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EDITORIAL

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Capturing the rapidly evolving study of adaptation

Abstract

Research on the genomics of adaptation is rapidly changing. In the last few decades, progress in this area has been driven by methodological advances, not only in the way increasingly large amounts of molecular data are generated (e.g. with high-throughput sequencing), but also in the way these data are analysed. This includes a growing appreciation and quantitative treatment of covariation among units within the same data type (e.g. genes) or across data types (e.g. genes and phenotypes). The development and adoption of more and more integrative tools have resulted in richer and more interesting empirical work. This special issue – comprising methodological, empirical, and review papers – aims to capture a 'snapshot' of this rapidly evolving field. We discuss in particular three important themes in the study of adaptation: the genetic architecture of adaptive variation, protein-coding and regulatory changes, and parallel evolution. We highlight how more traditional key themes in the study of genetic architecture (e.g. the number of *loci* underlying adaptive traits and the distribution of their effects) are now being complemented by other factors (e.g. how patterns of linkage and number of *loci* interact to affect the ability to adapt). Similarly, apart from addressing the relative importance of protein-coding and regulatory changes, we now have the tools to look in-depth at specific types of regulatory variation to gain a clearer picture of regulatory networks. Finally, parallel evolution has always been central to the study of adaptation, but now we are often able to address the question of whether – and to what extent – parallelism at the organismal or phenotypic level is matched by parallelism at the genetic level. Perhaps most importantly, we can now determine what mechanisms are driving parallelism (or lack thereof) across levels of biological organization. All these recent methodological developments open up new directions for future studies of adaptive changes across traits, levels of biological organization, demographic contexts and time scales.

1 | INTRODUCTION

The study of adaptation occupies a central position in evolutionary biology. Understanding how the evolutionary process results in adaptation allows us to clarify how a substantial portion of the biological diversity around us has arisen. Researchers strive to use the most appropriate tools to uncover the mechanisms of adaptation and their genomic bases. Perhaps the most obvious example of this has been the gradual shift towards techniques which allow us to obtain large amounts of genetic data. While in the early 1990s studies often adopted one or very few genetic markers, such as mitochondrial DNA fragments, today studies utilizing thousands of *loci* scattered throughout the genome, scored with genome complexity reduction techniques such as RAD-Seq (Franchini et al., 2017; Peterson et al., 2012), are the norm. In fact, when assaying genetic variation throughout the entire genome, studies without genome reduction techniques are now commonplace due to the rapid decline in sequencing costs.

Increasing the amount of data obtained, however, does not necessarily bring new or deeper insight about the evolutionary process. In other words, the rush to "sequence more" does not, in itself, provide the answer to any evolutionary question. Sequencing more is extremely popular in the field because it allows us to capture variation that may not otherwise be captured, which in turn may permit greater understanding of the evolutionary process. This seemingly trivial point is the reason behind another trend in the field: the development of analytical methods that take advantage of the properties of large-scale data, now regularly considering patterns of covariation within and across data types.

When genome scale datasets started accumulating, the obvious methodological choice was to score the same kind of statistics at each position of the genome as previously used on one or a few genetic markers, for instance F_{ST}. These SNP-by-SNP "scans" of the genome – and related approaches such as averaging a given statistic over several SNPs in a window – are still common, useful and used, also in our own work (Christmas et al., 2021; Fruciano et al., 2016; Jones et al., 2019; Raffini et al., 2017; Xiong et al., 2021). However, these approaches are now being complemented by other analytical tools that capitalize on patterns of covariation. For instance, a recent genome-scale approach allows the detection of adaptive introgression by analysing patterns of genetic diversity at groups of neighbouring *loci*. Such analyses often exhibit a "volcano" shape with reduced genetic diversity at the locus of introgression, in combination with increased diversity relative to background in the flanking

regions (Setter et al., 2020). This method – which exploits the fact that genetic variation is scored at high resolution throughout the genome and focuses on patterns of covariation among neighbouring *loci* – is clearly conceptually distinct from an approach where genetic variation is scored separately at each locus or averaged across *loci*. Similar reasoning applies to approaches (and their empirical applications) that make use of recombination rate variation for improved parameter inference, or which describe covariation in gene expression among transcripts by using networks (Fruciano et al., 2019; Langfelder & Horvath, 2007; Ravindran et al., 2021; Zhang & Horvath, 2005). Conceptually, all these tools make use of covariation *within* a certain data type. Similarly, tools that quantify, describe and exploit covariation *across* data types are increasingly popular. These tools typically represent each data type as a multivariate array to quantify or characterize the covariation between them. This novel approach permits investigation of questions as diverse as the association between ecological variables and genetic variation (Capblancq et al., 2018), or the genetic basis of variation in adaptive traits (Fruciano et al., 2016; Maga et al., 2015; Mitteroecker et al., 2016).

