Historical recombination maps diverge between Eurasian blackcap populations with distinct migratory strategies

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Abstract

Recombination generates new combination of alleles, whereby it maintains haplotype diversity and enhances the efficacy of selection. Despite the apparent stasis in positioning recombination events in birds, recombination rates differ widely across the genome and within species. The causes of recombination rate variation and its evolutionary impact on natural populations remain poorly understood. We used whole-genome resequencing data of 167 individuals of the Eurasian blackcap (Sylvia atricapilla) to characterise the historical recombination landscape variation at broad and fine scales among populations with distinct migratory phenotypes. We additionally evaluated the interplay between recombination rates with patterns of genetic diversity, population divergence (based on Fst and dxy), and potential signs of selection. Our comparative analyses revealed: i) Lower divergence of recombination maps at the broad scale and higher variability at fine scales. Resident island populations showed higher variability in recombination patterns among them and with continental populations. Recombination rates were more conserved in continental populations regardless of the migratory phenotype. ii) The degree of divergence between recombination maps correlated with population differentiation. It could also recapitulate population-specific demographic history and genetic structure. iii) Recombination rates correlated negatively with Fst and positively with nucleotide diversity and dxy, suggesting that recombination may reduce the effect of linked selection over the loss of neutral diversity. We identified chromosomal regions with potential signs of linked selection. This study evidences that recombination is a variable trait that shapes the diversity and evolution of population differentiation in the blackcap.

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Running title: Intra-specific recombination rate variation

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Abstract

Recombination generates new combination of alleles, whereby it maintains haplotype diversity and enhances the efficacy of selection. Despite the apparent stasis in positioning recombination events in birds, recombination rates differ widely across the genome and within species. The causes of recombination rate variation and its evolutionary impact on natural populations remain poorly understood. We used whole-genome resequencing data of 167 individuals of the Eurasian blackcap (*Sylvia atricapilla*) to characterise the historical recombination landscape variation at broad and fine scales among populations with distinct migratory phenotypes. We additionally evaluated the interplay between recombination rates with patterns of genetic diversity, population divergence (based on Fst and dxy), and potential signs of selection. Our comparative analyses revealed: i) Lower divergence of recombination maps at the broad scale and higher variability at fine scales. Resident island populations showed higher variability in recombination patterns among them and with continental populations. Recombination rates were more conserved in continental populations regardless of the migratory phenotype. ii) The degree of divergence between recombination maps correlated with population differentiation. It could also recapitulate population-specific demographic history and genetic structure. iii) Recombination rates correlated negatively with Fst and positively with nucleotide diversity and dxy, suggesting that recombination may reduce the effect of linked selection over the loss of neutral diversity. We identified chromosomal regions with potential signs of linked selection. This study evidences that recombination is a variable trait that shapes the diversity and evolution of population differentiation in the blackcap.

Keywords

historical recombination maps, nucleotide diversity, population divergence, linked selection, population genomics, bird migration

Introduction

Meiotic recombination facilitates novel combinations of alleles, contributes to generating and maintaining genetic diversity along the genome, and potentially leads populations to adapt and evolve over prolonged periods of time (Felsenstein, 1974; Keightley & Otto, 2006). When selection acts over physically linked loci (i.e., Hill-Robertson interference, Hill & Robertson, 1966), recombination breaks up this linkage. It reshuffles haplotypes, fundamentally influencing the efficacy of selection in two ways: First, modulating the speed of purging deleterious mutations and spreading advantageous alleles in the population (Betancourt et al., 2009; Crow & Kimura, 1965; Hickey & Golding, 2018). Secondly, affecting the strength of linked selection and maintaining neutral diversity physically linked to the loci that are under either positive (selective sweeps) or negative selection (background selection) (Castellano et al., 2020; Charlesworth et al., 1993; Chase & Mugal, 2022; Cutter & Payseur, 2013). Recombination further plays a critical role in influencing the degree of gene flow and introgression between populations (Martin et al., 2019; Schumer et al., 2018). High recombination rate is associated with greater population divergence (dxy) (Burri et al., 2015; Nelson et al., 2021), whereas low recombining regions are more related to loss of nucleotide diversity due to linked selection, population differentiation, and speciation (Burri et al., 2015; Cutter & Payseur, 2013; Henderson & Brelsford, 2020; Samuk et al., 2017). Given the impact of recombination on the evolution and adaptation of populations, variation in recombination rates emerges as an exciting phenomenon to be investigated in light of population genomics.

Variability of recombination rates at different scales has been widely described over the last few years, spanning from variation within the genome, between sexes and individuals, to populations, species as well as different taxa (Peñalba & Wolf, 2020; Peterson & Payseur, 2021; Smukowski & Noor, 2011; Stapley et al., 2017). Birds lack a functional PRDM9 protein responsible for positioning and initiating recombination events in many mammals. The majority of recombination events ("hotpots") cluster in promoter-like regions or regions where open chromatin stretches allow access to the transcription machinery, presumably conferring more conservation to the recombination landscape (Singhal et al., 2015). Recombination landscapes in birds appear conserved at broad scales (genome-wide); however, remarkable differences in recombination

rates are evident at the fine scale (Kawakami et al., 2017; Singhal et al., 2015; Bascon Cardozo et al., 2022). Recombination variation within the avian genome is associated with the presence and distribution of specific genomic features. High recombination rates are enriched in GC-rich content sequences, including CpG islands, regulatory regions such as promoters, transcription start sites, 5'UTR regions, and specific families of transposable elements (TEs) (Bascón-Cardozo et al., 2022; Kawakami et al., 2017; Peñalba et al., 2020; Singhal et al., 2015; Smeds et al., 2016). Low recombining regions associate with intergenic regions, chromosomal rearrangements (i.e. inversions) and long tandem repeats (Bascón-Cardozo et al., 2022; da Silva et al., 2019; Ishigohoka et al., 2021; Kawakami et al., 2017). Moreover, the recombination rate is negatively associated with chromosome size (Backström et al., 2010; Bascón-Cardozo et al., 2022; Kawakami et al., 2017; Peñalba et al., 2020; Smeds, et al., 2016). Despite these striking correlative patterns, broad and fine scale recombination rate variation and its implications in natural populations remain poorly studied. To disentangle recombination variation and its impact throughout evolution in natural populations, it is crucial to use consistent approaches to estimate and systematically compare recombination maps at different scales, across and within species.

