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Social information from immigrants: multiple immigrant-based sources of information for dispersal decisions in a ciliate

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Summary

1. Dispersal is increasingly recognized as being an informed process, based on information organisms obtain about the landscape. While local conditions are often found to drive dispersal decisions, local context is not always a reliable predictor of conditions in neighbouring patches, making the use of local information potentially useless or even maladaptive. In this case, using social information gathered by immigrants might allow adjusting dispersal decisions without paying the costs of prospecting. However, this hypothesis has been largely neglected despite its major importance for ecological and evolutionary processes.

2. We investigated three fundamental questions about immigrant-informed dispersal: Do immigrants convey information that influences dispersal, do organisms use multiple cues from immigrants, and is immigrant-informed dispersal genotype dependent?

3. Using *Tetrahymena thermophila* ciliates in microcosms, we manipulated the number of immigrants arriving, the density of congeners, the resource quality in neighbouring patches, matrix characteristics and the level of cooperation of individuals in the neighbouring populations.

4. We provide the first experimental evidence that immigrants convey a number of different cues about neighbouring patches and matrix (patch quality, matrix characteristics and cooperation in neighbouring populations) in this relatively simple organism. Furthermore, we demonstrate genotype-dependent immigrant-informed dispersal decisions about patch quality and matrix characteristics.

5. Multiple cues from immigrants and genotype-dependent use of cues have major implications for theoretical metapopulation dynamics and the potential for local adaptation.

Key-words: condition-dependent dispersal, connectivity, emigration, metapopulation, non-random dispersal, social information, *Tetrahymena thermophila*

Introduction

Dispersal, the ability of individuals to move from one place to another, has widespread effects on evolution, affecting the colonization–extinction dynamics of metapopulations, species range distribution, life-history strategies and local adaptation (Clobert *et al.* 2001, 2012; Hanski & Gaggiotti 2004; Bowler & Benton 2005; Ronce 2007; Stevens *et al.* 2014). However, our understanding of the causes and consequences of this major process in ecology and evolutionary biology is rather limited (Bowler & Benton 2005; Ronce 2007; Clobert *et al.* 2012; Edelaar & Bolnick 2012). Dispersal has generally been considered in models as either a fixed or a random behaviour, independent of individual phenotype and environmental conditions (Patterson *et al.* 2008; Clobert *et al.* 2009). However, in a landscape partly composed of unsuitable habitats, individuals should benefit from obtaining information about their environment to perform appropriate habitat choice ('informed dispersal; Clobert *et al.* 2009; Schmidt, Dall & van Gils 2010; Chaine, Legendre & Clobert 2012, 2013). A large variety of abiotic and biotic factors could be used by organisms as information sources about their environment, such as temperature, resources or the presence and performance of conspecifics (Danchin

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et al. 2004; Doligez, Pärt & Danchin 2004; Dall *et al.* 2005; Clobert *et al.* 2009; Delgado *et al.* 2014), yet empirical investigation of information use is rare.

The last two decades have seen the emergence of studies showing that dispersal decisions can vary depending on individual phenotype or local context (Clobert *et al.* 2009), which are expected to strongly affect the potential for local adaptation and metapopulation dynamics (Clobert *et al.* 2009, 2012). In cases of spatially or temporally heterogeneous environments where the local context is not always a reliable predictor of neighbouring patches, using local information can be useless or even maladaptive (Kubisch *et al.* 2014). Since emigrating in a lower quality patch can lead to lower fitness or even death (Clobert *et al.* 2001, 2012; Bonte *et al.* 2012), obtaining information about neighbour patches prior to emigration can provide organisms with the opportunity to make adaptive habitat choices during dispersal (Holt 1985; Kubisch *et al.* 2014).

Gathering information about neighbouring patches can either occur through sampling nearby patches, which can be costly and time-consuming (Delgado *et al.* 2014), or by using indirect cues about the surrounding environment brought to the natal patch (Reed *et al.* 1999; Cox & Kesler 2012; Chaine, Legendre & Clobert 2013), yet empirical examples of the use of indirect cues are very rare. In a first study, Cote & Clobert (2007) showed that juvenile common lizards (*Lacerta vivipara*) use indirect information from immigrants about the density of neighbouring patches to adjust their dispersal behaviour. Immigrants can thus be a source of information about density in neighbouring patches to adjust dispersal decisions without paying the costs of prospecting (Cote & Clobert 2007). This process might thus be a form of social information use, which can either be based on evolved signals or cues inadvertently provided by immigrants (Danchin *et al.* 2004; Doligez, Pärt & Danchin 2004; Dall *et al.* 2005). In the context of dispersal decisions, the existence of social information use might affect metapopulation and evolutionary dynamics (Cote & Clobert 2007; Clobert *et al.* 2009). Indeed, extensive knowledge of the landscape is assumed in several ecological hypotheses related to the distribution and movement of individuals in the landscape (e.g. ideal free distribution, Fretwell & Lucas 1970; Kennedy & Gray 1993; least cost path, Adriaensen *et al.* 2003). Indirect information from immigrants could greatly enhance knowledge beyond that of prospecting, making the distribution of organisms in the landscape more easily approaching an ideal free distribution.

