

Seeing the whole picture: What molecular ecology is gaining from whole genomes

1 | INTRODUCTION

Whole genome sequences are rapidly becoming the marker of choice in molecular ecology. We attribute this partly to factors such as decreasing sequencing and library preparation costs. Yet, of greater consequence is the increase in information content over most reduced representation library (RRL) based methods. Whole genome sequencing (WGS), depending upon strategy (e.g. low or high coverage), theoretically generates *all* the markers. For example, rare alleles, which form the basis of many site frequency spectrum (SFS) based statistics and downstream demographic inference, are sampled in WGS whereas many will be missed by RRL methods (Figure 1a). Similarly, all genealogies are sampled in WGS (Figure 1a), which can be key for detecting minor ancestry components (e.g. Neanderthal ancestry in modern human populations). The contiguity between markers provided by WGS data is then informative of the age of distinct ancestry segments (when recombination maps are available), based upon the length of such segments. Contiguity and marker density provide increased resolution of the genomic landscape, and the detection and length estimates of features such as runs of homozygosity (ROH), targets of selection indicated by elevated metrics such as F_{ST} , and structural variation such as inversions (Figure 1a). Beyond such patterns are the inferences that can be drawn on causal or consequential processes, such as admixture, drift and demographic shifts, recombination, or selection. In this special issue of *Molecular Ecology*, we aim to showcase an array of studies that leverage the resolution of WGS to provide new insights into the molecular ecology of a range of species and ecosystems.

This special issue started life as a symposium planned for the 2020 Canadian Society for Ecology and Evolution and organised by Evelyn Jensen (Yale University and Newcastle University), Rebecca Taylor (Trent University) and Namrata Barai (CGEn). However, '2020' had other plans, and like many meetings the CSEE meeting was cancelled due to the COVID19 pandemic. Searching for another outlet for discussing the role of whole genome sequencing in ecology and evolutionary studies, the idea of a special issue was born. After a call for expressions of interest generated over 100 proposals, it soon became clear that there was an appetite for such a volume. Indeed, at one point we were contemplating a special trilogy rather than a singular issue. However, likely also due to the strains of home officing, laboratory and institutional shutdowns, supply disruptions and other COVID-related restrictions in 2020, the final list of articles reduced to fit a single volume special issue. However, this issue is

brimming with exciting and novel content, as the breadth and quality of the articles we present are testament to the value and utility of WGS. Here, we direct readers to potential articles of interest within the sub-disciplines of molecular ecology, which include inference of adaptation, demographic history, introgression, structural variation and new methods proposed to analyze WGS data.

2 | METHODOLOGICAL APPROACHES AND ADVANCES FOR WGS

Much of the reason behind the increasing utility of WGS for molecular ecology research, aside from reducing sequencing costs, are the increasing number of technologies and analytical pipelines to sequence, assemble, and analyse whole genome data. The first series of papers included in this special issue tackle some crucial aspects of the recent and methodical advances, as well as highlighting important future considerations.

As we have noted, contiguity is a key asset in the information content of whole genome sequences versus RRL methods, and contiguity can be inferred at chromosomal scales through the assembly of short- and long-read sequence data, and scaffolded using Hi-C data. Yamaguchi et al. (2021) discuss the role of Hi-C data in allowing chromosome scale genome assemblies to be widely available in non-model organisms without available linkage maps, and present a detailed description of the Hi-C method and provide important technical considerations.

Blom (2021) addresses the increasing availability and advantages of long-read sequencing within the field of molecular ecology, and the potential of reference-free assemblies for multiple individuals of a species for a better representation of the full genetic variation within and between populations. A major focus of this review, however, is on the urgent need to collect and preserve high-quality samples given drastic global biodiversity declines. Blom (2021) includes a call for support to ensure interdisciplinary collaborations and increased funding for field biologists, genomicists, and Natural History Collections, to ensure the variation underlying contemporary biodiversity can be available as a resource for future research.

Wold et al. (2021) advocate for the characterization of structural variants (SVs) in conservation genomic studies given their high frequency within the genome and that they are more likely than individual SNPs to overlap with regions of the genome impacting fitness. They discuss SV discovery-based methods from both short- and

