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Managing forest genetic resources for an uncertain future: findings and perspectives from an international conference

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Abstract

As climate change intensifies, the fate of many of the world's forests is becoming a major concern. Meanwhile, the European Union (EU) member states have committed to the goal of becoming the first climate-neutral continent by 2050, which will involve the planting of 3 billion additional trees by 2030. This challenge can only be met by robust and efficient management and conservation strategies, based on intense sharing of knowledge and tools among experts, practitioners and policymakers. The B4EST International Conference '*Managing Forest Genetic Resources (FGR) for an Uncertain Future*', held on 20–23 June 2022 in Lisbon (Portugal), brought together stakeholders from the public and private sectors, researchers and policymakers to explore issues around implementation of sustainable management and conservation of European forests. The conference illustrated the promise of genomic technologies for supporting the tree breeding sector, how Forest Genetic Resources (FGR) and Forest Reproductive Material (FRM) could be optimally deployed and play a key role in building climate resilient forests, and the role experts play in the present context of uncertain climate and societal changes.

Keywords Forest genetic resources · Forest reproductive material · Climate change · Forest management and conservation strategies · Forest resilience

Introduction

Covering 35% of the European land area (227 million hectares; Ferretti et al. 2020), forests are reservoirs of biodiversity and provide multiple ecosystem services, in particular

through their role in the water cycle, regulation of global (via carbon storage) and local (via evapotranspiration) climate, prevention of soil erosion and provision of wood (e.g. timber) and non-wood products (e.g. food, cork, resin, oils). The forestry sector accounts for about 1% of European gross domestic product and about 42% of timber is used for energy

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generation, 24% for sawmills, 17% for the paper industry and 12% for the panel industry (Ferretti et al. 2020). Forests also hold an essential place in European culture, history and tourism, and contribute to the well-being of urban and rural communities (EC 2021).

Climate change has triggered an increase in biotic and abiotic threats to forests, including gradual climatic shifts, more frequent extreme climatic events (e.g. droughts or frosts), large fires (not restricted to the traditionally fire-prone areas), severe storms (e.g. in western and central Europe) and insect outbreaks (Seidl et al. 2018; Forzieri et al. 2021; Obladen et al. 2021). How natural and managed forest tree populations will cope with these threats is highly uncertain. Indeed, although the range of tree species and populations are shifting northward and to higher elevations, these processes are unlikely to be fast enough to keep up with the current rate of climate change (Boisvert-Marsh et al. 2014; Davis and Shaw 2001). Without human intervention, natural forest tree populations will have to persist where they are, by relying on their phenotypic plasticity (Nicotra et al. 2010) and adaptive capacity, which depends on the genetic variation of the populations and on the presence of alleles that confer adaptive advantage under future climates. Predicting which populations will survive the changes is an active research area (Alberto et al. 2013). In managed forests, implementing strategies for the deployment of forest genetic resources (FGR, the genetic variation in trees of present or potential benefit to humans; FAO 1989) and tree breeding programmes, including low-input ones, will be key to developing forests that are resilient to the upcoming changes. In particular, conservation and management strategies must take into account the uncertainty of future climate predictions by ensuring that sufficient levels of genetic variation are maintained within populations, i.e. that the adaptive potential is high enough to cope with new conditions.

