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Integrating evolutionary genomics of forest trees to inform future tree breeding amid rapid climate change

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ABSTRACT

Global climate change is leading to rapid and drastic shifts in environmental conditions, posing threats to biodiversity and nearly all life forms worldwide. Forest trees serve as foundational components of terrestrial ecosystems and play a crucial and leading role in combating and mitigating the adverse effects of extreme climate events, despite their own vulnerability to these threats. Therefore, understanding and monitoring how natural forests respond to rapid climate change is a key priority for biodiversity conservation. Recent progress in evolutionary genomics, driven primarily by cutting-edge multi-omics technologies, offers powerful new tools to address several key issues. These include precise delineation of species and evolutionary units, inference of past evolutionary histories and demographic fluctuations, identification of environmentally adaptive variants, and measurement of genetic load levels. As the urgency to deal with more extreme environmental stresses grows, understanding the genomics of evolutionary history, local adaptation, future responses to climate change, and conservation and restoration of natural forest trees will be critical for research at the nexus of global change, population genomics, and conservation biology. In this review, we explore the application of evolutionary genomics to assess the effects of global climate change using multi-omics approaches and discuss the outlook for breeding of climate-adapted trees.

Key words: forest trees, climate change, multi-omics, evolutionary genomics, breeding

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INTRODUCTION

The heightened emission of greenhouse gases and rapid climate change contribute to the increased frequency and intensity of extreme weather events, such as severe droughts, floods, frosts, and heat waves, as well as the proliferation of pests (Baker et al., 2018). These events are significantly altering distribution patterns and posing escalating threats to global biodiversity (Bellard et al., 2012). Forest trees, serving as foundational components of terrestrial ecosystems, not only provide diverse habitats for various organisms but also serve as crucial sources of raw materials essential for human needs, including building materials, paper products, and various tree-crop foods (Hamrick, 2004; Bonan, 2008). Concurrently, as primary carbon sinks in terrestrial ecosystems, forest trees play an increasingly pivotal role in combating and mitigating the effects of global climate change (Alberto et al., 2013; Borthakur et al., 2022). Nevertheless, the adverse impacts of abiotic and biotic stresses on forests due to the swift pace of climate change are expected to endure. This will impede the normal growth and development of trees, potentially even resulting in combined stress events (Seidl et al., 2017). Furthermore, for long-lived organisms such as trees, marked by long generation times and large population sizes, the risks of widespread maladaptation and/or adaptational lag in response to environmental changes are expected to be more severe (Gougherty et al., 2021).

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Understanding the genomic basis of local climate adaptation is crucial for assisting forests in coping with challenging environments (Savolainen et al., 2013; Hoban et al., 2016). Given the escalating unfavorable environmental fluctuations, the adaptability and vulnerability of species to climate change are going to be influenced predominantly by standing genetic variation (Barrett and Schluter, 2008). Standing variation forms the foundation for future climate adaptations, enabling species to shift distributions to new, available habitats and enhance their stress tolerance in response to changing environments (Waldvogel et al., 2020; Bernatchez et al., 2024). Consequently, there is a pressing need for concerted efforts to thoroughly explore the genetic components and molecular mechanisms underlying climate adaptation and stress tolerance in natural forest populations (Fitzpatrick and Edelsparre, 2018).

To achieve this, fundamental evolutionary theory needs to be leveraged and integrated into forest breeding and management, particularly in the context of global climate change (Aguirre-Liguori et al., 2021). In addition, comprehensive prediction and assessment of vulnerability to climate change are strongly needed for many threatened forest tree species (Bay et al., 2017; Capblancq et al., 2020a). Such knowledge will not only streamline the breeding process for more stress-resilient trees but will also provide a thorough background for devising more effective mitigation, conservation, and management strategies in response to local climate-change-induced extinctions before it is too late (Holliday et al., 2017; Varshney et al., 2018; Cortés et al., 2020; Fady et al., 2020).

In this review, we begin with a comprehensive overview of how evolutionary genomic approaches, alongside population and landscape genomics methods, can deepen our understanding of local climate adaptation in forest trees. Subsequently, we evaluate advances made by various omics technologies over the past decade, emphasizing the use of diverse methodologies to explore the interaction between natural genetic variation and epigenetic modification in influencing phenotypic evolution and climate adaptation. Finally, we outline future avenues for breeding and conservation of trees resilient to global climate change. Our objective is to integrate evolutionary genomic approaches into the design and implementation of future forest tree breeding strategies, ultimately leading to the cultivation of forest trees capable of adapting to changing climates.

THE VALUE OF INTEGRATING EVOLUTIONARY GENOMICS FOR UNDERSTANDING AND RESPONDING TO RAPID CLIMATE CHANGE IN FOREST TREES

Evolutionary genomics research has played a vital role in understanding and predicting the responses of species to a changing climate (Waldvogel et al., 2020). The identification of species, populations, and genotypes at greatest risk offers promising avenues for optimization of management and conservation strategies. This involves implementing methods such as assisted migration and genetic rescue, genetic monitoring of relocated populations, conservation of genetic diversity *in situ*, genome editing for climate resilience, and accelerated breeding programs specifically tailored for climate-adapted trees (Capblancq et al., 2020a; Isabel et al., 2020).

Advances in sequencing technologies, especially high-throughput sequencing technologies, have significantly broadened access to genomic resources, even for non-model species. However, it is undeniable that substantial gaps persist between our ability to generate data and our understanding of the processes that underlie adaptive evolution and responses to climate change. With the urgency to address more extreme environmental stresses, genomics emerges as a critical tool for understanding evolutionary history, local adaptation, and anticipated responses to climate change in natural forest trees. This understanding is crucial for research at the nexus of global change, population genomics, and conservation biology (Figure 1 and Supplemental Table 1).

Speciation and hybridization in the evolutionary history of forest trees

Characterizing the evolutionary history of a species or closely related species is crucial for advancing our knowledge and understanding of causation in biology. This includes insights into the origin of species, the history of migration and hybridization, and the evolutionary forces shaping patterns of genetic variation (Bourgeois and Warren, 2021). Prior to inferring the evolutionary history of any tree species, it is necessary to establish information on relatedness and population structure among individuals, populations, and species. Multiple methods are commonly used as a starting point to estimate population structure and delineate species; these include linear dimensionality reduction-based principal component analysis (Price et al., 2006), Bayesian clustering-based structure (Pritchard et al., 2000), and maximum-likelihood clustering-based admixture (Alexander et al., 2009). Furthermore, both maximum-likelihood methods, such as RAXML (Stamatakis, 2014), and Bayesian methods, such as BEAST (Drummond and Rambaut, 2007), are commonly used to construct phylogenetic trees and infer genealogical relationships among individuals.

Once species have been delimited, speciation histories and demographic processes can be inferred using methods based on the site frequency spectrum (SFS) and/or sequentially Markovian coalescent models (Beichman et al., 2018). Popular SFS-based methods, such as Fastsimcoal2 (Excoffier et al., 2021), are frequently used to infer divergence and demographic histories in forest trees. For instance, after selecting the best demographic model from 18 different models, two widespread tree species in the Northern Hemisphere, *Populus tremula* and *Populus tremuloides*, were found to have diverged around 2.2–3.1 million years ago (Wang et al., 2016). This timeframe coincides with the onset of Pleistocene climate oscillations and the existence of the Bering land bridge. In addition, various coalescent-based approaches have been developed to infer changes in population size over evolutionary histories; these include PSMC (Li and Durbin, 2011), MSMC (Schiffels and Durbin, 2014), SMC++ (Terhorst et al., 2017), and the recently developed FitCoal (Hu et al., 2023). These methods have been used to infer past demographic histories in numerous tree species, such as poplar (Wang et al., 2020a), ginkgo (Zhao

