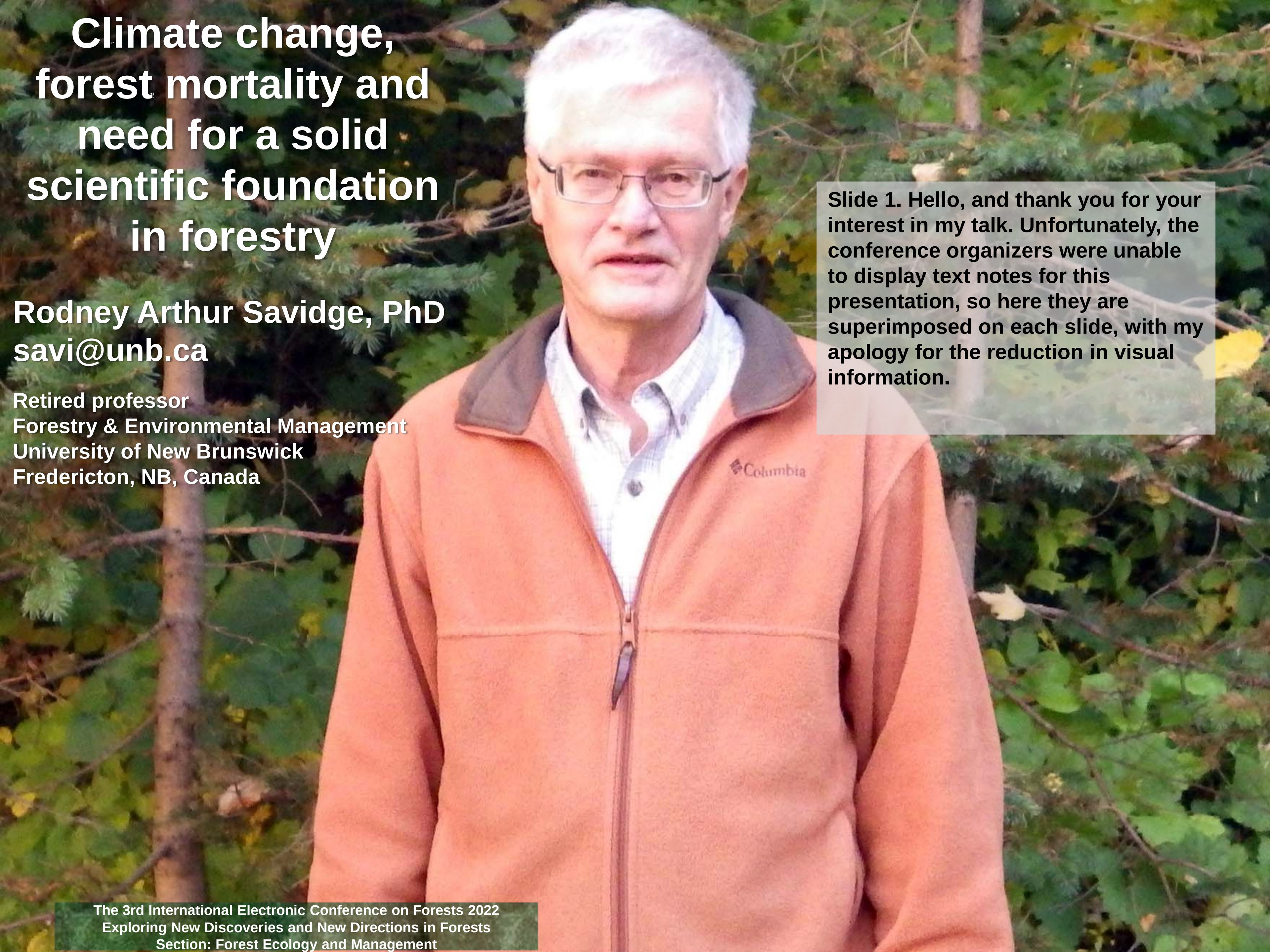

Climate change, forest mortality and need for a solid scientific foundation in forestry

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Slide 1. Hello, and thank you for your interest in my talk. Unfortunately, the conference organizers were unable to display text notes for this presentation, so here they are superimposed on each slide, with my apology for the reduction in visual information.

The 3rd International Electronic Conference on Forests 2022
Exploring New Discoveries and New Directions in Forests
Section: Forest Ecology and Management

Climate change, forest mortality and need for a solid scientific foundation in forestry

Slide 2: Graphical abstract: This slide shows an example of forest mortality in northern Canada. The wild population of spruce trees shown here has experienced widespread mortality, the cause uncertain. But note the scattered survivors; one is arrowed in red.

Slide 3: To satisfy the presentation guidelines, this slide shows the abstract that was originally approved for this presentation.

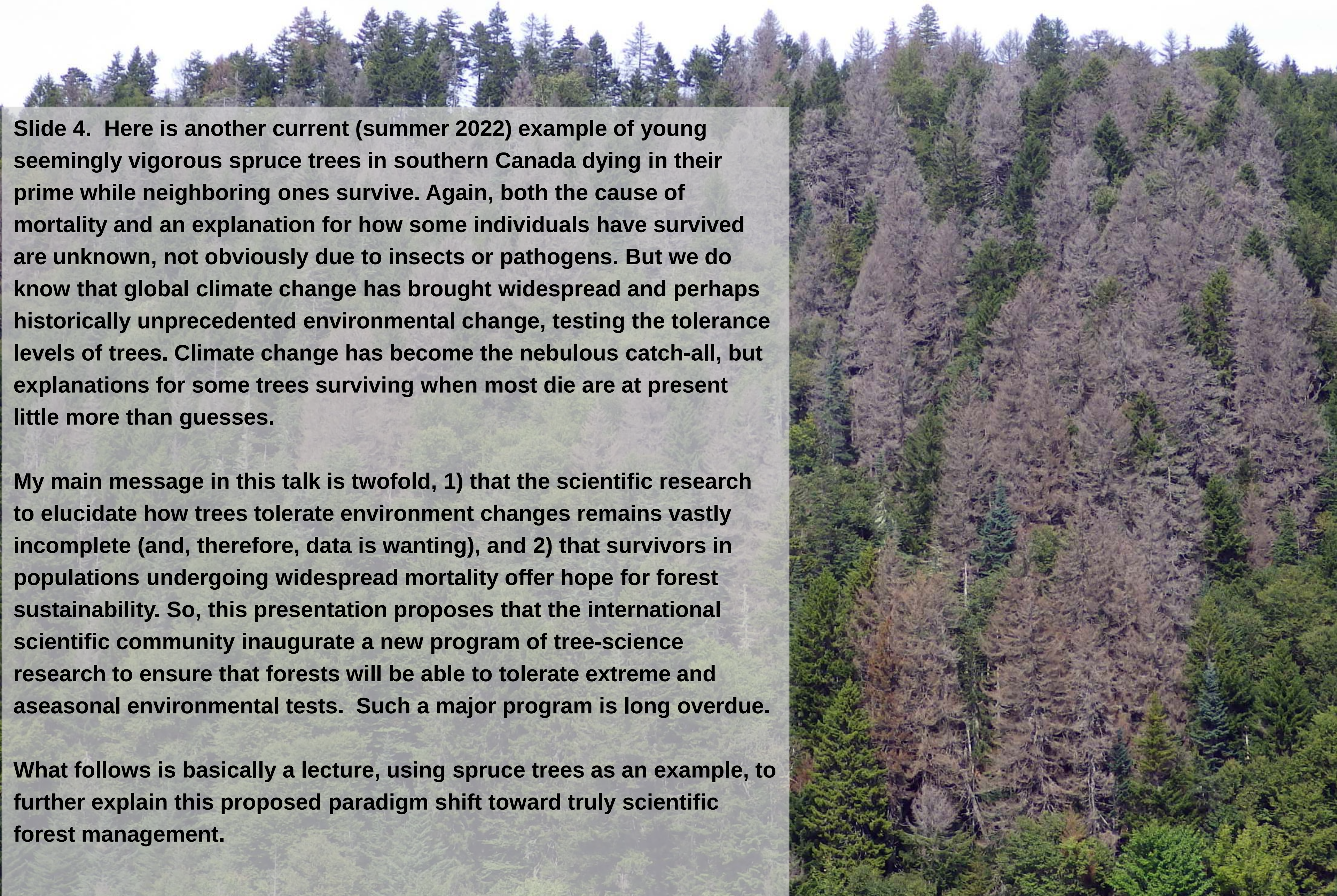
ABSTRACT - The fossil record allows the inference that the intrinsic attributes engendering survival of wild forest trees originated over millions of years of natural selection following physical, chemical and biological tests. Current thinking is that tolerance of, hence survival in, ever-changing environments is a physiological attribute influenced by both synecological associations and autecological changes. However, in terms of genetics and biochemistry, the fundamental basis for survival fitness remains incompletely known.

