, that is, dispersal could occur or not.

Before the experiment batch cultures of *T. pyriformis*, *Colpidium* sp. and *P. aurelia* were grown to carrying capacity (see Fig. S1). Subsequently, the batch cultures were centrifuged (centrifuge: Sigma 3-16PK; Sigma, Osterode, Germany; 3893 g; 5 min), the supernatant liquid was discarded and the pellet, which contained the protists, was resuspended in freshly bacterised medium (see Altermatt *et al.* 2015). This washing procedure largely eliminated chemical cues that were present in the batch cultures. Such chemical cues were previously found to potentially trigger intraspecific density-dependent movement (Fronhofer *et al.* 2015). We are therefore confident that the dispersal and movement behaviour observed here was not biased by cues remaining from the batch cultures. This implies that the differences in movement and dispersal between single-species metapopulations and multispecies metacommunities observed here can be attributed to a condition-dependent response with regard to interspecific interactions, since we controlled for intraspecific density.

Depending on the treatment (single-species metapopulations, two- or three-species metacommunities), start patches received populations or communities of one (Tet, Col or Pau), two (Tet–Col, Tet–Pau and Col–Pau) or three protist species (Tet–Col–Pau) from the washed batch cultures. In order to make consistent comparisons across all treatments, individual species were always added at one fourth of their respective carrying capacity and filled up with freshly bacterised medium to a total volume of 15 mL. Target patches always received 15 mL freshly bacterised medium without protists.

Communities acclimatised to the new conditions in the start patch for 1 h, during which protists could acquire information on abundance and presence of conspecifics and allopecifics. Then, the connecting tubes were opened and dispersal between the start and the target patch was allowed for 14 h. This period of time was determined through pilot experiments in order to allow the least dispersive species (Pau) to be detected in the target patch (this was usually the case after *c.* 10–12 h). After the dispersal phase, clamps were closed and movement as well as dispersal data were collected. All species combinations (treatments) were replicated eight times in independent blocks.

Data collection

Movement

We collected individual-based movement (velocity, tortuosity, net distance travelled) and morphological data (length of the protist along major and minor axes, area) after the dispersal phase from the communities in the start patch using video analysis (for detailed protocols see Altermatt *et al.* 2015). We followed the same procedure as described in Fronhofer *et al.* (2015): using a Nikon SMZ1500 stereo-microscope (Nikon Corporation, Kanagawa, Japan) with a Hamamatsu Orca Flash 4 video camera (Hamamatsu Photonics K.K., Hamamatsu city, Japan), we recorded videos for 20 s (500 frames) at a 20-fold magnification.

Subsequently, we used the free image analysis software ImageJ (version 1.46a U.S. National Institutes of Health, Bethesda, MD, USA, <http://imagej.nih.gov/ij/>) and the MOSAIC particle tracker plug-in (Sbalzarini & Koumoutsakos 2005) for the video analysis. By sequentially subtracting frames from the video, the software determines moving particles of a given size range (particle area determined by previous experimentation: 5–600 pixels). Thereafter, the particle tracker plug-in re-links the locations taking into account a predefined link distance (here: 20 pixels) over subsequent frames (for details of the algorithm refer to Sbalzarini & Koumoutsakos 2005). As described in Fronhofer *et al.* (2015), we used these movement paths to extract velocities, tortuosity (the circular standard deviation of the turning angle distribution) and net distance travelled (Euclidean distance from start to end of a movement path) as descriptive parameters that characterise a movement path.

Species within metacommunities were identified after the video analysis based on the collected morphological parameters (size and aspect ratio; see Fig. S2). We used a classification tree model (Statistical Software Package R version 3.1.2; package ‘tree’ version 1.0-35, function ‘tree’) with aspect ratio

and length along the major body axis as explanatory variables.

