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Avian Genomics in Ecology and Evolution

From the Lab into the Wild

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Population Genomics and Phylogeography

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Abstract

Population genetics is the study of genetic variation within populations and how allele frequencies change over space and time. This field largely focuses on the five fundamental evolutionary processes that influence genetic variation: mutation, genetic drift, gene flow, natural selection, and recombination. In this chapter, we review how genomic data from avian species have advanced our understanding of each of these five processes, including an emphasis on their interactions in shaping contemporary genetic diversity on the scale of whole populations. In general, genomic data has increased the potential for fine-scale resolution of population structure and determination of population boundaries and population membership. However, delineating populations is not always straightforward, and populations tend to fall on a continuum from isolation to panmixia. Mutation is the ultimate source of all genetic variation within populations. The ability to sequence whole genomes resulted in better estimates of mutation and substitution rates in particular genomic regions (e.g., coding vs. noncoding DNA) and along

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different avian lineages. The uncovered variation in these rates will further advance our knowledge of bird evolution. A genomic perspective on other evolutionary forces, such as genetic drift (tightly linked with the concept of effective population size [N_e]), migration, and selection, allows for more detailed reconstructions of demographic and phylogeographic history. In addition, the estimates of genome-wide recombination rates and their relationship with linked selection and GC-biased gene conversion will improve the match between population genetic models and biological reality.

Keywords
Assortative mating · Demography · Effective population size · GC-biased gene conversion · Gene flow · Linked selection · Natural selection · RADseq · Recombination · Substitution rates

1 Introduction

The field of population genomics, defined as the "process of simultaneous sampling of numerous variable loci within a genome and the inference of locus-specific effects from the sample distributions," was first conceptualized by Black IV et al. (2001). This initial conceptualization emphasized distinguishing between factors that influence unlinked loci independently (locus-specific effects), such as mutation, recombination, nonrandom mating, and selection, from those factors that have a similar influence on loci throughout the genome (genome-wide effects), such as genetic drift, gene flow, and inbreeding. Rather than emphasizing locus-specific effects, Luikart et al. (2003) defined population genomics more broadly as "the simultaneous study of numerous loci or genome regions to better understand the roles of evolutionary processes [. . .] that influence variation across genomes and populations" (p. 981). In contrast to Black IV et al. (2001), Luikart et al. (2003) concluded that the most important contribution of genomic sampling is to provide better inferences of population demography and evolutionary history. Hartl and Clark (2007) similarly adhered to a broader definition, "the application of population genetics on a genomic scale" (p. 469). In this review, we use this more general definition of population genomics and examine the fundamental evolutionary processes that influence genetic variation: mutation, genetic drift, migration (i.e., gene flow), natural selection, and recombination (Sects. 3–7).

Genetic diversity within populations is the result of these five fundamental evolutionary forces. For the most basic model, equilibrium values of genetic diversity are a function of mutation and genetic drift, both of which are a function of population size (N). Because more mutations occur and genetic drift is less efficient at removing variation in larger populations, genetic diversity should be directly proportional to N (Wright 1931), a relationship that has been supported by empirical studies (Soulé 1976; Frankham 1996, 2012). However, this simple model makes a

number of assumptions, including no immigration, no selection, constant N (i.e., drift-mutation equilibrium), nonoverlapping generations, and random mating (Wright 1931, 1938; Frankham 1995). In these mathematical models, N is not what ecologists would count when they go out in the field and ask "how many individuals are there?" The latter question refers to the census population size, usually specified as N_c. In population genetics, we typically calculate the effective population size N_e, which is a rather abstract quantity that reflects the genetic diversity of a population under study but includes the effects of inbreeding and subdivision, among others (Hartl and Clark 2007). Typically, N_e is much smaller than N_c (for details see Sect. 2 in this chapter). The effectiveness of selection is also dependent on N_e (Ohta 1972, 1992; Gillespie 2001; Ellegren 2009). Specifically, if the product $2N_es$ (where s is the selection coefficient) $\gg 1.0$, selection will override drift in determining the fate of mutations, whereas if $2N_es \ll 1.0$, drift will dominate. The emerging field of population genomics has revealed compelling evidence that directional selection, balancing selection, purifying selection, and hitchhiking are pervasive throughout the genome, causing widespread departures from neutral models (Hahn 2008; McVicker et al. 2009; Charlesworth 2012; Burri 2017a). However, some genomic features can also be explained by nonadaptive processes, such as genetic drift (Lynch 2007).

2 What Is a Population?

The term population has been defined in a variety of ways throughout the scientific literature (Waples and Gaggiotti 2006). At one extreme, population is essentially synonymous with sampling location, referring to a group of individuals sampled from a single location. Hartl and Clark (2007) defined a population in a more biologically relevant way: "a group of organisms of the same species living within a sufficiently restricted geographical area so that any member can potentially mate with any other member of the opposite sex" (p. 45). In an ideal population of sexually reproducing individuals, mating is random, and any individual has an equal probability of mating with any other individual from the same population (i.e., the population is panmictic). However, it is questionable whether any population is truly panmictic. Mating is rarely, if ever, completely random, but rather individuals are more likely to mate with individuals in close proximity. In other words, the probability of mating decreases with increasing distance between individuals, and this nonrandom mating results in a spatial organization of genetic variation (i.e., isolation by distance), even in the absence of any other factors such as mate choice or mobility. When making inferences about demographic histories or selection, the distribution of alleles across space becomes critically important.

Most definitions of a population are not operational in the sense that they fail to provide quantitative criteria for determining which individuals belong to the same or a different population. Waples and Gaggiotti (2006) suggested using the number of effective migrants per generation (N_em, where N_e is the effective population size and m is the migration rate) as an operational criterion for determining whether groups of

individuals could be considered a population. The threshold for this criterion is somewhat arbitrary, and estimating N_em can be cumbersome, especially with genomic datasets. Moreover, calculating N_em requires some a priori knowledge about which individuals are grouped. Therefore, the first hurdle in delineating populations is determining which individuals are sufficiently similar that they can be considered part of the same population.

