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Gene flow favours local adaptation under habitat choice in ciliate microcosms

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Local adaptation is assumed to occur under limited gene flow. However, habitat-matching theory predicts dispersal should favour rather than hinder local adaptation when individuals selectively disperse towards habitats maximizing their performance. We provide experimental evidence that local adaptation to the upper margin of a species' thermal niche is favoured by dispersal with habitat choice, but hindered under random dispersal. Our study challenges the idea that high gene flow precludes local adaptation, and provides unique experimental evidence of habitat choice as an overlooked mechanism responsible for adaptation under rapid environmental changes.

Classical evolutionary theory predicts that moderate-to-high gene flow in heterogeneous environments should hinder local adaptation and restrict speciation by homogenizing local gene pools[1,2]. In contrast, recent theory has shown that dispersal, the movements potentially leading to gene flow[3], could facilitate local adaptation when involving habitat choice[4–8]. When individuals either stay in or disperse towards habitats that maximize their performance, the resulting gene flow would involve a non-random subset of genotypes that are locally adapted[5–7,9]. In contrast to the common view, even high dispersal rates might thus facilitate rather than hinder local adaptation[4–8,10]. By generally assuming random gene flow, we might deeply misjudge the consequences of dispersal for eco-evolutionary dynamics and underestimate species adaptive potential facing environmental changes[4–7,10,11]. Despite the major impact habitat choice could have on local adaptation and the extensive empirical evidence for non-random phenotype- or context-dependent dispersal[12], experimental validation of this theoretical framework is lacking.

We experimentally tested whether local adaptation can occur under high gene flow if directed by habitat choice using microcosms of *Tetrahymena thermophila*, a ciliate that performs active dispersal and habitat choice[13,14] and reproduce clonally in our culture conditions. We focused on adaptation to temperature at the upper margin of the species' thermal niche where growth rate is significantly reduced. Temperature is an environmental factor of great importance to the fitness of many organisms, and quantifying adaptive potential at the margins of a species' thermal niche is highly relevant in the context of current global environmental changes and species range shifts. Furthermore, this model species, which naturally lives under thermal spatiotemporal variability in freshwater ponds, shows genetic variability in performance along a thermal gradient (Supplementary Fig. 1)—a condition required for habitat choice to lead to non-random gene flow[5,7].

To quantify habitat choice effects on local adaptation, we first tested whether individuals choose their habitat to match their thermal performance ability using *T. thermophila* maintained in axenic liquid media (see Methods). Genetically variable populations composed of ten clonal genotypes showing variation in performance along a temperature gradient (Supplementary Fig. 1) were used to inoculate the central patch of linear three-patch dispersal systems and allowed to disperse towards the two adjacent empty patches (Supplementary Fig. 2a). The temperature in the central and neighbouring patches was set to either 23 °C (thermal niche core; Supplementary Fig. 1) or 35 °C (upper thermal niche margin) to test for habitat choice at emigration (stay or disperse through the corridors) and immigration (join one of the neighbouring patches; Supplementary Fig. 2a). Single-patch systems were inoculated and kept either at 23 °C or 35 °C as controls in which cells had no possibility of dispersing. After 24 h, we transferred the cells from each patch into fresh media at 35 °C and quantified the growth rate as a measurement of fitness at the upper thermal niche margin (Supplementary Fig. 2a).

Our results provide support for the habitat-matching hypothesis: individuals that chose to stay or join the thermal niche margin (red points in Fig. 1) had significantly higher growth rates at 35 °C than those that chose to stay in or join 23 °C patches (blue points in Fig. 1; analysis of variance: $F_{1,34} = 12.66$; $P = 0.001$). Alternative hypotheses, such as selection, plasticity or drift, cannot explain these results (see Supplementary Materials). For instance, rapid selection on a subset of genotypes that better fit the local temperature would have led to higher fitness at 35 °C for cells from isolated 35 °C patches than isolated 23 °C patches (that is, when no dispersal was allowed). However, individuals kept for 24 h at either 23 °C or 35 °C in isolated patches did not significantly differ in growth at 35 °C (grey points in Fig. 1; $F_{1,10} = 0.09$; $P = 0.77$). Our results thus demonstrate that cells showed increased growth rate at 35 °C because they preferred to stay in or join the temperature that matched their thermal performance.