The Eurasian blackcap, *Sylvia atricapilla* (referred to as blackcap in the following) is a powerful study system for investigating genetic variation in behavioural traits such as migration in an evolutionary framework. Blackcaps are night-migratory songbirds encompassing populations that exhibit the entire repertoire of migratory phenotypes, including variation in the propensity to migrate, migratory distance, and orientation (e.g., Berthold et al., 1992; Helbig, 1991; Merlin & Liedvogel, 2019). Populations of blackcaps throughout the distribution range started to diverge as recent as ~30,000 years ago (ya), resulting in an overall low genetic differentiation, as well as limited gene flow between migratory populations, as suggested by the contemporary genetic structure between a subset of the populations studied previously (Delmore et al., 2020). At the same time, these populations differ in their demographic history, indicating that they may evolve differently and have potentially experienced different strengths of selective pressures. Hence, blackcaps provide an ideal empirical scenario to study recombination variation and evaluate their association with population dynamics.

In a previous study, we characterised the fine-scale historical recombination map in the blackcap system, revealing variable recombination rates across the genome and within chromosomes associated with specific genomic features (Bascón-Cardozo et al., 2022). In this context, we were able to identify divergent chromosomal regions between the blackcap and one of its closest sister species, the garden warbler (*Sylvia borin*). Comparative studies using genetic linkage maps were also carried out in more distantly related species (Backström et al., 2010; Peñalba et al., 2020), however little is known about the variation between different populations within the same species. This raised our interest to focus our evaluation of recombination rate variation on the population scale, specifically contrasting populations with divergent migratory phenotypes and evaluating the association with patterns of nucleotide diversity, population differentiation and potential signatures of selection. For that, we first inferred population-scaled recombination rates of twelve populations using an approach based on Linkage Disequilibrium (LD) taking population-specific demography into account. With this, we assessed the following questions: (i) Do historical recombination maps vary between populations with different migratory strategies at broad and fine scales? ii) What is the association of recombination rates with specific population-genetic parameters such as nucleotide diversity and Tajima's D within each population, and (iii) is the variation of recombination rate associated with relative and absolute population divergence (Fst, dxy)?

2. Materials and Methods

2.1 Genomic Data

We analysed whole genome resequencing data of 167 blackcap individuals across the species' range, including all migratory phenotypes published in Delmore et al. (2020) and Ishigohoka et al. (2021). The resident populations include continental residents (cont-res) (see Table S1), as well as island populations, which include Azores (AZO), Cape Verde (CAVE), Canary Islands (CAN), Madeira (MAD), Mallorca (MAL), and Crete (CRE). Continental migrants are separated by migratory distance: short-, medium-, and long-distance (short, medium, long) and further subdivided by migratory orientation: south-west (SW), north-west (NW),

and south-east (SE) (see **table S1**).

Sequence reads obtained by Illumina NextSeq 500, HiSeq 4000 or NovaSeq 5000 were mapped to a chromosomal-level reference genome (available under NCBI BioProject PRJNA558064, accession number GCA_009819655.1) at a median coverage of 15.1 ± 11.1X. The sample collection and genome assembly details are further described in Ishigohoka et al., 2021. A VCF containing polymorphic sites (SNPs) (published in Ishigohoka et al., 2021) was filtered using GATK version 4.1.6.0 (McKenna et al., 2010) and VCFtools (Danecek et al., 2011) with the following: minimum Genotype Quality of 20, a minimum depth of 10, a minor allele count (mac) of 1 and depth per site calculated as three times higher than the average (=< 10443), while ensuring only variant sites remain. After extracting each population separately, we used VCFtools to filter out sites with missingness greater than or equal to 0.7 to yield a collection of high-quality SNPs for downstream analysis (the number of SNPs retained for each population is summarised in **Table S1**). We additionally removed singletons for the estimation and analysis of recombination rates.

2.2 Inference and comparison of recombination maps between different populations

We estimated population recombination rates for each population separately using Pyrho (Kamm et al., 2016; Spence & Song, 2019), an LD-based approach that estimates and scales the per-generation per-base recombination rate (r) using historical population-specific effective population sizes (Ne) and mutation rate. Demography for each population was inferred as described below (2.3 demography inference), and we used the mutation rate of a related species, the collared flycatcher ($4.6x10^{-09}$ site/generation) (Smeds et al., 2016) for all the estimations. We generated lookup tables with pyrho "make table". Then, we input unphased genotypes in VCF format and assign a block penalty of 20 and a window size of 50 for the recombination rates estimation with pyrho "optimise". Recombination rates were inferred for each population separately. The estimates of Pyrho (scaled-recombination per site per generation rate) were converted to cM/Mb, and the linkage genetic map (genetic distance in cM) was calculated for each population with a custom script (Bascón-Cardozo et al., 2022).

To compare recombination maps between all populations, we calculated average recombination rates in 100 kb non-overlapping windows (as in Bascón-Cardozo et al., 2022) and performed genome-wide pairwise comparisons between all populations considering only autosomes. We measured the correlation coefficient for all the comparisons using Kendall's rank correlation test in R version 4.0.5 (R Core Team 2021) and visualised them as a heatmap with ggplot (Wickham, 2016). To illustrate local recombination patterns, we plotted the intra-chromosomal distribution of recombination rates for all populations. Finally, we calculated the recombination rate variance per window, including all the populations, to identify regions across the genome with higher variability in recombination patterns.