In association with the rapid rate of global climate change, there are now increasing incidents of forest mortality. Global sustainability of healthy forests requires ongoing survival fitness of forest organisms, in particular that of trees. Over the last century, tree-improvement programs selected and crossed individual mother trees having desired traits, to produce seed orchards and clones for reforestation/afforestation and related purposes. However, selections of preferred genotypes were based on their growth performance under earlier environmental conditions, and cultivars were selected mainly on the basis of commercial attributes rather than on their ability to survive extreme events.

Consequently, the possibility exists that survival fitness of preferred cultivars and their progeny has been compromised, relative to wild types. The needed research remains to be done, but a solid scientific foundation to manage future forests is clearly lacking at present. This presentation reviews the current state of knowledge about these concerns and suggests future research priorities. The limits of tolerance of trees to unpredictable extreme events can begin to be estimated by subjecting seedlings to controlled environmental tests.

Keywords: adaptation; landscape genomics; survivotype; tolerance

When mortality is recognized, what immediate or futuristic remedial reaction is available?

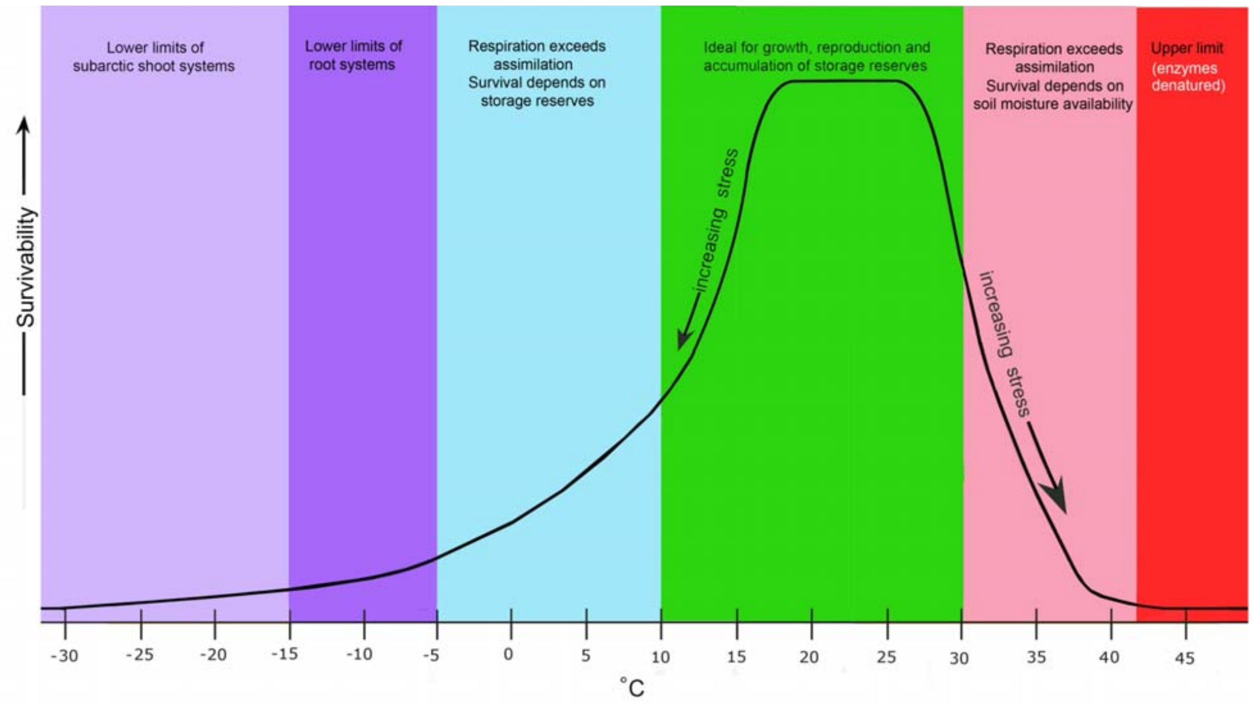


Slide 4. Here is another current (summer 2022) example of young seemingly vigorous spruce trees in southern Canada dying in their prime while neighboring ones survive. Again, both the cause of mortality and an explanation for how some individuals have survived are unknown, not obviously due to insects or pathogens. But we do know that global climate change has brought widespread and perhaps historically unprecedented environmental change, testing the tolerance levels of trees. Climate change has become the nebulous catch-all, but explanations for some trees surviving when most die are at present little more than guesses.

My main message in this talk is twofold, 1) that the scientific research to elucidate how trees tolerate environment changes remains vastly incomplete (and, therefore, data is wanting), and 2) that survivors in populations undergoing widespread mortality offer hope for forest sustainability. So, this presentation proposes that the international scientific community inaugurate a new program of tree-science research to ensure that forests will be able to tolerate extreme and aseasonal environmental tests. Such a major program is long overdue.

What follows is basically a lecture, using spruce trees as an example, to further explain this proposed paradigm shift toward truly scientific forest management.