Dispersal

Data on dispersal was collected by manually counting and identifying a representative sub-sample of protists from both start and target patches that had been conserved with Lugol after the experiment (for a detailed protocol see Altermatt *et al.* 2015). As the species varied widely in densities (Fig. S1 and Table S1), sub-sample volumes and rates were adjusted accordingly (0.01–1 mL; 2–15 sub-samples). Dispersal rates were calculated as the ratio of dispersers (individuals per volume in the target patch) to the sum of all individuals (sum of individuals per volume in start and target patch) at the end of the experiment, that is, after 14 h.

The time window we used for dispersal was relatively long, especially in relation to the reproductive rate of the fastest reproducing species (Tet; Fig. S1 and Table S1). Therefore, the measured dispersal rates could potentially be biased as a consequence of differential growth in start and target patch. In order to exclude this source of bias in our data, we used a two-patch metapopulation model (eqns S4–S7) which we fit using a least-squares approach to the collected population density data from both patches. This model allowed us to estimate the corrected dispersal rates that take into account density-dependent growth in both patches and the potential impact of Allee effects (see above). While the corrected and measured dispersal rates differed from each other, these values were highly correlated (LM: $N = 23$, $t = 40.58$, $P < 0.001$, $R^2 = 0.987$; Fig. S5; for more detailed information and results, see Supporting Information). We therefore performed all analyses on the original, raw data.

Population growth and interspecific competition

The necessary data to estimate growth rates (r_0), carrying capacities (K) as well as all pairwise interspecific competition coefficients (α_{ij} ; relative effect of species j on species i) were collected in separate experiments using the same microcosms and experimental setup, yet without allowing for dispersal. In order to obtain information on growth rates and carrying capacities, we recorded population growth of all three protist species independently over 10 days (Fig. S1) and subsequently fit a logistic growth model (eqn. S1) to the collected time-series data using a least-squares approach. Competition coefficients were estimated analogously: we followed the community dynamics of all 2-species combinations over more than one month (Fig. S3), and fit Lotka-Volterra models of interspecific competition (eqns S2–S3) to the time-series data, and extracted the relevant parameter estimates. See Supporting Information for details. Growth parameters are reported in Table S1 and competition coefficients can be found in Table 1 and in more detail in Table S3.

Statistical analysis

Data were analysed at the population level (means over all individuals) using linear mixed models (LMMs) with ‘replicate’ as a random effect. This random effect structure was used as individual replicates, including all species combina-

tions were run in temporally independent blocks. In case of overdispersion an observation-level random effect was added. Specifically, dispersal rates were analysed as ratios of counts using generalised linear mixed models (GLMM) with a binomial error structure. In case other data did not allow a Gaussian error structure an appropriate GLMM was used. All statistical analyses were performed with the software package R version 3.1.2. (functions 'lmer' and 'glmer' from the 'lmerTest' package; version 2.0-6). For pairwise comparisons, we used Tukey *post hoc* tests (function 'glht' from the 'multcomp' package; version 1.3-7).

The relative difference in movement and dispersal between single-species metapopulations and multispecies metacommunities was analysed using one-sample *t*-tests ($\mu = 0$). If needed, data were transformed to satisfy the normality assumption. See Table S5 for further information.

RESULTS

Relationship between movement and dispersal

We found large differences in dispersal rates between species: *Colpidium* sp. showed an order of magnitude higher dispersal rates compared to both *T. pyriformis* and *P. aurelia* (Fig. 2a; see Table S4 for the detailed and full overview of all statistical analyses). Analogous differences were found in movement behaviour (Fig. 2b–d; Table S4): just as for dispersal, *Colpidium* sp. exhibited the highest net distance travelled. Generally, differences in net distance travelled were reflected in differences in velocity and tortuosity. Overall, higher velocities and less tortuous paths (narrower turning angle distribution) resulted in larger net distances travelled and vice versa (Fig. 2b–d; Table S4).

The qualitative correspondence of dispersal and movement reported for single-species metapopulations was found more generally, across all three species and in all metapopulations and -communities analysed in our experiments (Fig. S6). The

strong nonlinearity of the relationship between movement and dispersal is in good accordance with the results of Fig. 2: small differences in movement (Fig. 2b–d) potentially led to large differences in dispersal (Fig. 2a). This nonlinearity may be due to changes in the shape of the distribution of net distances travelled (Fig. S7): increased dispersal events are likely the result of long-distance movement events (fat-tailed movement distributions).