Additionally, we calculated the average recombination rate per chromosome in cM/Mb, weighted by the physical distance between each pair of sites where recombination was estimated, for each population. We calculated and compared average recombination rates among all populations using nonparametric pairwise Wilcoxon rank sum tests, Bonferroni corrected statistics with no assumption of equal variances (Mann-Whitney test) with the function function‘ pairwise.wilcox.test' in R.

2.3 Demography inference

For demography inference, we used whole-genome resequencing data, including 167 blackcaps used in Ishigohoka et al., 2021. The SNP data in VCF (variant call format) were statistically phased using SHAPEIT2 (Delaneau et al., 2013), using the blackcap genetic map inferred in (Bascón-Cardozo et al., 2022) with Pyrho. We further polarised the phased SNPs according to allele frequencies in outgroup samples (five garden warblers and three African hill babblers). We used Relate (Speidel et al., 2019) to infer genome-wide genealogy of the 167 individuals. Coalescent patterns of samples within and across focal populations were extracted from the inferred genealogy. Effective historical population sizes and relative cross-coalescent rates were computed based on the distribution of coalescent times.

2.4 Simulation analysis

We performed a simulation to investigate whether different demographic histories affect the inference of recombination rate using samples of diverse populations. For that, we used msprime (Baumdicker et al., 2022) to simulate an ancestral population of 1,000,000 diploids which splits at 10,000 generations ago into three populations that undergo three different demographic trajectories: constant size, ten times expansion, and 1/10 contraction over the time until the present. We simulated a chromosome of 10 Mb with a mutation rate of4.6×10^{-9} (/base-pair/generation) and constant recombination rates: 1, 4 and 10 times the mutation rates. We sampled 50 individuals per population and saved phased genotypes in VCF format. Subsequently, we estimated recombination rates for the three populations separately using Pyrho with block penalty of 25 and window size of 50. Then recombination rates (r) were converted to cM/Mb and compared among the three populations.

2.5 Evaluating recombination association with nucleotide diversity and population divergence

To characterise the relationship between recombination rates and patterns of diversity and population divergence, we calculated nucleotide diversity (π) for each population and F_{st} and dxy for all population pairs using a VCF file containing all callable sites (meaning polymorphic and non-polymorphic sites that had mapping support) and varying tools from the "genomics general" toolkit (Martin et al., 2020). We used parseVCFs.py (https://github.com/simonhmartin/genomics_general/VCF_processing release 0.4) to filter the described VCF with min-depth >5 and max <60 and ran popgenWindows.py (https://github.com/simonhmartin/genomics_general release 0.4) with a window size of 100 kb, ensuring that at least 10 kb were called in each window. Missingness was set to 0.7 (minData), taking the proportion of individuals covering at least 10kb per window.Genome-wide pairwise comparisons between recombination rates with nucleotide diversity (π), $F_{st,}$ and dxy were carried out in 100 kb windows for all populations. We used the "ggcorrplot' package (**https://github.com/kassambara/**ggcorrplot) in R to measure Kendall's rank correlation coefficients with a significance threshold of 5 %.

Studies in flycatchers and mice suggested that Fst outliers tend to occur in regions where recombination is low or suppressed (Burri et al., 2015; Cruickshank & Hahn, 2014; Nachman & Payseur, 2012; reviewed in Ravinet et al., 2017), which we also assess for the blackcap genome here. We first identified populations with elevated genome-wide Fst values. Subsequently, we identified windows with Fst outlier taking the 95th and 99th percentiles, and we plotted them together with the recombination maps of the respective populations.

Since we used recombination rate estimations for each population and evaluated the correlation coefficients among all pairs of populations, we additionally assessed the relationship of dissimilarity in recombination maps with population differentiation (Fst). We calculated recombination dissimilarity by subtracting the genome-wide pairwise correlation measurements among all pairs of populations from the maximum value (1). We estimate Spearman and Kendall's correlation between recombination dissimilarity and Fst values for all population pairs. To support our statistical analysis, we performed Mantel tests implemented in the R-package 'vegan' (Oksanen et al. 2020), which statistically compares distance matrices. For that, we converted our data sets of recombination dissimilarity to a matrix and the pairwise comparisons of Fst values to a genetic distance matrix (Fst matrix), including all populations. We compared both matrices using the Mantel test with the Kendall-rank method and randomly permuting 9,999 times the rows and columns of one of the matrices. We performed all statistical analyses encompassing all populations. We also ran the same analysis on a subset of the data contrasting all continental with all island populations.

Recent studies suggest that elevated levels of divergence (dxy) occur in regions with elevated recombination rates (Burri et al., 2015; Nelson et al., 2021). Analogous to these studies, we defined Highly Recombining Regions (HRR) as windows with an LD-based recombination rate exceeding four times the background recombination rate (genome-wide-average recombination rate) for each population. We then calculated the average dxy within HRR for each population weighted by the number of sites within each window. We compared these with the genome-wide weighted average dxy separately for each population pair using a one-sample Wilcoxon signed-rank test.

2.6 Recombination and Tajima's D

To allow for an association between recombination rate and possible patterns of selection, we calculated Tajima's D to distinguish between genomic regions neutrally evolving and regions evolving via non-random processes. Tajima's D calculates the difference between two measures of genetic diversity: the mean number of pairwise differences and the number of segregating sites. We calculated Tajima's D for each population in 100 kb windows using VCFtools. Then, we characterised their association with recombination rates by performing partial correlations using "ppcor" package (Kim, 2015) and treating nucleotide diversity as a confounding variable.

To complement our analysis, we also included the annotated gene density described in Bascón-Cardozo et al., 2022 and calculated gene count in 100 kb windows along the genome. Using Kendall's rank coefficient, we measured the genome-wide association of gene density with recombination rates for each population. Finally, we visualized the distribution of gene density together with recombination rates, nucleotide diversity, and Tajima's D using the R package ggplot.

