

Chromosomal inversions can limit adaptation to new environments

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Abstract

Chromosomal inversions are often thought to facilitate local adaptation and population divergence because they can link multiple adaptive alleles into non-recombining genomic blocks. Selection should thus be more efficient in driving inversion-linked adaptive alleles to high frequency in a population, particularly in the face of maladaptive gene flow. But what if ecological conditions and hence selection on inversion-linked alleles change? Reduced recombination within inversions could then constrain the formation of optimal combinations of pre-existing alleles under these new ecological conditions. Here, we outline this idea of inversions limiting adaptation and divergence when ecological conditions change across time or space. We reason and use simulations to illustrate that the benefit of inversions for local adaptation and divergence under one set of ecological conditions can come with a concomitant constraint for adaptation to novel sets of ecological conditions. This limitation of inversions to adaptation may contribute to the maintenance of polymorphism within species.

KEYWORDS

adaptive constraints, balancing selection, genome architecture, linkage, population divergence, recombination, supergenes

1 | BACKGROUND

In evolutionary biology, there is a common notion that chromosomal inversions facilitate local adaptation and population divergence. Inversions create different physical arrangements of a genomic region, which often lead to non-viable gametes when recombination between these arrangements occurs (Navarro et al., 1997; Sturtevant & Beadle, 1936). As a result, realized recombination between different inversion arrangement types is strongly reduced at the population level, and alleles within one arrangement type become strongly linked and can behave similarly to a single allele of large selective effect. Selection should thus be more efficient in maintaining sets of inversion-linked alleles, if they are adaptive, and driving them to high frequency in a population, particularly under gene flow from a population adapted to a different environment (Rieseberg, 2001). Indeed, theory suggests that local adaptation of a population can be achieved more readily when multiple, locally

adaptive alleles are contained within the same inversion arrangement type (Charlesworth & Barton, 2018; Feder & Nosil, 2009; Kirkpatrick & Barton, 2006).

Consistent with the idea of inversions facilitating local adaptation and population divergence, one inversion arrangement type is often found at a relatively high frequency within populations, and populations from different environments often differ strongly in their frequency of arrangement types (e.g., Faria et al., 2019; Wellenreuther & Bernatchez, 2018). However, recent work has highlighted that reduced recombination between inversion arrangement types can hinder the purging of unconditionally (i.e., environment-independent) deleterious mutations, such as premature stop codons or recessive lethals (Berdan et al., 2021; Jay et al., 2021). The accumulation of such deleterious mutations may thus counteract the adaptive potential of inversions for local adaptation. For recessive deleterious variants, the reduction in recombination resulting from inversions may also lead to patterns of associative overdominance, where there

is an apparent heterozygous advantage due to masked deleterious variants (Gilbert et al., 2020). This type of balancing selection or the combination of both beneficial and unconditionally deleterious variants within a single inversion provide possible explanations for why inversions may often be maintained as polymorphisms within species (Berdan et al., 2021; Jay et al., 2021).

Another limitation to adaptation from inversions could occur when selection favours new combinations of inversion-linked alleles. This can happen due to temporally or spatially varying selection. When selection changes in direction, pre-existing inversion arrangements could pose a constraint to further adaptation because recombination cannot build optimal combinations from pre-existing alleles bound within inversions. The idea that inversions could constrain selection from favouring optimal allele combinations at inversion-linked adaptive loci is distinct from the accumulation of unconditionally deleterious mutations and could represent an important explanation for the evolution and maintenance of chromosomal inversions in species.

