Commentary

Dendroecology meets genomics in the common garden: new insights into climate adaptation

In this issue of *New Phytologist* (pp. 630–645), Housset *et al.* bring together old and new tools to address an important global change problem: they combine a common garden experiment, association genetics, and dendroecology to gauge the adaptation of trees to climate variation, laying the foundation for a genotype-to-phenotype-level approach to managing forests of the future. Better anticipation and management of the effects of climate change on forests qualifies as one of the grand scientific and natural resource management challenges of the twenty-first century: among other ecosystem services, forests play an important role in the global carbon cycle, having sequestered approximately 30% of the excess greenhouse gasses added to the atmosphere by humans over the period 1959–2015 (Le Quéré *et al.*, 2016). Trees are locally adapted with respect to climate (as are all organisms), and risk becoming maladapted if the rate of climate change exceeds their capacity to respond through migration, plasticity or *in situ* evolutionary adaptation. Maintaining key ecosystem services provided by forests thus involves adaptation in two senses of the word: better understanding the basis for *evolutionary adaptation* to climate in trees to help develop *climate adaptation strategies* – i.e. management actions that can be taken to mitigate the negative effects of climate change.

> '*Altogether, Housset* et al. *link genotype, phenotype, and environment in an unique way by treating response to climate – considered at three timescales – as traits.*'

Something old

Common garden experiments have a long history in ecology: Turesson (in the 1920s) and Clausen, Keck, and Heisey (in the 1940–1950s) investigated population differentiation, local adaptation, and their genetic underpinning, establishing that

climatic factors shape adaptive traits in wild species (Aitken & Bemmels, 2016). Forestry provenance trials, including common garden and partial reciprocal transplant designs, pre-date these seminal studies in ecological genetics by some 200 years and have long been used to examine local adaptation to climate (Aitken & Bemmels, 2016). More recently, they have been repurposed towards the development of climate adaptation strategies (Alberto *et al.*, 2013).

Something new

Genomic sequencing technologies have sparked excitement about the potential to link variation at specific genetic loci to variation of important phenotypes. Entire genome sequences from many individuals can be used to test correlations between each locus and phenotypes of interest (genome-wide association studies, or GWAS). Most genetically-based traits of interest in trees are likely controlled by many genes, thus genome-wide approaches offer a more complete picture than traditional approaches sequencing just a few genes (Savolainen *et al.*, 2007; McKown *et al.*, 2014). Genomic tools, such as reference genome sequences and single nucleotide polymorphism (SNP) sets, are now available for a number of forest tree species to apply GWAS. Genotype–phenotype association (GPA) studies in trees so far, ranging from dozens to thousands of loci (Eckert *et al.*, 2009; McKown *et al.*, 2014), have pointed to specific genes underlying adaptive trait variation, and these results are being aligned with genotype–environment and phenotype–environment associations to establish robust links between genotypes, phenotypes, and environment (Sork *et al.*, 2013; Bragg *et al.*, 2015).

Something old and new

Annual growth rings are an old source of information on the growth of trees that are enjoying a renaissance of new uses. The increment borer was invented in a forestry context in the mid-nineteenth century. Since then, tree-ring time series have been used to date events, reconstruct past climate, investigate forest disturbance processes and stand dynamics, and most recently, tree physiological processes (Fonti *et al.*, 2010; Eilmann *et al.*, 2014; Weigt *et al.*, 2017) and global carbon cycle-related questions (Babst *et al.*, 2014). The ability to generate multi-decade to multi-century time series of individual performance with annual or sub-annual resolution, and hence analyze a tree's response to climate variation across this range of timescales, make tree-ring data an exceptional resource for addressing global change questions.

Bringing these three elements together, Housset *et al.* used tree-ring data collected in a forestry provenance trial to identify climatic constraints on growth and evaluate local adaptation; tree-ring-derived growth metrics were then associated with

This article is a Commentary on Housset *et al.*, **218**: 630–645.

