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COMMENTARY

A claim for a 'next generation' of multisite range-wide forest genetic trials built on the legacy of ecological genetics to anticipate responses to climate

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Forests provide invaluable environmental services to the planet and essential renewable goods for humanity, such as fibre, timber, chemicals and energy. Nevertheless, temperate and boreal forests are challenged by the climate crisis and other associated ecological threats, such as alien forest pests and pathogens. As a result, in some species whole populations are at extinction risk, and genetic diversity is lost. Therefore, maintaining the current distribution of forests and the ecosystem services these forests supply requires unprecedented coordinated efforts from the scientific community for understanding, forecasting and mitigating such impacts. Additionally, since the total area of tree plantations and exploited forests are already more extensive than those of unmanaged forests, we must provide first-class information to policy-makers to sustain evidence-based forest management.

The chance of a given species or a population variant persisting in a given region will depend, for in situ adaptation, on its adaptive potential, which is related to the standing genetic variation. However, within an assisted migration (*sensu lato*) context, the adaptive potential at the species level will be determined by the existence of populations already adapted or lineages with enough plasticity for accommodating to the new conditions. For example, the population, as an adaptive unit, has been reported as the source of improved fitness values for some forest tree species (fast growing, pest resistance, pathogen tolerance or drought resilient). Therefore, providing knowledge on forest tree species' genetic variation, phenotypic plasticity, and genetic variation in plasticity to climate changes is

essential for forecasting forest tree species' responses to the ongoing climate crisis.

It is on this point that the review paper presented by Leites and Benito-Garzón (2023) in this issue is interesting, novel and valuable. The authors make an excellent call for attention to the value of existing networks of genetic trials in trees and directly go to the need to establish a new generation of genetic trials specifically designed to pinpoint cues of adaptation in forest species. The authors first state the framework for understanding the relevance and value of the networks of provenance forest genetic trials. Then they perform a systematic and comprehensive literature review to identify strengths, gaps and opportunities. Lastly, they review the results offered by the publications that study at least three replicated common gardens (i.e. pure multisite forest genetic trials), summarizing current knowledge on the topic.

Multisite provenance forest genetic trials established in the second half of the 20th century are unique jewels for gathering information about species biology, predicting tree population responses to climate and facilitating forest management tools. Furthermore, the primary and applied information obtained from some of these networks have provided high-value papers not only in the field of forestry, but also for plant evolutionary ecology, as they are perfect tools for studying the evolution of genetic adaptations and phenotypic plasticity. Below we discuss some ideas arising from this topic that we would like to highlight.

One central value of a multisite provenance genetic trial design is the power to reveal the nature of the interactions between the

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genetic component (populations, families or clones) and the site, which is the genetic variation in phenotypic plasticity among the genetic units. Multisite forest genetic trials have been designed particularly for this purpose. Genetic variation in phenotypic plasticity (or differences in genotype-by-environment interaction, $G \times E$) is a crucial concept for theoretical and applied evolutionary genetics, providing key information for predicting adaptation to climate change, species distribution models and assisted migration (e.g. Lancaster et al., 2017).

Agricultural and animal breeding programs (all on organisms with short life cycles) have traditionally considered trait stability a positive value, and have therefore looked for lineages with fixed trait values with relatively low phenotypic plasticity. That is worthwhile when looking for more accuracy in forecasting productivity. However, phenotypic plasticity could be a key attribute for population persistence in the case of long-lived species such as forest trees. There is currently a lack of knowledge about genetic variation in plasticity for most tree species, which is one primary reason why more forest genetic trials are required. Analyses of multisite genetic trials have contributed to understanding the evolution and adaptive value of phenotypic plasticity, particularly for traits related to intraspecific competition, such as growth rate. For example, in Ponderosa pine, de la Mata et al. (2022) observed greater phenotypic plasticity in populations from drier and hotter environments, and populations with higher phenotypic plasticity in those traits showed lower quantitative genetic variation within populations. But this pattern may be species specific and more empirical data are required to know in what cases phenotypic plasticity is advantageous under high resource availability and phenotypic stability under harsh environments in order to maintain a conservative resource-use strategy.

