A grove of healthy redbays *(Persea borbonia)* resulting from the study by Huges et al. (2022). A small but important proportion of the population, these specimens were identified as resistant to laurel wilt, a disease that rapidly wiped out most of the species.

SCIENCE AND TECHNOLOGY

Focus Forestry on Genetic Diversity

By Jiri Hulcr and Matias Kirst

Introduction

Foresters are increasingly concerned about the "unknown unknowns:" pests and diseases that unpredictably arrive from overseas and sometimes devastate entire tree species, or unprecedented climatic anomalies. The best, if not the only, insurance against an unpredictable future is genetic variation within tree populations. Here we describe how the genetic diversity perspective can move from theory into practice at different levels of forestry. The first step is to recognize that genetic variation within a species is an irreplaceable heritage accumulated over millions of years.

Epidemics Happen

The COVID-19 epidemic forced all of us to reflect on an important biological phenomenon. New diseases can emerge suddenly and affect the entire species. Forest health epidemics also happen. Cases of continental-scale tree mortality are on the rise with increasing introductions of pathogens and pests with global commerce. The American chestnut, the Dutch elm disease, laurels wilt, the emerald ash bores, the white pine blister rust, the hemlock wooly adelgid, the beech bark disease ... do we need to continue?

But this article is not about doom and gloom. This onslaught also led to a new, forward-looking understanding of forest health. Possibly the most hopeful is the paradigms shift from the standard whack-a-mole approach to managing pests and diseases by killing them one by one, to the understanding that we need to grow resistant and resilient forests. Usually, after any new disease sweeps through, a few individuals of the afflicted tree species survive. The magic is genetic variation.

Breeding for Genetic Diversity

What does it mean to grow forests for genetic diversity? First, it's not your regular breeding for pathogen resistance. It is the opposite. In most contemporary genetics-based tree breeding, when a pathogen attacks a particular tree crop, we identify tree genotypes that are resistant, and clone them. An individual tree can be resistant to an individual pathogen, however, only a genetically diverse population can have enough resistance to all of the perils of the Anthropocene.

These days, many tree species are attacked by a plethora of pathogens, and more are coming from overseas. On top of that, native, formerly secondary pathogens, are showing greater virulence, synergized by increasingly stressful climatic conditions.

We can surely develop a blight-resistant American chestnut, but planting the clones back may still not be possible with new *Phytophthora* species in our soil. Not to mention pest insects, which are rarely involved in the gene-for-gene evolutionary arms race like fungi, and can resist broader ranges of host defense chemistry.

Breeding for resistance to the one specific pathogen that happens to be most important right now almost guarantees lowering the overall diversity, and that will make it harder to find resistance against future problems. The path forward leads through maintaining and increasing genetic variation in the tree populations.

Expanding Our Perspective

What's the time horizon of your forestry objectives? Is it a quarterly profit report? Is it a stand rotation? Is it the longevity of your land that you plan to pass on to your family? Or might it actually be the entire posterity, thousands of years, ensuring that the land maintains its resilience to the current

challenges, as well as the future ones that may not even exist yet? Perhaps we should treat our forestry heritage as if we have inherited it from the future generations, and take the longest perspective.

For that, genetic diversity is indispensable. It should not be a part of silviculture. It should be its ultimate goal, the most important result that we need to pass on. A perspective of a hundred years requires genetic diversity to be broad, because we don't know what the next, future challenge will be.

The perspective of thousands of years requires more. It requires evolvability. It requires having the genetic material to evolve new resistance, even evolve traits that are not yet present in the population. By selecting for any trait that happens to be important now, we are preventing this evolvability. We are squandering the existing variation, an irreplaceable heritage that has taken millions of years to accumulate.

Most biological systems, from forest to agricultural to marine, now struggle with similar rapid changes, namely new pathogens and the changing climate. Livestock breeding programs are scrambling to save small ancient domestic populations, as mainstream breeds fail to withstand climate-related stresses. To rebuild corals reefs, coral individuals are now selected for genetic diversity, since we do not know which genotypes will maintain the association with the symbiotic algae as sea temperatures continue to rise. Prioritizing genetic diversity is becoming the new paradigm for managers across many different natural resources.

We Don't Need New Tools

Silviculture for genetic diversity does not need a new set of tools. It can use the same good old forestry approaches we've been developing over centuries. What's new is the prioritization of objectives. Just like when ecological forestry came aboard, it adopted standard, stand-level management developed for commercial timber. Only the objective moved from maximizing yield to maximizing ecological function (Palik and D'Amato, 2017).

The most common current response to a known pathogen is genetic improvement. An example is the successful breeding of southern pines for resistance to pitch canker. The most effective management of forests for *unknown future* pathogens may be the opposite: maintaining genetic variation. When laurel wilt eliminated redbays from the southeastern US forests, a few individuals survived (Hughes et al., 2022).

Before the challenge by this novel pathogen, these individuals were indistinguishable from the rest; now they are the only hope for the species. We just need to propagate them. Or better yet, breed the resistance into a wide, genetically diverse pool, by crossing those resistant trees with the remaining material.