In the past, statistical power from only a small number of genetic markers from distant regions of the genome has often been insufficient to unveil weak population structure, and increasing the number of markers has clearly shown that more markers give better signals (Kraus et al. 2015). Population genomics uses technology to increase the number of genetic markers by orders of magnitude (Kraus and Wink 2015; Wink 2019), thereby offering the potential for fine-scale resolution of population structure and determination of population boundaries and population membership. Peters et al. (2016) conceptualized a quantitative framework for using large-scale genetic datasets to delineate "conservation units." This framework, largely inspired by approaches in Harvey and Brumfield (2015), can be applied to delineating populations. Using the mottled duck (*Anas fulvigula*) and genotypes obtained from a reduced representation genomic approach, double-digest restriction-associated DNA sequencing (ddRAD-seq), Peters et al. (2016) used a variety of analytical methods to distinguish between apparent panmixia, discrete population units, and isolation by distance. Specifically, they demonstrated that the Florida and Western Gulf Coast populations of mottled ducks were discrete units—genotypes were sufficiently similar within regions and different between regions that (1) all individuals grouped together in population-specific clusters on the basis of ddRAD-seq genotypes (Fig. 1a), (2) all individuals were assigned unambiguously to their populations of origin, (3) the geographic area separating these populations was a better predictor of allele frequency differences than geographic distance alone, and (4) there was limited evidence of admixture and gene flow between these populations. In contrast, there was no evidence of population structuring within Florida or the Western Gulf Coast. Therefore, in the case of mottled ducks, delineating population boundaries was unambiguous. Other studies of avian taxa have used similar approaches with ddRAD-seq data to demonstrate discrete differences in multilocus genotypes between geographic groups (Parchman et al. 2013; Harvey and Brumfield 2015; Kopuchian et al. 2016), and such discrete population structure has been used as evidence for species delimitation (Oswald et al. 2016).

In contrast to the discrete population units found in mottled ducks, studies of some avian taxa found ambiguous evidence of population boundaries (Kraus et al. 2013; Lavretsky et al. 2015). For example, Lavretsky et al. (2015) used principal component analyses (PCA) to cluster individuals based on ddRAD-seq genotypes in mallards (*Anas platyrhynchos*) and Mexican ducks (*A. diazi*). Although there was some evidence of discrete or nearly discrete populations (e.g., eastern and western populations of mallards and mallards vs. Mexican ducks), individuals could not be unambiguously assigned to populations and there appeared to be substantial admixture. Overall, a pattern of isolation by distance seemed to describe the geographic

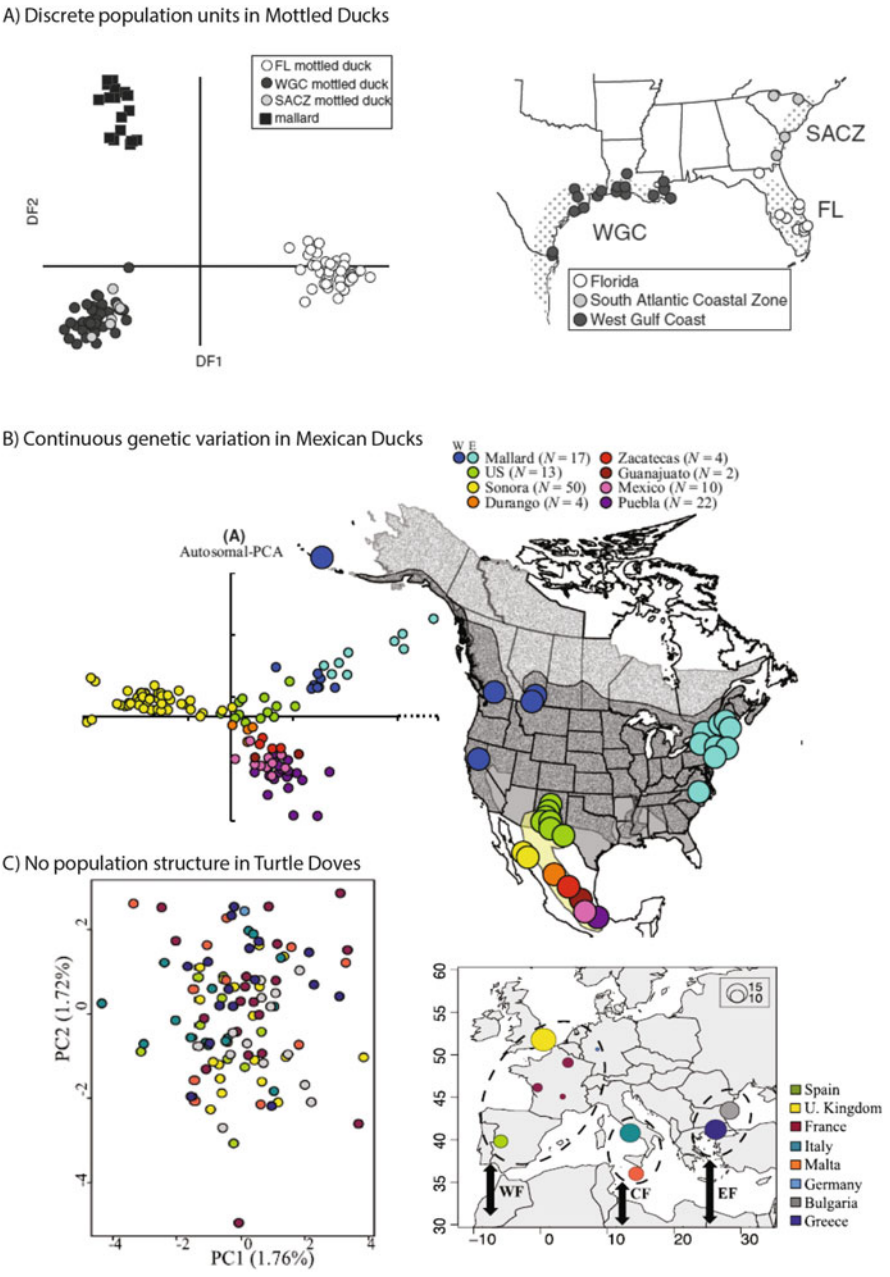

Fig. 1 Examples of the gradient of possible outcomes when applying genomic data to inferences of population boundaries, including (**a**) discrete population units in mottled ducks (Peters et al. 2016), (**b**) continuous variation with possible isolation by distance in mallards and Mexican ducks (Lavretsky et al. 2015), and (**c**) apparent panmixia in turtle doves (Calderón et al. 2016)

distribution of alleles (Fig. 1b); for example, western mallards, which are geographically closer to Mexican ducks, were genetically intermediate between eastern mallards and Mexican ducks, and Mexican ducks sampled from the United States were genetically intermediate between mallards and Mexican ducks sampled from Mexico. Within Mexico, there was a stepping-stone pattern of genetic differentiation: individuals from the most geographically distant sampling locations were the most genetically differentiated (e.g., Sonora vs. Puebla), whereas there was substantial overlap in principal component (PC) scores among individuals from neighboring sites (e.g., Puebla vs. the state of Mexico). A similar pattern of isolation by distance was also found among subspecies of dark-eyed junco (*Junco hyemalis*) in North America: the principal components showed a striking resemblance to geographic distribution (Friis et al. 2016). Although the slate-colored junco (*J. h. hyemalis*) does appear to be a discrete population, it is important to emphasize that all the individuals examined were sampled from the same location; more comprehensive sampling across their range will be necessary to determine whether this subspecies represents a discrete population or if it fits within a broader pattern of isolation by distance. Otherwise, for both juncos and Mexican ducks, the challenge is that delineating population boundaries is not possible given the gradation in multilocus genotypes over space, despite clear evidence of population structure. Thus, the use of population genomics to infer aspects of population demography, history, and selection necessitates models that incorporate isolation by distance.

