Tansley review

'Chimes of resilience': what makes forest trees genetically resilient?

Authors for correspondence:
Antoine Kremer
Email: antoine.kremer@inrae.fr

Martin Lascoux
Email: martin.lascoux@ebc.uu.se

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Antoine Kremer[1], **Jun Chen**[2] **and Martin Lascoux**[3]

[1]UMR BIOGECO, INRAE, Université de Bordeaux, Cestas, 33612, France; [2]College of Life Sciences, Zhejiang University, Hangzhou, 310058, China; [3]Department of Ecology and Genetics, Evolutionary Biology Centre, Uppsala University, Uppsala, SE-75236, Sweden

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Summary

Forest trees are foundation species of many ecosystems and are challenged by global environmental changes. We assemble genetic facts and arguments supporting or undermining resilient responses of forest trees to those changes. Genetic resilience is understood here as the capacity of a species to restore its adaptive potential following environmental changes and disturbances. Importantly, the data come primarily from European temperate tree species with large distributions and consider only marginally species with small distributions. We first examine historical trajectories of trees during repeated climatic changes. Species that survived the Pliocene–Pleistocene transition and underwent the oscillations of glacial and interglacial periods were equipped with life history traits enhancing persistence and resilience. Evidence of their resilience also comes from the maintenance of large effective population sizes across time and rapid microevolutionary responses to recent climatic events. We then review genetic mechanisms and attributes shaping resilient responses. Usually, invoked constraints to resilience, such as genetic load or generation time and overlap, have limited consequences or are offset by positive impacts. Conversely, genetic plasticity, gene flow, introgression, genetic architecture of fitness-related traits and demographic dynamics strengthen resilience by accelerating adaptive responses. Finally, we address the limitations of this review and highlight critical research gaps.

I. Introduction

All organisms have experienced repeated climate changes and environmental disturbances during their evolutionary history, and this constitutes a natural testing ground of their resilience.

Resilience is a broadly used word these days, and a definition is in order here to avoid misunderstandings. We extend Holling's (1973) broad definition of ecosystem resilience and of the forest resilience concepts (Anderson-Teixeira *et al.*, 2013; Nikinmaa *et al.*, 2020) to the genetic level of forest trees, as the

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capacity of a woody species to withstand or to recover from adverse ecological conditions and disturbances by maintaining its adaptive potential. Such constraints can be generated by extreme events (e.g. earthquakes, frost spells, droughts, windstorms and pest outbreaks) or result from steadily increasing stress due to biotic or abiotic continuous directional changes. Whatever the cause, a resilient species would be more likely to avoid extinction during adverse ecological periods and recover and thrive as more favorable conditions return. Importantly, our understanding of resilience does not assume return to the predisturbance state of the species, but its capacity to evolve and eventually adapt to postdisturbance conditions. Evolutionary trajectories leading to resilience thus encompass genetic rescue by natural means, that is without any human restoration, and adaptation and bring into play genetic as well as demographic processes. Concerns about resilience are today raised most often for trees in the context of climate change (Dymond *et al.*, 2014; Nikinmaa *et al.*, 2024). It has become common place to state that trees, in general, and forest trees in particular, are ill-equipped to face climate change, the main argument being that their long generation time will prevent them from adapting fast enough to a rapid climate change (Aitken *et al.*, 2008; Bisbing *et al.*, 2021), although earlier reports supported rapid microevolution (Petit & Hampe, 2006; Kremer, 2007). Concerns were further reinforced by reports of increasing forest tree mortalities following repeated drought events (Allen *et al.*, 2015; Changenet *et al.*, 2021; George *et al.*, 2022). In this review, we attempt to assemble genetic facts and arguments supporting or undermining resilient responses of trees, focusing primarily on species of the Northern Hemisphere.

It is important to state outright that we are in no way questioning the need to take urgent actions against ongoing climate change. Also, it is worth stressing that, while emphasis is on resilience to climatic change, forest trees also have to be resilient to a host of biotic factors. As a matter of fact, as witnessed by the ash dieback in Europe or the chestnut blight dieback of the American chestnut, some of the greatest recent threats experienced by forest trees did not come from climate change but from the spread of diseases and pests. However, the genetic characteristics of trees that allow for rapid adaptation to climate change should also facilitate adaptation to biotic agents of selection.

Our review proceeds in two steps. In the first part, we will draw lessons from the past. Trees have experienced dramatic and repeated climatic changes during the Late Pleistocene at different time scales (Rull, 2020; Huntley *et al.*, 2023), and their trajectories have been well reconstructed using complementary disciplines such as palynology, phylogeography and population genetics (Petit *et al.*, 2005; Gavin *et al.*, 2014; Birks & Tinner, 2016; De Lafontaine *et al.*, 2018; Milesi *et al.*, 2024). What does the evolutionary history of individual tree species tell us? Were forest trees particularly vulnerable during adverse climatic periods? Can one observe shared features of tree responses to climatic changes, or, instead, were those responses to climate change primarily idiosyncratic? We will focus on species of the Northern Hemisphere and, more specifically, on Europe, as it was strongly affected by glaciation and is the part of the world we are most familiar with. However, we will also consider other geographic areas, especially when those offer an interesting contrast with Europe. Importantly, we mostly will not consider large groups of tree species, such as insect-pollinated tropical trees, which often have limited distributions, and to which some of our conclusions may not apply. With a few exceptions (Eucalypts and acacias *sensu* largo), these species remain understudied in view of their ecological importance.

In the second part of our review, we will revisit conclusions inferred from contemporary studies of key genetic mechanisms either constraining or shaping resilient responses across spatiotemporal scales. Large genetic surveys have been conducted during the last decades in widely distributed tree species, highlighting contrasting distributions of neutral and adaptive diversity across ecological gradients (Alberto *et al.*, 2013; Leites & Benito Garzon, 2023). Similarly, genetic and genomic studies, both intensive and comparative, conducted in breeding and natural populations have enriched our understanding of the genetic, mating and dispersal systems of trees and their functioning in different ecological settings (Austerlitz *et al.*, 2004; González-Martínez *et al.*, 2006; Savolainen *et al.*, 2007). What have we learned from different species about the factors that may have triggered or limited resilience? Which evolutionary processes are at stake during recovery from the contemporary ecological crisis? Finally, we will conclude by addressing current challenges and future prospects.

II. Lessons from the past

1. Legacies of the Pleistocene

Woody floras underwent severe climatic and macroecological events since the Late Pliocene. In the Northern Hemisphere, these climatic fluctuations resulted in a succession of extinctions followed by repeated sequences of extreme demographic expansions and contractions of the remaining species. At the Pliocene–Pleistocene transition (*c.* 2.6 million years ago (Ma)), the climate in the Northern Hemisphere changed dramatically with the onset of the glacial-interglacial cycles, resulting in large-scale extinction of trees, especially in Europe (Rull, 2020). The modern flora represents less than 30% of the tree genera present during the Tertiary (Latham & Ricklefs, 1993; Eiserhardt *et al.*, 2015) and species that went extinct were widespread before their disappearance (Magri *et al.*, 2017). During and following these extinctions, the remnant species retracted and expanded their distributions in response to the oscillations of glacial and interglacial periods (Box 1).

While extinctions selectively eliminated cold-sensitive species (Svenning, 2003), an additional selective filtering took place in the aftermath of extinction. Post-extinction scenarios involve replacement and diversification dynamics associating the expansion of preexisting species, evolution of new taxa and invasion by nonlocal species (Jablonski, 2001, 2008). In the case of the Pliocene–Pleistocene (5 Ma to *c.* 0.8 thousand years ago (ka), Box 1) extinction of trees, replacement dynamics with preexisting species sharing invasiveness attributes dominated. Indeed, surviving species rapidly colonized southern Europe, as the overall forested area had only slightly decreased during the extinction (Magri *et al.*, 2017), thus suggesting the expansion of preexisting local species. These new species shared invasiveness attributes such as

Box 1. Climate variations and tree extinctions during the Pliocene–Pleistocene

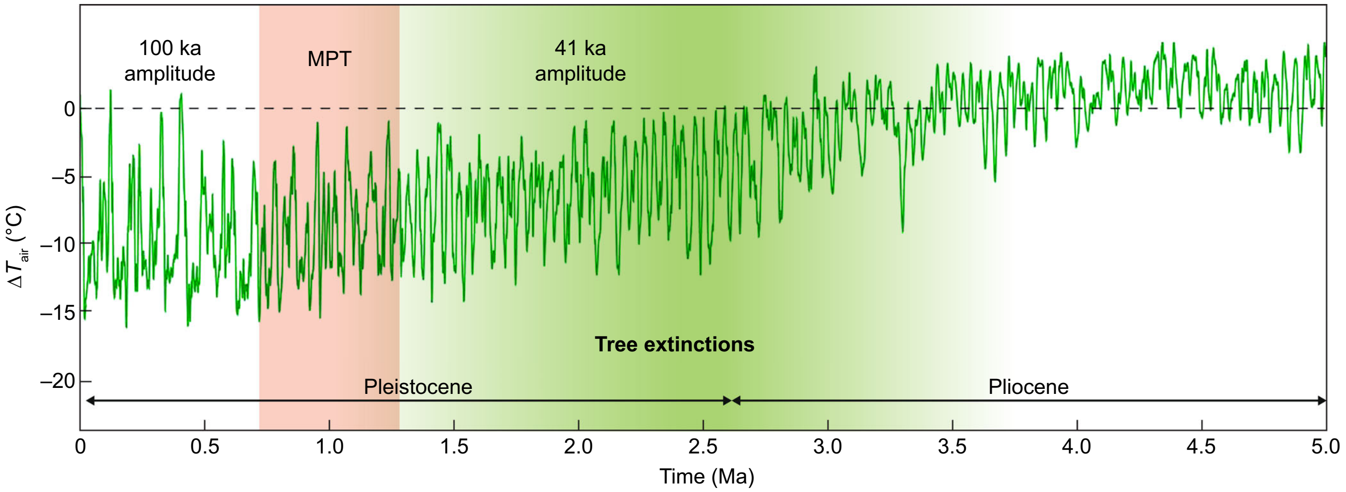

Fig. B1 Climate variations and tree extinctions during the Pliocene–Pleistocene transition. The graph represents the variation of the surface–air temperature anomaly (Δ_{air}(°C)) over Antarctica reconstructed from changes in benthic oxygen isotope records ($\delta^{18}O$). From data in De Boer *et al*. (2014).