Condition-dependent dispersal and movement in metacommunities

Dispersal and the underlying movement strategies were strongly impacted by the presence of competing species (Fig. 3). For all statistical analyses, please refer to Table S5. In two-species metacommunities *T. pyriformis* always exhibited higher dispersal rates compared to the single-species reference (Fig. 3a and e). The presence of *Colpidium* sp., a relatively strong competitor ($\alpha_{Tet,Col} = 2.85$; Table 1), led to a 34% increase in the dispersal rate (Fig. 3a). The even stronger competitor *P. aurelia* ($\alpha_{Tet,Pau} = 18$; Table 1) increased *Tetrahymena*'s dispersal rate by 780% (Fig. 3e). In both cases, increased dispersal rates were reflected in altered movement patterns: the presence of competitors led to higher net distances travelled (20 and 30% respectively; Fig. 3b and f) due to higher movement velocities (Fig. 3c and g). We therefore found a generally positive relationship between the strength of competitive interactions and dispersal in *Tetrahymena*. The same positive relationship held for net distance travelled as well as movement velocity and the strength of competitive interactions (Fig. S8).

Colpidium sp. did not alter its dispersal rate in the presence of the weak competitor *T. pyriformis* ($\alpha_{Col,Tet} = 0.32$; Table 1; Fig. 3a). On the contrary, it reduced its net distance travelled (14%; Fig. 3b) by increasing movement tortuosity (Fig. 3d). The stronger competitor, *P. aurelia* ($\alpha_{Col,Pau} = 2.53$; Table 1), even decreased the dispersal rate of *Colpidium* sp. (41%; Fig. 3i) which was associated with a decrease in net distance

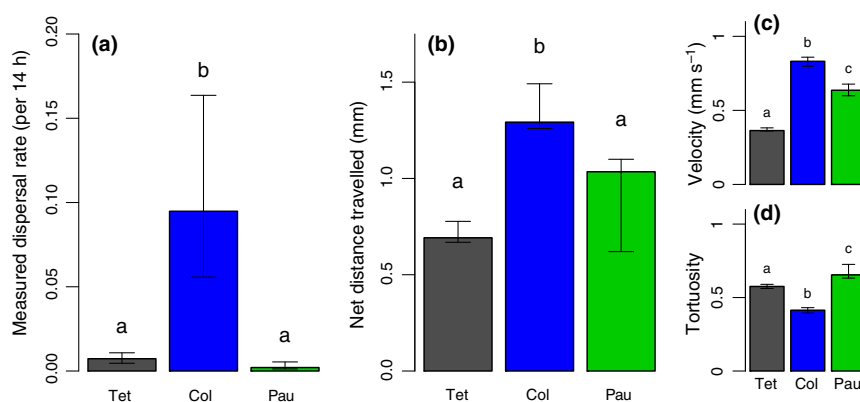


Figure 2 Dispersal and movement in single-species metapopulations. (a) Measured dispersal rates for *Tetrahymena pyriformis* (Tet), *Colpidium* sp. (Col) and *Paramecium aurelia* (Pau) in single-species, two-patch metapopulations. (b) Net distance travelled, that is, distance from start to end of one individual movement trajectory in the same metapopulations. (c) Velocity. (d) Tortuosity measured as the standard deviation of the circular turning-angle distribution. Differences in dispersal can be explained qualitatively by differences in net distance travelled. These differences are also consistent with the measured velocities and tortuosities, with faster and less tortuous movement paths leading to more displacement and dispersal. We always report the median as well as the 25 and 75% percentiles over eight replicates. The letters indicate significant differences between species ($P < 0.05$; GLMMs and Tukey *post hoc* contrasts; see Table S4 for details).