2 | THE ADAPTIVE LIMITATION HYPOTHESIS OF INVERSIONS

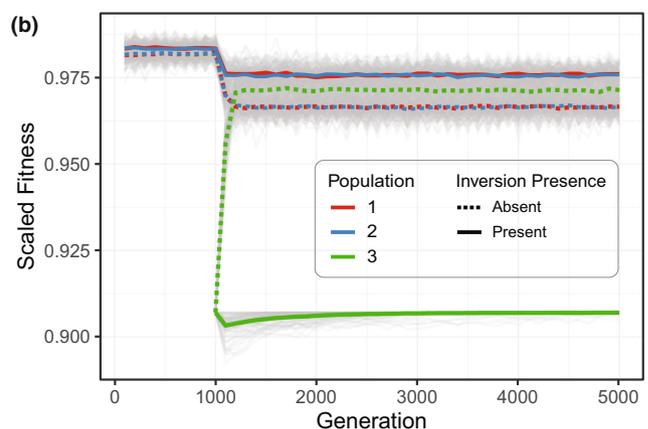
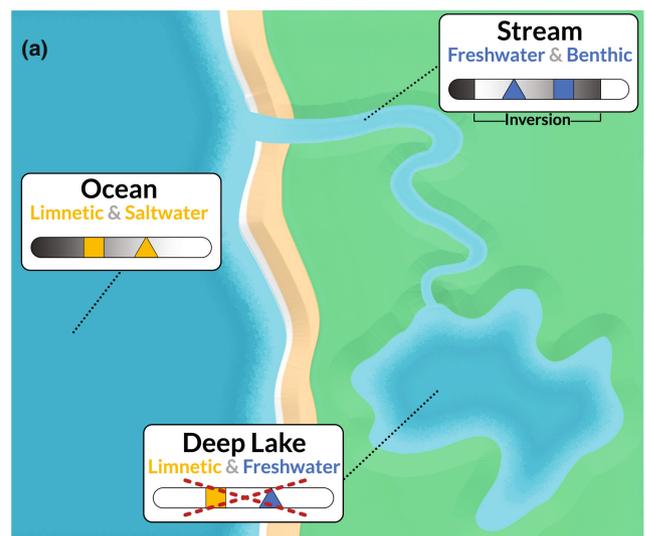
Mounting empirical evidence suggests that standing genetic variation is the main source of genetic variation for the early phases of adaptation in nature (e.g., Barrett & Schluter, 2008; Chaturvedi

et al., 2021; De Lafontaine et al., 2018; Haenel et al., 2019; Jones et al., 2012; Lai et al., 2019; Lescak et al., 2015; Louis et al., 2021; Messer & Petrov, 2013; Owens et al., 2021; Renaut et al., 2011; Whiting et al., 2021). Whether and how rapidly a population can adapt to a new ecological challenge therefore depends on how efficiently selection can reshape pre-existing alleles into new optimal combinations. Inversions may limit such genetic reshaping.

Imagine a scenario where each of two different inversion arrangements contains alleles that are beneficial in one habitat type and maladaptive in another. Then, a new third habitat type becomes available favouring a novel combination of these alleles from the two arrangements. The lack of recombination between the arrangement types will hinder reshaping of optimal allele combinations and hence can limit rapid adaptation into the new habitat (Figure 1a). Similarly, if ecological conditions, and thus selection, change for one or both of the initial populations, the lack of recombination of pre-existing alleles between arrangement types could impede adaptation compared to when adaptive alleles are not inversion-linked and thus free to recombine. Both of these scenarios, a novel habitat appearing or an existing habitat changing, are representative of multitudes of real-world scenarios, which can drastically alter the direction of natural selection.

To illustrate this idea, we explored whether inversions limit adaptation in forward-time individual-based simulations mimicking these

