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► **To cite this version:**

| Antoine Kremer, Jun Chen, Martin Lascoux. Are forest trees genetically resilient?. 2024. <hal-04775124>

HAL Id: hal-04775124

<https://hal.science/hal-04775124v1>

Preprint submitted on 9 Nov 2024

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1 **Are forest trees genetically resilient?**

2

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12 **Keywords:** Forest trees, genetic resilience, Quaternary, local adaptation, gene flow, effective population size

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14

15 **Abstract**

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

33

34

35

36 **Introduction**

37 All organisms have experienced repeated climate changes and environmental disturbances
38 during their evolutionary history and this constitutes a natural testing ground of their
39 resilience. Resilience is a broadly used word these days and a definition is in order here to
40 avoid misunderstandings. We extend Holling's broad definition of ecosystem resilience
41 (Holling, 1973) and of the forest resilience concepts (Anderson-Teixeira *et al.*, 2013; Nikinmaa
42 *et al.*, 2020) to the genetic level of forest trees, as the capacity of a woody species to withstand
43 or to recover from adverse ecological conditions and disturbances by maintaining its adaptive
44 potential. Such constraints can be generated by either extreme events (e.g. earthquakes, frost
45 spells, droughts, windstorms, pest outbreaks) or result from steadily increasing stress due to
46 biotic or abiotic continuous directional changes. Whatever the cause, a resilient species would
47 be more likely to avoid extinction during adverse ecological periods and recover and thrive as
48 more favourable conditions return. Importantly, our understanding of resilience does not
49 assume return to the pre-disturbance state of the species, but its capacity to evolve and
50 eventually adapt to post-disturbance conditions. Evolutionary trajectories leading to
51 resilience thus encompass genetic rescue by natural means and adaptation and bring into play
52 genetic as well as demographic processes. Concerns about resilience are today raised most
53 often for trees in the context of climate change (Dymond *et al.*, 2014; Nikinmaa *et al.*, 2024).
54 It has become common place to state that trees, in general, and forest trees, in particular, are
55 ill-equipped to face climate change, the main argument being that their long generation-time
56 will prevent them from adapting fast enough to rapid climate change (Aitken *et al.*, 2008;
57 Bisbing *et al.*, 2021), although earlier reports supported rapid microevolution (Petit & Hampe,
58 2006; Kremer, 2006). Concerns were further reinforced by reports of increasing forest tree
59 mortalities following repeated drought events (Allen *et al.*, 2015; Changenet *et al.*, 2021;
60 George *et al.*, 2022). In this review, we attempt to assemble genetic facts and arguments
61 supporting or undermining resilient responses of trees primarily on species of the Northern
62 Hemisphere.

63 It is important to state outright that we are in no way questioning the need to take urgent
64 actions against ongoing climate change. Also, it is worth stressing that, while emphasis is on
65 resilience to climatic change, forest trees also have to be resilient to a host of biotic factors.
66 As a matter of fact, as witnessed by the ash dieback in Europe or the chestnut blight dieback

67 of the American chestnut, some of the greatest recent threats experienced by forest trees did
68 not come from climate change but from the spread of diseases and pests. However, genetic
69 characteristics of trees that allow for rapid adaptation to climate change should also facilitate
70 adaptation to biotic agents of selection.

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

87 In a second part, we will revisit conclusions inferred from contemporary studies of key genetic
88 mechanisms either constraining or shaping resilient responses across spatio-temporal scales.
89 Large genetic surveys have been conducted during the last decades in widely distributed tree
90 species highlighting contrasting distribution of neutral and adaptive diversity across ecological
91 gradients (Alberto *et al.*, 2013; Leites & Benito Garzon, 2023). Similarly, genetic and genomic
92 studies, both intensive and comparative, conducted in breeding and natural populations have
93 enriched our understanding of the genetic, mating and dispersal systems of trees and their
94 functioning in different ecological settings (Austerlitz *et al.*, 2004; González-Martínez *et al.*,
95 2006; Savolainen *et al.*, 2007). What have we learned from different species about the factors
96 that may have triggered or limited resilience? Which evolutionary processes are at stake

97 during recovery from the contemporary ecological crisis? Finally, we will conclude by
98 addressing current challenges and future prospects.

