Molecular Ecology

WILEY

MOLECULAR ECOLOGY

INVITED REVIEW

Population Genomics of Adaptive Radiation

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Received: 1 April 2024 | **Revised:** 26 August 2024 | **Accepted:** 12 September 2024

Handling Editor: Joanna Freeland

Funding: This work was supported by NSF Grants 2224892 and 1556963 to C.E.W. J.A.R. was supported by an NSF Postdoctoral Research Fellowship in Biology (Award 2109825). L.L.C. was supported by a Four Year Fellowship from the University of British Columbia.

Keywords: adaptation | hybridization | macroevolution | phylogenetic theory and methods | population genetics – empirical | speciation

ABSTRACT

Adaptive radiations are rich laboratories for exploring, testing, and understanding key theories in evolution and ecology because they offer spectacular displays of speciation and ecological adaptation. Particular challenges to the study of adaptive radiation include high levels of species richness, rapid speciation, and gene flow between species. Over the last decade, high-throughput sequencing technologies and access to population genomic data have lessened these challenges by enabling the analysis of samples from many individual organisms at whole-genome scales. Here we review how population genomic data have facilitated our knowledge of adaptive radiation in five key areas: (1) phylogenetics, (2) hybridization, (3) timing and rates of diversification, (4) the genomic basis of trait evolution, and (5) the role of genome structure in divergence. We review current knowledge in each area, highlight outstanding questions, and focus on methods that facilitate detection of complex patterns in the divergence and demography of populations through time. It is clear that population genomic data are revolutionising the ability to reconstruct evolutionary history in rapidly diversifying clades. Additionally, studies are increasingly emphasising the central role of gene flow, re-use of standing genetic variation during adaptation, and structural genomic elements as facilitators of the speciation process in adaptive radiations. We highlight hybridization—and the hypothesized processes by which it shapes diversification—and questions seeking to bridge the divide between microevolutionary and macroevolutionary processes as rich areas for future study. Overall, access to population genomic data has facilitated an exciting era in adaptive radiation research, with implications for deeper understanding of fundamental evolutionary processes across the tree of life.

1 | Introduction

The high-throughput sequencing revolution has fundamentally changed the research possible in many fields of evolutionary biology, and the study of adaptive radiation is no exception. Adaptive radiations, instances of rapid origination of ecologically diverse species (see Section 2), have long garnered attention in evolutionary biology because of their impressive species diversity, diverse phenotypes, and rapid diversification (Schluter and Schenk 2000; Osborn 1902). However, this very nature of what draws our attention to adaptive radiations is what has also made them difficult to study. For example, speciation events that have occurred in rapid succession and with little chance for lineage sorting are impossible to study phylogenetically without large genomic datasets (e.g., Wagner et al. 2013; Stolting et al. 2013). Likewise, studying the genetic basis for phenotypic evolution greatly benefits from genomic-scale datasets (e.g., Nakamura et al. 2021; Roberts Kingman et al. 2021; Moest et al. 2020; Aguirre et al. 2022) and is further facilitated by the ability to readily generate reference genome sequences from high-throughput sequencing and, increasingly, long-read technologies (e.g., Brawand et al. 2015; Jones et al. 2012; Dasmahapatra et al. 2012). Additionally, while the species richness of some adaptive radiations has posed a major challenge to data collection, technological advancements in DNA sequencing now allow us to collect genome-wide genetic data at the population level for many species simultaneously and have thus fundamentally changed the research that is possible in these challenging situations. These data have already facilitated great breakthroughs in the study of adaptive radiation and will continue to do so.

We here review the progress that population genomic data has enabled in adaptive radiation research and discuss perspectives for subsequent research directions based on genomic datasets. By "population genomic data", we refer to various kinds of genomic datasets which utilise intraspecific sampling of the genome to study processes in population divergence and to identify the genetic basis of phenotypic divergence (Box 1 and Table 1). We begin with a review of what is meant by adaptive radiation, in an effort to circumscribe our focus (Section 2). However, we also emphasise that many of the processes that make adaptive radiation interesting are relevant to a broad range of evolutionary situations, and thus the work discussed here also has applicability beyond research in adaptive radiations. Likewise, the knowledge of evolution we gain from studying adaptive radiations will contribute to a broader understanding in evolutionary biology: adaptive radiations are case studies for understanding the fundamental processes constraining and facilitating evolution. We focus our discussion on how population genomic data has contributed to advances in adaptive radiation research in five key areas: (1) phylogenetics, (2) hybridization, (3) timing and rates of diversification, (4) the genomic basis of trait evolution, and (5) genome structure.

Adaptive radiation is a macroevolutionary phenomenon. All definitions agree at some level that adaptive radiation is not diagnosed by the microevolutionary processes occurring within it but by the resulting patterns in diversity at and above the species level. One theme that emerges throughout the sections of

BOX 1 | What is population genomics?

Population genomics is the study of genomic data collected at the population level. The term first emerged in the late 1990's in reference to nascent efforts to study the genetic underpinnings of disease traits in human populations (Gulcher and Stefansson 1998; Siniscalco et al. 1999). The next-generation sequencing revolution opened the possibility of population genomic work to studies of non-model organisms by cost-effectively generating orders of magnitude more sequence data than traditional sequencing approaches. Thus, next-generation sequencing technologies represented a crucial step forward in being able to scale genomic work to multiple individuals within and among populations and species. Given that work on adaptive radiations by definition involves multiple species, this was a huge advancement for the field. Additionally, these technologies facilitated the sequencing of many more reference genomes, thereby allowing additional genomic work in non-model adaptive radiation systems (e.g., Brawand et al. 2015; Alföldi et al. 2011).

At first, population genomic work in non-model organisms focused on reduced-representation genomic sequencing approaches (i.e., RAD: Baird et al. 2008; ddRAD: Peterson et al. 2012; GBS: Elshire et al. 2011). Baited-capture approaches, which target a reduced portion of the genome by sequencing regions isolated through probes designed for particular genomic targets, also emerged (e.g., Faircloth et al. 2012; Lemmon, Emme, and Lemmon 2012). As sequencing costs have continued to drop with improvements in sequencing technologies, there are an increasing number of studies using population-scale whole genome data in non-model organisms (e.g., Enbody et al. 2021, 2023), in some cases facilitated by low-coverage whole genome sequencing approaches (Lou et al. 2021) and inclusion of long-read sequences to target assembly of complex genomic regions and investigate structural genomic variation (see Section 7). Emerging functional genomics approaches, which assess interactions between genes and non-coding elements in the genome, are also becoming increasingly accessible. Some other approaches use transcriptomic data (e.g., Wickett et al. 2014) as a reduced representation genomic sequencing method for phylogenomics. With appropriate sample design, these methods can assess differences in gene regulation and expression across taxa, an emerging focus of interest as we seek to understand the functional genomic implications of DNA sequence divergence (e.g., Singh et al. 2017; Zhang et al. 2019).

Population genomic work in non-model organisms has also expanded substantially thanks to the generation of high quality reference genomes for many organisms. Although this work is possible even without sequenced reference genomes using de novo assembly approaches and pipelines (e.g., Catchen et al. 2011; Eaton and Overcast 2020), annotated reference genomes greatly expand the possibilities for studying functional genomics, the genetic basis of traits, identifying regions of the genome under selection, and studying structural genomic variation.

The rapid pace of emerging sequencing technologies and their associated fields of study present promising new directions for population genomic data that will contribute to studies of adaptive radiation. There is a plethora of approaches enabled by these emerging and advancing technologies—e.g., CHIP-seq, long-read sequencing, genome editing, approaches to studying epigenomics—that are opening the door for future studies to further explore the contribution of non-coding genomic elements during rapid speciation or in the early states of ecological differentiation during adaptive radiation. Long-read technologies are making high quality genome assemblies increasingly feasible, facilitating functional genomic work and work on structural genomic variation at the population level. Genome editing technologies (i.e., CRISPR-Cas9) may especially serve to elucidate the role that key genes or genic pathways, including structural elements such as inversions, may play during the process of speciation (e.g., Rossi et al. 2024; Sommer-Trembo et al. 2024). We target our discussion in this paper to work in adaptive radiations which utilises intraspecific genomic sampling as a key component in addressing questions related to the origins, divergence, and diversity of adaptive radiations.

TABLE 1 | Some of the sequencing methods used for generating population genomic data, including examples in which each type of data have been used in adaptive radiation research.

Method	Description	Examples in adaptive radiation research
Reduced representation genomic sequencing approaches (RADseq, ddRAD, GBS)	This suite of methods target sequences that are adjacent to restriction sites located throughout the genome. This provides a genome-wide window into genetic variation, while reducing the number of targeted sequencing regions to allow for high levels of individual multiplexing	Martin and Feinstein (2014); Meier, Marques, et al. (2017); Meier, Sousa, et al. (2017)
Sequence capture approaches (RAPTURE, ultraconserved elements, exome capture, Hyb-Seq)	These methods target particular regions of the genome for sequencing by making use of "baits" to focus sequencing effort and coverage on pre-selected regions. These methods are often used for resolving deep phylogenetic splits and for degraded samples, so that sequencing effort is focused on specific pre-defined regions with high probability of sequencing	Moest et al. (2020); Weitemier et al. (2014)
RNA-seq/Transcriptome sequencing	RNA-seq captures sequence data from expressed genes. It can be used to generate whole transcriptome sequences, which can be used as a reduced representation genomic sequencing method in phylogenomics. Additionally, with appropriate sampling design it can be used to examine patterns of differential gene expression	Singh et al. (2017); Pease et al. (2016); Zhang et al. (2019); Nevado et al. (2016); Bernal et al. (2022); McGirr and Martin (2021)
Low-coverage whole genome sequencing	These methods allow whole genome sequencing, but do so at low coverage so as to enable sequencing of many individuals at low cost. Coverage is too low to allow for confident genotype calls at the individual level, so downstream analyses rely on genotype uncertainty information	Enbody et al. (2021, 2023)
Whole genome sequencing	Increasingly, whole genome sequencing is affordable enough to allow for sequencing of multiple individuals even at relatively high coverage (>20x). Thus population genomic work at the whole genome scales is increasingly common	Kautt et al. (2020); Choi et al. (2021); Richards et al. (2021); Meier et al. (2023)

this review is that the ability to collect genome-scale data at a population level facilitates research questions spanning the microevolutionary–macroevolutionary divide (Box 2). When "traditional" genetic data (e.g., Sanger sequence data, microsatellites) reinforced the separation of population genetic and phylogenetic work given that these research areas required entirely different datasets relevant to these two scales of analysis, genomic data allows us to move fluidly across these scales. The genomic datasets used to answer population genetic questions are the same datasets that in many cases can be used to address questions at phylogenetic scales. Our ability to break down the micro–macro barrier with genomic datasets presents an exciting potential for all of evolutionary biology, but particularly for research on adaptive radiations.

