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SYNTHESIS

Comparative phylogeography in the genomic age: Opportunities and challenges

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Abstract

Aim: We consider the opportunities and challenges comparative phylogeography (CP) faces in the genomic age to determine: (1) how we can maximise the potential of big CP analyses to advance biogeographic and macroevolutionary theory; and (2) what we can, and will struggle, to achieve using CP approaches in this era of genomics.

Location: World-wide.

Taxon: All.

Methods: We review the literature to discuss the future of CP - particularly examining CP insights enabled by genomics that may not be possible for single species and/or few molecular markers. We focus on how geography and species' natural histories interact to yield congruent and incongruent patterns of neutral and adaptive processes in the context of both historical and recent rapid evolution. We also consider how CP genomic data are being stored, accessed, and shared.

Results: With the widespread availability of genomic data, the shift from a single- to a multi-locus perspective is resulting in detailed historical inferences and an improved statistical rigour in phylogeography. However, the time and effort required for collecting co-distributed species and accruing species-specific ecological knowledge continue to be limiting factors. Bioinformatic skills and user-friendly analytical tools, alongside the computational infrastructure required for big data, can also be limiting.

Main conclusions: Over the last ~35 years, there has been much progress in understanding how intraspecific genetic variation is geographically distributed. The next major steps in CP will be to incorporate evolutionary *processes* and community perspectives to account for patterns and responses among co-distributed species and across temporal scales, including those related to anthropogenic change. However, the full potential of CP will only be realised if we employ robust study designs within a sound comparative framework. We advocate that phylogeographers adopt such consistent approaches to enhance future comparisons to present-day findings.

KEYWORDS
community genomics, congruence, discordance, landscape community genomics, macrogenomics, multi species analysis

1 | INTRODUCTION

The term *phylogeography* was first proposed in 1987 to describe the phylogenetic analysis of genetic data in a geographic context (Avise et al., 1987). In addition to advocating for a combined phylogenetic and population genetic perspective, phylogeographers pushed for the extrapolation of micro-evolutionary processes into the macro-evolutionary realm (Avise et al., 1987; Hickerson et al., 2010; McGaughran, 2015). Although the initial concept was framed as explicitly comparative, many papers that followed often considered only a single species (Knowles, 2009), making it difficult to identify shared responses by many co-distributed taxa to the same landscape-level event. By identifying common patterns among co-distributed taxa, we can better uncover the underlying effects of geography, species (i.e. traits), and their interactions, to eventually encompass biogeographic scales (Blanchet et al., 2017; Riddle, 2016). Such is the ambition of *comparative phylogeography* (CP) (Bermingham & Moritz, 1998).

It is 35 years since Avise et al.'s (1987) pioneering paper, with influential decadal review papers by Bermingham and Moritz (1998), Hickerson et al. (2010), Edwards et al. (2021, 2022), and various contributions to a Proceedings of the National Academy of Sciences CP special issue (Avise et al., 2016). Despite an increasing uptake in both phylogeography and CP research in the years since, most studies still focus on micro-evolutionary processes within single species (Figure 1). Yet, over time, the potential for phylogeography has moved well beyond a reliance upon a single organellar locus, such as animal mitochondrial DNA (mtDNA), to include genome scale investigations. Likewise, CP has moved to comparisons of genomes across multiple species. Next generation sequencing technologies have enabled *genomic* approaches, where intraspecific variation can be extracted from thousands of markers up to entire genomes to address complex phylogeographic questions for many species of interest (Edwards et al., 2015; Hendricks et al., 2018). However, there are also signs that perhaps phylogeographic studies have reached their apex in popularity and that comparative studies have always struggled to gain traction (Figure 1, Edwards et al., 2021). Thus, now is a good time to consider the opportunities and challenges we face in the genomic era and our potential motivations for CP over coming decades. For example: What can CP practitioners do with genomic data that we could not do with data from one or a few loci? What insights do genomic comparisons across species enable? How can we weave together population and landscape genomic data with phylogenomics to deepen our understanding of the relationships between micro- and macro-evolution?

Large-scale *comparative* population genomic research can greatly advance biogeographic and macroevolutionary theory (Blanchet et al., 2017; Marske et al., 2013; McGaughran, 2015). With better ways of estimating evolutionary parameters (e.g. divergence times, gene flow, population size), we can go beyond asking whether *patterns* are concordant and see whether *processes* are concordant among co-distributed species. In some scenarios (e.g. simple vicariance), we have a good understanding of neutral processes, but our growing ability to genotype increasing numbers of putatively adaptive loci will enable us to contrast spatial patterns of adaptive divergence with neutral (non-adaptive) spatial patterns to identify the underlying geographic contributors to selection. Further, a comparative genomic framework gives us the ability to develop expectations and improve forecasting regarding evolution in the Anthropocene when, among other factors, selective pressures, dispersal rates, and species interactions are changing at an unprecedented pace.

Our purpose in this review is to discuss CP in the genomic age, using a broad definition of phylogeography to encompass studies of intraspecific genetic variation in a geographic context regardless of specific analytical approaches. We span three major topics: (1) Recognising temporal and spatial congruence; (2) Considering adaptive and neutral population processes; and (3) CP in the Anthropocene. We also discuss ways that CP practitioners can store, access, and share CP outcomes (Box 1).