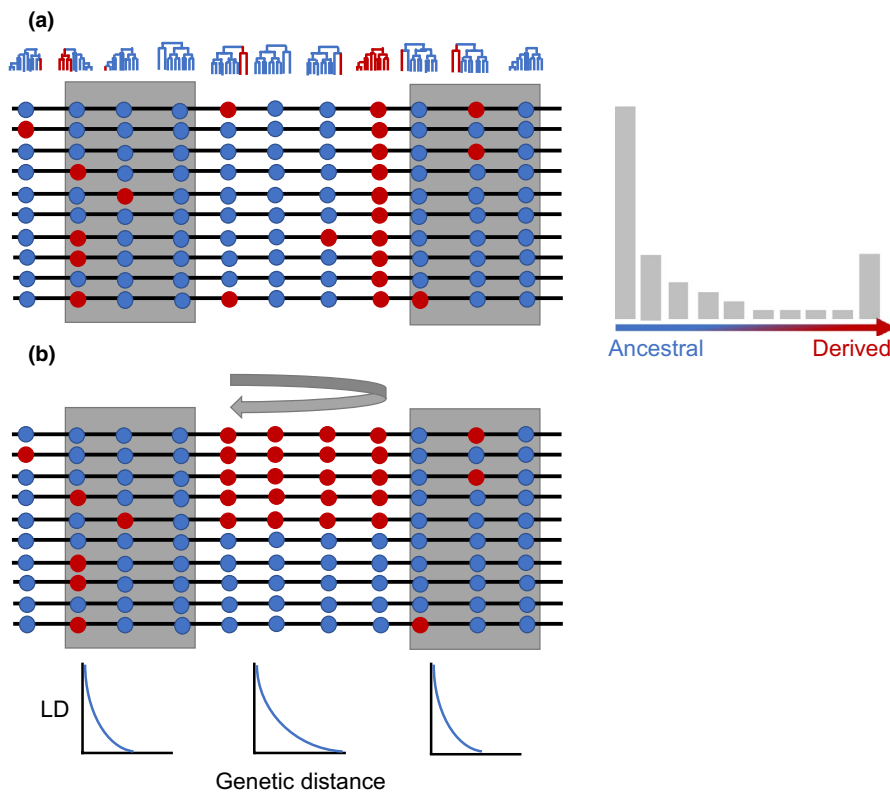


FIGURE 1 (a) Schematic figure of 10 haploid genomes sampled through WGS or RRL (markers within grey boxes). WGS samples the full diversity of genealogies and allele frequency spectrum, whereas rare variants will not all be sampled using RRL. (b) WGS also provides increased resolution of contiguity, linkage and marker density, which increase the probability of detecting genomic landscape features such as structural variants (e.g. inversions, as represented in the schematic), runs of homozygosity and outlier peaks in F_{ST} or other metrics

long-read sequencing data, and describe the advantages of generating a pangenome, or the characterization of variation within the group or species of interest rather than relying on one reference genome, a concept also promoted by Blom (2021).

A key constraint to sequencing population-level datasets has been the associated costs. However, the development of suites of methods that infer genotype likelihoods to account for uncertainty has resulted in increasing popularity of low-coverage whole genome sequencing (lcWGS). Lou et al. (2021) give a detailed road-map outlining the theory and advantages behind lcWGS in population genomics. The authors outline the costs of generating lcWGS in comparison to other commonly used sequencing strategies (e.g. RAD-seq), and the increasing number of analyses which can be performed with low coverage data within a probabilistic framework. By making scripts available for a suite of analyses from raw data onwards, the authors make this a highly valuable resource for anyone new to lcWGS data.

Lou et al. (2021) are not the only authors to demonstrate advantages of WGS over RRL strategies. Both additions to the special issue by Szarmach et al. (2021) and Duntsch et al. (2021) directly compare the performance of whole genome sequencing to RRL using empirical datasets. In the case of Szarmach et al. (2021), the divergence landscape as measured by the commonly used F_{ST} sliding window approach is compared using whole genomes, GBS, and ddRAD-seq data from yellow-rumped warblers. ddRAD-seq data was found to be the least cost effective and unable to capture the heterogeneous divergence landscape between subspecies, with WGS data giving superior resolution overall when compared to GBS. Duntsch et al. (2021) focus on measuring inbreeding in the New Zealand hihi using

whole genomes at different sequencing depths, RAD-seq, and SNP array genotypes. Low density markers were found to either miss runs of homozygosity (ROH) or inflate ROH lengths due to combining homozygous regions, and high levels of missing data biased ROH detection. It is also possible, however, that researchers may need to combine multiple data types. Ribeiro et al. (2021) provide a bioinformatics pipeline able to do just that, demonstrating an example using WGS and target capture data which works even in the absence of a reference genome.

As well as articles demonstrating the power and cost effectiveness of WGS for various research questions, the contribution by Bourgeois and Warren (2021) provides an exhaustive resource for those looking for available tools for population genomic analyses of WGS data. Featuring detailed discussion of methods for unravelling population structure and history as well as detecting evolutionary processes, their article features over 100 methods organised into handy summary tables. Additionally, they are maintaining a website which will be continually updated with lists of resources (www.methodspopgen.com).

