

# FORESTS AND THEIR INTERACTIONS WITH THE ENVIRONMENT

EDITED BY: Sofia Valenzuela, Sanushka Naidoo and Amy Brunner

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# FORESTS AND THEIR INTERACTIONS WITH THE ENVIRONMENT

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# Modern Strategies to Assess and Breed Forest Tree Adaptation to Changing Climate

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Studying the genetics of adaptation to new environments in ecologically and industrially important tree species is currently a major research line in the fields of plant science and genetic improvement for tolerance to abiotic stress. Specifically, exploring the genomic basis of local adaptation is imperative for assessing the conditions under which trees will successfully adapt *in situ* to global climate change. However, this knowledge has scarcely been used in conservation and forest tree improvement because woody perennials face major research limitations such as their outcrossing reproductive systems, long juvenile phase, and huge genome sizes. Therefore, in this review we discuss predictive genomic approaches that promise increasing adaptive selection accuracy and shortening generation intervals. They may also assist the detection of novel allelic variants from tree germplasm, and disclose the genomic potential of adaptation to different environments. For instance, natural populations of tree species invite using tools from the population genomics field to study the signatures of local adaptation. Conventional genetic markers and whole genome sequencing both help identifying genes and markers that diverge between local populations more than expected under neutrality, and that exhibit unique signatures of diversity indicative of “selective sweeps.” Ultimately, these efforts inform the conservation and breeding status capable of pivoting forest health, ecosystem services, and sustainable production. Key long-term perspectives include understanding how trees’ phylogeographic history may affect the adaptive relevant genetic variation available for adaptation to environmental change. Encouraging “big data” approaches (machine learning—ML) capable of comprehensively merging heterogeneous genomic and ecological datasets is becoming imperative, too.

**Keywords:** genomics of adaptation, genomic prediction, genome-wide association studies, genome-wide selection scans, assisted gene flow, machine learning, big data

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## INTRODUCTION

How trees will respond to climate change is a pressing question both in the contexts of natural forests and tree plantations (Kremer et al., 2014; Holliday et al., 2017; Isabel et al., 2020). Forests offer key ecological services, boosting significant resources of biodiversity in terms of species and habitats, while help mitigating the impact of excess air pollutants (Phillips et al., 2019; Pennisi, 2020). Trees also source natural renewable materials (i.e., wood itself, cellulose for the pulp industry,



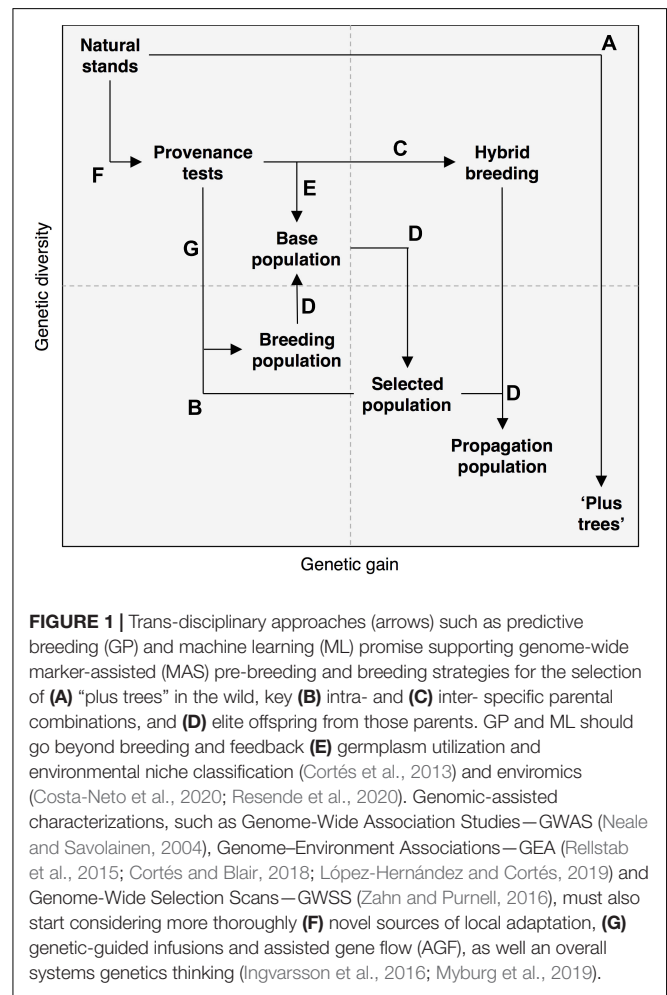
and lignin and hemicelluloses for energy production), likely to increase in the future as sustainable alternatives to fossil fuels (Carlson et al., 2014).

Yet, forest tree species are being threatened by climate change (Sullivan et al., 2020) due to fluctuations in the frequency and intensity of heat, drought, salinity (Naidoo et al., 2019), and the incidence of pathogens and pests (Naidoo et al., 2014; Christie et al., 2015). Hence, now more than ever it is essential to explore changing abiotic (Chakhchar et al., 2017; Alcaide et al., 2019b) and biotic (Meyer et al., 2016) interactions. Rampant phenotypic plasticity (Berlin et al., 2017; Hallingback et al., 2019) to climate gradients is presumed in trees, arguing resilience to variability throughout their long lives. Still, forests adaptability should also be assessed in the light of spatially varying local environmental selective pressures (Savolainen et al., 2013), and trees' genetic and evolutionary potentials (Howe and Brunner, 2005). Both directly reflect and feedback overall adaptive genetic variation. Hence, understanding the genomic drivers that underpin adaptive trait variation becomes vital for conservation and industrial goals.

Developments in plant genomics (Brunner et al., 2007a; Neale and Kremer, 2011) have already disclosed the genetic basis of various useful traits (Khan and Korban, 2012; Tuskan et al., 2018). Yet, this information has limitedly been utilized in tree improvement and conservation (Flanagan et al., 2018), despite genetic gains (Figure 1) and optimized management are urgently required due to environmental issues (Scherer et al., 2020). Besides, breeding woody perennials is primarily bottlenecked by their outcrossing reproductive systems, prolonged juvenile phases (Grattapaglia et al., 2018), large genome sizes lacking elimination mechanisms of long-terminal transposons (Nystedt et al., 2013), and an excessive focus on productivity (Burdon and Klápště, 2019) that omits adaptive traits (Table 1; Li et al., 2019). Thus, here we discuss ways to side step these limitations by arguing how predictive genomics can increase selection accuracy and shorten generation intervals (Grattapaglia et al., 2018), assist the detection of exotic variants from tree germplasm (Migicovsky and Myles, 2017), and disclose the genomic potential of adaptation to different climates (Lind et al., 2018). These efforts will ultimately inform conservation and breeding to enhance forest health, ecosystem services, and sustainable production.

## PREDICTIVE BREEDING PROMISES BOOSTING FOREST TREE GENETIC IMPROVEMENT

The aim of forest tree breeding is rarely to develop new varieties, but instead advance gradual population improvement through recurrent selection and testing (Neale and Kremer, 2011). Because of the long generation times of forest trees, their breeding has traditionally relied on phenotypic selection from natural stands by choosing “plus-trees” (Figure 1A). Their superior phenotype (primarily productivity and tree architecture, and seldom adaptability) is often measured *in situ* or in provenance trials. This starting pool of preferred trees constitutes the base population, an arboretum from which further selection is carried out to build a selected population with elite seed/scion donors.



**FIGURE 1 |** Trans-disciplinary approaches (arrows) such as predictive breeding (GP) and machine learning (ML) promise supporting genome-wide marker-assisted (MAS) pre-breeding and breeding strategies for the selection of (A) “plus trees” in the wild, key (B) intra- and (C) inter-specific parental combinations, and (D) elite offspring from those parents. GP and ML should go beyond breeding and feedback (E) germplasm utilization and environmental niche classification (Cortés et al., 2013) and enviromics (Costa-Neto et al., 2020; Resende et al., 2020). Genomic-assisted characterizations, such as Genome-Wide Association Studies—GWAS (Neale and Savolainen, 2004), Genome-Environment Associations—GEA (Rellstab et al., 2015; Cortés and Blair, 2018; López-Hernández and Cortés, 2019) and Genome-Wide Selection Scans—GWSS (Zahn and Purnell, 2016), must also start considering more thoroughly (F) novel sources of local adaptation, (G) genetic-guided infusions and assisted gene flow (AGF), as well an overall systems genetics thinking (Ingvarsson et al., 2016; Myburg et al., 2019).

Their estimated combinatory ability is gathered from genetic tests such as progeny trials, and parental re-selection (Figure 1B) from top families and single trees (White et al., 2007). After three steps of selection (from the natural, base, and selected populations), eroded genetic diversity may jeopardize overall population's productivity and resilience due to inbreeding depression. In order to minimize this risk, a breeding population is established to increase genetic variability. Intermating may rely on infusions from external populations. Outbred multi-parental populations (Scott et al., 2020) hence become the base population of a second generation. A bottleneck of this approach is that each generation would last at least nine or 18 years, for seedling or elite clone identification, respectively, in a fast growing tree species such as *Eucalyptus* (Resende et al., 2012).

Shortcuts to speed up the traditional cycle of forest tree genetic improvement rely on hybrids and backcrossing. Hybrid breeding (Figure 1C) aims harnessing heterotic effects (hybrid vigor) due to dominance and over-dominance already existing in nature, capable of increasing yield and adaptability (Schilthuisen et al., 2004; Seehausen, 2004). Dominance refers to the masking of deleterious effects of recessive alleles as a consequence of the increased heterozygosity resulting from hybridization

**TABLE 1** | Predictive breeding (genomic prediction—GP, also known as genomic selection—GS) studies in forest tree species published during the last years.