Temperature tolerance and survivability

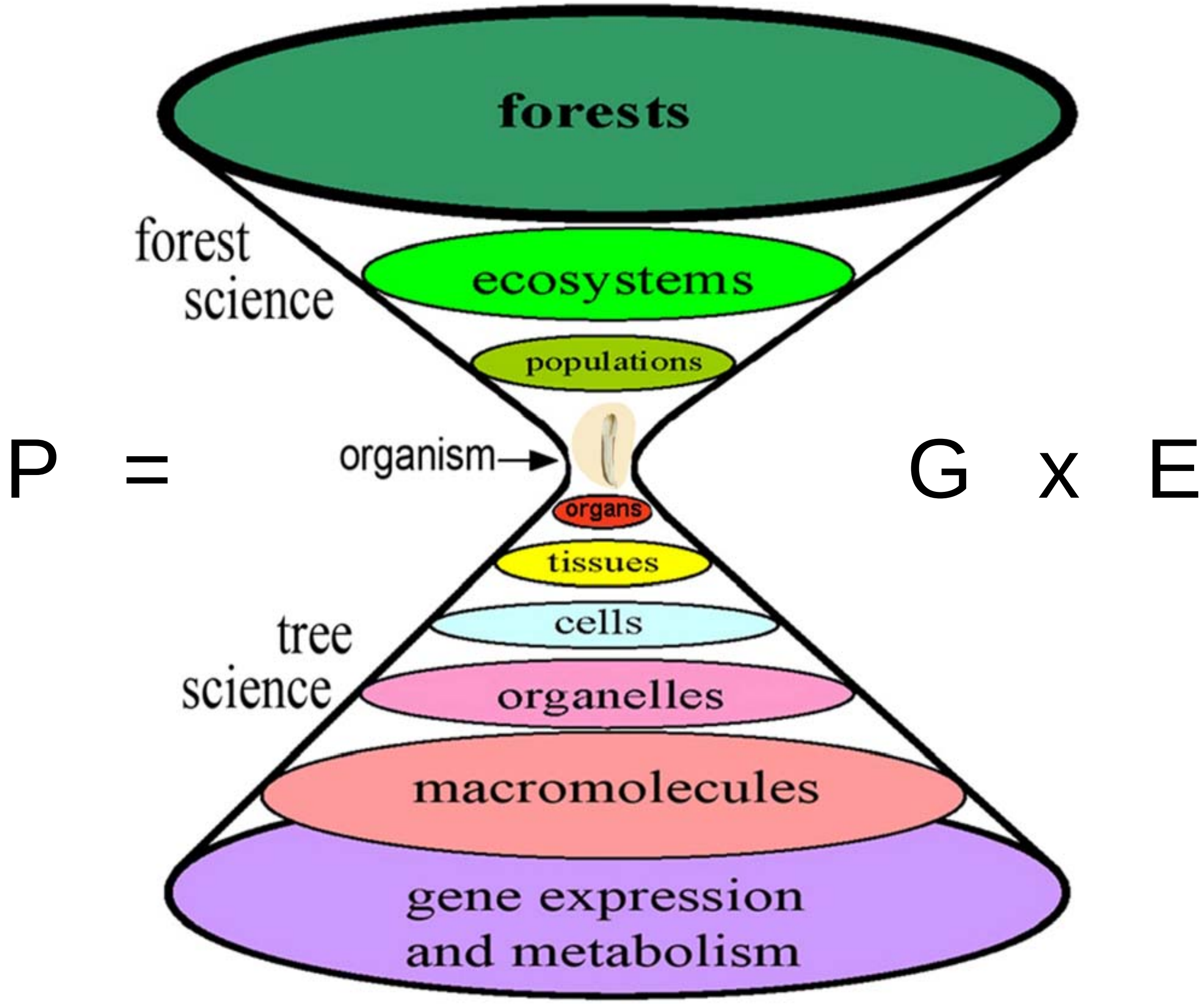


Slide 5. Environment comprises many considerations, and trees must cope with all simultaneously. This slide attempts to generalize the concept of tolerance in relation to temperature. Biological tolerance is the ability to survive unfavorable or out-of-the-ordinary environmental conditions.

Some individuals within a species are better than others at surviving sub-zero temperatures, others at surviving heat shock. This variable fitness has long been recognized in population genetics. For example, a half century ago, high levels of within-provenance and within-family variability in eucalypt seedling survival were found in response to low temperatures. But still today, the physiological, biochemical and genetic bases for the limits of tolerance varying among trees remain unresolved.

The aim of landscape genomics is to identify suitably 'adapted' planting stock to combat future mortality. However, that approach probably would not focus on the individual survivors in the mortality locations shown earlier, and it probably would assume that seeds earlier collected from those geographic regions were suitably adapted, when the subsequent mortality has revealed otherwise.

It is time to place emphasis on survivors in regions undergoing mortality, to elucidate their genes, biochemistry and overall physiology and discover how they differ from those of dying trees. As progress is made, genomics will use information diagnostic of the exceptional ones, thereby increasing confidence that planting stock is suitably adapted.



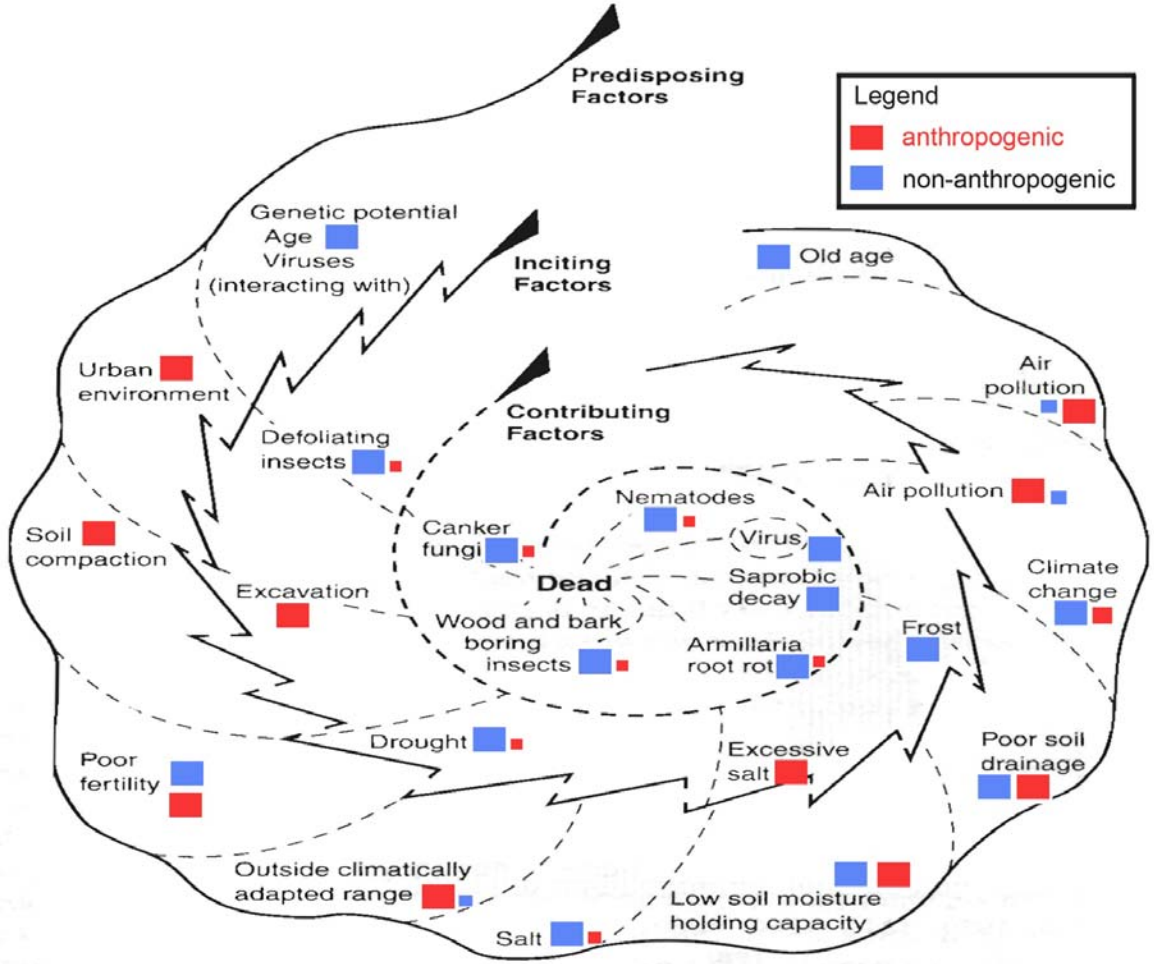
Slide 6. Genotype - environment interactions are the general explanation for biological variation, but tolerance is an invisible phenotypic trait.