Clearly, the field is currently experiencing an exuberance of new integrative ways of studying adaptation and new knowledge amassed by using them. We aimed to capture a snapshot of recent advances in the study of adaptation when organizing a symposium on the 'Genetics and genomics of adaptation' at the 2019 Congress of the European Society for Evolutionary Biology. The congress was held in Turku (Finland), and was one of the last large conferences in our field prior to the COVID-19 pandemic. The special issue assembled here represents the logical next step after the symposium. We think the symposium – and this special issue – are timely because a suite of analytical and methodological advances are being adopted very rapidly and are transforming the way we study adaptation. We suggest that the support our symposium received, with one of the highest numbers of submissions, reflects not only the popularity of the topic of adaptation, but also the fact that the field is rapidly developing and thus facilitating the growth of a wealth of new ideas and tools. This special issue aims to crystallize, in journal article form, a diverse and exciting set of methodological novelties and empirical findings. For instance, Schneider et al. (2021) conducted a simulation study to explore how well diverse statistics can detect selective sweeps in recently diverged populations. They find that, among 16 summary statistics, a recently developed summary statistic and a more traditional F_{ST} performed best. Importantly, by simulating several conditions, Schneider et al. (2021) show that different summary statistics perform best in different conditions. Selveshwari et al. (2021), in contrast, utilized a combination of experimental evolution and high-throughput sequencing approaches. These authors used the bacterial system *Escherichia coli* to investigate: (a) whether the same selection pressure (ultraviolet radiation, UV) might lead to different evolutionary outcomes depending on the organism's physiological state (i.e. whether selection is applied during the lag or the exponential growth phases of these bacteria); and (b) whether the similar significant reduction in sensitivity to UV observed in both aforementioned treatments relative to control populations were accompanied by convergent or distinct genomic signatures. These two papers flank the diverse spectrum of topics covered in this special issue (Table 1). We note that the genomics of adaptation field is very extensive. Thus, rather than reviewing the field in its entirety, we here focused on three key topics in the study of adaptation examined by articles in this special issue: the genetic architecture of adaptive variation, the relative importance of regulatory and protein-coding evolution, and parallel evolution.

2 | GENETIC ARCHITECTURE OF ADAPTIVE VARIATION

Traditionally, "genetic architecture" refers to how genotypes are mapped to phenotypes. This includes the number of genes and alleles underlying a given trait, the distribution of effect sizes (i.e. the relative contribution of each gene to the final phenotype), as well as the relationships between genes and alleles (e.g. pleiotropy, dominance, epistasis) and with the environment (Hansen, 2006; Mackay, 2001; Timpson et al., 2018). We can expect that these properties of genotype-phenotype mapping influence whether and how adaptive evolution unfolds.

TABLE 1 List of papers in this special issue

Paper	Taxon	General topic
Hartke et al. (2021)	*Crematogaster levior* (ants)	Genetic parallelism
Kelley et al. (2021)	*Poecilia Mexicana* (Teleost fish)	microRNA expression
Montoya et al. (2021)	Coronaviridae (viruses)	Selection during host switch
Ravindran et al. (2021)	*Daphnia galeata* (Cladoceran crustacean)	Response to predation risk
Schneider et al. (2021)	Methodological	Detection of signatures of selection
Selveshwari et al. (2021)	*Escherichia coli* (bacterium)	Evolution of resistance
Vanhove et al. (2021)	*Quercus suber* (tree)	Climatic adaptation
Yamaguchi et al. (2021)	Chondrichthyans and other nonosteichthyan vertebrates (fish)	Evolution of opsin genes
Zueva et al. (2021)	*Salmo salar* (fish)	Genetic parallelism