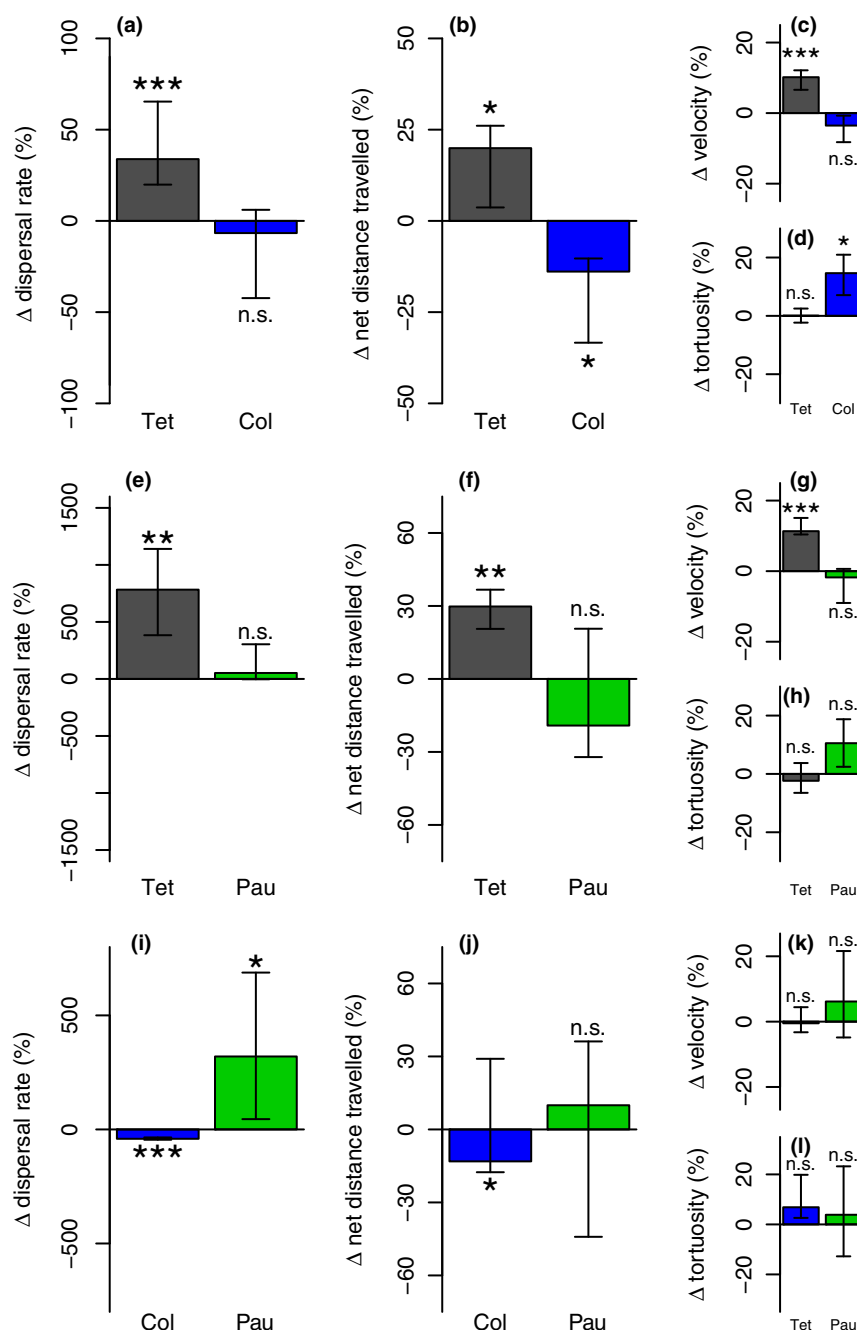


Figure 3 Difference in dispersal and movement behaviour between single-species metapopulations and two-species metacommunities. Positive (negative) values indicate more (less) dispersal/ movement in the metacommunity relative to the single species context. (a)–(d) *Tetrahymena pyriformis* (Tet) and *Colpidium* sp. (Col); (e)–(h) *T. pyriformis* (Tet) and *Paramecium aurelia* (Pau); (i)–(l) *Colpidium* sp. (Col) and *P. aurelia* (Pau). We always report the median as well as the 25 and 75% percentiles over eight replicates. The statistical analysis was performed using one-sample *t*-tests ($\mu = 0$) on the differences (see Table S5). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Note that the y-axes extensions differ among panels. Since we show effect sizes relative to single-species movement and dispersal our results depict the effect of interspecific competition only.

travelled (13%; Fig. 3j) and a non-significant increase in tortuosity (Fig. 3l).