FIGURE 1 Exemplary scenario and simulation of how inversions can limit adaptation to new environments. (a) in this exemplary scenario, inversion-linked alleles at two biallelic loci confer adaptation to two different original habitats in an aquatic organism: saltwater and limnetic alleles (ocean habitat) vs. freshwater and benthic alleles (stream habitat). Such an inversion will limit optimal adaptation into a novel third habitat (deep lake) that requires the combination of freshwater and limnetic alleles. (b) Results from forward-in-time simulations using SLIM (Haller & Messer, 2019), based on the scenario outlined in (a). Population 3 forms at generation 1000 and represents the novel deep lake habitat, which in the absence of an inversion can be successfully colonized, reaching relatively high population fitness in the face of migration-selection balance (dashed lines). In the presence of the inversion (solid lines), however, fitness is reduced in the novel habitat as optimal adaptation is prevented from the alleles locked within the inversion. In these simulations, each allele has an equal selective and thus fitness effect, being beneficial in one of the two original habitats and detrimental in the other, with $s = \pm 0.1$. In population 3, the allele favoured in population 1 at the first locus and the allele favoured in population 2 at the second locus are favoured. Migration between the populations occurs throughout the simulations at $m = 0.01$. Adaptation of each population is expressed as the mean population relative fitness scaled against the maximum possible relative fitness based on the known optimal genotypes (i.e., a scaled fitness of 1 represents optimal adaptation of a population). Thick lines in colour indicate the mean scaled fitness of 100 replicate simulations (grey lines). De novo mutation and double crossovers were not considered in these simulations. See the supporting information for further details on the simulations as well as alternative scenarios and parameter combinations tested, including a polygenic model (Figure S3).



two scenarios. Simulations begin with a two-deme model in which each of two populations adapts to a distinct environment. Individuals are diploid and have genomes with two loci, each with two fully additive alleles conferring adaptation to either one of the two environments, respectively (i.e., these loci are under divergent selection between the populations). Populations exchange migrants and thus alleles throughout the duration of the simulation. In one scenario, we then introduce a new third habitat which can be colonized (Figure 1b; Figure S1). Alternatively, in a second scenario, we change the environment for one of the existing populations (Figure S2). In both cases, the novel selective pressure now favours a new combination of alleles at the two loci: selection favours the allele adaptive in population 1 at one locus, and the allele adaptive in population 2 at the other locus. We ran these simulations both with and without an inversion that captured one of the two sets of alleles adaptive in either one of the two initial populations as an arrangement. Overall, these simulations confirm our intuition that an inversion can limit adaptation to a new adaptive optimum compared to simulations without inversions where optimal combinations of pre-existing alleles can be created easily via recombination (Figure 1b; Figures S1 and S2).

These simulations are intentionally simplified and do not explore the full range of conditions under which an inversion can limit adaptation to changing adaptive optima. Yet, these results do demonstrate that, in principle, inversions can limit rapid local adaptation and hence adaptive divergence between populations. Although we placed reciprocally adaptive/maladaptive alleles within alternative inversion arrangements, a similar (albeit weaker) effect could be generated by an inversion that was polymorphic but unrelated to the change in selection (e.g., because it contains a recessive lethal allele). In this case, a reduction in average recombination in the inverted region would result in the limitation of adaptation via standard Hill–Robertson interference (Hill & Robertson, 1966). Future theoretical work could explore how dominance or epistatic effects of loci within inversions may influence this constraint as well as the timescale on which it is relevant.

Our described constraint of reduced recombination at inversions for adaptation is conceptually related to the long-standing idea for why asexual reproduction is particularly disadvantageous when environments change frequently over time or space. That is, maladaptive genetic associations built by past selection or brought to a different environment through migration cannot be rebuilt into favourable combinations in the absence of recombination as in asexually reproducing organisms (Maynard Smith, 1978; Otto, 2009). Another conceptual parallel can be drawn to the constraint described previously for pleiotropy, where a single gene affects multiple traits and may therefore hinder the evolution of optimal trait combinations under varying ecological conditions (Cheverud, 1984; Pavličev & Cheverud, 2015). These conceptual parallels between asexual reproduction, pleiotropy and inversions can help explain how the absence of recombination can constrain adaptive evolution, yet the dynamics of inversions are unique and worthy of special consideration since recombination is only reduced in individuals carrying both arrangement types (i.e., in heterozygotes).