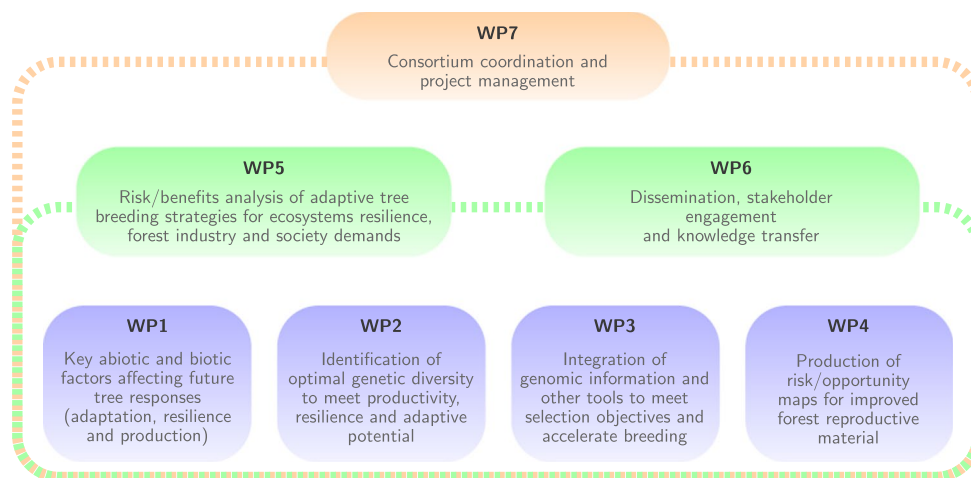
In light of the challenges of climate change, new genomic technologies hold the potential to better anticipate the response of tree populations, to better characterise FGR and to accelerate breeding. For instance, tree populations at risk of maladaptation may be identified based on the disruption of their gene-environment relationships (e.g. Fitzpatrick and Keller 2015). Large genomic datasets will allow improved characterisation of FGR, such as precise delineation of gene pools, quantification of genetic diversity or identification of the genetic variation underlying disease resistance or drought tolerance. Such data have also proven highly useful for genomic selection (GS), in which all available genomic markers are used to predict the additive genetic value of individuals (Meuwissen et al. 2001), leading to tremendous progress in livestock improvement (García-Ruiz et al. 2016) and increasingly in tree breeding. In addition, combining transcriptomics and metabolomics (i.e. multi-omics data)

with genomics may result in more accurate prediction of phenotypes.

Faced with accelerating climate change and environmental degradation, European countries committed in 2020 to the European Green Deal, a strategy for transition to a sustainable economy and with the overarching objective of becoming the first climate neutral continent by 2050. Within this framework, the EU Biodiversity Strategy for 2030 has the ambitious goal of ensuring that natural ecosystems are restored, resilient and adequately protected by 2050. Forest management and conservation are expected to play a central role in reaching European biodiversity goals. In parallel, the New EU Forest Strategy for 2030 proposes actions to improve the quantity and quality of European forests and to enhance their protection, restoration and resilience in the face of climate uncertainty. Among the measures proposed is a commitment to improve the area and biodiversity of forests by planting 3 billion more trees by 2030, in addition to current plantation efforts. Last, the EU Bioeconomy Strategy, updated in 2018, includes the objective of sustainable management of natural resources, and mitigation and adaptation to climate change.

Deploying management and conservation strategies to address climate change will involve sharing new scientific knowledge among experts, practitioners and policymakers. It is therefore essential to make the latest research and tools easily accessible and to strengthen the links among the various actors in the forestry sector. With this as a central objective, the B4EST project funded by the EU's research and innovation funding programme H2020 (www.b4est.eu) ran from 2018 to 2022 (Fig. 1). The project provided forest tree breeders, forest owners, managers and policymakers with scientific knowledge to increase forest survival, health, resilience and productivity in the face of climate change, while maintaining genetic diversity and key ecological functions. As a finale, an international Conference, 'Managing Forest Genetic Resources (FGR) for an Uncertain Future' (<https://b4est.eu/b4est-conference>), was held on 20–23 June 2022 in Lisbon, Portugal, at the Instituto Superior de Agronomia, University of Lisbon. The conference brought together a wide range of stakeholders from both the public and private forestry sector, researchers and policy authorities (Table 1, Supplementary Information). It had four sessions, each addressing a key topic for sustainable management and conservation of European forests, namely (1) rethinking and accelerating breeding to cope with new challenges and an uncertain future; (2) the role of forest genetic resources (FGR) in building resilient forests to climate change; (3) potential of forest reproductive material (FRM) deployment in different European countries and forest types in a context of climatic and societal change; and (4) strengthening the interface among scientists, policymakers and stakeholders for a better mitigation, adaptation and risk management

Fig. 1 Structure of the B4EST project and its different work packages (WPs). B4EST stands for B-FO(U)R-EST, with ‘B’ referring to ‘breeding’ and ‘FO(U)R-EST’ referring to ‘forest’. The full title of the project is ‘Adaptive BREEDING for productive, sustainable and resilient FORESTs under climate change’



in forestry. In addition, the presentation of different tools developed under B4EST (Table 2, Supplementary Information) and two training courses completed the conference programme (Table 3, Supplementary Information).