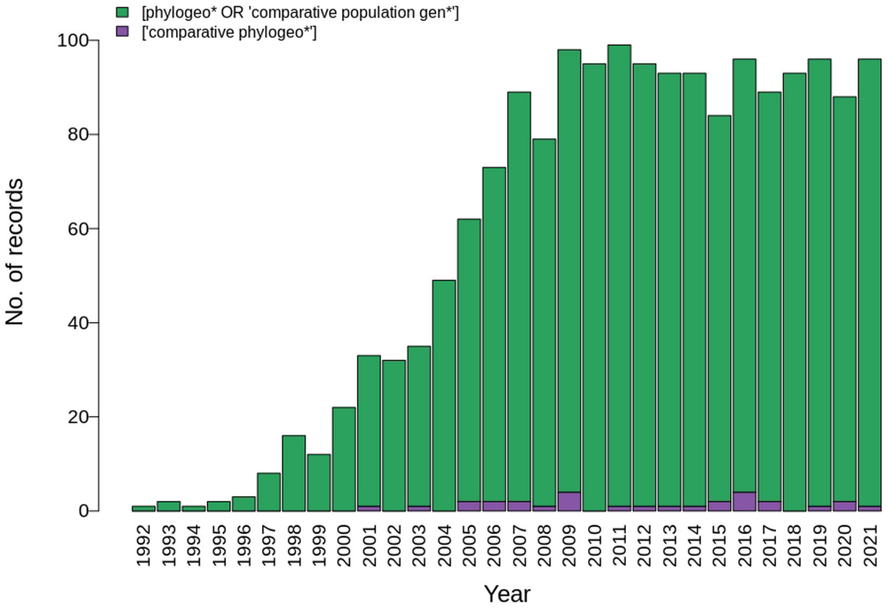

FIGURE 1 Uptake of phylogeography and comparative phylogeography research since Avise et al. (1987) coined the term 'phylogeography'. Searches were performed on Web of Science (28 February 2022) using the terms [phylogeo* OR 'comparative population gen*'] and ['comparative phylogeo*'] applied to title, abstract, and author key words. The number of records in each year from 1992 to 2021 is plotted here, with the number of records obtained from the latter search term presented as a fraction (purple) of the number obtained with the former search term (green).

BOX 1 Accessing and sharing CP data

Performing investigations that are both truly comparative and genomic necessitates large efforts for sample acquisition and subsequent analysis. Thus, reuse and re-analysis of previously published genomic surveys is appealing and can augment new empirical investigations. Previous CP approaches have included mining literature for genetic summary statistics (e.g. Gaither et al., 2013; Lawrence et al., 2019; Selkoe et al., 2014; Sexton et al., 2014), or retrieving existing data from sequence repositories (e.g. Gratton, Marta, Bocksberger, Winter, Trucchi, et al., 2017; Miraldo et al., 2016) using automated data retrieval (e.g. custom scripts: Barrow et al., 2020; SequinR: Charif & Lobry, 2007; rentrez: Winter, 2017), followed by georeferencing, quality control and analysis (e.g. Diversity of the Indo-Pacific database, 'popgendb': https://github.com/DIPnet/popgenDB, phylogatR: Pelletier et al., 2022). While these approaches deliver compelling portrayals of intraspecific genetic patterns across multiple species (reviewed in Leigh et al., 2021), their utility for CP studies interested in the *processes* determining multi-species *genomic* patterns is limited given that: raw data supporting new analyses might not be accessible; there may be biases or deficiencies in which data and metadata are deposited (Paz-Vinas et al., 2021; Toczydlowski et al., 2021); and samples across species are not likely to be spatially or temporally aligned.

Another approach has been the formation of coordinated research networks, where researchers co-sample species towards a common goal (e.g. the IntraBioDiv Consortium of 27 alpine plant species: https://www.wsl.ch/en/projects/intrabiodiv.html) or curate and contribute datasets (e.g. Diversity of the Indo-Pacific Network with >200 marine organism datasets: https://diversityindopacific.net/). By aggregating raw data, these coordinated efforts provide a greater diversity of potential analyses and comparative inferences. These large collaborative exercises have also guided best-practice required to enable datasets to be interoperable and re-usable for future CP research. Whereas genomic data are readily available in public repositories (e.g. INSDC: http://www.insdc.org/; DataDryad), the associated metadata to provide a full context for phylogeographic research (i.e. location and date of sampling) are often missing (Gratton, Marta, Bocksberger, Winter, Keil, et al., 2017; Pope et al., 2015; Toczydlowski et al., 2021). Nonetheless, coordinated efforts have informed metadata standards appropriate for raw genomic sequence data (e.g. the Minimum Information about any Sequence [MIxS] metadata standards; Field et al., 2008) and the development of "metadatabases", such as the Genomic Observatories Metadatabase (GEOME: www.geome-db.org; Deck et al., 2017; Riginos et al., 2020). GEOME is a keep-safe for metadata relevant to genomic datasets held in INSDC repositories, providing contextual information that is important for informing CP analyses (e.g. georeferences, associated organisms, and whether the individual was sampled from a wild population). The platform also enables the coordination of collaborative projects (e.g. the Ira Moana Project; Liggins et al., 2021), where researchers can design a common metadata template, share tissue availability, sequencing progress (Riginos et al., 2020), and cultural permissions and responsibilities pertaining to the data (e.g. Liggins, Anderson, & Hudson, 2021). Uptake in the use of community metadata standards and best-practice deposition to complement the community's uniform use of INSDC would ensure greater resources for CP in future.

Future CP studies would also be enhanced through increased availability and interoperability of (meta)data repositories for relevant biological, ecological, and environmental data not already described (e.g. including phylogenetic corrections and/or ecological niche models that draw from occurrence records, Marske et al., 2013). For instance, advances in the genomic resources available for human populations and agricultural systems, and corresponding phenotypic data have instigated the generation of public repositories for phenotype data alongside genomic data (e.g. NCBI dgGaP database, Mailman et al., 2007; International Grapevine Genome Program: https://www6.inrae.fr/iggp, Adam-Blondon et al., 2016; GnPIS, Steinbach et al., 2013). These systems enable persistent links between genotype–phenotype (and sometimes environment) data, allowing a greater diversity of analyses than currently possible for CP studies on wild populations.