Similar to Mexican ducks and dark-eyed juncos, population genomics suggests that red crossbills (*Loxia curvirostra*) comprise a mix of discrete, nearly discrete, and non-discrete ecotypes that loosely correspond to geographic populations (Parchman et al. 2016). However, in this case, there was no overall pattern of isolation by distance, at least partly as a result of their nomadic behavior. For example, PCA clusters individuals from the western and eastern parts of the red crossbill's range to the exclusion of individuals from the interior. Parchman et al. (2016) concluded that adaptation to conifer species, rather than geography, was a better explanation of the observed genetic differentiation. In addition, the population from South Hills, Idaho, USA, appeared to be a discrete population that was genetically distinct from other crossbills, and these results coupled with differences in morphology and calls have resulted in the recognition of a distinct species, the Cassia crossbill (*L. sinesciuris*) (Chesser et al. 2017).

In some cases, population genomics might fail to reveal population structure, even for species with broad geographic distributions. For example, Calderón et al. (2016) sampled European turtle doves (*Streptopelia turtur*) from locations throughout eastern and western Europe and obtained genomic data using ddRAD-seq. Using PCA on single-nucleotide polymorphisms (SNPs; pronounced *snips*), they found that PC scores overlapped substantially among individuals from different sampling locations (Fig. 1c). Thus, despite its widespread distribution, genetic variation within European turtle doves is consistent with a single, panmictic population. On ecological timescales, populations from the different regions may or may not be demographically independent; however, on evolutionary timescales, there is sufficient genetic connectivity (i.e., gene flow, range expansion) that detectable population

structure does not emerge. Population genomic data likewise failed to reveal population structure in mountain chickadees (*Poecile gambeli*), despite geographically structured phenotypic variation and evidence of local adaptation in life history (Branch et al. 2017). Thus, for the purpose of population genomics, samples from different regions could be pooled and analyzed as a single population for inferences of evolutionary history.

The above case studies illustrate possible outcomes of inferring population structure using genomic data and multivariate statistics. Waples and Gaggiotti (2006) provided a visual representation of the continuum of population differentiation, from isolation to panmixia, and PCA and other similar orthogonal transformations (e.g., discriminant function analysis) offer the ability to visualize where species of interest fall within this continuum. For instance, the examples discussed above illustrate this continuum; mottled ducks (Fig. 1a) clearly fit the scenario of isolation or "complete independence," Mexican ducks (Fig. 1b) fit both "modest connectivity" (Sonora, USA, and inland sampling locations) and "substantial connectivity" (inland locations: Zacatecas, Guanajuato, Mexico, and Puebla), whereas European turtle doves (Fig. 1c) best fit "panmixia." Further advances could be made by developing methods for quantifying this structure to facilitate comparisons across taxa from different studies. Also, such approaches are applicable to the opposite end of distribution of genetic variation when this leads into speciation (Ottenburghs 2019).

3 Mutation

The ultimate source of all genetic variation within populations is mutation, which changes the nucleotide sequences within a region of DNA through a point mutation (a single base pair change), insertion or deletion of one or more nucleotides, inversions, etc. Mutation is independent in different populations. In the absence of homoplasy (i.e., recurrent mutations, back mutations to the previous state) and gene flow, new mutations that arise after populations split will be unique to a single population and cause populations to genetically diverge over time.

Mutation rates have been estimated across the tree of life, from simple RNA viruses and bacteria to higher eukaryotes, and vary widely from 7.2×10^{-7} to 7.2×10^{-11} per base pair per generation (Drake et al. 1998). In humans, this estimate translates to a germline mutation rate of about 0.5×10^{-9} per base pair per year (Scally 2016). The number of new mutations that enter a population each generation is a function of N_e. However, many mutations are lethal or strongly deleterious and are not passed to future generations. Therefore, in population genetics, we consider the substitution rate, which is the rate at which new mutations accumulate over time. The substitution rate depends on both the rate at which mutation adds new variants and the rate at which natural selection removes deleterious or lethal mutations (see Box 1 in Barrick and Lenski 2013). In the case of strictly neutral evolution, when new variants do not affect biological fitness, the substitution rate is equal to the mutation rate. However, with genomic data, the substitution rate is lower than the

mutation rate, and in the absence of mutation accumulation experiments (Barrick and Lenski 2013) in birds, we can only measure the long-term substitution rates.

Genomic substitution rates vary considerably among lineages of birds. Substitution rates have been estimated for fourfold degenerate sites in coding regions. Fourfold degenerate refers to the observation that each of the 4 nucleotides at a site results in the same amino acid. A substitution at a fourfold degenerate site is also referred to as a synonymous substitution. The substitution rate at these sites was estimated to be approximately 3.3×10^{-9} substitutions per site per year (s/s/y) for Passeriformes (perching birds) and $<1.0 \times 10^{-9}$ s/s/y for Struthioniformes (ostriches) (Zhang et al. 2014). The global rate across all avian lineages was approximately 1.9×10^{-9} s/s/y (Zhang et al. 2014). Similarly, Nam et al. (2010) found a nearly twofold difference in substitution rates at fourfold degenerate sites ($1.23–2.21 \times 10^{-9}$ s/s/y), with the lowest rates in ancestral bird lineages and the highest rates in a representative of Passeriformes. The substitution rate estimated from ddRAD-seq, which generates a pseudorandom sampling of the genome and includes sequences from both coding and noncoding regions, was similar to that found at fourfold degenerate sites—approximately 1.75×10^{-9} s/s/y for a lineage of Anseriformes (waterfowl) (Peters et al. 2016). However, the substitution rate for ultraconserved elements (UCEs) and their flanking regions was found to be about an order of magnitude lower, 2.59×10^{-10} s/s/y, in a lineage of Charadriiformes (shorebirds) (Oswald et al. 2016).

Substitution rates also vary across the genome. As a general rule, substitutions accumulate more rapidly in noncoding regions of the genome, such as introns and intergenic regions, than in protein-coding exons. However, avian genomes contain an estimated 3.2 million highly conserved elements (HCEs) interspersed throughout both noncoding and coding DNA (Zhang et al. 2014), and these HCEs contribute to high variation in substitution rates even within classes of DNA. Similarly, overall substitution rates also vary among chromosomes. Based on analyses of transcriptomes for ten species of birds, d_S (divergence at synonymous sites) was negatively correlated with chromosome size, suggesting that the synonymous substitution rate is lower for larger chromosomes than for smaller chromosomes (Künstner et al. 2010). They also found that d_S was higher for the Z chromosome than for autosomes, a pattern that was also observed by Zhang et al. (2014) in a comparative analysis of full genomes from 45 avian species.