3 | OUTCOMES AND FUTURE INVESTIGATIONS

There are several ways by which the adaptive limitation of inversions could resolve itself genetically. Gene conversion events or double crossovers could allow for rare genetic exchange (gene flux) between inversion arrangement types, thereby allowing for the build-up of combinations of pre-existing alleles that are favourable under changed ecological conditions. De novo mutations in pre-existing inversion arrangements as well as in other regions of the genome could also build newly favoured allele combinations. While both of these routes could resolve the limitation that inversions can pose to adaptation, they will necessitate longer waiting times than a normally recombining genomic region. The rates and hence efficiency of gene conversion, double crossovers and de novo mutations in resolving the limitation of inversions to adaptation will also vary depending on species and genome region (e.g., Baer et al., 2007; Korunes & Noor, 2017). Moreover, these considerations emphasize the need for a greater appreciation of genetic variation within—and not only between—inversion arrangement types.

The idea described here of how inversions may limit rapid adaptation to changing ecological conditions seems compatible with observations in nature. For instance, quantitative trait loci (QTL) underlying trait variation that is important for adaptive divergence across a major habitat transition have been mapped to chromosomal inversions in populations of threespine stickleback fish and *Littorina* snails (stickleback: Liu et al., 2021; Peichel & Marques, 2017; *Littorina*: Koch et al., 2021). However, both of these species have recently been exposed to new niches imposing novel selection pressures, possibly favouring novel combinations of these inversion-linked QTL (stickleback: Bell & Foster, 1994; Reid et al., 2021; Roesti et al., 2015; *Littorina*: Morales et al., 2019).

Direct tests of how frequently inversions limit adaptation in nature will be challenging, especially because genetic variants within inversions are in strong linkage and therefore difficult to assay individually. A promising yet challenging approach would be to unlock inversion-linked genetic variants by flipping one arrangement type using CRISPR/Cas9-induced double-strand breaks, thereby restoring collinearity and thus recombination between different inversion arrangement types (Schmidt et al., 2020). This would subsequently allow for estimating how selection targets individual alleles that were previously inversion-linked. An adaptive constraint of inversions would be implicated if selection targeted some of the previously linked alleles within an arrangement type in the opposite direction within the given ecological context. Another less direct test of the adaptive limitation hypothesis of inversions could use QTL mapping of ecologically important trait variation (analogous to a QTL sign test; Orr, 1998). An adaptive constraint of an inversion may be implicated if the trait effects of some within-inversion QTL were reversed to what would be expected under optimal adaptation. Finally, if inversions are indeed hotspots of adaptive loci, one might expect that the genetic variation unique to the different arrangements of

a (single) large inversion is unlikely to play a key role in the rapid diversification of a taxon into many niches, and may even pose a constraint for such adaptive radiations. Similarly, successful colonization of new habitats could be hindered altogether if many adaptive loci were inversion-linked. This constraint could be counteracted, in part, by the existence of several inversions if each inversion captures a combination of alleles that allows successful adaptation in the face of gene flow across independent environmental axes.

4 | CONCLUSION

While an inversion can link unique adaptive allele combinations into non-recombining genomic blocks (haplotypes) and thereby favour local adaptation under one set of ecological conditions, this benefit may come with a concomitant constraint in adaptation to a novel set of ecological circumstances. Indeed, inversions linking unique allele combinations into distinct haplotypes may also be prone to be maintained as polymorphisms within species under spatially and/or temporally varying selection and gene flow. While searching for evidence of such adaptive limitations imposed by inversions in nature will be challenging, further investigation of this phenomenon will broaden our understanding of the processes shaping diversity across variable environments and during rapid adaptive radiations.

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AUTHOR CONTRIBUTIONS

Marius Roesti conceived of the original idea described in this paper, coordinated the study, contributed to designing/writing the simulations, and led the paper writing. Kimberley J. Gilbert contributed to further developing the paper's idea, to designing/writing the simulations, and to paper writing. Kieran Samuk contributed to further developing the paper's idea, led the writing of and ran the final simulations, contributed to paper writing.

CONFLICT OF INTEREST

The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

The code to run, analyse and illustrate the simulations is available at https://github.com/ksamuk/inversion_constraint.

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