2 | RECOGNISING TEMPORAL AND SPATIAL CONGRUENCE

A fundamental and long-standing goal of CP is to determine whether there are common geographic and temporal patterns of genetic diversity and divergence among populations of co-distributed species that have arisen in response to common historical events and processes. Because pre-genomic investigations could only describe phylogeographic diversity for one or a few genetic loci (notably organellar sequences such as mtDNA for animals and chloroplast DNA for plants, along with microsatellite genotyping across taxa), precision and accuracy in the parameter estimates suffered from limited genetic sampling. Genome-wide surveys, such as RADseq (reviewed by Andrews et al., 2016) and increasingly whole genome sequencing (reviewed by Bourgeois & Warren, 2021; Therkildsen & Palumbi, 2016), have refined methods for interrogating historical demographic processes—particularly changes in effective population size and joint estimates of divergence and gene flow. Many loci can yield additional resolution for CP inferences about historically recent events (i.e. Holocene and Anthropocene). Concurrently, fine scale geographic and environmental information (e.g. http://www.paleoclim.org/) has become readily available, allowing associations between landscape and genomic diversity to be explored. Finally, a growing interest in species traits within ecology and evolution (Violle et al., 2014), including within a phylogeographic context (Donihue et al., 2020; Papadopoulou & Knowles, 2016; Zamudio et al., 2016), provides a lens for more nuanced questions about concordance and discordance. Together, these new tool sets and approaches allow comparative phylogeographers to test refined hypotheses focusing on the *processes* that shape genetic biodiversity.

Coalescent approaches that can support demographic inferences aiming to infer divergence timings, population size changes, and gene flow are now a standard component of the CP toolkit (see Edwards et al., 2021 for extended review). Often historical parameters are appraised for each species individually and commonalities are observed or related to expectations based on geographic history and species traits (e.g. Edwards et al., 2016; Marske et al., 2020; Satler & Carstens, 2017; Thomaz & Knowles, 2020). This is the case, for example, for the widespread use of sequentially Markovian coalescent methods, where users often overlay species plots showing changes in effective population size through time in order to make broad inferences about congruent (or incongruent) species responses to paleo events (Li & Durbin, 2011; Schiffels & Durbin, 2014). Unified demographic analyses drawing upon approximate Bayesian computation (Hickerson et al., 2006; Oaks, 2019; Oswald et al., 2017; Xue & Hickerson, 2015; Xue & Hickerson, 2020) advance these approaches in a specific CP context by formalising comparisons across species to identify sets of taxa that have experienced demographic events with concordant timing. Such analyses have been used to show synchronous population expansions (e.g. for grass species of the sky islands in the trans-Mexican volcanic belt, Mastretta-Yanes et al., 2018); identify co-distributed species with synchronous, and asynchronous population expansions (e.g. for reef fishes of the Pacific Ocean, Delrieu-Trottin et al., 2020; and Australian tropical skinks, Potter et al., 2018); and reveal that the timing and locations of population expansions differ among species (e.g. for three South American lizards; Prates et al., 2016). Similarly, examinations of demographic vicariance dates have provided evidence for synchrony (such as for eight population pairs of riverine anadromous versus freshwater lampreys Xue & Hickerson, 2020) and asynchrony for population pairs of co-distributed species (for instance, six Peruvian birds separated by a common biogeographic barrier, Xue & Hickerson, 2020; and geckos across never connected Philippine islands, Oaks, 2019). These studies have been remarkable in quantifying certainty in temporal concordance, however in comparing species in a hierarchical model that treats species' traits as 'nuisance' parameters that are not inferred with data (even if they are paramaterised to vary across taxa; e.g. effective population sizes, generation times, etc), they primarily focus on shared patterns.

Hierarchical models developed for this kind of 'trait-less' inference can nevertheless consider species traits explicitly, as exemplified by landmark studies in gall wasps (Bunnefeld et al., 2018; Stone et al., 2012). In the more recent work, Bunnefeld et al. (2018) tested four competing models of community assembly for four herbivorous gall wasps and nine of their parasitoids from the Western Palearctic. Composite likelihood frameworks that accommodated uncertainty of parameter estimates for each species were used to show that community history was not random and yet hosts and parasitoids did not necessarily share a concordant history, thereby refuting scenarios of strict co-dispersal or host tracking (Bunnefeld et al., 2018). This work highlights a promising direction for exploring how temporal concordance and discordance results from interactions between traits and environments—an essential but mostly unrealised objective of CP.

To date, methodological developments to confirm or refute concordance have focused nearly exclusively on temporal aspects, while methods for detecting spatial concordance have been less integrated with coalescent theory and continue to emphasise pattern (i.e. comparative landscape genomics: Rissler, 2016) over process. Similar to temporal concordance, spatial patterns are typically appraised for each species individually and then qualitatively compared. However, summary statistics derived from genomic data could readily be interrogated with established methods for identifying and testing multi-species spatial phylogeographic concordance, such as boundary detection (as in Soltis et al., 2006; Garrick et al., 2008; Pelc et al., 2009; Rissler & Smith, 2010) or genetic diversity shifts (Arranz et al., 2022). In principle, the aforementioned multi-species spatial methods could be based on demographic parameter estimates, such as genetic effective population size, changes in population size, and dispersal; for example, Crandall et al. (2019) showed that spatial patterns inferred from coalescent genealogy sampling among co-distributed marine species in the Hawaiian archipelago were largely consistent with stepping-stone migration among islands. Unified methods that can interrogate spatial commonalities for demographic processes among multiple species, however, remain to be developed. Although not CP in context, recent advances in spatial population genomic simulation pipelines (e.g. SLiM, Haller & Messer, 2019; msprime, Kelleher et al., 2016) allow modelling of demographic inference at different spatial scales (Battey et al., 2020; Bradburd & Ralph, 2019). The SLiM and msprime-associated tree-sequence methodology is of particular note, as it incorporates all ancestry information for an entire simulated population (Haller et al., 2018; Kelleher et al., 2018). Such approaches are increasingly relevant to the evolutionary dynamics of wild populations and their unification with CP could be transformative.