However, our understanding of immigrant-informed dispersal is still scarce (Cote & Clobert 2007, 2010; Clobert *et al.* 2009; Schmidt, Dall & van Gils 2010). Recently, Chaine, Legendre & Clobert (2013) used a theoretical model to show that immigrant-informed dispersal could evolve simultaneously to the use of local information about population density. Furthermore, they found that the simultaneous use of local and immigrant information sources reduces extinction risk and favours metapopulation persistence compared to local density-dependent dispersal only (Chaine, Legendre & Clobert 2013). Whereas one might expect direct local information to be much more reliable (i.e. contain less noise) than indirect immigrant-informed information, this study pointed out the importance of information from immigrants in ecological and evolutionary processes. Candidate dispersing individuals might benefit from obtaining information about various aspects of neighbouring patches in a metapopulation beyond current density including the difficulty of travel to and the social make-up of those patches. However, whether immigrants simply convey information about the presence or density of conspecifics in neighbour patches, or whether more complex information and multiple cues are conveyed and used by organisms to adjust dispersal decisions still remains unanswered (Cote & Clobert 2007; Clobert *et al.* 2009; Chaine, Legendre & Clobert 2013). Furthermore, whether this process can affect nonrandom gene flows and consequently the potential for local adaptation requires genotype-dependent immigrant-based dispersal decisions (Edelaar, Siepielski & Clobert 2008; Edelaar & Bolnick 2012), which has yet to be investigated.

In this study, we used experimental microcosms of a ciliated protist, *Tetrahymena thermophila*, to test whether immigrants arriving in a population convey information about the neighbouring patches and matrix that influences dispersal decisions and to what extent this relatively simple organism can use cues from immigrants about different aspects of the environment. Moreover, we used six genetically different clonal lines of *T. thermophila* in our experiments to test for genotype-dependent differences in immigrant-based dispersal decisions. We manipulated independently five types of information that might be conveyed by immigrants to test whether a focal population modified its dispersal rate accordingly. To obtain immigrants, we introduced cells in one side of a two-patch system (Fjerdingstad *et al.* 2007; Schtickzelle *et al.* 2009; Chaine *et al.* 2010; Pennekamp *et al.* 2014) and then collected cells that dispersed to the target patch. These disperser cells were then used as immigrants who had actually undergone dispersal of their own accord. We transferred a standard number of these immigrants in new populations placed in the start patch of a two-patch system. We then let cells disperse and measured dispersal rate as the proportion of cells in the target patch. Specifically, we manipulated the number of immigrants arriving, the density of congeners and resource quality in neighbouring patches, matrix characteristics and the level of cooperation of individuals in the neighbouring populations.

Materials and Methods

CULTURE CONDITIONS AND CELL SAMPLING

T. thermophila cells were maintained in rich liquid growth media (2% Difco proteose peptone, 0·2% yeast extract) at 22°C (Fjerdingstad *et al.* 2007; Schtickzelle *et al.* 2009; Chaine *et al.* 2010;

Pennekamp *et al.* 2014). All manipulations were performed in sterile conditions under a laminar flow hood.

We used a standardized procedure to measure cell density and morphology in *T. thermophila* cultures based on automatic analysis of digital images (Pennekamp & Schtickzelle 2013). From each culture, we measured 5 samples (10 μL) each pipetted into one chamber of a multichambered counting slide (Kima precision cell 301890), and took digital pictures under dark-field microscopy (Fjerdingstad *et al.* 2007; Schtickzelle *et al.* 2009; Chaine *et al.* 2010). Digital pictures were analysed using IMAGEJ software (version 1.47, National Institutes of Health, USA, http://imagej.nih.gov/ij; *see* Pennekamp & Schtickzelle 2013) to obtain the overall number of cells on the picture, later transformed into density per mL.

TWO-PATCH SYSTEMS TO MEASURE DISPERSAL

To measure dispersal rate in *T. thermophila*, we used standard two-patch systems consisting of two habitat patches (1·5-mL standard microtubes), connected by a corridor (4-mm internal diameter silicon tube, 2·5 cm long) and filled with growth media (Fjerdingstad *et al.* 2007; Schtickzelle *et al.* 2009; Chaine *et al.* 2010; Pennekamp *et al.* 2014). At the beginning of each experiment, cells were placed in the start patch and the corridor was opened to allow dispersal towards the target tube. At the end of the dispersal time, the corridor was clamped to separate residents (cells remaining in the start patch) from dispersers (cells that moved to the target patch), and both patches were sampled as previously described.

For any given two-patch system, dispersal rate was computed as the proportion of the cells present in the target patch (target/(start+target)). This measure of dispersal, used in several previous studies (Fjerdingstad *et al.* 2007; Schtickzelle *et al.* 2009; Chaine *et al.* 2010), has been shown to be insensitive to density-dependent effects on growth that might lead to differences in growth rate between patches over the timeframe of the experiment (Pennekamp *et al.* 2014). Moreover, temperatures used in Pennekamp *et al.* (2014) were higher than in our study, which means generation time is longer in our work (about $^1/_2$ - 1generation at 23°C; Chaine *et al.* 2010) and density effects should therefore be even smaller.

EXPERIMENTAL PROCEDURES

All experiments we conducted focused on the addition of 'immigrants' into a new population, but experiments differed in the conditions that immigrants experienced prior or during dispersal. To obtain immigrants, we introduced cells (150 000 cells mL^{-1} unless stated otherwise) in one side of a two-patch system. After 5 h, we collected cells that dispersed to the target patch (i.e. dispersers). These disperser cells were then used as immigrants who had actually undergone dispersal of their own accord. We transferred 5000 immigrant cells (unless stated otherwise) into a new focal population that consisted in 225 000 cells (150 000 cells ml^{-1}) in the start patch of a two-patch system as described above. We then let cells disperse for 17 h (about $^1/_2$ - 1generation at 23 °C; Chaine *et al.* 2010). All experiments were performed with 5 replicated two-patch systems for each immigrant treatment and each genetic line.