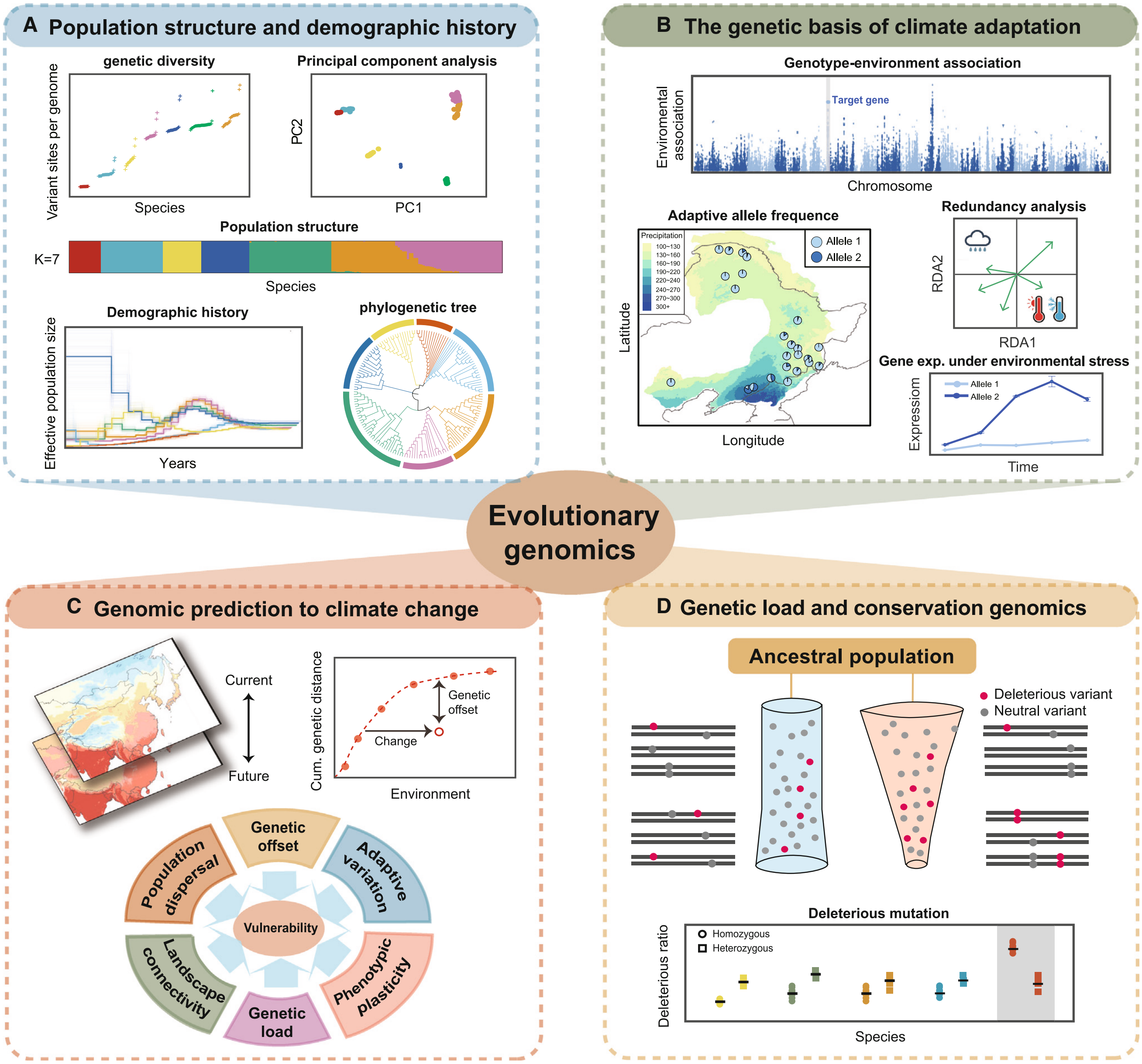

Figure 1. The value of integrating evolutionary genomics approaches and strategies for understanding and responding to rapid climate change in forest trees in four ways.

(A) Exploring population structure and demographic histories of targeted species and populations (adapted from Liu et al., 2022).

(B) Unraveling the genomic basis of local adaptation (adapted from Sang et al., 2022).

(C) Predicting genomic vulnerability to future climate change.

(D) Deducing genetic load and recent population fluctuations to guide conservation and management actions (adapted from Liu et al., 2022).

The corresponding software tools associated with each section are listed in Supplemental Table 1.

et al., 2019), oak (Liang et al., 2022), and the relict tree *Cercidiphyllum japonicum* (Zhu et al., 2020).

As we enter the era of whole-genome sequencing at the population level, genome-scale evolution has been found to be highly heterogeneous, with different genes and loci exhibiting distinct evolutionary histories. The discordance in gene trees across the genome poses a significant challenge to the estimation of species trees. Various biological processes and evolutionary events, including incomplete lineage sorting (ILS), ancient and recent hybridization, and natural selection, likely contribute to the pervasive heterogeneity in evolutionary histories observed across loci and genes throughout the Tree of Life (Stull et al., 2023). This complexity is particularly pronounced in forest tree species, which are generally characterized by large effective population sizes and high levels of genetic diversity, thus leading to prevalent ILS across species, lineages, and clades. In addition, as most tree species are outcrossing, interspecific hybridization and gene flow are important processes and are widely recognized to be both prevalent and important in genera such as *Populus* (Wang et al., 2020b), *Quercus* (Crowl et al., 2020), *Juglans* (Zhang et al., 2022), and other clades. Therefore, distinguishing the relative importance of ILS and hybridization in determining gene tree discordance has spurred the development of various summary statistics and approaches, such as ABBA-BABA statistics (Green et al., 2010), DFOIL (Pease and Hahn, 2015), HyDe (Blischak et al., 2018), and Twisst (Martin and Van Belleghem, 2017). Methods such as f_d statistics can be further used to quantify and identify introgressed genomic regions (Malinsky et al., 2021).

Recent studies have revealed that various evolutionary forces, such as demographic processes, hybridization load, natural selection, and recombination, have likely interacted in determining the ancestry landscape across the genome following hybridization (Moran et al., 2021; Liu et al., 2022). Analyses of genomic divergence between species during the early stages of speciation have consistently shown a heterogeneous landscape of genetic differentiation, with some regions exhibiting high levels of genetic divergence (i.e., F_{ST} and/or d_{xy}), often referred to as "genomic islands," that likely contain genes involved in mediating reproductive isolation (Bock et al., 2023). Numerous genome-scale studies have been conducted in tree species to identify genes potentially associated with speciation and reproductive isolation (Wang et al., 2016). A well-studied example is the origin of a homoploid hybrid species, *Ostryopsis intermedia*, which inherited alternative alleles from two parental species. One allele is associated with flowering time, and the other is linked to iron tolerance, resulting in premating isolation from both parents (Wang et al., 2021b). Taken together, a comprehensive exploration of the evolutionary histories of speciation, hybridization, demography, and divergent natural selection is crucial for understanding the factors that shape different patterns and levels of genetic variation within and among species.

The genetic basis of local adaptation in forest trees

Owing to high outcrossing rates, extensive gene flow, and significant phenotypic and genetic variation, long-lived perennial trees provide an excellent platform for comprehensive exploration of the genetic underpinnings of local adaptation across geographic landscapes (Savolainen et al., 2007; Isabel et al., 2020). Transplant experiments, including reciprocal transplant and common-garden trials, are considered the gold standard for investigating and assessing local adaptation across discrete habitats and environmental gradients (Sork, 2017). Reciprocal transplant experiments enable the examination of potential advantages specific to a home site by transplanting experimental accessions into at least two habitat types with contrasting environmental conditions (Price et al., 2018). In addition, provenance trial experiments involve more source populations and transplantation into multiple field gardens (VanWallendael et al., 2022). This is especially relevant for forest tree species whose geographic ranges span continuous environmental gradients rather than consisting of two or more distinct habitat types. Provenance studies also serve as invaluable resources for revealing the contemporary adaptational lag of local populations and assessing their capacity to cope with changing climates (Browne et al., 2019; Fady and Rihm, 2022; Leites and Benito Garzón, 2023).

Similarly, common-garden experiments facilitate the control of confounding effects across diverse environments. They also aid in understanding the relative contributions of genotype, environment, and genotype-by-environment interactions in shaping trait variation among populations from different regions (De Villemereuil et al., 2016). Common garden experiments are widely used in studies of local adaptation in forest trees (Savolainen et al., 2007). The adaptive traits measured in these experiments are often combined with genomic data from the same individuals to identify genes and variants associated with trait variation through genome-wide association studies (GWASs) (Savolainen et al., 2013). For instance, Wang et al. (2018) integrated common-garden experiments with whole-genome resequencing for GWASs. They identified a single genomic region containing the gene *PtFT2* that explained 65% of the observed genetic variation in the timing of bud set, a key adaptive trait that mediates local adaptation across populations along a latitudinal gradient in European aspen. The function of *PtFT2* was validated through functional genomics experiments, and the results showed that alternative alleles at the locus are maintained by natural selection. In addition, Capblancq et al. (2023) recently combined common gardens and genomic methods to identify a set of putatively adaptive genes, primarily involved in drought tolerance, cold hardiness, and phenology, that underlie local climate adaptation along different environmental gradients in red spruce.

Although reciprocal transplant and common-garden experiments have significantly advanced our understanding of local adaptation, these approaches are often time consuming, costly, and challenging to execute effectively for many species. An alternative approach is offered by population and landscape genomics, which are phenotype free and test for spatially varying selection between populations and/or associations between allele frequencies and environmental variables (Mahony et al., 2020; Lasky et al., 2023). In population genomics, genome scans for high interpopulation genetic differentiation that deviates from neutral model expectations (e.g., F_{ST}, d_{xy}) and scans for signatures of divergent and positive selection (e.g., XP-CLR, hapFLK) are commonly used to identify loci associated with population-specific adaptation (Bourgeois and Warren, 2021). In landscape genomics, genotype–environment association (GEA) studies have been rapidly adopted for detection of adaptive loci and variants highly associated with heterogeneous landscapes of environmental variables, providing insight into the evolutionary forces driving spatial patterns of climate-associated genetic variation (Rellstab et al., 2015; Lasky et al., 2023). Various GEA approaches, including univariate models that test associations between individual loci and environmental variables (e.g., latent factor mixed models) and multivariate models that simultaneously test associations between many loci and multiple environmental variables (e.g., redundancy analysis), have been developed and widely used to characterize the genetic basis of local adaptation in forest trees (Frichot and François, 2015; Forester et al., 2018; Capblancq and Forester, 2021).