Species	Populations	Trait data	Genotyping data	GP algorithm	Key conclusions	References
<i>Elaeis guineensis</i>	162 individuals from the Deli and Group B populations	Seven oil yield components	262 SSRs	PBLUP, GBLUP	Genomic selection (GBLUP) calibrated according to conditions of the experiment showed higher trait precision when using pedigree-based model	Cros et al., 2015
<i>Elaeis guineensis</i>	A × B hybrid progeny tests with almost 500 crosses for training and 200 crosses for independent validation	Seven oil yield components	(> 5,000 GBS-derived SNPs)	GBLUP, PBLUP	Preselction for yield components using GBS is the first possible application of GS in oil palm.	Cros et al., 2017
<i>Hevea brasiliensis</i>	332 clones from the F1 cross PB 260 × RRM1600	Rubber production	332 SSRs on site 1 and 296 SSRs on site 2	RKHS, BLR_A, RR-BLUP-A, BLR_AD, RR-BLUP_AD	Mean between-site GS accuracy reached 0.561 when using the 125–200 SSRs with the highest Ho. The simulations showed that by applying a genomic preselction among 3,000 seedlings in the nursery there is a greater precision of selection of the genomic preselction compared to the phenotypic preselction. Statistical method had no effect on GS precision	Cros et al., 2019
<i>Eucalyptus grandis</i> × <i>E. urophylla</i> hybrids	999 individuals from 45 families	Cellulose content, composition of lignin monomer, total lignin, WD	33,398 SNP	ABLUP, GBLUP, ssGBLUP	ssGBLUP is a tool with a great projection for the improvement of the precision and the bias of the classic GBLUP for the genomic evaluation in the improvement of <i>Eucalyptus</i>	Cappa et al., 2019
<i>Picea abies</i>	1,370 controlled-pollinated individuals from 46 unrelated parents	Quality features of solid wood, pilodyn penetration, acoustic speed	116,765 SNP	ABLUP-A, ABLUP-AD, GBLUP-AD, GBLUP-ADE	GBLUP-AD is a model with great utility in production and propagation. Tree breeders can use it for seedling selection, or family and full-siblings selection	Chen et al., 2019
<i>Eucalyptus globulus</i>	646 individuals out of approximately 10 individuals per family	WD, branch quality, DBH, HT	14,442 SNP	BRR, Bayes C, HAP, HAP-SNP	In general, the BRR and Bayes C methods had a higher predictive capacity for most of the traits. In particular, genomic models that included the haplotype effect (either HAP or HAP SNP) significantly increased the AP of traits with low heritability.	Ballesta et al., 2019
<i>Eucalyptus cladocalyx</i>	1,470 individuals from 49 families	DBH, HT, BHT, WD, STR, SLD, FI	3.8 K Illumina Infinium EUChip60K SNPs	Bayes A, Bayes B, Bayes C, BRR	An GSq approach outperformed GS models in terms of predictive ability when the proportion of the variance explained by the significant marker-trait associations was higher than those explained by the polygenic background and non-significant markers	Ballesta et al., 2020
<i>Eucalyptus</i> clones of <i>E. urophylla</i> × <i>E. grandis</i>	1,130 clones of 69 full-sib families	Biomass production, WUE, wood properties	3,303 SNPs	GBLUP	The inclusion of wood δ13C in the selection process may lead to <i>Eucalyptus</i> varieties adapted to marginal zones still presenting good performance for biomass and wood chemical traits	Bouvet et al., 2020
<i>Picea abies</i>	726 trees of 40 families of complete siblings from two localities	Density, microfibr angle, wood stiffness	5,660 Infinium iSelect SNP matrix SNPs from exome capture and sequencing	Single-trait: GBLUP, BRR, GBLUP, TGBLUP, ABLUP, Multi-traits: GBLUP	Genomic prediction models showed similar results, but the multi-trait model stood out when weevil attacks were not available. Most of the results indicate that the weevil resistance genotypes were higher when there was a greater proportion of height to diameter and greater rigidity of the wood.	Lenz et al., 2020
<i>Pinus radiata</i>	457 POP2 descendants of 63 parents, and 524 POP3 descendants of 24 parents	Branching frequency, stem straightness, internal verification, and external bleeding	1,371,123 exome sequencing capture SNPs	GBLUP, ABLUP	An efficient way to improve non-key traits is through genomic selection with a pedigree corrected using SNP information	Li et al., 2019
<i>Pseudotsuga menziesii</i>	13,615 individuals	HT, 13 environmental variables	66,969 SNPs	ssGBLUP	GS-PA can be substantially improved using ECs to explain environmental heterogeneity and G × E effects. The ssGBLUP methodology allows historical genetic trials containing non-genotyped samples to contribute in genomic prediction, and, thus, effectively boosting training population size which is a critical step	Ratcliffe et al., 2019

(Continued)



TABLE 1 | Continued

Species	Populations	Trait data	Genotyping data	GP algorithm	Key conclusions	References
<i>Shorea platyclados</i>	356 individuals from a half-sib progeny population	Seven important traits, including growth, branching quality, wood quality traits	5,900 Illumina Hi-Seq X SNPs	rrBLUP	Selective breeding for these traits individually could be very effective, especially for increasing the diameter growth, branch diameter ratio and wood density simultaneously	Savitri et al., 2020
<i>Hevea brasiliensis</i>	435 individual rubber trees at two sites. 252 F1 hybrids derived from a PR255 × PB217 cross, 146 F1 hybrids derived from a GT1 × RRIM701 cross, 37 genotypes from a GT1 × PB235 cross, and 4 testers (GT1, PB235, RRIM701, and RRIM600)	SC	30,546 GBS-derived SNPs	BLUP, SM, MM, MDs, Mde	Multi-environment models were superior to the single-environment genomic models. Methods in which GS is incorporated resulted in a fivefold increase in response to selection for SC with multi-environment GS (MM, MDe, or MDs)	Souza et al., 2019
<i>Fraxinus excelsior</i>	1,250 individuals	Tree health, ash dieback resistance	100–50,000 HiSeq X SNPs	RR-BLUP	Ash dieback resistance in <i>F. excelsior</i> is a polygenic trait that should respond well to both natural selection and breeding, which could be accelerated using genomic prediction	Stocks et al., 2019
<i>Eucalyptus nitens</i>	691 individuals	Solid wood production, height, DBH, stem straightness, WD, wood stiffness, wood shrinkage, growth strain	12,236 Illumina EUChip60K SNPs	BLUP, GBLUP	The greatest improvement in genetic parameters was obtained for tangential air-dry wood shrinkage and growth strain	Suontama et al., 2019
<i>Pseudotsuga menziesii</i>	A 38-year-old progeny test population (P1), selecting 37 of 165 families with complete siblings at random from 3 different settings. Validation population contained 247 descendants with controlled crosses from the 37 families	HT	Complete genotyping of exome capture	RR-BLUP, GRR, Byes-B	The validation of cross genomic selection of juvenile height in Douglas fir gave very similar results with the ABLUP predictive precision, but this precision may be linked to the relationship between training and validation conjugates	Thislethwaite et al., 2019a
<i>Pseudotsuga menziesii</i> , <i>Picea glauca</i> , <i>P. engelmannii</i>	1,321 Douglas-fir trees, representing 37 full-sib F1 families and 1,126 inter- spruce trees, representing 25 open-pollinated (half-sib) families	Mid-rotation height, WD	200–50,000 Illumina HiSeq 2000 SNPs	RR-BLUP	Reducing marker density cannot be recommended for carrying out GS in conifers. Significant LD between markers and putative causal variants was not detected using 50,000 SNPs	Thislethwaite et al., 2020
<i>Pinus contorta</i>	Half- and full-sibs represented by 57 base parents and 42 full-sib families with an calculated effective population size of 92	Growth and wood quality	51,213 Illumina HiSeq SNPs	Bayes C, Bayes B, BLUP, GBLUP, ABLUP	The predictions of Marker-based models had accuracies that were equal to or better than pedigree-based models (ABLUP) when using several cross-validation scenarios and were better at ranking trees within families	Ukrainetz and Mansfield, 2020
<i>Castanea dentata</i>	7,173 descendants of BC3F3 from 346 “Clapper” mothers and 198 “Serious” mothers. For the BC3F2 progeny, a total of 1,134 “Clapper” and 1,042 “Graves” were sampled	<i>Cryphonectria parasitica</i> fungus severity (BC3F3) or presence/absence data (BC3F2)	Sequencing of a <i>C. dentata</i> clone in the PacBio Sequel platform	HBLUP, ABLUP, Bayes C	By means of genomic prediction and estimation of hybrid indices, a trade-off is between resistance and a proportion of inherited genome. The results found show that the genetic architecture underlying the heritability of resistance to blight is complex	Westbrook et al., 2020
<i>Picea abies</i>	484 progeny trees from 62 half-sib families	WD, MOE, MFA	130,269 Illumina HiSeq 2500 SNPs	ABLUP, GBLUP, rrBLUP, BayesB, RKHS	This study indicates standing tree-based measurements is a cost-effective alternative method for GS. Selection for density could be conducted at an earlier age than for MFA and MOE	Zhou et al. (2020)

For a comprehensive summary of previous studies not included here see Grattapaglia et al. (2018). Detailed abbreviations are shown at the end of the table. WUE, water use efficiency; SC, stem circumference; WD, wood density; MOE, modulus of elasticity; MFA, microfibril angle; DBH, diameter at breast height; HT, total tree height; BHT, first bifurcation height; STR, stem straightness; SLD, slenderness index; FI, flowering intensity; SNP, single nucleotide polymorphism; SSR, simple sequence repeat; GBS, genotyping by sequencing.

(i.e., an escape from inbreeding depression). On the other hand, over-dominance corresponds to the increase in aptitude as the result of the additive and epistatic effects of alleles that are naturally maintained by balancing selection and only coincide in hybrid genotypes. Hybrid breeding is nowadays widely used at operational plantations to maximize circumference at breast height (e.g., *E. grandis* × *E. nitens* and *Pinus elliotti* × *P. oocarpa*), height (e.g., *P. caribaea* × *P. tecunumanii*) and resistance to *Fusarium* spp. (i.e., *P. patula* × *P. tecunumanii*), among other potential uses (Burkhart et al., 2017). Backcrossing helps targeting the introgression of desired traits from exotic sources into elite populations, as has been done to transfer resistance to chestnut blight into American populations from Chinese wild donors (Cipollini et al., 2017).

Molecular breeding approaches (Badenes et al., 2016), in which genetic markers are used to assist selection, offer promising alternatives to speed up traditional tree breeding cycles, as well as hybrid and backcrossing schemes. Marker-Assisted Selection—MAS (Butcher and Southerton, 2007; Muranty et al., 2014) and Backcrossing—MAB (Herzog and Frisch, 2011) provide frameworks to pyramid target genetic variants of simple Mendelian traits, which are those regulated by few major genes (e.g., resistance to biotic stresses). Gene editing (Doudna and Charpentier, 2014; Dort et al., 2020) and transgenics (Campbell et al., 2003) can also transfer or silence allelic variants of major effects within a single generation (Pereira-Lorenzo et al., 2019). These may replicate the success of tolerant chestnuts (Alcaide et al., 2019a; Westbrook et al., 2019) and promote reproductive sterility (Meilan et al., 2001; Fritsche et al., 2018). Yet, molecular breeding via MAS, MAB and gene editing is often inefficient to trace quantitative traits as growth and adaptation to abiotic stresses. Adaptation is often polygenic (Cortés et al., 2018b; Barghi et al., 2020) due to many low-effect genes and their second-order interactions (Boyle et al., 2017).