We performed five distinct experiments to test whether *T. thermophila* cells adjust dispersal decisions depending on different types of information from immigrants:

1. *Density in neighbouring patches*: in order to test whether the density in the immigrants' patch of origin affected the dispersal rate of a focal population, we used immigrant cells that came from populations at 3 different cell densities: 50 000, 150 000 and 300 000 cells mL^{-1}. Population density determines competition among individuals, and local density is often found to drive dispersal decisions (i.e. density-dependent dispersal; Fronhofer, Kropf & Altermatt 2014; Pennekamp *et al.* 2014; Rodrigues & Johnstone 2014). Since colonization success should depend on competition in the colonized habitat, we expect cells to adjust their dispersal decisions to information obtained from immigrants about the density in neighbouring patches.
2. *Number of immigrants*: we investigated whether cells modified dispersal behaviour depending on the number of immigrants transferred into a focal population: 5000 or 10 000 cells. The number of immigrants might indeed be indicative of both the presence of neighbouring habitats and of competition in these habitats. Consequently, cells should benefit from adjusting their dispersal decisions depending on the number of immigrants arriving.
3. *Cooperation strategy of immigrants*: we tested whether the composition of other populations in terms of life-history strategies influenced the decision to disperse. *T. thermophila* recognize kin and form aggregative groups between kin (Chaine *et al.* 2010) that cooperate through the exchange of specific molecules (Christensen *et al.* 1996, 2001). Cells should thus benefit from either staying or settling in groups of kin and should therefore adjust their dispersal decisions to information provided by immigrants about the kin structure of neighbouring habitats. Here, we tested whether the relatedness and relative cooperation level of immigrants affected the dispersal rate of a focal population. We used four genetic lines for this experiment, two being cooperative (i.e. E & Q) and two being selfish (i.e. 7 & 4A; Schtickzelle *et al.* 2009; Chaine *et al.* 2010). The two other lines used in other experiments are 'medium cooperative' (i.e. D3 & P) and so were not used here to simplify the design. Focal populations received immigrants from either i) the same genetic line as the focal population, ii) a different genetic line but with the same cooperation strategy or iii) a different genetic line with a different cooperation strategy.
4. *Matrix characteristics*: since dispersal behaviours are expected to be shaped by landscape matrix characteristics (Bonte *et al.* 2012), we expect individuals to adjust dispersal according to immigrant information about corridor diameter, a characteristic of the matrix that causes a greater reduction in dispersal rate than expected proportionally to the size of the opening in our model species (in contrast to corridor length which had no significant effect no dispersal rate; A.S. Chaine; unpublished data). Here, immigrants were cells that disperse through either normal corridors (4 mm in diameter) or thinner corridors (1·6 mm in diameter). Since immigrants that dispersed through thin corridors should be informative of a landscape with reduced connectivity, therefore increasing the potential costs of dispersal, we expect a lower dispersal rate compared to when immigrants came through normal corridors.
5. *Habitat quality in neighbouring patches*: we studied whether immigrants convey information about habitat quality of neighbouring patches by adding immigrants that originated from patches that were i) of the same quality as the focal population (standard medium), ii) poorer than the focal pop-

ulation (1/2 diluted medium) or iii) richer than the focal population (2 × concentrated medium). Since the quantity of resources in a given habitat is one of the main drivers of dispersal decisions (Bowler & Benton 2005; Bonte *et al.* 2012; Clobert *et al.* 2012), we expect cells to adjust their dispersal decisions according to information obtained about the expected quality of neighbouring habitats.

Additionally, during the experiment on habitat quality in neighbouring patches, we quantified dispersal rate without immigrants in addition to treatments with immigrants presented above. This control allowed us to test whether the range of dispersal rates differed according to the presence or absence of immigrants.

Since cells were not individually distinguishable when mixed, we could not determine whether cells that had dispersed at the end of our experiments were initially from the focal population or introduced immigrants. Immigrants could have different dispersal decisions than individuals from the focal populations. However, the 5000 immigrants introduced in our experiments represent only 2% of the resulting focal population (i.e. 5000 immigrants + 225 000 residents). Even in the hypothetical case where all these immigrants systematically either disperse or stay after their introduction to a new population, such a small proportion would have had little effect on our quantitative measure of dispersal.

To determine whether immigrants differed in some way from resident cells, we tested whether adding disperser versus resident cells as ‘immigrants’ into a new patch affected the dispersal rate of the focal population. To obtain ‘dispersers’ and ‘residents’, we allowed dispersal as described above, but then collected cells from either the start patch (i.e. residents) or the target patch (i.e. dispersers) for introduction into new focal populations.

STATISTICAL ANALYSES

For each of the five experiments, we first tested for genotype-dependent differences in immigrant information use using linear models with dispersal rate as a dependent variable, the immigrant treatment, the genetic line and their interaction as fixed factors. We computed linear models with a Gaussian distribution, and in all cases, residuals of these models followed a normal distribution (Fig. S1, Supporting information). Following a backward selection procedure, we removed the interactions and fixed factors from the models when nonsignificant (Table S1, Supporting information). The data can be downloaded from Dryad (Jacob *et al.* 2015).

Results

We found no significant effect of the density in the immigrant patch of origin on dispersal rate ($F_{2,82}$ = 0·22; P = 0·84; Table S1, Supporting information) and no significant interaction between immigrant patch density and the genetic lines ($F_{10,72}$ = 1·62; P = 0·12).

The number of immigrants did not have a significant effect on dispersal rate ($F_{1,53}$ = 3·35; P = 0·07; Table S1, Supporting information), and we found no significant effect of the interaction between genetic line and immigrant number on dispersal rate ($F_{5,48}$ = 0·90; P = 0·49).

We then tested whether the cooperation strategy of immigrants affected the dispersal rate of a focal population and found a significant main effect ($F_{2,53}$ = 3·95; P = 0·02; Table S1, Supporting information), but no significant interaction between immigrant cooperation strategy treatments and genetic line on dispersal rate ($F_{6,47}$ = 2·09; P = 0·07). We also found that the changes in dispersal rate in response to immigrants did not significantly differed depending on whether focal cells were cooperative and immigrants selfish or the converse (cooperation level * immigrant treatment: $F_{2,51}$ = 1·84; P = 0·17). This result consequently suggests that the four lines used in this experiment did not differ in how they use information about immigrant cooperation strategy to adjust their dispersal decisions. Compared to a control where immigrants were of the same genetic line as the focal population, we found that adding immigrants from the same cooperation strategy but a different genetic line had no significant effect on the dispersal rate (estimate ± SE = 0·003 ± 0·02; $F_{1,34}$ = 0·02; P = 0·882). In contrast, when immigrants were from a different genetic line with a different cooperation strategy, the focal population showed a significant decrease in dispersal rate (−0·05 ± 0·02; $F_{1,35}$ = 7·32; P = 0·011; Fig. 1).