In addition to providing information about the rate of evolution, estimates of substitution rates are necessary to calculate demographic parameters from sequence data. For example, percent sequence divergence (d) can be calculated directly from genomic data with the formula $d = 2\mu t$, where μ is the substitution rate and t is the time since divergence. Thus, having an estimate of μ (in substitutions per site *per year*) allows us to estimate the number of years since two species or populations began diverging. Similarly, genetic data can provide an estimate of the composite parameter θ (*theta*), where $\theta = 4N_e\mu$, and an estimate of μ (in substitutions per site *per generation*) can therefore be used to estimate effective population sizes. These estimates of demographic parameters are important for making inferences about evolutionary history, conservation priorities, and phylogeography.

4 Genetic Drift and Effective Population Sizes

Whereas mutation adds genetic variation to a population, genetic drift removes it. Genetic drift is the stochastic fluctuation in allele frequencies over time that results from the random survival of individuals and the random sampling of gametes during reproduction. In an idealized population of size N_c, the probability that two copies of a gene randomly sampled from a population are identical by descent (i.e., they were derived from the same ancestor in the previous generation) is $1/2N_c$. Lineages that fail to leave descendants go extinct, and any unique mutations within those lineages are lost. Because the rate at which genetic variation is lost is inversely correlated with population size, smaller populations lose variation more rapidly than larger populations. However, this relationship assumes a constant population size (i.e., population sizes remain the same between generations), generations that do not overlap, 1:1 sex ratios, equal variance in reproductive success between the sexes, and random mating. In reality, populations deviate from these assumptions, which usually results in a faster rate of genetic drift than expected given N_c. The N_e is the size of an ideal population that loses genetic variation at a rate equal to that of the actual population (Wright 1931). In other words, N_e quantifies the rate at which genetic drift decreases genetic diversity within a population. Across a wide range of studies, Frankham (1995) estimated that N_e averaged about $0.1N_c$.

Applications of genomics to inferences of N_e and the role of genetic drift have primarily focused on fluctuations in population sizes over evolutionary time, with a particular emphasis on the role of past climate changes. Calderón et al. (2016) used approximate Bayesian computation (ABC) to fit ddRAD-seq data from European turtle doves to five models of demographic history, including constant population sizes and various scenarios of fluctuating population sizes. They found that their data best fit a model that included a population expansion during the late Pleistocene (~78,000 years before present; ybp) followed by a population decline during the Holocene (~7600 ybp). Reductions in N_e have also been inferred from ddRAD-seq data for various species of dry forest birds from South America (Oswald et al. 2017). Interestingly, they found similar changes in N_e between ancestral and daughter populations among the six species studied, despite considerable variation in population divergence times. They attributed these long-term reductions in N_e to historical reductions in the geographic extent of dry forests in this region. One of the main strengths of these inferences lies within the hypothesis-driven framework that is often used in population genomics and phylogeography (Carstens et al. 2017; see Sect. 8). In particular, fitting the data to various models of population size changes and using a Bayesian or likelihood approach to choose the best-fit model make it possible to reject simpler models in favor of more complex models.

Whole-genome data from a single diploid individual can also provide information about past population size changes. In a comparative study of 38 bird species, Nadachowska-Brzyska et al. (2015) used the pairwise sequentially Markovian coalescent (PSMC, Li and Durbin 2009) model to show that demographic histories varied considerably among species and that the N_e of some species fluctuated by orders of magnitude. One prominent pattern was a major reduction in population

sizes associated with the last glacial period (LGP; ~110–12 kya). Surprisingly, however, Nadachowska-Brzyska et al. (2015) did not find a relationship between the extent of the decline and whether current ranges overlapped with regions severely influenced by glaciation (e.g., were formerly covered in ice or extreme deserts). Similar patterns of demographic fluctuations and major reductions in N_e associated with the last glacial period have been inferred from whole-genome sequences and the PSMC for grouse (*Lagopus* spp.) (Kozma et al. 2018), black-and-white flycatchers (*Ficedula* spp.) (Nadachowska-Brzyska et al. 2016), and geese (genera *Anser* and *Branta*) (Ottenburghs et al. 2017b).

5 Gene Flow

When a population gets subdivided, random genetic drift and selection can lead to genetic divergence among the subpopulations. Migration—the movement of organisms among these subpopulations—can act as a kind of genetic glue that binds the subpopulations genetically and sets a limit to the amount of genetic divergence that can accumulate (Hartl and Clark 2007). In the literature, migration and gene flow are often used interchangeably. However, there is an important difference between both terms: migration refers to the movement of individuals between subpopulations, while gene flow encompasses the movement of alleles and their establishment into a different gene pool (Tigano and Friesen 2016). Hence, migration does not necessarily result in gene flow (Verhulst and Van Eck 1996).

Direct estimates of migration often involve mark-recapture methods, which can be impractical and labor-intensive for large populations with low migration rates. Therefore, indirect measures based on genetic data are mostly preferred. Early studies estimating gene flow—expressed as N_em—from genetic data relied on F_{ST} or other measures of differentiation (Slatkin and Barton 1989). However, the population genetic models for these estimations assume unrealistic conditions, such as constant population size, symmetrical migration, and mutation-drift equilibrium (Whitlock and McCauley 1999; Wilson and Rannala 2003; Marko and Hart 2011). The development of non-equilibrium approaches provided the opportunity to assess more realistic scenarios of gene flow. Specifically, isolation-with-migration models enabled the joint estimation of gene flow, genetic diversity, and divergence times within a maximum likelihood framework (Hey and Nielsen 2004; Hey 2006; Hey et al. 2018). For example, isolation-with-migration analyses based on a multilocus dataset indicated asymmetrical gene flow from indigo bunting (*Passerina cyanea*) to lazuli bunting (*P. amoena*) (Carling et al. 2010). Alternative software packages, such as migrate-n (Beerli and Palczewski 2010), have also been used to quantify the degree of gene flow in migrating waterfowl populations of mallard (*Anas platyrhynchos*) (Kraus et al. 2013) and barnacle goose (*Branta leucopsis*) (Jonker et al. 2013).