Rethinking breeding strategies for an uncertain future

Genomic innovations in the last decade have led to improvements in the way tree breeding is conducted. The development of new genotyping tools is a cornerstone of this progress. The 4TREE Axiom 50 K single nucleotide polymorphism (SNP) array was developed within the B4EST project for four economically important species in Europe: poplar (*Populus* sp.), ash (*Fraxinus* sp.), maritime pine (*Pinus pinaster* Ait.) and stone pine (*Pinus pinea* L.). Based on existing and de novo sequencing resources, it is primarily aimed at breeders to provide low genotyping costs and foster collaboration between breeding programmes across Europe. Sanna Olsson (INIA-CSIC) showed how the 4TREE SNP array has been used to achieve unprecedented resolution of population structure and unambiguous clonal identification in stone pine.

The availability of large sets of genomic markers has enabled the use of more powerful statistical tools to predict phenotypes, in particular GS, which has already revolutionised animal breeding. Indeed, GS promises to accelerate genetic gain by shortening breeding cycles, reducing phenotyping costs through better targeting (replacing all or a portion of the phenotyping effort with genotyping) and improving predictive and explanatory analyses to decrypt phenomena and optimise performance in progeny. For example, Geoffrey Haristoy (CIRAD) showed how GS can be used to predict height, diameter and survival across generations in the ALTRI's breeding programme, which manages close to 70,000 hectares of *Eucalyptus globulus* in Portugal. Recent

developments in GS include the integration of multi-omics data in phenotypic prediction. Leopoldo Sánchez (INRAE) presented an approach combining genomic and transcriptomic data (expression quantitative trait loci, eQTLs) with ridge regression in black poplar (*Populus nigra* L.). Compared to using genomic data alone, phenotypic predictions were much improved by incorporating the eQTLs.

However, implementing GS in recurrent breeding programmes risks accelerating genetic diversity erosion and so long-term genetic gains may be compromised by higher inbreeding rates. Laurence Moreau (INRAE) gave a keynote talk on how GS can be used at different stages of a breeding programme to better manage genetic diversity over time. She showed how, in maize, GS models calibrated on combined diversity panels (i.e. panels with both primary genetic resources and recent elite materials) can identify sources of favourable alleles that could enrich a given breeding programme (Allier et al. 2020a). She then presented a breeding strategy in which GS and optimal cross-selection (i.e. optimal selection of crosses under a constraint on genetic diversity in the progeny) are combined to improve genetic resources (i.e. pre-breeding), close the gap between the improved genetic resources and elite materials (bridging), and manage the introduction of donors into the elite breeding population (Allier et al. 2020b). Such strategies are highly promising as they broaden the available genetic resources for commercial breeding programmes and have the potential to increase long-term genetic gain with only a limited reduction of short-term commercial gain (Allier et al. 2019). In a similar vein, Mathieu Tiret (UU) used the concept of group selection to show that maintaining genetic diversity can provide both long- and short-term genetic gains (i.e. through intraspecific interactions) in the breeding programme of black poplar.