I refer to the tolerance phenotype as the 'survivotype.' Similar to morphological phenotypes, survivotypes vary within a species.

Forest scientists have investigated populations and communities, trying to understand how they function and change. But identification and conservation of exceptional survivotypes remains to become an applied activity. Tree scientists have discovered how extrinsic factors influence growth and development, investigating sub-cellular phenomena at several levels. In principle, they can elucidate the basis for variable tolerances, but it is a work in progress.

In the meantime, we can recognize, conserve and learn from survivors following events of general mortality.

Paul Manion's 'decline-disease spiral' model



After PD Manion (1991) *Tree Disease Concepts*, 2nd ed., Prentice-Hall.
Red/blue indicators by RA Savidge

Slide 7: One hypothesis to explain a population undergoing mortality has trees becoming predisposed as a result of old age. However, what 'old age' actually means is uncertain. Longevity can span millennia, and so it remains uncertain if longevity is predetermined.

Other hypotheses have tree decline incited by some impairment in normal physiological functioning, or by biotic attack, resulting in weakening and a spiraling cascade of further compromises leading ultimately to death.

The problem is that until tree decline becomes overtly obvious, tree scientists for the most part remain unable to distinguish healthy versus unhealthy ones with other than speculative confidence.

Individual Tree Death

Slide 8: Isolated snags may be encountered within otherwise healthy forest communities, but scientific knowledge to do a post-mortem determination of what actually triggered dying when all around remain healthy is generally lacking.

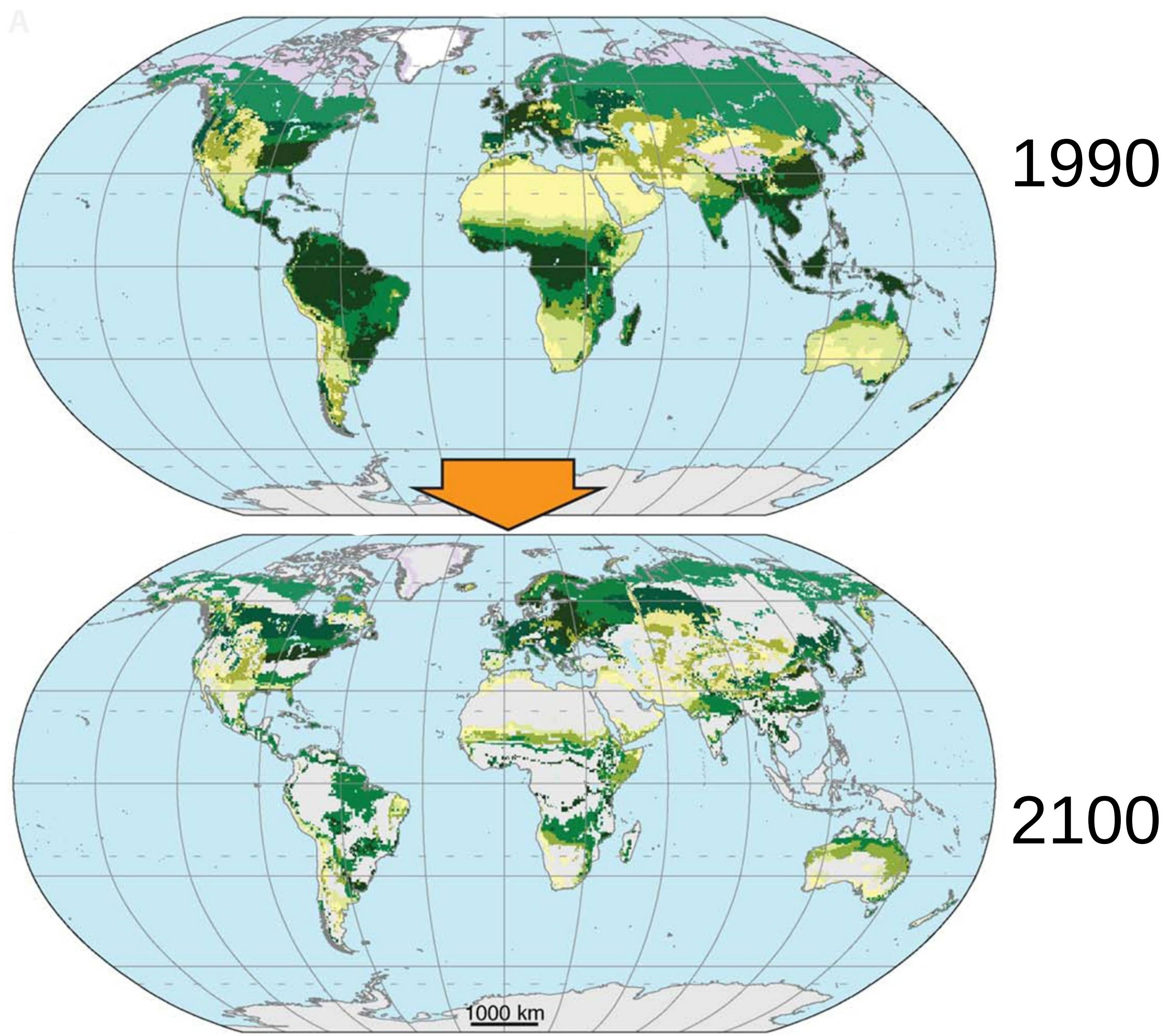
Those in silviculture use terms like ‘self-thinning’ and ‘inter-tree competition’, but they are imaginative pseudoscientific concepts having little if any value at the level of tree science for understanding or explaining the intrinsic basis for variation in survival fitness.