When individuals selectively disperse towards habitats that maximize their performance, dispersal is predicted to favour rather than hinder local adaptation[4–7,10], but this hypothesis remains unexplored experimentally. We performed a long-term selection experiment to test the effects of dispersal with habitat choice compared with random dispersal on local adaptation at the upper margin of the species' thermal niche (Supplementary Fig. 2b). We set up large genetically variable populations (that is, mixes of the 10 genotypes; ~250,000 cells in total) maintained at 35 °C for around 250 generations (6 weeks; 2–5 h generation time; Supplementary Fig. 2b) and receiving immigrants weekly from the initial genetically variable

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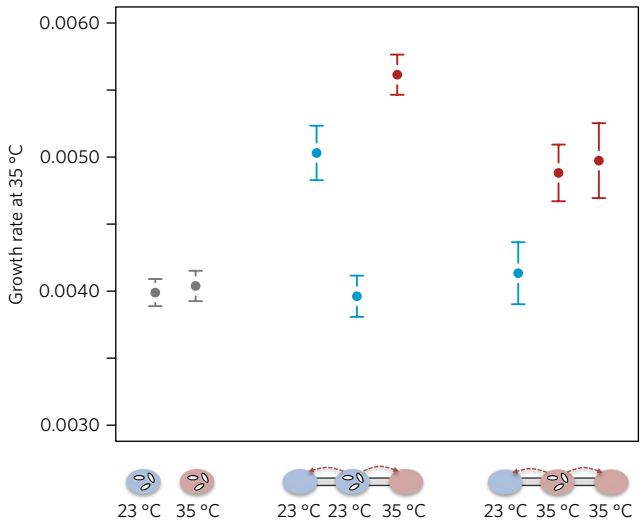

Fig. 1 | Habitat choice and thermal performance ability. Cells that chose to stay in or join the thermal niche margin through dispersal (red) had higher fitness in these marginal conditions than those that chose the other habitat (that is, the thermal niche core; blue) or did not have the opportunity to disperse (grey). The mean ± s.e. growth rate per hour at 35 °C of the cells from each population is shown ($n = 6$ replicates initially inoculated with 40,000 cells ml^{-1} in the central patch).

populations, mimicking regular movement of immigrants from core to marginal habitats. Immigrants came from a weekly reiteration of the first experiment, generating immigrants for either random or habitat choice dispersal. A random dispersal treatment consisted of introducing as immigrants a random subset of initial populations from isolated control patches ('no dispersal'; Supplementary Fig. 2a). Habitat choice treatments consisted of cells that chose a 35 °C patch (stayed at 35 °C or joined 35 °C from a 35 °C or 23 °C origin; red patches in Supplementary Fig. 2a). Control choice treatments consisted of cells that chose a 23 °C patch (blue patches in Supplementary Fig. 2a).

Adaptation to local conditions was estimated once a week by quantifying the growth rate at 35 °C of a sample of cells from each population placed in fresh media, and through 'local versus foreign' and 'home versus away' approaches[1,15]. Foreign populations consisted of the same initial genetically variable populations but maintained at 23 °C instead of 35 °C without immigration. Furthermore, because the intensity of gene flow should affect its consequences for local adaptation[1,16], we conducted the entire experiment at two levels of dispersal: 10% and 30% of the local population's initial carrying capacity. Additional controls for temporal changes in fitness consisted of genetically variable populations maintained at 23 °C and receiving either random dispersal or habitat choice dispersers from 23 °C to 35 °C.

Our results show that dispersal with habitat matching favours local adaptation: local adaptation to the niche margin increased through time when dispersal entailed habitat choice towards the niche margin (linear mixed model: $F_{1,59} = 39.63$; $P < 0.001$; Fig. 2a, Supplementary Table 1 and Supplementary Figs 4 and 5) together with an increase in the population sizes (Supplementary Fig. 6). This was true regardless of whether the immigrants were cells that chose to disperse toward a 35 °C habitat, or cells that did not disperse but rather stayed in a 35 °C habitat (Fig. 2b). Thus, the positive effect of habitat choice on local adaptation resulted from the choice of habitat itself, and not from a potential higher competitive or colonization ability of dispersers that would appear only when immigrants consisted of dispersers[17]. In contrast, local adaptation did

