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SYNTHESIS

The drivers of intraspecific trait variation and their implications for future tree productivity and survival

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Abstract

Forests are facing unprecedented levels of stress from pest and disease outbreaks, disturbance, fragmentation, development, and a changing climate. These selective agents act to alter forest composition from regional to cellular levels. Thus, a central challenge for understanding how forests will be impacted by future change is how to integrate across scales of biology. Phenotype, or an observable trait, is the product of an individual's genes (G) and the environment in which an organism lives (E). To date, researchers have detailed how environment drives variation in tree phenotypes over long time periods (e.g., long-term ecological research sites [LTERs]) and across large spatial scales (e.g., flux network). In parallel, researchers have discovered the genes and pathways that govern phenotypes, finding high degrees of genetic control and signatures of local adaptation in many plant traits. However, the research in these two areas remain largely independent of each other, hindering our ability to generate accurate predictions of plant response to environment, an increasingly urgent need given threats to forest systems. I present the importance of both genes and environment in determining tree responses to climate stress. I highlight why the difference between G versus E in driving variation is critical for our understanding of climate responses, then propose means of accelerating research that examines G and E simultaneously by leveraging existing long-term, large-scale phenotypic data sets from ecological networks and adding newly affordable sequence (-omics) data to both drill down to find the genes and alleles influencing phenotypes and scale up to find how patterns of demography and local adaptation may influence future response to change.

KEYWORDS

climate selection, eco-evo integration, genetic variation, genomics, long-term research, plant traits, scaling, trees

Forest ecosystems provide enumerable benefits to society beyond their simple extractive value. Forests can filter drinking water (Blumstein et al., 2015; Thompson et al., 2016), stabilize coastlines (Spalding et al., 2014), and provide local cooling to urban heat islands (Bowler et al., 2010). Forests are also a stabilizing force to the climate, as they remove approximately one third of anthropogenic carbon emissions from the atmosphere globally each year (Le Quéré et al., 2015). However, whether forests will continue to serve as carbon sinks into the future is in question.

Over the past several decades, forest cover has decreased worldwide (Global Forest Watch, 2022). This decrease is the result of a conversion of land to agriculture/development and mortality from climate-induced disturbances. Increased wildfires, prolonged drought, and invasive insect outbreaks associated with globalization and climate change have resulted in large-scale, tree mortality events (Hammond et al., 2022). These selective agents have acted to alter forest composition from the regional scale to the cellular level removing individuals that once lived in a locality and leaving the remaining resilient individuals to reseed the next generation. Thus, to understand whether, and to what degree, forests may continue to serve as carbon sinks requires us to integrate data across disciplines (ecology and evolution) and scales of biology to predict how tree species will respond to climate change.

WE ARE IN AN ERA OF BIG (TRAIT) DATA

In this current data-rich era, trees can be measured from space, airplanes, and inexpensive unmanned aerial vehicles (UAVs). Using sensors mounted on these platforms, we can remotely capture resolutions as low as 30 cm from space (e.g., Pléiades Neo ESA, 2023) and to 1 cm with UAVs (Schiefer et al., 2020). Not only can we get high-resolution snapshots, some satellites have now been collecting images for up to 50 years (e.g., Landsat Neigh, 2023), enabling us to examine change over time and geographic space. These images can be used to measure variation in plant functional traits or the measurable characteristics of individuals that influence their fitness (i.e., growth, reproduction, or survival) (Violle et al., 2007). These traits, such as leaf lifespan or height, have been combined into trade-off axes to infer plant life-history strategies, such as conservative vs. competitive resource users (Reich et al., 2003; Wright et al., 2005a) and to understand how climate shapes these trade-offs (Wright et al., 2005b; Blumstein et al., 2022a).