Recent progress in GEA studies has revealed that many genes and genetic variants are involved in environmental and climate adaptation, supporting the polygenic or even oligogenic architecture of adaptation (Hoban et al., 2016; Fagny and Austerlitz,

Species	Data	Spatial scale	Local adaptation identification approach	Genomic prediction model	Reference
Betula nana	RADseq	United Kingdom	RDA, Bayenv2, BayeScan	RONA	Borrell et al., 2020
Corymbia calophylla	DArTseq	Western Australia	Bayenv2, BayPass, LFMM	GDM	Ahrens et al., 2019
Dalbergia cochinchinensis and *Dalbergia oliveri*	GBS	Southeast Asia	LFMM	GF	Hung et al., 2023
Eucalyptus melliodora	GBS	Australia	NA	GDM	Supple et al., 2018
Eucalyptus microcarpa	DArTseq	Australia	Bayenv2, BayeScan, FDIST2, hierarchical FDIST2, Bayenv XTX	RONA	Jordan et al., 2017
Euptelea polyandra and *Euptelea pleiosperma*	RADseq	China and Japan	BayeScan, Arlequin	GF	Cao et al., 2020
Fagus sylvatica	Whole-genome resequencing	Europe	LFMM	RONA	Mueller et al., 2023
Fagus sylvatica	ddRADseq	French Alps	RDA	RDA	Capblancq et al., 2020b
Melaleuca rhaphiophylla and *Nuytsia floribunda*	DArTseq	Southwestern Australia	LFMM, RDA	GDM	Walters et al., 2020
Picea abies and *Picea obovata*	Exome capture sequencing	Northern Europe	Pcadapt, RDA	RONA	Karunarathne et al., 2024
Picea rubens	Exome capture sequencing	Eastern America	RDA, GF	GF	Lachmuth et al., 2023a
Pinus bungeana	GBS	Central China	RDA	GF	Guo et al., 2022
Pinus cembra	Pooled exome capture sequencing	Central Europe	LFMM, BayPass	RONA	Dauphin et al., 2021
Pinus contorta	Exome capture sequencing	Western North America	RDA	RDA	Capblancq and Forester, 2021
Pinus densata	Exome capture sequencing	Western China	Bayenv2, Pcadapt	GF	Zhao et al., 2020
Pinus pinaster	Illumina Infinium SNP array	Europe	RDA, pRDA, LFMM, BayPass, GF	GF, RDA, LFMM, GDM	Archambeau et al., 2024
Platycladus orientalis	GBS	China	Pcadapt, Bayenv2, BayeScan, RDA	GF	Jia et al., 2020
Populus balsamifera	Targeted genotyping	North America	LFMM, Bayenv2	GDM, GF	Gougherty et al., 2021
Populus balsamifera	Targeted genotyping	North America	F_{ST} outlier tests, Bayenv, GPA	GF, GDM	Fitzpatrick and Keller, 2015
Populus koreana	Whole-genome resequencing	Northeast China	LFMM, RDA	RONA, GF	Sang et al., 2022

Table 1. Examples of studies that have used landscape genomic approaches to assess the vulnerability of forest trees to climate change.

(Continued on next page)

Species	Data	Spatial scale	Local adaptation identification approach	Genomic prediction model	Reference
Populus tremula	Whole-genome resequencing	Sweden	LFMM	GDM	Ingvarsson and Bernhardsson, 2020
Pseudotsuga menziesii var. *menziesii*, *Pseudotsuga menziesii* var. *glauca*, and *Pinus banksiana*	Exome capture sequencing	North America	WZA, BayPass	GF, RONA	Lind et al., 2024
Pterocarya macroptera	RADseq	China	Bayenv, LFMM	RONA, GF	Wang et al., 2023
Quercus acutissima	Whole-genome resequencing	China	LFMM, BayPass	GDM,GF	Yuan et al., 2023
Quercus petraea, *Q. pubescens*, and *Q. robur*	Poolseq	Switzerland	LFMM	RONA	Rellstab et al., 2016
Quercus rugosa	GBS	Mexico	BayeScan, LFMM	GF	Martins et al., 2018
Quercus suber	GBS	Western Mediterranean	BayeScan, BayPass, SelEstim	RONA	Pina-Martins et al., 2019

Table 1. *Continued*

DArTseq, diversity arrays technology sequencing; GBS, genotyping-by-sequencing; GDM, generalized dissimilarity modeling; GF, gradient forest; GPA, genotype–phenotype association; LFMM, latent factor mixed model; Poolseq, whole-genome sequencing of pools of individuals; RADseq, restriction-site-associated DNA sequencing; ddRADseq, double digest restriction-site-associated DNA sequencing; RDA, redundancy analysis; RONA, risk of non-adaptiveness; BayPass, Bayesian population association analysis.

2021). However, fully accounting for the confounding effects of demography and population structure is challenging, especially for species in which environmental and geographic distributions are closely linked to population structure, which inevitably leads to false positives (Kemppainen et al., 2021). Moreover, the assumption of monotonic clines between allele frequency and environment may not hold true for most alleles involved in climate adaptation, limiting the effectiveness of GEA methods in detecting actual causal loci (Lotterhos, 2023). Consequently, there is a growing need for more sophisticated methodologies that explicitly consider and model the genomic complexity of polygenic adaptation to unravel the genetic architecture underlying the adaptation of forest trees to their environment (Barghi et al., 2020; Yeaman, 2022).

Harnessing landscape genomics to predict climate change response in forest trees

After candidate adaptive loci or variants for climate adaptation have been identified, an increasingly popular approach in recent forest tree studies involves incorporating current adaptive genetic variation to estimate the amount of genomic change (genomic vulnerability) needed to track changing climates from the current landscape patterns of GEA (Table 1) (Capblancq et al., 2020a). To measure the climate-change vulnerability of a population using genomics, the first step is typically to establish current geographic patterns of adaptive genomic composition across the landscape through a composite frequency turnover of the identified adaptive allele frequencies. Subsequently, the spatial pattern of adaptive genetic variation is projected forward in time, and the magnitude of genetic changes, typically estimated as the cumulative effects of allele or genotype frequencies, is measured to quantify the genomic maladaptation of populations to their predicted new environmental conditions (Hoffmann et al., 2021; Rellstab et al., 2021).

Several approaches have been developed to estimate genomic vulnerability and maladaptation. The risk of non-adaptedness (RONA) approach was initially developed to estimate the expected allele frequency changes required under future environmental conditions using linear regression at the single-locus level of putatively adaptive variants (Rellstab et al., 2016). Pina-Martins et al. (2019) further enhanced this approach by introducing a correction to the average values based on the R^2 of each marker association, resulting in a more robust average RONA. In addition to RONA, the machine-learning-based gradient forest (GF) approach (Fitzpatrick and Keller, 2015) and the quadratic-distance-based geometric genomic offset (Gain et al., 2023) have also been used extensively in recent studies. Combined with powerful raster climatic visualization, genetic offsets demonstrate great untapped potential for predicting the non-adaptedness of populations to new environmental conditions, particularly in long-lived forest trees for which other experiments are often impractical or even impossible (Martins et al., 2018; Vanhove et al., 2021; Sang et al., 2022). Furthermore, to simultaneously consider the contributions of adaptation and migration to mitigating climate change risk, Gougherty et al. (2021) integrated three offset-based metrics, including local offset, forward offset, and reverse offset, to not only quantify the *in situ* risks of populations but also help predict populations that are poorly adapted to all projected conditions across the geographic area and identify locations where assisted migration is likely to be most effective (Gougherty et al., 2021).

However, as genomic offset-based metrics gain popularity for assessing climate change threats, it is essential to bear in mind the numerous limitations in interpreting and applying these approaches (Rellstab et al., 2021). For instance, genomic offset measures often assume that the magnitude and extent of environmental effects on the genetic architecture of climate traits will remain the same in the future, which is unlikely. Therefore, it is advisable to incorporate additional independent datasets, including information on population dispersal, phenotypic plasticity and variation, genetic load, and landscape connectivity, to further validate genomic offset predictions (Aguirre-Liguori et al., 2021). In particular, transplant experiments, such as common-garden or provenance trials, are highly needed to validate offset predictions by quantifying the performance of fitness-related phenotypes in the growing sites projected to the future climate from source populations (Lind et al., 2024). It is essential to perform such evaluations before incorporating genomic offset predictions into management practices aimed at restoration, conservation, and biodiversity management (Lind and Lotterhos, 2024).