A last-generation predictive breeding (Figure 1D) approach designed for quantitative polygenic traits is known as Genomic Prediction—GP (Desta and Ortiz, 2014; Crossa et al., 2017; Grattapaglia et al., 2018). GP standardizes infinitesimal marker-based additive predictive models by relying on historical phenotypic data (Meuwissen et al., 2001; Gianola et al., 2006; de los Campos et al., 2013). Trait data must be in Linkage Disequilibrium—LD or genetic auto-correlation (e.g., Kelleher et al., 2012), with the molecular markers or with the samples' genetic co-ancestry. GP utility has been demonstrated (Table 1) in model forest tree species such as *Eucalyptus* (Resende et al., 2012; Suontama et al., 2019), and conifers as *Pinus* (Resende M. F. et al., 2012; Li et al., 2019) and Douglas-fir (Thistlethwaite et al., 2017, 2019b), but also in non-model perennial crops such as coffee (Sousa et al., 2018), rubber (Cros et al., 2019; Souza et al., 2019) and oil palm (Cros et al., 2015). GP may even fit epigenetics (Roudbar et al., 2020), as well as multi-trait genomic models as was recently confirmed in Norway spruce for growth, wood quality and weevil resistance traits (Lenz et al., 2020). GP could also be coupled with somatic embryo-genesis for clonal propagation of elite genotypes by selecting elite zygotic embryos based on their genomic breeding value (Grattapaglia et al., 2018). GP has the potential to predict untested hybrid

genotypes (Technow et al., 2014) in woody perennials (Cros et al., 2017; Tan et al., 2017) by genotyping potential parental lines and phenotyping few F1 hybrids. Prioritizing inter-specific combinations for field trials can speed up hybrid breeding. Meanwhile, like already envision for chestnut (Westbrook et al., 2020), Genomic-Assisted Backcrossing (GABC) will replace MAB as the strategy to assist introgression breeding into elite populations from exotic germplasm.

## ASSISTING GENOMIC CHARACTERIZATION OF TREE GERmplasm TO CAPTURE NOVEL VARIANTS

Exploiting tree wild populations for genomics-assisted breeding (Figure 1E) is key to broaden the genetic basis of woody perennial breeding programs (Migicovsky and Myles, 2017). Specifically, diverse seed bank collections and novel tree provenances might source (Ulian et al., 2020) exotic variation (e.g., unique wood quality properties). They also help avoiding genetic erosion (e.g., via infusions) and increasing long-term adaptability to climate change (e.g., making forests more tolerant to abiotic stresses such as drought and heat). For example, genomic diversity analyses helped capturing rare variants in *P. trichocarpa* germplasm (Piot et al., 2019) often missed by Genome-Wide Association Studies (GWAS) in the related species *P. tremula* (Khan and Korban, 2012). Expanded phylogenomic (Wang M. et al., 2020) and species (Wang et al., 2020) diversity may source novel alleles to support selective breeding, as in wood quality traits for improved bioenergy feedstock. In turn, GP might go beyond breeding, the focus of the previous section, and feedback seed bank characterization (Hickey et al., 2017)—e.g., by predicting seed traits (Kehel et al., 2020) and overall yield (Crossa et al., 2007, 2016) in diverse accessions that otherwise could not have been tested at once in genetic field trials. Although the use of GP for germplasm characterization is latent, it has not been fully explored in forest tree species, a main research gap to be filled in the oncoming years.

Tree species rich in evolutionary diversity (Shang et al., 2020) could leverage breeding. Hybridization (Nieto Feliner et al., 2020), introgression (Burgarella et al., 2019), and polyploidy (Mason and Wendel, 2020) have already pumped morphological novelty by testing more genetic compatibilities than humans ever will. Yet, genomics of adaptive radiations (Seehausen, 2004; Madriñán et al., 2013; Cortés et al., 2018a; Marques et al., 2019) are challenging (Schilthuizen et al., 2004; de la Harpe et al., 2017). Long-living oaks—*Quercus* (Plomion et al., 2018; Leroy et al., 2020b; Plomion and Martin, 2020) are a classical syngameon (Cannon and Petit, 2020) – a promiscuous network of weakly isolated species that has driven peerless historical (Crowl et al., 2020; Hipp et al., 2020; Leroy et al., 2020c) and current (Leroy et al., 2020a) adaptive introgression (Kremer and Hipp, 2020).

In short, marker-assisted schemes are liable to be implemented at various stages during pre-breeding—e.g., in the selection of



“plus trees” from the wild (De Dato et al., 2018), of target parental pairs (Blair et al., 2013), and of superior offspring (Galeano et al., 2012). These approaches also aid conservation (Martín et al., 2012; Mattioni et al., 2017) and germplasm tracing (Cortés et al., 2011; Blair et al., 2012; Chiocchini et al., 2016). Still, genomic-assisted studies of germplasm may risk focusing on productive traits and disregard locally adapted trait variation.

## GENOMICS OF ADAPTATION TO DIFFERENT ENVIRONMENTS

Local genetic adaptation (**Figure 1F**) may prove useful in the reaction of forests to climate change (Savolainen et al., 2013; Lascoux et al., 2016), for instance via gene swamping of pre-adapted alleles (Kremer et al., 2014; de Visser et al., 2018). Nowadays there is a wide portfolio of genomic tools that appeal to environmental variables in order to infer the genetic basis of adaptation to abiotic stresses. Specifically, Genome-Wide Selection Scans—GWSS (Zahn and Purnell, 2016) and Genome–Environment Associations – GEA (Rellstab et al., 2015) aim detecting signatures of selection across environmental gradients by pinpointing sections in the genomes that correlate with habitat heterogeneity (Forester et al., 2016). These approaches have successfully been used to assess variation in bud-break phenology (McKown et al., 2018) and stomata patterning (McKown et al., 2014) as potential responses to climate warming in natural populations of *P. trichocarpa*. They have also allowed comparing the likelihoods of adaptive reactions at continental (Holliday et al., 2011; Evans et al., 2014; Zhou et al., 2014; Stölting et al., 2015) and regional scales (Eckert et al., 2010; Holliday et al., 2016; Pluess et al., 2016; Ingvarsson and Bernhardsson, 2020) across phylogenetically diverse taxa (Yeaman et al., 2016). Currently there are even multi-scale approaches to detect widespread divergent selection in non-model tree species experiencing population decline (Mayol et al., 2020).

Local adaptation to climate change can be further enhanced (**Figure 1G**) via assisted gene flow—AGF (Aitken and Whitlock, 2013). AGF aims minimizing endogenous negative, while maximizing exogenous positive, selection by trans-locating pre-adapted individuals to facilitate adaptation of planted forests to climate change (Aitken and Bemmels, 2016). Management of local adaptation in a changing climate was recently examined in populations from lodgepole pine (*P. contorta*) across western Canada (Mahony et al., 2020). Yet, operational uses of genomic data to guide seed transfer or AGF are still lacking. Alternatively, genetic containment may be desired for transgenic trees (Brunner et al., 2007b; Klocko et al., 2016). The utility of these approaches in tropical forests remains to be explored. Tropical trees are more at risk from warming because they are closer to upper thermal limits (Freeman et al., 2020; Sentinella et al., 2020), as in montane (Cortés and Wheeler, 2018; Feeley et al., 2020; Tito et al., 2020) and alpine (Wheeler et al., 2014, 2016; Valencia et al., 2020) habitats. Disclosing the genetic, pan-genomic (Bayer et al.,

2020), and epigenetic (Brautigam et al., 2013; Sow et al., 2018; Barrera-Redondo et al., 2020) bases of traits underlying adaptive responses in tree species will assist AGF, industrial milestones, and conservation priorities (Isabel et al., 2020) across meta-populations (Gonzalez et al., 2020), and even micro-habitats (Cortés et al., 2014; Abdelaziz et al., 2020).

## CONCLUDING REMARKS

A major question in the interface between forests and their environments that genomics have the potential to assist is whether tree adaptation to the fast pace of climate change can happen despite their long generation times (Holliday et al., 2017). Specifically, GP offers a feasible way to predict adaptation from allele frequencies in many genes of low effects underlying polygenic traits (Isabel et al., 2020). This way, the role of adaptive responses can be balanced in relation with range shifts (i.e., migration) and extinction as possible climate change outcomes for tree populations (Aitken et al., 2008; Alberto et al., 2013). This question is equally insightful for domesticated and wild stands of forest trees, and must be coupled with reflections regarding the best propagation and conservation schemes. For instance, the factual consequences on genetic diversity of clonal and seedling forestry (Ingvarsson and Dahlberg, 2018), and of assisted gene flow (Aitken and Whitlock, 2013; Aitken and Bemmels, 2016), must be compiled.

Forest genomics tends focusing on economically important species. Yet, the power of population genomics must be further extended to comprehend neutral and adaptive processes in non-commercial species of ecological value in order to advance not just productivity, but also climate adaptation, forest health and conservation (Isabel et al., 2020). In this sense, GP is starting to permeate novel non-key traits other than growth and wood density, but still of interest for breeding, such as branching, stem straightness and external resin bleeding (Li et al., 2019). GP is also predicting adaptive trait variation for abiotic (Eckert et al., 2010) and biotic (Westbrook et al., 2020) stresses. In parallel to an enrichment of target traits, emerging genomic technologies might unlock woody plant trait diversity beyond the model tree species poplar, eucalyptus, willow, oak, chestnut and pecan (Tuskan et al., 2018).

There is currently a rich mosaic of alternative genetic methods to carry out both explicit (direct) and implied (indirect) selection on economic- (Burdon and KlápšTě, 2019) and ecological-worth (Holliday et al., 2017; Isabel et al., 2020) functions. These different traits can enlighten our understanding of the consequences of genetic divergence on the reaction of tree populations to climate change (Kremer et al., 2014). However, novel methodological developments should target more comprehensively complex trait–environment relationships (Bruehlheide et al., 2018). They should also mingle between adaptive (Cortés et al., 2015b; Sedlacek et al., 2016) and range shift (Sedlacek et al., 2014; Wheeler et al., 2015) responses across altitudinal (Lenoir et al., 2008; Steinbauer et al., 2018), latitudinal (Chen et al., 2011) and micro-habitat (Sedlacek et al., 2015; Little et al., 2016) gradients.

## PERSPECTIVES

Exploring natural adaptation to changing climate and genetic breeding for tolerance to abiotic stress in forest tree species has traditionally been assisted by GWAS, GWSS, GEA (Cortés et al., 2020), and AGF techniques. These approaches have allowed identifying and utilizing naturally available, locally adapted, variants. More recently, major developments in the field of predictive breeding (i.e., GP) promise to speed up selection from natural sources, as well as within the breeding cycle, by shortening the generation intervals and increasing the selection accuracy prior field trials. We have already identified and discussed major improvements in this line, such as multi-trait GP models (Lenz et al., 2020), coupled with integrative selection scores (Burdon and KlápšTě, 2019) on novel non-key (Li et al., 2019) and ecological-worth (Holliday et al., 2017; Isabel et al., 2020) traits. These innovations can capture multi-scale trait–environment relationships (Bruelheide et al., 2018) in non-model tree species (Mayol et al., 2020). Given the complexity and heterogeneity of trans-disciplinary data sources, Machine Learning (ML) offers a timely predictive and synthesizing approach capable of merging the highlights of the GWAS, GWSS, GEA, AGF and GP techniques.