The strongest competitor in all pairwise comparisons, *P. aurelia* ($\alpha_{Pau,Tet} = 0.06$, $\alpha_{Pau,Col} = 0.01$; Table 1), did not react to the presence of *T. pyriformis*, although a non-significant trend to smaller net distances travelled as a consequence of more tortuous paths could be observed (Fig. 3f and h). By contrast, *Colpidium* sp., which is larger than *T. pyriformis*,

induced an important increase in dispersal rate (320%; Fig. 3i), which was accompanied by a non-significant increase in net distance travelled (Fig. 3j).

Scaling up from two- to three-species metacommunities

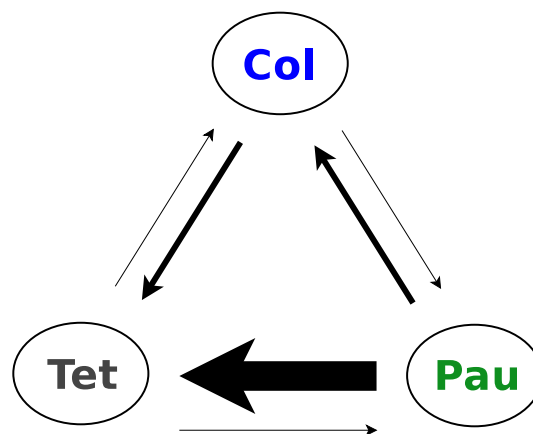
The patterns of condition-dependent dispersal and movement observed in two-species metacommunities (Fig. 3) were also

found in the three-species metacommunity (Fig. 4). The presence of competing species induced increased dispersal in *T. pyriformis* in comparison to single-species metapopulations (870%; Fig. 4a). This was associated with corresponding changes in net distance travelled and movement velocity (Fig. 4b and c). *Colpidium* sp. was found to have a reduced dispersal rate in the three-species metacommunity (50%; Fig. 4a) as in the presence of *P. aurelia* only (Fig. 3i). This pattern was accompanied by a reduction in net distance travelled (Fig. 4b) and velocity (Fig. 4c) as well as an increase in movement tortuosity (Fig. 4d). Similarly, *P. aurelia* had an increased dispersal rate in the three-species metacommunity (327%; Fig. 4a), as in the two-species metacommunity with *Colpidium* sp. (Fig. 3i). As in the two-species metacommunity, this change was not strongly reflected in changes in movement due to the large amount of variation.

DISCUSSION

We combined experiments in single-species metapopulations, as well as in two- and three-species metacommunities, to understand the effect of interspecific competition on condition-dependent movement and dispersal. Our experiments show that the presence of competing species leads to consistent and predictable changes in dispersal and movement dynamics in experimental metacommunities relative to the single-species metapopulations (Fig. 5). This strongly indicates that dispersal and movement are conditional with respect to interspecific competition, and that interspecific interactions have the potential to impact metacommunity dynamics and to change the number of coexisting species at local and regional scales. Furthermore, besides only depending on the strength of competitive interactions, we suggest that dispersal and movement also depend on the specific dispersal and movement behaviour of the interaction partners as outlined in the introduction. This dependence on community composition can only be understood if one takes into account the long-term fitness-relevant consequences of interactions and dispersal. Therefore, the specific multispecies context may introduce emergent phenomena that can only be understood in the