During the Late Pliocene, global temperatures were *c*. 2–4°C warmer than during the preindustrial period (Solomon *et al*., 2007), and seasonal climatic rhythms became more pronounced with dryer summers and cooler winters. Temperatures continued to drop with the emergence of the Pleistocene glacial–interglacial cycles (2.6 Ma), causing generalized dryer and cooler conditions with contrasted seasons during the glacial periods, and moister and warmer conditions during interglacial periods. During the earlier cycles, temperatures during the interglacial periods were still warmer than today. During the Mid-Pleistocene Transition (MPT, 1.2–0.6 Ma, orange area on the figure), climate severity increased sharply when glacial–interglacial cycles changed from low (41 thousand years ago (ka)) to high (100 ka) amplitudes, resulting in larger temperature changes between glacial and interglacial periods. Temperature changes during the last 10 cycles, varied between 5 and 8°C between glacial and interglacial periods (Berger *et al*., 2016) (Fig. B1).

The Late Pliocene and Pleistocene tree extinctions (green-shaded area on the Fig. B1) were driven by climatic changes and geographical constraints to tree migration. During the Pliocene, Europe was the home of diverse subtropical hygrophilous and thermophilous taxa that could not adapt to the increasingly cooling climate dominating the Early Pleistocene (Svenning, 2003). In addition, large amplitudinal climatic fluctuations forced by the glacial/interglacial cycles generated large-scale latitudinal migrations of trees. East–west-oriented mountain barriers in Europe (Pyrenees, Alps, Carpathians) and the Mediterranean Sea constrained severely the latitudinal retreat of many tree taxa, and contributed to their extinction (Gray, 1878; Latham & Ricklefs, 1993). While extinctions were more pronounced during the Late Pliocene and Early Pleistocene and highly variable across Europe, they lasted up to Mid-Pleistocene transition, with very rare occurrences during the last glacial-interglacial cycles (Magri *et al*., 2017; Suc *et al*., 2018).

prolificity, competitive ability and dispersal (Lamarque *et al*., 2011), which facilitated the replacement of the extinct species. Indeed, tree genera (*Carya, Tsuga, Liquidambar*, *Cathaya*, etc.) that disappeared from Europe during the Gelasian–Calabrian (2.8–0.8 Ma) were predominantly replaced during the Mid-Pleistocene by species such as *Quercus*, *Fagus*, *Betula*, *Carpinus*, *Pinus* and *Picea*, which still occupy most of Central and Northern Europe today (Combourieu-Nebout *et al*., 2015; Magri *et al*., 2017).

During extinctions and afterward, these genera were further reinforced by additional selective drivers triggered by orbitally forced range dynamics (ORD; Dynesius & Jansson, 2000). ORD refer to the succession of expansion/retraction range changes due to the recurrent sequences of glacial-interglacial cycles. Sequences with frequent (periodicity of 41 ka) and low climatic amplitude cycles during the early phase (2.6–0.8 Ma) were followed by less frequent (periodicity 100 ka) but high-amplitude cycles since the Mid-Pleistocene (Head & Gibbard, 2015) (Box 1). ORD selective drivers increased with the severity and amplitude of the latter cycles and favored fast colonizing, vagile and generalist species (Dynesius & Jansson, 2000; Jansson & Dynesius, 2002). High vagility, fertility and colonizing ability lead to increased migration rates and thereby facilitating demographic expansion. Low specialization also facilitates site capture and rapid establishment in new suitable habitats. Both vagility and broad niche contributed ultimately to the wide distribution of species. These inferences are supported by palynological records of the last interglacial period that also highlight high migration velocities (Giesecke *et al*., 2017; Giesecke & Brewer, 2018). According to these authors, tree migration was ‘faster than the predicted mean velocity of climate change’ (Loarie *et al*., 2009) reconstructed for the same period. Evidence of selection for rapid establishment and site capture comes from the present monitoring of tree recovery in agriculture-abandoned field land or other degraded areas. In these studies, the woody

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communities colonizing new areas are predominantly composed of early-successional species and establishment is extremely rapid, typically within a few decades (Wright & Fridley, 2010; Rehounková *et al.*, 2018). Interestingly, conifer or broad-leaved tree genera that disappeared in Europe during the Pleistocene (e.g. *Tsuga, Sequoia, Cedrus, Carya, Magnolia* and *Cathaya*) were mainly composed of species sharing late-successional attributes, while modern genera (*Quercus, Betula, Corylus* and *Pinus*) include mainly species sharing early- to mid-successional features.

Finally, there are two additional and more recent historical facts that reinforce the hypothesis of selection for climatic resilience during the Pleistocene (2.6 Ma to 11 700 ya) extinction and the subsequent ORD episodes. First, extinctions were rare during the most recent glacial-interglacial cycles during the Middle (1.25 Ma to *c.* 129 ka) and Late Pleistocene (from *c.* 129 ka and *c.* 11 700 ya), that is after the extinction crisis of the Early Pleistocene, which affected relictual genera such as *Zelkova* (Jasinska *et al.*, 2022) or *Pterocarya* (Corrado & Magri, 2011). Second, surviving species to the extinction and to ORD episodes demonstrated resilient responses during abrupt and short climatic changes that occurred within the interglacial periods. There are at least four reported abrupt changes during the current interglacial period (Bölling (warming), Alleröd (warming)/Bölling–Alleröd, 14 700–12 900 ya), Older Dryas (cooling, *c.* 14 000 ya) and Younger Dryas (cooling, *c.* 12 900–11 650 ya), with large climatic amplitude over a few hundred years (Peteet, 2000). Very rapid vegetation responses including local disappearance and substitution of local woody species were observed, followed by a rapid recovery of the original species (Tinner & Lotter, 2001; Cole, 2010). In summary, a large body of biogeographical data support the sorting of species equipped with life history traits enhancing persistence and resilience during the Early and Late Pleistocene as a result of extinctions and ORD episodes.

Box 2. Estimating effective population size

Classically, the effective size of a population, N_e, is defined as the size of an idealized population, typically a so-called Wright–Fisher population, that would produce the same rate of genetic drift as the population of interest (Wakeley, 2009). As pointed out by Waples (2022), this definition is technically correct but its rather abstract nature hides the simpler dependency of N_e on three main demographic parameters: the number of potential parents, and the mean and variance in the number of offspring per parent (see also Caballero (2020 Ch. 5)). These three main parameters will, in turn, be influenced by population structure and selection. The effective population size will rarely be equal to the census number, and it is therefore important to be aware that estimates of N_e provide only indirect information on past changes in census number. However, N_e is directly related to genetic variation and to the efficacy of selection and is therefore indicative of the evolutionary potential of a species. There are various approaches to reconstruct changes in N_e over time. They differ primarily in the source of information they are using, and this, in turn, determines the time scale on which inference can be made. Methods based on linkage disequilibrium will retrieve information on past N_e over a few hundred generations (GONE, Santiago *et al*., 2020), while methods based on the site frequency spectrum (StairwayPlot2, Liu & Fu, 2020; Fitcoal, Hu *et al*., 2023), or on the distribution of heterozygosity along the genome (PSMC, Li & Durbin, 2011; MSMC2, Schiffels & Wang, 2020; SMC++, Terhorst *et al*., 2017) will retrieve N_e trajectories across much deeper times but will have a low resolution for more recent ones. Finally, it is worth stressing that all these methods do not explicitly consider population structure, nor do they consider introgression from other species. So, while the resulting estimates of N_e are good estimates of the evolutionary potential of the species at a given point in time they should be interpreted cautiously in terms of demography.