The last two methodological contributions for the special issue focus on challenges which may now be addressed using WGS. Vekemans et al. (2021) address genomic regions which are problematic to assemble due to being repetitive in nature, highly heterozygous and/or divergent across individuals, but are important from an ecological and evolutionary viewpoint, named as 'special interest genomic regions' (SIGR) by the authors. Using a few key examples as case studies—the Major Histocompatibility Complex (MHC), sex-determining regions (SDRs) and the plant self-incompatibility locus (S-locus)—Vekemans et al. (2021) outline

current methods to study SGRs using new technological advances. Yoder and Tiley (2021), in contrast, highlight the power of high-coverage whole genome sequences to identify all rare variants in a genome, and how this can address the challenge of estimating de-novo mutation (DNM) rate within the germline, the process driving the generation of diversity for natural selection to act upon.

3 | INFERENCE OF DEMOGRAPHIC HISTORY

Several studies in this special issue draw inference from WGS data to gain new insights into demographic and evolutionary histories. For example, effective population size changes are inferred through time using variation in coalescent rates in individual genomes, and cross-coalescence between genomes from canids, caribou, horses, killer whales and sea turtles (see Sarabia et al. (2021); Taylor et al., (2021); Vershinina et al., (2021); Foote et al., 2021; Torres Vilaça et al., 2021 respectively). As noted by Vershinina et al., 2021, (and illustrated by Foote et al., 2021, Sarabia et al., 2021, Taylor et al., 2021 and Torres Vilaça et al., 2021), even just a few nuclear genomes can provide estimates of gene flow versus isolation, even within and among species with complex evolutionary histories.

Introgressed components within admixed ancestry can then contribute towards local adaptation, as elegantly demonstrated by Comeault et al. (2021), and the age of introgressed elements can be dated (Errbii et al., 2021). However, evolution can find other mechanisms to drive phenotypic convergence. For example, Owens et al. (2021), find limited evidence of introgression between their focal sunflower congeners, and argue that convergence arose from segregation of standing variation in the form of large inversions. Segregation of low recombining regions of ancient origins is also found in an exhaustive genomic investigation of the genomes of ~90 species spanning the *Formica* phylogeny (Purcell et al., 2021). Whole genome sequencing of different host species of *Rhagoletis* fruit flies highlighted the horizontal transfer of *Wolbachia* strains between hosts (Wolfe et al., 2021). Lastly, Santos et al. (2021) uncover a robust species tree between bighorn and thinhorn sheep, however the use of whole genomes demonstrated genealogical discordance throughout their genomes and evidence of ancient hybridization with implications for adaptation. WGS data is increasingly painting a complex picture of evolution that challenges basic bifurcating tree models.

As highlighted above and by North et al. (2021), whole genome sequences also have the advantage over RRL data of identifying rare variants. These alleles are expected to have shallower coalescence times, and so can reflect demographic histories over shorter timescales of a few generations. In a comprehensive review, North et al. (2021), encapsulate how many of the key attributes of WGS data can elucidate the demographic and evolutionary histories of invasive species over relevant timescales.

4 | CONSERVATION

In the midst of the biodiversity crisis, it is no surprise that molecular ecologists are eager to apply WGS to species of conservation concern. WGS is assisting conservation by providing conclusive assessments of population structure, which when coupled with analyses of demographic history is providing deeper understanding into how populations arrived at their present states (e.g., Iannucci et al., (2021); Jensen et al. (2021); Sarabia et al., (2021); Taron et al., (2021)). Particularly exciting insights are being gained into whether populations are newly small (i.e. recently declined), or have persisted as small over their evolutionary history; scenarios which have different implications for the expectations of genetic load. Despite documenting a dramatic loss of genomic diversity in Southern White Rhinos using temporal samples, Sánchez-Barreiro et al. (2021) found that there is no significant accumulation of genetic load. Similarly, the study by Iannucci et al. (2021) found the populations of Komodo dragons display very low diversity, even when compared to more endangered species of reptile, yet no evident signs of severe deleterious mutations. However, patterns of mutation accumulation are complex, and Jensen et al. (2021) found the rate of mutation accumulation to differ among lineages in the radiation of Galapagos giant tortoises, a surprising finding given their recent divergence.

One promising aspect of WGS analysis in a conservation context is the ability to estimate genome wide diversity in a way that is unbiased by marker choice, and comparable among species. Such estimates could then feed into conservation policy and perhaps be used to help assess status, for example with the IUCN Red List (Garner et al., 2020). Indeed, several papers in this issue specifically present a comparison of diversity within the genomes of their focal taxa to other related taxa (kea and kākā birds in Martini et al. (2021); Komodo dragons in Iannucci et al., (2021); Mexican wolves in Taron et al., (2021)). However, the diversity metrics they use for these comparisons are different (heterozygous SNPs/kbp in Martini et al., (2021), nucleotide diversity in Taron et al., (2021) and Watterson's Theta θ_w in Iannucci et al., (2021)), demonstrating that additional work is needed to achieve the full potential for WGS to provide comparability among species and studies.