Throughout the paper, we highlight outstanding questions and promising future directions for population genomic research focused on adaptive radiations. We additionally focus on the research methods that address challenges faced within adaptive radiation research (Figure 1), review recent progress for key areas in model systems of adaptive radiation (Figure 2), and discuss hypothesized processes that could explain how hybridization shapes radiations (Figure 3). While our knowledge of evolution within adaptive radiations has grown considerably, these breakthroughs have a much broader application beyond adaptive radiations alone and serve to inform our knowledge of evolutionary processes more broadly across the tree of life.

2 | What Is an Adaptive Radiation?

Since Osborn's introduction of the term in 1902 (Osborn 1902), the concept of adaptive radiation has been widely embraced (Simpson 1953; Schluter and Schenk 2000; Gillespie et al. 2020), and research on adaptive radiation has advanced our understanding of many topics across ecology and evolution. Despite its widespread acceptance and empirical and theoretical focus (Gavrilets and Losos 2009), disagreements linger regarding its precise definition. Substantial effort has been dedicated to appraising the concept of adaptive radiation and detailing its origins (e.g., Givnish 1997, 2015; Schluter and Schenk 2000; Gillespie

BOX 2 | Linking micro- and macroevolution.

One fundamentally challenging aspect of studying evolution is addressing processes across hierarchical scales: how do processes at the population level influence patterns at phylogenetic scales? What are the key links between microevolutionary processes and macroevolutionary patterns? Historically, work at the population genetic level has used entirely different genetic markers than work at the phylogenetic level; this disconnection in data has reinforced a divide across these scales of study. With recent technological revolutions in DNA sequencing, we are now in an era in which large-scale DNA sequencing is feasible, and the data we collect at the population genetic level are the same that can be used to reconstruct phylogeny. Genomic data themselves thus have the potential to act as a bridge connecting microevolutionary and macroevolutionary questions.

Macroevolution is broadly defined as "evolution above the species level" and focuses on understanding the origins of differential diversity among clades and geographic regions (Futuyma and Kirkpatrick 2022). Adaptive radiation is fundamentally a macroevolutionary phenomenon: radiations are often hypothesized to possess innovations which may underlie their shifts in diversification rate (Simpson 1945, 1959; Erwin 2021; Rabosky 2017; see Section 6), and core to understanding adaptive radiation as a process is identifying factors underlying their differential diversity when compared to related clades (Gillespie et al. 2020; Yoder et al. 2010; see Section 5). Population genomic work is contributing to our understanding of both of these dimensions of adaptive radiation. Particularly for non-model organisms which comprise most adaptively radiating taxa, population genomic data are facilitating work on the genetic basis of traits and trait evolution (see Section 6). This work holds promise for making great strides into understanding how the genomic architecture of traits may relate to their evolutionary dynamics and impacts on diversification (see Section 7). Likewise, population genomic data pose exciting new possibilities for studying links between population genetic processes and macroevolutionary patterns.

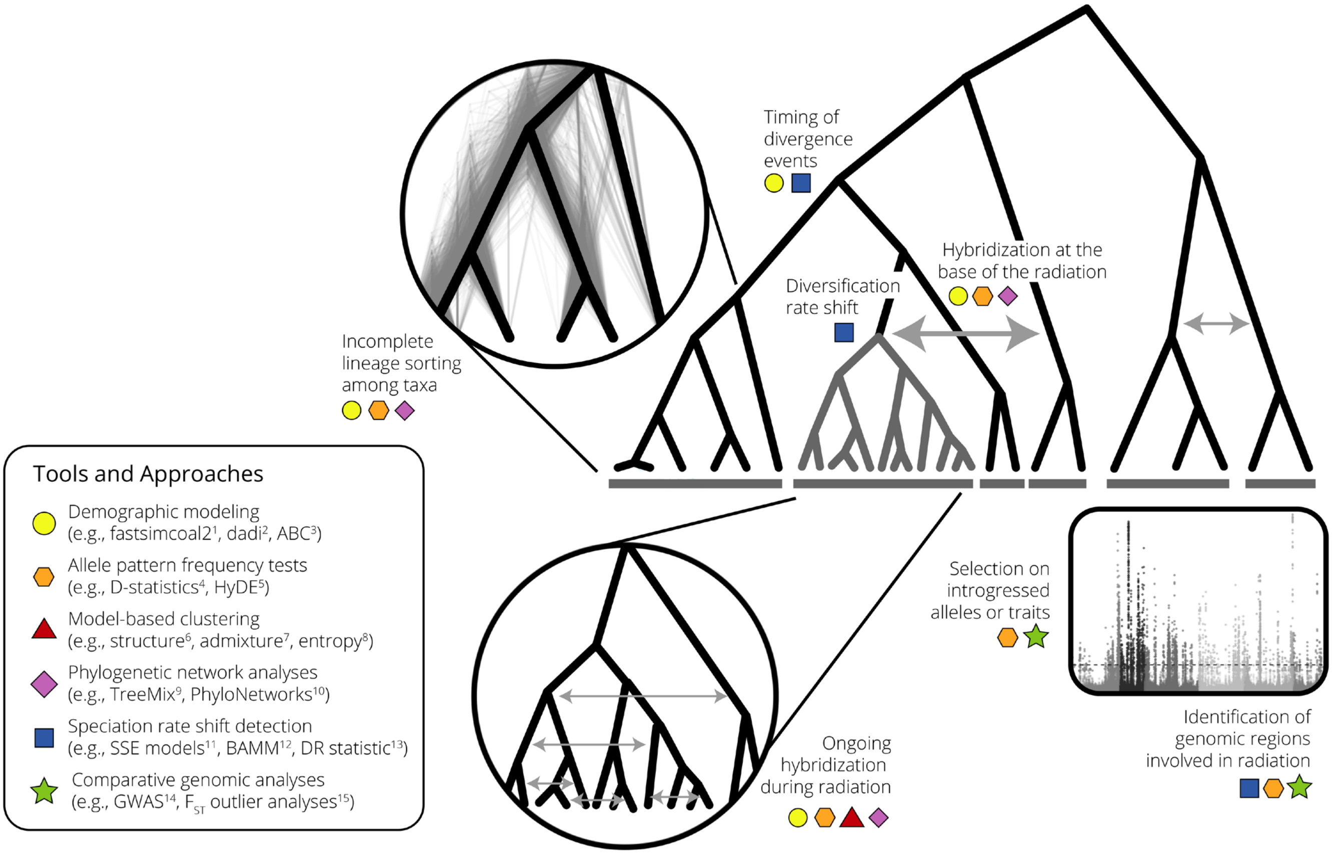
Population genetic variation may impact a lineage's propensity to diversify in various ways. Genetic variation may limit adaptive potential and influence clade diversification dynamics (Dobzhansky 1937; Lloyd and Gould 1993). Additionally, the arrangement of genetic variation across the landscape, and degree of genetic isolation between spatially differentiated populations, may impact the propensity for a lineage to split (e.g., Vrba and Gould 1986). Alternatively, species with highly fragmented populations may be more likely to go extinct, negating the impact of high population structure on realised diversification rates even if speciation rates are increased (Jablonski 2008). In general, increasing attention is needed on the demographic controls on speciation, including the propensity for lineage splitting, but also persistence of newly diverged populations through time, as well as dynamics of the evolution of barriers to gene flow (Harvey, Singhal, and Rabosky 2019). Being able to collect high-resolution genomic data at the individual level for many populations and species thus represents a key advance in the ability to test such long-hypothesized but infrequently tested relationships between microevolution and macroevolution. These data allow us to simultaneously infer genetic variation, patterns of spatial genetic structure, and phylogenetic relationships that feed into the inference of speciation rates. New and emerging work is starting to provide such tests (Riginos et al. 2014; Harvey et al. 2017; Singhal et al. 2022), and although these studies have rarely included adaptive radiations (but see Singhal et al. 2018), adaptive radiations present particularly exciting case studies with which to test these relationships by nature of their exceptional diversification.

Additional potential for linking microevolutionary and macroevolutionary scales arise in the effort to link community ecological processes to diversification (e.g., Weber et al. 2017; Hembry and Weber 2020). Attempts in this area include mechanistic modelling at the community level that builds predictions about genetic diversity and diversification (e.g., Overcast et al. 2021). Modelling frameworks such as this rely on high resolution genomic data collected from many individuals at the whole-community level.

Finally, understanding the processes contributing to adaptive radiations provides opportunities to link mechanisms across scales of hierarchical organisation. For example, loci derived from historical hybridization may provide functional diversity important for subsequent adaptive radiation (e.g., Figure 3; Meier, Marques, et al. 2017). Hybridization at the base of a lineage has long been hypothesized to provide important genetic variation to facilitate adaptive radiation (e.g., Seehausen 2004), but compelling tests of this hypothesis have only begun to emerge with large genomic datasets (e.g., Stankowski and Streisfeld 2015; Meier, Marques, et al. 2017; Irisarri et al. 2018; Box 3).

et al. 2020), and we defer to these works for in-depth discussions of these topics. For this review, we take an intentionally permissive view of adaptive radiation, considering cases of adaptive radiation broadly as clades with multiple ecologically differentiated species with recent common ancestry. We focus on cases that previous work has viewed through the lens of adaptive radiation. However, we also here briefly circumscribe the main themes and difficulties surrounding definitions of adaptive radiation.