Remotely sensed data are complemented and often validated by data collected by ecological research networks. These networks typically aim to study ecological phenomena by instituting the same methodologies at sites around the world and often overlap with each other. For example, the Ameriflux network (Novick et al., 2018) is a series of towers set above the forest canopy around the world that measure water and carbon fluxes in each tower footprint. These towers are often placed at existing research networks, such as long-term ecological research sites (LTERs) and national ecological observatory network sites (NEON) because they require a fair amount of infrastructure such as internet and power. Given that the towers extend beyond the canopy and are electrified, they are also prime candidates for placing cameras and other sensors, such as the standard red-green-blue cameras used by the Phenocam Network (Seyednasrollah et al., 2019) to measure phenology. Some of these sites, particularly LTER sites, have been taking ground-based measurements of plant traits for up to decades, providing large data sets that have been used to examine regional to global patterns in trait variation (e.g., Wang et al., 2022).

Finally, the coordination of many individual studies into trait databases has also provided an invaluable resource for examining the trait variation of individuals across geographic and climatic space. One such example is the TRY database, where researchers can upload their spatially referenced data for use by the wider community (Kattge et al., 2020). Others such as the Xylem Functional Traits (Choat et al., 2012; Hammond, 2023) and Nonstructural Carbohydrate (NSC) (Blumstein et al., 2022a) databases include more specialized subsets of plant physiological traits. In sum, these resources enable researchers to examine how traits vary with climate (e.g., Figure 1A) and how this variation might enable or constrain plant response to future global change.

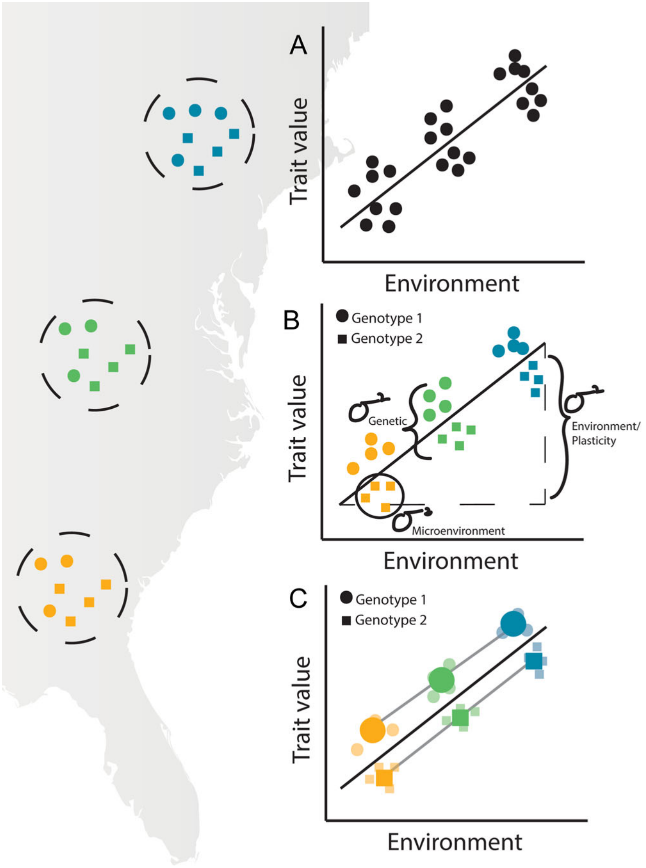

FIGURE 1 Conceptual diagram demonstrating how (A) trait variation collected from across a geographic range can be formed by (B) variation (σ^2) driven by plasticity, microenvironment, and genetics together. In this simplistic example, when (C) genetics are accounted for (solid circles and squares represent genetic estimates of the trait), the reaction norm for each genotype is revealed, enabling us to quantify the drivers of trait variation.

While insights on phenotypic variation from all of these sources are valuable, because these data are collected largely in observational studies, with a few exceptions (e.g., Melillo et al., 2011), it is impossible to tease apart whether environment alone is driving patterns of variation or whether genetics is also a factor.