Another conservation relevant aspect of genetic diversity that WGS is unlocking is the ability to discriminate between recent inbreeding and ancient coalescence via analysis of ROH. An exciting example of this is Foote et al. (2021). They combined ROH identification and analyses of changes in effective population size through time to differentiate between high background relatedness due to coalescence of haplotypes deep within the pedigree and recent inbreeding (leading to long ROH) in populations of known conservation concern. Analysis of temporal samples can also be powerful for discerning the causes of ROH, which were found to increase in maximum length, mean length and total proportion of the genome in ROH between samples pre- and post-bottleneck in both white rhino sub-species (Sánchez-Barreiro et al., 2021).

5 | GENETIC BASIS OF ADAPTATION

The origins of the diversity on earth and the changes in species through time have fascinated the general public since ancient times. But, as these evolutionary processes are associated with interactions of multiple biotic and abiotic forces, mechanistic dissection of adaptive evolution has been challenging (Charlesworth et al., 2017). The genetic basis of adaptive traits has been an elusive long-standing question in the field of evolutionary biology (Orr, 2005). But progress in such studies was always hampered by the absence of genomic perspectives and lack of marker resolution. There has been a resurgence of interest in studying the genetic basis of adaptive traits in recent times, mostly driven by the desire to integrate genomics into long-standing knowledge of natural history and organismal biology, reviewed in Lamichhane et al. (2019). Enormous progress in high throughput sequencing technologies in the last decade has allowed sequencing genomes at a population scale and generated toolkits that have facilitated the integration of ecological and genomic data for many species.

A series of papers in this special issue have utilized whole-genome sequencing approaches to explore the genetic basis of adaptive traits in a range of study systems. Montejo-Kovacevich et al. (2021) studied the genetic basis of wing shape in Neotropical butterflies and identified a highly polygenic basis to wing aspect ratio variation, emphasizing the role of polygenic adaptation in ecological traits. In a similar finding, Pereira et al. (2021) employed an experimental evolution method in F2 interpopulation hybrids of the copepod *Tigriopus californicus* to identify the complex architecture of mitonuclear incompatibilities and polygenic adaptations. Nunez et al. (2021) used northern acorn barnacles as a model to examine the genetic basis of adaptation to a highly heterogeneous environment and utilized a pooled-sequencing approach to identify genomic signatures associated with ecologically extreme microhabitats across the North Atlantic basin. Batley et al. (2021) analysed whole genomes of 53 Indo-Pacific bottlenose dolphins and identified genes associated with innate and adaptive immune responses, and cytokine signalling pathways that were exposed to highly infectious Cetacean morbillivirus (CeMV). Similarly, Moreno Santillán et al. (2021) undertook a comparative genomic study of 37 ecologically divergent bat species to explore unique immune system adaptations, and found selection on genes involved in antiviral immunity as well as gene losses related to inflammatory responses, all perhaps involved with facilitating resistance to viral infections within bat species.

There are a variety of confounding factors that generate a heterogeneous pattern of variation across the genome and thereby create a challenge in the robust identification of genomic regions associated with certain adaptive traits. DeRaad et al. (2021) utilized a genome-environment association (GEA) testing approach to leverage publicly available *Anopheles gambiae* genomes to differentiate true signals of genome environment adaptation from background variation resulting from alternative evolutionary processes. Colicchio et al. (2021) utilized similar GEA approaches using whole-genome re-sequencing data from *Mimulus guttatus* populations to identify candidate genes

associated with climatic variables in specialized metabolism, drought resistance, and development.

6 | CONCLUSION

The collection of articles within this special issue showcase some of the many applications of WGS, and demonstrate how WGS is rapidly advancing the field of molecular ecology. This progress is set to continue as sequencing technology and computational methods further advance. WGS, once restricted to model organisms, is now feasible for most taxa, and we anticipate an explosion of whole genome resources going beyond just one reference genome for each taxon.

The contributions presented in this special issue herald a new era in molecular ecology, as we anticipate that a burgeoning and widespread application of WGS will provide unprecedented insights into consequential questions in ecology and evolution. Further technological, methodological and analytical advances will enable our community to tackle deeply vexing questions in non-model systems, and may lead to the shifting of key paradigms in adaptation, speciation and conservation, as well as revealing a horizon of new questions. It's an exciting time to be a molecular ecologist!

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