Conceptualizations of adaptive radiation frequently feature some combination of three themes (Glor 2010; Schluter and Schenk 2000; Givnish 1997): (1) multiplication of lineages from a common ancestor, (2) an expansion of ecological diversity and associated phenotypes, and (3) notable diversification rate. The first theme involves the splitting of an ancestral lineage into multiple daughter lineages and can be diagnosed using phylogenetic tools with increasing ease given rapid advancements in the generation of genomic data and phylogenetic and species delimitation methods. The second theme represents the "adaptive" component of adaptive radiation. Ecological disparity in adaptive radiation is typically thought to evolve via natural selection and competition for resources, which results in phenotypic differentiation as species adapt to contrasting environments (Schluter and Schenk 2000). This process is promoted by ecological opportunity—either through the existence of accessible but underused niche space (e.g., a species colonises a vacant island) or an evolutionary innovation that facilitates the exploitation of resources that hitherto were inaccessible (Schluter and Schenk 2000). The most widely used criterion for estabilishing the adaptive component of adaptive radiation, proposed by Schluter and



[1]Excoffier et al. 2013 • [2]Gutenkunst et al. 2010 • [3]Approximate Bayesian computation, reviewed in Csilléry et al. 2010 • [4]Green et al. 2010 • [5]Blischak et al. 2018 • [6]Pritchard et al. 2000 • [7]Alexander et al. 2009 • [8]Gompert et al. 2014 • [9]Pickrell and Pritchard 2012 • [10]Solís-Lemus et al. 2017 • [11]State-dependent speciation and extinction, reviewed in Ng & Smith 2014 • [12]Rabosky 2014 • [13]Jetz et al. 2012 • [14]Genome-wide association studies, reviewed in Hirschhorn & Daly 2005 • [15]Reviewed in Narum & Hess 2011

FIGURE 1 | Examples of current tools and approaches used to characterise the evolutionary history of adaptive radiations using population genomic data. For each process, references indicate examples of approaches that can be used to infer the evolutionary processes contributing to patterns observed in the population genomic data. Methods are further detailed in Box 4, and the different hybridization hypotheses are elaborated on in Figure 3.

Schenk (2000), examines the utility of traits within an environmental context to build a case for their adaptive value, thus suggesting that adaptive evolution allowed individuals to expand into novel niches. The third theme, notable diversification rate, has received the most debate regarding its inclusion in defining adaptive radiation. Many authors include a burst of diversification in their definitions or suggest that elevated diversification is frequently associated with adaptive radiation (e.g., Simpson 1953; Schluter and Schenk 2000; Naciri and Linder 2020). Others object to the inclusion of elevated diversification and argue that the pattern of ecological disparity within a multiplying lineage should be the focus and that the rate of diversification (the "explosive" nature of diversification in some lineages) should be considered separately (Givnish 1997, 2015; Losos and Mahler 2010).

Circumscribing adaptive radiation becomes even more complicated when examining the potential defining features in more detail. One issue is that these features exist on continua, and thus it is unclear how to demarcate a meaningful threshold for the number of species, degree of ecological disparity, and rate of diversification necessary for a lineage to be considered an adaptive radiation. This well-recognised dilemma has led to two reactions. First, some have called for the abandonment of the concept as a construct that has outlived its utility (Olson and Arroyo-Santos 2009). Others have accepted the ambiguity that can arise when classifying lineages as adaptive radiations but argue that the term should be reserved for lineages considered to possess remarkable diversity (Losos and Mahler 2010) and have diversified "rapidly and interpretably" (Grant 2013). Additional complications emerge with the recognition that a variety of evolutionary routes can potentially lead to the same archetypal pattern in which several ecologically differentiated species share recent common ancestry (Rundell and Price 2009).

In this review, we consider our intentionally permissive view of adaptive radiation as constructive for two reasons. First, it is clear that manifold processes and factors can underpin the same pattern ascribed to adaptive radiation. Similar to Losos and Mahler (2010), instead of taking a narrow stance on what drove diversification in order for it to be deemed an adaptive radiation, we consider it more productive to focus on the general pattern (e.g., notable species and/or ecological diversity that often arises in rapid succession) and use the underlying complexity to frame hypotheses about the drivers of adaptive radiation. For example, instead of including the correspondence of speciation and ecological divergence as a defining criterion (Rundell and Price 2009), we can ask how often these two phenomena co-occur in lineages that exhibit the pattern of adaptive radiation. Second, and more pragmatically, we recognise that it is often difficult to comprehensively assess the criteria that have been proposed to identify

BOX 3 | Combinatorial mechanisms.

As recently formed species are increasingly investigated with genomic data, a growing body of research suggests that genetic variation that arose well before the onset of speciation ("old genetic variation") can play a key role in speciation and diversification. An emerging idea from this work is that old genetic variation and the sorting of this variation into new combinations ("combinatorial mechanisms") can prompt rapid speciation (Marques, Meier, and Seehausen 2019). This idea is gaining substantial traction as an explanation for the observation that incipient diversity arises quickly in many adaptive radiation systems.

Combinatorial mechanisms can foster radiation in several ways (see Figure 3). At the phenotypic level, new combinations of existing genetic variants can create phenotypes outside the observed range of either parental species in a phenomenon called transgressive segregation (Seehausen 2004; Bell and Travis 2005). Theory and simulations predict that transgressive traits should be most effective at promoting adaptive radiations when hybridization is accompanied by vacant ecological niches, such as after an environmental disturbance (Seehausen 2004; Kagawa and Takimoto 2018). Recombining ancient alleles with standing variation in a population can also sort genetic incompatibilities into new viable combinations: mixing partially incompatible lineages may generate many unfit hybrids, but may eventually create new and viable combinations of alleles that are reproductively isolated from parental combinations (Schumer et al. 2018; Powell et al. 2020; Moran et al. 2021). Another potential mechanism involves linkage of co-adapted gene complexes into haplotypes with large effect on ecologically-relevant phenotypes. If the breakdown of these haplotypes can be prevented by fixing them in an emerging species or by reducing recombination (e.g., via inversions, such as in *Rhagoletis*; Feder et al. 2003), theory predicts that they can be selected for (Ishii and Charlesworth 1977; Nei and Li 1980). These combinatorial mechanisms can work alone or in concert to produce reproductive isolation, even in sympatry and on evolutionarily short timescales.

Population genomics can help identify the role of combinatorial mechanisms by characterising the distribution of sequence divergence times and phylogenetic relationships within radiations across the genome (Figure 1). Sliding window analyses do this by identifying differences in sequence divergence (d_{xy}) or phylogenetic relationships between species in different genomic windows (e.g., Martin and Van Belleghem 2017). For example, in *Heliconius* butterflies genome scans revealed that introgression of regions flanking a wing pigmentation controller likely facilitated the origination of two lineages by enabling them to express novel pigmentation phenotypes (Enciso-Romero et al. 2017). Additionally, although identifying genetic incompatibilities remains challenging, population genomic tools can aid in identifying these loci in some situations (Schumer et al. 2018; Powell et al. 2020), a first step toward clarifying their role in speciation mechanisms. Such analyses, employed in the study of adaptive radiations, could provide evidence for the syngameon hypothesis (sensu Seehausen 2004, see Section 4) in demonstrating the functional role of ongoing hybridization.

adaptive radiation (e.g., Schluter and Schenk 2000), which has led to surprisingly few systems fully satisfying these criteria (Gillespie et al. 2020). More generally, we feel that systems can still offer valuable insights into questions of adaptive radiation regardless of whether they have explicitly been demonstrated as satisfying particular criteria. Indeed, a key theme of this paper is that adaptive radiations are interesting because of the perspectives they offer on the processes constraining and facilitating evolution generally.

3 | Phylogenomic Approaches in Adaptive Radiation

The evolutionary process is commonly modelled as serial bifurcations that give rise to new lineages, and the estimation of phylogenetic relationships is a central goal of evolutionary biology. Because of the rapid diversification characteristic of many adaptive radiations—combined in some cases with high species richnesses, which can hamper obtaining complete taxon sampling—radiations have posed some of the most persistent challenges to phylogenetic reconstruction. However, high-throughput sequencing methods (Table 1) have revolutionised the amount of data available for phylogenetic studies (reviewed in Delsuc, Brinkmann, and Philippe 2005; Bravo, Schmitt, and Edwards 2021). Large genomic datasets have now helped resolve relationships in recently radiating lineages and lineages that rapidly radiated in the distant past (Wagner et al. 2013; Twyford and Ennos 2012; MacGuigan and Near 2019; Olave and Meyer 2020; Nelson et al. 2021). Given the attainability of population genomic data and advancements in computational approaches, the range of taxa for which genomic data are available will continue to increase, enabling researchers to study the phenomenon of adaptive radiation across a more representative sample of the tree of life. Furthermore, the ability to collect genomic data at the population level provides novel data for disentangling mechanisms contributing to gene discordance, testing species boundaries, assessing intraspecific variation, and linking these mechanisms across hierarchical scales of biological organisation (See Boxes 2 and 4).

The examination of hundreds, thousands, or even tens of thousands of loci has become routine in the field of phylogenomics, and this requires inferring phylogenetic relationships when the history of individual loci differs (gene tree/species tree discordance; Duchene 2021). Theoretical studies have revealed that many phenomena including incomplete lineage sorting (ILS), hybridization, horizontal gene transfer, recombination, gene duplication and loss, and historical non-random mating may lead to discordance between gene and species history (Kong and Kubatko 2021). Importantly, rapidly diversifying clades may have pervasive ILS, leading to topological incongruence across the genome. Such genomic mosaicism may also result from ancient or recent hybridization (Folk et al. 2018; Kong and Kubatko 2021). Indeed, at the early stages in an adaptive radiation, the diversification process may produce scenarios more akin to a network-like evolutionary history of species that resist the classic, overly simplistic models of serial bifurcation (Marques, Meier, and Seehausen 2019). Recent methodological advances in phylogenomic approaches particularly target discordance arising from ILS and hybridization and have made progress in elucidating the complex evolutionary history of rapidly diversifying clades. Species tree inference methods explicitly account for ILS, and some of these are now feasible for large genomic datasets (e.g.,

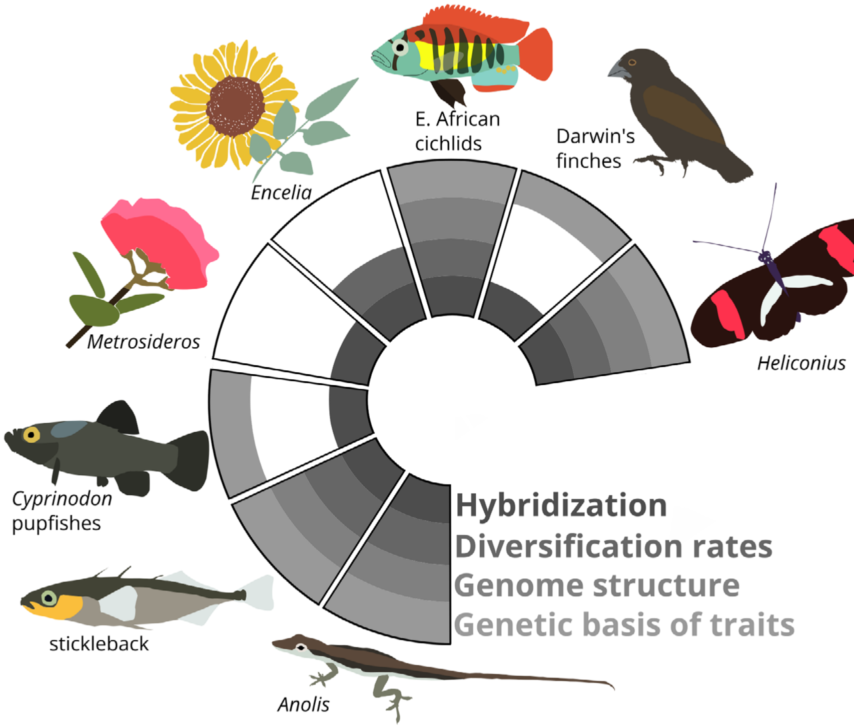


FIGURE 2 | A diagram of select study systems that are cited in this review, which illustrates the taxonomic breadth that features in adaptive radiation research. Filled circle segments symbolise whether published studies have investigated a particular aspect of adaptive radiation research within the given study system. The categories of study correspond to sections within this review.