Additionally, because spatial concordance varies among co-distributed species, incorporation of species' traits (including ecology and life history) into hypotheses can yield significant insights into the interaction between phenotype and landscape history in shaping genomic variation (Papadopoulou & Knowles, 2016; Zamudio et al., 2016), thereby extending to focus on underlying spatial processes. For example, population genomic results matched species-specific expectations for past habitat connections for two broadly co-distributed mountain sedges with distinct ecological niches (Massatti & Knowles, 2016). Similarly, a promising approach for inferring spatial locations of past refugia (He et al., 2017) was applied to hickories to show that putative refugial locations and subsequent routes of expansion differed between the two tree species, consistent with their contrasting ecological attributes (Bemmels et al., 2019).

The data richness of genomic CP datasets also greatly expands our ability to infer detailed species' histories of landscape usage, including gene flow and range expansion, potentially informing when concordance should be expected. For example, Marske et al. (2020) investigated regional phylogeographic patterns in two forest beetles and found that concordance of process (geographic expansion) was only detected in regions of New Zealand that were recolonised by both species following glaciation. In contrast, species-specific range dynamics were detected in regions previously shown to harbour glacial refugia for at least one of the two species (Marske et al., 2012), highlighting a relationship between landscape history and likelihood of phylogeographic concordance among species. Similarly, Thom et al. (2021) tested for cross-species associations between distribution, latitude, and elevation for 21 Neotropical bird species *prior to* generating species-specific estimates of genetic connectivity. They found that genomic differentiation among populations was predictable according to Janzen's hypothesis that suggests rates of dispersal in tropical mountains are lower than in mountains at other latitudes (Janzen, 1967; Thom et al., 2021). These studies and other detailed evaluations (e.g. Petkova et al., 2016) re-affirm the importance of species-specific natural history in informing expectations of spatial congruence and point to promising new approaches within CP to evaluate expectations a priori (e.g. the use of species distribution models, Carnaval et al., 2009; including models and patterns of co-occurrence, Pollock et al., 2014; and incorporating evolutionary dynamics and environmental change, Bocedi et al., 2021).

A practical challenge common across CP is the need for co-distributed samples to be able to make robust inferences, especially to test hypotheses based on spatial patterns and processes. Whereas genomic studies have greatly increased the number of loci per species, spatial resolutions (number of sampled locations, number of individuals sampled per location) are typically lower in phylogenomic studies as compared to classical low marker phylogenetic studies (Garrick et al., 2015). Sparse spatial coverage, especially when several species are sampled from somewhat different locations, can contribute to spatial pseudocongruence (sensu Soltis et al., 2006), whereby multi-species genetic attributes are concordant at a coarse spatial resolution but incongruent at fine scale resolutions, suggesting different causative processes among species. However, few ecological communities can realistically be sampled comprehensively across species, geography, and loci given time and budget constraints. A nice exception is the work of Salces-Castellano et al. (2019), who barcoded all members of a beetle assemblage in Tenerife and then applied reduced representation sequencing to the 16 species that spanned the whole study system in order to identify shared locations where alleles abruptly shift frequency (while reliance on a single locus is not genomic, the sampling strategy is inspiring). In a second CP study notable for standardised geographic sampling, large-scale replication, and use of phylogenetic contrasts, Harvey et al. (2017) showed that genomic diversity and differentiation in 20 species-pairs of Amazonian birds were greater in birds living in upland forests versus those inhabiting floodplains, matching expectations based on birds' dispersal opportunities in these two habitats. The systematic geographic sampling in these examples is an excellent first step, while incorporating homologous loci would extend the capacity for functional insights from these comparisons. Baited target capture is a variant of reduced representation sequencing (Jones & Good, 2016) that might be especially useful for CP focused on certain taxon groups, as homologous loci can be sequenced from each species (e.g. using ultra-conserved elements, 'UCE,' baits; Lim et al., 2020) provided they share these loci. Data synthesis approaches that utilise best-available, rather than purpose-collected, data will undoubtedly continue to be used for comprehensive insights into the influence of species attributes and geographic histories on CP but necessitate spatial interpolation or averaging due to uneven sampling across species (Box 1), so that authors and readers should be alert to conclusions potentially affected by spatial pseudocongruence. For the foreseeable future, compromises are required with respect to number of species, extent and density of sampled locations, and number and type of loci, with optimisation appropriate to a study's intent (Gagnaire, 2020).