3. Results

Our analyses revealed that at the broad scale, genome-wide recombination maps of different blackcap populations across the species' distribution range appear highly similar (**Fig 1A**). Higher correlation coefficients were observed among migratory populations (Kendall's tau (r_τ)>0.82, p<0.0001), except for the long-distance migrants, which are mainly characterized by low SNP density and the lowest correlation coefficients of all comparisons (r_τ=0.4-0.5, p<0.0001) (**Fig 1A)** . The continental resident population was more similar to continental migratory populations compared to resident island populations. Island populations showed lower levels of inter-population correlation with variable patterns among islands and also with resident and migratory continental populations (**Fig 1A**). Correlation coefficients between the island and continental populations were highest in Madeira and Canary Islands (**Fig 1A**). When we calculated and compared genome-wide recombination rate averages between populations, we found that they ranged between 0.8 to 6.2 cM/Mb (**Table S2** ,**Fig1B**). Island populations showed lower genome-wide average recombination rates compared to continental populations (Wilcoxon rank sum test p<0.0001), with the exception of long-distance migrants that showed overall the lowest average recombination rate (0.8 cM/Mb, **Fig1B**). Generally, recombination rates were higher in micro-chromosomes than macro-chromosomes in all populations, and chromosome Z showed one of the lowest averages of recombination rates (**Fig 1B**).

In contrast to the nearly consistent broad-scale patterns across blackcap populations, recombination rates were highly variable at a finer scale. Intra-chromosomal comparisons revealed divergent patterns of recombination between populations across different chromosomes (**Fig 1C** , **Fig S1, S2**): Island populations showed different patterns among populations, e.g., chromosome 18 in the Crete population (**Fig 1C, Fig S2**), whereas continental populations showed more variability in the smoothness of recombination maps (**Fig 1C, Fig S1)** . The variation was more prominent in micro-chromosomes (e.g., chromosomes 18, 23, 26, 28, 29 in **Fig 1C** , **Fig S4**) than in macro-chromosomes. In the largest macro-chromosomes, the recombination landscapes were more consistent among populations (**Fig S4**), with high recombination rates towards the end of chromosomes and lower recombination rates in the center (e.g., chromosomes 1, 2, 4, **Fig 1C, Fig S1, S2**). Recombination rates in chromosome Z were conserved across populations at both broad and fine scales. All populations consistently show suppressed recombination along the entire Z chromosome and a peak of historical recombination at one chromosomal end which may represent the pseudoautosomal region (PAR) (**Fig S1, S2**).

3.1 The strong relationship between recombination and nucleotide diversity

All populations show a strong positive association between recombination rate and nucleotide diversity (π) (r_τ>0.55, p<0.0001, **Table S2**). The lowest coefficient of positive correlation was observed in the long-distance migrants (r_τ=0.44, p<0.001). Genomic regions where decreased nucleotide diversity coincided with low or suppressed recombination were shared across all populations (**Fig 2**). Interestingly, in some chromosomes, potential targets of selection represented as genes were not entirely depleted within these regions (see chromosomes 16, 22,26 **Fig 2**). In chromosomes 20 and 29, a substantial number of genes was

more evident (**Fig 2**).

3.2 Variation in recombination rates and distortion of the Site-frequency spectrum (SFS) as potential means of selection

We found recombination rates weakly correlated with Tajima's D in all blackcap populations when we performed partial correlations controlling for nucleotide diversity for each population (**table S2**). The correlation was slightly positive in continental populations and insignificant for the short-distance population. In contrast, island populations show a negatively weak correlation **Table S2**). Genome-wide average Tajima's D in island populations was greater ([?] 0) compared to continental populations, which showed values below 0 (**Fig S5**). Interestingly, when we looked into the intra-chromosomal distribution of Tajima's D, we identified a distortion, either a peak or drop in the site-spectrum frequency (SFS), coinciding with some of the chromosomal regions characterised by decreased recombination rates, low nucleotide diversity and intermediate gene density described in the previous section (**Fig 2** see chromosome 16,20,26 and 29).

3.3 The interplay of variable recombination rates with relative and absolute population divergence

The pairwise comparisons among all populations revealed different associations between relative divergence or differentiation (Fst) and recombination rates between populations (**Fig 3, Fig S6**). Fst calculated for each population pair with their respective recombination maps was negatively correlated in some, but not all populations (**Fig 3** , **Fig S6**). Fst outliers ($95^{th}$and 99^{th} percentile) in these populations occurred predominantly in regions of low or suppressed recombination. This was consistent in both recombination maps from the populations where Fst was calculated (see CRE-MAL **Fig 3A** , also see cont_res-CRE, CAVE-CRE, short-MAD, AZO-CRE in **Fig S6**). Among continental populations, short, medium-distance migrants and resident populations show negative correlation coefficients between recombination rate and Fst when compared with the long-distance population (for instance, Fst resident_cont-long: r_τ =-0.31 for resident_cont and r_τ =-0.068 for long). In the comparison between medium-distance populations with different migratory orientations and short-distance populations, a weak positive association of recombination and Fst was seen (Fst medium-SE_short, r_τ =0.06 for medium_SE, r_τ =0.08 for short). However, not all populations showed a consistent association. For instance, the Fst calculated between Azores and Mallorca (Fst AZO-MAL) was significantly associated with recombination rates of Mallorca but not Azores (**Fig 3B**). Additionally, in the comparison between the Azores and medium_SW migrants, Fst AZO-medium_SW correlated positively with recombination rates of medium_SW (r_τ=0.13) but negatively with recombination rates of AZO (r_τ =-0.12, see also: Fst AZO-medium_SE, Fst AZO_medium_NW, and Fst short-MAL**Fig S6**). Thus, the recombination rate in one population was differentially associated with Fst compared to the other population.