`ASTRAL`, Rabiee, Sayyari, and Mirarab 2019; `SNAPP`, Bryant et al. 2012; `SVDquartets`, Chifman and Kubatko 2014). Other methods can infer non-bifurcating networks for a limited number of taxa (e.g., `PhyloNetworks`; Solís-Lemus and Ané 2016). A related challenge is that phylogenies derived from large genomic datasets often have high statistical support despite substantial discordance among nucleotide sites and loci, thereby challenging our confidence in bifurcating phylogenies from classic metrics of branch support (e.g., Dell'Ampio et al. 2014). New metrics to explicitly quantify genealogical concordance provide insight into branch-specific concordance across loci/sites and complement classic metrics of branch support (e.g., Minh, Hahn, and Lanfear 2020).

Additional methods can transform discordant noise into valuable information about the genomic processes that led to discordance, including inference of historical admixture (e.g., *D*-statistics; see Box 4) and the partitioning of discordance into portions attributable to ILS versus admixture (e.g., `QuIBL`; Edelman et al. 2019). Importantly, *D*-statistics require an appropriate species tree hypothesis and thus should be calculated in the context of careful phylogenetic inference. These recent developments in phylogenomic methods provide enormous potential to identify, discern, and better understand processes involved in adaptive radiation. For example, a recent reconstruction of the phylogeny of Midas cichlids scrutinised gene tree discordance using phylogenomic approaches (e.g., PhyloNetworks, Solís-Lemus and Ané 2016; `HyDe`, Blischak et al. 2018), paired with extensive population sampling, and found signatures of both ILS and hybridization (Olave and Meyer 2020). Likewise, Edelman et al. (2019) used a novel method (`QuIBL`) to disentangle the signals of ILS and admixture in the evolutionary history of *Heliconius* butterflies. Hybridization may also lead to polyploidization, particularly in plant radiations, which may itself facilitate adaptive radiation (Schenk 2021) while also posing substantial challenges to phylogenetic reconstruction (Rothfels 2021).

Sampling multiple individuals per species also provides important information for inferring species boundaries from genomic data. Collecting sufficient genomic data from sympatric species and applying phylogenetic models may reveal species boundaries simply by delimiting monophyletic groups (e.g., Wagner et al. 2013). The spatial distribution of sympatric taxa allows a natural test of species boundaries: if genetic differentiation remains and hybrids are not detected in sympatry, then this provides strong evidence for the reciprocal reproductive isolation of these taxa (in that context). However, in cases where species boundaries are not tested by natural sympatry, decisions regarding species delimitation can be much more challenging, particularly when dealing with large genomic datasets for which spatial genetic variation is readily detectable at fine geographic scales. Although in many cases, genomic data will lead to an increase in the number of recognised taxa due to its ability to distinguish cryptic species, in some rare cases, genomic data may alternatively lead to a reduction in the number of recognised species because of taxonomic oversplitting from phenotypic assessment alone, as was the case in Antarctic barbeled plunderfishes (Parker et al. 2022).

The multispecies coalescent (MSC) extends the coalescent model to multiple species, one implication of which is the provision of a statistical approach to delimit taxonomic groups (i.e., `BPP`; Yang 2015). Although these methods can be challenging to use for large genomic datasets, new methods seek to tackle this challenge (e.g., Rabiee and Mirarab 2021). Furthermore, the MSC can confound divergence driven by spatial structure with that driven by species boundaries (e.g., Sukumaran and Knowles 2017). New methods seeking to address the distinction between intraspecific spatial divergence and species boundaries provide interesting developments in this area (Sukumaran, Holder, and Knowles 2021). Although these approaches have not yet been used in the context of adaptive radiation, opportunities are ripe as population genomic data accumulates. In general, clear articulation of the species concepts being applied in circumscribing species in adaptive radiations is crucial for generating data that can be used in a comparative framework. Differences in taxonomic tradition can have a major impact on comparative species richnesses (e.g., Genner et al. 2004), and examinations of broader scale patterns in species richness must be able to account for these biases. We encourage future work in genomics and phylogenomics of adaptive radiations to openly define a working species concept for their study systems.

4 | The Role of Hybridization in Adaptive Radiations

Hybridization has long been proposed as a driver and facilitator of adaptive radiations (Seehausen 2004; Anderson and Stebbins 1954). Despite the role of hybridization in the collapse and extinction of numerous species (e.g., Grabenstein and Taylor 2018), the past several decades have also identified its importance in facilitating adaptive radiation based on theoretical models (Seehausen 2013; Kagawa and Seehausen 2020), simulations (Kagawa and Takimoto 2018), and empirical studies of adaptive radiations (Meier et al. 2019; Pardo-Diaz et al. 2012; Papadopulos et al. 2013; Richards and Martin 2017; Meier et al. 2023; Bell and Travis 2005; Herder et al. 2006; Glaubrecht and von Rintelen 2008; Meier, Marques, et al. 2017; Meier et al. 2023; Grant and Grant 2019). The emergence of population genomic-level data has fueled rapid advancement in this area of research because these data can facilitate identification of both recent and ancient hybridization, and can test mechanisms related to the functional role that hybridization has played in the history of adaptive radiations.

Hybridization may influence adaptive radiation in several distinct ways (Figure 3). Hybridization at the base of a radiation (“hybrid swarm origins”; Seehausen 2004) can increase the amount of heritable genetic variation in the founding population, thereby decoupling diversification from the slow rate of mutation accumulation (Seehausen 2004; Marques, Meier, and Seehausen 2019). Hybridization during adaptive radiation (“syngameon hypothesis”; Seehausen 2004) may provide further opportunity for recombining adaptive variation in novel ways that can facilitate ongoing radiation (Marques, Meier, and Seehausen 2019; Box 3). One way in which hybridization in this latter context can contribute directly to species diversity is through the process of hybrid speciation, in which hybridization directly results in speciation and reproductive isolation from parental taxa (Mavarez et al. 2006; Salazar et al. 2010; Schumer, Rosenthal, and Andolfatto 2014). Fusion–fission dynamics happen when clades emerge from hybrid swarm origins, collapse, and subsequently re-form, facilitating exceptionally rapid diversification (Meier et al. 2023). Population genomic data have contributed evidence in all of these arenas concerning hybridization's role in adaptive radiation, and we review this evidence here.

Most empirical studies have focused on documenting hybridization's presence and prevalence in radiating lineages. We now have strong evidence that hybridization has featured prominently in the history of many radiations (Figure 2) including some of the most celebrated adaptive radiations such as East African cichlids (reviewed in Svardal et al. 2020), Darwin's Finches (Lamichhaney et al. 2015), stickleback (Guo et al. 2019), *Heliconius* butterflies (Edelman et al. 2019), *Anolis* lizards (Wogan et al. 2023), and radiations on the Hawaiian islands (e.g., Choi et al. 2021). However, to gain a more in-depth understanding of hybridization's effects on adaptive radiation, including testing its hypothesized roles in facilitating diversification, we must not only document the prevalence and timing of hybridization but also the fate and impact of the genetic material gained through hybridization. Recent work has made strides in this direction, but this will remain a challenge and focus of continuing research in this area.

In a population genomic context, one general strategy for characterising the impact of introgressed genetic material is to examine whether variants gained from hybridization have been the targets of selection. For example, one recent approach uses patterns of allele sharing between lineages within and outside the radiation to bin variants by their putative origin; these include ancient polymorphisms, variants that have recently arisen within the radiation, and variants derived from hybridization (Meier, Marques, et al. 2017; Pease et al. 2016). These variant classes can then be investigated to determine whether particular categories of variants have likely been the targets of selection, often by identifying the unique patterns of genomic diversity generated by selective sweeps or comparing the prevalence of highly differentiated loci between variant origin classes. Existing applications of these approaches in cichlid fishes in Lake Malawi and the Lake Victoria region, *Solanum* tomatoes, and Hawaiian *Metrosideros* plants, have revealed that hybridization-derived variants and ancient polymorphisms frequently show signatures of positive selection (Pease et al. 2016; Meier, Marques, et al. 2017; Meier et al. 2023; Svardal et al. 2020; Choi et al. 2021), suggesting that hybridization-derived genetic variation has facilitated divergent adaptation in these radiations. In a recent study on *Heliconius* butterflies, an adaptively introgressed region associated with mimicry and red colour preference was found to have introgressed between related species, continuing to build the case that adaptive introgression may play a key role in trait and behavioural evolution during adaptive radiation (Rossi et al. 2024).

Some studies have made links between the hybrid origin of alleles and adaptive traits. Colour patterns in *Heliconius* butterflies (Moest et al. 2020; Rossi et al. 2024), novel trophic strategies in *Cyprinodon* pupfish (Richards et al. 2021), and visual acuity derived from variation at the LWS opsin allele in cichlids (Meier, Marques, et al. 2017) are three examples. In pupfish, Richards and Martin (2017) found that species divergence mostly arose from selective sweeps of standing variation, but genes associated with important axes of phenotypic and ecological divergence derive from hybridization with taxa from other locations. In Darwin's finches, the influence of natural selection on introgression was determined by tracking changes in the amount of introgressed material within populations

BOX 4 | Approaches for inferring complex histories.