(a) Strength of interspecific competition



(b) Condition-dependence of dispersal and movement

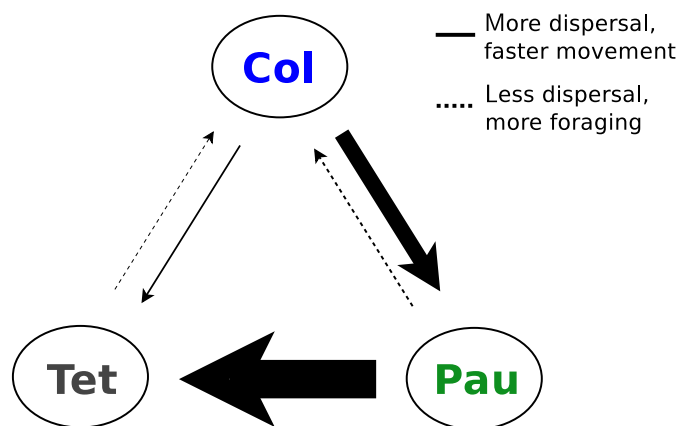


Figure 5 Condition-dependent movement and dispersal in metacommunities of competing species. (a) Strength of interspecific competitive interactions in all pairwise comparisons. (b) Resulting impact on dispersal and movement behaviour. Faster and straighter movement translates (nonlinearly) into more dispersal. We interpret slower and/or more tortuous movement as foraging behaviour. The width of all arrows scales with effect strength. See also Table 1 and Table S3.

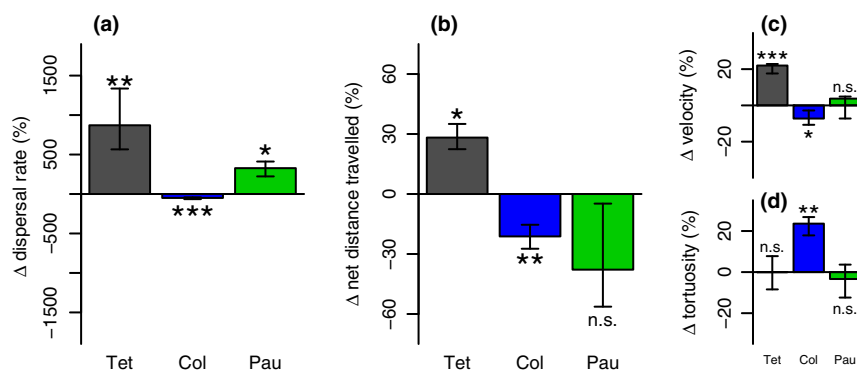


Figure 4 Difference in dispersal and movement behaviour between single-species metapopulations and three-species metacommunities (*Tetrahymena pyriformis* (Tet), *Colpidium* sp. (Col) and *Paramecium aurelia* (Pau)). Positive (negative) values indicate more (less) dispersal/ movement in the metacommunity relative to the single species context. We always report the median as well as the 25 and 75% percentiles over eight replicates. The statistical analysis was performed using one-sample *t*-tests ($\mu = 0$) on the differences (see Table S5). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

metacommunity context and cannot be predicted from single-species behaviour only. As a consequence, our work suggests that predictions based on dispersal and movement estimates gained from species in isolation are likely to fail.

Dispersal and movement are condition-dependent with respect to interspecific competition

Consistent with our theoretical predictions (Fig. 1b), a generally positive condition-dependence of dispersal and movement was found for the least competitive species, *T. pyriformis*, which also exhibits the weakest Allee effect (Figs 3, 4 and Figs S5e, S8). At the same time, the competing species did not alter their dispersal rate, which is also in line with our predictions. These results imply that models of condition-dependent dispersal, more exactly density-dependent dispersal (Metz & Gyllenberg 2001; Poethke & Hovestadt 2002), can be transferred from a single-species metapopulation context to a multispecies metacommunity context as indicated in Fig. 1b if one takes into account interspecific interactions.