In populations where recombination maps are less conserved such as island populations, recombination patterns showed higher variability in regions of elevated Fst in some of them (See AZO-MAL **Fig 3B**). Therefore, we evaluated the relation between genome-wide dissimilarity of recombination maps between populations and population differentiation (Fst). This revealed a positive association ($r_{\tau=}$0.29, p<0.001, **Fig 4**), which was further supported by comparing recombination dissimilarity matrices and Fst matrices for all population pairs (Mantel's test r=0.13, p<0.001, 9999 permutations). This relationship was driven by island populations (**Fig 4**), and when we separated island populations from continental populations, the association in island populations became even stronger ($r_{\tau=}$0.45, p<0.05, Mantel's r=0.23 p<0.001, **Fig 4**). Whereas, the correlation pattern within continental populations disappeared (in Mantel's r= 0.1, p>0.05) or turned negative (r_τ =-0.61, p<0.01, **Fig 4**).

Our results revealed a positive association between recombination rates and absolute divergence (dxy) between all populations (r_τ>0.55 -r_τ>0.36, p<0.0001). Again, the long-distance migratory population showed the weakest correlation coefficient, albeit positive. When we focused only on dxy within HRR, we found a significantly greater dxy average compared to the genome-wide dxy in all population pairs (Wilcoxon test p<2.2e-16,**Fig 5**), suggesting an increase in population divergence within HRR.

4. Discussion

4.1Recombination rate variation between different populations at broad and fine scales

We compared historical recombination maps at genome-wide (broad-scale) and intra-chromosomal (fine-scale) levels in 100 kb windows among blackcap populations with different migratory phenotypes. Our data shows that recombination maps of distinct populations have diverged at fine scales, while patterns at broader scales are more conserved. This pattern of similarity in broad-scale recombination rates has previously been found between and within other bird species (Kawakami et al., 2017; Peñalba et al., 2020; Singhal et al., 2015) as well as in mammals (Betancourt et al., 2009; Campbell et al., 2016; Myers et al., 2005), fish (Shanfelter et al., 2019), and reptiles (Schield et al., 2020). The variation of recombination rates at the genome-wide scale can be attributed to genetic factors, epigenetic regulation (e.g., DNA methylation), and mutations in genes involved in meiosis and/or double-strand break repair pathways (Brand et al., 2018; Charlesworth, 2018). Hence, the conservation of recombination rates at broad-scales could reflect molecular mechanisms shaping recombination dynamics. For example, it is often observed the enrichment of recombination events in open chromatin regions and functional elements in organism lacking the protein PRDM9 such as birds and yeast, where recombining patterns are often stable (Lam & Keeney, 2015; Singhal et al., 2015). This similarity in genome-wide recombination rates could also be a common pattern in organisms containing recombination hotspots since this is not observed in organisms that lack of them, such as *Drosophila*(Samuk et al., 2020).

Our observed variation in the level of correlation among recombination landscapes of distinct blackcap populations may recapitulate population structure and demography (Delmore et al., 2020, Bours et al. in preparation). Blackcap population stratification suggests the majority of island populations cluster separately, while continental migrant populations form one genetic cluster. Even continental resident populations are more similar to the continental migratory population than to the resident populations on islands (Delmore et al., 2020). This mirrors the higher pairwise correlation of recombination maps among continental populations regardless of the migratory phenotype, suggesting that recombination patterns are predominantly formed by genetic divergence and the evolutionary history of the populations. Contact zones across a migratory divide separating populations with distinct migratory behaviour exist in central Europe between medium-distance SW and SE migrants, in line with that, recombination rates between both populations share the highest similarities.

Long-distance migrants were the exception, showing lower correlation coefficients with all the rest of the populations, probably due to their overall low SNP density (despite good coverage), diversity, and sample size. In contrast to other populations, samples for the long-distance migrant phenotype were not exclusively sampled at the breeding locations but included samples taken during migration, thus, the sample pool likely covers a broader population range. Adding further individuals with known breeding origins to complement the samples from this phenotype in the future would be ideal for clarifying whether recombination rate in this population is indeed exceptional due to molecular, biological, and evolutionary reasons or because the resolution was too low in our current study to allow for accurate characterisation of this population.

Reflecting what is known for the genetic structure, island populations show less similarity among themselves and with continental populations, except for Crete, which clusters closer to the continental populations in comparison to the rest of the island populations and didn't show an exceptionally high correlation with continental populations. The Mallorca population showed higher recombination rate divergence with islands and continental populations, mirroring the separation reported in PC2. Macaronesian islands form two genetic clusters, one between the Canary Islands and Madeira which are closer to the migrant continental populations and this was reflected in higher correlation in recombination maps between both populations and with the continent. A second cluster was formed by Cape Verde and Azores that did not show increased similarity levels compared to the rest of the populations. Thus, additional factors, for example, population sub-structure likely also contribute to observed patterns of similarity and variation of recombination maps between populations.

Population demography is another important factor that affects the variation in recombination rates. Our simulations with bird-specific parameters corroborated that the approach used in this study to infer recombination rates is not biased by population-specific demography (**Fig S3**). Therefore, the divergent recombi-

nation maps may reflect biological factors and different evolutionary histories in the populations. Blackcap populations split into different migratory phenotypes about 30,000 ya. After the split, island populations experienced a reduction of effective population size (Ne), whereas Ne in continental populations increased (Delmore et al. 2020). Consistent with that, the genome-wide average of Tajima's D was significantly lower in continental populations compared to island populations, indicative of expansion and contraction events in these populations (Tajima, 1989). Perhaps, due to the low Ne in island populations, selection (directional or purifying selection) is less efficient (selection relaxation), and genetic drift has larger effects (Charlesworth, 2009; Gravel, 2016; Ohta, 2013; Wright, 1931), resulting in divergent recombination landscapes. Continental populations with higher Ne may have more substantial selective pressures over migratory traits, maintaining "optimal" recombination rates and lowering the effect of genetic drift, which may contribute to the conservation of recombination maps. Probably that also relates to the difference in genome-wide recombination rates among continental populations showing higher recombination rates than island populations. However, as populations differ in population size and SNP density and additional population-specific factors may influence recombination rates, one should be cautious when comparing absolute values. The pairwise correlation between recombination rates and Tajima's D was positive for continental populations and negative for island populations, probably reflecting the role of recombination in the efficacy of selection in populations with different histories. However, correlations were only weakly significant.