2. Maintenance of the effective population size across time

Another source of evidence about the resilience of forest trees to past climate change comes from recent studies inferring change in effective population size (N_e) over time (see Box 2 and Nadachowska-Brzyska *et al.* (2015) for the estimation of N_e, and for what N_e is and what it is not). Many studies have estimated changes in N_e over time in forest trees using one of the methods mentioned in Box 2. Of particular interest are comparative studies. Estimates of N_e obtained for seven major European forest tree species with StairwayPlot2 (Box 2) showed a continuous increase over time (Fig. 1a,b; Milesi *et al.*, 2024). For some species, for instance *Quercus petraea* and *Fagus sylvatica*, this time period extended very far back in time (up to 15 Ma in *Q. petraea*). And they both had a very large current N_e, especially *Q. petraea* (800 000). These large N_e could be the result of introgression from related species (e.g. Leroy *et al.*, 2020). Interestingly, N_e trajectories could be clustered into three groups (Fig. 1c), suggesting that they were not entirely determined not only by environmental factors but also by the biology and demographic history of the species. Scots pine was part of these seven species and was analyzed independently by Bruxaux *et al.* (2024) who, using a large, rangewide sampling, also observed an overall increase in estimates of N_e obtained with StairwayPlot 2 (Box 2) over a period of 1 Ma. As for *Quercus* and *Fagus*, recent N_e was generally very large (5×10^5–10^6). In oaks, a large and rather stable N_e does not seem to be specific to *Q. petraea* as a similar pattern was also observed in other oak species, in North America (*Quercus lobata*; Sork *et al.*, 2022) and East Asia (*Quercus acutissima*; Fu *et al.*, 2022). Helmstetter *et al.* (2020) also estimated temporal changes in N_e with the StairwayPlot2 method on three palm and four Annonaceae species from West African tropical forests. Again, N_e trajectories were strongly species-dependent, suggesting that they were not entirely determined by environmental factors. Interestingly, the N_e of the three palm species, all of which had large N_e (up to 500 000), increased continuously over the time period under which N_e values were estimated. Finally, Bai *et al.* (2018) used Pairwise Sequentially Markovian Coalescent (PSMC) (Box 2) to estimate the change in N_e for 11 temperate *Juglans* (walnut) species. As in the two previous studies, the different species did not react similarly to the climatic oscillations following the Early Pleistocene cooling, and species-specific factors seemed to have played a prominent role. However, in this case, most species exhibited a decline in N_e, but there was a large variation in the importance of N_e decline. In summary, these widely distributed tree species appear to have been very resilient to past environmental changes, as suggested by the maintenance of their large effective population size. It should also be pointed out that another indirect source of evidence for the maintenance of fairly

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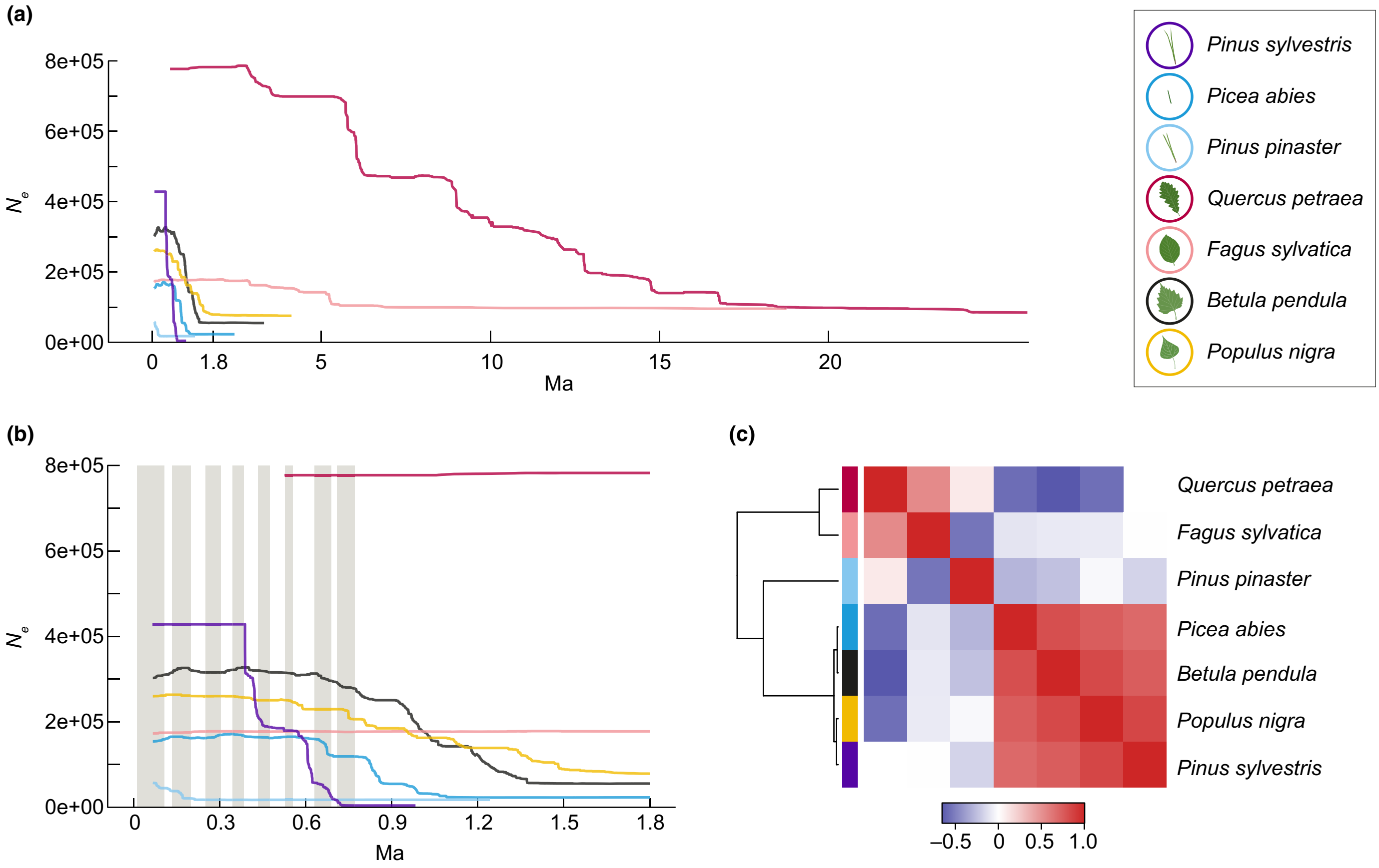

Fig. 1 Genetic resilience of seven common European tree species. (a) Change in effective population size (N_e) through time (million years ago, Ma), inferred with Stairway Plot 2 (lines, with one-sample-per-population). The median changes in N_e are reported. (b) A zoom-in of (a) focusing on the 0–1.8 Ma period. Grey-shaded rectangles delineate periods of glacial advance. (c) Species can be grouped based on their N_e trajectories. Heatmap based on Kendall's correlation coefficients computed from changes in N_e through time between each pair of species. The order of species along the *x*-axis is the same as that along the *y*-axis. Blue and red colors represent negative and positive correlation values, respectively. Adapted from Milesi *et al*. (2024).

large long-term N_e and weak random genetic drift is the large number of shared polymorphisms observed across related species, even in species that diverged a long time ago and are today found on different continents (e.g. Chen *et al*., 2010; Feng *et al*., 2019). Finally, it is worth stressing that all three comparative studies cited previously indicate that species' responses are partly idiosyncratic but that their biological properties and their geographical location also led to some shared patterns. Those shared patterns and the relative role of biological properties and historical contingencies played in establishing them certainly deserve further attention.

3. Rapid tree microevolution

A long-standing question and nowadays recurrent concern about the resilience of forest trees is the pace of microevolution in response to ongoing climate change. Considerable research has been conducted in common gardens (known as provenance tests) of trees highlighting extensive genetic differentiation between populations for quantitative traits, some of which might be related to fitness (Langlet, 1971; Wright, 1976). One century of provenance tests research has amply confirmed that tree populations are locally adapted across different biomes of the Northern Hemisphere (Leites & Benito Garzon, 2023). Notably, trees exhibit striking genetic clines for growth and phenological traits along climatic gradients (Morgenstern, 1996; Sáenz-Romero *et al*., 2019), suggesting adaptive responses to climatic changes. Provenance research corresponds to synchronic approaches to assess genetic variation. Provenance tests afford estimates of population differentiation between extant populations, but they do not provide an assessment of the rate of microevolution resulting in population differentiation (Hendry & Kinnison, 1999). While most temperate European tree populations are in place since several millennia (Giesecke *et al*., 2017; Giesecke & Brewer, 2018), no genetic diachronic approach allowed the estimation of the timeframe needed to achieve local adaptation. Did trees evolve gradually over several generations during the postglacial period, or did adaptation proceed over much shorter periods as short temporal pulses? There is indirect evidence that trees were able to adapt gradually. For instance, Li *et al*. (2022) analyzed a contact zone separating the two main genetic clusters of Scandinavian populations of Norway spruce. Under the Last Glacial Maximum (18 000 ya), Scandinavia was covered by ice. As the ice melted away, trees (and other organisms) recolonized Scandinavia from both the North and the South, leading to the current contact zone. The latter

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matches very closely the border between the two main Köppen climate regions of Scandinavia, suggesting that the contact zone was shaped and maintained by selection, something that was confirmed by selection tests (Li *et al*., 2022). Because the trees recolonized Scandinavia some 8000–12 000 ya, and assuming a generation time of at least 50 years, these data suggest that the pattern of local adaptation to the main climatic regions and the establishment of the contact zone took place over, at most, a few hundred generations. Of course, part of this pattern of local adaptation likely also reflects some levels of preadaptation in the trees that recolonized Scandinavia.

Were trees also able to adapt during shorter timescales? Longitudinal temporal monitoring of genetic changes in trees remains an experimental challenge due to their long generations and has been discarded in the past. Access to ancient DNA has overcome these constraints but fails for the time being to recover data at the level of whole populations (Wagner *et al*., 2018, 2024). Dendroecological studies based on tree ring analysis, although retrospective, do not take into consideration the temporal demographic changes (mortalities) as they are conducted on surviving trees. Furthermore, they do not allow separating genetic from plastic responses to environmental changes. Despite experimental constraints to track temporal evolutionary changes, there are a few emerging results that indicate that adaptive processes are active at ecological timescales (a few centuries). A first series of data provides estimates of population differentiation between populations that were recently separated from their known common source population. Typical examples of such cases correspond to population transfers by human intervention, as the introduction of North American species in Europe during the last two centuries (Krumm & Vitkova, 2016). When the introduced populations were compared with their source populations in common garden experiments, significant genetic differences of fitness-related traits suggested that natural selection was the most parsimonious explanation for the recent divergence observed (Daubree & Kremer, 1993; Kremer & Hipp, 2020). Although these differences were detected between modern extant populations, the very recent divergence provides evidence that adaptive evolution can occur over a very few generations.