Another challenge for GS is to simultaneously select for multiple traits (e.g. growth and drought resistance). Victor Papin (INRAE) estimated breeding values that vary along

environmental gradients (e.g. different levels of aridity) for a dendrophenotype (ring surface) in maritime pine and emphasised the importance of selecting genotypes that perform well in a wide range of environments or in specific environments. Giorgio Tumino (WUR) used the 4TREE SNP array to predict phenotypic variation for resistance to ash dieback disease in common ash (*Fraxinus excelsior* L.), showing that genomic predictions were more accurate for lesion length than for the percentage of defoliation. Chiara Biselli (CREA) identified loci for resistance to the woolly poplar aphid (*Phloeomyzus passerinii* L.) in poplar and showed that molecular markers explained more than 50% of the total phenotypic variance for resistance. Since most cultivated poplar clones are susceptible to the disease, this study is a step towards building a collection of resistant clones that could enrich poplar breeding. Lastly, Ricardo Alía (INIA-CSIC) presented a review on genetic correlation between growth and resistance/tolerance to abiotic/biotic stresses in forest trees, resulting from B4EST research, in which he suggested that genetic correlations among traits will not constrain genetic improvements for most traits.

Forest genetic resources and adaptation to climate change

Predicting how natural and plantation forest tree populations will fare in their current location or respond to new environments (e.g. after translocations) is a difficult task (Aitken et al. 2008), yet necessary for effective management and conservation strategies (Aitken and Bemmels 2015). Meanwhile, projections of future climates are still very uncertain (Lindner et al. 2014), especially those related to future precipitation (IPCC 2021), and there is a need for development of methods to incorporate these uncertainties into predictions. In this session, case studies and statistical approaches were presented that aimed to improve predictions of the short-term responses of forest tree populations to new climatic conditions using a wide range of concepts and tools from population and quantitative genetics, spatial modelling and community-level modelling.

In his keynote talk, Tongli Wang (UBC) shared his perspective on recent method development for predicting tree population responses to climate change. Future ranges were first predicted with climate niche models, which have the limitations of not considering intraspecific variation and of relying on the realised rather than the fundamental niche of the species. Transfer and response functions were then developed based on phenotypic data from multi-site common gardens to predict trait variation across the range, and called universal response functions (URF) as both transfer and response functions were combined in a single model (Wang et al. 2010). Predictions from those functions rely

on the association between trait variation and the climate-of-origin of the populations (i.e. genetic component) and the climatic conditions in the common gardens (i.e. plastic component). The approach has been shown to provide less pessimistic predictions of population responses than climate niche models (Benito Garzón et al. 2019). As access to genomic tools has improved, a new set of approaches have been developed to predict population responses to future climatic conditions based on genomic data. Wang showed an example in which landscape genomics methods were used to define seed and breeding zones in lodgepole pine (*Pinus contorta* Douglas) (Yu et al. 2022).

Together the speakers gave a complementary overview of methods and traits for forecasting the responses of European trees to climate change. Katharina Liepe (Thünen IFG) and Zhi-Qiang Chen (UPSC) applied the URF framework to height data from 20 common gardens and 1100 provenances in Norway spruce (*Picea abies* L.) and found that most height variation was explained by phenotypic plasticity, although the two studies did not identify the same climatic drivers. Liepe showed that height models predicted a substantial contraction of the species range towards the core of the distribution, though these predictions were less alarming than those from occurrence-based species distribution models. She also suggested that transferring optimal populations may help maintain growth where the species persists. Chen showed that using the optimal populations in each common garden may enhance productivity by 51.1% and 30.7% for temperature increases of 1 °C and 2 °C, respectively. Still on Norway spruce, Arne Steffenrem (NIBIO) investigated an understudied plastic response in forest trees: the effects of the maternal reproductive environment. He suggested that temperatures during reproduction and seed maturation can have long-lasting and predictable effects on seedling phenology. Controlling such maternal effects in management and conservation programmes may prove useful for maximising the performance of trees grown in nurseries. Transgenerational effects were also investigated by Marta Callejas-Díaz (INIA-CSIC) in a common garden experiment of maritime pine. She showed that seedling height and ontogeny were influenced by the interacting effects of seedling cohorts and mother genotype (Callejas-Díaz et al. 2022). Last, using seven southeastern Baltic provenances of Scots pine (*Pinus sylvestris* L.) grown in five common gardens in Germany and Latvia, Āris Jansons (Silava) found that the highest genetic variation for climatic sensitivity of radial growth (measured from tree rings) was mostly associated with the summer heat moisture regime.