Population genomics for conservation in forest trees

After populations particularly vulnerable to future climate threats are identified, it is crucial to gather additional evolutionary information before making conservation decisions (Allendorf et al., 2010; Supple and Shapiro, 2018). First, because temporal changes in effective population size (N_e) can vary significantly among different populations, the inference of recent population trends provides a powerful means of diagnosing the conservation status of populations (Luikart et al., 2010). In addition to the demographic history inference approaches at the species level mentioned above, several novel approaches for estimating contemporary N_e fluctuations, such as SNeP and $N_{e\text{-LD}}$, have been developed by analyzing patterns of linkage disequilibrium (Barbato et al., 2015; Novo et al., 2022). Given the complex relationship among neutral genetic diversity, degree of vulnerability, and recent population declines, understanding how intrinsic and extrinsic factors influence the trajectory of N_e can inform strategies to mitigate their effects on local populations (Teixeira and Huber, 2021; Forester et al., 2022).

Second, although all populations harbor deleterious mutations, purifying selection is less effective at eliminating harmful variations in populations that are undergoing prolonged decline and bottlenecks (Dussex et al., 2023). This leads to a greater accumulation of slightly and mildly deleterious mutations in such populations. Furthermore, genetic drift in small populations can exacerbate inbreeding depression, causing recessive deleterious mutations to express in a homozygous state, which further reduces individual fitness and increases the likelihood of extinction (Mathur and DeWoody, 2021; Bertorelle et al., 2022). Numerous population genomics tools are available to predict the effects of genomic variants and investigate the dynamics of load in declining populations. For example, snpEff categorizes variants using the gene annotations of the target genomes, identifying, for example, synonymous, non-synonymous, start-loss, stop-gain, and intronic mutations (Cingolani et al., 2012); SIFT 4G classifies single nucleotide polymorphisms (SNPs) into categories such as synonymous, tolerated, deleterious, and loss-of-function (LoF) (Vaser et al., 2016); and GERP calculates sequence conservation scores across the genome by incorporating data from multiple additional species (Davydov et al., 2010). By employing these population genomics tools, Yang et al. (2018) found that purging of highly deleterious variants, such as LoF variants, was remarkably efficient in the critically endangered ironwood tree (*Ostrya rehderiana*) (Yang et al., 2018). This resulted in a gradual reduction in inbreeding depression, allowing the species to survive at low population sizes over extended periods of time, and may further mitigate extinction when anthropogenic disturbances are eliminated. Liu et al. (2022) found that compared with other related species, *Populus qiongdaoensis* exhibited a genome-wide relaxation of purifying selection against weakly deleterious mutations, consistent with its isolated and restricted island distribution (Liu et al., 2022).

Lastly, population genomics provides many new applications for informing conservation and management actions. These include the expansion of genomic resources to many threatened species (e.g., the European Reference Genome Atlas), increased resolution for cryptic species delineation, and determination of optimal management strategies (e.g., *in situ* or *ex situ* conservation management) by identifying populations that are especially adapted or vulnerable to future threats (Hohenlohe et al., 2021; Theissinger et al., 2023). Therefore, in conservation decision making, particularly in the context of complex environmental and climate change, it is crucial to integrate evolutionary potential components—comprising ecological disturbance, demographic stochasticity, adaptive capacity, and genetic load—into species' vulnerability and extinction risk assessments (Milot et al., 2020).

ADVANCES IN MULTI-OMICS FUNCTIONAL GENOMICS FOR REVEALING THE MOLECULAR MECHANISMS OF CLIMATE ADAPTATION IN FOREST TREES

In addition to the advent and rapid development of high-throughput sequencing technologies, which have revolutionized our understanding of how species and populations respond to environmental changes (Ansorge, 2009; Amarasinghe et al., 2020), recent cutting-edge approaches in multi-omics analyses and applications have expanded the scope. These encompass high-quality reference genome assemblies, population genomics, epigenetics, transcriptomics, metabolomics, and microbiomics, which collectively offer new avenues for exploration of enduring questions regarding the long-term evolution and adaptation of forest trees to their diverse environments (Figure 2 and Supplemental Table 2). These approaches are instrumental in resolving evolutionary units and identifying the functional genes and associated molecular mechanisms that contribute to environmental adaptation, which are essential for selecting and breeding trees resilient to global climate change

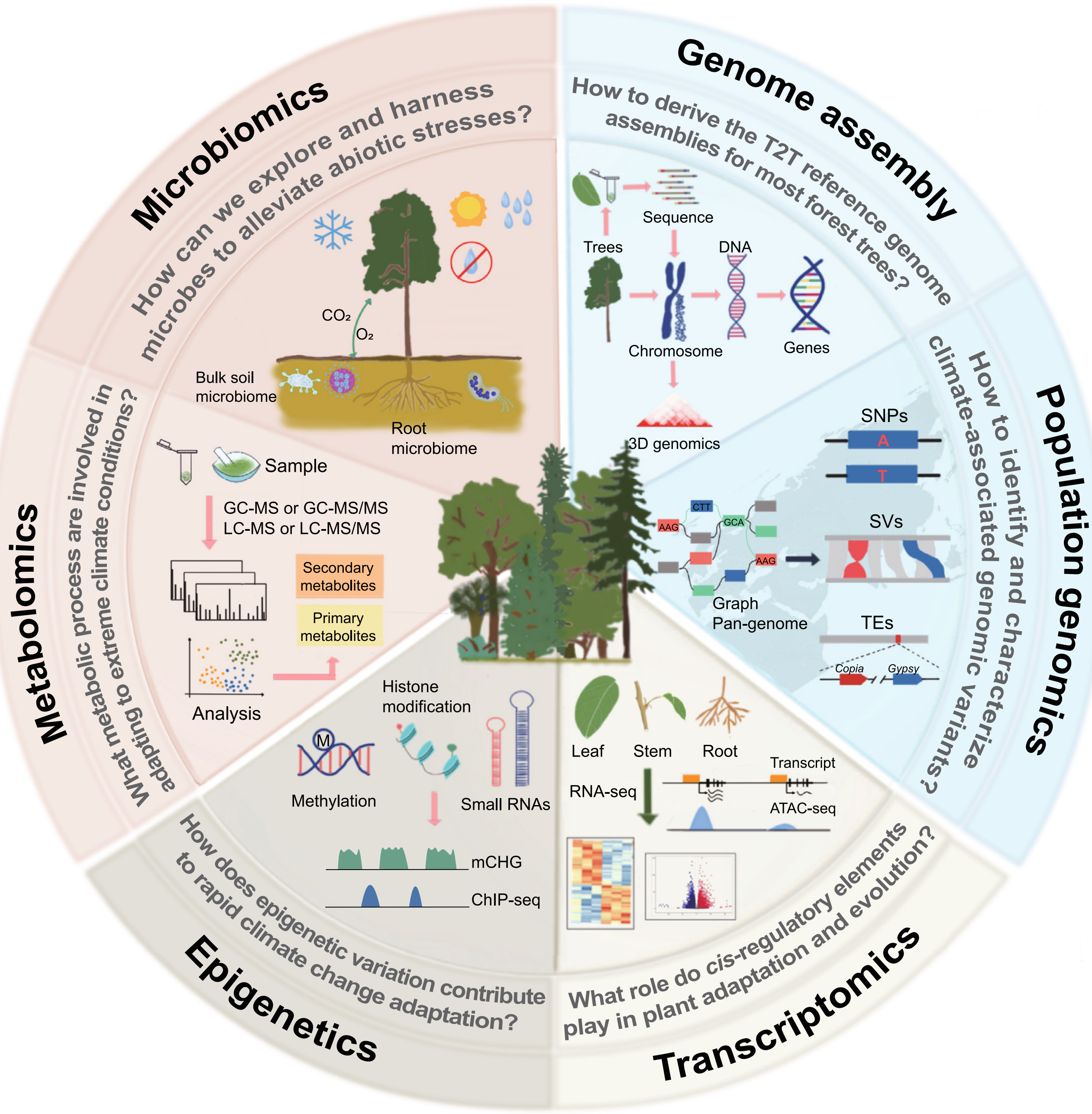

Figure 2. Recent cutting-edge approaches for multi-omics analyses and applications.
(1) Reference genome assemblies to create T2T genomes. (2) Pangenome population genomics to capture complete genomic variation. (3) Transcriptomics and regulatomics to characterize the evolution of gene expression. (4) Epigenetics to decipher the epigenetic variation involved in environmental adaptation. (5) Metabolomics to detect metabolic diversity. (6) Microbiomics to understand plant–microbe interactions. All these fields are key to paving the way for exploring how forest trees will respond to future climate change.

(Hohenlohe et al., 2021; Theissinger et al., 2023; Webster et al., 2023).

Reference genome assemblies

Recent advances in genomics are becoming increasingly integrated into the field of forest tree research. The first completely sequenced genome of a forest tree species was that of *Populus trichocarpa* (Tuskan et al., 2006). To date, hundreds of tree genomes have been sequenced and assembled (Chen et al., 2018a), primarily those of angiosperm trees with relatively small genome sizes, such as poplars, eucalypts, and oaks (Myburg et al., 2014; Lin et al., 2018; Plomion et al., 2018) (Supplemental Table 3). Despite this, advanced long-read sequencing technologies have facilitated the construction of chromosome-scale and high-quality assemblies, even for conifer species known for their large and complex genomes (Nystedt et al., 2013; Niu et al., 2022).