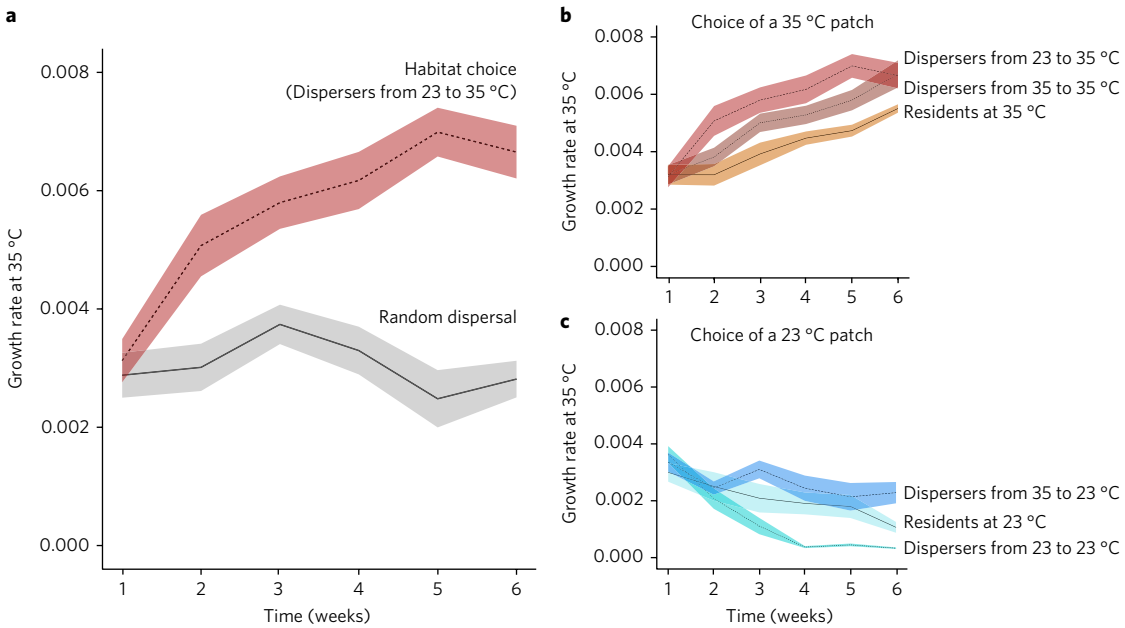

Fig. 2 | Habitat choice favours local adaptation at the thermal niche margin. a, The growth rate at the thermal niche margin (35 °C) did not significantly change over time under random dispersal (grey), whereas it significantly increased when incoming dispersers actively chose to leave a 23 °C patch to join a 35 °C patch (red). Estimating local adaptation as 'local versus foreign' and 'home versus away' showed a similar pattern (Supplementary Figs 3 and 4). **b**, Local adaptation increased when dispersal involved adaptive habitat choice, regardless of whether the immigrant cells chose to disperse towards a 35 °C habitat, or did not disperse but rather stayed in a 35 °C habitat. **c**, Local adaptation to 35 °C was prevented or decreased when immigrants chose to stay in or join a 23 °C patch. The lines connect the mean values of the growth rate per hour for all the populations in each treatment ($n = 12$ per treatment; the two immigration rates are not distinguished here as the differences were mostly not significant; see Supplementary Table 1). The coloured areas represent s.e.

not occur under random dispersal ($F_{1,59}=0.49$; $P=0.48$; Fig. 2a), as predicted by classical theory[1]. Finally, populations receiving immigrants consisting of cells that chose a 23 °C habitat showed unchanged or even decreased local adaptation (Fig. 2c). All populations started with equal population sizes and received a fixed number of immigrants each week, meaning that treatment effects were very unlikely to result from drift or differences in mutational input rates (see Supplementary Materials). Cells from control populations maintained at 23 °C showed no change in fitness at 35 °C over time (Supplementary Table 2).

While the potential for local adaptation should decrease with increasing gene flow under random dispersal in temporally stable landscapes[1,16], local adaptation can be maximal for intermediate gene flow levels under temporal variability through an increase in local genetic diversity[15]. In contrast, gene flow may favour local adaptation even in temporally stable landscapes when involving habitat choice[5–7]. Accordingly, local adaptation increased faster with a 30% immigration rate compared with a 10% immigration rate when immigrants were dispersers that chose to join a 35 °C patch from a 35 °C original habitat (Supplementary Table 1). Increasing the immigration rate did not, however, affect the rate of local adaptation in all other treatments, suggesting that a 10% immigration rate was sufficient to completely hinder or favour local adaptation depending on the type of dispersal involved[15]. A next critical step will be to identify and compare the tipping points at which the effect of dispersal on local adaptation is reversed with and without habitat choice[18].