More recent diachronic approaches combining genomic and phenotypic surveys have confirmed these conclusions. In two recent studies (Saleh *et al*., 2022; Caignard *et al*., 2024), temporal genetic changes were assessed in multicentennial oak trees during the transition between the Little Ice Age (1450–1850) and the Anthropocene warming (1850–today) (Box 3). The Little Ice Age was a cold period with repeated extreme winters documented by historical reports of tree mortalities and damages (Fagan, 2002). Temperatures increased afterward by > 1.5°C to the present (Pfister & Wanner, 2021). Significant temporal genetic changes were found during the transition between the cold Little Ice Age and the Anthropocene warming at the genomic and phenotypic levels (Box 3). There are three lessons to be learned from this retrospective analysis regarding the pace of microevolution. First, evolution was rapid as changes were detectable on an ecological timescale. Second, evolutionary changes fluctuated in response to climatic transition as the direction of genetic changes switched in the opposite direction between the Little Ice Age and the Anthropocene warming. Third, the genomic imprint of genetic changes was distributed over the whole genome with limited allelic frequency shifts at a large number of single nucleotide

Box 3. Microevolutionary changes during climate transitions

Assessments of temporal genetic changes in forest trees over successive generations are very rare given the time constraints imposed by long-lived species. In a recent study, genome-wide allelic frequency changes (Δ) were assessed in four different age-structured cohorts in sessile oak (*Q. petraea*) even-aged managed forests to track temporal changes during the transition from the cold period of the Little Ice Age to the warming Anthropocene (from 1680 to 2008). The experiment was repeated in three different forests (Saleh *et al*., 2022). Under even-aged silvicultural regimes, natural selection is strongest at the juvenile stage, when > 95% of seedlings are eliminated. These age-driven demographic dynamics were the rationale for using a retrospective monitoring of evolutionary changes based on age-structured cohorts, despite the lack of access to discrete separate generations. To separate stochastic genetic changes from one cohort to the next (due to genetic drift or other demographic causes) from systematic changes due to natural selection, covariations of Δ values were examined over different time periods (e.g. between $\Delta_{1680-1850}$ and $\Delta_{1850-1960}$). (Fig. B3) Under stochastic sources of variation, the covariations (r) are expected to be zero, while similar systematic sources as natural selection will raise positive values, and opposing sources will generate negative values (Buffalo & Coop, 2019). The results showed temporal genome-wide allelic frequency changes in the same sign during the cold period (r_{cold}-positive) and in the warm period (r_{warm}-positive), the two periods being considered separately (Saleh *et al*., 2022). Conversely, covariations were negative when comparing Δ values between cold and warm periods ($r_{\text{cold,warm}}$-negative). These results were further confirmed at the phenotypic level in common garden experiments in which open-pollinated progenies originating from the different age-structured cohorts were compared. In particular, genetic changes in height growth and phenology-related traits were reoriented between the cold and warm periods (Caignard *et al*., 2024). Overall, these results show that microevolutionary changes can occur over ecological timeframes in trees and that the direction of evolution can change with climate change.

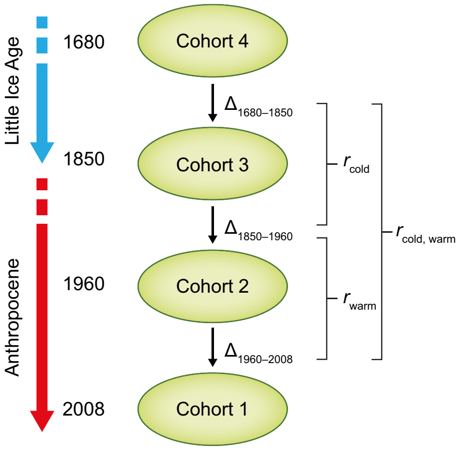

Fig. B3 Estimating linked selection from temporal genome-wide allelic frequency changes. See text for explanation.

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polymorphisms (SNPs). Furthermore, evidence of rapid and directional genetic changes was underpinned by diachronic observations conducted over two successive generations in oaks at contemporary timescales (Alexandre *et al.*, 2020). Taken together, these findings suggest that adaptation is tracking climatic changes very closely and could thereby contribute to tree resilience to environmental changes.

III. Lessons from the present

1. Limited impacts of genetic load and inbreeding depression

Inbreeding and inbreeding depression can severely decrease the adaptive potential of a species. Many surveys have shown that long-lived perennials, such as forest trees, have higher levels of inbreeding depression than annuals and shrubs (Lesaffre & Billiard, 2021). Indirect estimates of the measure of inbreeding depression ($\delta \equiv 1 - w_i / w_o$, where w_i and w_o are the fitness of inbred and outbred individuals, respectively) amounted to 0.24 for short-lived herbaceous, 0.53 for long-lived herbaceous and 0.66 for woody species (Duminil *et al.*, 2009). Inbreeding depression is particularly high and well-documented in conifers (Williams & Savolainen, 1996). It is still disputed whether inbreeding depression is higher in long-lived perennials than in annuals because they accumulate more somatic mutations or because inbreeding depression is expressed across multiple life stages, but recent surveys of genome-wide molecular variation indicate that long-lived outcrossing perennials tend to accumulate more deleterious mutations than short-lived ones (Chen *et al.*, 2017). These authors calculated zero- and fourfold pairwise nucleotide site diversity, π_0 and π_4, respectively. Zerofold nucleotide diversity is a proxy of nonsynonymous changes in protein coding sequences while fourfold pairwise nucleotide site diversity is a proxy of synonymous diversity. The former is assumed to be under selection while the latter evolves under neutrality. Those pairwise nucleotide diversities were then used to calculate the ratio of zero- to fourfold nucleotide diversity, $\pi_0 : \pi_4$, which provides a good measure of the efficiency of selection in purging deleterious mutations. In trees (outcrossing long-term perennials), estimates of $\pi_0 : \pi_4$ were significantly higher than the value observed in outcrossing annuals and at a similar level to selfing annuals and selfing short-term perennials (Fig. 2). Other approaches, based on site conservation across species (e.g. SIFT, Ng & Henikoff, 2003; PROVEAN, Choi *et al.*, 2012), were used to estimate the importance of deleterious mutations in forest trees. They also led to the conclusion that the mutational load of forest trees is relatively high (Zhang *et al.*, 2016; Conte *et al.*, 2017). However, caution was recommended when interpreting or comparing these estimates (Conte *et al.*, 2017).

Since, under the nearly neutral theory (Ohta & Gillespie, 1996), $\pi_0 : \pi_4$ decreases with effective population size, one might have expected to observe relatively low values in trees. Independently of its source and causes of its maintenance, the high genetic load observed in many forest tree species should limit their evolutionary potential, particularly in marginal populations in which the genetic load is expected to be higher than in central ones. However, this is not observed in broadly distributed tree species, such as *Q. petraea* or *Picea abies*, in which the ratio $\pi_0 : \pi_4$ varies little across populations (James *et al.*, 2023). This may be a consequence of gene flow linking marginal and central populations and/or of the fact that the current values of $\pi_0 : \pi_4$ are more closely associated to the deeper part of gene genealogies, which is shared across populations than to the most recent part, which is more population specific. At any rate, it appears that the adaptive response and resilience of many forest trees have not been badly affected by the presence of the high genetic load observed across the species range. Possibly, the very large number of offspring produced during a tree's lifetime and the strong selection at the seedling stage combine to make the genetic load bearable.

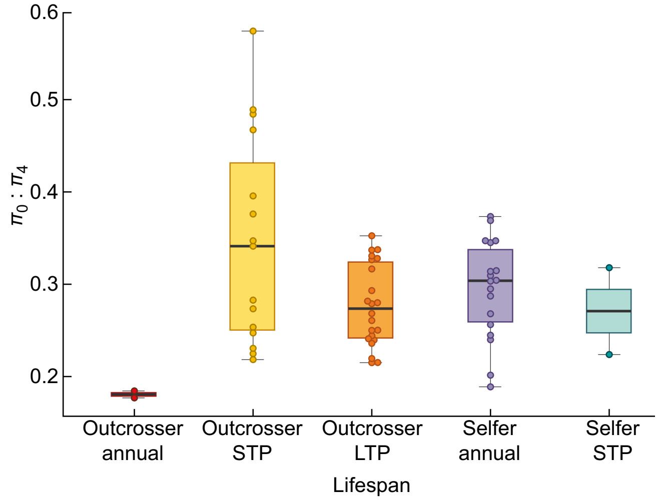

Fig. 2 Ratio $\pi_0 : \pi_4$, where π_0 is nucleotide diversity at zerofold sites (nonsynonymous) and π_4 is nucleotide diversity at fourfold sites (synonymous), differs between combinations of mating system and lifespan. Each dot corresponds to a species. Box limits indicate the range of the central 50% of the data, and the central line marks the median value. The ratio $\pi_0 : \pi_4$ is as high in long-term perennials as in annual selfers, suggesting that they accumulate deleterious mutations at the same rate. LTP, long-term perennial; STP, short-term perennial. The list of the species used to draw the figure is given in Supporting Information Table S1.