Even a casual look at empirical studies of adaptive evolution reveals an abundance of genetic architectures underlying adaptive variation. Indeed, traditionally a contrast – a rift almost – has existed among evolutionary biologists between a perspective emphasizing one or few major or exclusive *loci* affecting a given trait versus a perspective postulating many *loci* of small effect. Exemplifying the former perspective of few relevant genes are the many studies focusing a priori on specific genes and gene families, which are typically chosen based on prior knowledge suggesting higher than average adaptive effects. A case in point is opsins – a family of genes classically studied in evolutionary biology because of their relevance for vision. Despite the broad interest it elicits in the scientific community, this gene family has not been studied with equal effort across clades. Yamaguchi et al. (2021) review our current knowledge about opsins in cartilaginous fishes, an evolutionarily and ecologically important clade in which the study of these genes has not been as extensive as in other groups. Not only do Yamaguchi et al. (2021) review the functional role of variation in visual opsins for adaptation to various environments; they also discuss a group of nonvisual opsins and caution against drawing simplistic conclusions on the presence of a given opsin in a given species or clade based solely on assembled genomes. Indeed, despite recent methodological progress, de novo assemblies of genomes are often fragmented and incomplete, making it hard to conclusively rule out the presence of a given opsin gene in a species based on a genome assembly alone (Yamaguchi et al., 2021).

At the same time, a plethora of other studies make the more or less explicit assumption that several *loci* of small effect drive adaptation, particularly in the field of quantitative genetics (Sella & Barton, 2019). These studies often seek to identify *loci* of small effect and therefore must overcome both the problems of detection limits (which prevent the detection of all genetic variation underlying a given trait) and inaccurate effect size estimation (Slate, 2013; Xu, 2003). A vast body of research subscribes to this 'several-*loci*-of-small-effect' perspective by addressing questions such as the distribution of effect sizes (e.g. Baxter et al., 2009; Sinclair-Waters et al., 2020) and the importance of epistasis (e.g. Huang et al., 2012; Shao et al., 2008). Recent progress in sequencing technologies and analyses of 'omic' data have further bolstered the importance of genes of small effect, and more generally of polygenic adaptation (Barghi et al., 2020; Barton et al., 2017; Boyle et al., 2017; Kautt et al., 2020; Sella & Barton, 2019). On the one hand, the availability of large genomic datasets has allowed us to pick up subtle variation. On the other hand, sequencing more has spawned a series of methodological problems. For example, the number of SNPs analysed in genome-wide association studies (GWAS) has increased over time. At first, the potentially higher power of detecting variation brought about by dense genome-wide genotyping was counteracted by a loss of power due to having to correct for multiple tests (as essentially one test was performed on each SNP). However, the subsequent development of more lenient approaches to control for multiple comparisons (Storey & Tibshirani, 2003), as well as methods which increase power in other ways such as controlling for background variation (e.g. Lee et al., 2011; Tucker et al., 2014), has provided us with an effective increase in power. That is, with the combination of high-throughput sequencing and more sophisticated data analysis we can now identify more loci *and* loci of smaller effect. It is not surprising, then, that in recent years a great deal of emphasis has been placed on genes of small effect, both in theoretical and empirical work (Barton et al., 2017; Boyle et al., 2017).

Recently, interest in other factors that affect the ability to adapt has complemented the study of genetic architecture of polygenic adaptive traits as traditionally defined (Barghi et al., 2020). Sources of heterogeneity which, given a certain architecture of a polygenic trait, affect the ability to adapt include recombination, the distribution of *loci* across the genome, and more generally patterns of gene linkage (Barghi et al., 2020). For instance, different studies have asked whether the genes responsible for the variation in adaptive traits are randomly distributed throughout the genome or rather cluster in specific regions of the genome (e.g. Fruciano et al., 2016; Jacobs et al., 2017). These questions inform our understanding of adaptation because the fact that genes are not independent from each other (i.e. the physical linkage of two genes on the same chromosome) can promote rapid divergence (Flaxman et al., 2014). Because adaptive variation can be observed both within (populations or species) and between evolutionary units (e.g. different populations adapted to different conditions), and because linkage can promote rapid divergence, linkage can potentially account for our ability to observe distinctly adapted evolutionary units.

Similar perspectives (e.g. about the number of genes underlying adaptation or their distribution across the genome) arise not only when studying a clearly defined focal trait of adaptive value, but also when investigating adaptation to certain environments more generally. For example, Vanhove et al. (2021) used landscape genomics to investigate population structure and genetic variation in cork oak (*Quercus suber* L. 1753) across the Mediterranean basin and found evidence of weak population structure along an east-west gradient. The authors also identified 265 SNPs associated with various environmental factors, particularly temperature. This evidence suggests that climatic adaptation is highly polygenic in this species.