Our results reveal variation at fine scales between different populations of the Eurasian blackcap. We identified chromosomal regions with divergent recombination patterns between populations across several chromosomes, predominantly in micro-chromosomes. The level of variation differed between populations that exhibit different migratory behaviour. More specifically, resident island populations showed higher variation in their recombination patterns, whereas continental populations mostly varied in the intensity (smoothness) of recombination at specific genomic regions, possibly influenced by variation in sample sizes and SNP densities between populations. Incidences of local recombination variation have also been described in other bird species (Backstrom et al., 2010; Kawakami et al., 2017; Stapley et al., 2010; van Oers et al., 2014), and may therefore represent a common phenomenon in birds. This fine-scale variation could be attributed to structural variation such as inversions and large deletions suppressing recombination, which have been described in several studies in the blackcap and other species (Hooper & Price, 2017; Ishigohoka et al., 2021; Morgan et al., 2017; Volker et al., 2010). In addition, the presence of other specific genomic features, such as retrotransposons, the genetic and epigenetic regulation of CpG islands, and particular genes may also affect local recombination variation (Bascon-Cardozo et al., 2022; Kawakami et al., 2017; Penalba et al., 2020; reviewed in Stapley et al., 2017). The areas identified with more significant variability in recombination rates between populations could be associated with structural variants or differential gene regulation providing exciting targets for further exploration in genotype-phenotype association studies. Perhaps some of these regions are associated in the evolution and regulation of the migratory behaviour. However, this is purely speculative at present, as migratory and resident blackcap populations also experience different selective environmental pressures that could influence recombination variation among populations.

Previous studies reported both an increase and decrease in recombination rates with changes in temperature, solar radiation, and precipitation (Dreissig et al., 2019; Lloyd et al., 2018; Zhang et al., 2017). Populations studied here are also subjected to different environmental pressures, particularly between the island and continental populations, as well as broad latitudinal changes with varying temperatures and precipitation levels (Cropper 2013). Furthermore, migrant populations encounter different biotic and abiotic conditions throughout their migratory journey and may have different adaptation strategies to adjust to different habitats. Potentially, many adaptations to changing environments might also be influencing recombination rates and driving recombination differentiation between continental migrants and resident populations.

4.2 Putative regions under linked selection: Conserved regions in low recombination associated with reduced nucleotide diversity and potential signs of selection

Our results corroborate that a strong relationship exists between nucleotide diversity and recombination rate across the genome, as has been shown for other bird species (Kawakami et al., 2017; Mugal et al., 2013;

Singhal et al., 2015), as well as a broad range of other taxa (reviewed in Cutter & Payseur, 2013; McGaugh et al., 2012; Smukowski & Noor, 2011). This result hints at linked selection, indicating that the effects of selection on linked neutral (or weakly selected) diversity are strong in the blackcap. This is particularly evident in conserved regions across all populations, where low recombination rates coincide with low diversity. As recombination events could be undetectable due to the lack of suitable markers (Hudson & Kaplan, 1985; Stephens, 1986), we cannot exclude that these regions may represent regions where historical recombination events are masked rather than genuinely absent. However, given the high quality of our dataset and the remarkably consistent pattern across all populations, they may be indicative of regions with strong linked selection. Some of the regions of low recombination could also represent regions under background selection (Burri et al., 2015; Chase & Mugal, 2022; McGaugh et al., 2012, reviewed in Cutter & Payseur, 2013). Signatures of background selection would show a pattern of reduced recombination and reduced diversity associated with a considerable density of genes (Cutter & Payseur, 2013; Talla et al., 2019; Vijay et al., 2016). Several identified regions match this consistent pattern, e.g., chromosomes 20 and 29. It could be the case that recombination in regions with a high gene density is disfavored. Thus, a majority of recombination events reshuffling these alleles may be deleterious and thus rapidly purged from the population (reviewed in Dapper & Payseur, 2017; Otto et al., 1994). Distortion in the site-frequency spectrum (SFS), measured here with Tajima's D, can be identified at these regions where recombination and nucleotide density are low, patterns that are indicative of background selection and selective sweeps (Campos et al., 2014; Cvijović et al., 2018; Kim, 2006). However, it is essential to point out that Tajima's D can be influenced by recombination and linkage disequilibrium (Thornton, 2005), and thus interpretations should be treated with caution.

Moreover, recurrent hard sweeps and putative chromosomal inversions would yield a similar pattern of low recombination rates coinciding with reduced diversity (Andolfatto, 2001; Sanchez-Donoso et al., 2022). Here, we would expect a drop in Tajima's D (skewing the SFS towards rare variants over neutral expectation) to signal selective sweeps (Kim, 2006), a pattern that we observe, for example, in chromosomes 20 and 22 and 26. Thus, even though we cannot fully disentangle whether low nucleotide diversity is a side-effect, a cause, or a consequence of low recombination, these loci are relevant for further investigation. After all, these regions may indicate long-term background selection, selective sweeps, and harbours of structural variants.

4.3 Recombination rates association with genetic differentiation (Fst) and absolute divergence (dxy)

Although genetic differentiation between blackcap populations is generally low, we identified regions where Fst outliers coincide with low recombining regions. This pattern has previously been reported for other bird species , as well as other taxa (Burri, 2017 Burri et al., 2015; Henderson & Brelsford, 2020; Samuk et al., 2017). Interestingly not all of the populations showed the same pattern: we also found examples of populations where Fst outliers were enriched in regions with high recombination rates, and these regions show variable recombination maps between populations. We found the divergence of recombination maps among populations (recombination dissimilarity) in association with population differentiation (Fst), which indicates that not only the suppression of recombination but also the divergence in recombination rates among populations could contribute to population differentiation. Similar results were also reported in plants such as wheat (Danguy des Déserts et al., 2021) and cocoa tree, where population differentiation decreased the percentage of hotspots overlapping among populations (Schwarzkopf et al., 2020). Additionally, chromosomal rearrangements could also cause these patterns, as has been described in Alves et al., 2014, where genetic differentiation given by a chromosomal inversion was positively correlated with dissimilarity in recombination maps.