High dispersal has long been assumed to homogenize populations in structured landscapes, thereby hindering local adaptation and speciation[1,2]. In agreement with this classical theory, we found that random dispersal hinders local adaptation. However, when dispersal results from habitat matching, local adaptation is facilitated[4–7,10]. Our study demonstrates how the behaviours underlying dispersal—random versus active habitat choice movement—can shift the effects of gene flow from constraining to facilitating local adaptation. Habitat choice should drastically increase a species' ability to adapt to new environmental conditions, especially compared with expectations from current models on the consequences of climate change, which largely assume random dispersal. For instance, the loss of genetic variation during range expansion is typically expected to reduce adaptive potential, but the empirical evidence is mixed at best[19,20]. Habitat matching during range expansion may, in contrast, increase the adaptive potential and thereby facilitate rather than constrain range expansion[6,21], which could also explain successful range expansions in some species[22]. The results of our microcosm experiments stress the need to identify the environmental conditions required for the evolution of habitat choice (for example, environmental variability, information availability and reliability, and dispersal costs), to quantify its effects in sexually reproducing systems where recombination occurs, and to integrate this process into current theoretical and predictive frameworks[5–7,22].

Methods

Culture conditions and genotypes. *T. thermophila* is a 30–50 µm ciliated unicellular eukaryote naturally living in freshwater ponds in North America. The species is a model organism in cell and molecular biology, and its maintenance under laboratory conditions benefits from decades of experience. Here, we used ten genotypes originally sampled by F. P. Doerder in North America[23] (genotypes D1, 2, 3, 4, 6, 10, 12, 13, 15 and 17; see Supplementary Table 3), which reproduced clonally in our culture conditions.

Cells were maintained in axenic rich liquid growth media (2% Difco proteose peptone and 0.2% yeast extract) at 23 °C and propagated weakly (5% transfer to fresh media). 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 automated analysis of digital images. From each culture, we measured 5 samples (10 µl) pipetted into one chamber of a multi-chambered counting slide (Kima precision cell 301890), and took digital pictures under dark-field microscopy. Digital pictures were analysed using IMAGEJ software (version 1.47, National Institutes of Health; http://imagej.nih.gov/ij) to obtain the overall number of cells on the picture, which was later transformed into density per ml.

Dispersal and habitat choice. To quantify habitat choice, we used dispersal systems consisting of three linearly connected patches (5 ml standard Eppendorf tubes; Supplementary Fig. 7) connected by corridors (4 mm internal diameter silicon tubes; 5 cm long) and filled with growth media. The cells were placed in the central patch (that is, the 'start patch'; ~200,000 cells) and the corridors were opened. The cells could therefore choose to either stay in the 'start' patch or disperse, and if they dispersed they could choose where to go.

Population growth and fitness. We quantified the fitness of individuals from each patch in the habitat choice experiment and under different gene flow treatments in the local adaptation experiment using standard population growth analyses. Small numbers of cells (~100 cells) from each patch or population were transferred to 96-well plates (250 µl wells) filled with growth media. Cultures were maintained at 23 or 35 °C and absorbance measurements at 550 nm were performed every 1 h for 1 week using a microplate reader (Infinite M200, Tecan). Absorbance was significantly and linearly correlated with cell density within the range of densities observed in this study ($F_{1,22}=145.94$; $P<0.001$; $R^2=0.87$; Supplementary Fig. 8). The growth rate of each population was computed using the gcfit function (grofit R-package[24]) with spline fit (illustration in Supplementary Fig. 2).

Data availability. The data that support the findings of this study are available from https://doi.pangaea.de/10.1594/PANGAEA.876499.

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Author contributions

S.J., D.L., A.S.C., D.B. and J.C. defined the research theme. S.J., D.L., A.S.C., D.B., M.H. and J.C. set up the experimental protocols. S.J. performed the experiments and analysed the data with the help of M.H. and N.S. S.J. wrote the manuscript. D.L., A.S.C., D.B., N.S. and J.C. contributed substantially to the revisions.

Competing interests

The authors declare no competing financial interests.

Additional information

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