We found a significant interaction between matrix characteristics (i.e. corridor diameter) experienced by immigrants and the genetic line on the dispersal rate of the focal population ($F_{5,48}$ = 3·20; P = 0·014; Fig. 2; Table S1, Supporting information). Analyses within each genetic line revealed that two lines decreased their dispersal rate when immigrants came through thinner corridors (line 4A: −0·08 ± 0·03; $F_{1,8}$ = 5·95; P = 0·041; line P: −0·07 ± 0·03; $F_{1,8}$ = 6·01; P = 0·040; Fig. 2), whereas 4 showed no significant change (all P > 0·12).

By modifying the habitat quality in neighbouring patches (quantity of resources in the immigrants’ patch of

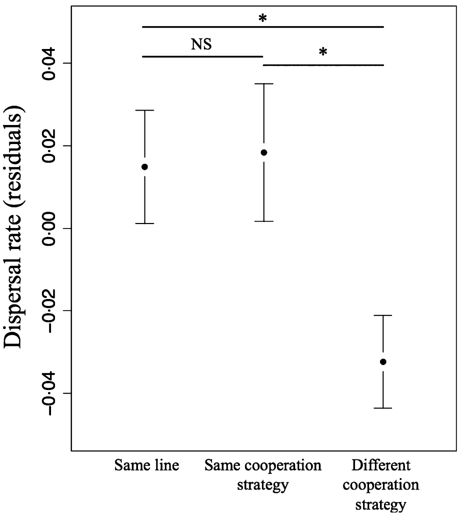

Fig. 1. Dispersal rate was influenced by immigrant cooperation strategy. Mean ± SE of residuals of dispersal rate after statistically correcting for differences among the genetic lines is shown for each type of immigrant. Stars indicate significant differences (*P <0·05) and ‘NS’ indicates differences where P > 0·05.

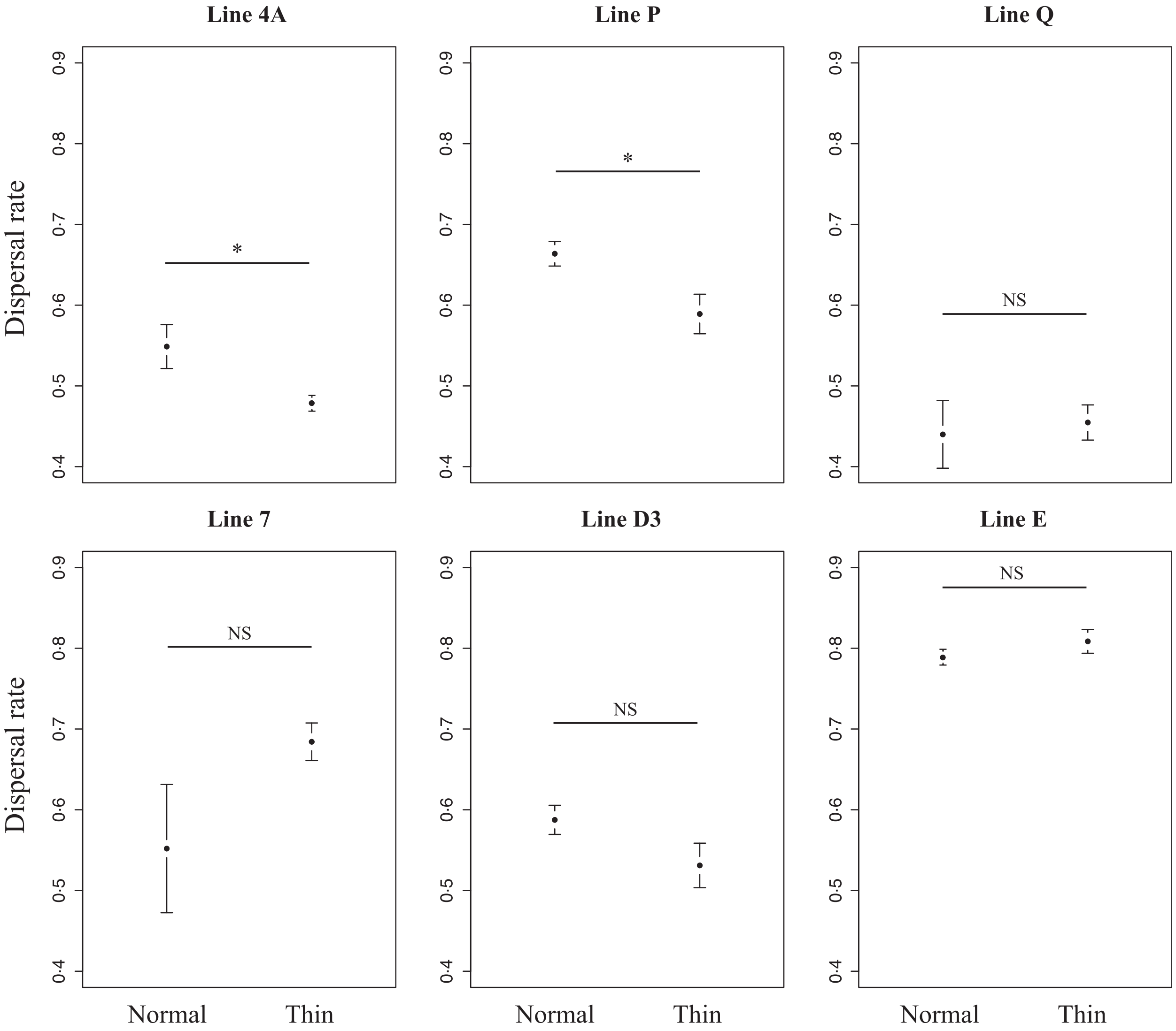

Fig. 2. Landscape matrix characteristics (i.e. corridor diameter) experienced by immigrants influenced dispersal rate. Each panel shows the dispersal rate (mean ± SE) of a single genotype responding to immigrants who had previously dispersed through normal or thin corridors. Both the intensity and direction of the relative response to immigrant dispersal conditions varied among genotypes ($F_{5,48}$ = 3·20; P = 0·014). Stars indicate significant differences (*P <0·05) and 'NS' indicates differences where P > 0·05.