Moving forward, we anticipate that CP investigations will increasingly draw upon ecological principles to test for consistent histories based on species traits and associations—for example, strong concordance could be more frequent among co-distributed species with similar ecological attributes or among those that are closely interacting—thereby bringing the field closer to the longstanding goal of community phylogeography (Hickerson et al., 2010; Marske et al., 2013). Such focused endeavours will provide key insights into the dynamics of ecological communities over time, especially during periods of past rapid climate change (Hand et al., 2015; Moritz & Agudo, 2013). Along with improved methodologies, and quantitative modelling, genomic-scale phylogeographic datasets present bioinformatic and analytical challenges and these hurdles clearly increase with the number of species. Consequently, unified multi-species phylogeographic analyses (such as Bunnefeld et al., 2018; Xue & Hickerson, 2020) will continue to require considerable initial study to propose a small set of reasonable and likely population models for testing from the large number of possible models. Genome-wide loci also present challenges for molecular dating of events that inherently relies upon valid estimates of mutation rates (as well as species generation times), which are not well known for most species and loci. Additionally, recombination rates affect covariances among loci (Gagnaire, 2020). Locus-specific selection histories (see next section) and genetic architecture will also certainly affect phylogenomic inference, yet we have no tools at present for incorporating these factors into multi-species comparisons. Thus, there is great scope for analytical developments that can detect a variety of phylogeographic patterns across many loci, many populations, and many species (Garrick et al., 2015; Oaks et al., 2020).

3 | CONSIDERING ADAPTIVE AND NEUTRAL POPULATION PROCESSES

Whereas there is a rich literature regarding comparative investigations of intraspecific histories (see previous section), comparative research on adaptive diversity is just beginning. Enabled by our recent capacity to genotype putatively adaptive loci across multiple taxa, such approaches aspire to reveal spatial patterns of adaptive divergence. Ultimately, a comparative programme of adaptive diversity will seek to uncover the extent to which causes of environmental selection are concordant (and therefore predictable) or idiosyncratic across geographies and species.

Identifying loci that are adaptive even for a single species, however, remains a daunting proposition. Often researchers will employ criteria based on tests of selection to categorise loci as adaptive versus neutral (discussed in Balkenhol et al., 2017; Liggins et al., 2019). But this simplification represents a false dichotomy given that the extent to which a locus' history has been shaped by selection is contingent upon its linkage relationships, recombination neighbourhood, and interactions with other loci (Cutter, 2013). Indeed, methods for detecting outlier loci that are candidates for selection are burgeoning and most empirical studies report a surprisingly high prevalence of outliers (e.g. reviews by Ahrens et al., 2018; Riginos et al., 2016). Instead of environmental attributes, these outliers may correspond with other mitigating factors, such as genomic regions of reduced recombination (so called islands of differentiation) and intrinsic reproductive isolation between co-occurring ecotypes (Bierne et al., 2013; Booker et al., 2020; Cruickshank & Hahn, 2014; Stevison & McGaugh, 2020; Yeaman & Whitlock, 2011).

Only a few studies have explicitly examined spatial patterns of adaptive genetic diversity among co-distributed taxa by looking for replicated associations between outlier genotypes and environmental variables (genotype environment association tests–GEA: reviewed by Rellstab et al., 2015). These studies have highlighted a diverse array of outcomes. For example, Hanson et al. (2017) used the IntraBioDiv dataset (Meirmans et al., 2011) to show that multivariate environmental gradients predicted modest amounts of allelic turnover in outlier AFLP (amplified fragment length polymorphism) loci for 8 out of 27 European Alp plant species, suggesting weak but predictable concordance for adaptive diversity among some species in this community. This study illustrates spatial replication across species but not necessarily shared genomic response given that AFLP loci are undoubtedly not homologous. In a contrasting example, environmental variables and outlier loci completely differed in spatial responses in a SNP (single nucleotide polymorphism) survey of lodgepole and jackpole pine sister species (Cullingham et al., 2014). Similarly, comparison of two co-distributed corals found that ~0.1% of RAD (Restriction site associated DNA) loci of the brooded (low dispersal) species were outliers that showed replicated allelic associations with depth, whereas none of the outlier RAD loci for the broadcast (high dispersal) species showed allelic differentiation by depth (Bongaerts et al., 2017). Finally, in a striking example of genomic and phenotypic concordance, early and normal migrating phenotypes of both steelhead and cutthroat salmon were strongly associated with the genomic region encompassing the *GREB1L* gene, suggesting a potential role for this gene in premature dispersal (Prince et al., 2017). These behavioural phenotypes (and associated alleles) were sympatric in some populations for each salmon species and thus the genomic architecture of adaptation appears concordant, although adaptive diversity was not strictly concordant geographically (Prince et al., 2017). Collectively, these early examples hint at the diversity of possible outcomes that might be observed as the number of studies examining adaptive genetic diversity in a CP framework grows.

In general, convincingly demonstrating GEA is difficult and, as more studies seek to compare spatial patterns of adaptive diversity across co-distributed species, it is important to consider the sorts of situations that could lead to spurious spatial concordance of putatively adaptive variants. For example, using GEA to identify shared environmentally-structured gradients between species is problematic as the input environmental attribute(s) for each species would be inherently correlated: asking whether species share common GEA patterns may just recapitulate correlations arising from the shared environmental predictors (Figure 2). However, finding that the same locus or loci with similar functions respond to the same environmental variables would constitute convincing evidence for convergence or parallelism. In general, aspatial criteria for detecting outlier loci are more defensible in the context of uncovering concordance (or discordance) among species, as concerns with latent spatial correlation structures are reduced.

