Centuries of provenance trials: towards predictive infrastructures for forest adaptation under climate change

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Abstract

Provenance trials are among forestry's most valuable experimental legacies. Established over centuries to compare species and provenances, they laid the foundation for understanding local adaptation and supported tree breeding, but remained focused on growth, timber quality, and ranking provenances by performance. Climate change calls for a next generation of comparative trials that can help forecast forest regeneration, persistence, and adaptation. We use a backcasting approach, starting from this desired future state and working backward to identify future needs. We argue for an integrative approach that covers the whole life cycle, including regeneration and biotic stress responses, and that incorporates ecological realism. We also need to better exploit legacy experiments and develop coordinated, distributed experiments across environmental gradients, including extreme conditions, and involving stakeholders. Next-generation trials should be conceived as training populations for genomic prediction and exploit opportunities offered by remote sensing technologies for high-throughput phenotyping. Coordinated networks can transform static experiments into evolving predictive infrastructures for adaptive forest management today.

Interest in comparing the performance of different forest tree species and provenances in a given environment dates back to the 16^{th} century, when the shipbuilding industry recognized that timber origin affects quality and performance. The royal navies of France and England are thought to have conducted the first so-called *provenance trials* (Box 1, Fig. 1a) [1]. These experiments laid the foundation for understanding how genetic variation interacts with the environment and can be regarded as forestry's most significant contribution to evolutionary biology [2]. Together with the pioneering work of plant ecologists [3, 4], they contributed to the development of the concept of *local adaptation* and established *common garden trials* as a major experimental approach for studying adaptation in natural populations. With the post-war development of tree breeding, several *progeny* and *clonal trials* (Box 1) were established, enabling the estimation of breeding values and achievement of genetic gains through selection (Fig. 1a), yet the focus remained on increasing wood production and improving timber quality [5].

Today, with climate change, for the first time in the history of *comparative trials*, the primary use of these experiments is the need to understand and anticipate tree responses to rapid environmental change [6, 7]. In the Mediterranean and temperate zones, forest governance seeks provenances that can survive and deliver essential ecosystem services [8], while in the boreal zones, those that can assure stable wood production in a fast-warming and rapidly urbanizing world. New objectives include restoring damaged sites, ensuring that trees can complete their rotation period, and enhancing the climate resilience of existing forests [9, 10]. The stakes are high: forests provide ecosystem services that we long believed came for "free", such as clean water [11]. Forests also buffer climate change by cooling the environment and structuring the landscape to create diverse habitats that support biodiversity [12, 13]. Addressing these new needs exposes the limitations of existing comparative trials and calls for new approaches for studying adaptation in forest trees.

In this *Perspective*, we critically examine the literature of comparative trials in forest trees, highlight the strengths and weaknesses of past experiments, and propose a more integrative approach for future trials. Our analysis focuses on Europe, but our findings are relevant to forest research worldwide. Specifically, we argue that despite the rich history of European trials and their rediscovery for tackling climate change [6, 14–17], some of their fundamental assumptions have not been questioned, and proposals for the design of future trials have yet to emerge. We argue that comparative trials need to be redesigned and move from ranking provenances by mean performance into predictive infrastructures for forecasting forest regeneration, persistence, and adaptation under climate change (Fig. 1). Throughout this Perspective, we use comparative trial (Box 1) as an umbrella term for provenance, progeny, and clonal trials. We explicitly distinguish among these trial types whenever their objectives, experimental designs, or inferential power differ.

Challenges to predict forest adaptation under climate change using past provenance trials

When does differentiation indicate adaptation?

A fundamental assumption of provenance trials is that provenance differences observed in a common environment reflect adaptation to local climatic conditions (Fig. 1a), yet they may equally arise from demographic history, including postglacial recolonization, founder effects, expansion load, admixture, and gene flow, all of which shape present-day genetic structure independently of current adaptation [18–21]. The extent to which demographic history confounds adaptive inference depends strongly on spatial scale and life history. Species with large effective population sizes and extensive pollen flow may show little geographic differentiation despite broad distributions, whereas species with shorter dispersal distances may exhibit much more pronounced provenance differences [19, 21]. Provenance differentiation at a short spatial scale may reflect family structure [22–24], while continental-scale trials inevitably capture deeper historical signals, including glacial refugia, recolonization routes, admixture, and human-mediated transfers [25–27]. As a result, provenance trials almost always detect differences among populations, but the evolutionary significance of these differences cannot be inferred without accounting for demographic history. This limitation is inherent to provenance trials, which compare populations as the unit of observation. In contrast, progeny trials retain pedigree relationships, enabling the estimation of additive genetic variation and evolutionary potential, while clonal trials replicate genotypes and enable direct estimation of genotypic variation. Statistical methods that test whether phenotypic differentiation among populations exceeds expectations under drift provide a significant step forward [24, 28–32], although limited sampling across both geographic and environmental gradients can still confound inference.

With the advent of the genomic era, researchers increasingly sought to uncover the genomic architecture of traits (Fig. 1a), often with limited success, due to the highly polygenic architectures of adaptive traits [33–35]. At the same time, genotype-environment association studies offered a complementary route for identifying candidate adaptive variation without direct phenotypic observations. These approaches identify correlations between allele frequencies and environmental gradients, whereas genomic forecasting methods, such as RONA (Risk of Non-Adaptedness) and Gradient Forest, project fitted genotype-environment relationships across space or under future climates [36–38]. Interpreting such associations as signatures of adaptation assumes that they predominantly reflect environment-mediated selection rather than demographic history. Yet range expansion, founder effects, and isolation by distance can generate neutral allele-frequency clines that resemble adaptive signals [39, 40]. Prediction uncertainty becomes especially important when models are transferred across weakly related populations or extrapolated beyond the genomic and environmental conditions represented during calibration [41, 42]. Consequently, experimental validation in comparative trials re-

mains essential for testing whether genomic offsets and other genomic forecasts correspond to realized differences in performance across environments and life stages [38, 41–43].

Do the traits we measure represent fitness?

The second major challenge is that past comparative trials have historically focused on economically relevant growth traits (Fig. 2). While growth and biomass are key fitness components, they are not proxies for adaptation [5, 6]. Instead, adaptation emerges from coordinated life-history strategies rather than from individual traits [44]. Life-history theory predicts trade-offs among growth, reproduction, and survival that define a fast-slow continuum in trees [45]. Additional trade-offs between growth and defense [46], and between growth and abiotic stress tolerance [32], further shape adaptive strategies. Many of these relationships are environment-dependent and become apparent only under stressful conditions, meaning that trials established under favorable environments may substantially misinterpret adaptive differentiation [45, 47].

