

Review

Recombination Rate Evolution and the Origin of Species

Daniel Ortiz-Barrientos,^{1,4,*} Jan Engelstädter,^{1,4} and Loren H. Rieseberg^{2,3}

A recipe for dissolving incipient species into a continuum of phenotypes is to recombine their genetic material. Therefore, students of speciation have become increasingly interested in the mechanisms by which recombination between locally adapted lineages is reduced. Evidence abounds that chromosomal rearrangements, via their suppression of recombination during meiosis in hybrids, play a major role in adaptation and speciation. By contrast, genic modifiers of recombination rates have been largely ignored in studies of speciation. We show how both types of reduction in recombination rates facilitate divergence in the face of gene flow, including the early stages of adaptive divergence, the persistence of species after secondary contact, and reinforcement.

Introduction

In the absence of geographic barriers between populations, sexual reproduction is considered the greatest obstacle to the origin of new species [1]. While divergent natural selection creates distinct populations, sexual reproduction, through the homogenizing effects of genetic recombination, dissolves them. Cognizance of this antagonism has prompted many evolutionary biologists to deem that speciation within freely (sympatric) or between partially (parapatric) interbreeding populations is improbable [2]. However, recent theoretical and empirical results suggest that speciation in the face of gene flow should be feasible, and is perhaps common in nature [3–5]. Unfortunately, owing to our incomplete understanding of the genetics of speciation, the plausibility of key assumptions underpinning theoretical models of the process remain controversial. In the few instances where we do have some limited understanding (e.g., *Drosophila* and *Rhagoletis* fruit flies [6,7], *Ficedula* flycatchers [8,9], *Heliconius* butterflies [10], *Mimulus* monkeyflowers [11], and *Helianthus* sunflowers [12]), the genetics of speciation with gene flow appears to revolve around a key process: reduction of recombination between the genes that are responsible for reproductive isolation and those contributing to local adaptation [13,14].

Recombination generates new genetic combinations every generation, making it a rapid source of genetic variability upon which natural selection can operate [15]. However, recombination also breaks apart favorable combinations of alleles, potentially reducing the average fitness of a population [16,17]. This two-sided evolutionary effect of recombination is at the heart of both the evolution of sex [18] and the formation of new species when there is gene flow [19]. More specifically, the conditions that impede the evolution of sex and recombination are largely the same as those that facilitate speciation with gene flow. Alas, this connection is infrequently made, and therefore biological connections between the two processes have been often overlooked (but see [13,20]).

To visualize this connection, consider a situation where chromosomes carrying alleles *ABCD* or *abcd* confer high fitness, but chromosomes carrying any other combination of alleles produce

Trends

An often-overlooked connection between the evolution of sexual recombination and the origin of new species with gene flow suggests that the conditions for speciation with gene flow may be less restrictive than previously anticipated.

Evolutionary scenarios for which mathematical models predict selection for reduced recombination can provide insights into how ecological speciation and reinforcement can proceed.

Recent advances in our understanding of the molecular mechanisms of recombination in eukaryotes have provided first insights into how recombination rates can be modified within and between species.

In addition to the well-established role of chromosomal inversions during speciation, more subtle changes in recombination rates through modifier genes influencing the frequencies and distributions of crossover across the genome might also be important.

A better understanding of genomic patterns of differentiation during speciation could be gained by taking into account that recombination rates can themselves evolve.

¹The University of Queensland, School of Biological Sciences, St. Lucia, Queensland, Australia

²University of British Columbia, Department of Botany, Vancouver, British Columbia, Canada

³Indiana University, Biology Department, Bloomington, IN 47405-7005, USA

⁴These authors contributed equally

*Correspondence: d.ortizbarrientos@uq.edu.au (D. Ortiz-Barrientos).

low fitness. Now assume a population with only *ABCD* and *abcd* chromosomes, in other words strong **linkage disequilibrium** (LD, see [Glossary](#)). Recombination would then reduce mean population fitness, and mutations that reduce recombination can be favored if they are linked to the *ABCD* loci [17]. During speciation with gene flow, a similar situation arises: if alternative combinations of alleles are favored in two populations (*abcd* and *ABCD*, respectively), then gene flow and recombination between them will generate new genotypic combinations of low fitness, reducing levels of LD in each population. Therefore, we expect that modifiers that prevent or reduce recombination would also be favored during speciation. Such **recombination modifiers** would preserve the original genotypes and maintain high fitness in the population via the increase and maintenance of high levels of LD within populations [18]. On the other hand, speciation with gene flow is dependent on divergent natural selection, and rates of adaptation can be greater in sexual than asexual populations [18]. Therefore, it is important to keep in mind that, during speciation driven by natural selection, sex and recombination can be favored within populations, but not between diverging lineages.