origin), we found a significant interaction between habitat quality and genetic line on the dispersal rate of the focal population ($F_{10,72}$ = 6·94; P < 0·001; Fig. 3; Table S1, Supporting information). We found that 2 lines significantly decreased their dispersal rate when immigrants came from poor quality patches (estimate ± SE; line 4A: −0·11 ± 0·04; $F_{1,8}$ = 6·86; P = 0·031; line Q: −0·26 ± 0·06; $F_{1,8}$ = 20·42; P = 0·002; Fig. 3), one showed a slight but nonsignificant tendency to increase dispersal (line 7: 0·18 ± 0·09; $F_{1,8}$ = 4·01; P = 0·08), and 3 lines showed no significant change in dispersal rate (all P > 0·10). Surprisingly, only one line showed an increase in dispersal rate when immigrants came from high-quality habitats (line E: 0·15 ± 0·05; $F_{1,8}$ = 9·59; P = 0·015), whereas 3 lines decreased their dispersal rate (line 7: -0·26 ± 0·10; $F_{1,8}$ = 6·48; P = 0·034; line P: -0·21 ± 0·04; $F_{1,8}$ = 27·77; P = 0·001; line Q: -0·25 ± 0·04; $F_{1,8}$ = 34·42; P < 0·001) and two showed no significant change in dispersal (all P > 0·62).

In order to test whether the range of dispersal rates differ according to the presence of absence of immigrants, we compared dispersal when no immigrants were added relative to treatments with immigrants (all treatments pooled) in the experiment on habitat quality in neighbouring patches. As in previous studies, we found extensive differences in dispersal tendency between genetic lines (Fjerdingstad *et al.* 2007; Pennekamp *et al.* 2014), with dispersal rate in the absence of immigrants ranging from 0·27 to 0·78. In the presence of immigrants, dispersal rate ranged from 0·16 to 0·86, and there was no significant interaction between immigrant presence/absence and genetic lines ($F_{5,108}$ = 1·56; P = 0·18) and no main effect of immigrant presence/absence on the average dispersal rate ($F_{1,113}$ = 0·33; P = 0·57).