Further, past comparative trials focus on a narrow window of the life cycle, typically beginning two to three years after establishment and seldom tracking trees until the first reproduction (Fig. 2). Germination and seedling establishment represent major demographic bottlenecks and important stages of natural selection [44, 48–52]. Early life-history traits are shaped by trade-offs between seed size, fecundity, dispersal, and establishment, that are well studied across phylogenies and communities [53, 54], but rarely quantified within species and even less in comparative trials [55–59]. Combined with limited sampling of provenances across the species' range and of mother trees within a population, this likely misses adaptive variation in regeneration strategies [60].

Further, comparative trials implicitly assume that vegetative performance translates into reproductive success. Yet reproduction is a fundamental component of fitness and a major life-history axis on its own [6]. Flowering, fecundity, mast frequency, and regeneration respond differently to environmental variation than growth [61–63], while climate change and forest aging are altering masting dynamics across Europe [64], with cascading consequences for regeneration [65, 66]. Very few comparative trials were designed to study reproductive traits (Fig. 2) and, if so, such trials never sought to capture long-term reproductive strategies, potentially biasing estimates of adaptive differentiation and trait correlations. Yet, evidence shows that reproductive performance itself is heritable in many tree species [67, 68]. Consequently, comparative trials restricted to early vegetative growth capture only a fraction of the life-history processes determining long-term persistence.

Finally, comparative trials have traditionally been designed to maximize statistical power by reducing sources of environmental variation unrelated to the questions of interest [5]. Although they are often established on operational forest sites that retain considerable environmental heterogeneity, trials typically simplify the biotic environment by using monocultures, reducing herbivory and pathogen pressure, and selecting sites that avoid environmentally ex-

treme conditions. While this design has been effective for quantifying genetic variation under comparatively controlled conditions, it contrasts with the growing recognition that forest ecosystems are shaped by complex interactions among abiotic and biotic processes and that biodiversity plays a key role in enhancing forest resilience [69].

Are transfer functions suitable to predict future adaptation?

The third challenge is the continued reliance on the so-called transfer functions as the primary analytical tool for predicting responses under future climates. Transfer functions (Box 1) relate the average performance of a provenance to the climatic distance between its source and planting sites [70–72]. They rely on the assumption that spatial variation in provenance performance can substitute for temporal responses to future climate, an approach equivalent to the space-for-time substitution widely used in ecology [73]. While this framework has been extremely influential, its validity under rapid climate change has increasingly been questioned [74]. Robust transfer functions require observations spanning the environmental conditions over which populations are expected to respond, including stressful environments where growth and survival decline. Yet provenance trials have generally been established at relatively few sites and preferentially under favorable conditions for establishment and growth [5, 6, 75]. Consequently, transfer functions are frequently extrapolated beyond the climatic range over which they were calibrated, particularly when *genotype-by-environment interactions* (G×E, Box 1) alter provenance rankings across environments.

Another major limitation of transfer functions is that they are based solely on 'average' provenance characteristics and do not account for the large phenotypic and genetic diversity that usually exists within forest tree populations [14, 76, 77]. Transfer functions predict expected mean provenance performance under climatic transfer, but do not quantify whether within-population additive genetic variation provides the capacity for an evolutionary response. Yet predicting forest adaptation to climate change also requires estimates of evolutionary potential within populations [78]. Unfortunately, historical provenance trials were usually not designed to jointly estimate the population transfer functions and the quantitative genetic parameters that determine the evolutionary potential of populations. Currently, we still have limited knowledge of how adaptive potential is distributed across species' ranges [79]. More generally, forecasts of species vulnerability and extinction risk under climate change commonly ignore within-population genetic diversity, despite its importance in determining a population's potential to respond to environmental changes [80].

Future comparative trials in forest trees: integrating new knowledge and tools to address today's challenges

Limitations of past and present comparative trials help reveal opportunities to overcome them. We adopt a *backcasting* approach [81, 82], which starts from a desired future state and works backward to identify the needs to achieve it (Fig. 1b). Our aim is to predict the regeneration, persistence, and adaptation of forests under climate change. To achieve this, we propose transforming comparative trials from experiments that rank provenances based on economic criteria into predictive systems. Achieving this vision will require coordinated advances in five complementary areas (Fig. 1b). First, to capture adaptive processes, we need to consider the entire life cycle. Second, we must incorporate greater ecological realism into our trials, including resistance to pathogens. Third, experiments must become more informative by better leveraging legacy datasets and harnessing novel distributed experimental designs. Fourth, future trials could also be seen as training populations for *genomic prediction* (Box 1). Finally, thanks to technological developments in Earth observation, traits can be monitored through high-throughput observations. These new technologies may also enable the scaling of traits across space and time, provided they are accompanied by suitable benchmarking through extensive field observations and stakeholder involvement.

Trees are long-lived: it is time to consider their whole life cycle

If the goal is to predict forest regeneration and persistence under climate change, future comparative trials must capture the complete life cycle. In long-lived species, the traits most relevant to adaptation are not constant across ontogeny: germination and emergence are fitness components of early stages, reproduction is an important fitness component only during maturity, and defense is critical throughout the life cycle [44]. Complementing this ontogenetic perspective, relevant traits also span levels of biological integration and response times, ranging from fast-changing mechanistic to stable integrative traits. Fast-changing traits include, for example, rapid responses mediated by enzymatic and hormonal activity (Fig. **??**). Intermediate, functional traits emerge from multiple mechanisms over time, while slow-changing, integrative traits are the most stable across replicate measures of an individual and within species [83]. While genetics plays a role in the expression of all these traits, the most rapid traits tend to be the most plastic, and genetic influences are often most apparent in more integrative traits [84, 85].

Early-life regeneration processes represent a major but largely overlooked component of adaptive potential (Fig. 2). *Direct seeding* (Box 1) has a long history in Europe and was actually the dominant artificial regeneration method for some species during the 18^{th} and 19^{th} centuries. Over the 20^{th} century, tree planting became widely employed in forestry, supported by extensive nursery infrastructure. Today, there is renewed interest in direct seeding for

reforestation following severe drought, bark beetle outbreaks, and fires. Its key advantages resemble those of natural regeneration: seedlings can develop and adapt to local microsites with an undisturbed taproot, transplant shock and soil disturbance can be avoided, as well as the risk of transferring pathogens from the nursery to the field [86–88]. Direct seeding also exposes genetic material to natural selection during germination and establishment, capturing adaptive variation across early demographic bottlenecks that conventional planting bypasses. Species differ markedly in germination and establishment success, with seed mass emerging as a strong predictor of direct-seeding performance (Table 1) [57, 58, 87, 89]. Even when the percentage of seeds producing established seedlings is generally low, high sowing densities can still result in sufficient seedling numbers for successful reforestation, even for small-seeded species (Table 1) [86, 90]. Although seed predation can be substantial, experiments comparing protected and unprotected sowing have not always detected the effect of predator exclusion [89], indicating that seed quality, microsite conditions, and post-emergence mortality are equally or more important [59]. Incorporating direct seeding into future comparative trials would therefore enable these interacting drivers to be evaluated across environments [91, 92].