The evolutionary histories of adaptive radiations are complex, involving multiple lineages and complicated patterns of divergence, gene flow, changes in population sizes, etc. Population genetic theory makes predictions about the allelic and haplotypic patterns and variation expected to result from particular evolutionary phenomena, and these predictions can be leveraged to infer various aspects of a radiation's evolutionary history from genomic data (Figure 1). Although this task is formidable, especially when one is limited to contemporary sampling, exciting methodological advances are making it increasingly feasible. The fields of phylogenomics and population genomics have both developed approaches for inferring evolutionary patterns and processes, with the former generally being tree-based and the latter generally (although not always; e.g., Fan et al. 2023) making use of population genetic statistics and patterns (e.g., allele frequencies, patterns of identity-by-descent, or patterns of linkage disequilibrium). In the study of adaptive radiation, both of these classes of models can be valuable, and the strongest conclusions frequently come from working on both sides of the phylogenomics–population genomics divide (see Box 1) to combine the advantages of these methods (Figure 1).

A variety of tree-based methods have been employed to characterise the complex evolutionary histories of adaptive radiations. *D*-statistics (also known as ABBA-BABA tests) can help to disentangle the confounding effects of incomplete lineage sorting and differential admixture within a clade and thereby provide evidence for ancient hybridization by examining imbalances in the frequency of discordant gene tree topologies (Green et al. 2010). *D*-statistics can provide a genome-wide estimate of introgression between a pair of taxa. By applying modifications of these statistics in sliding windows across the genome, it is possible to localise regions of the genome involved in introgression (e.g., Martin, Davey, and Jiggins 2015). These regions can then be targeted in tests for selection on admixed regions (e.g., Moest et al. 2020; Svardal et al. 2020; Irisarri et al. 2018; Richards and Martin 2017; Stryjewski and Sorenson 2017), which can help reveal the functional role that introgression has played, including through increasing diversification rates in a clade of interest (see Section 5). Introgression events can also be inferred using information contained in the branch lengths of gene trees, such as the method implemented in `QuIBL` (Edelman et al. 2019), which uses the branch lengths of gene trees to locate introgressed regions by estimating the likelihood that a given region displays its gene tree topology due to introgression rather than ILS.

Tree-based admixture tests have frequently been employed in work on adaptive radiations, including in cichlids (Meier et al. 2019; Malinsky et al. 2018; Ronco et al. 2021; Poelstra, Richards, and Martin 2018), pupfish (Richards and Martin 2017), tomatoes (Pease et al. 2016), *Jaltomata* nightshades (Wu et al. 2018), and *Dendrocincla* woodcreepers (Pulido-Santacruz, Aleixo, and Weir 2020). Although *D*-statistics cannot resolve the directionality of gene flow in introgression events, methodological extensions have targeted this question (e.g., D-FOIL, Pease and Hahn 2015). In one notable case, Pease et al. (2016) identified substantial ILS-caused tree discordance as well as evidence for interspecific introgression in a radiation of wild tomatoes (*Solanum* spp.). They then used sliding-window based analyses to identify introgressed regions of the genome (Pease et al. 2016). *D*-statistics can reveal patterns consistent with hybrid swarm origins of adaptive radiation, and for the syngameon hypothesis (Figure 3). However, tests of these mechanisms require additional evidence for the functional implications of these hybridization events.

Demographic modelling (referring both to methods that infer population size changes through time, and methods for inferring population splits and mixture events over time; Beichman, Huerta-Sanchez, and Lohmueller 2018) represents a powerful collection of approaches to reconstruct many evolutionary phenomena that are of central interest in adaptive radiation research. A diversity of analytical approaches have been used to infer demographic histories from population genomic data, but they usually rely on compressions of genetic diversity into a summary statistic (e.g., site frequency spectrum, SFS; the distribution of allele frequencies across the genome for one or more populations or interest), blocks of ancestry that are identical-by-descent (IBD), or both for making inferences (reviewed in Beichman, Huerta-Sanchez, and Lohmueller 2018). Demographic histories can be inferred from both historical mutation events and historical recombination events. Both SFS and IBD-based methods use these patterns of sharing among individuals in a population or among individuals in separate populations, comparing the distribution of observed frequencies (SFS) or lengths (IBD) to the distribution expected under the inferred demographic model (Beichman, Huerta-Sanchez, and Lohmueller 2018). Demographic modelling has figured prominently in probing the formation of incipient diversity in adaptive radiations. For example, modelling with the coalescent-based genetic simulation program `fastsimcoal2` (Excoffier et al. 2013) helped tease apart the complexities of speciation in the *Pundamilia* cichlids of Lake Victoria, which involved the repeated formation of similar pairs of species facilitated by admixture (Meier, Sousa, et al. 2017). In the adaptive radiation of *Chorthippus* grasshoppers, the diffusion approximation-based program *δaδi* (Gutenkunst et al. 2009) was used to reconstruct the process of divergence among species including the timing of divergence and gene flow events as well as population size changes (Nolen et al. 2020). Robust demographic inference remains a substantial challenge (e.g., Momigliano, Florin, and Merilä 2021; Johri et al. 2021), and the application of these methods and interpretation of their results should be approached with caution (Momigliano, Florin, and Merilä 2021) and ideally in conjunction with other, complementary approaches that can be used for corroboration. Nonetheless, we expect that the value of demographic inference will continue to grow in adaptive radiation research, especially given that ongoing methodological innovation (e.g., Tran et al. 2023; Fan et al. 2023; Marchi, Kapopoulou, and Excoffier 2024) is increasing the flexibility, accuracy, and efficiency of available methods.

that had been characterized from population genomic data generated from decades of sampling (Enbody et al. 2023). Collectively, these findings provide mounting evidence that not only is hybridization prevalent in adaptive radiation but that hybridization-derived genetic material produced from hybridization pre- and post-dating the origin of the adaptive radiation can play an active and creative evolutionary role, thus providing evidence for both hybrid swarm origins and the

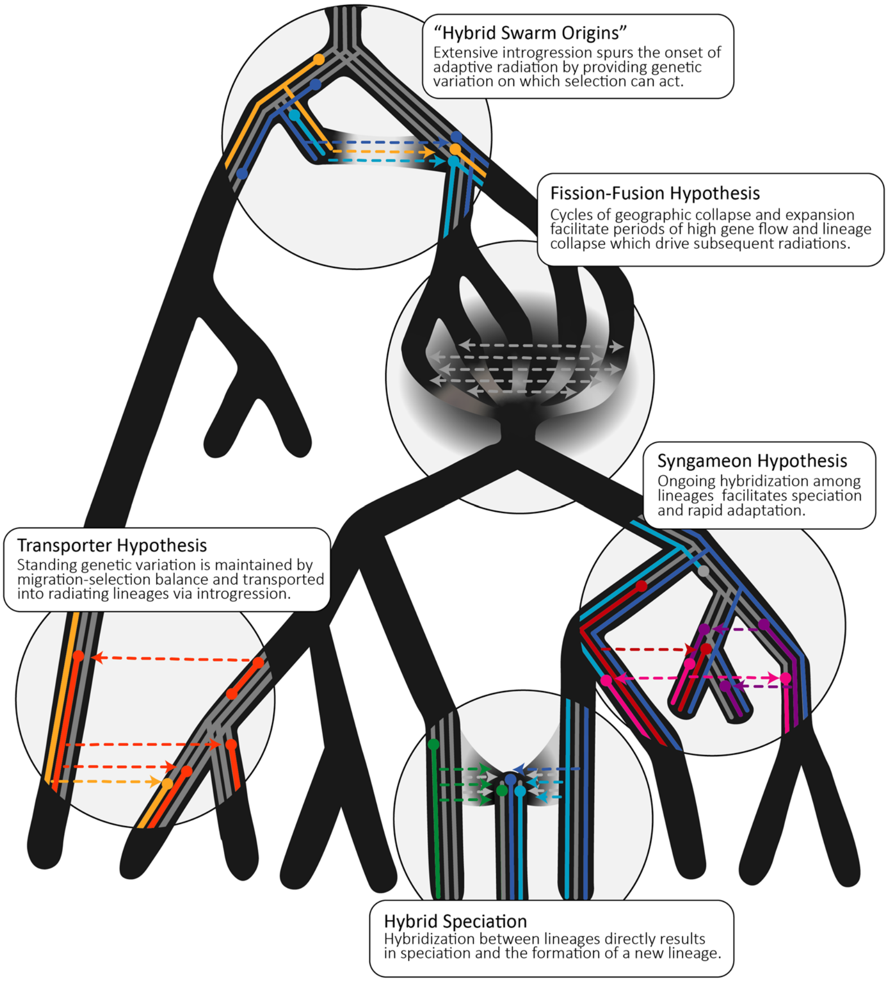


FIGURE 3 | Several hypotheses have been proposed to describe the role of hybridization in promiting adaptive radiation. (Top) Hybrid swarm origins of adaptive radiations describes the phenomenon wherein adaptation and speciation proceed rapidly from a hybrid population. (Upper Right) Relatedly, the fission–fusion hypothesis describes how the repeated growth and collapse of radiations results in a lineage with a high propensity to radiate. (Lower Right) The syngameon hypothesis posits that introgression during the radiation provides the genetic material by which lineages continue to radiate rapidly. (Lower Left) The transporter hypothesis describes how mutation-selection balance may serve to maintain adaptive alleles or standing genetic variants which can be re-used during subsequent adaptation within the radiation. (Bottom) Hybridization may also lead to hybrid speciation when hybridization directly results in the formation of new lineages or species within a radiation.

syngameon hypothesis. Indeed, the interaction between these distinct processes may be key in promoting some of the world's most dramatic adaptive radiations (Meier et al. 2023).

Demonstrating the functional role of hybridization in adaptive radiation requires elucidating cases of positive selection on variants derived from hybridization, but population genomic data can give us a clearer picture of selection *against* introgression-derived genetic variation. Both in and outside the context of adaptive radiation, population genomic studies are showing that hybrid ancestry often declines precipitously following the hybridization event for a variety of reasons but most commonly due to the purging of alleles that are deleterious in the new genomic background (Schumer et al. 2018; Martin et al. 2019; Moran et al. 2021; Edelman et al. 2019). Evaluating the balance between selection for and against introgressed alleles, and how these dynamics play out in systems of different age, diversity, and context for hybridization, is an exciting area of study that we predict will play a prominent role in future research.