The co-existence of two different perspectives – one focusing on one or a few genes and the other focusing on very many genes underlying adaptive variation – highlights that these perspectives are not really antithetic but are part of a continuum. This is likely why there has been a recent shift of focus towards the question of which conditions – rather than how many genes – promote adaptive change. These 'conditions' may include the interplay between gene number, patterns of linkage and gene flow, how many traits are actually involved in adaptation and their genetic correlations, plus other factors. For instance, in sticklebacks different numbers of *loci*, effect sizes and patterns of linkage of these *loci* have been identified depending on the specific trait being investigated (Chan et al., 2010; Miller et al., 2014; Peichel & Marques, 2017). Among many other factors to consider, a temporal perspective is useful, because whether we detect a few 'dominating' genes may often depend on the phase of the adaptive process we are looking at. This is perhaps more easily appreciated in fast-evolving clades. For example, Montoya

et al. (2021) analysed molecular evolution and adaptation in seven RNA viruses (including SARS-CoV-2) belonging to the Coronaviridae family that are known to have gone through host-switching events (zoonoses). By looking at genomic data, they observed that unlike other viral replication proteins, in the spike protein the sites under positive selection are inversely related to the time since the virus colonized the human population. Montoya et al.'s (2021) results highlight the value of understanding the mechanisms of adaptation in coronaviruses following host shifts – knowledge that can inform public health responses. Perhaps more importantly in the context of this special issue, their study also reinforces the idea that observing different phases of the adaptive process may suggest different scenarios in terms of the distribution of effects across *loci* and their relative importance for adaption. This is because when sampling soon after a host switch (as opposed to later), one would infer a much greater contribution of a given gene relative to others that may become involved or detectable only later.

While distinct studies of the same process (such as in the stickleback case) are useful for understanding the conditions under which certain elements of genetic architecture aid in adaptation, future work seeking quantitative integration of disparate factors (e.g. several traits) within studies should facilitate even more insight into the genetic architecture of adaptation.

3 | PROTEIN-CODING VERSUS REGULATORY ADAPTIVE VARIATION

Another long-standing question in evolutionary biology revolves around whether adaptive genetic variation occurs predominantly in protein-coding or in regulatory regions of genes (Carroll, 2005; Hoekstra & Coyne, 2007; Wray, 2007). Historically, the evolution of coding sequences has been considered the most prominent source of phenotypic evolution. For this reason, and because of technological limitations, studies aimed at understanding the molecular mechanisms behind adaptive divergence mainly targeted protein-coding sequence variation (Hoekstra & Coyne, 2007; Wittkopp & Kalay, 2012; Wray, 2007). However, since the seminal work by Britten and Davidson (1969) – who first proposed that regulatory changes play a fundamental role in phenotypic diversification –there has been a steady increase in research on the gene regulatory mechanisms that underpin intra- and inter-specific variation in gene expression and how such mechanisms can promote adaptive divergence (Hill et al., 2020).

In the last decade in particular, tremendous progress in molecular biology and bioinformatics has facilitated the development of new, widely accessible toolboxes for analysing genome-wide variation and for quantifying the expression of thousands of genes from several samples or experimental conditions in both model and non-model species. For instance, Ravindran et al. (2021) sought to uncover the genetic basis of phenotypic variation in *Daphnia* for traits of adaptive value under high predation risk. By using genotypic and phenotypic data in genome-wide association in combination with weighted gene co-expression network analyses, these authors identified several candidate transcripts associated with relevant life-history traits. This work emphasizes the complexity of the interaction between genotype, phenotype and environment, as well as the importance of regulatory evolution.

Thanks to recent methodological advancements, the general comparison of protein-coding and regulatory regions as main drivers of adaptive evolution is rapidly shifting towards quantitative rather than qualitative procedures. The increased resolution at which we can address this general question has also brought about a clear set of sub-questions. Similar to research on the genomic architecture of adaptive traits, one can now ask whether the number of genetic changes is larger in protein-coding or regulatory regions, how different their average effect is, and even whether the cumulative effect of protein-coding changes is greater than the cumulative effect of regulatory changes, or what the relative importance of the two changes is at different time scales. This methodological progress thus allows us to look deeper into the broad categories of "protein-coding" and "regulatory" genomic region variation.