2. Mixed effects of overlapping and long generation intervals

Long and overlapping generations have mixed effects on the resilience of trees. When forest stands are renewed either by natural means or by human interventions under even or uneven management regimes, seedlings are produced by open matings between adult trees. However, the age of parent trees varies between seed trees and pollinating trees. The former are composed of the oldest trees of the population just before their removal after natural death or by artificial cutting, while the latter are part of all surrounding trees producing pollen, which are trees of different ages starting from sexual maturity. As a result, the age at reproduction, for seed trees and pollen trees, exceeds the age at first breeding, and the generation interval is no longer the age when parent trees first reproduce but becomes the average age of parent trees at the birth of their offspring (Bijma & Woolliams, 1999). While generation time has rarely been estimated precisely in trees (Petit & Hampe, 2006),

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this, nonetheless, means that the generation interval in many temperate forest trees may exceed 100 years. Thus, generation times of most tree species outpace by far the Intergovernmental Panel on Climate Change timeframe of climatic predictions, and the predicted genetic changes needed to meet climate requirements exceed the known rate of past microevolution. This is why a long generation interval is recurrently claimed as a major limitation of tree evolution to match the velocity of climate change (Kremer, 2007; Aitken *et al.*, 2008). Evolutionary constraints generated by this reduced generation turnover have been highlighted in simulation studies under climate change scenarios (Kuparinen *et al.*, 2010), in which the rate of evolutionary change in two target species (*Betula pendula* and *Pinus sylvestris*) deviated continuously from the rate of climatic change, leading to an increasing adaptational lag. Under the simulation assumptions, the removal of adult trees changed this trend and facilitated adaptive evolution to climate change. Furthermore, long generation time in trees is accompanied by overlapping generations, which also have evolutionary consequences in the context of climate change, especially when combined with long generation times.

More generally, there are at least five evolutionary consequences of long and overlapping generations. Some are potentially positive, and others are negative for tree resilience. Let us start with the negative effects. (1) Overlapping generations lead to a decrease in effective population size, N_e, compared with the effective size expected under the classical Wright–Fisher model with nonoverlapping generations (Nunney, 1993; Wakeley, 2009; Caballero, 2020). Under neutrality, Nunney (1993) concluded that, under fairly general conditions, when the average generation time in an age-structured population is lengthened, then N_e approaches $N/2$, where N is the number of adults. So, everything else being equal, overlapping generations should lead to a lower genetic diversity than would have been observed had the species been an annual following the Wright–Fisher model. (2) Long generation time implies that generation turnover is limited, and thus, recombination cycles that promote new allelic associations prone to selection are reduced. (3) Generation overlap implies crossings between parent trees belonging to different age cohorts and thus generates temporal gene flow. Under continuous directional climatic variation with time, the fitness of age-structured cohorts is likely to vary linearly with age, older trees exhibiting lower fitness than younger cohorts (Caignard *et al.*, 2024). Thus, temporal gene flow will increase the adaptational lag due to the maintenance of long generation intervals.

However, generation overlap can also have positive effects. (1) First, generation overlap can act as a reservoir of genetic variation, as multiple age cohorts that underwent different selection regimes during their lifetime are maintained. This temporal variation can create ecological niches even in the absence of spatial variation in selection pressure and lead to a so-called storage effect that contributes to the maintenance of genetic variation (Ellner & Hairston Jr, 1994; Svardal *et al.*, 2015). Under fluctuating selection, this will increase the overall genetic variation of the population (Ellner & Hairston Jr, 1994; Yamamichi *et al.*, 2019) and thus enhance selection responses. (2) Second, generation overlap and long generations decrease the effect of drift during colonization (Austerlitz *et al.*, 2000). During colonization, overlapping generations will basically reduce founder effects. Because of the length of the juvenile phase, a newly established population will grow through the arrival of new migrants. This will increase the number of founders and therefore decrease the founder effect (Austerlitz *et al.*, 2000). Interestingly, both simulations (Austerlitz *et al.*, 2000) and experimental data in long-lived semelparous species (species that reproduce once in their lifetime and then die) (Liu *et al.*, 2024) indicate that it is really the overlapping generation and not only the long generation times that lead to this effect: the semelparous species *Puya raimondii* stays in a rosette form until it reaches *c.* 60 yr and produces a massive inflorescence and, shortly after that, dies. In contrast to what is observed in most forest tree species, a recent genomic study showed that drift in such species is very strong – at any rate much stronger than in its relative, *Puya macrura*, which is iteroparous – and population differentiation very pronounced (Liu *et al.*, 2024).

3. Genetic architecture of fitness-related traits facilitates rapid evolution

The genetic dissection of fitness-related traits in trees has considerably improved our understanding of how adaptive variation builds up and evolves in natural populations and contributes to their resilience. Genetic dissection breaks down phenotypic traits into the number, frequency, effect size and genomic distribution of genes, resulting in the genetic architecture of traits. Three major results have emerged from studies linking genetic architecture to adaptive variation in trees. First, quantitative trait loci (QTL) detection in segregating populations and genome-wide association studies in natural populations confirmed that most adaptive traits are controlled by a large number of genes, typically amounting to several hundreds, leading to a polygenic architecture (Hall *et al.*, 2016; De La Torre *et al.*, 2019), although theory suggests that antagonistic effects between migration and selection, which are common in trees (paragraph 2.5), may shape genetic architectures with fewer genes with larger effects (Yeaman & Whitlock, 2011). Second, the genetic variation of adaptive traits fueling local adaptation builds on a minor contribution of variation at each single gene and a much larger contribution of the covariation among the different genes (Le Corre & Kremer, 2003, 2012). And third, the multiple associations of different genes contributing to adaptive traits generate genetic redundancy, that is the occurrence of different associations resulting in the same phenotype (Yeaman, 2015; Laruson *et al.*, 2020).

To sum up, it is not only the cumulative contribution of single gene effects but also the contribution of the multiple combinatory associations of genes that underpin adaptive variation. While the former contribution has been supported by numerous results in breeding and natural tree populations, the latter contribution was inferred on the basis of the contrasting observed differentiation between adaptive traits and their underlying genes in trees (Kremer & Le Corre, 2012). The polygenic architecture of adaptive traits, the combinatory effects and genetic redundancy lead to important consequences on tree population evolution. First, large evolutionary changes in adaptive trait values can be triggered by the

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standing variation of numerous loci, each one of small effect (Sella & Barton, 2019; Höllinger *et al.*, 2023). Second, effective selection on standing genetic variation can occur over a limited number of generations (Kremer & Le Corre, 2012; Ehrlich *et al.*, 2021). Third, polygenic architecture and genetic redundancy facilitate the maintenance of variation of adaptive traits (Laruson *et al.*, 2020; Bataillon *et al.*, 2022). As a result, adaptive traits with polygenic redundant architecture enhance genetic resilience. Just as functional redundancy insures community resilience at the species level (Biggs *et al.*, 2020), genetic redundancy may trigger genetic resilience at the population level as variable combinations of redundant alleles offer multiple opportunities to reach optimal fitness at short timescales (Ehrlich *et al.*, 2021).

Besides genetic redundancy of the architecture of adaptive traits, there is a second level of redundancy that may be considered concerning resilience, which is redundancy at the genome level. While the evolution of the genome of flowering plants is paved by multiple phases of genome and gene duplications (Wang *et al.*, 2012), recent whole genome sequences of oak species have highlighted the increased duplication of defense-related genes (Plomion *et al.*, 2018; Sork *et al.*, 2022). Enrichment of resistance genes was interpreted as a means to withstand variable biotic selection pressures to which long-lived species such as trees are exposed. Finally, structural variation (SV) has recently been explored as a potential source of rapid adaptation in tree species (e.g. Prunier *et al.*, 2019). Early results in crop species (Todesco *et al.*, 2020) are very encouraging, but the contribution of SV to adaptation and genetic resilience in forest trees remains understudied.

4. Synergistic contributions of plastic and genetic effects to adaptive evolution

Phenotypic plasticity, defined as the capacity of a given genotype to respond differently to environmental conditions, has received much attention in trees that are exposed to repeated ecological changes over their lifetime (Chambel *et al.*, 2005). Empirical assessments of plastic responses of trees have mostly been investigated at the population level in multisite common garden experiments (Park & Rodgers, 2023), starting with the discovery of widespread genotype–environment (GE) interactions in most economically important species (Li *et al.*, 2017). Implicitly, the presence of GE interactions unveiled the underlying different responses of populations to site conditions, which are called norms of reaction and modeled as linear (Gregorius & Kleinschmit, 2001) or quadratic functions (Wang *et al.*, 2006) to environmental variables. The slopes (coefficients of the norm of reactions) are the key parameters accounting for the plastic response of the traits. Lessons gained from the assessments of the norms of reaction in multisite common garden experiments can be summarized in four major outcomes. First, the slopes of the norms of reaction at the species or population level are nonzero for most adaptive traits (Chambel *et al.*, 2005; Leites & Benito Garzon, 2023). Second, population differences exist, indicating genetic differentiation of plastic responses (Rehfeldt *et al.*, 2002; Sáenz-Romero *et al.*, 2019). Third, genetic variation of plastic responses is maintained within populations (Marchi *et al.*, 2022). Taken together, these results indicate that plasticity in trees has a genetic basis and can evolve. However, despite significant differences among populations, the level of genetic differentiation in plasticity among populations remains low, and amounts to the magnitude observed for neutral traits in the only known experiment in which intra- and interpopulation genetic variation of plasticity were assessed (Soularue *et al.*, 2023). Maintenance of genetic variation and low genetic differentiation among populations of the slope of the norms of reaction suggests that past evolution has generated a 'generalist' type response in trees maintained in all populations. Evolution toward an optimum plastic response, in which genotypes can reach optimal fitness in all environments, is also predicted by theory for long-lived species experiencing large spatiotemporal environmental heterogeneity and composed of populations connected by extensive gene flow (Scheiner, 2013; Hendry, 2016). The 'generalist' type of response increases the ability of populations to persist under a wide range of environmental disturbances and thus contributes to their resilience (Ghalambor *et al.*, 2007).