“Supervised” ML typically utilizes “labeled” training datasets in order to cross-validate the “recall” rate of a target classification (e.g., selection). ML powerfully handles high-dimensional inputs of heterogeneous “features” without a joint probability distribution (Schridder and Kern, 2018). This way, algorithmically generated non-parametric models that avoid rejection sampling sidestep the “curse of dimensionality” and offer new ways to reveal complex systems (Myburg et al., 2019). ML has historically been utilized in functional genomics (Libbrecht and Noble, 2015) and ecological niche modeling (Phillips et al., 2017). Yet, it is now transitioning into GWAS-coupled MAS (Cortés et al., 2015a), GP (Crossa et al., 2019; Abdollahiarpanahi et al., 2020), GWSS (Schridder and Kern, 2018), and demographics—as when coupled with Approximate Bayesian Computation (Elleouet and Aitken, 2018; Liu et al., 2019).

We anticipate that ML techniques will brace GP predictions for various traits in multi-environment trials that aim disentangling the additive genetic variance and the genotype  $\times$  environment components. Novel developments in the field of ML will further allow building more accurate predictions by merging environmental variables, microhabitat diversity, and genome-wide divergence, all within a tree-breeding context to pivot “plus tree” selection, hybrid breeding and GABC schemes, as well as in terms of adaptation to climate change in natural forests. Integrative assessments (Ingvarsson et al., 2016) via ML promise harnessing adaptive trait variation in forest tree species.

## REFERENCES

Abdelaziz, M., Anderson, J. T., Rochford, M. E., Bemmels, J. B., Jameel, M. I., and Denney, D. A. (2020). Small spaces, big impacts: contributions of micro-environmental variation to population persistence under climate change. *AOB PLANTS* 12:plaa005. doi: 10.1093/aobpla/plaa005

## AUTHOR CONTRIBUTIONS

AC conceived this review. MR-M and LB-C collected literature and prepared summary tables. AC wrote the first draft of the review with later edits made by MR-M and LB-C.

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Abdollahiarpanahi, R., Gianola, D., and Peñagaricano, F. (2020). Deep learning versus parametric and ensemble methods for genomic prediction of complex phenotypes. *Genet. Sel. Evol.* 52:12.

Aitken, S. N., and Bemmels, J. B. (2016). Time to get moving: assisted gene flow of forest trees. *Evol. Appl.* 9, 271–290. doi: 10.1111/eva.12293

- Aitken, S. N., and Whitlock, M. C. (2013). Assisted gene flow to facilitate local adaptation to climate change. *Annu. Rev. Ecol. Syst.* 44, 367–388. doi: 10.1146/annurev-ecolsys-110512-135747
- Aitken, S. N., Yeaman, S., Holliday, J. A., Wang, T., and Curtis-McLene, S. (2008). Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evol. Appl.* 1, 95–111. doi: 10.1111/j.1752-4571.2007.00013.x
- Alberto, F. J., Aitken, S. N., Alia, R., Gonzalez-Martinez, S. C., Hanninen, H., Kremer, A., et al. (2013). Potential for evolutionary responses to climate change - evidence from tree populations. *Glob. Chang. Biol.* 19, 1645–1661. doi: 10.1111/gcb.12181
- Alcaide, F., Solla, A., Cherubini, M., Mattioni, C., Cuenca, B., Camisón, Á., et al. (2019a). Adaptive evolution of chestnut forests to the impact of ink disease in Spain. *J. Syst. Evol.* 58, 504–516. doi: 10.1111/jse.12551
- Alcaide, F., Solla, A., Mattioni, C., Castellana, S., and Martín, M. A. (2019b). Adaptive Diversity and drought tolerance in *Castanea Sativa* assessed through genetic markers Est-Ssr. *Forestry* 92, 287–296. doi: 10.1093/forestry/cpz007
- Badenes, M. L., Fernandez, I. M. A., Rios, G., and Rubio-Cabetas, M. J. (2016). Application of genomic technologies to the breeding of trees. *Front. Genet.* 7:198. doi: 10.3389/fgene.2016.00198
- Ballesta, P., Bush, D., Silva, F. F., and Mora, F. (2020). Genomic predictions using low-density Snp markers, Pedigree and Gwas information: a case study with the non-model species *Eucalyptus Cladocalyx*. *Plants* 9:99. doi: 10.3390/plants9010099
- Ballesta, P., Maldonado, C., Perez-Rodriguez, P., and Mora, F. (2019). Snp and Haplotype-based genomic selection of quantitative traits in *Eucalyptus Globulus*. *Plants* 8:331. doi: 10.3390/plants8090331
- Barghi, N., Hermisson, J., and SchloöTterer, C. (2020). Polygenic adaptation: a unifying framework to understand positive selection. *Nat. Rev. Genet.* doi: 10.1038/s41576-020-0276-2 [Epub ahead of print].
- Barrera-Redondo, J., Pinero, D., and Eguiarte, L. E. (2020). Genomic, transcriptomic and epigenomic tools to study the domestication of plants and animals: a field guide for beginners. *Front. Genet.* 11:742. doi: 10.3389/fgene.2020.00742
- Bayer, P. E., Golicz, A. A., Scheben, A., Batley, J., and Edwards, D. (2020). Plant pan-genomes are the new reference. *Nat. Plants* 6, 914–920. doi: 10.1038/s41477-020-0733-0
- Berlin, S., Hallingbäck, H. R., Beyer, F., Nordh, N. E., Weih, M., and Rönning-Wästljung, A. C. (2017). Genetics of phenotypic plasticity and biomass traits in hybrid willows across contrasting environments and years. *Ann. Bot.* 120, 87–100. doi: 10.1093/aob/mcx029
- Blair, M. W., Cortés, A. J., Penmetsa, R. V., Farmer, A., Carrasquilla-Garcia, N., and Cook, D. R. (2013). A high-throughput Snp marker system for parental polymorphism screening, and diversity analysis in common bean (*Phaseolus Vulgaris* L.). *Theor. Appl. Genet.* 126, 535–548. doi: 10.1007/s00122-012-1999-z
- Blair, M. W., Soler, A., and Cortés, A. J. (2012). Diversification and Population Structure in Common Beans (*Phaseolus vulgaris* L.). *PLoS One* 7:e49488. doi: 10.1371/journal.pone.0049488
- Bouvet, J.-M., Makouanzi Ekomo, C. G., Brendel, O., Laclau, J.-P., Bouillet, J.-P., and Epron, D. (2020). Selecting for water use efficiency, wood chemical traits and biomass with genomic selection in a *Eucalyptus* breeding program. *For. Ecol. Manage.* 465:118092. doi: 10.1016/j.foreco.2020.118092
- Boyle, E. A., Li, Y. I., and Pritchard, J. K. (2017). An expanded view of complex traits: from polygenic to omnigenic. *Cell* 169, 1177–1186. doi: 10.1016/j.cell.2017.05.038
- Brautigam, K., Vining, K. J., Lafon-Placette, C., Fossdal, C. G., Mirouze, M., Marcos, J. G., et al. (2013). Epigenetic regulation of adaptive responses of forest tree species to the environment. *Ecol. Evol.* 3, 399–415. doi: 10.1002/ece3.461
- Bruehlheide, H., Dengler, J., Purschke, O., Lenoir, J., Jiménez-Alfaro, B., Hennekens, S. M., et al. (2018). Global trait–environment relationships of plant communities. *Nat. Ecol. Evol.* 2, 1906–1917.
- Brunner, A. M., Difazio, S. P., and Groover, A. T. (2007a). Forest genomics grows up and branches out. *New Phytol.* 174, 707–710.
- Brunner, A. M., Li, J., Difazio, S. P., Shevchenko, O., Montgomery, B. E., Mohamed, R., et al. (2007b). Genetic containment of forest plantations. *Tree Genet. Genomes* 3, 75–100. doi: 10.1007/s11295-006-0067-8
- Burdon, R. D., and KlápšTě, J. (2019). Alternative selection methods and explicit or implied economic-worth functions for different traits in tree breeding. *Tree Genet. Genomes* 15:79.
- Burgarella, C., Barnaud, A., Kane, N. A., Jankowski, F., Scarcelli, N., Billot, C., et al. (2019). Adaptive introgression: an untapped evolutionary mechanism for crop adaptation. *Front. Plant Sci.* 10:4. doi: 10.3389/fpls.2019.00004
- Burkhart, H. E., Brunner, A. M., Stanton, B. J., Shuren, R. A., Amateis, R. L., and Creighton, J. L. (2017). An assessment of potential of hybrid poplar for planting in the Virginia Piedmont. *New Forests* 48, 479–490. doi: 10.1007/s11056-017-9576-6
- Butcher, P., and Southerton, S. (2007). “Marker-Assisted Selection in Forestry Species,” in *Marker-Assisted Selection – Current Status and Future Perspectives in Crops, Livestock, Forestry and Fish*, eds E. Guimarães, J. Ruane, B. Scherf, A. Sonnino, and J. Dargie (Rome: FAO).
- Campbell, M. M., Brunner, A. M., Jones, H. M., and Strauss, S. H. (2003). Forestry’s fertile crescent: the application of biotechnology to forest trees. *Plant Biotechnol. J.* 1, 141–154. doi: 10.1046/j.1467-7652.2003.00020.x
- Cannon, C. H., and Petit, R. J. (2020). The oak syngameon: more than the sum of its parts. *New Phytol.* 226, 978–983. doi: 10.1111/nph.16091
- Cappa, E. P., De Lima, B. M., Da Silva-Junior, O. B., Garcia, C. C., Mansfield, S. D., and Grattapaglia, D. (2019). Improving genomic prediction of growth and wood traits in *Eucalyptus* using phenotypes from non-genotyped trees by single-step Gblup. *Plant Sci.* 284, 9–15. doi: 10.1016/j.plantsci.2019.03.017
- Carlson, C. H., Gouker, F. E., Serapiglia, M. J., Tang, H., Krishnakumar, V., Town, C. D., et al. (2014). “Annotation of the *Salix purpurea* L. genome and gene families important for biomass production,” in *Proceedings of the Plant and Animal Genetics Conference XXII*, San Diego, CA.
- Chakhchar, A., Haworth, M., El Modafar, C., Lauteri, M., Mattioni, C., Wahbi, S., et al. (2017). An assessment of genetic diversity and drought tolerance in Argan tree (*Argania Spinosa*) populations: potential for the development of improved drought tolerance. *Front. Plant Sci.* 8:276. doi: 10.3389/fpls.2017.00276
- Chen, I. C., Hill, J. K., Ohlemuller, R., Roy, D. B., and Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science* 333, 1024–1026. doi: 10.1126/science.1206432
- Chen, Z. Q., Baison, J., Pan, J., Westin, J., Gil, M. R. G., and Wu, H. X. (2019). Increased prediction ability in Norway Spruce Trials marker X environment interaction and non-additive genomic selection model. *J. Hered.* 110, 830–843. doi: 10.1093/jhered/esz061
- Chiocchini, F., Mattioni, C., Pollegioni, P., Lusini, I., Martín, M. A., Cherubini, M., et al. (2016). Mapping the genetic diversity of *Castanea Sativa*: exploiting spatial analysis for biogeography and conservation studies. *J. Geogr. Information Syst.* 08, 248–259. doi: 10.4236/jgis.2016.82022
- Christie, N., Tobias, P. A., Naidoo, S., and Kulheim, C. (2015). The *Eucalyptus Grandis* Nbs-Lrr gene family: physical clustering and expression hotspots. *Front. Plant Sci.* 6:1238. doi: 10.3389/fpls.2015.01238
- Cipollini, M., Dingley, N. R., Felch, P., and Maddox, C. (2017). Evaluation of phenotypic traits and blight-resistance in an American chestnut backcross orchard in Georgia. *Glob. Ecol. Conserv.* 10, 1–8. doi: 10.1016/j.gecco.2017.01.004
- Cortés, A. J., and Blair, M. W. (2018). Genotyping by sequencing and genome – environment associations in wild common bean predict widespread divergent adaptation to drought. *Front. Plant Sci.* 9:128. doi: 10.3389/fpls.2018.00128
- Cortés, A. J., Chavarrá, M. C., and Blair, M. W. (2011). Snp marker diversity in common bean (*Phaseolus vulgaris* L.). *Theor. Appl. Genet.* 123, 827–845. doi: 10.1007/s00122-011-1630-8
- Cortés, A. J., Garzón, L. N., Valencia, J. B., and Madriñán, S. (2018a). On the causes of rapid diversification in the Páramos: isolation by ecology and genomic divergence in *Espeletia*. *Front. Plant Sci.* 9:1700. doi: 10.3389/fpls.2018.01700
- Cortés, A. J., Liu, X., Sedlacek, J., Wheeler, J. A., Lexer, C., and Karrenberg, S. (2015a). *Maintenance of Female-Bias in a Polygenic Sex Determination System is Consistent with Genomic Conflict. On the Big Challenges of a Small Shrub: Ecological Genetics of Salix Herbacea L.* (Uppsala: Acta Universitatis Upsaliensis).
- Cortés, A. J., Monserrate, F., Ramírez-Villegas, J., Madriñán, S., and Blair, M. W. (2013). Drought tolerance in wild plant populations: the case of common beans (*Phaseolus vulgaris* L.). *PLoS One* 8:e62898. doi: 10.1371/journal.pone.0062898
- Cortés, A. J., Skeen, P., Blair, M. W., and Chacón-Sánchez, M. I. (2018b). Does the genomic landscape of species divergence in phaseolus beans coerce parallel signatures of adaptation and domestication? *Front. Plant Sci.* 9:1816. doi: 10.3389/fpls.2018.01816