99 **1. Lessons from the past**

100 **1.1. Legacies of the Pleistocene**

101 Woody floras underwent severe climatic and macroecological events since the late Pliocene.
102 In the northern hemisphere, these climatic fluctuations resulted in a succession of extinctions
103 followed by repeated sequences of extreme demographic expansions and contractions of the
104 remaining species. At the Pliocene-Pleistocene transition (around 2.58 million years ago
105 (Mya)) the climate in the northern hemisphere changed dramatically with the onset of the
106 glacial-interglacial periods, resulting in large-scale extinction of trees, especially in Europe
107 (Rull, 2020). The modern flora represents less than 30% of the tree genera present during the
108 Tertiary (Latham & Ricklefs, 1993; Eiserhardt *et al.*, 2015) and species that went extinct were
109 widespread before their disappearance (Magri *et al.*, 2017). During and following these
110 extinctions, the remnant species retracted and expanded their distributions in response to the
111 oscillations of glacial and interglacial periods.

112 While extinctions selectively eliminated cold sensitive species (Svenning, 2003), an additional
113 selective filtering took place in the aftermath of extinction. Post extinction scenarios involve
114 replacement and diversification dynamics associating expansion of pre-existing species,
115 evolution of new taxa and invasion by non-local species (Jablonski, 2001; Jablonski, 2008). In
116 the case of the Plio-Pleistocene (5 Mya to about 12 kya) extinction of trees, replacement
117 dynamics with pre-existing species sharing invasiveness attributes dominated. Indeed,
118 surviving species rapidly colonized southern Europe, as the overall forested area had only
119 slightly decreased during the extinction (Magri *et al.*, 2017), thus suggesting expansion of pre-
120 existing local species. These new species shared invasiveness attributes such as prolificity,
121 competitive ability, dispersal (Lamarque *et al.*, 2011) that facilitated the replacement of the
122 extinct species. Indeed tree genera (*Carya*, *Tsuga*, *Liquidambar*, *Cathaya*, ..) that disappeared
123 from Europe during the Gelasian-Calabrian (2.8 Mya to 0.8 Mya) were predominantly replaced
124 during the Mid Pleistocene by species such as *Quercus*, *Fagus*, *Betula*, *Carpinus*, *Pinus* and
125 *Picea*, that still occupy most of Central and Northern Europe today (Combourieu-Nebout *et*
126 *al.*, 2015; Magri *et al.*, 2017).

127 During extinctions and afterwards, these genera were further reinforced by additional
128 selective drivers triggered by orbitally forced range dynamics (ORD, (Dynesius & Jansson,
129 2000)). ORD refer to the succession of expansion/retraction range changes due to recurrent
130 sequences of glacial-interglacial cycles. More than fifteen sequences paved the Pleistocene
131 with frequent (periodicity of 41 kya) and with low climatic amplitude cycles during the early
132 phase (2.6 Mya to 1.8 Mya), gradually followed by less frequent (periodicity 100ka) but with
133 high amplitude cycles since the mid Pleistocene (Head & Gibbard, 2015). ORD selective drivers
134 increased with the severity and the amplitude of the latter cycles and favored fast colonizing,
135 vagile and generalist species (Dynesius & Jansson, 2000; Jansson & Dynesius, 2002). High
136 vagility, fertility and colonizing ability lead to increased migration rates and thereby facilitate
137 demographic expansion. Low specialization also facilitates site capture and rapid
138 establishment in new suitable habitats. Both vagility and broad niche contribute ultimately to
139 the wide distribution of species. These inferences are supported by palynological records of
140 the last interglacial period that also highlight high migration velocities (Giesecke *et al.*, 2017;
141 Giesecke & Brewer, 2018). According to these authors, tree migration was «faster than the
142 predicted mean velocity of climate change (Loarie *et al.*, 2009)» reconstructed for the same
143 period. Evidence of selection for rapid establishment and site capture comes from present
144 monitoring of tree recovery in agriculture abandoned field land or other degraded areas. In
145 these studies, the woody communities colonizing new areas are predominantly composed of
146 early successional species and establishment is extremely rapid, typically within a few decades
147 (Wright & Fridley, 2010; Rehounková *et al.*, 2018).