For maintaining genetic diversity within a forest stand, we may still spray paint dots on the trees to be removed in the next thinning so that the forest grows well. However, instead of keeping only the straight and tall ones, we may need to explore other approaches. They can range from keeping representation of all phenotypes, to genotyping the population and selecting individuals that encompass most of the diversity.

To increase the diversity of genes in a population, there is not much we need to do; open pollination does the magic. That is what sex is for nature—increasing genetic variation leads to greater survival. The elephant in the room is that the populations need support.

The main threat to forests, and the genetic diversity within, is conversion to other land uses. Justifying why forest land needs to remain forested is beyond this article; suffice it to say that there are many different justifications. One of them is economic. Where the situation demands single-species stands, we may look for high-yielding genotypes that are sufficiently diverse from each other to capture most of the remaining genetic diversity.

Where focus on more than one species is possible, the forestry community may need to diversify not only the forests, but also the markets for them. We typically grow what the industry wants, but we may need to work with the industry so they use what grows well. We also need to think beyond just the main timber species: while there are still plenty of pines and a few hardwoods species, populations of many other species are declining in abundance, or have not recovered after most American forests have been cutover. From the Atlantic white cedar to the western sequoias, many important tree species have rather small genetic population sizes.

Where a substantial change of current practices is needed is reforestation. Many programs around the world—from climate change mitigation for policy mandates, to large-scale commercial timber plantings—routinely use seedlings grown *en masse* in nurseries from a few lineages. In terms of long-term forest health and resilience, this practice is counterproductive. Where foresters are not in a rush, such as in long-lived northern conifers, in forests for natural regeneration, or for carbon capture, it may be better for the forest to establish itself, with some help.

As most foresters know, a forest will grow wherever the soil and water availability allows. It may not be the structure and species composition that we desire right now. The natural transition from a pre-forest through early succession to standing timber may be longer than short-term planting programs expect. For the long-term forest survival, instead of manually planting clones, it may be more productive to safeguard naturally regenerated seedlings: for genetic variability, for rhizosphere development, for the restoration of biodiversity and bioabundance.

Protecting entire populations will likely be the focus of agencies that manage forests at such scales. But even timber companies are not exempt from the rules of biology, and would be advised to not put all of their eggs in one basket. Imagine the southeastern forests if a laurel wilt-like pathogen hit the few dominant clones of loblolly pine. There is a reason to keep pine diversity on the land.

Some of the most progressive eucalyptus breeding companies in the southern hemisphere are experimenting with open pollination in their plantations. They hope to prevent the large waves of mortality experienced in clones which were improved for a few traits but impoverished for overall diversity.

Companies and agencies in the northern US and in Europe are going even further. After heat waves and bark beetles wiped out unprecedented swaths of spruce plantations, the entire industry is suddenly looking fondly at uneven-aged forestry, which not only guarantees a diversified portfolio of species and genes, but also produces profit with greater regularity. The good news is that genetic diversity and timber yield can be positively correlated, even on the stand level, if done right (Carter et al. 2020).

Redirecting at least some of our attention away from plantation silviculture would address another, sneakier problem: forestry education. As immediate profits drive jobs towards plantations, there has been a substantial global decline in bona fide forestry schools. (We are intentionally distinguishing between plantations characterized by rotations, and forests characterized by selective logging, uneven-age structure, and self-seeding.) Particularly in the global south dominated by plantation timber production, university forestry degrees are in decline (McGlone et al., 2022; Victoria State Government). We need to attend to this trend, before genuine silviculture of diverse forests is forgotten.

Future is Possible

We are increasingly able to predict new and future pests and diseases. This is a substantial improvement compared to the situation 20 years ago, when we borrowed the military jargon and talked about the "unknown unknowns." There are now many "known knowns;" pests or pathogens that we have confirmed to have the potential for damage.

Surely, we cannot predict all the pests and diseases, but research has demonstrated several to which we can now prepare (Dong et al., 2024, Li et al., 2022). In addition to exotics, native pathogens switch from being inconspicuous molds to pine killers depending on moisture in the air (Pandit et al. 2020). In theory, we know that, to address these challenges, we need genetic diversity in our forests. Now we need to put it into practice.

The largest danger is lack of community mobilization. If COVID can teach us anything, it is that society's response can make all of the difference. The most hopeful sign is that the forestry industry is starting to appreciate the danger of forest health threats. Will we be lulled to comfort by the fact that no major pathogen has yet wiped out southern pines? Or will the big players take seriously the signs of pathogen emergence and spikes of temperature? Will agencies and industry leaders focus on genetic diversity of trees as a factor in their plans?

Conclusion: What You Can Do

We will be able to prevent the next big epidemics of tree deaths if we elevate population resilience among our priorities. Help promote it wherever you are. If you are a part of a company that deals with natural resources, talk about diversifying timber portfolios. If you work in an agency, talk about genetic diversity. If you are in an educational institution, learn from the managers of the future: your students, as the new generation seems to understand the need to diversify instinctively. If you grow trees and you see a potential problem, please tell someone. A great venue for sharing observations is the Southeastern Forest and Tree Health Diagnostics online forum (SFTHD 2024). FS

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