Masting, the intermittent and often synchronized production of large seed crops, has long attracted the attention of ecologists [62, 63], yet this research has remained disconnected from comparative trials in trees (Fig. 2). Masting is a key life-history dimension in studies of reproductive strategies across the landscape [60] and life-history trade-offs [45]. Since reproductive traits often respond differently to environmental conditions than growth traits do, they provide complementary information on adaptive potential [61]. Forest trees typically reach reproductive maturity between 10 and 60 years of age, with wide variation among species, environments, and management conditions [93], making it difficult to integrate direct measures into comparative trials. However, monitoring of flowering phenology, fecundity, age at first reproduction, reproductive allocation, and masting of mother trees in seed stands would allow integration of reproductive traits with the performance of their offspring in existing and future trials. Long-term monitoring of seed stands is also essential, given that masting dynamics show increasing temporal variability [64]. Finally, repeated measurements of reproductive traits and seed collections from the same mother trees across years, combined with standardized progeny trials, could help disentangle maternal genetic effects, interannual maternal environmental effects, and transgenerational plasticity, while also improving seed collection strategies and predictions of future regeneration.

Survival, tolerance to abiotic stress, and defense against biotic stressors are key components of fitness, but remain underrepresented in past comparative trials [94, 95] (Fig. 2). Responses to drought, heat, and frost have received considerably more attention than resistance to pests and pathogens, reflecting the central role of climate-related mortality in forest persistence. Nevertheless, biotic stressors are becoming increasingly important as climate change, global trade, and assisted migration expose forests to novel pests and pathogens for which local populations may possess little resistance [96–98]. Future comparative trials should therefore quantify stress responses across the full trait continuum, from rapidly responding molecular, biochemical, and

physiological traits to integrative whole-tree outcomes (Fig. **??**). For abiotic stress, informative traits include stomatal conductance, hydraulic conductivity, and resistance to hydraulic failure [99, 100]. For biotic stress, candidate measurements include constitutive and induced defense metabolites, such as terpenes, phenolics, and volatile organic compounds, which play central roles in resistance to pathogens and herbivores [101, 102]. Beneficial microbial associations may further modify plant defense and resilience, while metabolomic approaches can reveal how genetic, abiotic, and biotic factors jointly shape defensive chemistry within species [103, 104]. At the whole-tree level, repeated scoring of crown condition, drought or frost damage, disease progression, growth reduction, recovery, and survival provides integrative measures of resistance and tolerance that can be linked to genomic prediction models. Some physiological and structural traits, together with canopy symptoms of abiotic stress and pathogen damage, are increasingly measurable through high-throughput phenotyping and remote sensing (Fig. **??**), allowing repeated, standardized assessments across large, distributed experiments.

Integrating ecological realism: environmental heterogeneity and biotic interactions

Measuring a broader range of stress-response traits will not be sufficient if genotypes continue to be evaluated under simplified or predominantly favorable conditions. Yet, abiotic microsite heterogeneity [105] and biotic interactions, including competition, facilitation, herbivory, and pathogen exposure, can strongly influence trait expression and fitness [106]. Therefore, future trials should extend G×E to include biotic context (G×E×B), moving towards the prediction of genotypic responses under ecologically realistic conditions. Fine-scale environmental heterogeneity within sites can reveal biologically meaningful differences in how genotypes respond to variation in microclimate, soils, and resource availability [17, 107, 108]. Genetic variation in stress responses can be assessed through standardized drought and temperature manipulations [e.g., 32, 109], experimental herbivory [e.g., 110], and controlled pathogen inoculations [e.g., 111], the latter providing standardized resistance phenotypes that can be incorporated into breeding and genomic prediction [112].

Provenances and genotypes performing well in monoculture are not necessarily optimal in species mixtures or resistant to pests and pathogens. Although these issues have rarely been assessed in forest tree trials, biodiversity–ecosystem functioning experiments demonstrate that species diversity and genetic diversity can substantially influence growth and productivity across environments [113]. Some experiments explicitly incorporate both species and genetic diversity gradients, enabling the identification of genotypes or seed families with high performance in mixtures [114]. Similar ideas are emerging in agriculture, where participatory breeding seeks to select genotypes under heterogeneous field conditions [115], and optimal crop mixtures [116]. Finally, one has to keep in mind that European forests are largely managed ecosystems [117]. Comparative trials using different seeding, planting, and thinning options could help understand how forest management can leverage intraspecific diversity to design

new management practices that reduce forests' vulnerability to climate change [118].

A significant yet often overlooked aspect is the risk of pests and pathogens being transmitted through plant material to new habitats during assisted migration [96]. Given the ongoing and anticipated substantial trade of seeds over long distances, planting seeds can be vectors of *endophytic microorganisms* (Box 1) [119]. Their introduction to new habitats can facilitate interactions among otherwise geographically isolated populations of microorganisms, potentially leading to the formation of novel hybrid strains with increased virulence traits [120]. These microorganisms may also switch to local susceptible host species and spread through populations, eventually becoming invasive and/or pathogenic [e.g., 97, 98]. In this context, the *sentinel planting approach* (Box 1), in which surveillance of sentinel plants enables early identification of potential pests [121], should become an integral part of future trials.

Digitization, databasing, distributed and gradient experiments with traceable origins

Predicting forest responses across Europe requires experiments and data infrastructures that explicitly capture environmental gradients and genotype-by-environment interactions. Existing comparative trials already provide a substantial foundation for this effort. Digitization, database integration, and meta-analysis are transforming many fields of biology [122, 123], and several studies have demonstrated the value of synthesizing data across comparative forest trials [95, 124–126]. Although differences in experimental design, trait definitions, measurement protocols, and environmental coverage constrain joint analyses, harmonizing legacy datasets can transform geographically dispersed trials into coordinated data infrastructures that support cross-site inference and integration with new experimental networks. Large Language Models may further assist with extracting and translating information from non-English and gray literature, although their outputs will require expert validation and traceability to the original sources. Statistical methods can also improve the comparability of legacy data. For example, within individual trials, iterative kriging can account for fine-scale spatial heterogeneity and improve the estimation of genetic effects before cross-site synthesis [127]. However, statistical correction cannot compensate for missing metadata or fundamental incompatibilities among experimental designs, emphasizing the importance of standardized, complete, and traceable records in future trials.