SNPs. In particular, the novelty of Housset *et al.*'s GPA study is their choice of 'phenotypes'. Most GPA studies in trees have focused on phenotypes measured at a single time point. Housset *et al.* realized that trees contain much more information about climate response in their annual growth rings. Three growth metrics – average growth over the period 1993–2014, growth anomaly in response to particularly cold autumn and spring temperatures in 2002–2003, and the sensitivity of growth to monthly climate variables – were treated as phenotypes. These phenotypes were then associated with (1) mean annual temperature of the provenances, revealing clinal variation indicative of local adaptation (Fig. 1), and (2) genetic variants (SNPs) at loci with previously-demonstrated links to local climate adaptation. Altogether, Housset *et al.* link genotype, phenotype, and environment in an unique way by treating response to climate – considered at three timescales – as traits.

Notably, the fastest-growing provenance in the common garden was not the local one, rather a more southern, warmer provenance (a pattern corroborated in a meta-analysis by A. Angert *et al.*, unpublished). This suggests that the effects of global warming on performance are already in progress – i.e. local phenotypes (and their underlying genotypes) are showing signs of maladaptation. While assisted migration is one potential tool to address such local maladaptation, it carries the risk of missing the mark if genotypes are moved too far, too fast (Aitken & Whitlock, 2013). Complex geographic clines in adaptive traits, poor understanding of the genetic mechanisms underlying species' responses, and uncertainties in the sign and magnitude of projected climate change further make the design of assisted migration a challenging task. Indeed,

Housset *et al.* found opposing geographic clines of cold and drought sensitivity (Fig. 1; see also Montwé *et al.*, 2015). Southern provenances were more tolerant of summer drought, but they were also more negatively impacted by a particularly cold autumn and spring. Simply moving provenances north may not be successful if they will be exposed to climatic stresses (cold) to which they are not adapted. Extreme events of all kinds are projected to increase in intensity and frequency (Sillmann *et al.*, 2013). It should also be kept in mind that abiotic (climatic) factors are not the only ones influencing fitness in wild populations – interactions between trees and insect pests are also expected to change with climate (Logan *et al.*, 2003). Understanding the genetic mechanisms underlying adaptation to climate – e.g. drought tolerance, cold hardiness, and phenological traits that influence insect outbreaks – may be necessary to develop novel phenotype combinations for successful poleward transplanting, including adaptation to future 'no-analog' climates.

Housset *et al.* have set the stage for the analysis of additional loci and tree-ring traits. Their GPA study included a relatively modest set of loci, and because of large tree genomes and polygenic traits, such targeted sequencing methods likely miss many of the genetic loci underpinning trait variation. In the future, more exhaustive GWAS will capture more of that underlying genetic variation. Other tree-ring traits can provide insight into tree physiology (i.e. water and carbon dynamics) and deepen our mechanistic understanding of adaptation to climate. Wood anatomical traits, such as cell lumen area and cell wall thickness, offer information on resistance to drought- or frost-induced cavitation, as well as xylem plasticity (Eilmann *et al.*, 2014). Together with stable isotope ratios of $\delta^{18}O$ and $\delta^{13}C$, which reflect stomatal response to environmental conditions and water-use efficiency (Gessler *et al.*, 2014; Weigt *et al.*, 2017), the water-use strategies of trees can be quantified and associated with genetic variation (M. Isaac-Renton *et al.*, unpublished). Plasticity, in particular, is a poorly understood and poorly studied aspect of adaptive capacity (Nicotra *et al.*, 2015) that tree rings offer an excellent window into, since they record the response of a given genotype to time-varying environmental conditions. Tree-ring time series also offer a window into how climate sensitivities might change over the lifetime of a tree, i.e. the environmental conditions necessary for regeneration vs adult persistence (*sensu* Grubb, 1977).