148 Finally, there are two additional and more recent historical facts that reinforce the hypothesis
149 of selection for climatic resilience during the Pleistocene (2.58 Mya to 11,650 ya) extinction
150 and the subsequent ORD episodes. First, extinctions were rare during the most recent glacial-
151 interglacial cycles-during the Middle (1.25 Mya to c. 129 kya) and Late Pleistocene (from c.
152 129 kya and c. 11,700 ya), i.e. after the extinction crisis of the early Pleistocene (close to 2.58
153 Mya), which affected relictual genera such as *Zelkova* (Jasinska *et al.*, 2022) or *Pterocarya* (
154 Corrado & Magri, 2011). Second, surviving species to the extinction and to ORD episodes
155 demonstrated resilient responses during abrupt and short climatic changes that occurred
156 within the interglacial periods. There are at least four reported abrupt changes reported
157 during the current interglacial period (Bölling (warming), Alleröd (warming) /Bölling-Alleröd,

158 14,700 ya – 12,900 ya), Older Dryas (cooling, c. 14,000 ya) and Younger Dryas (cooling, (c.
159 12,900 ya–11,650 ya)), with large climatic amplitude over a few hundred years (Peteet, 2000).
160 Very rapid vegetation responses including local disappearance and substitution of local woody
161 species, were observed, followed by rapid recovery of the original species (Tinner & Lotter,
162 2001; Cole, 2010). In summary, a large body of biogeographical data support the sorting of
163 species equipped with life history traits enhancing persistence and resilience during the early
164 and late Pleistocene as a result of extinctions and ORD episodes.

165 **1.2. Maintenance of the effective population size across time**

166 Another source of evidence about the resilience of forest trees to past climate change comes
167 from recent studies inferring change in effective population size (N_e) over time (see Box 1 and
168 (Nadachowska-Brzyska *et al.*, 2015) for estimation of N_e , and for what N_e is and what it is not).
169 Many studies have estimated changes in N_e over time in forest trees using one of the methods
170 mentioned in Box 1. Of particular interest are comparative studies. Estimates of N_e obtained
171 for seven major European forest tree species with StairwayPlot2, showed a continuous
172 increase over time (Figure 1, Milesi *et al.*, 2024). For some species, for instance *Quercus*
173 *petraea* and *Fagus sylvatica*, this time period extended very far back in time (up to 15 Mya in
174 *Quercus petraea*). And they both had a very large current N_e , especially *Quercus petraea*
175 (800,000). Interestingly, N_e trajectories could be clustered into three groups, suggesting that
176 they were not entirely determined by environmental factors. Scots pine was part of these
177 seven species and was analysed independently by Bruxaux *et al.* (2024) who, using a large,
178 rangewide sampling, also observed an overall increase in estimates of N_e obtained with
179 StairwayPlot 2 over a period of 1 Mya. As for *Quercus* and *Fagus*, recent N_e was generally very
180 large (5×10^5 – 10^6). In oaks, a large and rather stable N_e does not seem to be specific to *Q.*
181 *petraea* as a similar pattern was also observed in other oak species, in North America (*Q.*
182 *lobata*; Sork *et al.*, 2022) and East Asia (*Q. acutissima*; Fu *et al.*, 2022). Helmstetter *et al.* (2020)
183 also estimated temporal changes in N_e with the StairwayPlot2 method on three palm and four
184 Annonaceae species from West Africa tropical forests. Again, N_e trajectories were strongly
185 species dependent, suggesting that they were not entirely determined by environmental
186 factors. Interestingly, the N_e of the three palm species, all of which had large N_e (up to
187 500,000), increased continuously over the time period under which N_e values were estimated.
188 Finally, Bai *et al.* (2018) used PSMC to estimate the change in N_e for 11 temperate *Juglans*

189 (walnut) species. As in the two previous studies the different species did not react similarly to
190 the climatic oscillations following the early Pleistocene cooling and species-specific factors
191 seemed to have played a prominent role. However, in this case, most species exhibited a
192 decline in N_e , but there was a large variation in the importance of N_e decline. In summary,
193 these widely distributed species tree species appear to have been very resilient to past
194 environmental changes, as suggested by the maintenance of their large effective population
195 size. Finally, it should be pointed out that, another indirect source of evidence for the
196 maintenance of fairly large long-term N_e and weak random genetic drift is the large number
197 of shared polymorphisms observed across related species, even in species that diverged long
198 time ago and are today found on different continents (e.g. Chen *et al.*, 2010).