Projected changes in potential vegetation

Slide 9: Mortality is occurring worldwide, and predictions are that global forest biomass will be substantially reduced by the end of this century.

Natural selection has operated on forests for about 394 million years, and everywhere nature has favored diversity, in the process sustaining itself. Tree improvement programs over the last century, by their ever increasing focus on productivity genotypes, have in essence said to Mother Nature that "we know a better way." An underlying assumption evidently has been that trees superior in growth must also be at least equal to wild types in survival fitness.

But scientific evidence to support that assumption is lacking. What if fast-growing trees are actually the weaker survivotypes? For example, photosynthate is essential for growth, but it also supports biosynthesis of storage reserves and production of secondary metabolites used in defense. If storage reserves and secondary metabolites are insufficient, the so-called "improved" stock may be the more vulnerable to extreme tests of survival fitness.



Source: Allen, C. D., D. D. Breshears, and N. G. McDowell. 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* 6:129. http://dx.doi.org/10.1890/ES15-00203.1

"… tree improvement programs improve the genetic value of the population while maintaining genetic diversity." G Namkoong, K Hyun and JS Brouard (1988) *Tree Breeding : Principles and Strategies.* New York: Springer-Verlag.

"The object of all plant breeding programmes, without exception, is the production of populations that are more profitable to grow than their predecessors."
NW Simmonds (1985) Perspectives on the evolutionary history of tree crops, pp 3-13 in *Attributes of Trees as Crop Plants*, edited by MGR Cannell and JE Jackson, NERC Press.

Slide 10: Recall that forest tree improvement programs began early in the 20th century. At the outset, there was still old growth forest available to harvest. To garner needed financial support ,it was claimed that the genetic value of populations could be improved while still maintaining genetic diversity.

Initially, tree genetics and improvement did include concerns about tolerance and survival fitness but, as industry became increasingly involved, that faded and the emphasis shifted toward commercial aspects. On the assumption that the extrinsic environment next year would be more or less the same as in earlier ones, it seemed self-evident that trees superior in growth had demonstrated the needed tolerance and survival fitness.

Recall that climate change was not on the radar until recently and, even after it had become obvious, many governments sat on the fence until 1990 and later.

Improvement of 'genetic value' was proclaimed, but what is it?
And what is genetic diversity?

What is “genetic value”? genetic gain?

Slide 11: A spruce tree genome contains about 20 picograms of DNA and 28,000 genes in its 24 diploid chromosomes. But that is not how genetic value is measured. ‘Genetic value’ has been an estimation of the monetary effect of a genotype’s productivity, relative to that of wild types. ‘Breeding value’ is synonymous but refers to the value after the genome has been inherited by progeny.
‘Genetic gain’ in the final analysis is gain in genetic value.
The concept of genetic gain justified increased harvesting and removal of wild-type forest, creation of plantations and subsequent silvicultural interventions such as herbiciding and pesticiding.
It is a fact that only a miniscule fraction of the extra profits gained have been little if at all allocated to research concerned with discovery of tolerance limits and identification of superior survivotypes.

What is “genetic diversity”?

Diversity in forest ecosystems

Type of diversity	Definition
Genetic diversity	Distribution of genotypes within a population or species
Alpha diversity	Variously measured as *species richness*, or number of species in a community; *species evenness*, or distribution of relative frequencies of different species; or *structure*, the spatial arrangement of plants (clumped, uniform spacing; single- or multilayered)
Beta diversity	Local landscape diversity, measured by different communities using the same attributes as for alpha diversity
Gamma diversity	Regional diversity, measured by biome richness and evenness

source: Table 2.4 in Edmonds, RL, Agee, JK and Gara, RI 2000. *Forest Health and Protection* McGraw Hill Publ.

Slide 12: Various perspectives exist about forest diversity. What might have been included in the list shown here is physiological diversity, the varied ability among individuals – among survivotypes – to tolerate and survive the extrinsic environment.

Genetic diversity usually is explained as differences between individuals of a population in their DNA nucleotide sequences. Nucleotide differences arise primarily through mutation, allelic recombination and sexual reproduction. There are approximately 1,000 nucleotide pairs of coding sequence per gene; so, given 28,000 genes in a spruce genome, there are 28 million pairs. In principle, nucleotide differences influence the nature of gene expression, hence primary and secondary metabolism, and adaptation in terms of natural selection.

The ability to discover and evaluate genetic diversity is now robotically and computer program routine, but the methods and results provide uncertain insight into altered metabolism, into identification of superior survivotypes.

Survivotype diversity is invisible.

Slide 13: The readily visible morphological variation here is an indication of underlying genetic diversity. Most of these trees are probably more than a hundred years old, growing on permafrost at 1000 m above sea level in Yukon Eastern Beringia, in the coldest region of North America. This region has never been disturbed by forestry operations, and there are no stumps and no charcoal fragments to be found in the frozen tundra soil. Over thousands and possibly millions of years of climatic fluctuations, through natural selection the trees growing in this region acquired the fitness to sustain the population, remarkable because no other species but some dwarf birch and shrubby willows, and very recently some young aspens, have been able to establish here (despite many seed sources of other species being only a few km distant). It is not possible to know by examination of variation in morphological phenotypes, but these trees are manifestly of similar survivotype. The genomic basis for this exceptional fitness could be revealed through research.

What fitness attributes will be needed for the globe’s future forests to survive?

Should genetic gain be redefined in terms of survival fitness?

Slide 14: Variation within adaptive metabolism or survivotype diversity is the insurance policy for biosphere sustainability despite environmental change. Forest managers need to know the full range of what the planting stock can tolerate, and they presently lack such information. Comprehensive testing to establish minimum – maximum tolerance ranges needs to be done. Such research would find broad pragmatic application for establishment of future plantations, and if brought down to the level of gene expression could benefit landscape genomics enormously. In other words, I am suggesting the need for a paradigm shift in tree- improvement programs , such that genetic gain is defined in terms of survival fitness.