Organizing legacy trials that persist as living collections into accessible databases can unlock new research questions and guide targeted re-measurement. By linking historical records with newly collected phenotypes, these trials can support the estimation of phenotypic plasticity in growth using dendroecological traits [e.g., 128]. They can also provide rare opportunities to assess the long-term consequences of assisted migration and gene flow. For example, a network of eleven century-old Oriental beech introductions established alongside native European beech forests has enabled the investigation of provenance origins, hybridization, and

the potential risks and benefits of assisted gene flow [129, 130]. As climate change advances, legacy trials are increasingly exposed to extreme climatic conditions and emerging pests and pathogens, creating opportunities to test whether historical differences in growth are associated with variation in resistance and resilience [131].

New comparative trials could draw inspiration from distributed and gradient experiments, which have long been used in ecology to quantify responses across environmental conditions [132, 133]. Such designs are particularly valuable for addressing context dependence by testing whether effects are general or vary predictably among locations [91, 134]. Specifically, *coordinated distributed experiments* (CDEs, Box 1) combine broad geographic coverage with standardized protocols, consistent metadata, and individual-level data, enabling researchers to evaluate both the generality of target effects and the environmental drivers of variation in their strength [135]. Unlike post hoc meta-analyses of independently designed studies [136], CDEs coordinate experimental treatments and measurements across sites while deliberately sampling, rather than controlling, environmental heterogeneity [137]. Their network structure can also accommodate new measurements, treatments, and participating sites as scientific questions evolve [138]. Networks of provenance trials already share some features with CDEs, but future comparative trials could adopt their stronger coordination, standardized data collection, and capacity for iterative development. A continental-scale oak experiment comparing direct seeding with planting illustrates how coordinated protocols can be used to study germination, emergence, and early establishment across contrasting environments [139, 140].

A further extension of the CDE framework is the concept of next-generation citizen science (NGCS) proposed by Bison et al. [91], which broadens participation beyond academic research teams to trained forestry professionals. In such cases, the risks can be distributed across many small, low-cost experiments, 302 across Europe in the case of MyGardenOfTrees, making it feasible to test extreme or failure-prone conditions that would be difficult or too risky to implement in conventional trials. Similarly, the Swiss provenance trial network [141] emphasized the critical role of stakeholder collaboration, which enabled testing at 57 sites, 18 species, and 117 seed sources. Living labs, such as the Mountain Forest Initiative, extend this participatory approach by co-designing research and management interventions with local actors [142]. Together, these models can support the deployment of standardized experimental units across heterogeneous environments, integrate local ecological knowledge, increase societal relevance, and expand experimental capacity beyond what research institutions could sustain alone.

Urban environments offer another complementary setting for distributed comparative experiments. Cities expose trees to climatic and edaphic extremes, including urban heat islands, restricted rooting volume, and water limitation, and may therefore provide partial analogs of conditions expected under future climates [143, 144]. Networks of cities spanning climatic gradients could be used to study tree responses across contrasting environments [145]. To function as comparative trials, future urban networks should use traceable planting material, standardized experimental designs and measurement protocols, and harmonized environmental

and management metadata. Because urban trees are readily accessible, such networks could support repeated phenotyping at relatively low cost, potentially involving municipal practitioners and citizen scientists. Although urban-tree monitoring initiatives already exist, they are rarely designed within the genetic and experimental framework of comparative trials.

Finally, *seed orchards* (Box 1) have played an instrumental role in producing improved forest reproductive material while managing relatedness and genetic diversity [5]. Future seed orchards could include climatically contrasting parental genotypes and be used to perform controlled crosses. This would broaden the range of genetic combinations available for testing under future-relevant environments, including selected interpopulation or interspecific hybrids where appropriate [146, 147]. When the resulting progeny are genomically characterized and evaluated across coordinated, long-term trials, they can form dynamic training populations for genomic prediction, enabling breeding values and prediction models to be updated through recurrent progeny testing [148]. Beyond producing improved forest reproductive material, such integrated orchard-and-trial systems could provide long-term platforms for studying adaptation, assisted gene flow, hybridization, and the evolutionary consequences of breeding strategies under changing climates.

Next-generation trials as training populations for genomic prediction

Predictive breeding requires comparative trials that function as genomic training populations. In this context, designs that incorporate within-population genetic variation through pedigree-based or genomic relatedness across environmental gradients are the most useful as they allow partitioning trait variation into population, family, and individual components and enable the estimation of adaptive potential and reaction norms (Box 1) [149, 150]. In agricultural applications, such *multi-environment trials* (METs, Box 1) are the gold standard [151], in which genotypic responses are modeled as functions of environmental covariates, enabling prediction beyond observed environments and improving the characterization of G×E [152, 153]. Because many phenotypic responses to environmental variation are nonlinear, it is essential to sample environmental gradients spanning the range of conditions that a species experiences or could experience under climate change, allowing reaction norms to be estimated rather than approximated [154–156]. Therefore, a distributed experimental design that integrates environmental heterogeneity does not imply a loss of statistical power but rather a gain in predictive power.

With decreasing sequencing costs and the development of bioinformatic pipelines and statistical methods, genomic prediction offers a unique opportunity to predict traits that will only be expressed in the future [34, 157]. This is particularly valuable in forest trees because it enables early selection for traits that normally require decades to measure, while increasing selection intensity in breeding programs [158, 159]. Accordingly, *genomic selection* (Box 1) reframes phenotyping from an endpoint of breeding into the process by which prediction models are trained [160]. Genomic prediction can also exploit conditionally neutral variation. Genetic differences

underlying disease resistance or tolerance to future abiotic stresses may remain unexpressed until the relevant stress occurs. Consequently, training populations must be phenotyped under the environmental conditions or stressors of interest so that genomic models can learn these genotype-phenotype relationships [161]. Once trained, such models can predict performance before these traits are expressed. In this context, it is essential that future comparative trials record multidimensional phenotypes, including pathogen-defense traits (Fig. **??**), to improve predictions of regeneration, persistence, and resilience under future disturbance regimes.

Genomic prediction, however, is only as good as the experimental populations used to train it. Realized prediction depends on the quality of the training population, relatedness between training and prediction sets, multigenerational pedigrees, and genotype-by-environment interactions [162]. Historical progeny trials were not designed with these objectives in mind. They frequently rely on legacy datasets from mature trials with ungenotyped parents, use offspring as the reference population, and focus predominantly on growth traits measured under relatively favorable conditions [159]. Consequently, prediction accuracy often declines across generations, environments, or unrelated populations, particularly for highly polygenic traits such as growth. This limitation should not be interpreted as a failure of genomic prediction itself, but rather as a consequence of training populations that were not designed for predictive breeding. Prediction accuracy depends critically on the design of the training population, the relatedness between the training and target populations, the environments of the target population, and the representation of relevant environmental variation [160, 162].

