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DISPATCH

Evolution: How important is the dimensionality of natural selection in local adaptation?

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Organisms adapt to their local environments, which may vary in one aspect, or many. A new study shows that such dimensionality matters, as it impacts the magnitude and dynamics of local adaptation, with broader ecological consequences such as the evolution of generalists.

Evolution by natural selection may be best evidenced by the existence of local adaptation, that is, when individuals have a higher fitness in their native environment than in a foreign environment. It has become an important concept in evolutionary biology both because it reveals the process of adaptation within the current time frame and because it is fundamental to the evolution of diversity¹. Divergent selection favours intra-specific variation and may underlie speciation when reproductive isolation evolves alongside eco-geographic differentiation between populations². Studying ecological speciation has put a spotlight on the importance of the dimensionality of divergent selection³. Reproductive isolation appears stronger when it involves multiple barriers linked to multiple traits and multiple ecological axes than in cases of unidimensional divergence³⁻⁵. The matter of dimensionality also arises at the intra-specific level when studying local adaptation^{6,7}. Environments can differ in one aspect (for example, temperature, salinity, or humidity) or multiple aspects, and fitness may involve one trait (such as colour, growth rate, or size) or multiple traits. How does such dimensionality in divergent selection affect the evolutionary dynamics of local adaptation? Would local adaptation be stronger or weaker if two sites differ in one or multiple environmental variables? Will adaptation arise faster or slower? These fundamental questions are addressed by Nathan White and colleagues in an elegant empirical study published in this issue of *Current Biology*⁸.

To investigate the effects of environmental dimensionality on local adaptation, White and collaborators⁸ designed an ambitious experimental-evolution set up using a species of monogonont rotifer, *Brachionus plicatilis*, a type of small aquatic invertebrate. Population pairs of *B. plicatilis* were split between environments differing by either one or three stressors (Figure 1). Local adaptation was then measured by assessing fitness in home versus away environments at regular intervals, including enough replicates to overcome the vagaries of experimental evolution (four unidimensional and four multidimensional pairs, with four replicates per pair of environments). This experimental design represents an impressive amount of work led over months (40 cycles of 7 days) that was tailored to test the impact of dimensionality on local adaptation. Fitness was quantified in all environments, consistently and at regular time intervals, allowing the authors to measure both the magnitude and dynamics of adaptation. Moreover, by ensuring that the intensity of selection was similar in all environments, the experiment readily tested the impact of dimensionality without being confounded by a putative difference in total selection intensity.

Predictions about how the dimensionality of divergent selection affects local adaptation are ambivalent. On the one hand, spreading selection across multiple orthogonal traits may hasten and strengthen adaptation both by affecting more genes and by reducing fitness of migrants and hybrids^{3,5-7}. On the other hand, spreading selection across multiple traits and loci may lead to a weaker effect on fitness and adaptation may be slowed down by gene flow and recombination for unlinked loci^{3,6}. The results presented by White *et al.*⁸ partially validate and contradict both predictions. In their study, both unidimensional and multidimensional divergent selection led to local adaptation, but they differed in magnitude over time. In multidimensional pairs, local adaptation quickly increased, supporting the first prediction. This result agrees with a meta-analysis suggesting that adaptation is stronger when dimensionality is higher⁷. However, over the course of the experiment, local adaptation between multidimensional environments declined⁸. In contrast, unidimensional divergence ultimately led to stronger local adaptation than multidimensional divergence, but occurred more slowly⁸. Overall, the dynamic of adaptation appears as a crucial parameter that is affected by the dimensionality of environmental divergence.