Regulators of gene expression are commonly categorized into *cis* and *trans* components, depending on how they control the expression of a specific gene. While *cis* elements (e.g. promoters, enhancers, microRNA binding sites) modify the expression of a physically linked gene in an allele-specific fashion, *trans* elements are diffusible products (e.g. transcription factors, RNA molecules) that can regulate the expression of distant genes by binding their *cis*-regulatory DNA sequences (Signor & Nuzhdin, 2018). Among the gene regulatory candidates, *cis*-regulatory mutations have long been proposed as the most promising targets for adaptive phenotypic evolution (Benowitz et al., 2020; Wittkopp & Kalay, 2012). Differently from protein-coding sequences that are thought to evolve under strong purifying selection, *cis*-regulatory elements are subjected to more relaxed selective constraints. That is because changes in protein-coding sequences equally affect every single cell and stage of an organism. Therefore, these changes can typically have more pleiotropic effects than changes in *cis*-regulatory elements. Likewise, *trans* regulatory elements are thought to have a high degree of pleiotropy because of the large number of *cis*-regulatory regions they can potentially bind to. For this reason, and because their effects are often recessive, *trans* elements are considered highly conserved. Conversely, *cis* components can affect gene expression only spatially (i.e. in merely some cells or tissues) or at different developmental stages. Further, *cis*-regulated genes tend to occupy less central positions within transcriptional networks (Benowitz et al., 2020; Yang & Wittkopp, 2017). This evidence suggests that *cis*-mutations are less likely to be deleterious and can accumulate (slowly) over time under selective pressures and contribute to between-species divergence (Gordon & Ruvinsky, 2012; Nourmohammad et al., 2017).

Several evolutionary studies investigating genetic polymorphism in noncoding regions have detected signatures of positive selection in the *cis*-regulatory sequence space, suggesting that polymorphisms in these regions might play a substantial role in local adaptation. Among the best examples, Chan et al. (2010) found that

the molecular changes driving the repeated reduction in the pelvic girdle observed in separate populations of sticklebacks, a stunning case of phenotypic adaptation, reside in a noncoding genomic region controlling the linked Pituitary homeobox transcription factor 1 gene (*Pitx1*). Similarly, Real et al. (2020) revealed how regulatory genomic rearrangements are associated with adaptive intersexuality in the Iberian mole (*Talpa occidentalis*). These authors found that altered expression of the androgen-converting gene CYP17A1 and the pro-testicular factor gene FGF9 could be a key molecular mechanism promoting female mole masculinization. Mole-specific misexpression of these genes was linked to structural reorganization of *cis*-elements with enhancer activity that is present exclusively in the mole lineage.

The unprecedented availability of massive genomic resources now allows us to study the complex interplay between *cis* and *trans* mechanisms in driving the evolution of gene expression. For instance, error-free chromosome-level genome assemblies (Rhie et al., 2021) are now used to produce high quality whole-genome alignments in which thousands of regulatory elements from different species can be annotated and analysed in a phylogenetic framework to identify signatures of selection. These genomic signals, when combined with gene expression profiling from both genome-wide or candidate approaches and with phenotypic measures of traits with known or potential adaptive value, are providing new insights for the emerging field of adaptation genomics.