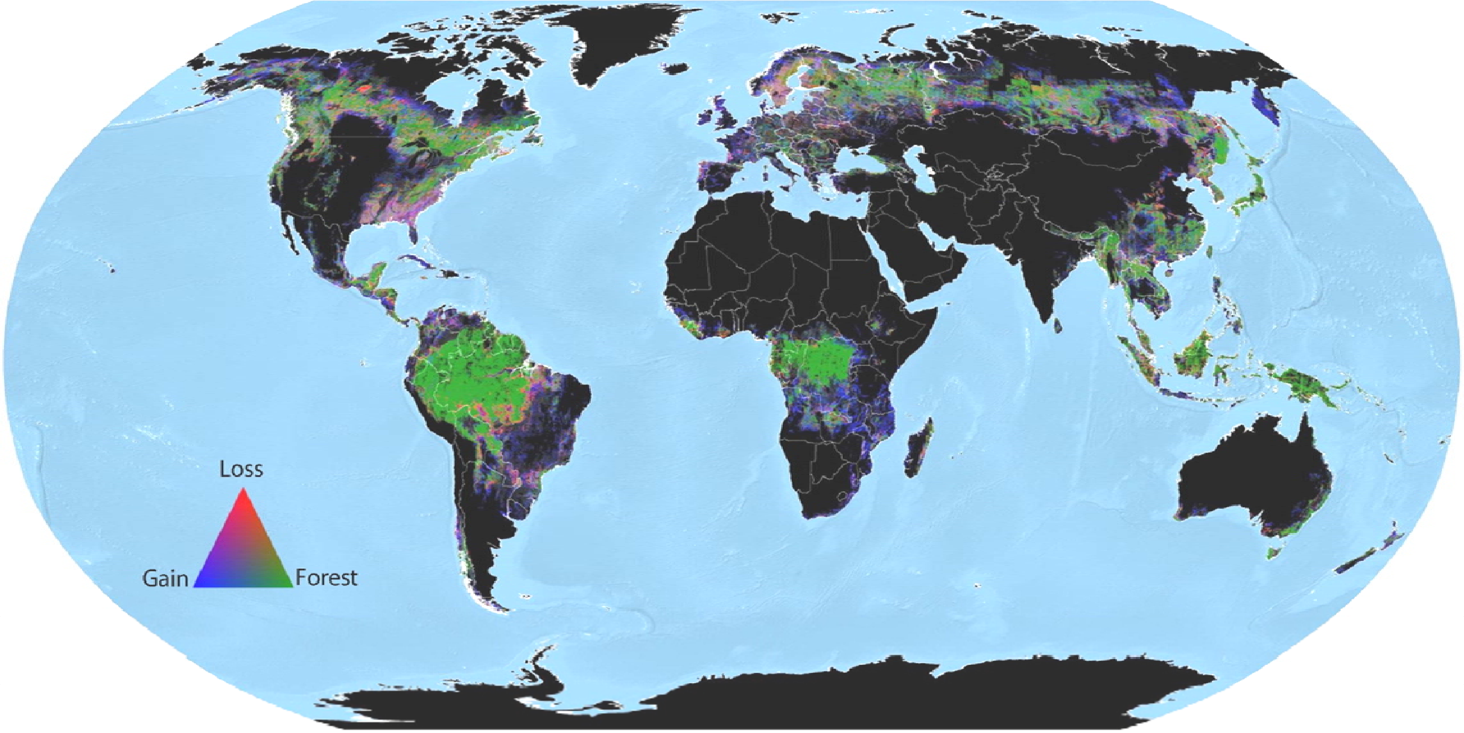
Survival value: Are plantation trees better than wild types?

Slide 15: At present the paucity of information available about how much tolerance has been gained, or lost, in fast-growing plantations is cause for concern. Abrupt inexplicable mortality is becoming increasingly common, and once a plantation begins dying, it's back to square one. Because so little information is presently available, it is difficult to envisage how landscape genomics can usefully address such threats to survival.

Some landscape genomics researchers have nevertheless suggested that appropriately adapted stock can be identified merely by mining existing genomics databases, correlating selected nucleotide loci with historical climate records, no need for garden tests. But again, one brief extreme environmental change, beyond what a geographic region has ever previously experienced, may initiate general mortality in trees presently perceived to be well adapted.

Source: thelearningplanet.files.wordpress.com/2013/03/eucalyptus-forest-plantation-lg.jpg

Is landscape genomics the answer?



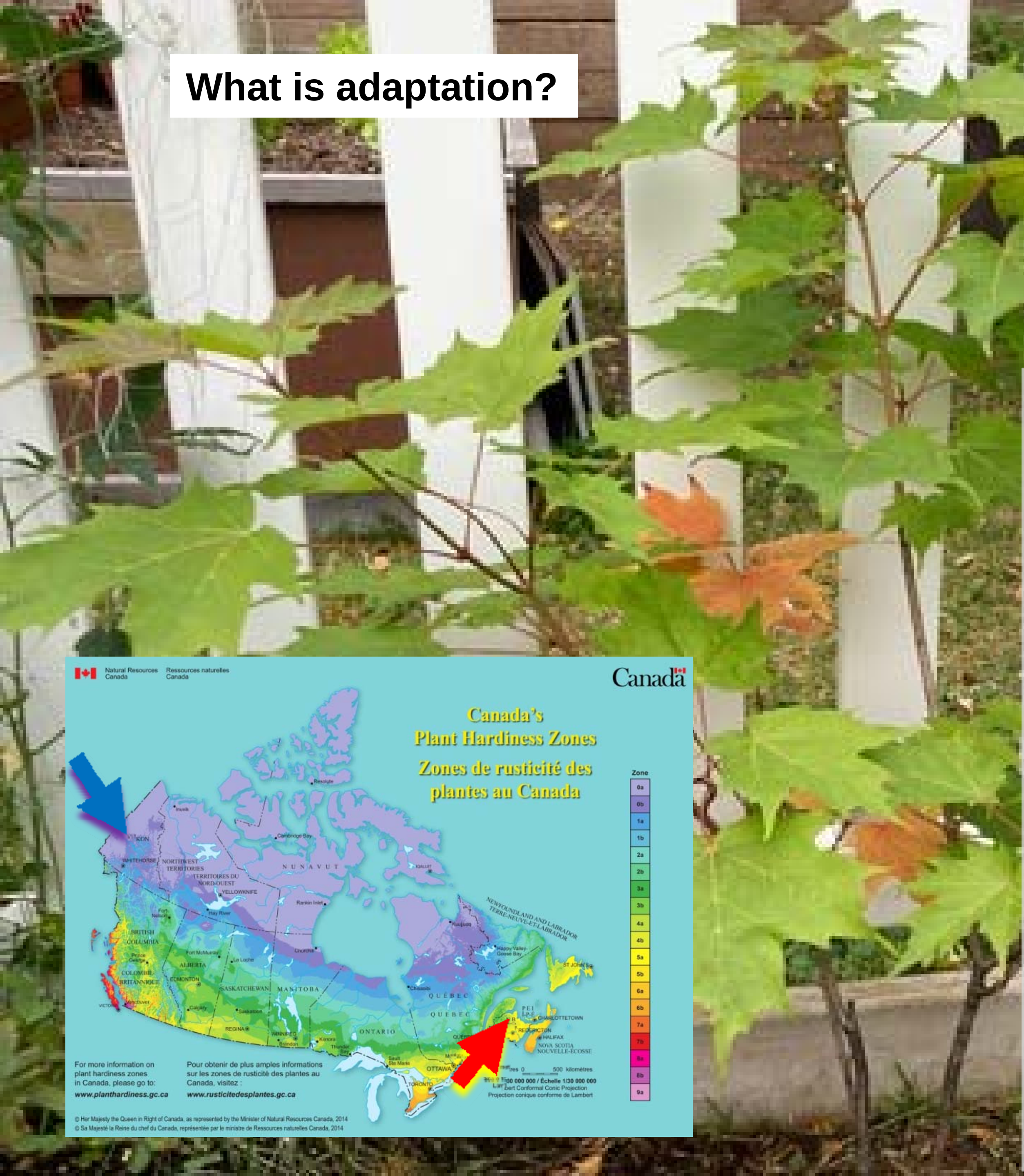
Source: Kim, D.-H., J.O. Sexton, P. Noojipady, C. Huang, A. Anand, S. Channan, M. Feng. J.R. Townshend. (2014) Global, Landsat-based forest-cover change from 1990 to 2000. *Remote Sensing of Environment* DOI: 10.1016/j.rse.2014.08.017.