5 | Estimating the Timing and Rates of Diversification

Understanding diversification dynamics—or how and why speciation and extinction rates vary across time, space, and taxa—has long interested evolutionary biologists (Ricklefs 2007), and reconstructing the process of diversification is critical to understanding adaptive radiation. While divergence times and patterns have been estimated historically from morphological, fossil, and genetic data, genome-scale data have enabled finer-scale modelling and analysis of complicated divergence processes, such as those involving rapid radiation from a common ancestor, or complex scenarios of hybridization and admixture (e.g., Meier, Marques, et al. 2017). In particular, the next-generation sequencing revolution has enabled expansion of genomic datasets to the population level, facilitating simultaneous investigation of processes occurring both within and among well-defined species. The pairing of population genomic and phylogenomic investigations has opened the door to powerful suites of analyses that bridge evolutionary scales (Box 4).

Population genomic data have enabled increasingly accurate estimation of divergence times using both population genomic and phylogenomic methods. While traditional molecular clock-based phylogenetic methods for divergence time estimation can be used with population genomic data, having large numbers of sites across the genome in addition to multiple individuals per species present challenges to some of these methods because of dataset sizes. At the same time, these data open the door to additional methods for inferring dated phylogenies. Specifically, demographic modelling methods can make use of population genetic predictions for divergence times given genetic diversity data and known mutation rates. Such estimates derived from population genetic models provide an independent source of information from traditional molecular clock-based phylogenetic methods. In addition, analyses can be strengthened by combining genomic data with other lines of evidence, commonly fossil dating, morphological, or spatial data (Pyron 2015). Advances in the ways in which fossil, morphological, and genomic data can be combined, such as in `RevBayes` (Hohna et al. 2016), `BEAST` (Bouckaert et al. 2019), and their numerous associated packages, have allowed these independent lines of evidence (with all of their independent biases and assumptions) to be modelled together, thereby strengthening inferences of divergence times. In particular, analyses that combine multiple types of data are important for understanding the key innovations associated with shifts in diversification rates within a clade, lending support for hypotheses about the *adaptive* component of adaptive radiations.

An important extension to estimating more accurate divergence times is the ability to test predicted diversification patterns in adaptive radiations. Some models of adaptive radiation predict that fast early diversification is followed by a decrease in speciation rates as ecological niches are filled (e.g., Gavrilets and Vose 2005; Yoder et al. 2010; Moen and Morlon 2014). Although other phenomena can decrease diversification rates (i.e., speciation rate minus extinction rate) over time (Moen and Morlon 2014), many studies have found evidence that speciation rates slow through time in adaptive radiations. Such conclusions have been possible for decades with phylogenetic data; however, increasingly available population genomic data has enabled the generation of high-resolution molecular phylogenies for a growing number of taxa, thereby increasing the number of systems for which such analyses are possible. One example of how increasingly availabile of genomic data has improved our ability to estimate speciation rates, and to use those estimates to test diversification hypotheses, is in the radiation of *Liolaemus* lizards in South America. Esquerré et al. (2022) used a combination of mitochondrial and reduced-representation genomic data to resolve the clade's phylogeny and test the relative contributions of introgression and geologic events (the uplift of the Andes Mountains and glacial–interglacial cycles) to diversification. Similarly, Singhal et al. (2021) used extensive taxon sampling to resolve the phylogeny of a radiation of shrubs in the genus *Encelia*, which then allowed the characterisation of diversification and disparification (evolution of trait disparity throughout a clade) rates and an investigation into the role that climatic oscillations and habitat heterogeneity have played in facilitating divergence within the clade.

Adaptive radiations, as a consequence of their rapid diversification, have high rates of ILS, and therefore a critical part of understanding their divergence history is disentangling ILS and hybridization. Advances in phylogenomic methods (see Section 3) have made progress in working to disentangle these signals. Additionally, methods designed to take advantage of large amounts of population genomic data, such as a suite of demographic inference methods—that is, methods for finding a particular model describing population size changes as well as population split and mixture events over time (Beichman, Huerta-Sanchez, and Lohmueller 2018; Marchi, Schlichta, and Excoffier 2021)—complement strictly phylogenetic methods through their ability to model specific diversification scenarios and to account for gene flow between clades and the changes in population size concomitant with these events (see Box 4). Other population genomic methods, such as *D*-statistics (Green et al. 2010) and the related *f*-statistics (Reich et al. 2009; Patterson et al. 2012), can be used to inform these models (see Section 4) as well as to identify regions of the genome that contain elevated signals of introgression.

Genomic data, while offering clear advantages, do not fully eliminate existing limitations, and also pose new challenges for estimating the timing and rate of speciation within adaptive radiations, and thus these tasks remain formidable. First, it can be difficult to accurately estimate phylogenetic branch lengths with genomic data (Duchene et al. 2017; Bromham 2019; Brown et al. 2010), and the way that data are acquired and processed prior to phylogenetic or population genetic analyses can exacerbate these challenges. Taxon sampling, locus sampling, bioinformatic filtering, and the choice of phylogenomic analysis methods can all have notable impacts on branch length estimation (Bromham et al. 2018; Bromham 2019; Rick et al. 2024). More fundamentally, recent work by Louca and Pennell (2020) showed that under a commonly used model for examining diversification dynamics, phylogenies of extant taxa are associated with infinite diversification scenarios, which has led to questions of whether diversification rates should even be estimated (Pagel 2020). These challenges illustrate our progress in harnessing the power of genomic data for examining the timing and rates of diversification but also its limitations. Encouragingly, the inference of diversification dynamics is an active area of methods development in evolutionary biology and statistics, and thus we expect rapid progress in addressing existing pitfalls. This is exemplified by recent work spurred by Louca and Pennell (2020), including rigorous appraisals of existing methods and the development of approaches that circumvent some of the issues with statistical identifiability in diversification models (Morlon, Hartig, and Robin 2020; Helmstetter et al. 2021; Legried and Terhorst 2021).

6 | The Genetic Basis of Trait Evolution in Adaptive Radiations

The incredible diversity of traits involved in adaptive radiations is famously varied and inextricably linked to the processes that drive radiations across diverse taxa. Many traits define or strengthen species boundaries, determine niche use during adaptation, and compose the phenotypic aspects on which selection acts to drive adaptive divergence, making the genomic basis of trait evolution a key process to study during the progression of adaptive radiation. Now, with access to population genomic data, we are poised to better understand the genomic and genetic mechanisms (i.e., the genes, gene complexes, or physical and heritable elements in genome structure) enabling rapid divergence across systems. Studies using population genomic data have substantially advanced our understanding of the role of standing genetic variation (Roberts Kingman et al. 2021), the extent of the genome involved in adaptation (Nakamura et al. 2021), and the role of structural elements and hybridization (Marques, Meier, and Seehausen 2019) in diverse trait evolution. However, many questions remain and future work should extend population genomic investigation into non-model systems and focus on documenting parallel patterns for the genetic basis of trait evolution across radiations in diverse taxa. Here, we briefly highlight recent developments in our understanding of the genetic basis of traits in both plant and animal radiations and discuss broad trends and outstanding questions that emerge from the study of trait evolution in adaptive radiation.

Much research has focused on what extent of the genome is involved in adaptive evolution. Is rapid phenotypic change and incipient speciation driven by just a handful of key genes with pleiotropic effects (Thompson 2020)? Or many small-effect loci across large spans of the genome? Data attainability and methodological advances such as genome-wide association studies (GWAS) have found evidence for both patterns: in some radiations, adaptive traits are driven by a few key large-effect loci (Enbody et al. 2023) whereas in other cases hundreds of loci are associated with adaptive traits (Roberts Kingman et al. 2021). Little more than a decade ago our understanding of the genetic basis of trait variation in stickleback was limited to the identification of a handful of large-effect loci associated with variation in pelvic spines and lateral plates (Coyle, Huntingford, and Peichel 2007; Shapiro, Bell, and Kingsley 2006; Colosimo et al. 2005). Now, our understanding of trait evolution in the stickleback genome has expanded to include hundreds of loci across the genome that are repeatedly identified as regions of ecotype variation between freshwater and marine stickleback populations in parallel adaptive divergences (Jones et al. 2012; Roberts Kingman et al. 2021; Reid, Bell, and Veeramah 2021). Similarly, quantitative trait loci (QTL) mapping in African cichlids previously identified a few key loci repeatedly associated with variation in trophic traits such as craniofacial or jaw morphology (Albertson, Streelman, and Kocher 2003; Concannon and Albertson 2015). Now the development of high-quality, annotated cichlid reference genomes (Brawand et al. 2015) and genome-wide comparison studies with whole-genome and trait data has identified large portions of genomes that are associated with phenotypic shifts (Nakamura et al. 2021). In both systems, the availability of annotated reference genomes, the development of analytical tools, and the incorporation of whole-genome sequence data have led to the detection of numerous regions across the genome that facilitate adaptation and are associated with phenotypic shifts in complex traits, often revealing extensive selection on small-effect loci across large portions of the genome. However, although population genomic tools and data provide valuable insights into evolutionary patterns at the whole genome scale, these observations will ultimately need to be linked to genes and genetic mechanisms that facilitate trait evolution. Despite the detection of small-effect loci across the genome, "genomic hotspots" of divergence via large-effect loci have emerged as important evolutionary drivers, especially for certain key traits, or in contexts when rapid, repeated evolution is adaptive. Such key loci often harbour many genes, although they can also include relatively few genes with pleiotropic effects (Feller and Seehausen 2022; Morris et al. 2019). For example, studies in *Heliconius* butterflies—both historically with QTL studies and more recently with population genomic data—have repeatedly identified only a small handful of large-effect loci and a few regulatory mechanisms and moderators that drive the extensive phenotypic diversity of the wing colour pattern (Jiggins and McMillan 1997; Mavarez et al. 2006; Kronforst, Kapan, and Gilbert 2006; Joron et al. 2006; Supple et al. 2014; Moest et al. 2020). Trait studies in Darwin's finches similarly identify few divergent loci among species associated mainly with genes that control craniofacial morphology and development (Lamichhaney et al. 2015; Rubin et al. 2022; Chaves et al. 2016; Enbody et al. 2023), and in *Helianthus* sunflowers, genes underlying trait adaptation among ecotypes are clustered on inversions (Todesco et al. 2020). These examples highlight the variety of genetic mechanisms associated with trait change—ranging from the clear contribution of a small number of large-effect loci to the involvement of hundreds of loci across large portions of the genome, or a balance of both (De-Kayne et al. 2022; Enbody et al. 2023). Disentangling similarities and differences across traits and taxa is a fascinating future challenge of this work as case studies accumulate. Additionally, identifying genetic mechanisms that predispose some regions of the genome to be used repeatedly in adaptation, for example via recombination rate variation or structural properties (see Section 7), will provide critical insights into the mechanism of adaptive parallelism across radiations. For instance, the gene responsible for repeated loss of an ecologically important pelvic spine trait in stickleback occurs in a genomic region where double-stranded DNA breakage is more likely (Xie et al. 2019). Study of "adaptation hotspots" in adaptive radiation research is only possible with genomic data and may help answer long-standing questions about the mechanisms that allow the striking ecological divergence and rapid speciation that characterise adaptive radiations.