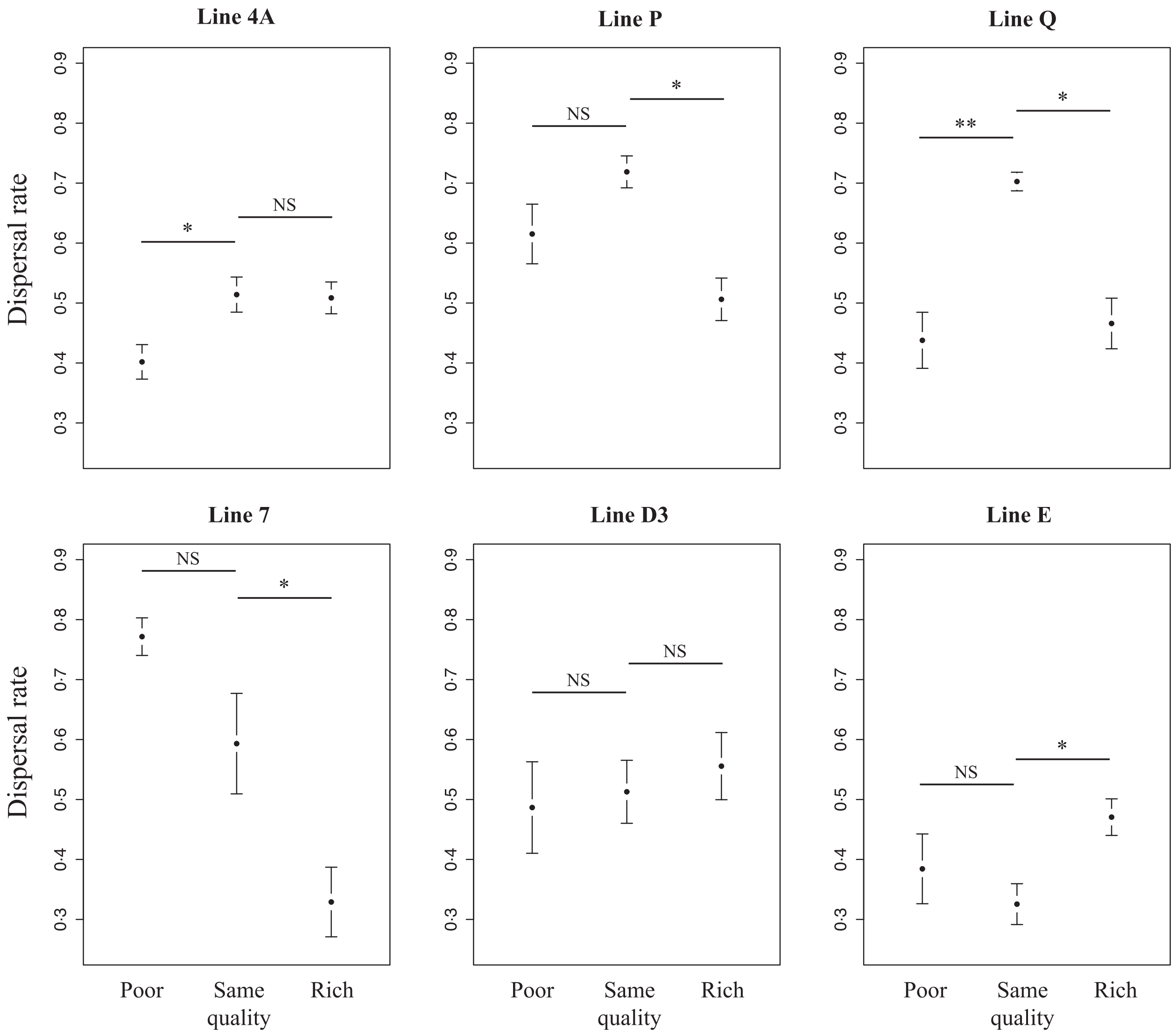

Fig. 3. Effects of habitat quality in neighbouring patches (quantity of resources in the immigrants' patch of origin) on dispersal rate. Each panel shows how a single genotype modified dispersal rate (mean ± SE) according to immigrants coming from patches that were poorer, the same as, or richer than the focal patch. Genotypes differed extensively in both the degree and direction of their reaction to immigrants of different types ($F_{10,72} = 6{\cdot}94$; $P < 0{\cdot}001$). Stars indicate significant differences (*$P < 0{\cdot}05$; **$P < 0{\cdot}01$) and 'NS' indicates differences where $P > 0{\cdot}05$.

We found a significant interaction between the status of cells (i.e. resident *versus* disperser cells) added as immigrants in the new populations and genetic line on the dispersal rate of the focal population ($F_{5,48} = 4{\cdot}45$; $P = 0{\cdot}002$), suggesting dispersers and residents provide different cues when added into a new population and that the genetic lines responded in different ways to this immigrant information.

Discussion

In this study, we experimentally tested whether immigrants convey information about the environmental and social conditions outside the local habitat, and to what extent a relatively simple organism can use cues from immigrants about different aspects of the environment to adjust its dispersal decisions (Table 1). Our experiments revealed that *T. thermophila* cells were able to adjust their dispersal rate according to immigrant-borne information about a number of different biotic and abiotic characteristics of the environment including neighbouring patch quality, corridor characteristics and the cooperation strategy of the neighbouring populations. In contrast, the density in the immigrants' patch of origin and the number of immigrants that arrive in a patch appeared to have no significant effect on the dispersal rate. Importantly, we found differences among genotypes in the dispersal responses to some forms of immigrant information about neighbouring patches (habitat quality and matrix characteristics), but not to all types of information (the cooperation strategy

Table 1. Multiple cues from immigrants are used to adjust dispersal decisions in *Tetrahymena thermophila*, partly in a genotype-dependent way

Immigrant information	Information used	Genotype-dependent use of information
Density in neighbouring patches	No	No
Number of immigrants	No	No
Cooperation strategy of immigrants	Yes	No
Landscape matrix characteristics	Yes	Yes
Habitat quality in neighbouring patches	Yes	Yes

of the neighbouring population; Table 1). These results have important implications for our understanding of dispersal and its role in metapopulation dynamics.

MULTIPLE IMMIGRANT-BASED SOURCES OF INFORMATION FOR DISPERSAL DECISIONS

In this study, we provide the first experimental evidence for the use of multiple cues from immigrants in dispersal decisions. Cells of *T. thermophila* used information regarding three relatively complex features of distant populations. First, cells adjusted their dispersal rate according to the cooperation strategy of immigrants and consequently in neighbouring populations. The *T. thermophila* lines used in this experiment are able to recognize kin and orient their dispersal towards patches occupied by kin or nonkin according to their cooperation strategy (Chaine *et al.* 2010). Here, we found that *T. thermophila* using indirect information adopt the same dispersal rate whether immigrants are kin or nonkin with the same cooperation strategy, despite their ability to distinguish kin from nonkin (Chaine *et al.* 2010). However, when immigrants have a different cooperation strategy, we found that the dispersal rate decreased relative to both treatments where immigrants were kin and nonkin with the same cooperation strategy. Importantly, we found that the changes in dispersal rate in response to arrival of nonkin immigrants did not significantly differ depending on the focal cells' cooperation level. This result might appear surprising since recognition and preferential cooperation among kin is expected only in cooperative species (Hamilton 1964a,b). First, our results might indicate that mixing with nonkin exhibiting the same cooperation strategy does not entail significant costs, suggesting potential cooperative behaviours among closely related genetic strains in this species. In contrast, cells modified their dispersal decisions to avoid cells with a different cooperation strategy. Surprisingly, noncooperative cell lines decreased their dispersal when cooperative immigrants arrived despite potential advantages they might accrue from being in a population of cooperators. Such a pattern might arise if noncooperators stay to benefit from the arrival of cooperators (i.e. their social habitat quality has improved with the arrival of cooperative immigrants) or if cooperators can exclude or punish noncooperators. The former explanation seems more likely since our previous work showed that noncooperative lines preferentially orient towards populations with cooperative lines (Chaine *et al.* 2010). These results point out the need for further experiments to explore the mechanisms involved in recognition of kinship and cooperative status, and how cooperative behaviours that exist among kin within a clonal genetic line are modulated in the presence of cells from different genetic lines.

T. thermophila modified dispersal rates according to characteristics of the matrix experienced by immigrants during their dispersal, and this response differed between genetic lines. According to theory, higher fragmentation and/or costs of dispersal will not always lead to selection for reduced dispersal (Ronce, Perret & Olivieri 2000). While the costs of dispersal should impact performance and thus the evolution of dispersal behaviours (Bonte *et al.* 2012), the role that metapopulation characteristics (e.g. stability, fragmentation) play in shaping dispersal decisions is still debated (Ronce & Olivieri 2004; Ronce & Clobert 2012). Our findings point to a potential resolution to mixed results on the importance of landscape costs on dispersal: some genotypes might be more sensitive to landscape-induced costs of dispersal than others because of genotype-dependent variations in dispersal strategies (Clobert *et al.* 2009).