TRAITS ARE THE PRODUCT OF GENES AND ENVIRONMENT: DISCERNING THE CONTRIBUTIONS OF EACH MATTERS

While we have an immense ability to categorize variation in key traits, we have yet to effectively estimate the drivers of this trait variation. While "functional trait" has become a ubiquitous term in the literature, it is essentially another name for an adaptive phenotype—a measurable characteristic of an organism that conveys higher fitness in a given environment. Phenotypes are the products of an organism's genes, the environment in which an organism lives, and the interaction between the two (Figure 1B).

$$\text{Phenotype}(\text{P}) = \text{Genotype}(\text{G}) + \text{Environment}(\text{E}) + \text{GxE} \quad (1)$$

This is the classic nature versus nurture debate: To what degree does the plant's environment (nurture) versus its genetic background (nature) dictate its overall characteristics? Distinguishing one from the other is critical because each acts on different time scales and enables organisms to respond to climate selection in very different ways.

Variation due to environment, often referred to as plasticity, informs how much phenotypic space an individual has to respond to change within their lifetime (E in Eq. 1). Plastic variation is defined as the same genotype exhibiting different phenotypes when placed in novel environments (Scheiner and Goodnight, 1984). The phenological timing of leaf out is a common example of a trait that can exhibit plasticity; temperate, deciduous trees will alter the date of their leaf out each year in response to interannual variation in spring temperatures (e.g., Anderson et al., 2012). Trees are long-lived, immobile species and thus have always been reliant on plasticity in certain traits like phenology to persist in variable environments. However, as the global climate shifts and we enter non-analog climate futures, plants will likely be pushed beyond the limits of their plasticity (Jump and Penuelas, 2005), necessitating a shift in trait means via adaptive evolution and possibly even novel combinations. Thus, plasticity alone is unlikely to enable plants to respond to long-term change.

Alternatively, genetic variation can be passed onto offspring and therefore acted upon by natural selection (G in Eq. 1). Genetic variation encompasses the differences between individuals in their genomic sequences. Countless studies have demonstrated that genetics contribute significantly to variation in tree species traits (e.g., McKown et al., 2014) and that tree populations exhibit high degrees of local adaptation (Savolainen et al., 2007; Franks et al., 2014), indicating that geographic and climate trait variation patterns are driven to some degree by genetic differentiation, not just environmental conditions. Understanding the degree to which trait variation is driven by genetic differentiation is critical because this variation can be shaped by adaptive evolution and potentially produce novel phenotypes in future non-analog climate scenarios.

Genetics can also uniquely interact with environment to produce different reaction norms, a phenomenon known as genotype by environment interactions (GxE in Eq. 1; Des Marais et al., 2013). We have long acknowledged the importance of GxE in regard to disease in humans. For example, an individual may have an allele that predisposes them to developing a disease such as skin cancer, but that disease will only manifest in certain environments, say high sun exposure, but not in individuals without the allele (Hunter, 2005). These differential responses to environment based on an individual's genetic background has more recently gained traction. For example, in a large comparative study of wheat, researchers found that when a cultivar is selected for drought resistance in one environment, it may not be the most drought resistant among the same mix of cultivars in another (Xiong et al., 2021), indicating that GxE is critical to consider when optimizing crop outputs at a given locality.

While evolution is typically thought to be a slow process, I argue that microevolutionary forces such as local adaptation can play out in a relatively short period (~50–100 years) in tree species. In other species, local adaptation has been observed to occur in just a few generations (e.g., Cambell-Staton et al., 2017). For A species that takes ~25 years to be reproductive could undergo 3–4 generations in just 100 years. Locally adaptive evolution typically acts on standing genetic variation, removing unfit individuals and their alleles from populations, thus populating the next generation with alleles of higher fitness. For example, if a drought affects a population of trees and kills off 75% of the individuals with genetically lower tolerance to drought, the fitter individuals will survive and go on to populate the next generation. The following generation of trees will have a much higher drought tolerance on average, leaving it less vulnerable to extremes in the future. Thus, in just one extreme event, allele frequencies can shift, and trait means can adapt to new regimes.