Interestingly, for one species, *Colpidium* sp., the effect of interspecific competition was opposite to the results for the other species: dispersal decreased in the presence of all competitors (Figs 3i, 4 and Fig. S8). We suggest that this is due to a U-shaped competition-dependent dispersal/movement reaction norm as depicted in Fig. 1a (Kim *et al.* 2009; Fronhofer *et al.* 2015). Likely, *Colpidium* sp. shows the highest dispersal rate of all species in a single species-context (Fig. 2a) as a consequence of a relatively high species-specific Allee threshold (see Fig. S5e). In that case, an increase in competition may generally lead to a decrease in dispersal as evident from Fig. 1a. Clearly, increasing competition even further should eventually lead to positive condition-dependence. Alternatively, *Colpidium* sp. may have a globally negative density-dependent dispersal reaction norm which would lead to the same results as we report here. This would imply that *Colpidium* sp. does not suffer from intra or interspecific competition, or that the reaction norm is not an adaptation to escape from competition. Regardless of these details, our results show that dispersal and movement are conditional with respect to interspecific competition.

The most competitive species, *P. aurelia*, which is also least affected by the presence of both other species ($\alpha_{Pau,j}$ is always very small; Table 1), did not react to increased competition in a consistent manner (Fig. S8). Such a pattern can be understood and possibly generalised if one takes the impact of the focal species (here: *P. aurelia*) on the other species into account as outlined in the introduction. First, for highly asymmetric interactions (in our case this would be between *P. aurelia* and *T. pyriformis*; $\alpha_{Pau,Tet} = 0.06$ and $\alpha_{Tet,Pau} = 18$), the resulting impacts on dispersal and movement behaviour will be highly asymmetric as the weaker competitor has nearly no fitness-relevant impact on the focal species. We indeed found an increase in the dispersal rate of *T. pyriformis* by 780% while there was no effect on the dispersal rate of *P. aurelia*. Subsequently, the weaker competitor will eventually leave the local community and the stronger competitor does not experience any fitness advantages by altering its dispersal or movement behaviour. Second, if, however, the weaker competitor happens to suffer

from a strong Allee effect (here: *Colpidium* sp.) its dispersal rate may be decreased by the focal species, as described above. This has important consequences as competition will increase locally and the weaker competitor may start to have fitness-relevant negative effects on the focal species. While being a better competitor, the focal species could then experience fitness benefits by increasing its dispersal rate as depicted in Fig. 1b. This scenario potentially explains why *P. aurelia* consistently showed a comparatively strong increase in dispersal and movement in the presence of *Colpidium* sp. (a very weak competitor) in both two- and three-species metacommunities (Figs 3i and 4). Consequently, we suggest that dispersal and movement are not only condition-dependent with respect to interspecific competition, but may also depend on the specific dynamic behaviour of the interaction partner and the consequences of this behaviour.

While our results provide evidence for interspecific condition-dependence of movement and dispersal, we can only speculate with respect to the cues used to inform this plastic behaviour. Two possible candidate cues are the physical presence of the competing species and chemical cues secreted into the environment. Fronhofer *et al.* (2015) have recently provided evidence that intraspecific density-dependent movement in *Tetrahymena* is triggered by chemical cues. However, Fellous *et al.* (2012) report that physical cues seem to be used by *P. caudatum*. A conclusive study pinpointing optimal cues and elucidating the physiological mechanisms behind conditional dispersal and movement decisions remains to be conducted.

Relationship between movement and dispersal

All our experiments show that local movement behaviour can be used to explain differences in dispersal (Fig. 2 and Fig. S6). Straighter and faster movement leads to more dispersal while slower and more tortuous movement leads to less dispersal. Specifically, increased dispersal is mostly linked to higher velocities, while decreased dispersal and foraging-like behaviour is primarily linked to an increase in tortuosity (Figs 3 and 4). This holds across all species investigated in this study, although the quantitative relationship are species-specific (Fig. S6).

The relationship between movement and dispersal is nonlinear, such that, at specific starting conditions, already small differences in movement can lead to large differences in dispersal (Fig. S6). This nonlinearity mainly arises because the distributions of net distances travelled (Fig. S7) are asymmetric (skewed) and differ in the amount of long-distance movement (kurtosis), such that a small difference in median distances may imply a large amount of long-distance movement and dispersal. On a more speculative note, if one can scale up from movement kernels (Fig. S7) to dispersal kernels, the condition-dependence of the form of the kernel we observed can have important implications for species coexistence (Aiken & Navarrete 2014).