Much of the genetic variation on which selection can act during adaptive radiations must arise from either de novo mutations or from standing genetic variation (SGV) that is either present in the colonising population or introgressed among neighbouring lineages. Advances in population genomic analyses have explored the relative contribution of SGV—defined as the accumulated genetic diversity present within a population that can be utilised for adaptation—versus novel variation in facilitating trait evolution in adaptive radiations, and generally have found SGV, often in combination with introgression, to underlie traits and fuel phenotypic evolution (Roberts Kingman et al. 2021; Meier, Marques, et al. 2017; Frei et al. 2022). Notably, parallel adaptation of homologous loci drawn from much older SGV appears to be a key mechanism underlying trait evolution in many diverse systems that have been recently investigated with population genomic data (Roberts Kingman et al. 2021; Moest et al. 2020; Supple et al. 2014; Rubin et al. 2022; McGee et al. 2020). This is exemplified in the parallel adaptive radiation of stickleback into freshwater (Roberts Kingman et al. 2021; Jones et al. 2012; Reid, Bell, and Veeramah 2021; Lescak et al. 2015; Schluter and Conte 2009;

Bell and Aguirre 2013). Also, in adaptive radiations of *Heliconius* butterflies, colour pattern replication in co-mimics has occurred via repeated adaptation involving the same genomic locations (Kronforst, Kapan, and Gilbert 2006; Joron et al. 2006; Moest et al. 2020), suggesting that repeated selection on a few homologous loci associated with the same "supergene" underlie the wide diversity of phenotypes (Supple et al. 2014; Moest et al. 2020; Jiggins and McMillan 1997; Mavarez et al. 2006; Kronforst, Kapan, and Gilbert 2006; Joron et al. 2006).

Extensive hybridization, in combination with SGV, also plays an important role in the radiation of traits in East African cichlids (Meier, Marques, et al. 2017; Meier et al. 2023; Marques, Meier, and Seehausen 2019; McGee et al. 2020; Urban et al. 2021; Nakamura et al. 2021). The pattern of frequent lineage splitting in adaptive radiations may possibly dispose radiating lineages to utilise SGV more than lineages in non-adaptively radiating clades, but this comparison needs further examination. McGee et al. (2020) notes that ancient haplotypes correlate with adaptation to specific ecological niches and are recombined and reused during adaptive divergences to facilitate rapid speciation (McGee et al. 2020). This recombination of standing genetic variation into novel combinations, especially as the result of hybridization, has been termed the 'combinatorial mechanism' (Box 3 and Figure 3). Studies of adaptive radiation in Hawaiian *Metrosideros* also find that ancient haplotypes underlie diverse phenotypes and provide the genetic basis for recurring selection events across islands (Choi et al. 2021). A promising line of questioning that emerges from this narrative seeks to identify the origins of SGV, particularly by exploring the connection between SGV in a clade to cycles of historic geographic upheaval that result in the repeated expansion and collapse of usable habitats, as observed in (Meier et al. 2023). Are certain lineages—say those in volatile ecosystems or those consisting chronically of many small peripatric populations—more likely to experience evolution from the reuse of SGV? Indeed, are these lineages more likely to be those that adaptively radiate? How does the age, size, history of geographic instability, or extent of gene flow in a clade influence these patterns?

The emerging picture that SGV may be ubiquitous as fuel for rapid trait diversification across adaptive radiations is notable and has only been recently explored with the advent of population genomic data and analyses. Moreover, the observation that parallel evolution occurs from SGV provides an intriguing roadmap for predicting evolutionary change (Roberts Kingman et al. 2021; Moest et al. 2020; Supple et al. 2014; Rubin et al. 2022; McGee et al. 2020). However, many outstanding questions remain. For instance, the origins of SGV and the mechanisms by which it accumulates over time and space also remain largely unexplored. Expanding our knowledge in this area has promising implications for our understanding of how microevolutionary adaptations accumulate and lead to macroevolutionary change (Welch and Jiggins 2014; Meier et al. 2023). Finally, population genomic studies can also explore how SGV moves between and among populations and how commonly mechanisms such as the "transporter" process (Figure 3) facilitate trait evolution across diverse radiations (Schluter and Conte 2009).

Future work should strive to further understand when and why convergent patterns of trait evolution emerge (as in Roberts Kingman et al. 2021), especially across radiations, and how patterns of trait evolution drive barriers to gene flow, particularly through pleiotropic loci or genomic regions of low recombination such as inversions (Todesco et al. 2020). Increased accessibility to long-read sequence data will also aid in the exploration of trait evolution, since long-read data facilitates detection of selection on "gene clusters" or "supergene regions" among radiating lineages. Use of long-read sequence data also allows for haplotype mapping, which aids trait association mapping. Furthermore, the emerging accessibility of genome editing technologies will aid the experimental exploration of how key genomic regions, such as "hotspots of divergence" or structural elements, contribute to phenotypic evolution and even reproductive isolation (e.g., Rossi et al. 2024). Such methods can also be used to further explore the pleiotropic effects of key "speciation genes" or loci. Finally, future studies should seek to disentangle the role that elevated rates of gene flow via hybridization—as may be particularly common in adaptive radiations—play in the development of novel or rapid trait evolution. This hypothesis has been posed previously (e.g., Anderson and Stebbins 1954; Yakimowski and Rieseberg 2014) but is finally testable via population genomic methods.

However, future work is not without substantial challenges. While combining trait data with fine-scale whole-genome data continues to present exciting possibilities for adaptive radiation research, our understanding of trait evolution is biased toward traits that are easily measured or observed. Future work should expand the analysis of trait evolution to those behavioural or physiological traits that are undoubtedly important to speciation, but have been historically difficult to identify.

In sum, the rising prevalence of population genomic data has radically informed our understanding of the genetic mechanisms that underlie trait divergence in adaptive radiations and highlighted several key patterns. Although the traits implicated in adaptive radiations may be phenotypically and functionally diverse, the genetic underpinnings of trait divergence are often replicated across dissimilar systems. The incorporation of standing genetic variation emerges as a common facilitator of rapid adaptive divergence (Roberts Kingman et al. 2021; Moest et al. 2020; Supple et al. 2014; Rubin et al. 2022; McGee et al. 2020). Population genomic data has been crucial in the identification of numerous small effect loci in the adaptation of key traits (Jones et al. 2012; Roberts Kingman et al. 2021; Reid, Bell, and Veeramah 2021; Nakamura et al. 2021), and we expect that as more data accumulates, additional cases will emerge. The exploration of genome structure as it relates to trait origins and convergence in radiations may be a particularly promising area of exploration. The rising accessibility of population-scale genomic data has opened the doors for the study of trait evolution within adaptive radiation in non-model systems, and expanding data will allow for continued synthesis and exploration of these broad trends in both classic systems of adaptive radiation and non-model systems.

7 | Genomic Structural Variation

Variation in genome structure (hereafter *structural variation*) refers to differences in the abundance, presence, position, and orientation of nucleotide sequences (Merot et al. 2020). Structural variation exists along a size continuum ranging from single nucleotide sites to whole chromosomes or genomes and can involve insertions, deletions, duplications, inversions, or movement of genomic material (Merot et al. 2020). Evidence is accumulating that structural variation can substantially and importantly influence a variety of evolutionary processes including those relevant to adaptive radiation, such as speciation rate shifts and ecological adaptation linked with reproductive isolation. Nonetheless, potential connections between structural variation and adaptive radiation remain underexplored.

Until recently, the empirical study of structural variation has largely been confined to humans and model systems and generally limited to easily detectable variants (i.e., large inversions or genome duplications) owing to insufficient genomic data and methods that facilitate their discovery (Medvedev, Stanciu, and Brudno 2009). However, recent advancements in characterising structural variation are increasingly enabling their study in non-model systems. Of particular relevance is the rapid growth of long-read sequencing technologies, which can facilitate the discovery of structural variants that are often undetectable with short-read data. Relatedly, sequencing and bioinformatics advances are improving the assembly of reference genomes and pangenomes—representations of the collective contents of multiple genomes. These genomic resources improve our ability to characterize the structural genetic diversity present within and between populations (Siren et al. 2021). Thus, although evidence for the role of structural variation in adaptive radiation is currently modest, our capacity for studying this topic is rapidly growing (see Ho, Urban, and Mills 2020). Here, we discuss how structural variants could be implicated in adaptive radiation by examining their involvement in relevant evolutionary processes. We also highlight existing work that establishes preliminary connections between adaptive radiation and structural variation, which further motivates continued focus on these genomic features in adaptive radiation research.

Structural variants may play important roles within adaptive radiations by acting as rapid and potent generators of genomic and phenotypic variation, which increases the raw material on which natural selection can act. They may affect much larger regions of the genome than single nucleotide variants by reducing recombination across many genes or disrupting key gene pathways. Thus, although less is known about mutation rates and fitness effects of structural variants compared to single nucleotide variants, it is likely that selection on structural variants can produce large and rapid evolutionary change. For instance, evidence in plant and fish radiations suggests that whole-genome duplication may spur the onset of lineage diversification, perhaps by generating novel key innovations or by rapidly increasing genetic variation in the population (Glasauer and Neuhauss 2014; Schranz, Mohammadin, and Edger 2012), although these patterns are not always clear or consistent (Carretero-Paulet and Van de Peer 2020). Population-level variation in gene copy number variation (CNV) may also have a direct impact on the potential for populations to adapt due to functional redundancy, increased genomic diversity among populations, or from adaptation into novel habitats via neofunctionalization or changes in gene dosage effects. CNV has been associated with incipient speciation (Hirase et al. 2023) and generation of reproductive isolation (Rieseberg and Blackman 2010) yet has rarely been studied in the context of adaptive radiations (but see Chain et al. 2014).