Breakthroughs over the past decade in combining accurate single-molecule real-time sequencing (PacBio HiFi), nanopore sequencing (ultra-long reads), and long-range sequencing technologies (HiC) offer viable strategies for achieving gapless, telomere-to-telomere (T2T) genome assemblies, not only for humans but also for various plant species (Hoyt et al., 2022; Kille et al., 2022). However, the sequence assemblies of most forest tree genomes remain fragmented. The imperative for future efforts lies in achieving increasingly complete T2T genomes, which are essential for understanding and deciphering the "dark matter" of evolution and adaptation in the long-lived trees that dominate the world's forest ecosystems (Miga and Eichler, 2023).

Population genomics

In addition to the construction of high-quality reference genome assemblies, the advent of reduced-representation genome sequencing, specifically RADseq, and the increasing number of whole-genome resequencing initiatives have expanded the scope of population genomics beyond model plant species and important crops to encompass non-model organisms, including forest trees (Ellegren, 2014; Ingvarsson et al., 2016; Lou et al., 2021). The ongoing reduction in costs associated with short-read sequencing technologies facilitates the examination of genomic variation across hundreds or even thousands of individuals within natural populations of a target species (Song et al., 2023). The strides made in population genomics have significantly revolutionized our understanding of the evolutionary and demographic histories of species, the genetic basis of environmental adaptation, and the genetic load and vulnerability to climate change.

However, it has become evident that a single reference genome contains only a subset of genomic information for an individual species. Consequently, traditional variant detection approaches that rely on a single reference genome are primarily confined to SNPs and short insertions and deletions (indels), posing limitations in capturing large structural variations (SVs). With the rapid progress and reduced costs of long-read sequencing technology, it is now feasible to obtain population-scale representative genome sequences (De Coster et al., 2021). These sequences are then used to construct pangenomes and/or super-pangenomes within and across closely related species (Bayer et al., 2020; Khan et al., 2020; Raza et al., 2023). The release of the first super-pangenome of the genus *Populus* provides compelling evidence that genetic diversity, including allelic variations, dispensable and private genes, and SVs, is crucial for widespread adaptation and phenotypic diversity in this extensive forest tree genus (Shi et al., 2024). In the future, integration of pangenome graph approaches with large-scale short-read data can enable more comprehensive characterization not only of small variants but also of large SVs and transposable elements (TEs) at the population level (Qin et al., 2021; He et al., 2023). This approach provides further insights into their effects on transcriptional regulation, phenotypic evolution, and climate adaptation in forest tree species.

Transcriptomics

In addition to genetic variation, there is a substantial variation in gene expression among individuals, populations, and species, which often contributes significantly to adaptation and environmental responses (López-Maury et al., 2008; He et al., 2021). Advances in transcriptomic methodologies have facilitated initiatives such as the One Thousand Plant Transcriptomes project, encompassing the diversity of green plants (One Thousand Plant Transcriptomes Initiative, 2019). To characterize the evolution of gene expression, expression quantitative trait locus (eQTL) analysis treats gene expression as a molecular phenotype, correlating its association with genetic variation in natural populations (Doerge, 2002). This approach is increasingly used to decipher the genetic architecture of regulatory variation (Gilad et al., 2008). In comparison to *trans*-eQTLs, which result from the effects of distantly located genes and which usually have low statistical power, *cis*-eQTLs typically exhibit larger effect sizes and are more often directly linked to the regulation of gene expression and adaptation (Signor and Nuzhdin, 2018; Sun et al., 2023). In a study related to xylan acetylation in secondary cell walls of *Populus*, strong *cis*-eQTL and *trans*-eQTL regulation were identified for *PtRWA-C* through gene co-expression network and eQTL analysis, revealing the functional role of *PtRWA-C* in xylan acetylation and biomass energy conversion processes, along with its regulatory modules (Zhang et al., 2023).

Cis-regulatory variation is crucial for ensuring proper spatiotemporal gene expression, fostering phenotypic innovation, enabling response to the environment, and driving species divergence (Lu et al., 2018). In recent years, various experimental and sequencing methods, such as DNase-seq, MNase-seq, and ATAC-seq, have been developed to identify accessible chromatin regions indicative of active *cis*-regulatory regions involved in transcription factor binding (Song and Crawford, 2010; Buenrostro et al., 2015). Studies on model plants and key crop species have increasingly focused on investigating changes in chromatin accessibility and dynamic gene regulation in response to environmental cues (Hämälä et al., 2022; Bhaskara et al., 2023; Marand et al., 2023). Despite significant progress in high-throughput reporter assays and chromatin profiling in these species (Lu et al., 2018, 2019; Yan et al., 2024), studies on wild non-model species, such as forest trees, remain limited. In a study of vascular cambium development in *Populus trichocarpa*, *PtrWOX4a*, specifically highly expressed in the vascular cambium, was identified by RNA-seq, and further characterization through ChIP-seq and molecular experiments revealed that PtrVCS2 regulates the expression of *PtrWOX4a* via recruitment to the *PtrWOX4a* promoter through interaction with PtrWOX13a (Dai et al., 2023). Therefore, future research focusing on natural populations of widespread forest trees is crucial for understanding the genetic and regulatory factors contributing to the evolutionary dynamics of the transcriptional regulation that underlies phenotypic plasticity in response to changing environmental conditions (Marand et al., 2023).

Epigenetics

Epigenetic variation is typically characterized by non-sequence changes to DNA and/or chromatin, including DNA methylation, histone modification, and non-coding RNAs. These modifications play central roles in regulating gene expression, preserving genome integrity, and inducing stress-induced phenotypic plasticity (Bräutigam et al., 2013; Zhang et al., 2013; Meyer, 2015; Baduel and Sasaki, 2023). DNA methylation occurs primarily in CpG (regions of DNA where a cytosine resides next to a guanine), CHG, and CHH sequence contexts, where H can represent the base A, G, or C. It is one of the most extensively studied epigenetic modifications, known for its crucial role in regulating gene expression, silencing TEs, and influencing organismal development (Finnegan et al., 1998; Vaillant and Paszkowski, 2007).

Whole-genome bisulfite sequencing is generally applicable to both model and non-model plant species, although its application to species with large genome sizes and population-level samples is hindered by relatively high costs. Compared with those of angiosperms, DNA methylation maps of conifer species have revealed heavily methylated genomes influenced primarily by the high abundance of TEs present within their sizable genomes, as notably observed in spruces and pines (Ausin et al., 2016; Niu et al., 2022). Recent studies on pine species have demonstrated epigenetic clocks capable of predicting age in these long-lived forest trees. In *Pinus taeda*, CG and CHG contexts become hypomethylated with age (Gardner et al., 2023), whereas a gradual decline in CHG methylation is observed in *Pinus tabuliformis* at the 5′ end of the first intronic region of a conserved age timer gene (Li et al., 2023).

Furthermore, numerous studies indicate that DNA methylation exhibits plasticity and facilitates plant adaptation to harsh environmental stress (Dowen et al., 2012). For example, Gugger et al. (2016) demonstrated that DNA methylation, especially CG methylation, is involved in mediating local adaptation of valley oak populations to their environments. In the mangrove tree *Bruguiera gymnorhiza*, high-salinity environments induce genome-wide DNA hypermethylation of TEs, coupled with the transcriptional regulation of chromatin modifier genes (Miryeganeh et al., 2022). Song et al. (2024) identified a pattern of global increase in DNA methylation during the process of pear domestication and improvement. However, compared with research on DNA methylation, research on other epigenetic marks, including histone modifications (e.g., acetylation, methylation, phosphorylation, ubiquitination), as well as small RNAs (sRNAs) and longer non-coding RNAs (lncRNAs), is limited in forest trees. In addition, from the perspective of global climate change, the heritability of natural epigenetic variation and its contribution to local climate adaptation in wild populations has rarely been explored (Schmid et al., 2018; McGuigan et al., 2021). Moving forward, future studies integrating genomic variation, RNA profiling, ATAC-seq, and epigenetic modifications could offer a unique avenue to gain insight into the epigenetic mechanisms involved in transcriptional regulation and environmental adaptation.

Metabolomics

Plants generate a multitude of metabolites with diverse structures and functions to aid in defense against various abiotic and biotic stresses (Shulaev et al., 2008). In general, metabolites can be categorized into primary metabolites and secondary metabolites. Primary metabolites are mainly associated with the fundamental activities of plant growth and development. Secondary metabolites, which include terpenes, phenols, and sulfur- or nitrogen-containing compounds, are typically specialized, lineage-specific compounds with crucial roles in resistance to changing climates and biotic stresses (Wang et al., 2022a). Consequently, exploring quantitative and qualitative variations in metabolism across tissues, individuals, populations, and species provides valuable insights into plant development, environmental adaptation, and evolution (Keurentjes et al., 2006).