These new data are revealing how *cis* and *trans* factors might generally destabilize gene expression, but that a compensation between these two factors operates to re-stabilize it (Fraser, 2019; Signor & Nuzhdin, 2018). This is in line with previous work that proposed stabilizing selection as the main mode of evolution for gene expression (Hodgins-Davis et al., 2015). However, not only *cis*, but also *trans* regulatory adaptive variation can overcome this compensatory mechanism, be inherited, and give rise to lineage-specific expression patterns. Among *trans*-regulatory factors, microRNAs (miRNAs), short noncoding RNAs that repress the expression of a gene by preferentially binding its 3' untranslated region (3'UTR), are emerging as key players in the establishment of adaptive variation (Li et al., 2016). It has recently been shown how novel miRNAs could have a rapid turnover, as they can be easily gained and lost even across closely related taxa (Zlotorynski, 2019). This has been observed, for example, in cichlid fish, a lineage that is known to undergo extensive and fast adaptive radiations (Brawand et al., 2014; Franchini et al., 2016, 2019; Xiong et al., 2019). Reduced levels of purifying selection have been observed in miRNA binding regions of the 3'UTR in this rapidly evolving group of fish as compared to other clades (Brawand et al., 2014; Franchini et al., 2016, 2019; Xiong et al., 2019). This is consistent with the idea that noncoding portions of the genome – including target genes and their regulators – can be less constrained than coding portions. But more importantly, this finding in cichlid fish also suggests that for the same type of noncoding region relevant to gene regulation, the more 'flexible' clades at these regions (i.e. the ones able to accumulate more changes) are also more likely to produce adaptive change. Thus, substantial evidence shows that variation in miRNAs can promote diversification in rapidly evolving lineages so they quickly adapt to different environments. For instance, Kelley et al. (2021) identified several miRNAs differentially expressed in the gills of the freshwater fish *Poecilia mexicana* collected at two geographically nearby springs, one rich in hydrogen sulphide and the other not. This study paves the way for future studies to investigate the importance of miRNAs in fish adaptation to sulphidic environments. More generally, new research is demonstrating how both the gain of novel miRNAs and sequence variation at their target sites might represent an additional layer of regulatory complexity which can drive phenotypic divergence and adaptation (Franchini et al., 2019; Kelley et al., 2021; Li et al., 2016; Xiong et al., 2019). However, there is still much work to do to fully understand these complex regulatory mechanisms and their contribution to phenotypic diversity and lineage-specific adaptations.

Overall, future work focussing on positive, balancing and diversifying selection acting on genomic regions (either protein-coding or regulatory) as well as on intra and inter-specific *cis* and *trans* differences in gene expression under different environmental conditions will be crucial for better depicting their relative contribution to adaptation and speciation.

4 | PARALLEL EVOLUTION AND ADAPTATION

Parallel evolution constitutes a special focus in the study of evolution because it provides strong evidence for adaptation. It is commonly defined as the evolution of similar phenotypes or genotypes in multiple independent populations, in response to similar selection pressures, from similar initial conditions (Bolnick et al., 2018). Although traditionally there has been debate over how the term parallel evolution can be best defined, as well as how the terms convergent versus parallel are differentiated, a view that has recently been gaining impetus is that these terms are defined by the geometry of evolution in trait space (details reviewed in Bolnick et al. (2018)).

Importantly, taking advantage of the framework of parallel evolution can be extremely helpful when studying the genomic basis of adaptive variation. If the same adaptive pattern occurs in parallel, we can more easily assess which genomic-scale characteristics are also repeated, and studying multiple populations independently evolving in parallel enables us to distinguish deterministic selection from stochastic genetic differentiation (Berner & Salzburger, 2015; Haenel et al., 2019). Investigating the replicated independent evolution of similar traits when phylogenetically related taxa have been exposed to similar adaptive pressures increases the statistical power for inferring the genetic basis of adaptive variation (Elmer & Meyer, 2011; Manceau et al., 2010; Schluter, 1996; Walsh et al., 2019; Wood et al., 2005). That is, we are using instances of parallel evolution as a tool to understand the genetics and genomics of adaptation. At the same time, such instances of evolution of similar traits or trait

values – when supported by appropriate tests of parallel evolution – steer us towards the inference that evolution was driven by a deterministic process, often assumed to be natural selection (Bolnick et al., 2018; Harvey & Pagel, 1991).

In general, evolutionary biologists tend to use cases of repeated, parallel evolution of genes, phenotypes, or ecotypes to infer that (a) similar environments exert similar selection pressures, (b) selection favours only a few solutions and (c) the genes or traits that evolve in parallel are adaptations (Bolnick et al., 2018). However, the repeatability of these natural experiments in evolution is debated, and evidence for strong selection playing a role in parallel evolution at the genetic level is often equivocal because many different genetic routes can produce similar phenotypic outcomes (Bailey et al., 2016; Burns & Novikova, 2020).