Disentangling the amount of genetic variation in traits is critical for understanding not just how a stand will respond to selective events, but how trait physiology might change following selection. Traits often do not operate independently within organisms; an increase in a trait such as nonstructural-carbon storage due to selection will likely come at the cost of some other high carbon demand trait such as growth (Blumstein et al., 2022b). Thus, understanding whether variation is genetic will not only inform what percentage of plants might survive selective events, but how overall stand physiology might shift following these events, feeding back into ecosystem and climate-scale processes such as nutrient and carbon cycling.

HOW HAVE WE TRADITIONALLY SEPARATED THE TWO DRIVERS OF VARIATION?

Studies have been parsing genetic from environmental variation for over a century (Turesson, 1922; Clausen et al., 1941). Traditionally, individuals have been taken from across their range and planted in the same common garden. We assume that these designs control for the macroenvironment; thus, all differences measured between individuals are presumed to be genetic. The genotypes or families from these gardens can then be planted in replicated common gardens across a species range, enabling us to measure plasticity and GxE. These studies produce reaction norms (Figure 1C), which detail the amount of genetic, GxE, and plastic variation in a species. In sum, common garden studies and reciprocal transplant designs have provided invaluable insights into trait variation over the past century and should continue to be used. However, they are time consuming and difficult to set up anew, particularly for long-lived, slowly growing, large tree species. Given we are highly unlikely to meet the goal of limiting climate change to 1.5°C warming set by the Paris Climate Accord (Lamboll et al., 2023), we need to understand how one of the world's largest carbon sinks, forests, will respond to change and how we can intervene to enhance this carbon sink as quickly as possible.

COMMON GARDENS ARE TIME CONSUMING; IS THERE ANOTHER WAY?

Like the collection of ecological data, sequencing plant genomes has gotten cheaper and easier over the past several decades, which has led to an increase in reference genomes for ecologically important species (e.g., red oak; Kapoor et al., 2023) and a rapid expansion in the size and scope of projects. Like ecological studies, tree evolutionary genetics studies have also started to generate geographically broad and sometimes publicly available genomic and transcriptomic data of individual trees across many populations (e.g., NAFGS, 2023). These data of partial (i.e., RADseq) or even full-genomic sequences can be used in many ways, but their application in predicting plant response to climate selection is growing. These studies, often referred to as gene–environment association (GEA) studies, characterize how allele frequencies differ across populations of a species and how these differences map to climate (Wang et al., 2010; Lasky et al., 2023). Gene–environment association studies have highlighted alleles that are under climate selection and the degree to which these critical parts of the genome might shift in response to future climate change (e.g., Fitzpatrick and Keller, 2015; Blumstein et al., 2020). These studies have been invaluable in advancing our understanding of patterns of genetic variation with environment, local adaptation, and selection across tree species' genomes. However, they lack information on the adaptive phenotypes—or functional traits—that these alleles theoretically underly and how the two are linked.

Conversely, an immense amount of data has been generated on how ecological functional traits (i.e., adaptive phenotypes) vary across space and time from ecological studies, but the methods of collection (i.e., outside, controlled genetic designs like common gardens or without accompanying genomic information) inhibit our ability to tease apart the genetic from the environmental drivers of variation, a key piece in understanding response to climate change. I propose that it is time to combine these two forms of data collection and thinking to rapidly advance our understanding of the relationship between genotype, phenotype, and environment in large, long-lived tree species (Table 1, Figure 2).

My argument is simple: If we are going to sequence tree genomes and measure all of these traits, we should try to use the same trees. One way to do so is to focus efforts on ecological sites where data is already being collected and the trees can be tagged, geolocated, and easily returned to for further study. Relatedly, ecological research networks should start incorporating sequencing into their regular data collections and future collection plans. While genomic tree networks have been formed, these tend to exist in parallel, rather than in coordination with ecological trait networks. In this proposed design, researchers would gain a powerful understanding of the relationships between genotype, phenotype, and environment that would be informed by decades of phenotypic and environmental collection and newly added -omic sequences. Furthermore, this -omics data would have a long life and continue to inform future research projects layered on at these sites.