Finally, empirical results suggest that plastic and genetic variation contribute synergistically to phenotypic evolution of adaptive traits. Covariation of plastic and genetic effects in the same direction is expected when plastic responses to environmental changes ultimately result in increased fitness, thus contributing to the persistence of the species under altered conditions ('Baldwin effect'; Crispo, 2008). Under this scenario, plasticity first leads to phenotypic changes followed later by genetic changes, but alternative scenarios may occur as well (Crispo, 2008). Whatever the evolutionary sequence in trees, experimental results show that positive covariation of plastic and genetic effects of adaptive traits are more frequent in extant tree populations than negative covariation (Kremer *et al.*, 2014; Box 4). Several contemporary studies of variation in tree growth illustrate the positive covariation of plastic and genetic effects. Large-scale surveys of tree growth using increment cores conducted *in situ* indicated a steady increase in growth during recent decades due to higher atmospheric CO_2 concentration and nitrogen deposits (Maes *et al.*, 2019). Temporal genetic changes assessed in age-structured oak cohorts spanning the last two centuries (Caignard *et al.*, 2024) and genetic changes predicted over two successive generations (Alexandre *et al.*, 2020) showed a similar trend for tree growth. In this example, phenotypic changes, combining plastic and genetic responses, and genetic changes per se covary in the same direction. Monitoring of trait variation conducted *in situ* and in genetic tests (common gardens) exhibits mostly positive covariation of plastic and genetic effects (Box 4). Thus, both sources of variation amplify synergistically phenotypic responses to environmental changes and contribute more efficiently to persistence following perturbations.

5. Sustained local adaptation despite widespread gene flow within species

Most temperate forest trees are anemophilous and able to disperse pollen over long distances. Documented extreme effective pollen

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Box 4. Positive covariation of plastic and genetic effects in trees

Covariation of plastic and genetic effects can be assessed in trees by comparing genetic and phenotypic clines in common gardens and *in natura*. When different populations stemming from different geographic origins are compared under common garden conditions, most adaptive traits exhibit continuous population variation along some ecological gradient of their origins (Morgenstern, 1996; Leites & Benito Garzon, 2023). This pattern, called genetic cline, is the consequence of past divergent selection along the ecological gradient. Genetic clines can be compared with phenotypic clines, resulting from observations of the same traits made *in natura* along the same ecological gradient, and which are mostly shaped by plastic responses (Conover & Schultz, 1995; Conover *et al*., 2009). When both clines are oriented along the same direction, cogradient variation ensues (Conover *et al*., 2009) and plastic effects amplify adaptive genetic variation. However, when the two clines are in opposite directions, countergradient variation occurs (Conover *et al*., 2009) and plastic effects then offset genetic effects. We illustrate co- and countergradient variation for growth (a, b) and seed weight (c, d) in sessile oak (Caignard *et al*., 2021) along an elevational gradient in the French Pyrénées (Fig. B4). Height growth and seed weight were assessed in oak stands at various altitudes (a, c). The same traits were measured on offsprings collected on the same trees and raised in a common experiment (b, d). Both traits show clinal genetic and phenotypic variation, but positive covariation (cogradient) for height growth, and negative covariation (countergradient variation) for seed weight. The comparison between genetic and phenotypic clines for various adaptive traits (including growth, phenology, physiology and morphology) in oaks and eucalyptus showed that cogradient variation was overrepresented (Kremer *et al*., 2014) in comparison with Countergradient variation. Reported examples of Countergradient variation were interpreted as the consequence of compensation between environmental and genetic sources of variation (Caignard *et al*., 2021).

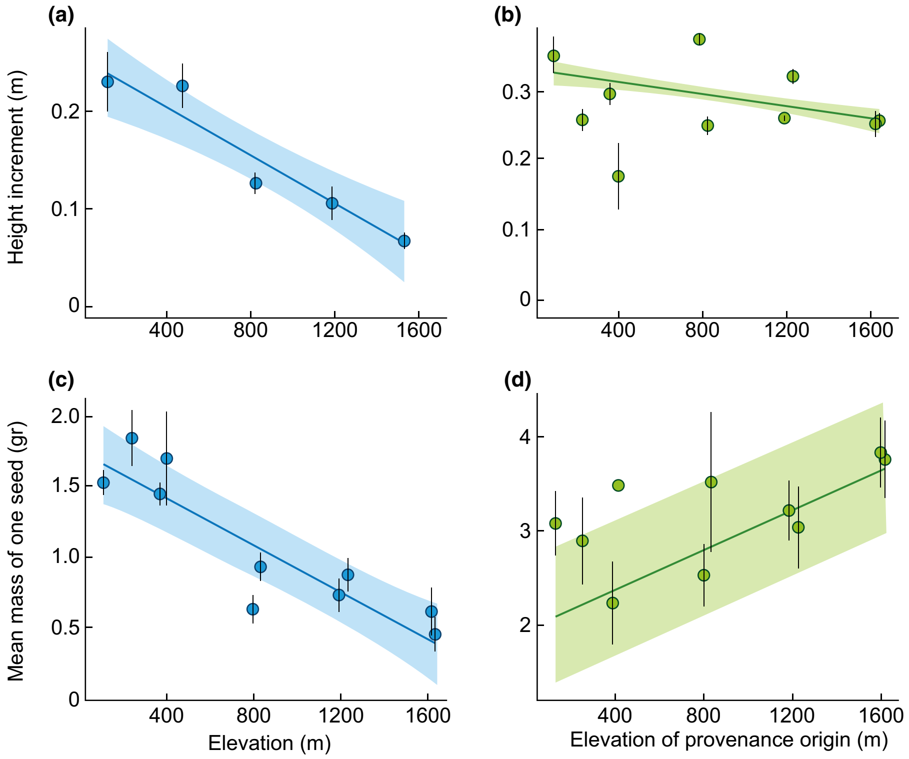

Fig. B4 Co- and countergradient variation for growth (a, b) and seed weight (c, d) in sessile oak along an elevational gradient in the French Pyrénées (based on data from Caignard *et al*., 2021).

dispersal – although rare – may reach hundreds of kilometers and, in Europe, is of the same magnitude as predicted shifts of climate during this century (Kremer *et al.*, 2012). In some species, gene flow can also take place by seed as well as via pollen, and in some tree species, for example *Sorbus aucuparia*, seed flow may even be more important than pollen flow (Bacles *et al.*, 2004). Under such circumstances, whether gene flow would facilitate or constrain adaptation to ongoing climate change has been a pressing issue that has been addressed recently by theoretical and experimental approaches (Savolainen *et al.*, 2007). From a theoretical standpoint, gene flow generates conflicting evolutionary trends (Lopez *et al.*, 2008). On the one hand, gene flow homogenizes allele frequencies among populations across space and increases the lag between the extant genetic value of populations and their expected optimal value, thus generating migration load. On the other hand, gene flow increases the standing genetic variation within populations and enhances their response to natural selection. Recent experimental results at a very local scale suggest that the latter effects of gene flow are dominating in ecological settings of closely located populations (Scotti *et al.*, 2023). Notably, adaptive divergence of nearby populations at individual SNPs is not prevented by extensive gene flow that connects close populations. In four

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conifers with contrasting life history traits, genomic differentiation correlated with local adaptation was maintained between close populations growing under contrasting environmental conditions. Fine-scale comparisons of immigrant with local gene pools indicated indeed that within-population genetic variation was increased by gene flow and enhanced adaptive differentiation (Gauzere *et al.*, 2020).

In the same vein, the ratio $\pi_0 : \pi_4$, which measures the efficiency of selection in purging deleterious mutations, did not vary across populations in six European forest tree species (James *et al.*, 2023), contrary to expectations that marginal populations would show a higher value than core populations. Altogether, these experimental results suggest that gene flow does not constrain adaptive differentiation when divergent selection is strong. Note, however, that the strong short-term response to selection observed at a very local scale may not necessarily translate into a high evolutionary rate when large time periods are considered (Messer *et al.*, 2016). A possible explanation is pervasive fluctuating selection as recently suggested by Saleh *et al.* (2022) in oaks and shown in *Mimulus* by Kelly (2022). In the latter, out of 1.8 M SNPs, 1796 SNP showed significant fluctuating selection and 40 significant directional selection, the rest behaving neutrally. Conversely, pollen flow may even amplify adaptation by introducing preadapted genes from distant populations into target populations under a directional shifting climate. Theory shows that in a heterogeneous environment changing linearly in space and time mimicking climate change along a geographic gradient, pollen dispersal will shift the ecological niche of a species to match the moving environmental change and accelerate the shift for species dispersing pollen at long distances (Aguilée *et al.*, 2016). Although we are lacking experimental results supporting these predictions, beneficial effects of pollen flow are likely to overcome negative effects, considering in addition that airborne pollen production of many tree taxa is stimulated by climatic change (Ziello *et al.*, 2012).

An extreme case of local adaptation in spite of gene flow is provided by Scots pine (*P. sylvestris*). Scots pine has one of the largest natural ranges among forest trees, extending from Scotland in the west to the Russian Pacific Coast in the east and from the Iberian and Balkans Mountain ranges in the south to the Barents Sea to the north. A recent rangewide genomic survey showed that genetic differentiation is weak and that genetic diversity is high and strikingly uniform across the range (Bruxaux *et al.*, 2024). Similarly, the ratio $\pi_0 : \pi_4$ was consistently high and barely varied across populations. Nonetheless, decades of common garden studies (known as provenance tests in the forestry literature) have repeatedly shown evidence of local adaptation. However, in the case of Scots pine, different factors underlie local adaptation in different parts of the range, with temperature playing a major role in the central part of the range, drought-related variables in Spain, and photoperiod in Scandinavia (Leites & Benito Garzon, 2023). Those regional patterns of local adaptation may, at least in part, explain the weak signal of genotype–environment association detected by Bruxaux *et al.* (2024) at the range level and, importantly, together with extensive gene flow maintaining the connections among populations, may have contributed to the maintenance of genetic diversity at the species level.