While most predictions of future population responses to climate change have been based on traits related to growth and wood properties, a more complete picture may be obtained by considering other trait, and incorporating information from the variation in allele frequencies along

climatic gradients or across generations. Annika Perry (UKCEH) presented an innovative study that combined a multispecies approach to identify SNP associated with growth and phenology traits with single species genomic prediction models (Perry et al. 2022). Model predictive ability was strongly limited by genotype-by-environment (GxE) interactions. However, using some of the height models as genomic selection tools would result in the selection of trees taller than the average for each site, highlighting the potential of the approach to accelerate tree breeding. Laura Guillard (Oxford University) addressed the issue of managing genetic diversity over generations when planted forests are converted to continuous cover forests, showing the first steps of two case studies comparing allelic frequency across different cohorts in plantations of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western red cedar (*Thuja plicata* Donn ex D.Don) under conversion. Last, Octávio S. Paulo (cE3c) illustrated how the estimation of current gene-climate relationships may inform the risk of population maladaptation under climate change, using landscape genomics approaches, i.e. Gradient Forests (Vanhove et al. 2021) and Risk of Non-Adaptedness (RONA) (Pina-Martins et al. 2019), in cork oak (*Quercus suber* L.).

Deployment of forest reproductive material

Successful deployment of FRM can be improved by careful definition of the required ecosystem services and the delivery to practitioners of scientific knowledge and decision support tools. This was illustrated by the keynote talk of Conceição Silva (UNAC), which dealt with FRM regulation, certification and markets in Portugal for the five main production tree species in the region, namely eucalypt (*Eucalyptus globulus* Labill.), cork oak, holm oak (*Quercus rotundifolia* Lam.), maritime pine and Mediterranean stone pine. Although private landowners (87% of forests in Portugal) consider climate change adaptation and mitigation as a priority, the cork, wood and pulp industry sectors struggle with a lack of raw material adapted to new climatic and biotic conditions. Until recently, breeding programmes have optimised genetic gain for traits related to growth and wood quality (e.g. in maritime pine and eucalypt) or the production of pulp (eucalypt), resin (maritime pine), cork (cork oak) or pinyons (stone pine). Now breeding programmes aim to improve tree resistance to pathogens, e.g. resistance to the pine wilt disease in maritime pine caused by the pine wood nematode (*Bursaphelenchus xylophilus*) and other traits. Another challenge for FRM deployment is addressing the trade-offs among traits of interest. Esteban Torres-Sánchez (CIF Lourizán) demonstrated in a Galician breeding population of maritime pine that selecting for wood quality at an early stage is possible due to phenotypic correlations

between juvenile and mature trees and will not result in a growth deficit (i.e. no trade-off between growth and wood quality). Last, Toms Kondratovics (Silava) presented results on using the light requirements of hybrid aspen (*Populus tremula* L. x *P. tremuloides* Michx) seedlings to optimise propagation rates in growth chambers and thereby accelerate breeding.

Besides sharing scientific knowledge, cooperation between researchers and practitioners requires the development of decision-support tools that are easy to access and use. Daniel Blanco-Ward (INIA-CSIC) presented an updated version of the forest map of Spain (FMS) providing information on FRM geographic origin, and Pauls Zeltiņš (Silava) showed how the generalised algebraic difference approach (GADA) can be implemented by foresters to predict height growth in young stands of improved Scots pine and silver birch (*Betula pendula* Roth). The B4EST project has supported the development of a web-based decision-support tool called the Planter's Guide which provides recommendations for a given regeneration site of the best available Scots pine and Norway spruce seedlings from seed orchards in Sweden and Finland. Mats Berlin (Skogforsk) presented the tool's new developments such as an interface that handles many sites and seed orchards simultaneously for stakeholders with large forest holdings (and nurseries). The next developments include expansion to other countries, incorporation of other future climate scenarios and better accommodation of prediction uncertainty.