To fully understand what shapes the dynamics of adaptation, it is worth returning to the initial definition. In White *et al.*⁸, local adaptation was defined following the classic measure of ‘home versus away’ fitness⁹ — that is, the difference between fitness in the local conditions and fitness in the contrasting conditions for each experimental pair of environments. However, examining changes in fitness separately reveals a more complex pattern. Whereas home fitness increases regularly in all environments, away fitness varies over time. In particular, away fitness increases in the last cycles in most multidimensional environments, resulting in a lower estimate of local adaptation but not in a loss of fitness (Figure 1). This is interpreted as an evolution of generalists that adapt to both environments, although no direct measure of phenotypes confirmed this explanation in White *et al.*'s study. Importantly, such an outcome reminds us that local adaptation does not always equate with antagonist pleiotropy, whereby alleles have opposite effects in home and away habitats. Some adaptive traits may be positive in one environment and neutral in another, and, even if they are doomed to be fixed in the long run, they can contribute to transitory differences between habitats¹⁰. Moreover, the evolution of generalists means that the dimensionality of selection has important consequences on ecological traits in communities. One could speculate that heterogeneous habitats varying in multiple independent stressors would favour the evolution of generalist species whereas environmental gradients varying on a single dimension would favour the evolution of specialists.

Overall, the research by White and colleagues⁸ provides a relevant and renewed point of view on local adaptation. First, it highlights that dimensionality matters and may influence not only the magnitude of adaptation but also its dynamic. Second, it shows that limiting local adaptation to antagonistic fitness between environments may hide more complex transitory processes. Third, it reveals that considering local adaptation from the perspective of fitness and ecological traits (generalist versus specialist, for instance¹¹) has different implications than considering local adaptation as early stages of speciation. Because reproductive isolation is an additional step that may, or may not, follow local adaptation, the impact of selection dimensionality on those evolutionary processes can differ^{2,6}. For instance, although multidimensional divergence may favour the completion of speciation between highly divergent populations³, it may rather impede early stages of local adaptation through the evolution of generalist populations⁸. Altogether, the question of how dimensionality in divergent selection impacts evolutionary dynamics thus appears non-trivial, and new studies like the one by White *et al.*⁸ will inspire complementary theoretical and empirical work to better refine predictions.

Besides selection by environment, local adaptation is conditioned by available variation, gene flow, genetic architecture, and recombination¹². This begs the question — how do such important features influence the impact of dimensionality on local adaptation? White *et al.*'s study is based on a species that is mostly clonal with a limited amount of sex and recombination. Would we observe similar patterns in an exclusively clonal species? For instance, the emergence of adaptive combinations of alleles allowing generalist adaptation may be prevented by limited recombination. On the contrary, would we observe such rapid adaptation in an obligatory sexual species in which gene flow and recombination might re-shuffle loci responding to multidimensional divergence? To address this and understand more broadly the impact of dimensionality on local adaptation, further studies are needed, such as theoretical models accounting for recombination, meta-analyses on a wide range of taxa, and experimental work — perhaps, for example, studies extending White *et al.*'s inspiring design to other species amenable to experimental evolution.

Comparing the results of White *et al.* to the literature on ecological speciation^{3,5} and quantitative genomics^{13,14} raises important questions. To what extent does the dimensionality of divergent selection play a different role for local adaptation at intra-specific levels versus emerging reproductive isolation between species? How is this impacted by the level of gene flow versus the strength of selection? Does multidimensional divergence lead to stronger or weaker genetic differentiation than unidimensional divergence? Does multidimensional versus unidimensional selection generate different landscapes of genetic differentiation along the genome? Again, experimental evolution would help to reveal the impact of dimensionality on other evolutionary processes, such as the colonisation of a new environment, phenotypic evolution, and speciation¹⁵. With the increasing availability of low-cost sequencing¹⁶, strategies called 'evolve and re-sequence'^{17,18} also open promising opportunities to better consider the complexity of multidimensional environments together with the genetic basis of adaptive traits and further our understanding of evolution.