199 **1.3. Rapid tree microevolution**

200 A long-standing question and nowadays recurrent concern about the resilience of forest trees
201 is the pace of microevolution in response to on-going climate change. Considerable research
202 has been conducted in common gardens (a.k.a. provenance tests) of trees highlighting
203 extensive genetic differentiation between populations for quantitative traits, some of which
204 might be related to fitness (Langlet, 1971; Wright, 1976). One century of provenance tests
205 research has amply confirmed that tree populations are locally adapted across different
206 biomes of the Northern hemisphere (Leites & Benito Garzon, 2023). Notably, trees exhibit
207 striking genetic clines for growth and phenological traits along climatic gradients
208 (Morgenstern, 1996; Sáenz-Romero *et al.*, 2019) suggesting adaptive responses to climatic
209 changes. Provenance research corresponds to synchronic approaches to assess genetic
210 variation. Provenance tests afford estimates of population differentiation between extant
211 populations, but they do not provide assessment of the rate of microevolution resulting in
212 population differentiation (Hendry & Kinnison, 1999). While most temperate European tree
213 populations are in place since several millennia (Giesecke *et al.*, 2017; Giesecke & Brewer,
214 2018), no genetic diachronic approach allowed the estimation of the time frame needed to
215 achieve local adaptation. Did trees evolve gradually over several generations during the post-
216 glacial period or did adaptation proceed over much shorter periods as short temporal pulses?
217 There is indirect evidence that trees were able to adapt gradually. For instance, Li *et al.* (2022)
218 analyzed a contact zone separating the two main genetic clusters of Scandinavian populations
219 of Norway spruce. Under the Last Glacial Maximum (18,000 ya) Scandinavia was covered by

220 ice. As the ice melted away, trees (and other organisms) recolonized Scandinavia from both
221 the North and the South leading to the current contact zone. The latter matches very closely
222 the border between the two main Köppen climate regions of Scandinavia suggesting that the
223 contact zone was shaped and maintained by selection, something that was confirmed by
224 selection tests (Li *et al.* (2022)). Because the trees recolonized Scandinavia some 8000-12000
225 ya, and assuming a generation time of at least 50 years, these data suggest that the pattern
226 of local adaptation to the main climatic regions and the establishment of the contact zone
227 took place over, at most, a few hundred generations. Of course, part of this pattern of local
228 adaptation likely also reflects some levels of pre-adaptation in the trees that recolonized
229 Scandinavia.

230 Were trees also able to adapt during shorter time scales? Longitudinal temporal monitoring
231 of genetic changes in trees remain an experimental challenge due to their long generations
232 and has been discarded in the past. Access to ancient DNA has overcome these constraints,
233 but fails for the time being to recover data at the level of whole populations (Wagner *et al.*,
234 2018; Wagner *et al.*, 2024). Dendroecological studies based on tree ring analysis, although
235 retrospective, do not take into consideration the temporal demographic changes (mortalities)
236 as they are conducted on surviving trees. Furthermore, they do not allow separating genetic
237 from plastic responses to environmental changes. Despite experimental constraints to track
238 temporal evolutionary changes, there are a few emerging results that indicate that adaptive
239 processes are active at ecological time scales (a few centuries). A first series of data provide
240 estimates of population differentiation between populations that were recently separated
241 from their known common source population. Typical examples of such cases correspond to
242 population transfers by human intervention, as the introduction of North American species in
243 Europe during the last two centuries (Krumm & Vitkova, 2016). When the introduced
244 populations were compared to their source populations in common garden experiments,
245 significant genetic differences of fitness related traits suggested that natural selection was the
246 most parsimonious explanation to the recent divergence observed (Daubree & Kremer, 1993;
247 Kremer & Hipp, 2020). Although these differences were detected between modern extant
248 populations, the very recent divergence provide evidence that adaptive evolution can occur
249 over a very few generations.