Modification of the quality of resources in the immigrants' patch of origin affected the dispersal rate of a population receiving these immigrants. Patch resource quantity, relative to competition, is thought to be one of the most important drivers of dispersal and lies at the foundation of ideal free distribution theory (Fretwell & Lucas 1970; Kennedy & Gray 1993; Clobert *et al.* 2001, 2012; Bowler & Benton 2005; Bonte *et al.* 2012). Our results show that *T. thermophila* immigrants convey information about habitat quality in the metapopulation, and individuals use this information to adjust their dispersal behaviour. The use of indirect information could greatly accelerate the approach to an ideal free distribution of individuals on patches relative to direct prospecting among patches. Interestingly, the responses to different immigrant habitat quality information differed between genetic lines: only two of six lines significantly decreased their dispersal rate when immigrants came from poor quality habitats. Surprisingly, only one line increased its dispersal rate when immigrants came from high-quality patches, whereas three lines significantly decreased dispersal. Overall, we found that the dispersal rate decreased when immigrants came from patches with levels of resources different from the focal patch regardless of whether that patch was of better or worse quality. While this result seems counterintuitive, one possible explanation is that our liquid growth media provide higher levels of resources than natural patches (i.e. bacteria in ponds), and thus, it is less costly to stay in an already good quality habitat than trying to move to one that will be at best slightly better. Alternatively, *T. thermophila* cells might not be able to obtain information about the relative quality of neighbouring patches from immigrants, but only detect whether neighbouring patches are of similar or different quality. The risk of leaving a good patch for a different, but occupied, patch in a heterogeneous metapopulation may be less advantageous than departure when other possible patches are not occupied (i.e. no immigrants from potential patches). Finally, immigrants might not provide information about the neighbouring patches but rather modify local conditions and as a result affect dispersal rates. We discuss below the likelihood of this hypothesis in our experiment.

The above results show that immigrants provide a wide range of information about the surrounding metapopulation, which begs the question of how this information is coded and transferred to residents. Our goal here was to demonstrate the use of information rather than the precise proximate basis of that information. Nevertheless, two main potential mechanisms might be involved in the process demonstrated here. Immigrant-informed dispersal decisions might first be based on chemical communication between cells. *T. thermophila* is indeed known to produce chemical compounds (Christensen *et al.* 1996, 2001) used in kin recognition (Chaine *et al.* 2010). Moreover, a recent study showed that cell movements are density-dependent in a ciliate (*Tetrahymena pyriformis*), a behavioural plasticity that is probably based on chemical cues (Fronhofer, Kropf & Altermatt 2014). Investigating whether immigrant-informed dispersal is based on chemical cues produced by cells, identifying the molecules potentially involved, and testing whether these chemicals function as cues or have specifically evolved to convey information (i.e. signals) will be a very exciting avenue for future research. Alternatively, effects of immigrants on dispersal decisions might result from demographic effects if immigrant arrival modifies local competition for resources that would in turn affect local dispersal rate. In such a case, immigrant-informed dispersal would not entail adaptive use of information about surroundings, but would be a consequence of modified local context affecting local information acquired by cells. In our experiments, the number of immigrants added was relatively limited compared to the focal population size (i.e. 2%, *see methods*), and adding 10 000 rather than 5000 immigrants did not significantly change the focal population dispersal rate. Since density is known to drive dispersal decisions in this species (Pennekamp *et al.* 2014), these results thus suggest that addition of small number of immigrants has little influence on local competition in our experiments. Nevertheless, if immigrants' arrival modifies local competition and by this way affects dispersal decisions, it means that the local conditions driving dispersal decisions are influenced by environmental and social conditions in the landscape. The benefits of dispersal decisions are likely to drastically differ depending on whether immigrant-informed dispersal decisions are based on socially acquired information about the landscape or on local information modified in some extent by immigrants, an important question that will require further experimental investigation.

Importantly, here, we found that dispersal rates in the presence of immigrants did not differ from when no immigrant arrived, thus showing that dispersal rate in the presence of immigrants was well within the normal dispersal rate of this species (i.e. when only local information is present and no immigrant arrived). However, even if the overall dispersal range was similar between the presence and absence of immigrants, the type of information brought by immigrants had a significant effect on dispersal behaviour as illustrated in the manuscript (Fig. 3). Our results thus suggest that the presence of immigrant per se is not determinant in shifting dispersal rates overall, but that differences in the information provided by immigrants do indeed modify dispersal rates. We can thus confidently argue that the type of information provided by immigrants and the characteristics of the genetic line (e.g. dispersal strategy and use of information provided) are the main drivers of immigrant-informed dispersal decisions.

IMMIGRANT-INFORMED DISPERSAL IS GENOTYPE DEPENDENT

Genetic variation in how information is used has not yet been considered in the dispersal literature, yet would have critical consequences for metapopulation theory. In addition to important differences in dispersal tendency between genetic lines (Fjerdingstad *et al.* 2007; Pennekamp *et al.* 2014; *this study*), the genetic lines used in our experiments also differed in how they adjusted dispersal according to information about neighbouring patch quality and matrix characteristics, but not to the cooperation strategy of immigrants despite a nonsignificant tendency. These results could reflect differences among genotypes in their response to immigrant information, differences among genotypes in what information is transferred or differences among genotypes in their ability to obtain information from immigrants.