6. Frequent hybridization in trees enhances adaptive introgression

Both hybridization and introgression have occurred frequently in forest trees, and hybridization was found to be positively correlated with perenniality (Mitchell *et al.*, 2019). Hybridization between different species and ensuing generations of backcrossing, that is introgression, is one of the most efficient genetic mechanisms to quickly introduce a vast amount of genetic variation into the genome of a given species (Soltis, 2013). While the importance of hybridization and introgression in plant species has been recognized for nearly a century, a systematic understanding of both processes in plants has only started over the last decades.

A first indication of the importance of hybridization and introgression in tree species was revealed by frequent conflict between chloroplastic and nuclear DNA, and between different nuclear genomic regions when reconstructing phylogenetic trees. However, only recently has the development of large-scale genomic sequencing allowed us to gain a global picture of the importance of historical gene flow on the evolution of a whole group of species, such as *Ficus* (Gardner *et al.*, 2023), *Fagaceae* (Zhou *et al.*, 2022), *Salix* and *Populus* (Sanderson *et al.*, 2023), and *Picea* (Karunarathne *et al.*, 2024). Even rare introgressed alleles can contribute to increase the number of adaptive mutations, which may be in short supply because of small N_e or low mutation rates. Studies in *Quercus* (Leroy *et al.*, 2020; Fu *et al.*, 2022) have revealed that adaptive introgressed alleles were common across the genome of widely distributed European and Asian oaks and that their proportion was influenced by genetic drift and environmental factors (Fig. 3). Introgression was affected by genetic divergence between pairs of populations and also by the similarity of the environments in which they live – populations occupying similar ecological sites tended to share the same introgressed regions. Fu *et al.* (2022) further pointed out that adaptive introgression did not affect the genes themselves but instead the *cis*regulatory elements regulating their expression, leading to similar expression profiles of closely related species in the same environment; and that although recombination facilitates the integration of introgressed alleles, suppression of recombination is necessary for the maintenance of adaptive introgressed alleles.

Suarez-Gonzalez *et al.* (2016) also identified linked adaptive introgression signals near a telomeric region in two *Populus* species. The suppressed recombination rate may help improve the efficacy of natural selection or reduce the so-called segregating load by preventing the breakdown of coadapted parental alleles (Moran *et al.*, 2021). In summary, while the exact mechanisms underlying adaptive introgression remain to be deciphered, introgression, by increasing the level of genetic diversity and bringing new adaptive alleles, will contribute to the resilience of forest trees.

7. Demographic dynamics boost genetic rescue

We have so far focused on genetic factors. As resilience was primarily viewed as an important evolutionary property, it made

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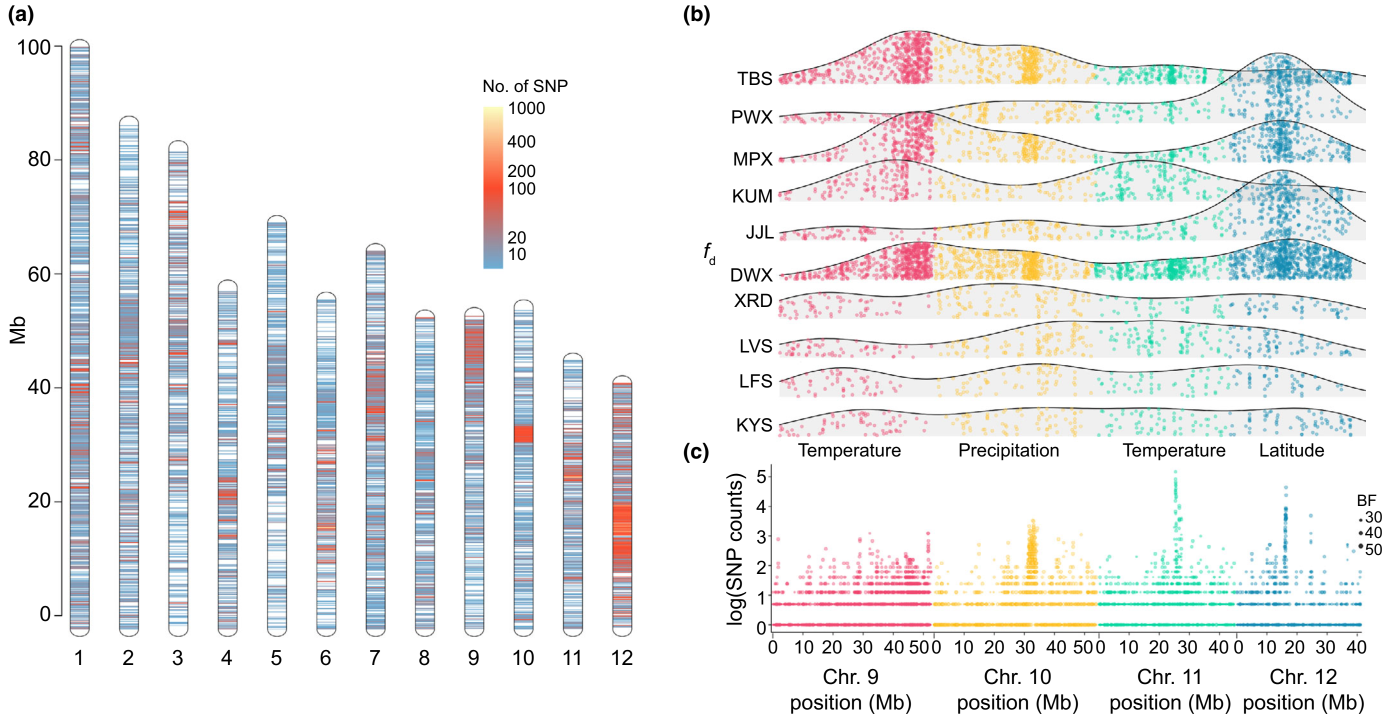

Fig. 3 Distribution of adaptive introgressed single nucleotide polymorphisms (SNPs) across the genome and their association with environmental factors. (a) Distribution of the number of SNPs under diversifying selection in windows of introgression for *Quercus acutissima* 12 chromosomes. The *y*-axis represents the coordinates of chromosomes, and the *x*-axis represents the 12 chromosomes. (b) Density distribution of introgression windows with significant evidence of introgression on Chr. 9–12. The *x*-axis shows the coordinates of each chromosome that was equally divided into 512 bins, and the *y*-axis gives the number of 10-kb sliding windows with significant evidence of introgression. Introgression is estimated by f_d, which quantifies the proportion of genomic regions affected by introgression (Martin *et al*., 2015). Each distribution curve corresponds to a population whose name is given at the start of the curve. (c) All four main introgressed regions in Chr. 9–12 are enriched with SNPs with frequency significantly associated with environmental/geographical factors (written in bold face), aligned vertically with each major introgression peak represented in (b, c). The size of the dots represents the mean Bayesian factor across all significant SNPs in the window. Figure adapted from Fu *et al*. (2022) (Creative Commons Attribution 4.0 International License).

sense to focus on those. However, resilience is also intrinsically a demographic property. And, while we have shown previously that empirical genetic and evolutionary evidence indicates that tree populations are prone to resilience, our understanding of how resilience is ultimately achieved remains limited. We are still lacking sufficient historical monitoring across generations to grasp the ecological and genetic mechanisms that triggered the recovery of populations to extreme environmental changes.

The question arises of how tree populations are maintained after repeated sequences of extreme climatic events that may have lethal consequences. The increased occurrence of extreme climatic events has stimulated world-wide monitoring of tree mortalities (Allen *et al.*, 2015). These reviews concentrated mostly on the abiotic causal drivers of mortality, rather than on the subsequent demographic changes in tree populations. Regional studies confirmed that increasing mortalities followed severe drought episodes in Europe (Senf *et al.*, 2020; George *et al.*, 2022). Reported mortality statistics described extreme spatial and temporal variation. Extant observed mortalities are the consequence of the background mortality preexisting in the population and the die-off generated by the extreme event, which have different temporal dynamics. Even die-off mortalities exhibit extreme spatiotemporal variation due to tree diversity, and microecological variation. Thus, forest stands undergoing dieback are characterized by the simultaneous persistence of dying and surviving trees, a situation that may subsist over years or decades.

Overall individual tree mortality, and tree population decline following extreme events, is a temporal gradual process (Changenet *et al.*, 2021). The Tree Decline Recovery Seesaw model (Whyte *et al.*, 2016) nicely illustrates the long duration during which tree populations maintain a decline status characterized by the coexistence of dying and surviving trees. One-off total tree mortalities are thus exceptions that may occur after fire or gale events but are unlikely the result of other biotic or abiotic events, including recent extreme droughts (as in 2003 or 2018–2019 (Senf *et al.*, 2020)). Canopy opening, resulting from the mortality of adult trees, favors recruitment resulting from open crossing between surviving trees (Martínez-Vilalta & Lloret, 2016). The time period during which partial mortalities will persist under steady state thus increases opportunities for genetic rescue to proceed by facilitating the renewal of the population. A long-distance pollen flow may prevent the breakdown of genetic diversity in the recruited seedlings and thus maintain the adaptive potential in the new generation. Ultimately, as the adult cohort may

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Table 1 Genetic attributes shaping tree genetic resilience.