- Cortés, A. J., Waeber, S., Lexer, C., Sedlacek, J., Wheeler, J. A., Van Kleunen, M., et al. (2014). Small-scale patterns in snowmelt timing affect gene flow and the distribution of genetic diversity in the alpine dwarf shrub *Salix Herbacea*. *Heredity* 113, 233–239. doi: 10.1038/hdy.2014.19
- Cortés, A. J., and Wheeler, J. A. (2018). “The environmental heterogeneity of mountains at a fine scale in a changing world,” in *Mountains, Climate, and Biodiversity*, eds C. Hoorn, A. Perrigo, and A. Antonelli (New York, NY: Wiley).
- Cortés, A. J., Wheeler, J. A., Sedlacek, J., Lexer, C., and Karrenberg, S. (2015b). *Genome-Wide Patterns of Microhabitat-Driven Divergence in the Alpine Dwarf Shrub Salix Herbacea L. On the Big Challenges of a Small Shrub: Ecological Genetics of Salix Herbacea L.* (Uppsala: Acta Universitatis Upsaliensis).
- Cortés, A. J., López-Hernández, F., and Osorio-Rodríguez, D. (2020). Predicting thermal adaptation by looking into populations’ genomic past. *Front. Genet.* 11:564515. doi: 10.3389/fgene.2020.564515
- Costa-Neto, G., Fritsche-Neto, R., and Crossa, J. (2020). Nonlinear kernels, dominance, and envirotyping data increase the accuracy of genome-based prediction in multi-environment trials. *Heredity* doi: 10.1038/s41437-020-00353-1
- Cros, D., Bocs, S., Riou, V., Ortega-Abboud, E., Tisné, S., Argout, X., et al. (2017). Genomic preselection with genotyping-by-sequencing increases performance of commercial oil palm hybrid crosses. *BMC Genomics* 18:839. doi: 10.1186/s12864-017-4179-3
- Cros, D., Denis, M., SaiNchez, L., Cochard, B., Flori, A., Durand-Gasselin, T., et al. (2015). Genomic selection prediction accuracy in a perennial crop: case study of oil palm (*Elaeis Guineensis* Jacq.). *Theor. Appl. Genet.* 128, 397–410. doi: 10.1007/s00122-014-2439-z
- Cros, D., Mbo-Nkoulou, L., Bell, J. M., Oum, J., Masson, A., Soumahoro, M., et al. (2019). Within-family genomic selection in rubber tree (*Hevea brasiliensis*) increases genetic gain for rubber production. *Ind. Crops Prod.* 138:111464. doi: 10.1016/j.indcrop.2019.111464
- Crossa, J., Burgueno, J., Dreisigacker, S., Vargas, M., Herrera-Foessel, S. A., Lillemo, M., et al. (2007). Association analysis of historical bread wheat germplasm using additive genetic covariance of relatives and population structure. *Genetics* 177, 1889–1913. doi: 10.1534/genetics.107.078659
- Crossa, J., Jarquin, D., Franco, J., Perez-Rodriguez, P., Burgueno, J., Saint-Pierre, C., et al. (2016). Genomic prediction of gene bank wheat landraces. *G3* 6, 1819–1834. doi: 10.1534/g3.116.029637
- Crossa, J., Martini, J. W. R., Gianola, D., Perez-Rodriguez, P., Jarquin, D., Juliana, P., et al. (2019). Deep kernel and deep learning for genome-based prediction of single traits in multi-environment breeding trials. *Front. Genet.* 10:1168. doi: 10.3389/fgene.2019.01168
- Crossa, J., Perez-Rodriguez, P., Cuevas, J., Montesinos-Lopez, O., Jarquin, D., De Los Campos, G., et al. (2017). Genomic selection in plant breeding: methods, models, and perspectives. *Trends Plant Sci.* 22, 961–975.
- Crowl, A. A., Manos, P. S., Mcvay, J. D., Lemmon, A. R., Lemmon, E. M., and Hipp, A. L. (2020). Uncovering the genomic signature of ancient introgression between white oak lineages (*Quercus*). *New Phytol.* 226, 1158–1170. doi: 10.1111/nph.15842
- De Dato, G., Teani, A., Mattioni, C., Marchi, M., Monteverdi, M. C., and Ducci, F. (2018). Delineation of seed collection zones based on environmental and genetic characteristics for *Quercus Suber* L. in Sardinia, Italy. *iForest* 11, 651–659. doi: 10.3832/ifer2572-011
- de la Harpe, M., Paris, M., Karger, D. N., Rolland, J., Kessler, M., Salamin, N., et al. (2017). Molecular ecology studies of species radiations: current research gaps, opportunities and challenges. *Mol. Ecol.* 26, 2608–2611. doi: 10.1111/mec.14110
- de los Campos, G., Hickey, J. M., Pong-Wong, R., Daetwyler, H. D., and Calus, M. P. (2013). Whole-genome regression and prediction methods applied to plant and animal breeding. *Genetics* 193, 327–345. doi: 10.1534/genetics.112.143313
- Destá, Z. A., and Ortiz, R. (2014). Genomic selection: genome-wide prediction in plant improvement. *Trends Plant Sci.* 19, 592–601. doi: 10.1016/j.tplants.2014.05.006
- de Visser, J. A. G. M., Elena, S. F., Fragata, I. S., and Matuszewski, S. (2018). The utility of fitness landscapes and big data for predicting evolution. *Heredity* 121, 401–405. doi: 10.1038/s41437-018-0128-4
- Dort, E. N., Tanguay, P., and Hamelin, R. C. (2020). Crispr/Cas9 gene editing: an unexplored frontier for forest pathology. *Front. Plant Sci.* 11:1126. doi: 10.3389/fpls.2020.01126
- Doudna, J. A., and Charpentier, E. (2014). Genome editing: the new frontier of genome engineering with Crispr-Cas9. *Science* 346:1258096.
- Eckert, A. J., Van Heerwaarden, J., Wegrzyn, J. L., Nelson, C. D., Ross-Ibarra, J., Gonzalez-Martinez, S. C., et al. (2010). Patterns of population structure and environmental associations to aridity across the range of loblolly pine (*Pinus Taeda* L., Pinaceae). *Genetics* 185, 969–982. doi: 10.1534/genetics.110.115543
- Elleouet, J. S., and Aitken, S. N. (2018). Exploring approximate bayesian computation for inferring recent demographic history with genomic markers in nonmodel species. *Mol. Ecol. Resour.* 18, 525–540. doi: 10.1111/1755-0998.12758
- Evans, L. M., Slavov, G. T., Rodgers-Melnick, E., Martin, J., Ranjan, P., Muchero, W., et al. (2014). Population genomics of *Populus trichocarpa* identifies signatures of selection and adaptive trait associations. *Nat. Genet.* 46, 1089–1096. doi: 10.1038/ng.3075
- Fay, M. F., and Palma-Silva, C. (2020). Professor Christian Lexer (23.05.1971–15.12.2019). *Bot. J. Linn. Soc.* 192, 589–591. doi: 10.1093/botlinnean/boaa006
- Feeley, K., Martinez-Villa, J., Perez, T., Silva Duque, A., Triviño Gonzalez, D., and Duque, A. (2020). The thermal tolerances, distributions, and performances of tropical montane tree species. *Front. For. Glob. Change* 3:25. doi: 10.3389/ffgc.2020.00025
- Flanagan, S. P., Forester, B. R., Latch, E. K., Aitken, S. N., and Hoban, S. (2018). Guidelines for planning genomic assessment and monitoring of locally adaptive variation to inform species conservation. *Evol. Appl.* 11, 1035–1052. doi: 10.1111/eva.12569
- Forester, B. R., Jones, M. R., Joost, S., Landguth, E. L., and Lasky, J. R. (2016). Detecting spatial genetic signatures of local adaptation in heterogeneous landscapes. *Mol. Ecol.* 25, 104–120. doi: 10.1111/mec.13476
- Freeman, B. G., Song, Y., Feeley, K. J., and Zhu, K. (2020). Montane species and communities track recent warming more closely in the tropics. *bioRxiv* [Preprint]. doi: 10.1101/2020.05.18.102848
- Fritsche, S., Klocko, A. L., Boron, A., Brunner, A. M., and Thorlby, G. (2018). Strategies for engineering reproductive sterility in plantation forests. *Front. Plant Sci.* 9:1671. doi: 10.3389/fpls.2018.01671
- Galeano, C. H., Cortés, A. J., Fernandez, A. C., Soler, A., Franco-Herrera, N., Makunde, G., et al. (2012). Gene-based single nucleotide polymorphism markers for genetic and association mapping in common bean. *BMC Genet.* 13:48. doi: 10.1186/1471-2156-13-48
- Gianola, D., Fernando, R. L., and Stella, A. (2006). Genomic-assisted prediction of genetic value with semiparametric procedures. *Genetics* 173, 1761–1776. doi: 10.1534/genetics.105.049510
- Gonzalez, A., Germain, R. M., Srivastava, D. S., Filotas, E., Dee, L. E., Gravel, D., et al. (2020). Scaling-up biodiversity-ecosystem functioning research. *Ecol. Lett.* 23, 757–776.
- Grattapaglia, D., Silva-Junior, O. B., Resende, R. T., Cappa, E. P., Muller, B. S. F., Tan, B., et al. (2018). Quantitative genetics and genomics converge to accelerate forest tree breeding. *Front. Plant Sci.* 9:1693. doi: 10.3389/fpls.2018.01693
- Hallingback, H. R., Berlin, S., Nordh, N. E., Weih, M., and Ronnberg-Wastljung, A. C. (2019). Genome wide associations of growth, phenology, and plasticity traits in willow [*Salix viminalis* (L.)]. *Front. Plant Sci.* 10:753. doi: 10.3389/fpls.2019.00753
- Herzog, E., and Frisch, M. (2011). Selection strategies for marker-assisted backcrossing with high-throughput marker systems. *Theor. Appl. Genet.* 123, 251–260. doi: 10.1007/s00122-011-1581-0
- Hickey, J. M., Chiurugwi, T., Mackay, I., Powell, W., and Implementing Genomic Selection in Cgair Breeding Programs Workshop Participants (2017). Genomic prediction unifies animal and plant breeding programs to form platforms for biological discovery. *Nat. Genet.* 49, 1297–1303. doi: 10.1038/ng.3920
- Hipp, A. L., Manos, P. S., Hahn, M., Avishai, M., Bodenes, C., Cavender-Bares, J., et al. (2020). Genomic landscape of the global oak phylogeny. *New Phytol.* 226, 1198–1212. doi: 10.1111/nph.16162
- Holliday, J. A., Aitken, S. N., Cooke, J. E., Fady, B., González-Martínez, S. C., Heuertz, M., et al. (2017). Advances in ecological genomics in forest trees and applications to genetic resources conservation and breeding. *Mol. Ecol.* 26, 706–717. doi: 10.1111/mec.13963
- Holliday, J. A., Suren, H., and Aitken, S. N. (2011). Divergent selection and heterogeneous migration rates across the range of sitka spruce (*Picea Sitchensis*). *Proc. Biol. Sci.* 279, 1675–1683. doi: 10.1098/rspb.2011.1805
- Holliday, J. A., Zhou, L., Bawa, R., Zhang, M., and Oubida, R. W. (2016). Evidence for extensive parallelism but divergent genomic architecture of adaptation along

