

Evolution of Chromosomal Inversions across an Avian Radiation

Ulrich Knief ^{1,2,*} Ingo A. Müller ^{1,3,4} Katherine F. Stryjewski ⁵ Dirk Metzler ¹
Michael D. Sorenson ⁵ and Jochen B.W. Wolf ^{1,*}

¹Division of Evolutionary Biology, Faculty of Biology, LMU Munich, 82152 Planegg-Martinsried, Germany

²Evolutionary Biology & Ecology, Faculty of Biology, University of Freiburg, 79104 Freiburg, Germany

³Department of Bioinformatics and Genetics, Swedish Museum of Natural History, 11418 Stockholm, Sweden

⁴Division of Systematics and Evolution, Department of Zoology, Stockholm University, 11418 Stockholm, Sweden

⁵Department of Biology, Boston University, Boston, MA 02215

*Corresponding authors: E-mails: ulrich.knief@biologie.uni-freiburg.de; j.wolf@biologie.uni-muenchen.de.

Associate editor: Emily Josephs

Abstract

Chromosomal inversions are structural mutations that can play a prominent role in adaptation and speciation. Inversions segregating across species boundaries (trans-species inversions) are often taken as evidence for ancient balancing selection or adaptive introgression, but can also be due to incomplete lineage sorting. Using whole-genome resequencing data from 18 populations of 11 recognized *munia* species in the genus *Lonchura* ($N = 176$ individuals), we identify four large para- and pericentric inversions ranging in size from 4 to 20 Mb. All four inversions cosegregate across multiple species and predate the numerous speciation events associated with the rapid radiation of this clade across the prehistoric Sahul (Australia, New Guinea) and Bismarck Archipelago. Using coalescent theory, we infer that trans-specificity is improbable for neutrally segregating variation despite substantial incomplete lineage sorting characterizing this young radiation. Instead, the maintenance of all three autosomal inversions (*chr1*, *chr5*, and *chr6*) is best explained by selection acting along ecogeographic clines not observed for the collinear parts of the genome. In addition, the sex chromosome inversion largely aligns with species boundaries and shows signatures of repeated positive selection for both alleles. This study provides evidence for trans-species inversion polymorphisms involved in both adaptation and speciation. It further highlights the importance of informing selection inference using a null model of neutral evolution derived from the collinear part of the genome.

Key words: trans-species polymorphism, speciation, ecological selection, *Lonchura*, *munia*.

Introduction

Chromosomal inversions are a long-known class of structural mutations changing DNA sequence orientation (Sturtevant 1921). In heterokaryotypic arrangements, recombination is suppressed, shielding alternate haplotypes from exchanging genetic variation. Given their substantial impact on processes mediating evolutionary change (Navarro et al. 1997; Kirkpatrick 2010; Peñalba and Wolf 2020), inversions have long been attributed an outstanding role in adaptation and speciation (Dobzhansky 1937; Noor et al. 2001; Rieseberg 2001; Navarro and Barton 2003; Hoffmann and Rieseberg 2008).

Theory predicts that the fate of genetic variation captured in the inverted sequence will depend on the fitness of homo- and heterokaryotypic arrangements (Faria, Johannesson et al. 2019). Originating from a single haplotype, most derived inversions will be quickly lost due to genetic drift or underdominance (e.g. gene disruption in

breakpoints, aneuploid gametes, capture of deleterious alleles, or negative epistatic variation; Kirkpatrick 2010; Faria, Johannesson et al. 2019). However, derived arrangements can also spread and eventually fix in a population if they capture beneficial, locally adapted gene complexes (Kirkpatrick and Barton 2006; Feder et al. 2011). A third and frequently observed possibility is the maintenance of both arrangements over extended periods of evolutionary time, which invokes forms of balancing selection, antagonistic pleiotropy, disassortative mate choice, or selection along ecological gradients (White 1977; Kirkpatrick and Barton 2006; Knief et al. 2017). Expectations are complicated by the usually unknown interactions of evolutionary processes (Faria, Johannesson, et al. 2019; Fuller et al. 2019; Berdan et al. 2021), and empirical access is impeded by often small fitness differences between arrangements that are difficult to measure in natural settings (Dobzhansky and Pavlovsky 1955; Knief et al. 2016).

Received: January 08, 2024. Revised: April 05, 2024. Accepted: May 03, 2024

© The Author(s) 2024. Published by Oxford University Press on behalf of Society for Molecular Biology and Evolution.

This is an Open Access article distributed under the terms of the Creative Commons Attribution License (<https://creativecommons.org/licenses/by/4.0/>), which permits unrestricted reuse, distribution, and reproduction in any medium, provided the original work is properly cited.

Open Access