Similar to the inference of genetic drift and effective population sizes, the development of ABC models allowed population geneticists to probe more complex models and evaluate the extent of gene flow by comparing simulated DNA sequence

evolution with empirical data (Beaumont 2010). For instance, a recent study compared 15 models (with different patterns and levels of gene flow) to assess the demographic history of pied flycatcher (*Ficedula hypoleuca*) and collared flycatcher (*F. albicollis*). ABC modelling based on whole-genome re-sequencing data from 20 individuals supported a recent divergence with unidirectional gene flow from pied to collared flycatcher after the Last Glacial Maximum (Nadachowska-Brzyska et al. 2013). Similar analyses have been performed to assess the demographic history of other bird species, such as *Melospiza* sparrows (Smyth et al. 2015), *Myrmeciza* antbirds (Raposo do Amaral et al. 2013), and *Platalea* spoonbills (Yeung et al. 2011). These studies indicate that model-based approaches are a fruitful avenue for the reliable estimation of gene flow (Ottenburghs et al. 2017a). Recently, machine learning techniques are being applied to population genomic questions (Schrider and Kern 2018), but this approach has not reached the ornithological community yet.

The development of more sophisticated tools in combination with the availability of genomic data led to important insights into the role of gene flow in population dynamics (Ottenburghs et al. 2017a). Similar to mutation, gene flow can introduce novel alleles into a population. Even between species this can be shown when modelling the probability of allele sharing between, e.g., related duck species with or without assuming hybridization (Kraus et al. 2012). The main difference with mutation is the speed at which this happens: the rate of migration is vastly greater than the rate of mutation (Hedrick 2013). The fate of these novel alleles depends on the specific genetic and environmental context in which they end up (Payseur 2010). In general, alleles can be divided into three categories: (1) neutrally evolving alleles that flow freely between populations, (2) alleles that confer an adaptive advantage and flow quickly, and (3) alleles that are not adapted to local conditions and are consequently selected against.

These allele-specific patterns of gene flow result in a heterogeneous genomic landscape in which some genomic regions are more prone to be exchanged between populations than others (Nosil et al. 2009; Ravinet et al. 2017; Wolf and Ellegren 2017). For example, a study comparing the genomes of hooded crow (*Corvus corone cornix*) and carrion crow (*C. c. corone*), two subspecies that interbreed along a narrow hybrid zone across Europe, uncovered a peculiar genomic landscape in which gene flow was relatively unrestricted across the genome except for one genomic region. This region harbored several genes involved in pigmentation and visual perception, suggesting a role in reproductive isolation (Poelstra et al. 2014).

In recently diverged populations, reproductive isolation can be caused by assortative mating, in which individuals with similar phenotypes mate with one another more frequently than would be expected under a random mating pattern (Ritchie 2007; Uy et al. 2018). For instance, the *alba* and *personata* subspecies of the white wagtail (*Motacilla alba*) mate assortatively based on head plumage patterns. This nonrandom mating results in a reduction in gene flow—estimated using almost 20,000 SNPs—between these subspecies (Semenov et al. 2017). The traits underlying assortative mating are various (e.g., song, plumage, behavior) and can originate in different ways (Uy et al. 2018). Sexual selection can drive changes in mating preferences and associated display traits (Ritchie 2007; Kopp et al. 2018).

Alternatively, natural selection can cause divergence in traits not related to mate choice, which may later be co-opted as mating signals, so-called magic traits (Servedio et al. 2011). In the end, natural and sexual selection can act in concert, culminating in a barrier to gene flow (Servedio and Boughman 2017). This synergy between natural and sexual selection is nicely illustrated by bird species in which different subpopulations are adapted to different food sources. Divergent natural selection can then result in distinct beak morphologies, which consequently produce different acoustic signals, such as songs or call types. Assortative mating based on song or call type can lead to a reduction in gene flow between subpopulations. This scenario has been described for *Loxia* crossbills (Parchman et al. 2006), *Melospiza* sparrows (Ballentine et al. 2013), and *Aphelocoma* scrub jays (Langin et al. 2015). So far, genetic data has allowed population geneticists to document these patterns, and genomics will lead to a more fine-grained picture of gene flow dynamics and provide the opportunity to pinpoint the genetic basis of the traits underlying assortative mating.

In addition to assortative mating, barriers to gene flow can also be physical. Numerous studies have documented how mountain ranges (Manthey et al. 2016; Moyle et al. 2017; Machado et al. 2018; Padró et al. 2018), rivers (Maldonado-Coelho et al. 2013; Fernandes et al. 2014), ecological transitions (Caro et al. 2013; Zhen et al. 2017; Garg et al. 2018), and sea currents (Munro and Burg 2017) can limit dispersal and act as barriers to gene flow. However, when assessing how geographical and topological barriers influence patterns of gene flow, it is important to keep the ecology and dispersal capacity of the species under investigation in mind. A study on Pleistocene land bridges in Sulawesi emphasizes this point: using ddRAD-seq data, the authors estimated the amount of ancient gene flow between the island populations of two bird species, the henna-tailed jungle flycatcher (*Cyornis colonus*) and the golden whistler (*Pachycephala pectoralis*). During the Pleistocene, the islands Peleng and Taliabu were connected by land bridges allowing animals to disperse from one island to the other. The analyses revealed little evidence of genetic exchange between the jungle flycatcher populations on Peleng and Taliabu, whereas there had been gene flow between island populations of golden whistler. The differences in gene flow dynamics probably depended on the ecology of the species: the jungle flycatcher is a specialized bird with poor dispersal capacities and does not venture outside forests often. The golden whistler, however, is a generalist that tends to explore new territories (Garg et al. 2018). Similarly, research on the role of Amazonian rivers as barriers to gene flow has culminated in contrasting results: some studies report clearly separated populations on each side of the river (Maldonado-Coelho et al. 2013; Fernandes et al. 2014), while other studies documented gene flow at headwaters (Weir et al. 2015; Sandoval-H et al. 2017). In summary, what might be a barrier for one bird species is not necessarily a barrier for another one.

6 Selection

Species are continuously adapting to ever-changing environments (Dobzhansky 1940; Bush 1975; Orr and Smith 1998). Genetic differences that arise through mutation or enter a population by gene flow result in populations of individuals with subtle morphological, ecological, or other differences (Coyne and Orr 2004). It is this diversity that selection works with, and thus these differences among individuals often dictate the "adaptability" of a species or population (Barton and Hewitt 1989; Orr 2001). Specifically, selection favors morphological, ecological, or other traits that increase survival and fecundity of an individual in a particular niche space (Fischer 1930; Price 1998; Rundle and Nosil 2005; Via 2009; Sobel et al. 2010; Wolf et al. 2010). In fact, it was in 1859 that Charles Darwin determined that the composition of a population or species changes (or evolves) due to the differential survival of individuals in varying environments and coined the responsible force as "natural selection" (Darwin 1859). Thus, evolution proceeds through the selection of traits that provide a competitive advantage, consequently increasing mating success. Finally, since Charles Darwin established natural selection as a dominant force in the evolutionary process, there has been a refinement regarding the types of selection. For example, the elaborate feathers and mating displays of birds are classical examples of sexual selection (Lande 1980; Andersson 1994; Johnsgard 1994; Promislow et al. 1994; Grant and Grant 1997; Price 1998; Clutton-Brock 2007; Krakauer 2008). In such a case, sexual selection confers higher mating success for the displaying sex despite any negative impact the trait may have via natural selection (i.e., predation).