Of course, there are alternative explanations for widespread regional phenomena that do not necessarily arise from environmentally-based selection. This includes range expansions out of refugia, which can affect allelic distributions among co-distributed species, especially when species ranges have shifted in spatially similar manners. In general, expansion fronts (Klopfstein et al., 2006) are associated with high drift and create population structure between the species core and the periphery; for example ~30% of polymorphic SNPs in humans show differences among continents (Hofer et al., 2009). Indeed, false positives in selection tests are often associated with population expansions (Lotterhos & Whitlock, 2014). Shared histories of range expansions among species, such as those out of glacial refugia, could lead to concordant spatial patterns between species for outlier loci (which may also align with environmental gradients: Figure 2). Therefore, a sensible precaution in designing a multi-species survey would be to consider past climate and habitat distributions to identify regions of the species' ranges likely to have been recently occupied. In addition, false positives are less prevalent directly along the axis of expansion as compared to those along an angle relative to the expansion (Frichot et al., 2015), so comparative studies should ideally sample along the most likely expansion direction.

Suture zones (sensu Remington, 1968), where many species have a history of secondary contact, also create situations where spatial concordance of allelic differentiation is expected and may be incorrectly attributed to environmentally-mediated selection (Figure 2). Intrinsic reproductive incompatibilities are well-known to arise in allopatry and will subsequently cause elevated genetic differentiation for affected genomic regions across zones of secondary contact (Barton & Bengtsson, 1986; Barton & Hewitt, 1985). It is less widely appreciated, however, that alleles from such intrinsic incompatibility

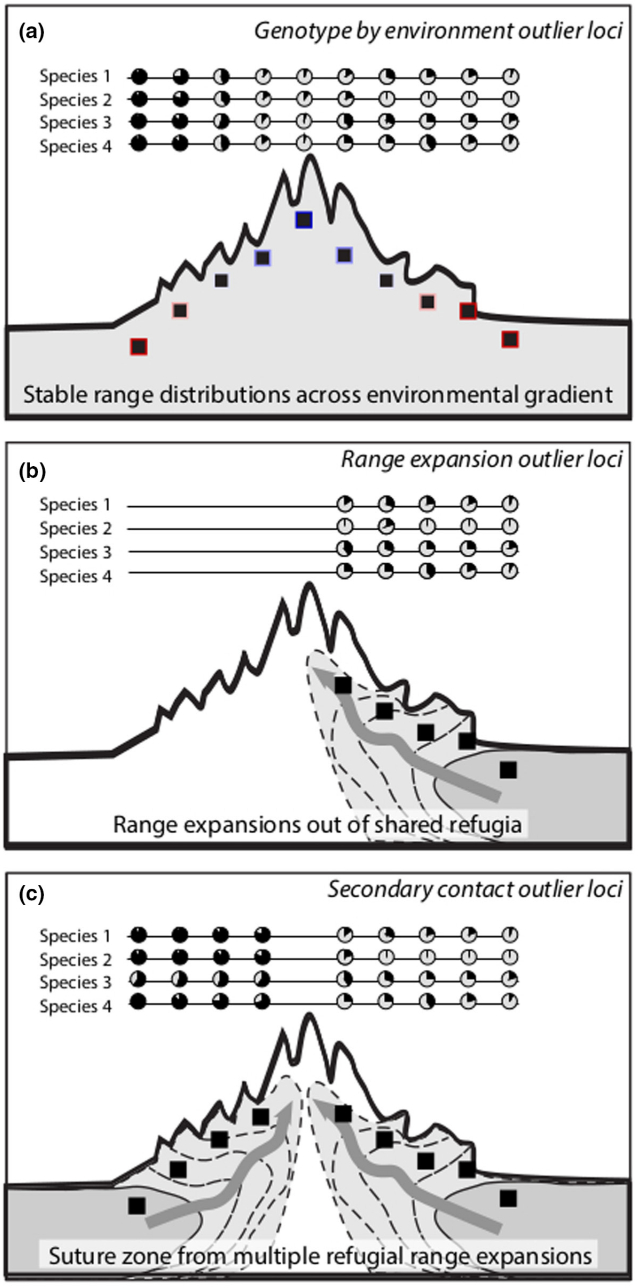

FIGURE 2 Scenarios leading to spatial concordance among allele frequency gradients of outlier loci from co-distributed species for a hypothetical scenario where multiple species inhabit a mountain and adjacent valleys. (a) Species are arrayed along one or more environmental gradients. Outlier loci identified by genotype by environment association analyses, where the same environmental variable (altitude-related temperature in this example) was used to identify outlier loci for each species. Because of the shared environmental predictor, the outlier loci will show correlated allele frequency shifts. (b) Species have common routes of expansion from a shared refugial area. Progressive bottlenecks arising from stepping-stone colonisation will enhance genetic drift and may result in correlated geographic structure for outlier loci across species just by chance. (c) Species have common routes of expansion out of multiple refugia and a suture zone of secondary contact (hybrid zone) maintains partial genetic differences among populations. Alleles can be trapped by geographies of low gene flow and may also be linked to genome regions that contribute to reproductive isolation between taxa. These three scenarios are not mutually exclusive. Squares indicate sampling sites (with ambient temperature on a red to blue gradient for a). Pie charts indicate allele frequencies for a single representative outlier locus per species sampled.

loci are also likely to show turnover coincident with environmental features (Bierne et al., 2011), and may become "trapped" by barriers to dispersal (Barton & Hewitt, 1985; see also several single species examples reviewed by Bierne et al., 2011, including complex mosaic hybrid zones). Because co-distributed species experience the same environmental features and may be affected by similar dispersal barriers, spatial patterns of genetic differentiation may be similar across species and may even show striking GEA without such loci necessarily being directly involved (or linked) with environmentally adaptive variants. Thus, comparative studies of adaptive diversity should be especially alert to sampling species and landscapes where admixture and semi-permeable dispersal barriers could be expected.