The relation between recombination dissimilarity and Fst was most evident in island populations with generally more variable recombination landscapes and greater Fst. In continental populations, the correlation flipped to negative or not significant, mostly driven by the long-distance migrants, which again behaves differently from all other populations showing high recombination dissimilarity and very low Fst. Nevertheless, it is also important to consider that the relative measure of divergence (Fst) can be inflated in regions where absolute genetic diversity is reduced and linked selection is strong (Burri et al., 2015; Cruickshank & Hahn,

2014; Martin et al., 2019; Noor & Bennett, 2009).

We also included absolute divergence (dxy) in our analysis and found a higher divergence between populations in HRR. This was a consistent pattern across all the populations. Together with our findings between recombination rates, nucleotide diversity, and Fst, this suggests that our blackcap populations may exemplify the model where genetic variation is affected by linked selection and recombination variation proposed by Nachman and Payseur (2012). Even though gene flow is a variable that was not considered in this study, previous work reported limited (or not detectable) gene flow among blackcap populations (Delmore et al., 2020). The linked selection model (Nachman & Payseur, 2012) was also reported in *Ficedula* flycatchers, another passerine species (Burri et al. 2015) where the heterogeneous landscape of differentiation evolves mainly as the result of background selection and selective sweeps in genomic regions of low recombination. Similarly, our results may lead to the identification of important putative genomic regions under background selection, selective sweeps, and regions with divergent recombination rates that may contribute to blackcap populations' differentiation and evolution.

In this study, we deciphered recombination rate variation from genome-wide to local chromosomal scale between blackcap populations across a wide geographical distribution, including island and continental populations and comprising a wide range of migratory phenotypes. Despite the generally assumed conserved recombination rates in birds and low differentiation between populations, which we also recovered on the broader scale, we detect striking differences in recombination rates at the fine scale between different populations of the same species. The interplay between recombination rate variation, nucleotide diversity, and population divergence suggests that linked selection may potentially contribute to the evolution of blackcap populations differentiation.

The correlation of population differentiation with reduced recombination rates was confirmed and recombination landscapes in blackcap populations were shown to vary with genetic divergence between populations. Our findings support the idea of recombination maps as a variable phenotype and highlight the importance of including them in population genomic analyses.

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Data accessibility

The primary and alternate haplotype assemblies for the Eurasian blackcap can be found under NCBI BioProject PRJNA558064, accession numbers GCA_009819655.1 and GCA_009819715.1 (Ishigohoka et al. 2021). The final dataset and all scripts used for the analyses will be uploaded to Dryad upon acceptance of the manuscript.

Benefit-Sharing Statement

All methods were carried out in accordance with relevant guidelines and regulations, all experimental procedures were approved and conformed to the applicable regulatory standards under permits by the Ethics committee of the respective authorities (permit numbers: AZ V242-62340/2016 (98-8/16), AZ 35-9185.81/G-16/43, AZ 3104-4/021/0033 and 1401-144/153-5.2.3)

Author Contributions

ML, LOH and KBC designed the study. KBC carried out population-specific recombination rate estimates, respective downstream analyses with population features and simulated data with support from LOH and ML. JI inferred population-specific demography and performed simulation analysis. The VCF file was generated and summary statistics estimated by AB. KBC wrote the manuscript with input from LOH and ML. All authors provided comments and feedback on the manuscript.

Figure captions

Figure 1. Recombination variation at different scales A) Correlation heatmap of recombination maps between all pairs of populations differing in migratory phenotype. Populations are classified between the island (resident) and continental (migratory and resident) populations. Heatmaps show Kendal rank test

correlations of pairwise comparisons between recombination rates calculated in 100 kb non-overlapping windows. **B)** Average recombination rates are given for each chromosome and all populations. The coloration gradient of dots reflects the genome-wide average recombination rate for larger (black) to shorter (light-grey) chromosomes. Chromosome Z is shown in blue dots. Red diamonds represent the genome-wide recombination rate average for each population. Mean values of recombination rates are significantly different between populations (Wilcoxon rank sum test,p <0,001), except for two populations from the Canary (CAN) and Madeira (MAD) islands (Wilcoxon rank sum test, p =0.25).**C)** Distribution of intra-chromosomal recombination rates (in cM/Mb) and genetic distance maps (in cM) across selected macro- (chromosomes 2 and 4) and micro-chromosomes (chromosomes 18, 23, 26) from migratory and resident populations subdivided into continental populations (top panel) and island populations (bottom panel) including continental residents in dashed lines.

Figure 2 . **Chromosomal regions with possible signs of linked selection** . Plots showing nucleotide diversity (π), recombination rates (rec rate), Tajima's D, and gene density distributions across selected chromosomes calculated in 100 kb non-overlapping windows for all populations (color coding as in Figure 1). The positive association between recombination rate and nucleotide diversity is reflected by highly similar patterns in all the populations. Grey bars highlight regions of low nucleotide diversity, reduced recombination rates and distortion in the site-frequency spectrum indicated by high or low patterns of Tajima's D and variable gene density.

Figure 3. Population differentiation and recombination rates variation . Recombination rates (rec rate) and Fst outliers in gray (with 95^{th} percentile in black and 99^{th} percentile in dark blue) across selected chromosomes for two island population comparisons: (A) between Crete (CRE)-Mallorca (MAL) and (B) between Azores (AZO) -Mallorca (MAL) on the left panels. Kendall correlations between Fst and recombination rates calculated in 100kb windows for the respective pair of populations are shown on the right panels. Colour coding for populations as in Figure 1.