Given that the number and survival of new mutations is largely dictated by population size (i.e., more mutations enter and are maintained in larger populations), selection is most effective in large populations (Ohta 1972, 1992; Gillespie 2001; Ellegren 2009), whereas genetic drift will dominate in smaller populations (Sect. 4). Thus, the probability of beneficial mutations to be lost due to genetic drift increases as population size becomes increasingly small. Due to a lag effect on the influence from selection on traits and associated genetic variation, the majority of new mutations are often lost due to genetic drift as a result of their naturally low frequency within any population if the selection favoring the new mutations is not very strong (i.e., relatively small selection coefficient s). In short, higher individual diversity increases the probability that a species survives challenges, such as changes affecting their current environment or when invading novel niche space (Turelli et al. 2001; Wu 2001; Coyne and Orr 2004). For example, a species that is comprised of largely clonal individuals (i.e., low genetic diversity) has little chance to survive new ecological or other challenges because none of the individuals have variants that would confer an adaptive response. Such scenarios are often an important issue for endangered or highly specialized taxa with small population sizes or ranges (e.g., islands) (Dickerson 1973; Templeton 1986; Lacy 1987; Hughes et al. 1997; Oyler-McCance et al. 1999; Mock et al. 2004). Captive breeding programs often need to contend with this issue (Elsbeth McPhee 2004; Fraser 2008; Cassin-Sackett et al. 2019). Conversely, a species comprised of a diversity of individuals is more likely to

have a proportion of individuals that may have the (genetic) variation necessary to survive the same challenges.

The emerging field of population genomics has revealed compelling evidence that directional selection, balancing selection, purifying selection, and hitchhiking are pervasive throughout the genome, causing widespread departures from neutral models (Hahn 2008; McVicker et al. 2009; Charlesworth 2012; Burri 2017a). Thus, in addition to variance in mutation (Sect. 3) and recombination (Sect. 7) rates, as well as differential gene flow (Sect. 5), the variance in selection also contributes to the heterogeneous nature of genomes. Importantly, just as with the other evolutionary forces, selective processes leave traceable signatures across the genomes of populations that researchers are now able to discern between (Wu and Ting 2004; Sabeti et al. 2006; Wolf et al. 2010; Schoville et al. 2012; Keller et al. 2013; Wray 2013; Seehausen et al. 2014; Andrews et al. 2016; Van Belleghem et al. 2018). Often, these genes or genetic regions are "needles in a haystack," and thus, increasing genomic coverage is essential for their discovery. Once a limitation by standard Sanger sequencing methods, the genomic era now enables researchers to attain sufficient genomic coverage required when searching for regions under selection in a genome (Kraus and Wink 2015; Jax et al. 2018b). Thus, by accessing larger portions of the genome, researchers are able to (1) determine how selection has operated in the evolution of their taxonomic system, (2) find important genes associated with adaptive traits in their systems, and (3) distinguish between differing selective signatures.

The identification of putative genes or genetic regions under selection is often accomplished through "genomic scans" in which markers are compared between taxa of interest with various summary statistics, such as relative (e.g., F_{ST}, Φ_{ST}) and absolute (e.g., d_{XY}) genetic divergence, as well as other measures of genetic diversity (e.g., pairwise nucleotide diversity π, Tajima's D). For example, conducting these genomic scans across ~3500 ddRAD loci, Lavretsky et al. (2015) were able to demarcate putative outliers (demarcated as regions of elevated genetic divergence) on the Z-sex chromosome and several autosomal chromosomes that may be linked to genes important in the divergence process between mallards and Mexican ducks (Fig. 2). Additionally, advances in Bayesian and maximum likelihood methods capable of analyzing large genomic datasets now allow researchers to assign statistical significance to each outlier (Pérez-Figueroa et al. 2010; Feng et al. 2015). In short, these programs often test each marker by comparing it to the overall genomic background to determine their statistical significance. For example, genomic scans and statistical tests revealed that the evolution of high-elevation adaptation for several Andean birds was due to the simple effect of positive selection on amino acid changes in hemoglobin for higher oxygen affinity (McCracken et al. 2009; Natarajan et al. 2015).

Sex-linked markers have been particularly interesting, as these have often been found to have significantly higher divergence patterns as compared to autosomal and/or mitochondrial markers. These patterns are especially detectable when speciation is at the earliest stage (Haldane 1948; Frank 1991; Reeve and Pfennig 2003; Phadnis and Orr 2009) and have been documented in birds (Minvielle et al. 2000;

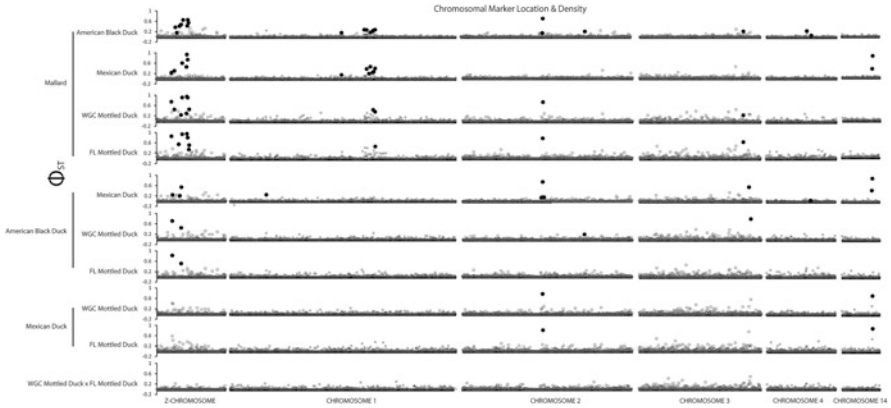

Fig. 2 Distribution of Φ_{ST} values for chromosomes containing significant outliers (chromosomes Z, 1, 2, 3, 4, and 14) for pairwise comparisons between mallards (MALL), American black ducks (ABDU), Mexican ducks (MEDU), Western Gulf Coast mottled ducks (MODUWGC), and Florida mottled ducks (MODUFL). Black dots denote markers identified to be putatively under diversifying selection in each pairwise comparison when analyzed in BayeScan v. 2.1 (Foll and Gaggiotti 2008). Such comparative analyses provide the opportunity to identify in which species divergent selection may be occurring in. For example, the outlier region within an ~11 Mbp region (1.0×10^8–1.2×10^8 bp) on chromosome 1 was found when comparing mallards to each of the monochromatic taxa, suggesting divergent selection occurring in mallards. Similarly, an outlier locus on chromosome 14 (position ~1.6×10^7; also see Lavretsky et al. 2015) was detected in all four comparisons involving Mexican ducks, suggesting directional selection at this or a linked locus in Mexican ducks only. The figure was adapted from Lavretsky et al. (2019)