Detailing the comparative geographies of adaptive genetic diversity represents an exciting new direction for phylogeography that will continue to increase in tractability as genomic methodologies become more accessible and less expensive. Nonetheless, it will be important for investigators to consider species' histories when designing sampling strategies and to robustly consider alternative (non-selective) explanations for emergent patterns. Genomic resources, especially genetic maps and recombination rates, will be invaluable for uncovering (or rejecting) such alternative explanations (Cutter, 2013; Hoban et al., 2016) and will, in some cases, provide greater insight regarding the nature of spatial adaptive variation (Yeaman & Whitlock, 2011). Given CP's longstanding concern with inferring demographic histories across geography, insights from CP can support appropriate sampling and subsequent interpretation of patterns revealed by putatively adaptive loci.

4 | CP IN THE ANTHROPOCENE

Although the tools of CP have advanced in leaps and bounds, there are inevitable limitations on the temporal resolution of environmental changes and species' responses when working with events thousands to millions of years before present. The Anthropocene (here defined as 1610 to present; Lewis & Maslin, 2015) provides an unprecedented opportunity for researchers to examine the kinds of processes that have shaped species ranges and phylogeographies through recent time, giving us valuable insight into the past and perhaps prescient warnings for the future. At the broad (community) scale, selective pressures may lead to coordinated shifts in species demography, resulting in a re-distribution of genetic diversity and adaptive potential across species ranges (see Sections 2 and 3). However, population responses will ultimately be determined by a combination of genetic, demographic, and species' attributes, as well as stochastic processes. Thus, the rapid change and short time frames over which populations are responding to anthropogenic change may plausibly lead to the detection of more stochasticity in individual species responses, and less synchronous responses across species, than recovered in CP studies in relation to historical events.

Anthropogenic activities, including landscape and atmospheric modification, are having increasingly detrimental impacts on the natural environment. The most comprehensive studies to date have used mitochondrial or microsatellite loci to link inferred strong changes in effective population size (and therefore reductions in genetic diversity) to climate-drivers. For example, a meta-analysis of marine fishes using 140 species and >11,000 microsatellite loci found that allelic richness was 12% lower in over-harvested populations (Pinsky & Palumbi, 2014). Similarly, mitochondrial analysis of >90,000 sequences from >4500 species found that habitats experiencing a greater scale of human impact hold less genetic diversity (Miraldo et al., 2016), but no such pattern was found in a later study of >175,000 mitochondrial sequences and >17,000 species (Millette et al., 2020). These findings suggest that the factors potentially impacting 'evolvability' (i.e. adaptive capacity) among species are complex and that 'global' analyses (reviewed in Leigh et al., 2021) may not best resolve impacts that are potentially location- and/or species-specific. However, such large datasets may be useful for 'predictive phylogeography', including the identification of cryptic diversity (e.g. Espíndola et al., 2016; see Fitzpatrick & Keller, 2014 for a smaller example that marries genomic data and community-level modelling). Linking changes in genomic data through time to environmental drivers (see Section 3) is a key requirement for future anthropogenic research.

One approach would be to study instances of parallel evolutionary responses to rapid environmental change. Although comprehensive exploration of synchronous responses (neutral or adaptive) to contemporary environmental change is lacking, Gagnaire (2020) outlined a standardised framework for this that combines historical demographic and selective parameters with contemporary measures of genetic connectivity among populations for species occupying the same geographic region. However, the emerging field of 'comparative population genomics' faces similar logistical challenges to those studies focused on historical concordance or shared adaptive variation — constrained by trade-offs, for example, between numbers of species/loci considered. Thus, current empirical work in this space predominantly uses pairs of different species, or time-separated pairs of the same and/or different species, to examine evolutionary changes through time. For example, Christmas et al. (2021) applied a comparative population genomics approach to cryptic bumblebee sister species and identified loci specific to sympatric populations that had acted as barriers to gene flow. Similar studies contrasting recently-diverged species (e.g. Papadopulos et al., 2019; Stankowski et al., 2019) will become increasingly important for understanding community genomic responses to anthropogenic impacts, such as habitat fragmentation (McGuire et al., 2016).

In another area for CP extension, single-species methods which co-infer demographic and selective parameters based on temporal shifts in allele frequency (e.g. Pavinato et al., 2021), could be extended to multi-species CP approaches based on homologous loci sampled over time to quantify the effects of selection and drift on populations and species. Another way to capture this information is provided by evolve-and-resequence studies, where populations are evolved under selective conditions and (re-)sampled over time. The covariance among time points and replicates can be used to estimate the fraction of allele frequency change through time that is driven by selection versus drift (which should lack a temporal association; Buffalo & Coop, 2020). Experimental evolution approaches are already providing information about the co-option of standing genetic variation towards rapid adaptation (Chaturvedi et al., 2021); moving forward, complex evolve-and-resequence experiments that combine a multi-species CP element with challenging environmental pressures could provide intriguing insights into concerted rapid evolutionary responses to anthropogenic changes.