Quantitative genetic approaches of forest tree breeding must be combined with those from ecological genetics and the advances in genomic resources for better forest science. It will be essential to re-analyse phenotypic information of multisite trial networks with information about population structure provided by new genomic data available for forest tree species. Importantly, determining population differentiation in a given trait or trait covariation with climate does not directly mean 'genetic adaptation to climate'. Considering unequal coancestry among populations when looking for clinal covariation between traits and geo-climatic variables is possible by integrating the matrix of population structure (Q) obtained from genomic information into the mixed models. Neutrality tests using genomic data are mandatory when looking for adaptive signals in phenotypic trait variation, as much of the population differentiation could not be adaptive but simply explainable by or overlapped with neutral evolutionary processes (López-Goldar et al., 2019).

We must consider how the integrated phenotype can react to the environment, as correlated responses of diverse connected traits could be expected to affect tree fitness. Such an idea (the existence of negative genetic correlations between life history traits) has been recognized and integrated into agriculture and animal breeding programs for managing genetic resources, but is still rare in forest management (but see Santini et al., 2019). Although valuable from

a physiological point of view, studies based on phenotypic correlations allow for limited evolutionary inference compared with studies based on genotypic or family correlations, which provide information on heritable, genetic-based trade-offs (Agrawal, 2020). Multisite forest genetic trials provide robust tools for studying trade-offs and their evolutionary relevance, although most are still awaiting to be uncovered. Trade-offs, traditionally identified across species, could occur across and within populations, with different consequences on the evolution of intraspecific trait variation. Besides, trade-offs are context dependent (nutrient availability, biotic interactions, abiotic stressors, etc.), and a central prediction is that context dependency contributes to the maintenance of intraspecific variation. Furthermore, here is where multisite trials replicated across the distribution range of the focal species are valuable.

Lastly, some methodological questions should be considered in re-analysing the existing databases and designing a new generation of multisite genetic trials. First, genetic trials have been often established using improved genetic material (already subjected to artificial selection, usually for productive criteria timber quality and growth potential). We know now that even one single selection event on phenotypic traits, such as growth rate, is enough to introduce bias in trait distribution and covariation with other characteristics such as reproduction (Santos-del-Blanco et al., 2015). In addition, if selected lineages with improved trait values ('plus families' using the forest breeding terminology) are included, selection intensity must be considered. We also need to move to a broader breeding perspective considering traits other than productivity, such as drought resilience and pest resistance, that could bring exceptional fitness value in the near future. Related to this point, genetic trials were usually located under 'regular' environments for the focal species, but we know that future conditions represent new and extreme environments for the trees. Establishing new trials in the distribution limits for the species could help detect hidden reaction norms or some new developmental constraints or trade-offs (Schlichting, 2008). Finally, one primary reason for urgency is that extant genetic trials are getting old. When intraspecific competition within the trial arises and mortality increases, information becomes increasingly dependent on the spatial design, and the value of inferences on adaptation quickly decreases.

In summary, we deeply agree with Leites and Benito-Garzón (2023), and would go even further, as we think that establishing a new network of tests is urgent and mandatory. We need a quick and coordinated effort to establish the next generation of multisite, range-wide provenance forest genetic trials focused on forest resilience to climate change. As scientists, we should facilitate tree population evolutionary responses to a new and changing climate and environment. Such efforts must be transnational, irrespective of differences in the development and objectives of forest genetics in each particular region. The scientific communities of countries with advanced breeding programs connected with the conservation of forest genetic resources and assisted migration (such as e.g. the US and Canada) have much to say in this challenge. Managers and policy-makers, and also readers of *Global Change Biology*, deserve

the best information for building new forest management decisions based on the best scientific evidence.

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CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analysed for the current article.

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