Saether et al. 2007; Pryke 2010), insects (Phadnis and Orr 2009; Martin et al. 2013), and mammals (Tucker et al. 1992; Sutter et al. 2013). For example, important reproductive isolation mechanisms, such as male sterility, sexually selected male plumage traits, and assortative mating, have all been linked to sex chromosomes (Minvielle et al. 2000; Saether et al. 2007; Turelli and Moyle 2007; Carling and Brumfield 2009; Phadnis and Orr 2009; Pryke 2010; Abbott et al. 2013; Pease and Hahn 2013; Stölting et al. 2013). In general, recent work suggests that due to the effect of recombination on the possible breakup of coadapted genes and admixture of alleles between diverging populations via gene flow, selection is more likely to lead to the adaptive divergence of traits linked to markers found in regions of low recombination because these regions are shielded from maladaptive gene flow from other populations (Delmore et al. 2015; Samuk et al. 2017). Thus, the probability of recovering markers linked to evolutionarily important regions on sex chromosomes is likely the product of their smaller absolute and effective size, as well as higher linkage disequilibrium as compared to autosomes (Bergero and Charlesworth 2009). For example, conducting genomic scans using ddRAD-seq data between mallards and Mexican ducks, Lavretsky et al. (2015) found 2–3% of Z-linked loci, compared to <0.1% of autosomal loci as outlier loci under divergent selection. Indeed, elevated Z-differentiation deviated from neutral expectations

when simulating data that incorporated demographic history and differences in effective population sizes between marker types. In contrast, Z-linked and autosomal differentiation ($\Phi_{ST} = 0.017$ and 0.013, respectively) were similar among the seven Mexican duck sampling locations, following a scenario of genetic drift and isolation by distance. Similar to Mexican ducks and mallards, Chaves et al. (2016) found that key adaptive traits (e.g., beak size) in Darwin's finches were also associated with a few genes (11 of 32,569 SNPs) but found these putatively evolutionary important genes across multiple chromosomes. Similarly, other studies also report genetic regions involved in adaptive divergence and reproductive isolation to be scattered throughout the genome (Parchman et al. 2013).

7 Recombination

Similar to other genomic parameters, such as gene density and mutation rate, recombination rate is highly variable along a genome. Regardless of chromosome size, at least one crossover per chromosome (or chromosome arm) is required for proper segregation of homologous chromosomes during meiosis (Fledel-Alon et al. 2009; Wang et al. 2012). This obligatory crossover results in a negative correlation between recombination rate and chromosomes size because the rate is calculated as a total genetic distance (in centimorgans, cM) divided by physical size of a chromosome (in Mb). Because of the large differences in chromosome size in bird genomes (Damas et al. 2019), recombination rate is an order of magnitude different between the largest and smallest chromosomes in birds (Groenen et al. 2009; Backström et al. 2010; Kawakami et al. 2014; van Oers et al. 2014). In addition, recombination rate is also variable within a chromosome, where the rate is lower near centromeres and increases away from them (Choo 1998; Talbert and Henikoff 2010). At a finer scale, birds and several other species have small genomic regions, referred to as recombination hotspots, where the rate is often hundreds or even thousands times higher than the surrounding regions (reviewed in Stapley et al. 2017). Genomic locations of recombination hotspots appear to be conserved over tens of millions of years during bird evolution (Singhal et al. 2015; Kawakami et al. 2017). Furthermore, the pseudoautosomal region (PAR), the only recombining region on sex chromosomes in the heterogametic sex (i.e., female birds with Z and W sex chromosomes), shows an extremely high recombination rate (>700 cM/Mb) (Smeds et al. 2014). Therefore, a highly heterogeneous recombination landscape is a hallmark of avian genomes, and characterizing detailed variation of recombination rate is a necessary step toward the understanding of how genetic variation changes over time in a genome.

There are at least two ways for recombination to affect genetic variation in a given genomic region, namely, "linked selection" and GC-biased gene conversion (gBGC). As discussed in Sect. 6, positive selection removes genetic variation at a locus under selection by fixation of an advantageous allele, while negative selection (purifying or background) reduces genetic variation because new mutations in functionally important regions, such as protein-coding genes and regulatory elements, cannot increase in frequency if they have a negative effect on fitness

(i.e., deleterious mutations). Removal of variants is not restricted to target loci under selection (positive and negative); variants at neighboring loci can also be removed from a population if those neighboring loci are physically linked to the target loci (hence referred to as "linked selection") (Cruickshank and Hahn 2014; Burri 2017b). Since the extent of linkage between loci under selection and neighboring loci depends on local recombination rate, there is a significant negative correlation between genetic diversity and recombination rate (Burri et al. 2015; Vijay et al. 2017). Because recombination rate variation is likely conserved between species (Singhal et al. 2015; Kawakami et al. 2017), patterns of genetic diversity along a genome are also likely similar between species (Burri et al. 2015; Dutoit et al. 2017; Vijay et al. 2017). Evaluation of baseline genetic diversity is particularly important in genomic scan analyses because measurement of relative genetic divergence between species is a function of genetic diversity within species and, consequently, low recombination regions tend to stand out as highly differentiated outlier regions even without direct involvement in the process of speciation.

Second, gBGC is a neutral, recombination-associated process that can leave a similar genetic footprint as positive selection by distorting the allele frequency distribution. Recombination is initiated by the formation of DNA double-strand breaks (DSBs), which are subsequently repaired as crossovers or noncrossovers. When crossovers occur, there is reciprocal exchange of DNA between homologous chromosomes (Fig. 3). During these repair processes, G or C nucleotides are preferentially transmitted over A or T nucleotides in regions close to DSBs with G:C and A:T base mismatches between paternal and maternal chromosomes (Duret and Galtier 2009; Mugal et al. 2015). Since gBGC takes place more frequently in regions experiencing frequent DSBs and recombination, highly recombining regions are more strongly affected by gBGC with stronger transmission bias toward G:C