Various technologies, such as NMR spectroscopy, gas chromatography–mass spectrometry (GC–MS), and liquid chromatography–mass spectrometry (LC–MS), are widely used for metabolomics measurements. Different strategies, including targeted, non-targeted, and widely targeted metabolomics, have been adopted for studies with distinct experimental designs and goals (Zhou and Liu, 2022). Multi-omics integration strategies are increasingly used to enhance our understanding of the genetic control and regulation of both primary and secondary metabolites. For instance, metabolite GWASs and mapping of metabolite-based quantitative loci are used to identify loci and/or genes that modulate metabolite profiles (Chen et al., 2014; Luo, 2015). A comprehensive analysis of genomics, transcriptomics, and metabolomics of hundreds of tomato genotypes by Zhu et al. (2018) revealed numerous changes in metabolites (i.e., nutritional and flavor metabolites) during tomato breeding. Zhou et al. (2022) used the latest graph pangenome approach to capture previously missing causal structural variants involved in the control of metabolite traits. Beyond crop domestication, metabolomics is frequently used to study plant adaptations to different ecological environments. For instance, separate studies on Tibetan hulless barley and Tibetan *Prunus* fruit trees revealed that natural genetic variations associated with genes in phenylpropanoid metabolic pathways are strongly linked to UV responses and high-altitude adaptation in species from extreme environmental conditions (Zeng et al., 2020; Wang et al., 2021a). Nevertheless, compared with those on other plant species, metabolomic studies on forest trees have been limited to date, necessitating future studies to explore metabolic diversity in trees with the goal of revealing the molecular mechanisms by which metabolic processes control extreme climate resilience in widespread tree species (Zahedi et al., 2021; Sun and Fernie, 2023).

Microbiomics

Plants encounter a diverse array of microbiota in natural environments, and their growth and development are closely tied to a broad range of microbial communities. Assembly of the plant-associated microbiome is a continual and intricate process, with microbiome members acquired either horizontally from the surrounding environment or vertically from their parents (Bakker et al., 2013; Lebeis, 2014). The beneficial effects of microbiota for host plants are diverse, ranging from nutrient transformation to protection of plants from abiotic and biotic stresses (Liu et al., 2020). In general, microbiota exists in almost all accessible plant tissues, and together with plants, they form a "holobiont" (Vandenkoornhuyse et al., 2015; Hassani et al., 2018). Forests comprise a myriad of microbial habitats, including foliage, roots, and wood, and the interactions between trees and their associated microbial communities are exceedingly complex (Baldrian, 2017; Lladó et al., 2018). For instance, the fungus *Clitopilus hobsonii* establishes an ectomycorrhiza-like association with its host tree *Populus tomentosa* (Peng et al., 2022). Under organic nitrogen conditions, this fungus significantly promotes plant growth and cell proliferation. However, under inorganic nitrogen conditions, leaf browning occurs after inoculation with the fungus, possibly owing to the production of certain toxic substances. Beyond the pivotal role of rhizosphere and phyllosphere microbes in bolstering woody plant resistance to biotic and abiotic stresses and ensuring plant survival, the stem and wood microbiome also has a significant influence on plant growth and development. For example, a study of culturable fungal endophytes from branch wood tissue of *Populus angustifolia* revealed that the composition of the endophyte community varied among tree genotypes in a common-garden experiment (Lamit et al., 2014).

From local to global scales, climate change has the potential to disrupt both aboveground and belowground plant–microbe interactions, further diminishing plant resistance and resilience to environmental challenges (Rudgers et al., 2020). In temperate forests, global climate change is often accompanied by shifts from ectomycorrhizal to arbuscular mycorrhizal tree species, leading to accelerated nitrogen turnover and increased volatile losses, among other consequences (Mushinski et al., 2020; Baldrian et al., 2023). Microbiomes, which play a key role in sensing and responding to environmental perturbations, are also crucial in shaping the responses of forest trees to biotic and abiotic stressors (Fitzpatrick et al., 2019). With the continuous development of high-throughput sequencing technology, complex plant microbial communities have gradually been discovered and analyzed (Hill et al., 2002). For example, a study on field-grown poplar trees showed that although rhizosphere microbiomes exhibited stability in niche differentiation, additional fine-tuning and adaptation were also observed in endosphere microbiomes of the leaf and stem compartments (Beckers et al., 2017). In addition, metagenome-wide association studies have been used to link microorganisms with their hosts, environmental changes, and physiological ecology (Wang et al., 2022b). Some QTLs involved in the interaction between plants and microbes during abiotic stress adaptation have been identified (Liu et al., 2020). However, despite significant progress in plant microbial research, the use of microorganisms to assist forest trees in coping with future climate change is still in its infancy. Methods such as genome mining, network analysis, and single-cell sequencing, as well as the integration of modeling and prediction, will provide platforms for screening new microorganisms that can increase plant fitness under stress conditions (Trivedi et al., 2020; Lan et al., 2024). With an increased understanding of plant–microbial interactions, rational management of the plant microbiome to facilitate reforestation and mitigate the adverse effects of climate change may prove to be a valuable strategy in the context of future global climate change (Busby et al., 2022; Addison et al., 2024).

Functional genomics screening by integrating multi-omics data

With continued progress in sequencing technology and the accumulation of large-scale multi-omics data, we are entering a new era of functional genomics (Figure 3). Advances in genomics, transcriptomics, epigenomics, chromatin profiling, and single-cell genomics are now being integrated with CRISPR-based functional genomics tools to enable comprehensive functional characterization of identified genes and regulatory elements. Although large-scale functional genomics approaches and genome manipulation have been broadly applied to model plants and important crop species (Marand et al., 2023; Lin et al., 2024), we are only beginning to investigate their versatility and utility in forest trees.

In the future, genome or even pangenome sequencing is expected to become routine (Schreiber et al., 2024), enabling detailed surveys of natural variation among haplotypes within and between species, particularly focusing on previously uncharacterized complex SVs (Figure 3A). TEs, often referred to as the "dark matter" of the genome, typically constitute a significant portion of the genomic content of trees. Emerging multi-omics technologies can help decipher the potential roles of TEs in shaping plant gene expression and function (Lisch, 2013). For instance, transposon insertions, in addition to silencing genes, can sometimes induce local three-dimensional genome reorganization, epigenetic changes, and alterations in chromatin accessibility. These changes can result in novel enhancer–promoter interactions and reprogram tissue-specific and/or stress-responsive expression patterns of specific genes (Figure 3B).

Traditional bulk molecular profiling provides mixed measures across cell types and is therefore unable to disentangle transcriptomes and regulatory chromatin accessibility specific to particular cell types or states. Recent advances in the ease and throughput of single-cell technologies have facilitated the discovery of previously unknown cell-type functions (Minow et al., 2023). For instance, Du et al. (Du et al., 2023) integrated high-resolution anatomical and spatial transcriptome analyses to identify previously undescribed meristematic-like cell pools within the phloem of the poplar stem. Although single-cell genomics in plants is still in its infancy, it is important to recognize the potential of single-cell technologies for examining changes in gene regulatory networks across different cell types, differentiation trajectories, environmental conditions, and plant–microbial interactions (Figure 3C).

FUTURE PERSPECTIVES FOR BREEDING OF FOREST TREES TO FACILITATE THEIR ADAPTATION TO RAPID CLIMATE CHANGE

The rapid pace of global climate change is exacerbating population declines and species extinctions, leading to an unparalleled loss of biodiversity. Like many other species, forest trees are increasingly vulnerable to the impacts of global climate change. Therefore, the urgent imperative to conserve and breed trees capable of thriving in present and future climate conditions cannot be overlooked. Building upon the reviews mentioned above, recent advances in multi-omics technologies are providing unprecedented insights into the genetic architecture of complex molecular or phenotypic traits involved in the environmental response, adaptation, and evolution of forest trees. Consequently, the integration of evolutionary and functional genomics stands as a powerful new tool that enables the bridging of genetic diversity and function, further facilitating the development of interdisciplinary systematic approaches for the design, conservation, and cultivation of future forests.