250 More recent diachronic approaches combining genomic and phenotypic surveys have
251 confirmed these conclusions. In two recent studies (Saleh *et al.*, 2022; Caignard *et al.*, 2024),
252 temporal genetic changes were assessed in multi-centennial oak trees during the transition
253 between the Little Ice Age (1450-1850) and the Anthropocene warming (1850-today) (Box 2).
254 The Little Ice Age was a cold period with repeated extreme winters documented by historical
255 reports of tree mortalities and damages (Fagan, 2002). Temperatures increased afterwards by
256 more 1.5°C to present times (Pfister & Wanner, 2021). Significant temporal genetic changes
257 were found during the transition between the cold Little Ice Age and the Anthropocene
258 warming at the genomic and phenotypic level (Box 2). There are three lessons to be learned
259 from this retrospective analysis regarding the pace of microevolution. First, evolution was
260 rapid as changes were detectable on an ecological timescale. Second, evolutionary changes
261 fluctuated in response to climatic transition as the direction of genetic changes switched in
262 opposite direction between the Little Ice Age and the Anthropocene warming. Third, the
263 genomic imprint of genetic changes was distributed over the whole genome with limited
264 allelic frequency shifts at a large number of SNPs. Furthermore evidence of rapid and
265 directional genetic changes was underpinned by diachronic observations conducted over two
266 successive generations in oaks at contemporary time scales (Alexandre *et al.*, 2020). Taken
267 together, these findings suggest that adaptation is tracking very closely climatic changes and
268 could thereby contribute to tree resilience to environmental changes.

269

270 **2. Lessons from the present**

271 **2.1. Limited impacts of genetic load and inbreeding depression**

272 Inbreeding and inbreeding depression can severely decrease the adaptive potential of a
273 species. Many surveys have shown that long-lived perennials, such as forest trees, have higher
274 levels of inbreeding depression than annuals and shrubs (Lesaffre & Billiard, 2021). Indirect
275 estimates of the measure of inbreeding depression ($\delta \equiv 1 - w_i/w_o$ where w_i and w_o are the fitness
276 of inbred and outbred individuals), amounted respectively to 0.24 for short-lived herbaceous,
277 to 0.53 for long-lived herbaceous and to 0.66 for woody species (Duminil *et al.* 2009).
278 Inbreeding depression is particularly high and well documented in conifers (Williams &
279 Savolainen, 1996). It is still disputed whether inbreeding depression is higher in long-lived

280 perennials than in annuals because they accumulate more somatic mutations or because
281 inbreeding depression is expressed across multiple life stages, but recent surveys of genome-
282 wide molecular variation indicate that long-lived outcrossing perennials tend to accumulate
283 more deleterious mutations than short-lived ones (Chen *et al.* 2017). These authors calculated
284 0- and 4-fold pairwise nucleotide site diversity, π_0 and π_4 , respectively. 0-fold nucleotide
285 diversity is a proxy of nonsynonymous changes in protein coding sequences while 4-fold
286 pairwise nucleotide site diversity, is a proxy of synonymous diversity. The former is assumed
287 to be under selection while the latter evolves under neutrality. Those pairwise nucleotide
288 diversities were then used to calculate the ratio of 0-4 fold nucleotide diversity, π_0/π_4 , which
289 provides a good measure of the efficiency of selection in purging deleterious mutations. In
290 trees (outcrossing long-term perennials), estimates of π_0/π_4 were significantly higher than the
291 value observed in outcrossing annuals and at similar level to selfing annuals and selfing short-
292 term perennials (Figure 2).

293 Since, under the nearly neutral theory (Ohta & Gillespie 1996), π_0/π_4 decreases with effective
294 population size, one might have expected to observe relatively low values in trees.
295 Independently of its source and causes of its maintenance, the high genetic load observed in
296 many forest tree species should limit their evolutionary potential, particularly in marginal
297 populations where the genetic load is expected to be higher than in central ones. However,
298 this is not observed in broadly distributed tree species, such as *Quercus petraea* or *Picea abies*,
299 where the ratio π_0/π_4 varies little across populations (James *et al.*, 2023). This may be a
300 consequence of gene flow linking marginal and central populations and/or of the fact that the
301 current values of π_0/π_4 are more closely associated to the deeper part of gene genealogies,
302 which is shared across populations than to the most recent part, that is more population
303 specific. At any rate, it appears that the adaptive response and resilience of many forest trees
304 have not been badly affected by the presence of the high genetic load observed across the
305 species range. Possibly, the very large number of offspring produced during a tree's lifetime
306 and the strong selection at the seedling stage combine to make the genetic load bearable.