Regardless of the cause, the degree of variation among genotypes in immigrant-informed dispersal might have important consequences for metapopulation dynamics and in particular for local adaptation. Genotype-dependent responses to immigrant information about neighbouring patch quality and matrix characteristics should lead to nonrandom gene flow in the landscape (Edelaar, Siepielski & Clobert 2008; Edelaar & Bolnick 2012). In contrast, if all individuals in a metapopulation exhibit the same dispersal response to immigrant information, as we found with regard to immigrant cooperation strategy, we would expect immigrant-informed dispersal to favour metapopulation homogenization and thus to decrease local adaptation (Ravigné, Dieckmann & Olivieri 2009; Thibert-Plante & Hendry 2011). It remains to be seen whether such genotype-dependent use of immigrant information exists in others species. Integrating variation in how genotypes use immigrant-informed dispersal into metapopulation theory should lead to a major shift in our understanding of metapopulation dynamics, local adaptation, species distribution range and evolution.

WHEN NOT TO USE INDIRECT INFORMATION

While immigrant-borne information influenced dispersal in some contexts, not all forms of information were used by residents to modify dispersal decisions. We found that the number of immigrants and the density of an immigrant's original patch – both of which would likely be linked to patch density throughout the metapopulation – had no influence on dispersal of residents in a new patch, at least within the range used in this study. Density often influences fitness, so it seems strange that such information would not be used. Juvenile lizards adjusted dispersal decisions to immigrant-transmitted information about neighbour patches density, but not to the number of immigrants (Cote & Clobert 2007) as also predicted by a recent theoretical model (Chaine, Legendre & Clobert 2013). Immigrant number could be a poor source of information on the density or quality of other patches, especially if genotypes vary greatly in the intensity and direction of density-dependent dispersal as in the case for *T. thermophila* (Pennekamp *et al.* 2014). This result highlights that information is not always useful, especially if it is a poor predictor of conditions in the metapopulation (Bocedi, Heinonen & Travis 2012).

The lack of a significant effect of the density in the immigrant patch of origin on the dispersal rate of the focal population is surprising. For example, density is known to be a major determinant of fitness in lizards (Lecomte *et al.* 1994; Cote, Clobert & Fitze 2007; Meylan, Clobert & Sinervo 2007), where both local and immigrant information about density have been found to affect dispersal (Massot *et al.* 1992; Cote, Clobert & Fitze 2007; Meylan, Clobert & Sinervo 2007) . We used a range of densities in *T. thermophila* similar to those shown to influence dispersal through direct local density (Pennekamp *et al.* 2014), so the information provided by immigrants should have been sufficient to influence dispersal decisions. Furthermore, immigrants from the different densities differed in morphology suggesting that information was potentially available. In species such as *T. thermophila*, which have a short life cycle and live in ephemeral patches, the density of a population is expected to change drastically over short time periods relative to the generation time. High variability in information is expected to decrease its reliability and thus decrease the potential for the evolution of information use (Boulinier & Danchin 1997; Doligez *et al.* 2003; Bocedi, Heinonen & Travis 2012). In contrast, the common lizard inhabits stable patches and lives relatively longer, and population density shows low temporal variation between subsequent generations (Massot *et al.* 1992), and therefore, information on density should be both reliable and useful. Further studies should investigate whether the use of immigrant information regarding density has evolved only in species where population densities are unlikely to change drastically within short time periods relatively to the generation time (Cote & Clobert 2007; Meylan, Clobert & Sinervo 2007). More generally, our experiments show that the presence of indirect information is not sufficient, and rather the reliability of that information in predicting future fitness is much more likely to drive the evolution of indirect information use.

CONCLUSION

In this study, we demonstrated that a relatively simple organism is able to use multiple cues from immigrants to adjust dispersal decisions. Obtaining information about the landscape through immigrant-informed dispersal without paying the costs of prospection is likely to strongly affect metapopulation dynamics. The local context is usually of great importance for individual fitness, and acquiring local information should allow individuals to adjust their decision to stay or leave a given habitat. However, obtaining information from immigrants about the landscape additionally to local information might allow individuals to make adaptive dispersal decisions (Chaine *et al.* 2010; Chaine, Legendre & Clobert 2013), especially when environmental conditions in the landscape are heterogeneous (Kubisch *et al.* 2014). The existence of such information transfer should increase individual knowledge of the landscape and thus favour a better match to an ideal free distribution relative to using locally acquired information only (Kennedy & Gray 1993; Cote & Clobert 2007; Clobert *et al.* 2009). Moreover, immigrant information led to either increased or decreased dispersal rates depending on cell genotype and the nature of the information conveyed. Therefore, immigrant-informed dispersal can in some cases reduce the extinction risk of a metapopulation through increased connectivity as predicted by models (Chaine, Legendre & Clobert 2013), but could also increase isolation through a reduction in dispersal rates and consequently increase extinction risks (Hanski 1998; Hanski & Gaggiotti 2004). At the same time, if indirect information allows individuals with specific phenotypes to target appropriate habitat patches, we should see an acceleration of local adaptation (Edelaar & Bolnick 2012). This process would be especially potent if genotypes differ in their reaction to the same information such that the match between genotype and environment is intensified. Globally, our results from highly controlled experiments in a relatively simple organism clearly show that immigrant-informed dispersal is likely to be common and will likely have very important effects on metapopulation dynamics, local adaptation and species evolution. Both empirical investigations in a broader array of organisms and theoretical exploration of the impact that immigrant-informed dispersal will have on meta-population dynamics have the potential to greatly alter our understanding of both ecological and evolutionary processes.

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Author contributions

ASC and JC designed the experiments. ASC and MH performed the experiments, SJ and NS performed picture analyses, and SJ analysed the data. SJ wrote the manuscript, and ASC, NS and JC contributed substantially to revisions.

Data accessibility

The data are available at Dryad: http://dx.doi.org/10.5061/dryad.gd8m9 (Jacob *et al.* 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Summary statistics for immigrant-based and genotype dependent dispersal decisions in each of our five experiments. Significant factors retained in the models after backward selection are presented in bold.

Fig. S1. Q-Q plots for dispersal rate, as used in linear models presented in Table S1.