The linkages between genotype, phenotype, and environment afforded by associating genetic variation with tree-ring traits in a forestry provenance context have the potential to eventually support genetic-based species distribution modeling. Ecophysiological models of tree growth that are parameterized with climate, tree-ring, and other data – e.g. the Vaganov-Shaskin model (or VSLite; Tolwinski-Ward *et al.*, 2011) and sink-limited growth models (Fatichi *et al.*, 2014) – can be linked to the genes responsible for tree-ring and other traits. Such a genetically-informed ecophysiological model could then be used to project performance spatially and forward in time as a function of future climate conditions (Sork *et al.*, 2013; Weinig *et al.*, 2014). Predicting the performance of novel genotypes in novel (no-analog) climates will be difficult, but likely necessary.
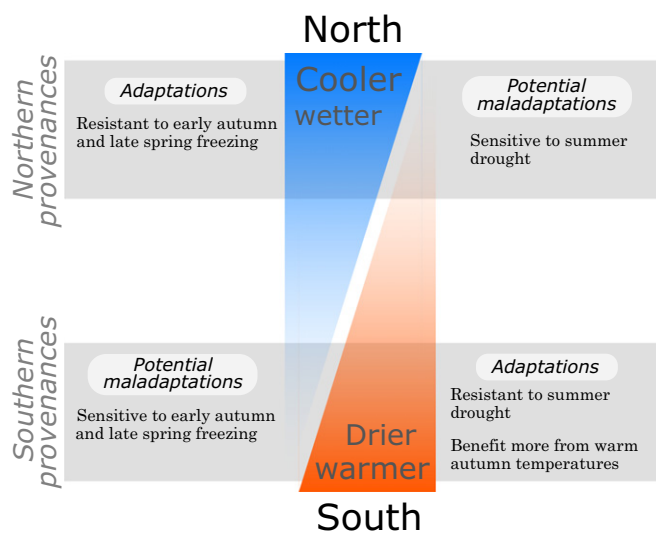

Fig. 1 Using tree-ring data from a forestry provenance trial, Housset *et al.* (in this issue of *New Phytologist*, pp. 630–645) found opposing geographic clines of drought and cold tolerance in *Pinus strobus*. Northern vs southern provenances evidenced both adaptation to local climate and the potential for maladaptation if moved (via assisted migration) against latitudinal climatic gradients. The ability to detect responses to climate variation on fine timescales – season and extreme variability – makes tree-ring-derived traits an appealing tool for investigating adaptation to climate and its genetic underpinning.

Combining the tools and talents of foresters, geneticists, dendroecologists, and physiologists will advance our understanding of climate-adaptive genetic variation in trees, how it varies in natural landscapes, and constraints to adaptation or tolerance. Only with the deeper insights gained from such interdisciplinary research will we be able to better assess population vulnerability and develop management priorities for sourcing seeds in a changing world (Aitken & Whitlock, 2013; Alberto *et al.*, 2013; Fitzpatrick & Keller, 2015) – for trees, crops, culturally-significant native plants and biodiversity as a whole.

Margaret E. K. Evans[1,2]*, **Paul F. Gugger**[3], **Ann M. Lynch**[1,4],
Christopher H. Guiterman[1], **Joshua C. Fowler**[1,2],
Stefan Klesse[1] and **Erin C. Riordan**[5]

[1]Laboratory of Tree-Ring Research, University of Arizona, Tucson, AZ 85721, USA;
[2]Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA;
[3]Appalachian Laboratory, University of Maryland Center for Environmental Science, Frostburg, MD 21532, USA;
[4]US Forest Service, Rocky Mountain Research Station, Tucson, AZ 85721, USA;
[5]Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095, USA
(*Author for correspondence: tel +1 520 621 0778;
email mekevans@email.arizona.edu)

References

Aitken SN, Bemmels JB. 2016. Time to get moving: assisted gene flow of forest trees. *Evolutionary Applications* 9: 271–290.

Aitken SN, Whitlock MC. 2013. Assisted gene flow to facilitate local adaptation to climate change. *Annual Review of Ecology, Evolution, and Systematics* 44: 367–388.

Alberto FJ, Aitken SN, Alia R, Gonzalez-Martinez SC, Hanninen H, Kremer A, Lefevre F, Lenormand T, Yeaman S, Whetten R *et al.* 2013. Potential for evolutionary responses to climate change – evidence from tree populations. *Global Change Biology* 19: 1645–1661.

Babst F, Alexander MR, Szejner P, Bouriaud O, Klesse S, Roden J, Ciais P, Poulter B, Frank D, Moore DJP *et al.* 2014. A tree-ring perspective on the terrestrial carbon cycle. *Oecologia* 176: 307–322.

Bragg JG, Supple MA, Andrew RL, Borevitz JO. 2015. Genomic variation across landscapes: insights and applications. *New Phytologist* 207: 953–967.

Eckert AJ, Bower AD, Wegrzyn JL, Pande B, Jermstad KD, Krutovsky KV, Clair JBS, Neale DB. 2009. Association genetics of coastal Douglas fir (*Pseudotsuga menziesii* var. *menziesii*, Pinaceae). I. Cold-hardiness related traits. *Genetics* 182: 1289–1302.