Scaling from two- to three-species metacommunities

Our results for two- and three-species metacommunities show that condition-dependent dispersal and movement are consistent across metacommunities of increasing diversity (Figs 3

and 4). The major patterns observed in the two-species systems, namely a general increase in dispersal and movement for *T. pyriformis*, a decrease in dispersal and movement for *Colpidium* sp. in the presence of *P. aurelia* and a simultaneous increase in dispersal for *P. aurelia* (Fig. 3), can all be recaptured in the three-species metacommunity (Fig. 4). The relative changes in effect size suggest a somewhat monotonic effect (see also Fig. S8 which includes data from both the two- and three-species metacommunities). We may thus speculate that the pairwise competition coefficients do not change qualitatively between two- and three-species communities. This is encouraging, as it suggests that predictions scaling up from simple to more complex communities are, in principle, possible and not elusive due to strong nonlinearities.

As a possibly interesting extension, our work also provides a mean of inferring dispersal rates from an interaction matrix (e.g. Table 1) and a reaction norm (e.g. Fig. 1). As dispersal, and the incentive to disperse, are notoriously difficult to assess in natural communities, the often much better known interaction terms (e.g. Carrara *et al.* 2015) may be a way to infer relative changes in dispersal rates across different communities.

Meta community consequences of conditional dispersal and movement

While condition-dependence is increasingly taken into account in single-species metapopulations, it has largely remained unexplored in a multispecies metacommunity context (but see Amarasekare 2010 for a theoretical model and De Meester *et al.* 2015 for empirical evidence). Our work demonstrates the importance of considering condition-dependent processes in studies of metacommunities, especially given the large effect sizes we report here (e.g. increases in dispersal rates up to 800% for some species; Figs 3 and 4). The metacommunity-level consequences of such drastic changes in dispersal remain to be explored in detail both theoretically and empirically. Given what we know about the consequences of density-dependent dispersal in metapopulations (see e.g. Amarasekare 2004; Enfjäll & Leimar 2009; Kubisch *et al.* 2011; Altwegg *et al.* 2013), the consequences are likely of large importance for population synchrony and stability in natural metacommunities (Koelle & Vandermeer 2004; Gouhier *et al.* 2010), coexistence (Amarasekare 2010), composition as well as the spatial distribution and temporal dynamics of food webs (Melián *et al.* 2015).

Interestingly, we did not find the classically reported competition-colonisation trade-off (e.g. Cadotte 2007), that is, weaker competitors showing higher dispersal abilities and vice versa in the single species metapopulations. In Fig. 2, the species are ordered by competitive rank and the pattern is clearly unimodal. By contrast, in the multispecies metacommunities conditional dispersal led to the emergence of what is usually termed 'competition-colonisation trade-off' as one can see in Fig. S9. Importantly, this negative correlation between dispersal and competitive ability is not a genuine genetic or cost-related trade-off between dispersiveness and competitive ability. This result has potentially far-reaching implications as competition-colonisation trade-offs have been linked to species coexistence and stability of meta communities (Calcagno *et al.*

2006; Livingston *et al.* 2012). Such behavioural plasticity will have important consequences for metacommunity dynamics and geographic distributions which underlines the need to take conditional dispersal into account.

CONCLUSIONS

Our experimental work shows that both dispersal and movement are conditional on and adjusted with respect to inter-specific competition. To a large extent, models of density-dependent dispersal and movement developed for single-species metapopulations can be amended to be applicable to metacommunities, highlighting that both intra- and interspecific interactions must be considered when understanding dispersal of species in a multispecies context. As we show that dispersal and movement strongly depend on the community context and likely also on the behavioural response of interacting species, our work implies that predictions based on dispersal and movement rates estimated in a single-species context only are likely erroneous and miss emergent, community-level phenomena.

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AUTHORSHIP

All authors designed the study. EAF and JK performed the experiments and analysed the data. EAF wrote the manuscript and all authors contributed substantially to revisions.

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