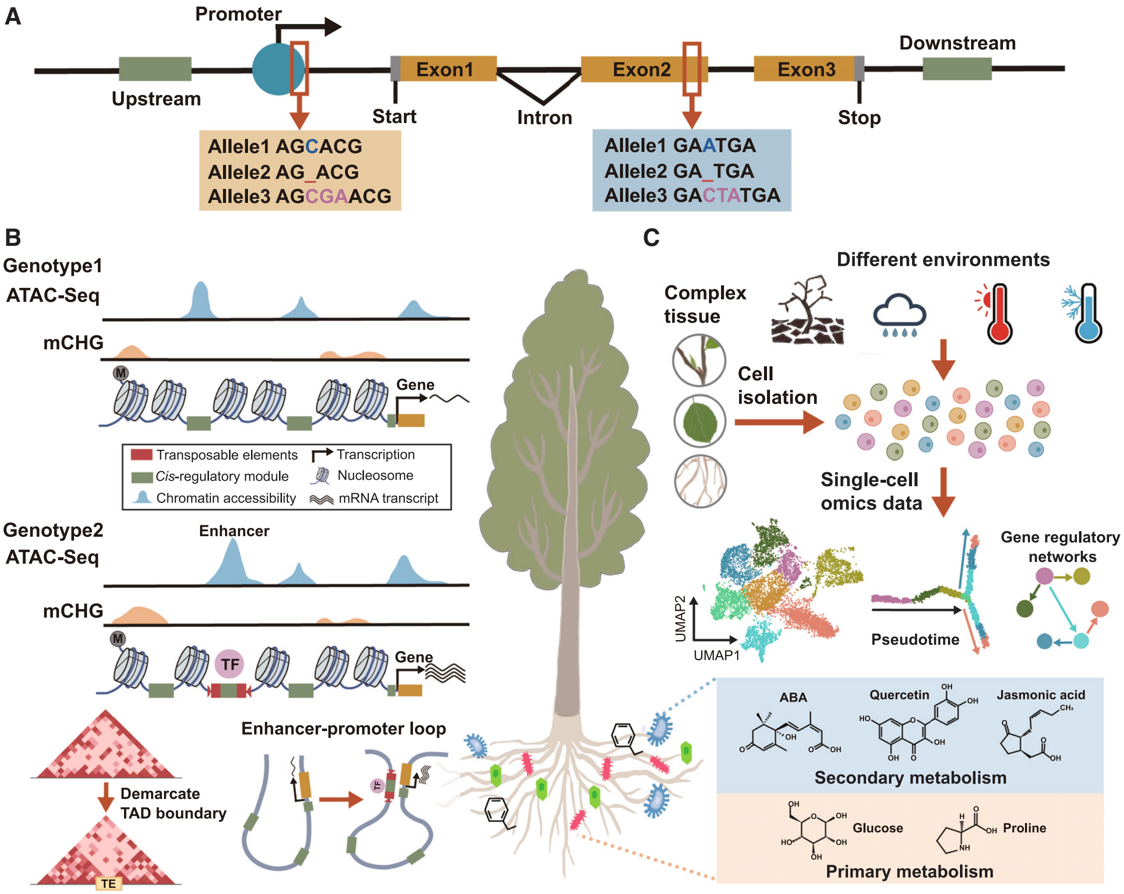

Figure 3. Directions for integrating functional genomics screening with multi-omics data.
(A) Advancing the characterization of natural genomic variation among haplotypes within and between species.
(B and C) (B) Deciphering the potential roles of previously unstudied structural variations, such as transposable element (TE) insertions, in creating novel enhancer–promoter interactions and determining the function of relevant genes, and **(C)** recognizing potential changes in gene regulatory networks across different cell types, differentiation trajectories, environmental conditions, and plant–microbial interactions.

To expedite and streamline the breeding of forest trees in anticipation of rapid climate change, it will be imperative to undertake various initiatives aimed at devising strategies and techniques (Figure 4). These endeavors should focus on enhancing both the yield of forest trees and their resilience to stress induced by climate changes. First, as reviewed above, the development and progression of omics technologies have contributed significantly to the identification of accessions and natural variations tolerant to environmental stress. These include not only SNPs but also other types of variations such as SVs, TE activities, and gene copy-number variations (Bayer et al., 2020; Khan et al., 2020; Raza et al., 2023). Coupled with the discovery and molecular mechanistic understanding of these adaptive genes and variants, genome-editing technologies via the CRISPR-Cas system, despite still exhibiting some significant off-target issues, offer a great opportunity for generating mutations in targeted genes to enhance adaptive traits, including stress tolerance, desirable properties of wood, and disease resistance (Bartlett et al., 2023).

Since the pioneering CRISPR-Cas-mediated genome editing of poplar in 2015 (Fan et al., 2015), there has been a notable increase in the number of tree species that have undergone genome editing (Cao et al., 2022). This advance shows great potential to revolutionize breeding processes for climate-resilient tree varieties. For instance, perennial trees are typically characterized by long reproductive cycles, which greatly hinder fundamental research and breeding improvement. To address this challenge, Ortega et al. (2023) developed a CRISPR-empowered *in vitro* flowering system that shortens the reproductive phase of poplars from 7–10 years to just a few months. This significant shortening of the reproductive cycle holds promise for accelerating breeding and improvement cycles in perennial trees in the future. In another example, Müller et al. (2020) used CRISPR-Cas9 to edit the *ARR17* gene, and CRISPR-Cas9-mediated knockout of *ARR17* triggered male flower development in an early-flowering female *P. tremula*, demonstrating that a single gene determines the sex switch in *Populus*. These findings show great potential for the development of a marker-aided sex-discrimination system for seedlings of poplar species, as sex selection is critical for controlling seed-hair pollution from poplar plantations in urban landscapes (Chen et al., 2023).

Moreover, recent advances in targeted genome-modification tools, such as base editing, prime editing, and other CRISPR-associated systems, enable precise editing of base substitutions,

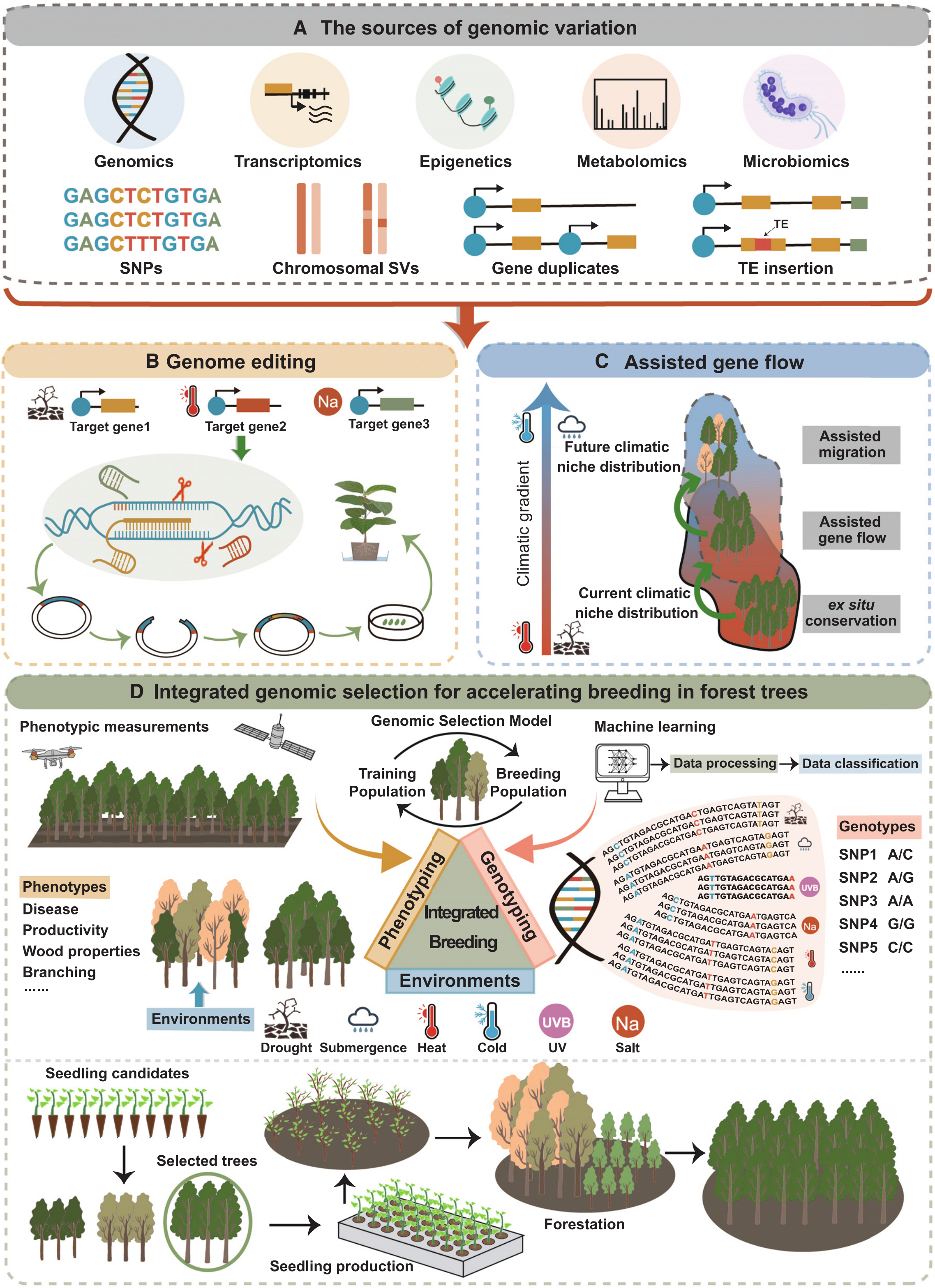

Figure 4. Future perspectives for facilitating the adaptation of forest trees to rapid climate change.
(A) More precise identification of causative natural genetic variations through multi-omics approaches.
(B) Implementation of genetic engineering for improving environmental stress tolerance through genome-/gene-editing technologies.
(C and D) (C) Actual management application of assisted gene flow/migration to mitigate maladaptation due to climate change (adapted from Aitken and Bemmels, 2016), and **(D)** integration of genomics, phenomics, and enviromics into genomic selection breeding strategies for rapid breeding of a new generation of environmentally adapted and healthy trees for future climates.

Glossary

Assisted gene flow: Assisted translocation of individuals within a species' range to facilitate adaptation to current or anticipated future local climate conditions.

Assisted migration: Translocation of individuals to areas outside the current species range that have become climatically favorable.