Eilmann B, Sterck F, Wegner L, de Vries SMG, von Arx G, Mohren GMJ, den Ouden J, Sass-Klaassen U. 2014. Wood structural differences between northern and southern beech provenances growing at a moderate site. *Tree Physiology* 34: 882–893.

Fatichi S, Leuzinger S, Korner C. 2014. Moving beyond photosynthesis: from carbon source to sink-driven vegetation modeling. *New Phytologist* 201: 1086–1095.

Fitzpatrick MC, Keller SR. 2015. Ecological genomics meets community-level modelling of biodiversity: mapping the genomic landscape of current and future environmental adaptation. *Ecology Letters* 18: 1–16.

Fonti P, von Arx G, Garcia-Gonzalez I, Eilmann B, Sass-Klaassen U, Gartner H, Eckstein D. 2010. Studying global change through investigation of the plastic responses of xylem anatomy in tree rings. *New Phytologist* 185: 42–53.

Gessler A, Ferrio JP, Hommel R, Treydte K, Werner RA, Monson RK. 2014. Stable isotopes in tree rings: towards a mechanistic understanding of isotopic fractionation and mixing processes from the leaves to the wood. *Tree Physiology* 34: 796–818.

Grubb PJ. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews* 52: 107–145.

Housset JM, Nadeau S, Isabel N, Depardieu C, Duchesne I, Lenz P, Girardin MP. 2018. Tree rings provide a new class of phenotypes for genetic associations that foster insights into adaptation of conifers to climate change. *New Phytologist* 218: 630–645.

Le Quéré C, Andrew RM, Canadell JG, Sitch S, Korsbakken JI, Peters GP, Manning AC, Boden TA, Tans PP, Houghton RA *et al.* 2016. Global carbon budget 2016. *Earth System Science Data* 8: 605–649.

Logan JA, Regniere J, Powell JA. 2003. Assessing the impacts of global warming on forest pest dynamics. *Frontiers in Ecology and the Environment* 1: 130–137.

McKown AD, Klápště J, Guy RD, Geraldes A, Porth I, Hannemann J, Friedmann M, Muchero W, Tuskan GA, Ehlting J *et al.* 2014. Genome-wide association implicates numerous genes underlying ecological trait variation in natural populations of *Populus trichocarpa*. *New Phytologist* 203: 535–553.

Montwé D, Spiecker H, Hamann A. 2015. Five decades of growth in a genetic field trial of Douglas-fir reveal trade-offs between productivity and drought tolerance. *Tree Genetics & Genomes* 11: 29.

Nicotra AB, Beever EA, Robertson LA, Hofmann GE, O'Leary J. 2015. Assessing the components of adaptive capacity to improve conservation and management efforts under global change. *Conservation Biology* 29: 1268–1278.

Savolainen O, Pyhajarvi T, Knurr T. 2007. Gene flow and local adaptation in trees. *Annual Review of Ecology Evolution and Systematics* 38: 595–619.

Sillmann J, Kharin VV, Zwiers FW, Zhang X, Bronaugh D. 2013. Climate extremes indices in the CMIP5 multimodel ensemble: Part 2. Future climate projections. *Journal of Geophysical Research: Atmospheres* 118: 2473–2493.

Sork VL, Aitken SN, Dyer RJ, Eckert AJ, Legendre P, Neale DB. 2013. Putting the landscape into the genomics of trees: approaches for understanding local adaptation and population responses to changing climate. *Tree Genetics & Genomes* 9: 901–911.

Tolwinski-Ward SE, Evans MN, Hughes MK, Anchukaitis KJ. 2011. An efficient forward model of the climate controls on interannual variation in tree-ring width. *Climate Dynamics* 36: 2419–2439.

Weigt RB, Streit K, Saurer M, Siegwolf RTW. 2017. The influence of increasing temperature and CO_2 concentration on recent growth of old-growth larch: contrasting responses at leaf and stem processes derived from tree-ring width and stable isotopes. *Tree Physiology* 29: 1–15.

Weinig C, Ewers BE, Welch SM. 2014. Ecological genomics and process modeling of local adaptation to climate. *Current Opinion in Plant Biology* 18: 66–72.