- altitudinal and latitudinal gradients in *Populus trichocarpa*. *New Phytol.* 209, 1240–1251. doi: 10.1111/nph.13643
- Howe, G. T., and Brunner, A. M. (2005). An evolving approach to understanding plant adaptation. *New Phytol.* 167, 1–5. doi: 10.1111/j.1469-8137.2005.01469.x
- Ingværsson, P. K., and Bernhardsson, C. (2020). Genome-wide signatures of environmental adaptation in European Aspen (*Populus Tremula*) under current and future climate conditions. *Evol. Appl.* 13, 132–142. doi: 10.1111/eva.12792
- Ingværsson, P. K., and Dahlberg, H. (2018). The effects of clonal forestry on genetic diversity in wild and domesticated stands of forest trees. *Scand. J. For. Res.* 34, 370–379. doi: 10.1080/02827581.2018.1469665
- Ingværsson, P. K., Hvidsten, T. R., and Street, N. R. (2016). Towards integration of population and comparative genomics in forest trees. *New Phytol.* 212, 338–344. doi: 10.1111/nph.14153
- Isabel, N., Holliday, J. A., and Aitken, S. N. (2020). Forest genomics: advancing climate adaptation, forest health, productivity, and conservation. *Evol. Appl.* 13, 3–10. doi: 10.1111/eva.12902
- Karrenberg, S., Buerkle, C. A., Field, D. L., and Savolainen, V. (2020). Dedication: Christian Lexer (1971–2019). *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 375:20200232. doi: 10.1098/rstb.2020.0232
- Kehl, Z., Sanchez-Garcia, M., El Baouchi, A., Aberkane, H., Tsivelikas, A., Charles, C., et al. (2020). Predictive characterization for seed morphometric traits for genebank accessions using genomic selection. *Front. Ecol. Evol.* 8:32. doi: 10.3389/fevo.2020.00032
- Kelleher, C. T., Wilkin, J., Zhuang, J., Cortés, A. J., Quintero, ÁL. P., Gallagher, T. F., et al. (2012). Snp discovery, gene diversity, and linkage disequilibrium in wild populations of *Populus tremuloides*. *Tree Genet. Genomes* 821–829. doi: 10.1007/s11295-012-0467-x
- Khan, M. A., and Korban, S. S. (2012). Association mapping in forest trees and fruit crops. *J. Exp. Bot.* 63, 4045–4060. doi: 10.1093/jxb/ers105
- Klocko, A. L., Brunner, A. M., Huang, J., Meilan, R., Lu, H., Ma, C., et al. (2016). Containment of transgenic trees by suppression of leafy. *Nat. Biotechnol.* 34, 918–922. doi: 10.1038/nbt.3636
- Kremer, A., and Hipp, A. L. (2020). Oaks: an evolutionary success story. *New Phytol.* 226, 987–1011. doi: 10.1111/nph.16274
- Kremer, A., Potts, B. M., Delzon, S., and Bailey, J. (2014). Genetic divergence in forest trees: understanding the consequences of climate change. *Funct. Ecol.* 28, 22–36. doi: 10.1111/1365-2435.12169
- Lafon-Placette, C., Vallejo-Marín, M., Parisod, C., Abbott, R. J., and Köhler, C. (2016). Current plant speciation research: unravelling the processes and mechanisms behind the evolution of reproductive isolation barriers. *New Phytol.* 209, 29–33. doi: 10.1111/nph.13756
- Lascoux, M., Glémin, S., and Savolainen, O. (2016). Local adaptation in plants. *Encycl. Life Sci.* 0025270, 1–7. doi: 10.1002/9780470015902.a0025270
- Lenoir, J., Gegout, J. C., Marquet, P. A., De Ruffray, P., and Brisse, H. (2008). A significant upward shift in plant species optimum elevation during the 20th century. *Science* 320, 1768–1771. doi: 10.1126/science.1156831
- Lenz, P. R. N., Nadeau, S., Mottet, M. J., Perron, M., Isabel, N., Beaulieu, J., et al. (2020). Multi-trait genomic selection for weevil resistance, growth, and wood quality in Norway Spruce. *Evol. Appl.* 13, 76–94. doi: 10.1111/eva.12823
- Leroy, T., Louvet, J. M., Lalanne, C., Le Provost, G., Labadie, K., Aury, J. M., et al. (2020a). Adaptive introgression as a driver of local adaptation to climate in European white oaks. *New Phytol.* 226, 1171–1182. doi: 10.1111/nph.16095
- Leroy, T., Plomion, C., and Kremer, A. (2020b). Oak symbolism in the light of genomics. *New Phytol.* 226, 1012–1017. doi: 10.1111/nph.15987
- Leroy, T., Rougemont, Q., Dupouey, J. L., Bodenes, C., Lalanne, C., Belsler, C., et al. (2020c). Massive postglacial gene flow between European white oaks uncovered genes underlying species barriers. *New Phytol.* 226, 1183–1197. doi: 10.1111/nph.16039
- Li, Y., Klápště, J., Telfer, E., Wilcox, P., Graham, N., Macdonald, L., et al. (2019). Genomic selection for non-key traits in radiata pine when the documented pedigree is corrected using DNA marker information. *BMC Genomics* 20:1026. doi: 10.1186/s12864-019-6420-8
- Libbrecht, M. W., and Noble, W. S. (2015). Machine learning applications in genetics and genomics. *Nat. Rev. Genet.* 16, 321–332. doi: 10.1038/nrg3920
- Lind, B. M., Menon, M., Bolte, C. E., Fiske, T. M., and Eckert, A. J. (2018). The genomics of local adaptation in trees: are we out of the woods yet? *Tree Genet. Genomes* 14:29.
- Little, C. J., Wheeler, J. A., Sedlacek, J., Cortés, A. J., and Rixen, C. (2016). Small-scale drivers: the importance of nutrient availability and snowmelt timing on performance of the alpine shrub *Salix Herbacea*. *Oecologia* 180, 1015–1024. doi: 10.1007/s00442-015-3394-3
- Liu, S., Cornille, A., Decroocq, S., Tricon, D., Chague, A., Eyquard, J. P., et al. (2019). The complex evolutionary history of apricots: species divergence, gene flow and multiple domestication events. *Mol. Ecol.* 28, 5299–5314. doi: 10.1111/mec.15296
- López-Hernández, F., and Cortés, A. J. (2019). Last-generation genome-environment associations reveal the genetic basis of heat tolerance in common bean (*Phaseolus vulgaris* L.). *Front. Genet.* 10:22. doi: 10.3389/fgene.2019.00954
- Madriñán, S., Cortés, A. J., and Richardson, J. E. (2013). Páramo is the world's fastest evolving and coolest biodiversity hotspot. *Front. Genet.* 4:192. doi: 10.3389/fgene.2013.00192
- Mahony, C. R., Maclachlan, I. R., Lind, B. M., Yoder, J. B., Wang, T., and Aitken, S. N. (2020). Evaluating genomic data for management of local adaptation in a changing climate: a lodgepole pine case study. *Evol. Appl.* 13, 116–131. doi: 10.1111/eva.12871
- Marques, D. A., Meier, J. I., and Seehausen, O. (2019). A combinatorial view on speciation and adaptive radiation. *Trends Ecol. Evol.* 34, 531–544. doi: 10.1016/j.tree.2019.02.008
- Martin, M. A., Herrera, M. A., and Martini, L. M. (2012). *In situ* conservation and landscape genetics in forest species. *J. Nat. Resour. Dev.* 2, 1–5.
- Mason, A. S., and Wendel, J. F. (2020). Homoeologous exchanges, segmental allopolyploidy, and polyploid genome evolution. *Front. Genet.* 11:1014. doi: 10.3389/fgene.2020.01014
- Mattioni, C., Martin, M. A., Chiocchini, F., Gaudet, M., Pollegioni, P., Velichkov, I., et al. (2017). Landscape genetics structure of european sweet chestnut (*Castanea Sativa* Mill): indications for conservation priorities. *Tree Genet. Genomes* 13:39.
- Mayol, M., Riba, M., Cavers, S., Grivet, D., Vincenot, L., Cattonaro, F., et al. (2020). A multiscale approach to detect selection in nonmodel tree species: widespread adaptation despite population decline in *Taxus baccata* L. *Evol. Appl.* 13, 143–160. doi: 10.1111/eva.12838
- McKown, A. D., Guy, R. D., Quamme, L., Klapste, J., La Mantia, J., Constabel, C. P., et al. (2014). Association genetics, geography and ecophysiology link stomatal patterning in *Populus trichocarpa* with carbon gain and disease resistance trade-offs. *Mol. Ecol.* 23, 5771–5790. doi: 10.1111/mec.12969
- McKown, A. D., Klapste, J., Guy, R. D., El-Kassaby, Y. A., and Mansfield, S. D. (2018). Ecological genomics of variation in bud-break phenology and mechanisms of response to climate warming in *Populus trichocarpa*. *New Phytol.* 220, 300–316. doi: 10.1111/nph.15273
- Meilan, R., Brunner, A. M., Skinnera, J. S., and Strauss, S. H. (2001). Modification of flowering in transgenic trees. *Prog. Biotechnol.* 18, 247–256.
- Meuwissen, T. H. E., Hayes, B. J., and Goddard, M. E. (2001). Prediction of total genetic value using genome-wide dense marker maps. *Genetics* 157, 1819–1829.
- Meyer, F. E., Shuey, L. S., Naidoo, S., Mamni, T., Berger, D. K., Myburg, A. A., et al. (2016). Dual Rna-sequencing of *Eucalyptus nitens* during *Phytophthora cinnamomi* challenge reveals pathogen and host factors influencing compatibility. *Front. Plant Sci.* 7:191. doi: 10.3389/fpls.2016.00191
- Migicovsky, Z., and Myles, S. (2017). Exploiting wild relatives for genomics-assisted breeding of perennial crops. *Front. Plant Sci.* 8:460. doi: 10.3389/fpls.2017.00460
- Muranty, H., Jorge, V., Bastien, C., Lepoittevin, C., Bouffier, L., and Sanchez, L. (2014). Potential for marker-assisted selection for forest tree breeding: lessons from 20 years of mas in crops. *Tree Genet. Genomes* 10, 1491–1510. doi: 10.1007/s11295-014-0790-5
- Myburg, A. A., Hussey, S. G., Wang, J. P., Street, N. R., and Mizrahi, E. (2019). Systems and synthetic biology of forest trees: a bioengineering paradigm for Woody biomass feedstocks. *Front. Plant Sci.* 10:775. doi: 10.3389/fpls.2019.00775
- Naidoo, S., Külheim, C., Zwart, L., Mangwanda, R., Oates, C. N., Visser, E. A., et al. (2014). Uncovering the defence responses of *Eucalyptus* to pests and pathogens in the genomics age. *Tree Physiol.* 34, 931–943. doi: 10.1093/treephys/tpu075
- Naidoo, S., Slippers, B., Plett, J. M., Coles, D., and Oates, C. N. (2019). The road to resistance in forest trees. *Front. Plant Sci.* 10:273. doi: 10.3389/fpls.2019.00273
- Neale, D. B., and Kremer, A. (2011). Forest tree genomics: growing resources and applications. *Nat. Rev. Genet.* 12, 111–122. doi: 10.1038/nrg2931