Slide 16: Landscape genomics correlates individual genetic loci of population genomes with GIS locations, hence with ecoregions and climate records, the aim beig to identify hypothetically useful adaptive variation. Time and climate change will reveal if this is a wise approach, but it may be placing the cart before the horse.

One concern resides in the established fact that considerable genetic diversity can exist within the somatic tissues of an individual tree, from one organ or tissue to the next, multiple genotypes within a genotype. It is unclear whether any of that diversity is linked to survival fitness. Nevertheless, that observation has raised doubt about all past interpretations of geographic populations based on molecular genomics data, because in general a single sample from each tree has been analyzed.

Let's suppose witin-tree genetic diversity is not an overriding issue. A more fundamental concern resides in longstanding assumptions about forest dynamics.

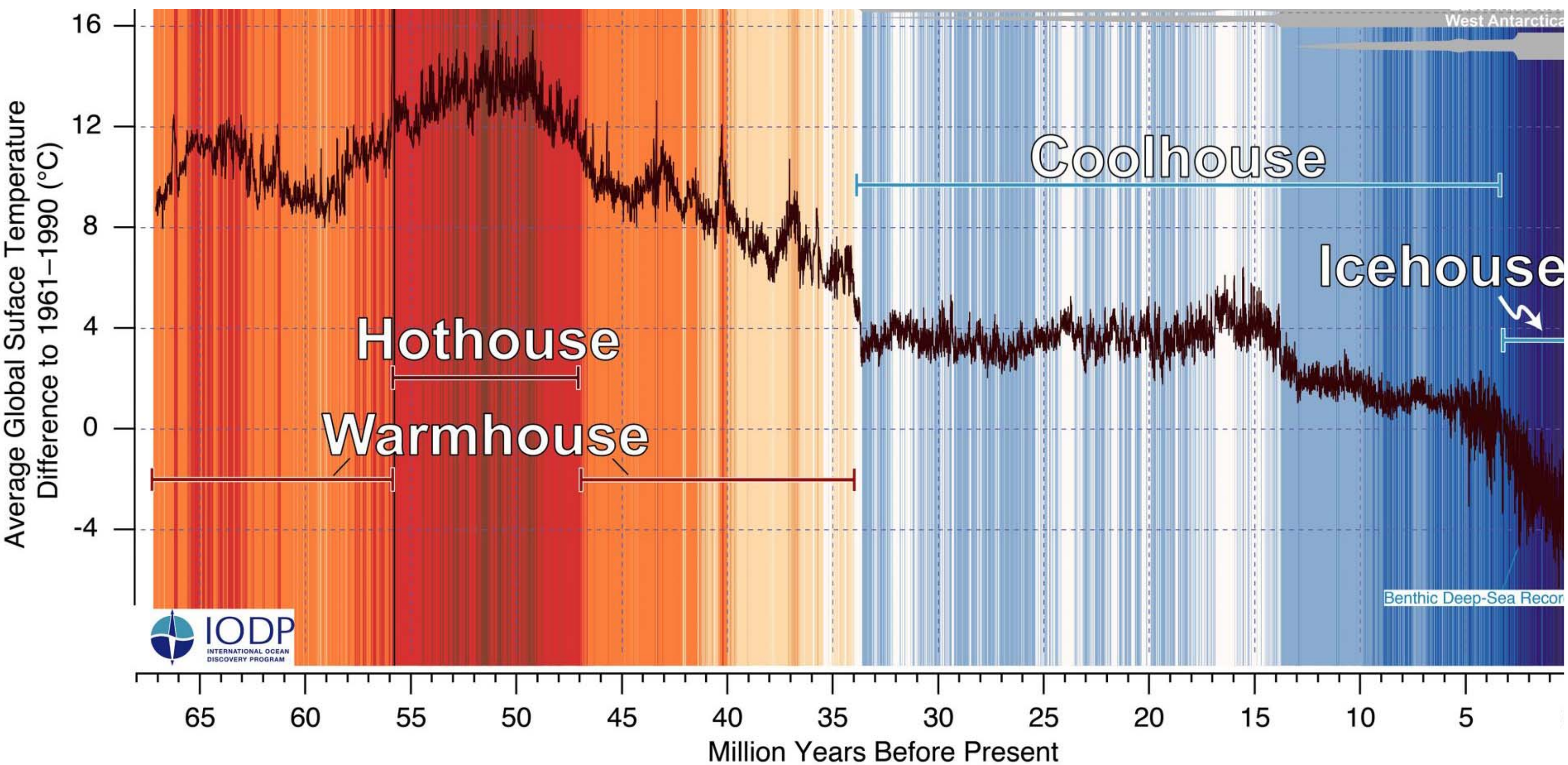
What is adaptation?



Slide 17: Plant hardiness zones as presently mapped are not, have never been, based on thorough physiological testing to discover the limits of tolerance in any species, rather on historical observations of geographic distributions and inductive assumptions about what can be tolerated.

Wild type distribution ranges mapped more than a century ago do not indicate the full adaptive competence of any tree species. For example, sugar maple has a northern hardiness limit indicated by the red arrow on this Canada plant hardiness map. In 2007, I transplanted several year-old seedlings from there to the location in Yukon indicated by the blue arrow, five hardiness zones beyond what these trees supposedly could tolerate. This photograph was taken in 2022; one has survived there for 15 years, an indication of survivotype diversity. Time will tell if it can continue to survive.

Presently healthy populations growing in locations where they are supposedly hardy may abruptly enter decline and proceed into general mortality, for no obvious reason. This inexplicble dying is on the increase around the globe. But the presence of survivors seems to be unequivocal evidence for genuine fitness, at least for the moment.