We argue that the next-generation comparative trials should be conceived as genomic training populations. Family-based designs with genotyped parents, measurements across multiple life-history stages and fitness components, coordinated environmental gradients, and sufficiently stressful conditions will provide the information needed to jointly estimate breeding values, genotype-by-environment interactions, and adaptive responses. Such trials will also create opportunities to estimate SNP-based heritability across environments, perform genome-wide association studies, identify loci underlying genotype-by-environment interactions, and improve genomic prediction by integrating biological information into prediction models. Such coordinated, genetically characterized experiments would provide the distributed training populations required to develop predictive genotype–phenotype–environment models.

Remote sensing enables phenotyping across the plant trait continuum in comparative trials

Scaling prediction from experimental plots to landscapes requires traits that can be repeatedly measured over large spatial and temporal scales. Traits along the fast-slow continuum are traditionally measured using separate methods and technologies from different disciplines (Fig. **??**). Remote sensing (RS) offers tools that can capture aspects of traits along the continuum, often using the same or similar technologies [163, 164]. This opens new possibilities for quantify-

ing and comparing genotype-by-environment interactions [165], monitoring stress responses, and tracking phenological dynamics at scales that are difficult to achieve with ground-based measurements alone. RS furthermore provides a powerful framework for scaling phenotypic observations from individual trees to regional or even global scales [166, 167]. However, especially when phenotyping by RS, genetic and environmental signals must be teased apart, and time scales on which processes act and produce different patterns must be interpreted [168].

A wide range of platforms and sensors is available (Table S1), enabling scalable measurements of canopy structure, physiology, and phenology across environmental gradients. By linking spectral and structural signals to traits, RS allows the characterization of multidimensional phenotypes that integrate information about chemical composition, water status, and tissue organization [169, 170]. Many RS techniques support multitemporal data acquisition, which can help determine trends and account for different response timescales and aspects of phenotypic variation that are more or less environmentally responsive. Field spectroscopy measurements in common gardens of *Fagus sylvatica* detected genetic and environmental components of trait variation [171], while multi-site experiments in *Populus fremontii* showed that spectral data can distinguish source populations with high accuracy and reveal heritable trait variation [172]. Similar approaches have detected genetic variation in canopy traits for *Pinus sylvestris* [173] and enabled species discrimination based on phenological differences in assisted migration contexts [174].

It is important to emphasize that RS does not replace field measurements, rather, it complements them [164]. Ground observations remain essential for calibration, validation, and ecological interpretation. In this context, combining RS with distributed experiments and citizen-based observations provides a promising pathway to linking fine-scale ecological processes with large-scale patterns of variation. Together, these approaches enable the integration of phenotype, environment, and spatial scale in ways that were previously not feasible in provenance research.

Conclusions

Comparative trials represent one of forestry's most valuable experimental legacies, but their future value will depend on our capacity to transform them into predictive infrastructures for forests under ongoing climate change. Backcasting from the goal of forecasting forest regeneration, persistence, and adaptation identifies five linked priorities: covering the full life cycle and relevant stress responses, incorporating ecological realism, coordinating legacy and new experiments across environmental gradients using traceable genetic material, designing genetically informative trials for reaction-norm and genomic prediction, and combining repeated field observations with remote sensing to scale phenotypes across space and time (Fig. 1b). While no single experiment can address all of these needs. Coordinated networks connecting legacy trials, new distributed experiments, predictive models, and stakeholders can neverthe-

less provide the long-term capacity to test assumptions, quantify uncertainty, and update recommendations as climates and forests change. The next generation of comparative trials should therefore be conceived not as static experiments, but as evolving research infrastructures grounded in ecological and evolutionary genetic theory and designed to support adaptive forest management.

1 Acknowledgments

K.C. was funded by the ERC Consolidator Grant MyGardenOfTrees (grant agreement no. 101003296) and by the VELUX Stiftung project TAMERS (Project ref. 2067). A.B.L. acknowledges project FireTran, funded by VELUX Stiftung (Project ref. 2540), and project Smart-Oak, funded by the European Union through FORWARDS (Horizon Europe Project No. 101084481) grants to third parties managed by the European Forest Institute.

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Boxes

Box 1: Glossary of terms

Clonal trial: A comparative trial evaluating genetically identical individuals (ramets) propagated vegetatively from selected genotypes (clones), for example, by cuttings or somatic embryogenesis.

Common garden trial: An experiment in which individuals are raised in a common environment to tease apart genetic and environmental trait variation.

Comparative trial: A term used in agriculture and forestry experiments to refer to experiments that compare the performance of various genetic entities such as clones, families, provenances, land races, and varieties.

Coordinated distributed experiments (CDEs): Experimental networks in which standardized protocols are used across many locations to quantify ecological or evolutionary processes over broad environmental gradients.

Genomic prediction: The prediction of phenotypic performance from genetic marker data using statistical models.

Genomic selection: The application of GP for breeding decisions using a training population with both phenotypic and genomic data.

Genotype-by-environment interaction ($G \times E$): It occurs when different genetic units (genotypes) express different trait values in response to environmental variation in different ways.

Local adaptation: A pattern in which local populations exhibit higher fitness than non-local populations in their home environment.

Multi-environment trials (METs): Experiments evaluating the same genetic material across multiple environments to quantify G × E, estimate reaction norms, and assess the stability and adaptability of genotypes.

Progeny trial: A comparative trial evaluating the offspring of known parental trees, usually organized as half-sib or full-sib families, enabling the estimation of quantitative genetic parameters, including additive genetic variation and breeding values.

Provenance trial: A comparative trial that evaluates trees originating from different geographic locations (provenances) in one or more common gardens, typically using seeds collected from multiple mother trees pooled together (bulk seed).

Reaction norm: A function that describes the phenotypic values of a genetic unit across a range of environments, providing a formal description of phenotypic plasticity.

Seed orchard: an intensively managed plantation of superior trees designed to produce high-quality seeds.

Transfer function: A statistical relationship describing how the performance of a provenance changes with climatic or geographic transfer distance between its origin and planting site.

Tables

Table 1: **Quantitative outcomes of direct-seeding experiments in European and North American forest tree species.** G is the percentage of germinated or emerged seeds at the estimated germination peak or monitoring time. S is the percentage of seeds that survived as seedlings at the final census: $S = 100 \times N_{\text{living seedlings, final}}/N_{\text{seeds sown}}$ [56]. Ranges in G and S represent variation across sites, provenances, seed batches, or experimental treatments. Methods to exclude seed and seedling predators are given. Species are ordered approximately by increasing reported seed mass.