- Neale, D. B., and Savolainen, O. (2004). Association genetics of complex traits in conifers. *Trends Plant Sci.* 9, 325–330. doi: 10.1016/j.tplants.2004.05.006
- Nieto Feliner, G., Casacuberta, J., and Wendel, J. F. (2020). Genomics of evolutionary novelty in hybrids and polyploids. *Front. Genet.* 11:792. doi: 10.3389/fgene.2020.00792
- Nystedt, B., Street, N. R., Wetterbom, A., Zuccolo, A., Lin, Y.-C., Scofield, D. G., et al. (2013). The Norway spruce genome sequence and conifer genome evolution. *Nature* 497, 579–584.
- Pennisi, E. (2020). Tropical forests store carbon despite warming. *Science* 368:813. doi: 10.1126/science.368.6493.813
- Pereira-Lorenzo, S., Ramos-Cabrera, A. M., Barreneche, T., Mattioni, C., Villani, F., Díaz-Hernández, B., et al. (2019). Instant domestication process of European chestnut cultivars. *Ann. Appl. Biol.* 174, 74–85. doi: 10.1111/aab.12474
- Phillips, J., Ramirez, S., Wayson, C., and Duque, A. (2019). Differences in carbon stocks along an elevational gradient in tropical mountain forests of Colombia. *Biotropica* 51, 490–499. doi: 10.1111/btp.12675
- Phillips, S. J., Anderson, R. P., Dudík, M., Schapire, R. E., and Blair, M. E. (2017). Opening the black box: an open-source release of maxent. *Ecography* 40, 887–893. doi: 10.1111/ecog.03049
- Piot, A., Prunier, J., Isabel, N., Klapste, J., El-Kassaby, Y. A., Villarreal Aguilar, J. C., et al. (2019). Genomic diversity evaluation of *Populus trichocarpa* germplasm for rare variant genetic association studies. *Front. Genet.* 10:1384. doi: 10.3389/fgene.2019.01384
- Plomion, C., Aury, J. M., Amsellem, J., Leroy, T., Murat, F., Duplessis, S., et al. (2018). Oak genome reveals facets of long lifespan. *Nat. Plants* 4, 440–452.
- Plomion, C., and Martin, F. (2020). Oak genomics is proving its worth. *New Phytol.* 226, 943–946. doi: 10.1111/nph.16560
- Pluess, A. R., Frank, A., Heiri, C., Lalague, H., Vendramin, G. G., and Oddou-Muratorio, S. (2016). Genome-environment association study suggests local adaptation to climate at the regional scale in *Fagus sylvatica*. *New Phytol.* 210, 589–601. doi: 10.1111/nph.13809
- Ratcliffe, B., Thistlethwaite, F., El-Dien, O. G., Cappa, E. P., Porth, I., Klápště, J., et al. (2019). Inter- and intra-generation genomic predictions for Douglas-Fir growth in unobserved environments. *bioRxiv* [Preprint]. doi: 10.1101/540765
- Rellstab, C., Gugerli, F., Eckert, A. J., Hancock, A. M., and Holderegger, R. (2015). A practical guide to environmental association analysis in landscape genomics. *Mol. Ecol.* 24, 4348–4370. doi: 10.1111/mec.13322
- Resende, M. D. V., Resende, M. F. R., Sansaloni, C. P., Petrolí, C. D., Missiaggia, A. A., and Aguiar, A. M. (2012). Genomic selection for growth and wood quality in *Eucalyptus*: capturing the missing heritability and accelerating breeding for complex traits in forest trees. *New Phytol.* 194, 116–128. doi: 10.1111/j.1469-8137.2011.04038.x
- Resende, M. F., Muñoz, P., Resende, M. D., Garrick, D. J., Fernando, R. L., Davis, J. M., et al. (2012). Accuracy of genomic selection methods in a standard data set of loblolly pine (*Pinus taeda* L.). *Genetics* 190, 1503–1510. doi: 10.1534/genetics.111.137026
- Resende, R. T., Piepho, H. P., Rosa, G. J. M., Silva-Junior, O. B., Silva, F. F., Resende, M. D. V., et al. (2020). *Enviromics* in breeding: applications and perspectives on envirotypic-assisted selection. *Theor. Appl. Genet.* doi: 10.1007/s00122-020-03684-z
- Roudbar, M. A., Momen, M., Mousavi, S. F., Ardestani, S. S., Lopes, F. B., Gianola, D., et al. (2020). Genome-wide methylation prediction of biological age using reproducing Kernel Hilbert spaces and Bayesian ridge regressions. *bioRxiv* [Preprint]. doi: 10.1101/2020.08.25.266924
- Savolainen, O., Lascoux, M., and Merilä, J. (2013). Ecological genomics of local adaptation. *Nat. Rev. Genet.* 14, 807–820. doi: 10.1038/nrg3522
- Sawitri, S., Tani, N., Na'iem, M., Widiyatno, Indrioko, S., Uchiyama, K., et al. (2020). Potential of genome-wide association studies and genomic selection to improve productivity and quality of commercial timber species in tropical rainforest, a case study of *Shorea platyclados*. *Forests* 11:239. doi: 10.3390/f11020239
- Scherer, L., Svenning, J. C., Huang, J., Seymour, C. L., Sandel, B., Mueller, N., et al. (2020). Global priorities of environmental issues to combat food insecurity and biodiversity loss. *Sci. Total Environ.* 730:139096. doi: 10.1016/j.scitotenv.2020.139096
- Schilthuizen, M., Hoekstra, R. F., and Gittenberger, E. (2004). Hybridization, rare alleles and adaptive radiation. *Trends Ecol. Evol.* 19, 404–405. doi: 10.1016/j.tree.2004.06.005
- Schloötterer, C. (2020). Christian Lexer: a lifelong passion for trees. *Mol. Ecol.* 29, 443–444. doi: 10.1111/mec.15363
- Schrider, D. R., and Kern, A. D. (2018). Supervised machine learning for population genetics: a new paradigm. *Trends Genet.* 34, 301–312. doi: 10.1016/j.tig.2017.12.005
- Scott, M. F., Ladejobi, O., Amer, S., Bentley, A. R., Biernaskie, J., Boden, S. A., et al. (2020). Multi-parent populations in crops: a toolbox integrating genomics and genetic mapping with breeding. *Hereditas*. doi: 10.1038/s41437-020-0336-6 [Epub ahead of print].
- Sedlacek, J., Bossdorf, O., Cortés, A. J., Wheeler, J. A., and Van-Kleunen, M. (2014). What role do plant-soil interactions play in the habitat suitability and potential range expansion of the alpine dwarf shrub *Salix herbacea*? *Basic Appl. Ecol.* 15, 305–315. doi: 10.1016/j.baec.2014.05.006
- Sedlacek, J., Cortés, A. J., Wheeler, J. A., Bossdorf, O., Hoch, G., Klapste, J., et al. (2016). Evolutionary potential in the alpine: trait heritabilities and performance variation of the dwarf willow *Salix herbacea* from different elevations and microhabitats. *Ecol. Evol.* 6, 3940–3952. doi: 10.1002/ece3.2171
- Sedlacek, J., Wheeler, J. A., Cortés, A. J., Bossdorf, O., Hoch, G., Lexer, C., et al. (2015). The response of the alpine dwarf shrub *Salix herbacea* to altered snowmelt timing: lessons from a multi-site transplant experiment. *PLoS One* 10:e0122395. doi: 10.1371/journal.pone.0122395
- Seehausen, O. (2004). Hybridization and adaptive radiation. *Trends Ecol. Evol.* 19, 198–207. doi: 10.1016/j.tree.2004.01.003
- Sentinella, A. T., Warton, D. I., Sherwin, W. B., Offord, C. A., Moles, A. T., and Wang, Z. (2020). Tropical plants do not have narrower temperature tolerances, but are more at risk from warming because they are close to their upper thermal limits. *Glob. Ecol. Biogeogr.* 29, 1387–1398. doi: 10.1111/geb.13117
- Shang, H., Hess, J., Pickup, M., Field, D. L., Ingvarsson, P. K., Liu, J., et al. (2020). Evolution of strong reproductive isolation in plants: broad-scale patterns and lessons from a perennial model group. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 375:20190544. doi: 10.1098/rstb.2019.0544
- Sousa, T. V., Caixeta, E. T., Alkimim, E. R., Oliveira, A. C. B., Pereira, A. A., Sakiyama, N. S., et al. (2018). Early selection enabled by the implementation of genomic selection in *Coffea arabica* breeding. *Front. Plant Sci.* 9:1934. doi: 10.3389/fpls.2018.01934
- Souza, L. M., Francisco, F. R., Goncalves, P. S., Scaloppi Junior, E. J., Le Guen, V., Fritsche-Neto, R., et al. (2019). Genomic selection in rubber tree breeding: a comparison of models and methods for managing GxE interactions. *Front. Plant Sci.* 10:1353. doi: 10.3389/fpls.2019.01353
- Sow, M. D., Allona, I., Ambroise, C., Conde, D., Fichot, R., Gribkova, S., et al. (2018). Epigenetics in forest trees: state of the art and potential implications for breeding and management in a context of climate change. *Adv. Bot. Res.* 88, 387–453. doi: 10.1016/bs.abr.2018.09.003
- Steinbauer, M. J., Grytnes, J. A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H., et al. (2018). Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature* 556, 231–234.
- Stocks, J. J., Metheringham, C. L., Plumb, W. J., Lee, S. J., Kelly, L. J., Nichols, R. A., et al. (2019). Genomic basis of European ash tree resistance to ash dieback fungus. *Nat. Ecol. Evol.* 3, 1686–1696. doi: 10.1038/s41559-019-1036-6
- Stöltzing, K. N., Paris, M., Meier, C., Heinze, B., Castiglione, S., Bartha, D., et al. (2015). Genome-wide patterns of differentiation and spatially varying selection between postglacial recolonization lineages of *Populus Alba* (Salicaceae), a widespread forest tree. *New Phytol.* 207, 723–734. doi: 10.1111/nph.13392
- Sullivan, M., Lewis, S. L., Affum-Baffoe, K., Castilho, C., Costa, F., Sanchez, A. C., et al. (2020). Long-term thermal sensitivity of earth's tropical forests. *Science* 368, 869–874.
- Suontama, M., Klápště, J., Telfer, E., Graham, N., Stovold, T., Low, C., et al. (2019). Efficiency of genomic prediction across two *Eucalyptus nitens* seed orchards with different selection histories. *Hereditas* 122, 370–379. doi: 10.1038/s41437-018-0119-5
- Tan, B., Grattapaglia, D., Martins, G. S., Ferreira, K. Z., Sundberg, B. R., and Ingvarsson, P. R. K. (2017). Evaluating the accuracy of genomic prediction of growth and wood traits in two *Eucalyptus* species and their F1 hybrids. *BMC Plant Biol.* 17:110. doi: 10.1186/s12870-017-1059-6
- Technow, F., Schrag, T. A., Schipprack, W., Bauer, E., Simianer, H., and Melchinger, A. E. (2014). Genome properties and prospects of genomic prediction of hybrid performance in a breeding program of maize. *Genetics* 197, 1343–1355. doi: 10.1534/genetics.114.165860