Finally, CP could be extended to utilise time-series data. In particular, signatures of rapid adaptation can be directly measured using preserved museum and/or herbarium specimens or ancient DNA (aDNA), with partial and even complete genomic sequences increasingly recoverable from historical and ancient remains (Slatkin & Racimo, 2016). For example, a study of alpine and lodgepole pine chipmunks used genomic data spanning >100 years to compare evolutionary responses to climate change and found that no SNPs had changed in frequency over time for the lodgepole pine chipmunk, nor for southern populations of the alpine chipmunk (Bi et al., 2019). However, a small number of sites in a gene coding for immune inflammatory response and hypoxia showed signals of selection consistent with climate change having caused substantial upward contraction of the alpine chipmunk's distribution (Bi et al., 2019). In another example, mollusc shells have been found to preserve not only the DNA of their host organism, but also the associated microbial community (Der Sarkissian et al., 2017, 2020). This rich archival source has already shed light on historical distributions of haplotypes (e.g. Hayer et al., 2021) and illustrates the potential for combining contemporary and historic population genomics to better understand the factors contributing to current phylogeographic patterns and to tell us what contemporary samples never can: what genetic variation has been lost. Access to entire communities in a microcosm further highlights the potential for detection of genomic community-scale responses through time (e.g. Lorenzen et al., 2011) if advances in next generation sequencing make aDNA research tractable in a comparative genomic framework. In particular, collaborative projects that will provide reference genomes for many species (see Box 1) will enable targeted analyses of homologous loci from species in an environmental DNA (eDNA) sample and advances in genome-skimming (Malé et al., 2014; Ripma et al., 2014; Weitemier et al., 2014) have the potential to liberate (meta)genome-scale information from aDNA and eDNA.

Although we have the sequencing technology to determine whether species have the genomic infrastructure to respond to change (e.g. by turning standing variation towards new functionality; Beheregaray et al., 2014; Chaturvedi et al., 2021; Rosenblum et al., 2010; Waters & McCulloch, 2021), the link between paleo- or historical-genomics and CP is currently largely unrealised (but see Fordham & Nogues-Bravo, 2018; Raxworthy & Smith, 2021). Future research aimed at comparing standing genetic variation from the past to that found today, in a multi-species CP framework, will reveal the extent to which signatures of rapid evolution may drive parallel or distinct genetic changes across both populations (Campbell-Staton et al., 2017; Schiebelhut et al., 2018) and species. This holds the promise of uncovering genomic patterns that will help us recognise and estimate the potential of groups of species to adapt to rapid and extreme environmental change in the future.

To decipher broad Anthropocene impacts on evolution, we need to better understand whether evolution is predictable (and therefore repeatable and reproducible), as well as identify the genomic signatures or features that motivate or facilitate rapid adaptation (McGaughran et al., 2021). Often, selection on important traits can be polygenic and different species or even populations may have a different genomic solution to the same problem. As whole genome data become more widely available, detecting multiple loci of small effect will become more tractable, but deciphering their meaning will remain a challenge. Careful CP genomic studies–particularly targeting the currently single- or few-species research outlined above–may enable us to better detect subtle shifts in community dynamics from background noise, leading to improved understanding of the importance of co-evolution in promoting the stability of communities experiencing anthropogenic impact (e.g. Hart et al., 2019; Nuismer et al., 2018). Such descriptive CP analyses will provide a rich diversity of studies to further examine the mechanisms of rapid evolutionary change by combining genomic analyses with quantitative genetics and experimental evolution (Bonneaud et al., 2011).

5 | CONCLUSIONS

In the 35 years since "phylogeography" was coined by Avise et al. (1987) and applied in a comparative context, we have made much progress in understanding how intraspecific genetic variation is geographically distributed. In the shift from a single- to a multi-locus perspective, we are starting to extract detailed historical inferences and have improved the statistical rigour of phylogeography (Hickerson et al., 2010). As outlined here, the next major steps in CP will be to incorporate evolutionary processes (selection, gene flow, etc.) and community perspectives to look for responses among co-distributed species and across temporal scales. But we caution that the full potential can be realised only if we also adopt a sound comparative framework.

We are less limited now by the challenges previously imposed by 'non-model' species (e.g. limited numbers of loci and the absence of a reference genome), and chromosome-scale reference genomes and widespread whole genome sequencing are now feasible, at least for species with modestly-sized (<0.5 Gb) genomes. A key emerging development is the use of whole genome sequencing for all individuals within a comparative population genomic study (e.g. Therkildsen & Palumbi, 2016) and we suspect the time when all sequences in such studies are reference quality is not that far off. As this happens, time and effort associated with collecting co-distributed species, robust study designs, and species-specific life history and ecological knowledge will each continue to be limiting factors. In particular, there is no substitute for an on-the-ground understanding of the natural history of the organisms we study or the nuances of the geography in which they occur—as such, in most regions of the world, acquiring this knowledge will be through collaboration with Indigenous peoples who have been stewards of the geographic regions and constituent species over the thousands of years we wish to study. And, while well-packaged and documented tools that lead a biologist from the field to the computer go a long way, bioinformatic knowledge and access to high powered computing resources can be limiting. Nonetheless, an important capacity-building question remains to be asked: assuming re-investment in fieldwork and unlimited computational power, are we actually ready for the analytical and collaborative challenges that CP in the genomic age brings?

With the advent of standard metadata use and infrastructures coincident with the burgeoning of genomics (Box 1), comparative phylogeographers stand to gain immense analytical power through breadth of datasets and depth of each included study. But, in an ideal world, we will see less segregation of fieldwork and bioinformatics, and more overlap from the field to data pipelines to inference. Thus, an emergent theme for the future is collaboration—in data gathering, storage and sharing, analysis, and dissemination.

With continued advances in modelling approaches and statistical rigour, collection of increasing numbers of genomic datasets for groups and communities of species, and the application of inference towards relevant and pertinent biological questions, including those related to the particular opportunities unfortunately provided by Anthropocene change, we are well positioned to advance CP towards new and exciting insights. In ensuing years, we particularly look forward to new understanding of the *processes* that account for patterns among co-distributed species and their genomic, and other (e.g. environmental) responses; and the harnessing of this new-found knowledge towards informed actions that address the challenges of the biodiversity crisis.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.-

DATA AVAILABILITY STATEMENT

No datasets were generated for this study.

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BIOSKETCH

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