Species	**Seed mass (mg seed^{-1})**	G (%)	S (%)	**Final census**	**Predation exclusion**	**References**
Betula pubescens[a]	0.079–0.248	11–14	0.31–0.34	7 years	Deer-fence	[86]
Alnus glutinosa[a]	1.8	60–73	0.40–0.45	7 years	Deer-fence	[86]
Sorbus aucuparia[b]	1.15–4.14	–	3.1–4.4	7 years	Deer-fence	[86]
Picea abies	4–7	22.1–23.2	4.5–8.6	4 growing seasons	None reported	[175]
Pinus sylvestris	5–8	27.6–29.1	4.3–7.0	4 growing seasons	None reported	[175]
Pinus resinosa	10	34.0	5.5	1 year	Treatments[c]	[89]
Pinus halepensis	15–20	1.3–18.2	0.2–4.6	2 growing seasons	Treatments[d]	[176]
Abies alba	37–65	–	0.83–13.3[e]	5 years	Not reported	[88]
Abies alba	46.8	10.3	0.17–2.63	3 growing seasons	Seed protectors[f]	[59]
Acer saccharum	60	5.8	3.3	1 year	Treatments[c]	[89]
Abies nordmanniana	67.2	15.8	0.27–4.03	3 growing seasons	Seed protectors[f]	[59]
Fagus caspica	243.4	4.7	0.02–2.05	3 growing seasons	Seed protectors[f]	[59]
Fagus sylvatica	244.3	10.1	0.05–4.41	3 growing seasons	Seed protectors[f]	[59]
Quercus cerris	2030–8990	0–89.8[g]	60	1 growing season	Seed shelters[h]; deer-fence; weeding	[140]
Quercus rubra	3140	57.2	52.5	1 year	Treatments[d]	[89]
Quercus robur	3150–7830	0–100[g]	70.7	1 growing season	Seed shelters[h]; deer-fence; weeding	[140]
Quercus ilex	2220–7960[i]	33.4	11.7–48.3	20 months	None reported; acorns buried at 5 cm	[90, 140]
Quercus suber	5870–8530[i]	66.4	22.3–49	20 months	None reported; acorns buried at 5 cm	[90, 140]

[a] Sowing rates of 1,020,000 or 2,040,000 viable birch seeds ha^{-1} were used; S therefore has viable seeds sown as its denominator. Seed mass is from [177].

[b] Seed mass is from [178].

[c] The experiment included protected and unprotected treatments, but protection had no detectable effect.

[d] Different microsite treatments were applied. Wood-chip cover produced $G = 18.2\%$ and $S = 4.6\%$, whereas the bare-ground control produced $G = 5.8\%$ and $S = 0.2\%$.

[e] Approximate S calculated using a sowing rate of 20 kg ha^{-1} and the reported final seedling density.

[f] Custom-designed cone-shaped fences protecting seeds and seedlings from predators.

[g] Range of eight-week germination percentages measured under controlled conditions. [h] Custom-designed biodegradable seed protectors [179]. [i] Seed mass is from [180].

Table 2: **The continuum of traits from rapidly responding molecular and biochemical traits to integrative measures of whole-tree performance and fitness relevant to future comparative trials.** The categories form a conceptual continuum rather than discrete classes. Rows highlight classic (eco-)physiology, phenology, and morphology traits, as well as traits future trials could measure more often: traits related to biotic defense and traits or proxies that can be measured or inferred using remote-sensing approaches. The expected strength of the genetic signal is approximate, and the references highlight reviews of classic traits as well as evidence for some of the future traits. Abbreviations: CI_{re}, red-edge chlorophyll index; EVI, enhanced vegetation index; NDVI, normalized difference vegetation index; VOC, volatile organic compound.

Trait level	**Molecular and biochemical**	**Physiological**	**Structural and anatomical**	**Phenological and life-history**	**Whole-tree performance and fitness**
Typical response time	Minutes to hours	Hours to days	Weeks to months	Seasonal	Years to decades
(Eco)physiology, phenology, morphology traits	Rubisco activity, nitrate reductase, catalase, peroxidase, osmolytes, phytohormones	Stomatal conductance, hydraulic conductivity, $\delta^{13}C$, non-structural carbohydrates, starch	Specific leaf area, leaf thickness, stomatal density, wood density, bark thickness, root:shoot ratio, seed mass	Bud burst, flowering time, bud set, leaf senescence, masting	Germination, survival, growth, biomass, age at first reproduction, fecundity
Biotic defense traits	Secondary metabolites (terpenes, phenolic compounds), phytohormones	Induced defense responses, VOC, resin flow	Bark thickness, resin ducts, leaf toughness	Timing of defense induction, recovery time	Disease severity, crown dieback, pathogen resistance, recovery
Remote sensing traits	Chlorophyll fluorescence, VOC	Canopy temperature, light-use efficiency, canopy water content	Structural canopy traits, crown architecture, hyperspectral traits	Green-up, flowering, senescence, vegetation indices, including NDVI, EVI, and CI_{re}	Crown dieback, mortality, regeneration success, disturbance impacts
Expected strength of genetic signal	Often low to moderate [102, 181, 182]	Low to moderate [183, 184]	Moderate [185]	Moderate to high [15, 84]	Moderate to high [84, 186, 187]