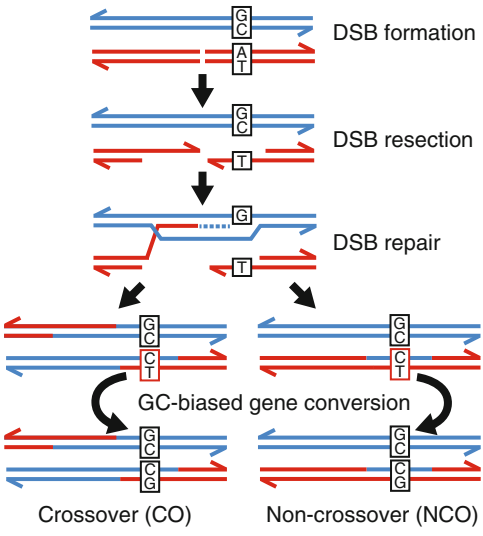

Fig. 3 DNA double-strand breaks (DSBs) are repaired as either crossovers (COs) or noncrossovers (NCOs). GC-biased gene conversion (gBGC) results from biased incorporation of GC over AT nucleotides in regions close to DSBs with base mismatches between paternal and maternal chromosomes (red and blue)

nucleotides. While positive selection increases allele frequency of "better-fit" alleles by virtue of their selective advantages, gBGC spreads G:C alleles independent of their effect on fitness. This causes a serious challenge in detecting a signature of selection because the strong effect of gBGC in high recombination regions can drive the fixation of potentially deleterious G or C alleles and, hence, counteract natural selection. In addition, the skewed allele frequency distribution by gBGC relative to neutral expectation can also affect inferences of demographic history and natural selection based on various population genetic statistics (Bolívar et al. 2018; Pouyet et al. 2018). Altogether, we must estimate the baseline genetic diversity by taking into account the effect of linked selection and gBGC in order to infer demographic history and detect signatures of selection (Mugal et al. 2015). Forward simulation approaches that take into account the variation of recombination rate, gene density, background selection, and demographic events can provide analytical framework to simulate genome-wide patterns of genetic diversity and divergence, with which an empirical data can be compared in order to detect outlier regions (Comeron 2017). In addition, machine learning approaches can jointly estimate effective population sizes and the impact of linked selection (both background selection and selective sweep) on the pattern of genetic diversity (Schrider and Kern 2016, 2018; Schrider et al. 2016; Sheehan and Song 2016).

8 Phylogeography: The Interface Between Population Genetics and Phylogenetics

The early study of mitochondrial DNA lineages when PCR and DNA sequencing became available (Wink 2019) revealed that branches of intraspecific gene trees often followed striking geographic patterns (Avise et al. 1987). The study of the relationship between gene genealogies and geography became known as phylogeography (Avise 2000). Some early examples of phylogeographic studies on avian mtDNA include snow goose (*Anser caerulescens*) (Avise et al. 1992; Quinn 1992), northern flicker (*Colaptes auratus*) (Moore et al. 1991), and common grackle (*Quiscalus quiscula*) (Zink et al. 1991). Phylogeography provides a bridge between phylogenetics (i.e., the reconstruction of evolutionary relationships) and population genetics, describing how genetic variation—introduced by mutation (see Sect. 3)—is geographically structured within and between populations by population genetic processes, such as genetic drift (see Sect. 4), gene flow (see Sect. 5), selection (see Sect. 6), and recombination (Sect. 7). For populations that have been separated historically and have experienced little or no gene flow, genetic differences can accumulate by these evolutionary processes, potentially resulting in speciation (Ottenburghs 2019).

Phylogeography relied heavily on non-recombining and rapidly evolving mtDNA to match gene genealogies with geography (Avise 2000). The advent of genomic data in combination with the development of coalescent theory (Kingman 1982a, b) has revolutionized the field (Edwards et al. 2015). In general, the application of next-generation sequencing technologies uncovers more detailed population structure that

is often missed by traditional markers, such as mtDNA and microsatellites. For example, using RADseq data, Ruegg et al. (2014) were able to more reliably distinguish between eastern and western populations of the Wilson's warbler (*Cardellina pusilla*) compared to previous studies based on mtDNA (Kimura et al. 2002; Paxton et al. 2013) and AFLPs (Irwin et al. 2011). In addition, the application of multilocus datasets revealed that different genes often result in different gene trees (Degnan and Rosenberg 2009). This phylogenetic incongruence can provide a more detailed picture of population history because different gene trees capture particular historical events and population genetic processes that have shaped the present patterns of genetic diversity. However, recent work has also uncovered high levels of reticulation due to recombination (see Sect. 7) and gene flow (Edwards et al. 2016). New statistical methods are being developed to deal with such reticulated scenarios (Dai et al. 2010; Ottenburghs et al. 2017a; Zhu et al. 2018).

9 Conclusions and Outlook

In this chapter we mostly dealt with questions relating to which inferences we can make from genetic variation data on a population scale, with respect to what we know about geological events as well as current and past geography. Traditionally, the study of phylogeography has a strong focus on demographic processes and distribution of genetic variation in time and space. The introduction of genomic techniques dramatically increases the statistical power with which we can answer questions and describe systems. In sections about the source, maintenance, and loss of genetic variation, we introduced the concepts of natural and sexual selection. This, in contrast to neutral variation that is shaped by demography, is the second and perhaps more innovative major addition that population genomics brings us compared to population genetics.

Measuring genetic variation everywhere in the genome, including both neutrally and adaptively evolving regions, allows us to understand demography and adaptation concurrently. Studies into the functional variation have so far only been possible on the interspecies level. Many studies in the past have analyzed the evolutionary history of genes known to be involved in key adaptations of a certain lineage. For instance, innate immunity in birds is well studied on the avian lineage scale. Cheng et al. (2015) deciphered evolutionary signals in effector molecules of the immune defense such as defensins and cathelicidins, and Velová et al. (2018) studied membrane proteins that control the identification and recognition of pathogens, the toll-like receptors. However, from our point of view, the really interesting studies are those taking into account the population approach and using population genetic theory to measure selection pressure. The first toll-like receptor population re-sequencing paper on wader species revealed purifying selection and domain-specific evolution (Raven et al. 2017). This was not a genome-wide study and lacked comparative information from a number of related genes, so the final conclusions remain tentative, but such studies are important next steps in understanding the relationship between functional and adaptive variation and offer a glimpse of what

may become possible in the future. A similar study on bird species with rather different phylogeographic histories curiously rejected the impact of natural selection (here, supposedly pathogen pressure) on the molecular evolution on this receptor family. Instead, the authors found that drift in small populations overrides the effects of natural selection (Gonzalez-Quevedo et al. 2015) as is expected on theoretical grounds under such conditions (Lynch 2007). Chapman et al. (2016) studied several toll-like receptor genes both on the lineage and population scale to place their evidence for diversifying selection into the broader evolutionary framework. Yet, the individual gene was studied in isolation from the rest of the genome. Whole-genome information on a population scale will make possible the study of selection patterns and their interaction with phylogeography, as the costs of sequencing continue to decline (Kraus and Wink 2015). New approaches to study functional variation not only within gene families (gene-centric) but also within and across biological pathways (pathway-centric) are now becoming possible. Jax et al. (2018a) showcase interactions between the functional variation and molecular evolution of more than 100 genes across several immune pathways in mallards and closely related ducks around the world and their geographic origin. The future development of population genomics might thus culminate in a more functional approach to avian evolution.

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