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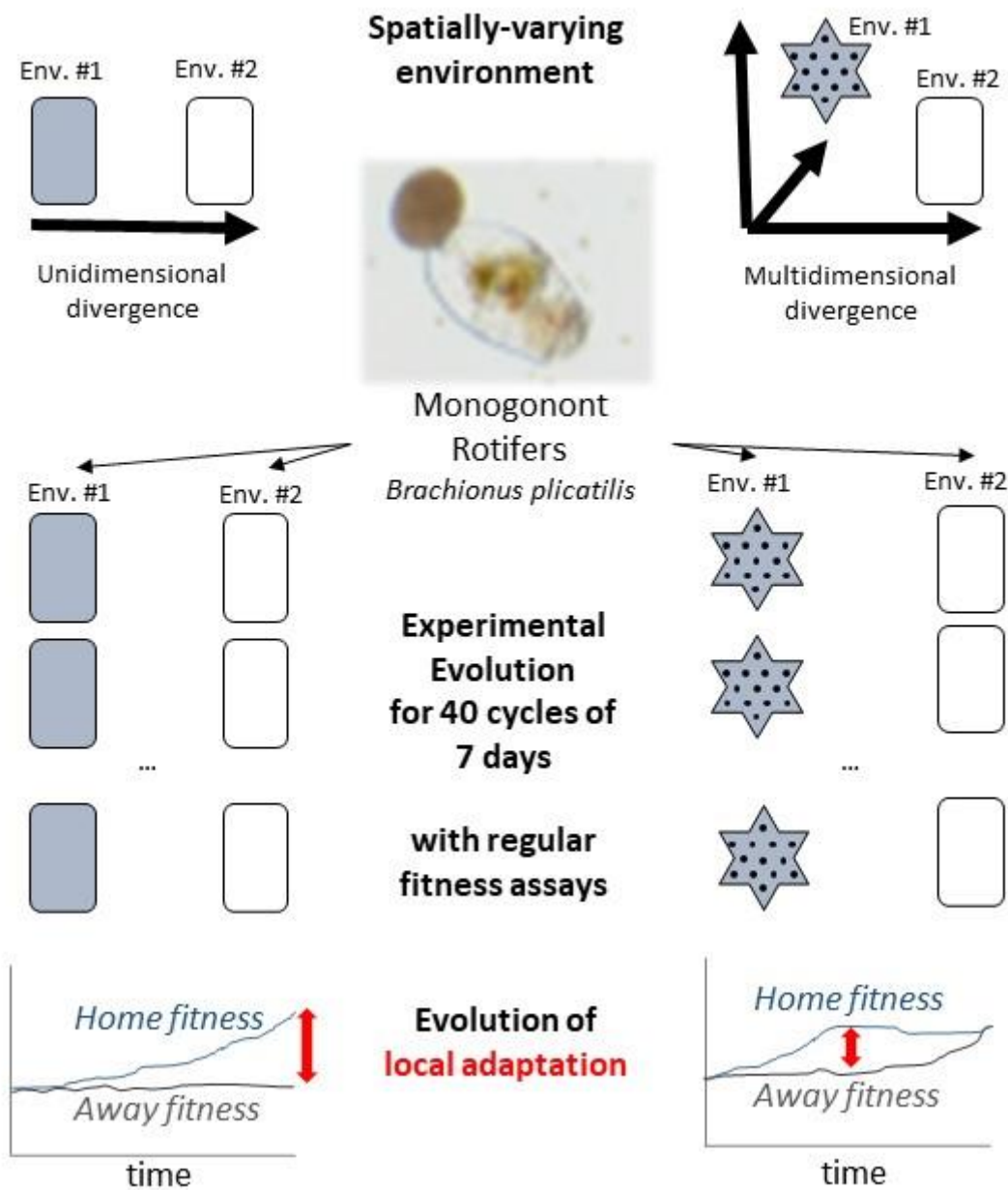


Figure 1: The impact of dimensionality on local adaptation.

The experiment contrasts two kinds of environmental pairs (represented here as Environment #1 and Environment #2), either varying in one stressor (unidimensional, on the left) or varying in three stressors (multidimensional, on the right). For each pair of environments (four unidimensional pairs, and four multidimensional pairs, with four replicates per pair), monogonont rotifers are raised for 40 cycles of seven days, and fitness is assessed every seven days on both the ‘home’ environment and the ‘away’ environment. Local adaptation is defined as a higher fitness in home versus the away environment. Photo credits: Agnieszka Urbanek.