Figures

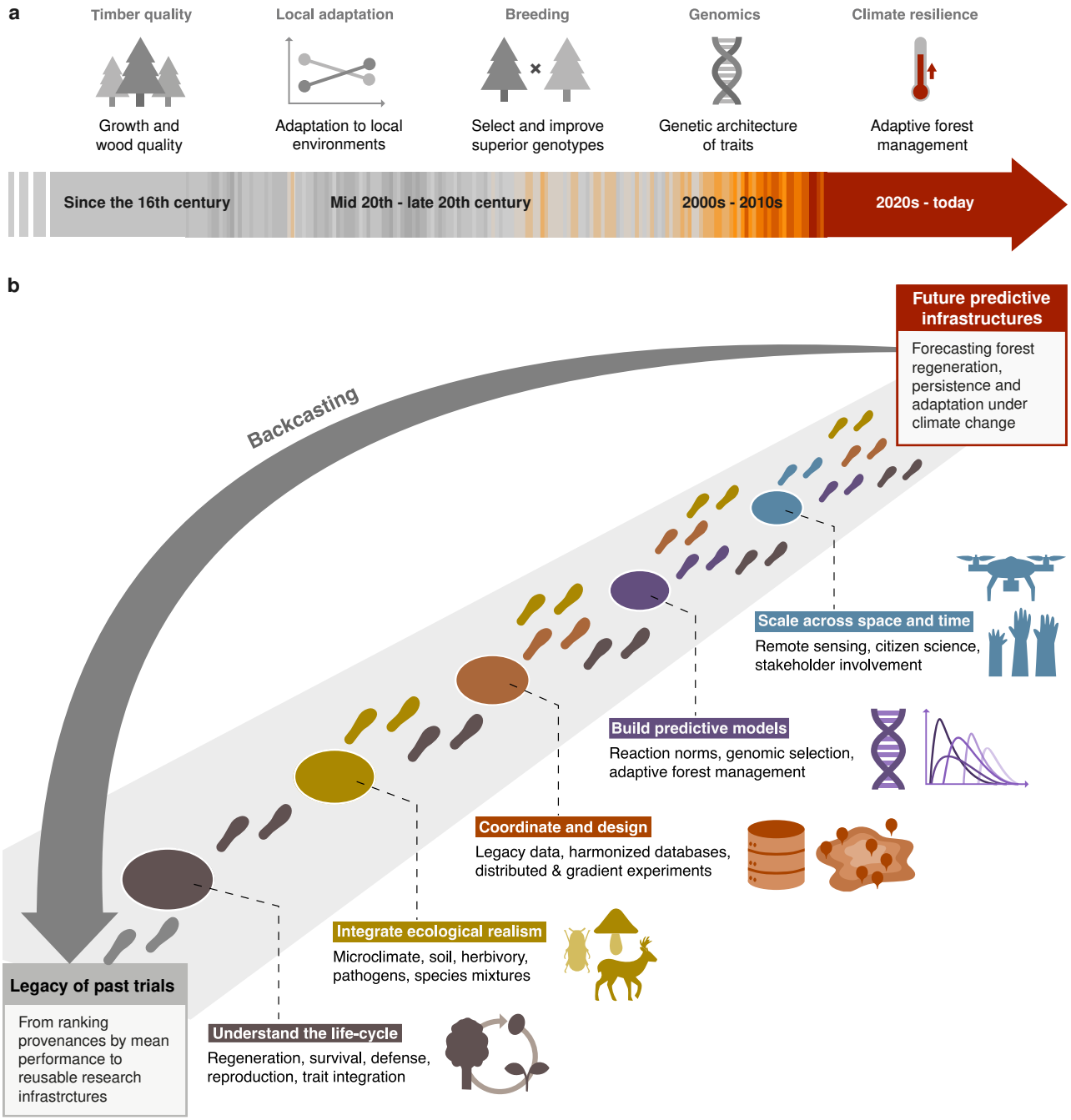

Figure 1: **From legacy comparative trials to future predictive infrastructures.** (a) Changing objectives of comparative trials in forest trees, from timber production and the study of local adaptation to tree breeding, genomics, and climate-resilient forest management, synthesized from [5]. (b) Backcasting framework for designing next-generation comparative trials. Starting from the long-term objective of forecasting forest regeneration, persistence, and adaptation under climate change, the framework identifies five complementary areas for development: coverage of the entire life cycle, greater ecological realism, coordinated experimental designs and data infrastructures, predictive modeling, and scaling across space and time. These areas are interconnected and iterative rather than a fixed linear sequence, indicated by the footsteps "walking together".

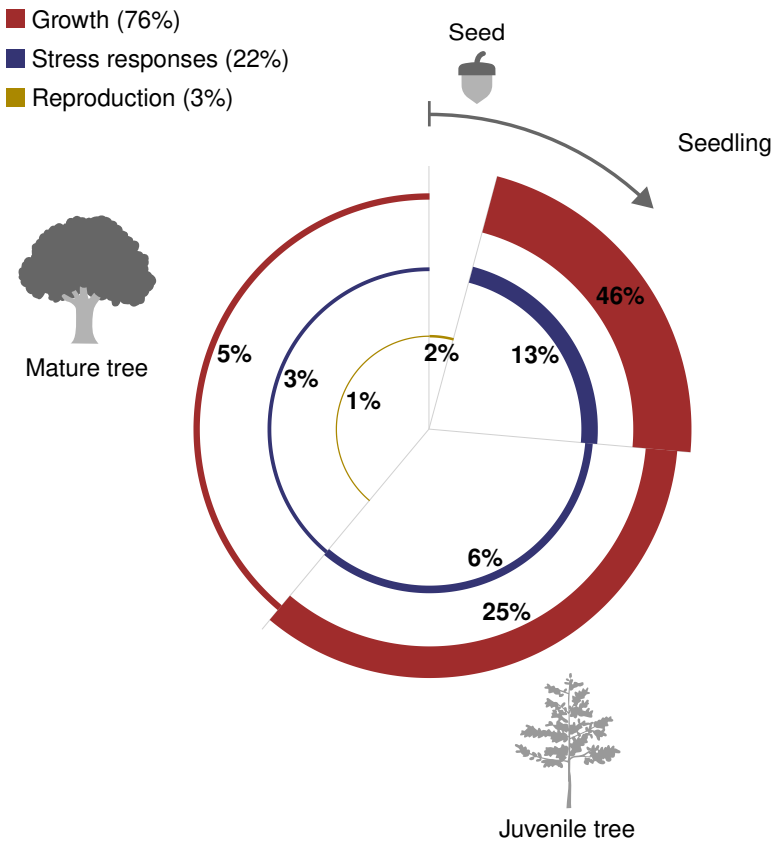

Figure 2: **Trait coverage across the tree life cycle in existing provenance trials.** Distribution of reported growth, stress-response, and reproductive traits across seed, seedling, juvenile, and mature life stages, based on the data compiled by [94]. The category "Stress responses" encompasses survival, tolerance to abiotic stress, and defense against biotic stressors. Percentages within ring segments represent the proportion of all classified study–trait–age records, and band thickness is proportional to the displayed percentage using a common linear scale across all rings. Percentages may not sum to 100% because of rounding. Life stages were defined as seedling (1–5 years), juvenile tree (6–30 years), and mature tree (>30 years). The "Seed" category comprises records of seed and germination traits measured at ages 0–4 years. Details of trait classification, age-class assignment, and data processing are provided in Supplementary Methods S1.

Supplementary Information for

Centuries of comparative trials in forest trees: time for the next generation to tackle climate change

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Contents

Table S1: Remote-sensing platforms and sensor types relevant for trait detection in common-garden trials of forest trees. Platforms determine the spatial and logistical feasibility of assessing genotype × environment ($G \times E$) responses, whereas sensor types determine the trait information that can be retrieved. Together, they provide opportunities to scale provenance performance from individual trees to landscapes. For a more detailed introduction to these techniques, see [167, 188, 189]. RPAS: remotely piloted aircraft system.