The session ended with a round table discussion including Juha Hakkarainen (FINSILVA), Brigitte Musch (ONF), Felipe Pérez (MITECO) and Christophe Orazio (IEFC). The panellists first defined the forest ecosystem services that are critically important in the context of climate change. This included provisioning of food, timber and other products, regulation of water, provision of a carbon sink, cooling in cities, prevention of erosion and desertification, maintenance of biodiversity, and contributing to human cultural and spiritual well-being. They argued that maintaining healthy and resilient forests will require dialogue among researchers, policymakers and practitioners, the establishment of protocols and open access databases, the development of breeding programmes for a wide range of species and provenance trials outside species ranges, and the development of new statistical or decision-support tools. These actions will have more impact if they benefit from a common legislation across countries, enabling better traceability of genetic material. Future FRM deployment will have to meet the challenge of providing trees that are resilient to new climates and resistant to diseases and pests, while maintaining genetic diversity. Holm oak dieback in Spain is a good example of where conservation strategies for natural populations will need to rely on improved material for biotic tolerance. A good balance will also have to be found

among forest production, social uses and conservation, and among forest management and naturalness. To this end, third-party labels may play a key role in protecting natural populations and ensuring sustainable forest management. In 2020, more than half of European forest area was certified by the Programme for the Endorsement of Forest Certification (PEFC), the Forest Stewardship Council (FSC), or both (Ferretti et al. 2020).

Science policy interface for mitigation, adaptation and risk management in forestry

The first three conference sessions demonstrated that investing in FGR management and FRM deployment has the potential to improve economic gains in tree breeding, forest resilience to climate change and the success of ecological restoration. However, the timescale of return on investment in research and development can be very long and priorities may shift due to political, economic or environmental changes. In this context, scientists have a responsibility to communicate both short and long-term benefits and the risks of new uses of FGR and FRM, to be clear and honest about prediction uncertainties, and to better understand practitioner's needs. With this in mind, Michele Bozzano (EUFORGEN, EFI), in his keynote talk, introduced the Forest Genetic Resources Strategy for Europe, a coordinated and cooperative effort supported by the European Forest Genetic Resources Programme (EUFORGEN), which aims to improve the conservation and sustainable use of European FGR. This strategy has three major objectives: (1) facilitate knowledge sharing and communication with key stakeholders (e.g. by improving the availability, access and quality of FGR information); (2) coordinate and monitor the conservation of FGR (e.g. by including genetic information to define conservation targets); and (3) promote the appropriate use of FGR. In addition, it defines principles for better coordination of policy.

Anssi Ahtikoski (LUKE) presented case studies from B4EST, in which the impacts of deploying improved FRM were evaluated in four regions of Europe with different growing conditions, forest structure, forest management procedures and expected risks of environmental change (climatic and biotic). The long-term benefits and risks of improved FRM were assessed by estimating biomass production, carbon sequestration, seed production resilience and biodiversity but also plywood production, biomass for bioenergy and phytoremediation in alluvial regions. This evaluation was performed on different species depending on the region (e.g. Scots pine and Sitka spruce in Scottish woodlands; maritime pine and stone pine in the Atlantic regions of southern Europe), and under different scenarios of future climate and forest management.

Isabel Carrasquinho (INIAV, FAO) presented how FGR are used in conservation and genetic improvement in Portugal. In 2020, five R&D projects were funded by the national operational programme (PROGEN) to evaluate diversity trends and status in maritime pine, cork oak, stone pine, prickly juniper (*Juniperus oxycedrus* L.) and white crowberry (*Corema album* L.). These innovative projects moved from a classical gene conservation strategy to a dynamic conservation approach with three main objectives: (1) to create the conditions for future evolution, (2) to conserve specific adaptations in marginal populations and (3) to save endangered populations. Seven species also benefit from breeding programmes aiming at improving a range of traits and supported either by public institutions or private actors, e.g. INIAV's breeding programme on maritime pine for resistance to pine wilt disease or higher resin production, or the two independent breeding programmes of RAÍZ and ALTRI in eucalyptus, selecting for higher pulp production.