	Facets constraining resilience	Facets mitigating constraints to resilience	Facets enhancing resilience
Properties of the genetic system	• Genetic load and inbreeding depression decrease fitness	• Genetic and genomic redundancy buffer responses to environmental changes	• Large standing genetic variation and polygenic architecture of traits increases the pace of microevolution • Synergistic contributions of plastic and genetic effects accelerate responses to environmental changes
Evolutionary drivers	• Temporal and spatial gene flow increases adaptational lag	• Microenvironmental divergent selection shapes local adaptation despite extensive gene flow	• Extensive intraspecific gene flow maintains large levels of diversity across the species range • Widespread interspecific geneflow generates adaptive introgression and increase the effective population size
Demographic drivers	• Long generation reduces the pace of microevolution	• Large fecundities offset genetic load • Long generation limits founder and drift effects during colonization, or after demographic collapses due to extreme events	• Generation overlap maintains genetic diversity • Large fecundities increase the rate of selection and contribute to rapid adaptation. It also decreases extinction risks due to demographic stochasticity • Regeneration is facilitated by demographic replacement dynamics

still be under a steady-state decline, the juvenile cohort originating from the surviving adult trees will develop and undergo selective screening under natural selection. Two cohorts following different evolutionary dynamics may then inhabit the same forest: the adult cohort undergoes steady decline while the juvenile cohort, given the higher expected selection intensity in the higher density among the seedlings, undergoes more rapid adaptive shifts to cope with the ongoing environmental changes. The coexistence of both cohorts over longer periods will reinforce the self-replacement as the seedlings may benefit from additional seeding years. In some cases, the two cohorts may be composed of different species and lead to replacement of the preexisting species (Cerioni *et al.*, 2024). However, self-replacement dynamics have also been observed following severe droughts (Margalef-Marrase *et al.*, 2022), but their genetic consequences remain poorly investigated. Such scenarios combining early expansion of new recruits benefiting from preexisting genetic diversity will contribute to important adaptive shifts to the ongoing stress episode, while the adult cohort may progressively disappear (‘silver-lining’ scenario; Coleman & Wernberg, 2020).

To sum up, we assembled facets of the genetic system of trees, and of evolutionary and demographic drivers that shape genetic resilience (Table 1). This synthetic overview emphasizes mixed contributions, ranging from facets constraining and limiting genetic resilience to facets increasing and enhancing it. Overall, the table illustrates that the latter dominate the former, suggesting that trees are better equipped than was formerly thought to withstand climatic changes.

IV. Conclusion

In this article, we have reviewed what is known about forest tree response to past climate changes and shown that species that did survive the Pliocene–Pleistocene transition had biological properties that helped them to survive the oscillations of glacial and interglacial periods that ensued. An important conclusion of this review is that resilience is a hallmark of the northern temperate zone’s trees, very likely due to their long history of surviving, even flourishing, through major environmental changes. Even under shorter time periods, repeated perturbations and disturbances expose trees to nonequilibrium conditions triggering evolutionary resilient responses, which have been poorly investigated so far. Our evolutionary perspective on trees has been dominated by the ultimate stable climax view of ecological systems, which are unlikely to apply to forest trees inevitably exposed during their lifetime to disturbance regimes. Eventually, such disturbance regimes may have led to some of the adaptive processes that we have outlined in the second part of this review.

While we still have a far-from-complete understanding of the evolutionary mechanisms contributing to forest tree resilience, some salient features have started to emerge. In particular, one key attribute of forest trees contributing to resilience appears to be their ability to combine large populations connected through extensive gene flow with pronounced local adaptation. This combination of features may have, in turn, enabled forest tree species to maintain high genetic diversity and survive their generally high genetic load. Even factors such as long and overlapping generation time may not have only negative consequences on resilience, and the ‘storage effect’ observed under fluctuating selection could also have contributed to the maintenance of genetic diversity. One practical implication of this review is that gene flow in forest trees is not something we need to worry about as it did not erase local adaptation and may even have contributed to it (Le Corre & Kremer, 2012). Finally, rapid adaptive responses to new selection pressures are indeed expected in populations combining high levels of standing genetic variation and polygenic architecture of fitness, and exposed to strong selection intensities (Kremer & Le Corre, 2012; Le Corre & Kremer, 2012). As we highlight in our review, tree species share these attributes and encounter severe selection intensities during the juvenile phase, thus demonstrating their high evolutionary potential (Box 5).

However, our review highlights the lack of understanding of the temporal frames at which these mechanisms are operating in

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Box 5. Evolvability and evolutionary potential of oaks

Fitness of an adult tree can be assessed by the number of surviving descendants it produces (as a male or female parent) in the next generation and having reached the same age as the parent tree. Its estimation *in situ* therefore requires access to two successive generations in the same population, and the reconstruction of the genetic relatedness between the trees of the two generations based on parentage analysis. Its measurement in the forest is therefore laborious and handicapped by the experimental constraints linked to the forest context. The mean standardized genetic variance of fitness within a population provides an estimate of the evolvability of this population, which corresponds to its evolutionary potential (Hansen *et al*., 2011, 2019). It measures the expected increase in fitness resulting from the response to selection on all adaptive traits, which can be interpreted as a component of resilience. Recently, fitness assessments of adult trees in a mixed forest of pedunculate oak (*Quercus robur*) and sessile oak (*Q. petraea*) were carried out (Alexandre *et al*., 2020) and their evolvabilities compared with measurements available in other plant and animal species that were compiled in a review (i.e. 82 estimates; Hendry *et al*. (2018)). The attached graph, adapted from Hendry *et al*. (2018), positions the values obtained for the two oaks (arrows) as compared to the distribution observed for the 82 values in plants and animals (distribution in green) (Fig. B5). This example illustrates the remarkable evolutionary capacities of trees in comparison with other animal or plant species, suggesting that they are prone to resilience.

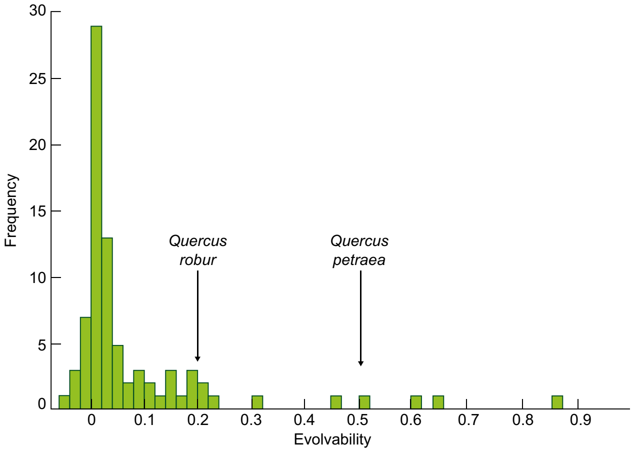

Fig. B5 Evolvability in oaks compared with other species. Based on data from Hendry *et al*. (2018) and Alexandre *et al*. (2020). See text for further explanations.

tree populations. As far as possible, we have distinguished short- and long-term processes, as inferred from population genetics or synchronic monitoring in common garden experiments. Temporal dynamics (allochronic approaches) are needed to grasp the pace at which resilience builds up in comparison with the strength and velocity of environmental changes. Yet, we illustrated in a case study that microevolutionary changes could occur rapidly during the transition between the Little Ice Age and the Anthropocene warming. Ancient DNA studies (a few millennia back in time) in trees may be a new avenue to explore temporal dynamics at various time scales. While they are still in their infancy, technical breakthroughs will undoubtedly usher a new era in evolutionary biology of forest trees as it did in humans (Irwing-Pease *et al*., 2024). A second limitation of our review comes from the focus on tree species sharing particular attributes, such as wide and continuous distribution, allogamy and longevity. Because they also share economic importance, their genetics, genomics and evolutionary biology have been more intensely studied and were thus preferentially prone to a review. It may well be that species with contrasting attributes (e.g. scattered vs narrow distribution, autogamy vs obligate outcrossing, short vs very long lifespan) behave differently. Comparative studies that span these life history traits and emergent attributes of species are needed to gauge the generality of our conclusions. Finally, we have put a bit more emphasis on genomic studies than on quantitative genetics simply because those allow easier historical inferences, not because we believe that quantitative genetics is not relevant. On the contrary, quantitative genetics is certainly going to play a central role in our efforts to understand the resilience of forest trees. Decade-long breeding programs, provenance tests and national forest surveys provide a vast trove of comparative data ready to be analyzed. Responding to the urgent conditions presented by ongoing climate change and environmental degradation demands that we keep working with these data to understand tree adaptive capacity and resilience even as we establish new experiments tailored to our evolving questions and needs.

Finally, our conclusions open new avenues to be explored for operational adaptive management in temperate forests. Among the various mechanisms and properties contributing to resilience that we have highlighted, some are intrinsic to species or evolutionary legacies and can hardly be shaped by human interventions, but others can be refined or manipulated through silvicultural practices. For example, the efficiency of natural selection could readily be improved by increasing the density of seedlings during natural seeding by accumulating seedlings over multiple years of fruiting. Thinning operations following early signals of mortalities due to extreme events should avoid clear cuttings or replacement by new species, but, instead, should facilitate renewal by natural regeneration of the declining species. It is out of the scope of this review to go through all potential applications. Instead, the results presented here should be viewed as a modest stepping stone toward more scientifically-based decisions in the management and conservation of tree species.

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Competing interests

None declared.

Authors contributions

AK, JC and ML wrote the paper.

ORCID

Jun Chen https://orcid.org/0000-0003-3187-7668
Antoine Kremer https://orcid.org/0000-0002-3372-3235
Martin Lascoux https://orcid.org/0000-0003-1699-9042

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Table S1 Data used to calculate the values used in Fig. 2.

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