Platform or sensor	Trait information captured	Strengths for provenance trials	Key limitations
Platforms			
RPAS	Centimetre-scale canopy reflectance and structure, depending on the sensor, over extents ranging from hundreds of square metres to several square kilometres per campaign.	Individual-tree monitoring; flexible repeat surveys at selected times; tree-level assessment of $G \times E$ responses in phenology, growth, and stress.	Limited spatial extent; payload-dependent equipment and operating costs; field effort for acquisition and validation; moderate logistical requirements; weather-dependent and campaign-based.
Piloted aircraft	Metre-scale canopy reflectance and structure, depending on the sensor, over moderate spatial extents of several square kilometres per campaign.	Suitable for multi-site trials; allows $G \times E$ responses to be compared across environments while retaining relatively high spatial detail.	Very high operating costs and moderate user costs; field validation required; substantial logistical constraints; weather-dependent and campaign-based.
Satellite-based	Metre- to kilometre-scale canopy reflectance and structure, depending on the sensor, with regular repeated coverage over large areas.	Long-term and repeated monitoring; supports scaling of provenance performance and $G \times E$ responses to landscape and regional levels.	Individual-tree discrimination is often limited; field validation is required; usable observations depend on acquisition timing, cloud cover, and sensor availability.
Sensor types			
Photography and photogrammetry *Passive*	Pigments, canopy colour, vigour, phenology, and, when structure-from-motion photogrammetry is used, three-dimensional canopy structure.	Monitoring of seasonal dynamics and productivity differences; supports assessment of $G \times E$ effects on phenology, vigour, crown dimensions, and growth.	Optical imagery is affected by clouds, illumination, and shadows; structural information is limited unless structure from motion or complementary LiDAR data are used.

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Table S1 continued from the previous page

Platform or sensor	Trait information captured	Strengths for provenance trials	Key limitations
Multispectral *Passive*	Pigments, canopy water status, vigour, and phenology, depending on the number and position of the spectral bands.	Efficient monitoring of seasonal dynamics, stress, and productivity differences; supports repeated assessment of $G \times E$ effects on canopy condition.	Cloud- and illumination-sensitive; spectral information is restricted to a small number of broad bands; limited structural information without photogrammetry or LiDAR.
Hyperspectral *Passive*	Leaf and canopy biochemistry, pigments, water status, stress signatures, and subtle phenotypic differences across many narrow spectral bands.	Detection of physiological and biochemical differences; can reveal subtle $G \times E$-driven variation that may not be visible in broad-band imagery.	Cloud- and illumination-sensitive; limited direct structural information; restricted platform availability; large datasets and complex calibration and processing requirements.
Thermal *Passive*	Canopy temperature, evapotranspiration, and indicators of water stress, depending on the target wavelengths and spatial resolution.	Detection of differences in drought response; supports evaluation of $G \times E$ effects on water stress, transpiration, and stomatal regulation.	Affected by atmospheric conditions, cloud cover, acquisition time, and surface energy balance; generally coarser spatial resolution than visible imagery; limited structural information.
LiDAR *Active*	Three-dimensional structure, including tree height, crown architecture, vertical canopy profiles, and biomass proxies, using laser pulses commonly in the near-infrared.	Direct comparison of structural traits; enables quantification of $G \times E$ effects on growth, biomass allocation, competition, and canopy architecture.	Usually limited to terrestrial, RPAS, aircraft, or selected satellite platforms; acquisition can be costly; point-cloud processing and individual-tree segmentation may be complex.
SAR/radar *Active*	Canopy structure, soil and canopy moisture, and some sub-canopy characteristics inferred from microwave backscatter.	Cloud-independent and largely weather-independent monitoring; useful in persistently cloudy regions; supports consistent assessment of structural and moisture-related $G \times E$ responses.	Speckle noise; complex processing and interpretation; sensitivity varies with wavelength, polarisation, viewing geometry, canopy structure, and soil conditions.

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Table S1 continued from the previous page

Platform or sensor	Trait information captured	Strengths for provenance trials	Key limitations
GNSS reflectometry *Passive/bistatic*	Soil or canopy moisture inferred from reflected global navigation satellite system signals in a narrow microwave-frequency range.	Potentially low-cost complementary moisture sensing; can provide repeated local observations using existing navigation-satellite signals.	High precision often requires dedicated field installations; spatial coverage and trait applications remain limited; the technique is still developing.

Supplementary Methods S1

We aimed to identify knowledge gaps in the traits and life stages represented in comparative trials. We grouped traits into three broad categories relevant to tree performance and fitness across the life cycle: **growth**, **stress responses**, and **reproduction**. Here, stress responses encompass survival, tolerance to abiotic stress, and defense against biotic stressors. To identify these gaps, we relied on a recent meta-analysis by Aspalter et al. [94], who conducted a systematic literature review of studies investigating intraspecific trait variation in European forest tree species. The exact search queries are provided in Appendix A of [94], and the resulting dataset is available from the Dryad repository at `https://doi.org/10.5061/dryad.v15dv424v`, which we downloaded in April 2026.

The dataset contains information from 269 unique articles and reports, for each study (`Paper.ID`), the measured trait (`Trait`), and the age at measurement (`Age`). Each trait is assigned to a group (`Group.y`) corresponding to one of the following categories: "Allocation", "Drought tolerance", "Frost tolerance", "Growth", "Leaf anatomy/Leaf morphology", "Leaf chemical composition", "Phenology", "Physiology", "Plant-animal interactions", "Plant morphology", "Plasticity indices", "Reproduction", "Root chemical composition", "Survival", "Stem chemical composition", "Wood anatomy", and "Other". The complete list of traits within each original category is provided in Appendix B of [94].

We reorganized the complete list of traits into the three broad categories as follows:

- **Growth** included traits related to growth and resource acquisition, including height, diameter and biomass, biomass allocation, vegetative phenology, such as bud burst and leaf senescence, morphological and anatomical traits measured at the leaf, root and whole-tree levels, chemical composition traits related to resource acquisition, such as chlorophyll and carbon content, and physiological traits related to photosynthetic activity, such as assimilation rate and water-use efficiency.

- **Stress responses** included direct measurements of survival, traits describing tolerance to abiotic stress, including drought, heat, and frost responses, traits describing defense against or damage caused by biotic stressors, including pests and herbivores, and growth, physiological, or morphological responses measured under experimentally imposed stress. This category also included chemical traits with established roles in abiotic stress tolerance or biotic defense, such as ferulic acid and epicuticular waxes. When an otherwise growth-related trait was measured under experimentally imposed stress, the resulting response was classified as a stress response rather than as growth.

- **Reproduction** included reproductive output, seed and germination traits, such as the weight of 1000 seeds or seedling recruitment, the percentage of empty seeds, and germination rate.

We did not classify traits belonging to the original categories "Other" and "Plasticity indices", and we removed records with ambiguous age information.

After these processing steps, 252 unique studies remained. Each study could contribute multiple records because the database contained one record for each unique combination of study, trait, and age at measurement. Thus, a study contributed multiple records when it examined several traits or measured the same trait at different ages. We assigned the remaining records to the following life stages: Seedling (1–5 years), Juvenile tree (6–30 years), and Mature tree (>30 years). The Seed category comprised records of seed and germination traits measured at ages 0–4 years. Because this category was defined jointly by trait type and age, it could overlap with the seedling category in age.

We then summarized the number of study–trait–age records within each combination of life stage and trait category. The resulting distribution revealed a strong bias towards growth-related traits and early life stages: 46% of all classified study–trait–age records represented growth-related traits measured at the seedling stage.