307 **2.2. Mixed effects of overlapping and long generation intervals**

308 Long and overlapping generations have mixed effects on the resilience of trees. When forest
309 stands are renewed either by natural means or by human interventions under even or uneven
310 management regimes, seedlings are produced by open matings between adult trees.

311 However, the age of parent trees varies between seed trees and pollinating trees. The former
312 are composed by the oldest trees of the population just prior to their removal after natural
313 death or by artificial cutting, while the latter are part of all surrounding trees producing pollen
314 which are trees of different ages starting from sexual maturity. As a result the age at
315 reproduction, for seed trees and pollen trees, exceeds the age at first breeding and the
316 generation interval is no longer the age when parent trees first reproduce, but becomes the
317 average age of parent trees at the birth of their offspring (Bijma & Woolliams, 1999). While
318 generation time has rarely been estimated precisely in trees (Petit & Hampe, 2006), this,
319 nonetheless, means that generation interval in many temperate forest trees may exceed 100
320 years. Thus, generation times of most tree species outpace by far the IPCC time frame of
321 climatic predictions, and the predicted genetic changes needed to meet climate requirements
322 exceed the known rate of past microevolution. This is why long generation interval is
323 recurrently claimed as a major limitation of tree evolution to match the velocity of climate
324 change (Kremer, 2007; Aitken *et al.*, 2008). Evolutionary constraints generated by this reduced
325 generation turnover have been highlighted in simulation studies under climate change
326 scenarios (Kuparinen *et al.*, 2010), where the rate of evolutionary change in two target species
327 (*Betula pendula* and *Pinus sylvestris*) deviated continuously from the rate of climatic change,
328 leading to an increasing adaptational lag. Under the simulation assumptions, the removal of
329 adult trees changed this trend and facilitated adaptive evolution to climate change.
330 Furthermore, long generation time in trees is accompanied by overlapping generations which
331 also have evolutionary consequences in the context of climate change, especially when
332 combined with long generation times. More generally, there are at least five evolutionary
333 consequences of long and overlapping generations. Some are potentially positive, and other
334 negative for tree resilience. Let us start with the negative effects. (i) Overlapping generations
335 lead to a decrease in effective population size, N_e , compared to the effective size expected
336 under the classical Wright-Fisher model with non-overlapping generations (Caballero 2020;
337 Nunney 1993; Wakeley 2009). Under neutrality, Nunney (1993) concluded that, under fairly
338 general conditions, when the average generation time in an age-structured population is
339 lengthened then N_e approaches $N/2$, where N is the number of adults. So, everything else
340 being equal, overlapping generations should lead to a lower genetic diversity than would have
341 been observed had the species been an annual following the Wright-Fisher model. (ii) Long
342 generation time implies that generation turnover is limited and thus recombination cycles

343 which promote new allelic associations prone to selection are reduced. (iii) Generation
344 overlap implies crossings between parent trees belonging to different age cohorts and thus
345 generates temporal gene flow. Under continuous directional climatic variation with time,
346 fitness of age-structured cohorts is likely to vary linearly with age, older trees exhibiting lower
347 fitness than younger cohorts (Caignard *et al.*, 2024). Thus, temporal gene flow will increase
348 the adaptational lag due to the maintenance of long generation intervals

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

370 **2.3. Genetic architecture of fitness related traits facilitates rapid evolution**

371 The genetic dissection of fitness related traits in trees has considerably improved our
372 understanding of how adaptive variation builds up and evolves in natural populations and
373 contributes to their resilience. Genetic dissection breaks down phenotypic traits into the