These genomic networks could be built for any species and could be utilized for many things, including using single-nucleotide polymorphisms (SNPs) to calculate the relative contribution of genetics to any given trait (i.e., heritability) via genomewide complex trait analyses (GCTAs); analyses developed for humans who also cannot be planted in common gardens (Yang et al., 2011). The prior limitation to these types of studies was largely the cost of sequencing so many individuals, but as the price has come down and the availability of tree reference genomes have risen, this sort of network has finally become attainable. I acknowledge that for some species, this goal is still out of reach due to their polyploid nature or excessively large genome. However, we can start developing these networks for many species (for a list of current tree reference genomes, see Wegrzyn et al., 2019), and eventually as genomic tools enable us to work with larger and more complex genomes, we can expand our efforts (Table 1).

For example, northern red oak (*Quercus rubra*) is the key driver of carbon sequestration in the eastern United States (Finzi et al., 2020) and has recently had a reference genome made available (Kapoor et al., 2023), which is diploid and relatively small (~750 Mbp or ~1/4 the size of the human genome). I am now sequencing red oaks in the Phenocam, Smithsonian ForestGeo, LTER, and NEON networks. In all of these places, I have detailed phenological leaf-out studies on individual organisms over many years and long-term environmental records from Phenocams and some human-observation records (e.g., Richardson et al., 2009). Thus, by sequencing a few hundred individuals, I am able to gain an expansive understanding of the genetic and environmental drivers of variation in leaf-out timing (Uffelmann et al., 2021). For just $50 a genome (5× median depth) and a few weeks in the field and lab, I can calculate the typical quantitative and population genetics metrics (e.g., narrow-sense heritability [h^2], quantitative trait vs. neutral genomic divergence [Q_{ST}/F_{ST}], etc.) on fully grown, mature trees that used to take decades to collect from a

TABLE 1 Common gardens and proposed method of sequencing wild populations to obtain phenotypic and genetic data to estimate contributions of genetics, environment, and their interaction. Such data are critical as the basis for most quantitative and population genetics analyses. Highlighted are a few common statistics that are used to examine genetic contribution and signatures of local adaptation of traits and some advantages and limitations of each approach. The proposed method may not work for all species now and requires larger sample sizes, but these quantities are very achievable if researchers work in a more coordinated way across ecological and evolutionary studies, particularly focusing collecting efforts at existing ecological research sites. These efforts could result in the fast generation of data sets human like the "thousand genomes projects" (Fairley et al., 2020), rapidly expanding our understanding of the relationship between genotype and environment in tree species.