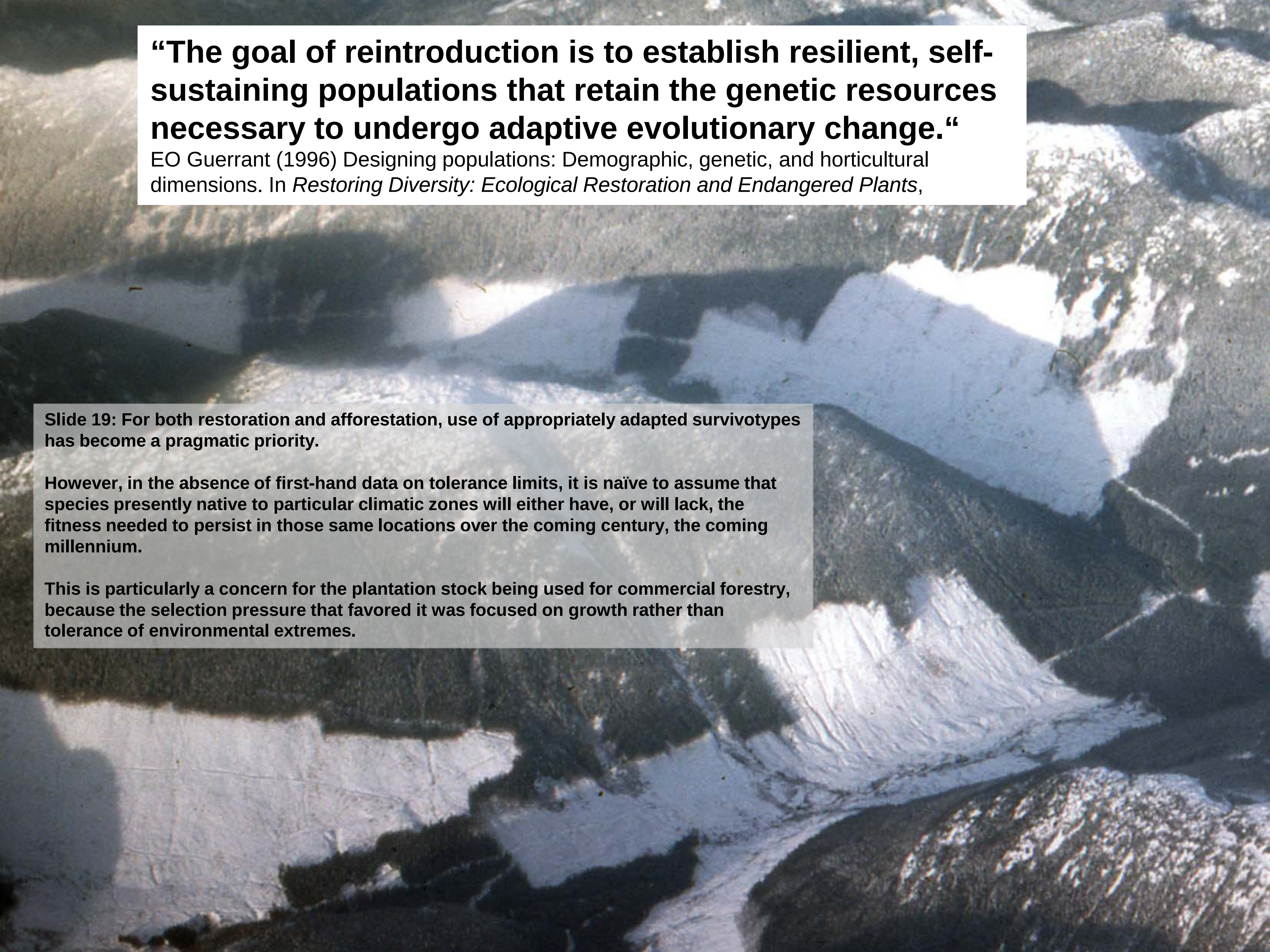


Source: T Westerhold, N Marwan, AJ Drury, D Liebrand, et a;/. (2020) An astronomically dated record of Earth's climate and its predictability over the last 66 million years. (2020) *Science* 369: 1383-1387.

Slide 18: Taking forest history to the extreme, palynological and macrofossil data indicate that our barren polar regions were forested many million of years ago. At the time, those regions were situated globally north of the Arctic circle and south of the Antarctic circle. Both broadleaved and conifer species, some similar to those now growing in temperate and subtropical regions, were present.

The global mean temperature was warmer then than now, so it is probable that polar regions were also warmer. Nevertheless, those trees had to tolerate several months of continuous winter darkness and photoperiod, light and UV phenomena quite different from anything experienced by the boreal forest or farther south. In other words, exceptional tolerance ranges may exist in some individuals of some species assumed to be intolerant, but if so they remain to be disclosed.

Forestry needs to think thousands of years into the future. Perhaps our globe will once again become a hothouse, or perhaps another ice age will begin. Either way, conservation of survivotypes capable of perpetuating the species should be the primary objective.



“The goal of reintroduction is to establish resilient, self-sustaining populations that retain the genetic resources necessary to undergo adaptive evolutionary change.“

EO Guerrant (1996) Designing populations: Demographic, genetic, and horticultural dimensions. In *Restoring Diversity: Ecological Restoration and Endangered Plants*,

Slide 19: For both restoration and afforestation, use of appropriately adapted survivotypes has become a pragmatic priority.

However, in the absence of first-hand data on tolerance limits, it is naïve to assume that species presently native to particular climatic zones will either have, or will lack, the fitness needed to persist in those same locations over the coming century, the coming millennium.

This is particularly a concern for the plantation stock being used for commercial forestry, because the selection pressure that favored it was focused on growth rather than tolerance of environmental extremes.

Tolerance limits can be discovered.

Slide 20: Tolerance limits of individual genotypes in relation to extreme and abrupt environmental change can be discovered by testing seedlings in controlled environment settings. Research along this line has been done for many decades with greenhouse seedlings, to determine their readiness to survive outdoors in nurseries and for out-planting, but the focus has been on stock improved for growth rate rather than to discover exceptional survivotypes.

It is time to focus on survivors in populations undergoing widespread mortality. Vegetative propagation of them in support of replicate testing would be essential.

It may well be that superior survivotypes will not be superior growers, and vice versa, but with such knowledge forest managers will be in a position to lean in favor of sustainability, or to risk it in favor of productivity. And, again, the tolerance limits found for survivors in regions of population mortality will establish baseline criteria against which presently favored plantation stock could be compared.

Knowing the genetic basis for the tolerance limits will enable landscape genomics to focus on loci that are reliably indicative of survival fitness.

Forestry cannot purport to be a profession of stewardship if it continues to assume that the extrinsic environment experienced by trees will be, in this or the next century, in the next millennium or further in the future, anything like that of the last century.

Slide 21: To summarize, forestry cannot purport to be a profession of stewardship if it continues to assume that the extrinsic environment experienced by trees will be, in this or the next century, in the next millennium or further in the future, anything like that of the last century.

Although the sustainability of the global forest is in question because of uncertainty about the impact of future environmental change on our forests, this can be viewed in a positive light because climate change has provided a wakeup call for scientifically well-founded knowledge and action to be achieved. Research to authenticate tolerance ranges and limits should be initiated without delay. There is an immense amount of research remaining to be done.

This concludes my presentation.

Acknowledgement: University of New Brunswick Libraries provided access to its resources.