Understanding how selection pressures are acting on species is particularly key in the face of anthropogenic habitat disturbance and a changing climate. This is especially so because the ability of models to predict evolutionary responses to environmental change rests on a high level of determinism of the process. Evidence suggests that evolution may be sufficiently predictable under some scenarios of climate change (Bolnick et al., 2018; Langerhans, 2018). Thus, tests for parallel local adaptation to climatic selection pressures of closely related insect species in sympatry (e.g. Hartke et al., 2021) can be useful in this context. Such studies of parallel evolution often address the general issue of the determinism of evolutionary change by testing whether similar adaptive outcomes at the organismal or phenotypic level depend on similar underlying genomic variation. In a sense, by asking how parallel evolution arises, these studies treat parallel evolution not as a tool, but as the object of investigation. For example, in this special issue, Hartke *et al*. investigated populations of two closely related largely sympatric cryptic ant species occurring along a climate gradient in neotropical French Guiana. The authors used genomic and environmental data, as well as variation in cuticular hydrocarbons. In social insects especially, cuticular hydrocarbons are not only important for protection against desiccation but are also used in communication and species recognition. All results were compared between the two species to understand whether local adaptation is operating in parallel or is lineage specific. Interestingly, Hartke et al. (2021) show that although these ant species are exposed to the same environmental selection pressures, genetic variation associated with local climate adaptation is largely nonparallel.

In a similar vein, Zueva et al. (2021) focused on investigating whether the same genetic architecture repeatedly underlies local adaptation in Atlantic salmon of the Barents-White Sea in north-eastern Russia and north-western Finland/Norway. The authors asked whether the same genomic regions are involved in local adaptation in salmon populations from three close but geographically distinct and genetically disjunct areas. Using a 220K SNP array the authors found that only a small fraction of those genomic segments (or haploblocks) putatively associated with local adaptation are shared across the three areas. Interestingly, the few shared haploblocks contain *loci* previously found to be associated with variation in life history traits and immune responses.

Results such as those found in Hartke et al.'s (2021) and Zueva et al.'s (2021) work highlight that replicated adaptive evolution can be due to largely nonparallel changes at the genetic level. Other recent studies have similarly documented limited parallelism at the genetic level despite substantial parallelism at the organismal or phenotypic level (e.g. Bainbridge et al., 2020; Elmer et al., 2014; Salisbury et al., 2020). In contrast, other studies find largely parallel, repeatable changes at the genetic level (e.g. Alves et al., 2019). Another level of complexity derives from the fact that even when the level of genetic parallelism is low, at the transcriptomic level highly parallel changes may be observed. For instance, high parallelism in gene expression and splicing, with at the same time limited genetic parallelism, has been reported across Arctic charr populations that independently evolved similar phenotypes (Jacobs & Elmer, in press). Such heterogeneity in findings across studies necessitates the reformulation of research approaches used when investigating parallel evolution. For instance, there is an increasing push for treating parallel evolution as a quantitative continuum from parallel to nonparallel, rather than as a binary phenomenon (Bolnick et al., 2018; Oke et al., 2017). This trend is also supported by improvements of how we conceptualize and quantify parallelism in the first place (e.g. De Lisle & Bolnick, 2020). Further, it is increasingly clear that adaptive parallel change at the phenotypic and organismal level can be the product of a mixture of parallel and nonparallel changes at the genetic level (Therkildsen et al., 2019). Finally, there is growing evidence that redundancy in the genotype-phenotype map (i.e. redundancy at the level of genetic architecture) can produce both parallel and non-parallel genetic changes underlying the same phenotypic adaptive variation (Barghi et al., 2020), thus highlighting the importance of other factors, including stochastic effects. These recent developments and the clear realization that there is no 'one-size-fits-all' answer open up new and exciting directions for future studies investigating adaptive changes across traits, levels of biological organization, demographic contexts and time scales along the parallel/nonparallel continuum.

5 | CONCLUSIONS

Did we succeed in capturing the enormous, rapid change in the study of adaptation? If we had aimed to capture all of the changes in the field, our efforts would have been in vain and misguided. The field is moving way too fast and in way too many directions to capture it completely in one special issue. Nonetheless, we suggest that this special issue crystallizes the current state of the field for a key set of topics in terms of open questions, new methods and empirical evidence. In this sense, we hope this special issue contributes to our understanding of how a substantial portion of the extraordinary diversity of life around us came to be.

KEYWORDS
adaptation, genetic architecture, genomics, genomics of adaptation, parallel evolution, regulatory evolution

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CONFLICT OF INTEREST
The authors have no conflict of interest to declare.

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All authors have created a first draft of the text and all of them have contributed to its refinement producing the final version.

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