	Reciprocal common gardens	Broad-scale sequencing of wild populations
General workflow		
1. Initial	Collect seeds/cuttings from wild populations, plant in uniform, reciprocal common gardens (need 10+ acres for trees)	N/A
2. Trait Measurement	Measure traits on replicated individuals/families within a common garden and across transplanted gardens	Measure traits on natural populations and collect genomic information (i.e., lcWGS, RadSeq), preferably colocated within established ecological research sites.
3. Analysis	Fit a mixed model with hierarchical structure (e.g., Phenotype ~ Garden + Population/Genotype/Replicate).	Many computational methods available (e.g., GREML Yang et al., 2015; Di Scipio et al., 2023), which can parse genetic, environmental and their interaction using SNP matrices.
4. Output	Variation due to genetics, plasticity, and the interaction between the two (GxE).	Variation due to genetics, plasticity, and the interaction between the two (GxE).
Calculable metrics		
1. Heritability	Calculate broad (H^2) or narrow-sense (h^2) heritability depending on design.	Calculate h^2 (Evans et al., 2018; Zhou et al., 2020).
2. Causal SNPs	If genomes sequenced, ~300–1000 individuals are needed to detect variants via GWAS.	~750–1000+ individuals are needed to detect variants via GWAS, since macroenvironment is not controlled for a priori.
3. Signatures of trait selection (Q_{ST}/F_{ST})[a]	Can calculate Q_{st}, using h^2 (narrow-sense, additive genetic variation) or approximate with P_{ST} by using H^2 (broad-sense, total genetic variation). If genomes are sequenced, can also calculate F_{ST}.	Given genetic estimates are additive genetic variation (h^2), can estimate Q_{ST}. This value can be compared to F_{ST} calculated from the genomes sampled.
Overall pros and cons		
1. Sample size	Because the experimental design is controlled, much smaller sample sizes are needed to calculate heritability and find causal SNPs (100s–1000 individuals).	Unmanaged sites have more sources of variation, so higher sample sizes are likely needed for most analyses (~750–1000+ individuals).
2. Cost	Costly in terms of time and resources to set up and maintain. For critical fitness traits (e.g., seed or pollen production), some tree species may not reach reproductive age for decades.	Genomic sequencing is cheap and continuing to decline; hundreds to thousands of trees could be sampled for the cost of establishing a new common garden. These genomic data can be taken from trees that already have phenotypic and environmental data available, further reducing time and monetary costs.
3. Species available	All species, although only some can clonally propagate easily and some are much easier to establish and grow.	In theory, any species, but costs and analysis potential are tied to genome size, ploidy, and availability of a reference genome. Methods are continuously being developed to deal with these challenges, and many tree reference genomes are already available (Wegrzyn et al., 2019).
4. Trait data collection	Collection efforts simple: trees are planted in a grid and usually near resources (e.g., power, internet, roads).	Collection may be more challenging as trees are not in neat rows and may be further from resources (power, roads, etc.)
5. Ontogeny	Trees all the same age, but trees may need years to decades to reach reproductive age and key fitness traits (e.g., seed number) determined.	Can target the age of tree best suited for trait of interest. However, additional work (e.g., taking dendrocores or cross-examining existing data at a given site) may be required to control for ontogenetic variation.

[a] Q_{st} is the phenotypic trait divergence across populations due to additive genetic variation; F_{ST} is the degree of genetic population differentiation explained by neutral processes.

FIGURE 2 Trait data is being collected at sites across the world at high frequencies. By adding -omics data to these collections, we can vastly expand the inferences of each study and begin to construct the relationships between genotype, phenotype, and environment at large scales for many species.

common garden. Not only that, I have now laid a foundation for years of research to come. These trees are tagged and geolocated in high-resourced ecological sites to encourage other researchers to layer additional traits for further studies. Like biobanks for humans (Sakaue et al., 2020), this type of research coordination could rapidly improve our understanding of the links between genotype, phenotype, and environment, which is critical not just for our understanding of how traits are formed, but for applications such as assisted migration of trees to bolster productivity under climate change, the discovery and replication of disease-resistant trees, and the success of forest restoration/planting efforts.

CONCLUSIONS

I have presented some "low-hanging fruit" methods of integrating ecology and evolution that are newly available given recent genomic advances. While there is still much to be learned from common gardens and reciprocal transplants, we are running out of time. Climate change is pressing; we are still on course for a "business as usual", or worse, climate trajectory (Lamboll et al., 2023). How forests respond to future change is a large part of the uncertainty in those predictions. Furthermore, nature-based climate solutions are currently being touted as the only viable option for removing additional carbon from the atmosphere. However, these projects are failing at a very high rate, in part due to a lack of data on what to plant where (e.g., Guizar-Coutino et al., 2022; Pearce, 2022). We need to better understand how tree phenotypes are shaped by both genetics and climate to improve our predictions of plant response and to develop effective intervention strategies.

AUTHOR CONTRIBUTIONS

M.B.: conceptualization; writing original draft, review, and editing.

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DATA AVAILABILITY STATEMENT

No new data were generated for this manuscript.

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