Richard Whittet (Forest Research) discussed opportunities for reopening the Scots pine breeding programme in Scotland. This programme started in the 1950s with the selection and testing of 1065 plus trees, but breeding work was discontinued (Lee 2002). If, as forecasted, the East of Great Britain becomes drier under climate change, it may become unsuitable for growing quality timber from Sitka spruce (*Picea sitchensis* (Bong.) Carr.), which is the main commercial species in the UK, making space for more drought-tolerant Scots pine. Analysis of Scots pine genetic trial data suggested that simultaneous improvement of growth and disease resistance (to *Dothistroma septosporum*) is possible, and was shown by a stakeholder survey to be of high public and private interest. Economic modelling also showed that the expected gains in growth and disease resistance for growers can cover their investment to do this. These ideas have been supported by the UK Government's Department for Environment, Food and Rural Affairs with funding for a three-year project to reinstate Scots pine breeding in Great Britain.

A round table discussion concluded the session, bringing views from different international organisations represented by Bent Leonhard (EFNA), Barry Gardiner (IEFC), Chris Kettle (Bioversity International) and Jarkko Koskela (FAO). A key role for experts, emphasised by all panellists, was to provide science-based, easy-to-understand information to policymakers and practitioners. This could include practical information such as the number of seeds to sow or nursery to use, or the risks and challenges specific to each tree species, geographical area. Experts should also provide more input into certification policies, decision-making and regulatory bodies, potentially through the creation of intermediaries, and by clearly articulating the short- and long-term effects of compromises. Experts can also help to ensure

that information is shared across borders and cultures and involves indigenous communities and traditional knowledge.

Conclusions and perspectives

The B4EST International Conference ‘Managing Forest Genetic Resources (FGR) for an Uncertain Future’ brought together people from across the forestry sector to share information and foster international collaboration among researchers, practitioners and policymakers, thereby promoting science-based innovations in forest management and conservation practices. As Catherine Bastien (INRAE) emphasised in her closing talk, B4EST has generated high value, novel scientific knowledge as well as easy-to-use methods and tools for tree breeding, identification and deployment of FRM, and management of FGR. For instance, climate-based URF (Wang et al. 2010; Leites et al. 2012), and more recently landscape genomics approaches (Capblancq et al. 2020), have proven effective to identify climate-adapted seed sources while GS approaches provide increasingly accurate selection of elite material in breeding (Wallace et al. 2018). Yet, most methods and tools can still be greatly improved and the risks and benefits of their large-scale implementation have yet to be explicitly quantified. As an example, GS is likely to take a leap forward with the integration of multi-omic information into predictions. In the meantime, scientists have warned about the decline in genetic diversity caused by the implementation of GS in tree breeding (Grattapaglia 2022), and have shown that counteracting this trend is in the interests of stakeholders, as the long-term benefits of maintaining sufficient genetic diversity in cultivated forests largely outweigh the short-term costs (Jannink 2010; De Beukelaer et al. 2017; Allier et al. 2019). Important knowledge gaps also remain, and identifying them is a priority for guiding future data collection and experimental design. One of the best examples is our current inability to determine which forest tree populations (managed or unmanaged) will be able to cope with climate change, and which are at risk of extinction and will require human intervention to persist. Indeed, population responses to changing environmental conditions are very complex and multifactorial (Chevin et al. 2010), and our understanding of the eco-evolutionary mechanisms underlying them is very limited, which prevents their integration into predictive models (Romero-Mujalli et al. 2019). Given the urgency of the situation, practitioners and policymakers will have to make decisions under great uncertainty regarding management and conservation strategies (Lindner et al. 2014). Close links among researchers and other actors in the forestry sector, such as those established and consolidated throughout the B4EST project, will therefore be a cornerstone of giving

our forests the greatest chance of resilience and adaptation to the multiple and uncertain changes ahead.

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Declarations

Conflict of interest The authors declare no competing interests.

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