We review here important aspects of the fundamental link between the origin of sex and the origin of new species. We start by describing the various forms in which LD arises within a population and produces selection on recombination rates. Next, we review the various mechanisms that could evolve to change recombination rates, including structural (e.g., **chromosomal rearrangements**) and allelic modifiers of recombination. We then show how selection on recombination rates is expected to play out in various stages of speciation. We finish by outlining some of the consequences of recombination rate evolution for our understanding of divergence and adaptation.

The Why and How of Recombination Rate Evolution

Natural Selection on Recombination Rates

Recombination reduces LD within a population but normally does not alter allele frequencies. Therefore, for recombination rates to be under natural selection, LD must be present in a population and altering levels of LD must have fitness consequences. LD can be generated by several evolutionary forces, three of which are illustrated in [Figure 1](#). Perhaps most importantly in the context of speciation, LD within a population will be induced by migration between two populations with different allele frequencies at two or more loci [21]. For instance, positive LD will build up when there is divergent selection in the two populations but polymorphism is maintained through migration ([Figure 1A](#)). This is most clearly seen in the extreme case where alleles *a* and *b* are fixed in one population and *A* and *B* in the other, such that one round of migration creates populations with both the *AB* and *ab* genotypes but no *Ab* or *aB* genotypes.

Second, LD is generated by natural selection in single populations when there is **epistasis** [22]: negative epistasis produces negative LD and positive epistasis produces positive LD ([Figure 1B](#)). This is intuitive because natural selection will produce an overabundance of intermediate genotypes (*Ab* and *aB*) when they are fitter than expected based on the average of the extreme genotypes *ab* and *AB* (negative LD), and vice versa (positive LD). Third, LD can arise as a result of random genetic drift or mutation. Over time and across many loci, drift and mutation *per se* will generate both positive and negative LD in equal amounts. However, when selection also acts on these loci, this distribution becomes biased towards negative LD through a mechanism known as the **Hill–Robertson effect**. According to this, genetic variation characterized by positive LD (e.g., only *ab* and *AB* genotypes present) will be eliminated more rapidly than genetic variation characterized by negative LD (e.g., only *Ab* and *aB*). This is because the former implies greater variance in fitness and hence more efficient natural selection. As a consequence, negative LD will predominate in the population ([Figure 1C](#)) [23]. Finally, LD can also be created by several other factors, including assortative mating and sexually antagonistic selection [19,24].

Glossary

Chromosomal rearrangement: a structural modification within or between chromosomes that affects the spatial location of genetic material.

Ecological speciation: the development of reproductive isolation between populations as a result of adaptation to different environments. It can take place in the face of gene flow.

Epistasis: non-independent effects of alleles at different loci. In particular, epistasis in fitness between two loci with alleles *A/a* and *B/b* can be defined in haploid organisms as $E = W_{ab}W_{AB} - W_{Ab}W_{aB}$, where *w* is the fitness of the respective genotype. Negative epistasis implies that the double mutant *AB* has a lower fitness than expected from the fitness effects of the two mutations *A* and *B* on the wild-type backgrounds *b* and *a*, respectively. Conversely, positive epistasis implies that *AB* has a higher fitness than expected from the individual effects of *A* and *B*.

Fitness trade-offs: alleles improving fitness in one environment reduce fitness in the other environment.

Hill–Robertson effect: negative LD arising from the interplay between random genetic drift and selection acting on several linked loci. Can produce selection for increased recombination rates.

Linkage disequilibrium (LD): non-random associations of alleles at different loci in a population. With two loci with alleles *A/a* and *B/b*, LD can be expressed as

$D = p_{ab}p_{AB} - p_{Ab}p_{aB}$, where *p* is the frequency of the respective genotype in the haploid phase. Negative LD thus indicates an overabundance of the *Ab* and *aB* genotypes, whereas positive LD indicates an overabundance of the *ab* and *AB* genotypes. Note that labeling of genotypes and thus the sign of *D* is often arbitrary, but in the case of natural selection acting on both loci the convention is to assign genotype labels *AB* and *ab* to the genotypes with the highest and lowest fitness, respectively, whereas the *Ab* and *aB* genotypes have intermediate fitness.

Recombination hotspots: regions of the genome where crossovers occur at high frequency.

Recombination modifier: a gene that affects the rate of crossovers between other genes. A modifier

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