Figure 4. Dissimilarity in recombination maps is associated with population differentiation in island populations. Correlation between genome-wide recombination dissimilarity and population differentiation (Fst) in all the populations, continental populations, and island populations. Correlations were measured with Mantel statistics and Kendall's rank tests.

Figure 5 . **Greater population divergence (Dxy) in High Recombining Regions (HRR).** Dot plots showing the comparison of genome-wide average dxy calculated for the focal population pairs across the whole genome in grey and within HRR corresponding to each population (denoted in color codes as in Figure 1). The plot shows a subset of selected populations with higher genome-wide dxy for visualization. The dots represent the means and error bars at the 95% confidence level. All the comparisons for each population pair are significantly different (Wilcoxon. test, p<0,001).

Figures

Figure1

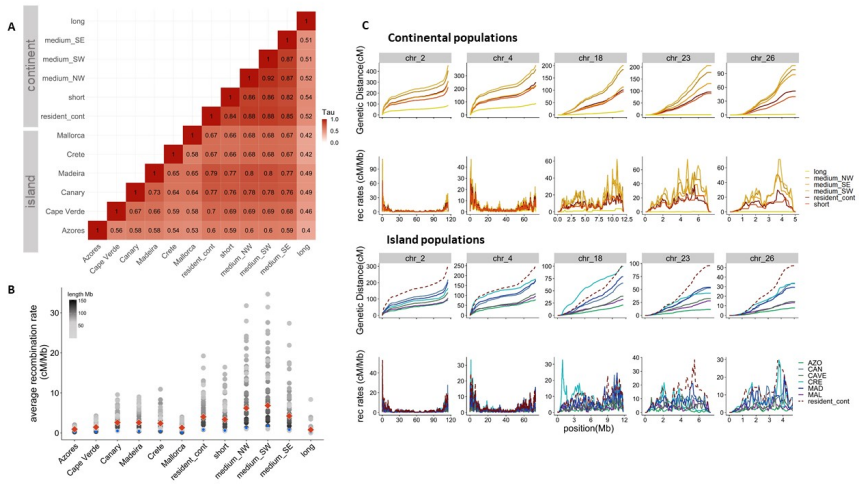

Figure 2

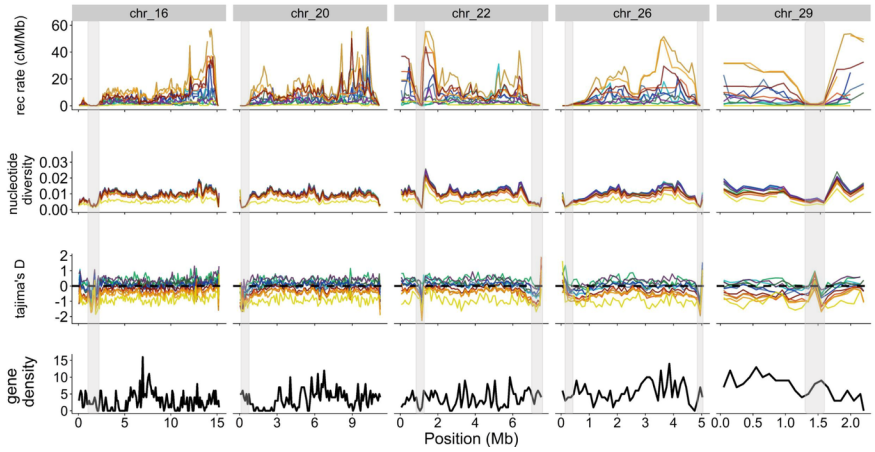

Figure 3

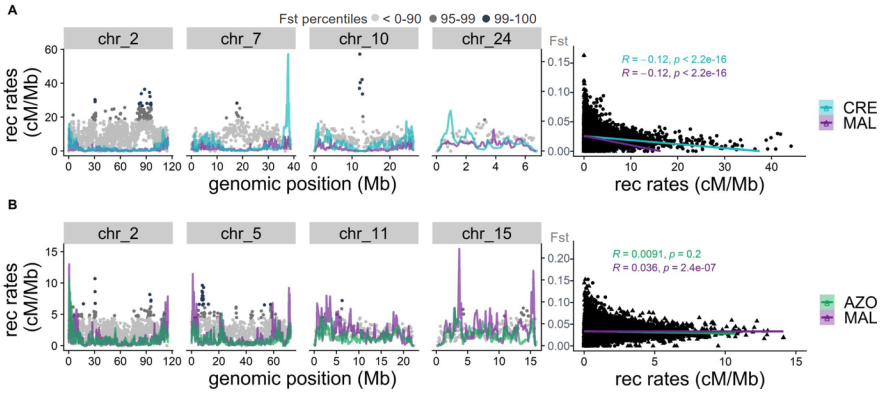

Figure 4

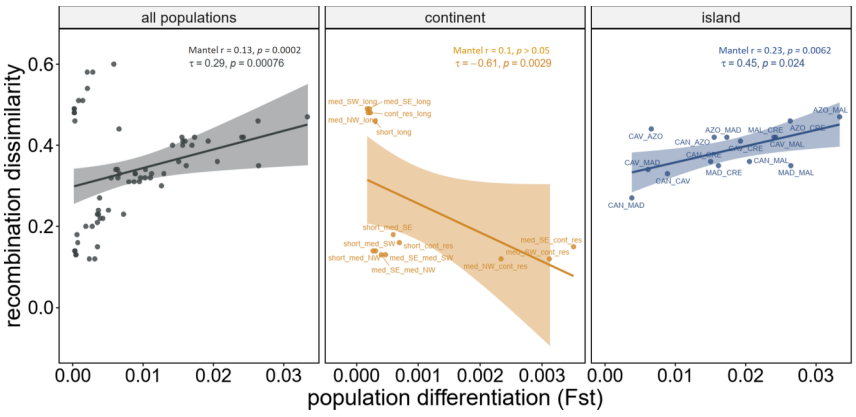

Figure 5