Transposable elements (TEs) have also received longstanding attention because they can generate considerable and variable changes in genome structure leading to phenotypic changes and can be induced via environmental stress (Casacuberta and González 2013; Catlin and Josephs 2022). Although the insertion of TEs is thought to be generally deleterious (Arkhipova and Meselson 2005), TEs may lead to evolutionarily significant variation if they alter the activity of ecologically relevant genes. Evidence is also mounting that TEs specifically represent a considerable and important source of genomic and phenotypic variation in adaptive radiations . For instance, in East African cichlids, Quah et al. (2024) discovered that ~75% of structural variation is attributable to TE activity, and TEs have alterated gene expression in the ecologically relevant visual opsin genes (Brawand et al. 2015; Carleton et al. 2020). Evidence also suggests that TEs associated with *Hox* genes in *Anolis* lizards drive the speciation rate in this clade, facilitating adaptive radiation (Feiner 2016).

Structural variation can also directly influence the process of local adaptation, especially by reducing effective gene flow between geographically proximate populations adapting to different ecological niches. Inversions and chromosomal fusions can directly reduce recombination between loci, maintaining linkage between sets of alleles that facilitate local adaptation (Kirkpatrick and Barton 2006; Guerrero and Kirkpatrick 2014). Inversions have been increasingly implicated in local adaptation and population divergence across the tree of life (Wellenreuther and Bernatchez 2018; Kirkpatrick and Barton 2006) and may be especially critical for speciation and local adaptation when gene flow occurs between geographically proximate but ecologically distal populations (Schaal, Haller, and Lotterhos 2022).

Capitalizing on our burgeoning capacity to characterize structural variants, a growing number of empirical population genomic studies are investigating the impacts of structural variation in remarkable detail. For example, in *Helianthus* sunflowers, dozens of haplotype blocks contained in structural variants (inversions, rearrangements) are associated with ecologically relevant traits that are distinct among similar sunflower ecotypes (Todesco et al., 2020; Huang et al., 2020). In the radiation of threespine stickleback. Freshwater vs. marine stickleback ecotypes are strongly associated with alternate inversion orientations, although the ecological traits mapping to these regions have not yet been identified (Jones et al. 2012; Roesti et al. 2015). Lastly, structural variation is increasingly a focus in studies of the East African cichlid radiations. For example, Penso-Dolfin et al. (2020) examined the genomes of several cichlid species and discovered a variety of structural variants, which were enriched for immune-related genes and genes associated with behaviour and development. Moreover, the most comprehensive investigation to date of structural variation in the context of adaptive radiation by Blumer et al. (2024) identified five large inversions segregating in the Lake Malawi cichlid radiation, which likely act as "supergenes" that play roles in ecological adaptation and sex determination. Interestingly, they found that the inversions likely spread through the radiation via gene flow between lineages, showcasing how the phenomena covered in this review can simultaneously and interactively shape the evolution of adaptive radiations.

Beyond their role in adaptation, structural variants may also facilitate speciation and reproductive isolation in adaptive radiations (Rieseberg 2001; Fuller et al. 2019; Zhang et al. 2021). First, structural variants can contribute to speciation by promoting the formation and strengthening of barriers to gene flow at various stages of the process. Structural variants can generate reproductive barriers by directly affecting fitness (e.g., causing infertility or inviability of heterokaryotypes), which has been demonstrated in several taxa including mice (Homolka et al. 2007) and *Drosophila* flies (Masly et al. 2006). They can also promote the formation of reproductive barriers through their suppression of recombination (Rieseberg 2001; Faria and Navarro 2010). The effects of structural variants on speciation can also promote ecological adaptation that simultaneously results in reproductive isolation. For example, an inversion in yellow monkeyflower (*Mimulus guttatus*) is involved in both local adaptation to water availability and multiple reproductive isolating barriers including flowering time, selection against immigrants, and extrinsic postzygotic isolation (Lowry and Willis 2010). Enabled by increasing accessibility of population-scale genomic data, empirical support for the involvement of structural variants in reproductive isolation and speciation is growing across diverse systems including birds (Hooper, Griffith, and Price 2019), insects (Noor et al. 2001; Brown et al. 2004; Lohse et al. 2015; Ayala, Guerrero, and Kirkpatrick 2013), snails (Le Moan et al. 2024), and plants (Lowry and Willis 2010; reviewed in Baack et al. 2015).

Finally, from a macroevolutionary perspective, accumulating work suggests connections between structural variation and broader diversification patterns, including those found in adaptive radiations. First, TEs have been associated with higher diversification rates, perhaps by rapidly generating genomic novelty and reproductive isolation (e.g., Naciri and Linder 2020; Feiner 2016; Oliver, McComb, and Greene 2013). A burst of TE activity preceded the onset of a bat adaptive radiation (Platt et al. 2014) and has been observed at the onset of recent speciation events in other taxa (Serrato-Capuchina and Matute 2018). Other macroevolutionary patterns also warrant attention. In the East African cichlid radiations, a positive relationship exists between indel enrichment and speciation rate (McGee et al. 2020), and whole genome duplications in plants may be associated with increased diversification at multiple evolutionary scales, including in the classic adaptive radiation of Hawaiian silverswords (Barrier et al. 1999) and more broadly in angiosperms (Tank et al. 2015).

Structural variants may be critical genomic features at all stages of adaptive radiations—from the formation of ecological divergence, to adaptation and speciation, to the macroevolutionary processes that govern speciation rates. A population genomic perspective will be especially valuable for understanding the impact of structural variants on adaptive radiation because structural variants frequently segregate both within and between species. Thus, population-level sampling and analyses across multiple species are necessary to reveal the prevalence and evolutionary impacts of structural variants on adaptive radiations. As both genomic resources and methods related to structural variant detection and analysis advance (reviewed in Ho, Urban, and Mills 2020; e.g., Siren et al. 2021; Song et al. 2022; Meier et al. 2020), we expect research on structural variants to increasingly emerge as an exciting frontier in the study of adaptive radiation.

8 | Conclusions and Future Directions

Here, we have reviewed recent work in adaptive radiation research facilitated by population genomic data in five key areas: phylogenomics, the study of hybridization, timing and rates of diversification, the genomic basis of trait evolution, and genome structure. Notwithstanding this progress, questions linger about the evolutionary processes underlying adaptive radiation, and ongoing work in these areas of research continues to uncover additional questions and promising directions of investigation. For instance, while we can now identify introgression as a common feature of radiating lineages, understanding the mechanistic link(s) between introgression and rapid radiation remains challenging. Documenting the fate of introgressed genetic material could help evaluate several hypotheses explaining how introgression facilitates adaptive radiation. Population genomic data will be particularly valuable for this and other endeavours because they can help disentangle incomplete lineage sorting, hybridization, and lineage divergence and facilitate more accurate estimates of diversification timing and rates.

It is also possible that the evolutionary processes elucidated through the study of population genomic data will help to distinguish adaptively radiating lineages from non-radiating clades (e.g., Meier et al. 2019, 2023). Nevertheless, the attributes of a lineage that predispose it to adaptive radiation remains an open question. For example, although one might assume that lineages with more genetic variation would be more prone to rapid ecological divergence, many if not most adaptive radiations have emerged in geographically isolated environments with relatively few founder individuals, presenting an intriguing paradox (Cerca et al. 2023). Alternatively, factors related to ecological opportunity and isolation may more accurately predict when adaptive radiations occur, or perhaps an interplay between intrinsic (e.g., genetic, trait-based) and extrinsic factors is more important (e.g., Wagner, Harmon, and Seehausen 2012; Meier et al. 2019).

Population genomic data have also facilitated exploration of the genomic mechanisms that facilitate phenotypic diversity and rapid adaptation of traits in adaptive radiations. We have identified the role of structural genomic variation, "genomic hotspots" like supergene regions, and the mechanisms by which reduced recombination (as in chromosomal inversions) can facilitate ecological divergence and eventual speciation. However, work remains to identify common mechanisms across radiations and determine the factors that distinguish the spectacular rates of divergence seen in adaptive radiations from non-radiating lineages. Population genomic data underlie a powerful arsenal of tools with which to revisit this question, especially by exploring the correlation between available SGV through time, or rates of hybridization among closely related lineages, to the propensity of lineages to speciate rapidly. The various hypotheses for the role of hybridization in facilitating rapid speciation (Figure 3) can be tested among radiating and non-radiating lineages to disentangle whether rates of gene flow are higher in adaptive radiations compared to their non-radiating counterparts (although greater opportunity for gene flow afforded by higher species richnesses in radiating clades also needs to be accounted for). More research is also needed to link ecological divergence to speciation by identifying pleiotropic regions in the genome that drive both reproductive isolation and adaptation, as well as investigating less explored mechanisms, such as structural elements (Section 7) or regions of fragile DNA, both of which can facilitate the rapid exploitation of ecological opportunity. Emerging sequencing technologies—such as genome editing, epigenomics, and metagenomic techniques—further open the door to novel approaches and questions. For instance, the use of genome editing technologies to study the re-use of key genes or genic pathways, including inversions or other structural elements, may shed light on the phenotypic effects contributed by key genomic regions and their ability to generate rapid evolutionary change.

The use of population genomic data—and the exciting discoveries that have characterised the last decade of research in adaptive radiation—have spurred a new and exciting era of evolutionary genomics research. These discoveries are not only relevant to adaptive radiation but have also enhanced our understanding of the pace and trajectory of evolution in diversifying lineages. Future research on the topics explored in this review will continue to deepen, and in some cases, revolutionize our understanding of adaptive radiations and the mechanisms that generate biodiversity.

Author Contributions

All authors contributed to circumscribing the scope of this paper, doing literature-based research on its subject, and writing the paper.

Acknowledgements

We would like to thank Dave Tank, Malia Santos, Sean Harrington, Josh Jahner, Dolph Schluter, the Schluter Lab at the University of British Columbia, and current and former members of the Wagner Lab at the University of Wyoming for comments on previous drafts of this manuscript. This work was supported by NSF Grants 2224892 and 1556963 to C.E.W. J.A.R. was supported by an NSF Postdoctoral Research Fellowship in Biology (Award 2109825). L.L.C. was supported by a Four Year Fellowship from the University of British Columbia.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

No new data was generated for this paper.

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