- Thistlethwaite, F. R., Gamal El-Dien, O., Ratcliffe, B., Klapste, J., Porth, I., Chen, C., et al. (2020). Linkage Disequilibrium Vs. Pedigree: genomic selection prediction accuracy in conifer species. *PLoS One* 15:e0232201. doi: 10.1371/journal.pone.0232201
- Thistlethwaite, F. R., Ratcliffe, B., Klápšti, J., Porth, I., Chen, C., Stoehr, M. U., et al. (2017). Genomic prediction accuracies in space and time for height and wood density of Douglas-Fir using exome capture as the genotyping platform. *BMC Genomics* 18:930. doi: 10.1186/s12864-017-4258-5
- Thistlethwaite, F. R., Ratcliffe, B., Klápšti, J., Porth, I., Chen, C., Stoehr, M. U., et al. (2019a). Genomic selection of juvenile height across a single-generational gap in Douglas-Fir. *Heredity* 122, 848–863. doi: 10.1038/s41437-018-0172-0
- Thistlethwaite, F. R., Ratcliffe, B., Klápšti, J., Porth, I., Chen, C., Stoehr, M. U., et al. (2019b). Genomic selection of juvenile height across a single-generational gap in Douglas-Fir. *Heredity* 122, 848–863. doi: 10.1038/s41437-018-0172-0
- Tito, R., Vasconcelos, H. L., and Feeley, K. J. (2020). Mountain ecosystems as natural laboratories for climate change experiments. *Front. For. Glob. Change* 3:38. doi: 10.3389/ffgc.2020.00038
- Tuskan, G. A., Groover, A. T., Schmutz, J., Difazio, S. P., Myburg, A., Grattapaglia, D., et al. (2018). Hardwood tree genomics: unlocking woody plant biology. *Front. Plant Sci.* 9:1799. doi: 10.3389/fpls.2018.01799
- Ukrainetz, N. K., and Mansfield, S. D. (2020). Assessing the sensitivities of genomic selection for growth and wood quality traits in lodgepole pine using Bayesian models. *Tree Genet. Genomes* 16:14.
- Ulian, T., Diazgranados, M., Pironon, S., Padulosi, S., Liu, U., Davies, L., et al. (2020). Unlocking plant resources to support food security and promote sustainable agriculture. *Plants People Planet* 2, 421–445. doi: 10.1002/ppp3.10145
- Valencia, J. B., Mesa, J., León, J. G., Madriñán, S., and Cortés, A. J. (2020). Climate vulnerability assessment of the *Espeletia* complex on PaiRamo sky islands in the Northern Andes. *Front. Ecol. Evol.* 8:565708. doi: 10.3389/fevo.2020.565708
- Wang, J., Street, N. R., Park, E. J., Liu, J., and Ingvarsson, P. K. (2020). Evidence for widespread selection in shaping the genomic landscape during speciation of *Populus*. *Mol. Ecol.* 29, 1120–1136. doi: 10.1111/mec.15388
- Wang, M., Zhang, L., Zhang, Z., Li, M., Wang, D., Zhang, X., et al. (2020). Phylogenomics of the genus *Populus* reveals extensive interspecific gene flow and balancing selection. *New Phytol.* 225, 1370–1382. doi: 10.1111/nph.16215
- Westbrook, J. W., Holliday, J. A., Newhouse, A. E., and Powell, W. A. (2019). A plan to diversify a transgenic blight-tolerant American chestnut population using citizen science. *Plants People Planet* 2, 84–95. doi: 10.1002/ppp3.10061
- Westbrook, J. W., Zhang, Q., Mandal, M. K., Jenkins, E. V., Barth, L. E., Jenkins, J. W., et al. (2020). Optimizing genomic selection for blight resistance in American chestnut backcross populations: a trade-off with American chestnut ancestry implies resistance is polygenic. *Evol. Appl.* 13, 31–47. doi: 10.1111/eva.12886
- Wheeler, J. A., Cortés, A. J., Sedlacek, J., Karrenberg, S., Van Kleunen, M., Wipf, S., et al. (2016). The snow and the willows: accelerated spring snowmelt reduces performance in the low-lying alpine shrub *Salix herbacea*. *J. Ecol.* 104, 1041–1050. doi: 10.1111/1365-2745.12579
- Wheeler, J. A., Hoch, G., Cortés, A. J., Sedlacek, J., Wipf, S., and Rixen, C. (2014). Increased spring freezing vulnerability for alpine shrubs under early snowmelt. *Oecologia* 175, 219–229. doi: 10.1007/s00442-013-2872-8
- Wheeler, J. A., Schnider, F., Sedlacek, J., Cortés, A. J., Wipf, S., Hoch, G., et al. (2015). With a little help from my friends: community facilitation increases performance in the dwarf shrub *Salix herbacea*. *Basic Appl. Ecol.* 16, 202–209. doi: 10.1016/j.baae.2015.02.004
- White, T., Adams, W., and Neale, D. (2007). *Forest Genetics*. New York, NY: CSIRO-CABI Publishing.
- Yeaman, S., Hodgins, K. A., Lotterhos, K. E., Suren, H., Nadeau, S., Degner, J. C., et al. (2016). Convergent local adaptation to climate in distantly related conifers. *Science* 353, 1431–1433. doi: 10.1126/science.aaf7812
- Zahn, L. M., and Purnell, B. A. (2016). Genes under pressure. *Science* 354:52. doi: 10.1126/science.354.6308.52
- Zhou, L., Bawa, R., and Holliday, J. A. (2014). Exome resequencing reveals signatures of demographic and adaptive processes across the genome and range of black cottonwood (*Populus trichocarpa*). *Mol. Ecol.* 23, 2486–2499. doi: 10.1111/mec.12752
- Zhou, L., Chen, Z., Olsson, L., Grahn, T., Karlsson, B., Wu, H. X., et al. (2020). Effect of number of annual rings and tree ages on genomic predictive ability for solid wood properties of Norway spruce. *BMC Genomics* 21:323. doi: 10.1186/s12864-020-6737-3

**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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