Conservation genomics: The application of genomic analysis to the preservation of the viability of populations and the biodiversity of living organisms.

Demographic fluctuation: The variation or oscillation in the size, structure, or distribution of a population over time.

Effective population size: The theoretical ideal population size experiencing an equivalent level of genetic drift as the observed population.

Epigenetics: A branch of studies for any heritable changes in chromosome organization that regulates gene activity in the absence of changes in nucleotide sequences.

Expression quantitative trait locus (eQTL): The quantitative trait locus that explain a fraction of the genetic variance of a gene expression phenotype.

Genetic load: The actual or potential reduction in mean population fitness owing to genetic causes including deleterious mutations, inbreeding and genetic drift.

Genetic offset: The amount of adaptive genetic change between present and future climate conditions required to maintain species current genetic–environmental association.

Genetic rescue: An increase in population fitness owing to immigration that enhances genetic diversity and alleviates inbreeding depression.

Genome assembly: The process of generating a contiguous sequences of all chromosomes of a genome from a large number of short-read or long-read DNA fragments, aided by genetic maps or proximity ligation techniques.

Genome editing: A type of genetic engineering in which DNA is inserted, deleted, modified or replaced in the genome of a living organism.

Genome-wide association studies (GWAS): The method that aim to identify associations of genotypes with phenotypes by testing for differences in the allele frequency of genetic variants between individuals who are ancestrally similar but differ phenotypically.

Genomics-assisted breeding: Utilizing genomic tools and technologies, such as high-quality genomes and QTL maps, to strategically select appropriate parents for diverse crossing programs, thereby generating novel combinations that ultimately produce elite breeding lines.

Genomic selection: A breeding methodology exploiting molecular genetic markers to design novel breeding programs and to develop new markers-based models for genetic evaluation.

Genotype-environmental association (GEA) studies: The method that uses statistical associations between allele frequency and environment of origin to test the hypothesis that allelic variation at a given gene is adapted to local environments.

Hybridization: Interbreeding of individuals from genetically distinct populations.

Inbreeding depression: Reduced fitness in offspring as a result of inbreeding.

Introgression: The transfer of genetic material from one species into the gene pool of another by the repeated backcrossing of an interspecific hybrid with one of its parent species.

Landscape genomics: The research filed that aims to identify the environmental factors that shape adaptive genetic variation and the gene variants that drive local adaptation.

Local adaptation: The greater fitness of local individuals in their home enviornments compared to that of nonlocal individuals, which results from natural selection.

Metabolomics: The study of the complete set of metabolites present within a biological cell, tissue, or an organism, which can uncover plant exudation in various environments and developmental stages.

Microbiomics: The science of characterizing and quantifying entire microbial communities, including their structure, spatiotemporal dynamics, genetic makeup, functional potential, and biochemical profiles.

Multi-omics: Combining two or more omics datasets to aid in data analysis, visualization, and interpretation to determine the mechanisms of biological processes.

Pangenome: The entire set of DNA sequences (or genes) of a species represented by the core genome and the accessory genome.

Population genomics: The research field that surveys patterns in the genome within and among populations to make inferences about evolution and the genome.

Super-pangenome: The approach involves developing pangenomes for diverse species within a given genus, or on a larger scale.

Transcrioptomics: The technology used to study an organisms' transcriptome, allowing for the identification of genes differentially expressed between individuals from different populations or species, and/or in response to different treatments.

Tree breeding: Develop genetically improved varieties for forestation through processes such as selection, breeding, and genetic testing.

small indels, and even large DNA segments at the kilobase level or above (Li et al., 2024). In addition to generating various types of mutations in beneficial trait genes, these advances have also enabled the manipulation of gene regulatory elements to produce novel alleles that regulate spatiotemporal patterns of gene expression (Rodriguez-Leal et al., 2017; Aguirre et al., 2023). More remarkably, the integration of cutting-edge artificial intelligence (AI) into modern genome-editing strategies offers a remarkable opportunity to design and modularize targeted gene combinations and regulatory pathways with enhanced precision and efficiency. For instance, Sulis et al. (2023) used machine-learning-based predictive models to identify gene targets for multiplex genome-editing strategies aimed at concurrently improving multiple wood traits, including lignin content, carbohydrate-to-lignin ratio, syringyl-to-guaiacyl ratio, and tree growth. These engineered trees hold great promise for enabling more efficient fiber pulping while simultaneously benefiting climate change mitigation and environmental conservation. However, despite the rapid development of advanced and powerful genome-editing tools, ethical, political, and societal concerns cannot be ignored and will remain at the forefront of global and deliberative discussions. This is especially true given the potential for long-term, unpredictable, and unwanted consequences, including complications arising from pleiotropic effects.

In addition to integrating genome-editing technologies for tree breeding, it is imperative to explore further applications of climate-conscious conservation and management that are vital for preserving the genomic resources necessary to mitigate the adverse impacts of climate change on natural forest trees (Aitken and Whitlock, 2013; Aitken et al., 2024). In addition to identifying populations at risk of maladaptation or extinction using landscape genomic approaches, other management strategies may include *in situ* and *ex situ* conservation collections, genetic rescue, assisted gene flow, and assisted migration (Aitken et al., 2024). For example, many forest trees, as foundation species in local ecosystems, are treated as prime candidates for assisted gene flow to enhance their adaptability to future environmental conditions by introduction of preadapted genotypes and alleles elsewhere in the species range (Aitken and Bemmels, 2016). However, in some cases, shifting from assisted gene flow within existing ranges to assisted migration beyond species ranges is also necessary (Aitken et al., 2024). This approach involves the deliberate translocation of tree species, including their seeds or individuals, to areas outside their current range where the projected future climate may be more suitable. Therefore, for actual management applications, it is crucial to pinpoint genotypes and existing populations that are best suited to act as potential donor sources and identify locations that are more effective as recipients for assisted migration under future climate change (Lachmuth et al., 2023a). Numerous approaches that integrate omics tools have been developed. For instance, two novel metrics, named donor importance (DI) and recipient importance (RI), were recently developed to quantify propagule transferability across the landscape by assessing the importance of each population serving as a seed source (donors) and any geographic location serving as a potential planting location (recipient) on the basis of the "not-to-exceed" offset thresholds (Lachmuth et al., 2023b). However, despite the potential benefits of approaches such as assisted migration, critics have raised concerns about potential ecological disruption, competition with existing species, genetic dilution, and unintended consequences for local ecosystems (McLachlan et al., 2007). Therefore, implementing and guiding these conservation actions for forest trees also demands careful planning, considering various ecological, ethical, and practical aspects, to balance biodiversity conservation with the associated risks and uncertainties (McLachlan et al., 2007).

Lastly, genomic-assisted breeding for climate-smart trees stands out as a crucial strategy for development of resilient tree populations better equipped to thrive under changing environmental conditions (Cortés et al., 2020). Traditional breeding methods, which involve controlled crosses and selection, have been used to enhance traits such as drought tolerance, disease resistance, and adaptation to specific environmental conditions. However, compared with other plant species, forest trees present more breeding challenges, including long breeding cycles, variable juvenile–mature correlations, complex genetic interactions among target traits (e.g., biomass production and wood quality), and in particular a limited understanding of the genetic basis of the most critical breeding target traits (Grattapaglia et al., 2018). As genotyping costs have declined, genomic selection has demonstrated immense potential to revolutionize forest tree breeding by offering more precise and efficient ways to identify superior trees with desired characteristics at an earlier age than is possible in traditional breeding programs, significantly shortening the breeding cycle

(Grattapaglia and Resende, 2011). Multiple genomic selection programs have been successfully tested in commercially important forest trees such as *Eucalyptus* (Resende et al., 2012; Tan et al., 2017) and conifers (Lenz et al., 2017; Chen et al., 2018b).

More recently, significant developments in high-throughput phenotyping promise to not only expedite breeding programs but also enable efficient collection of phenotypic data under diverse environmental conditions (Araus and Cairns, 2014; Araus et al., 2018). This makes it feasible to collect multi-trait data across multiple environments, enabling the exploration of possible correlations among different traits and of genotype-by-environment interactions. Future genomic approaches to selection breeding that integrate genomics, phenomics, and enviromics will undoubtedly have great potential to increase genetic gain and deliver materials with robust yields, even for currently untestable sites, in the face of future unfavorable environmental conditions (Crossa et al., 2021). Therefore, the integration of multi-omics information and the implementation of innovative predictive breeding strategies are crucial for future forest tree breeding programs, relying heavily on multidimensional big data and the application of AI (Xu et al., 2022). This, in turn, will pave the way for efficient and rapid breeding of a new generation of environmentally adapted and healthy trees for future climates.

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AUTHOR CONTRIBUTIONS

J.W. planned and designed the entire review. J.F., X.D., Y.C., Y.G., M.P., and J.W. wrote the manuscript. J.F. completed the figures. J.F., X.D., Y.C., Y.G., and Y.S. completed the tables. P.K.I. helped in the revision of the manuscript. All authors proofread and approved the final manuscript.

SUPPLEMENTAL INFORMATION

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