374 number, frequency, effect size and genomic distribution of genes resulting in the genetic
375 architecture of traits. Three major results have emerged from studies linking genetic
376 architecture to adaptive variation in trees. First, QTL (Quantitative Trait Loci) detection in
377 segregating populations and GWAS (Genome-Wide Association Studies) in natural populations
378 confirmed that most adaptive traits are controlled by a large number of genes, typically
379 amounting to several hundreds, leading to a polygenic architecture (Hall *et al.*, 2016). Second,
380 the genetic variation of adaptive traits fuelling local adaptation builds on minor contribution
381 of variation at each single gene and a much larger contribution of the covariation among the
382 different genes (Le Corre & Kremer, 2003; Le Corre & Kremer, 2012). And third, the multiple
383 associations of different genes contributing to adaptive traits, generate genetic redundancy,
384 i.e. the occurrence of different associations resulting to the same phenotype (Yeaman, 2015;
385 Laruson *et al.*, 2020). To sum up, it is not only the cumulative contribution of single gene
386 effects, but also the contribution of the multiple combinatory associations of genes that
387 underpin adaptive variation. While the former contribution has been supported by numerous
388 results in breeding and natural tree populations, the latter contribution was inferred on the
389 basis of the contrasting observed differentiation between adaptive traits and their underlying
390 genes in trees (Kremer & Le Corre, 2012). The polygenic architecture of adaptive traits, the
391 combinatory effects, and genetic redundancy lead to important consequences on tree
392 population evolution. First, large evolutionary changes in adaptive trait values can be
393 triggered by the standing variation of numerous loci, each one of small effect (Sella & Barton,
394 2019; Höllinger *et al.*, 2023). Second, effective selection on standing genetic variation can
395 occur over a limited number of generations (Kremer & Le Corre, 2012; Ehrlich *et al.*, 2021).
396 Third, polygenic architecture and genetic redundancy facilitate the maintenance of variation
397 of adaptive traits (Laruson *et al.*, 2020; Bataillon *et al.*, 2022). As a result, adaptive traits with
398 polygenic redundant architecture enhance genetic resilience. Just as functional redundancy
399 insures community resilience at the species level (Biggs *et al.*, 2020), genetic redundancy may
400 trigger genetic resilience at the population level as variable combinations of redundant alleles
401 offer multiple opportunities to reach optimal fitness at short time scales (Ehrlich *et al.*, 2021).
402 Finally, besides genetic redundancy of the architecture of adaptive traits, there is a second
403 level of redundancy that may be considered concerning resilience, which is redundancy at the
404 genome level. While the evolution of the genome of flowering plants is paved by multiple

405 phases of genome and gene duplications (Wang *et al.*, 2012), recent whole genome sequences
406 of oak species have highlighted the increased duplication of defence related genes (Plomion
407 *et al.*, 2018; Sork *et al.*, 2022). Enrichment of resistance genes was interpreted as a means to
408 withstand variable biotic selection pressures to which long-lived species such as trees are
409 exposed.

410 **2.4. Synergistic contributions of plastic and genetic effects to adaptive evolution**

411 Phenotypic plasticity, defined as the capacity of a given genotype to respond differently to
412 environmental conditions has received much attention in trees that are exposed to repeated ecological
413 changes over their lifetime (Chambel *et al.*, 2005). Empirical assessments of plastic responses of trees
414 have mostly been investigated at the population level in multisite common garden experiments (Park
415 & Rodgers, 2023), starting with the discovery of widespread genotype*environment (GE) interactions
416 in most economically important species (Li *et al.*, 2017). Implicitly, the presence of GE interactions
417 unveiled the underlying different responses of populations to site conditions, that are called norms of
418 reaction and modelled as linear (Gregorius & Kleinschmit, 2001) or quadratic functions (Wang *et al.*,
419 2006) to environmental variables. The slopes (coefficients of the norm of reactions) are the key
420 parameters accounting for the plastic response of the traits. Lessons gained from the assessments of
421 the norms of reaction in multisite common garden experiments can be summarized in four major
422 outcomes. First, the slopes of the norms of reaction at the species or population level are non-zero for
423 most adaptive traits (Chambel *et al.*, 2005; Leites & Benito Garzon, 2023). Second, population
424 differences exist indicating genetic differentiation of plastic responses (Rehfeldt *et al.*, 2002; Sáenz-
425 Romero *et al.*, 2019). Third, genetic variation of plastic responses is maintained within populations
426 (Marchi *et al.*, 2022). Taken together these results indicate that plasticity in trees has a genetic basis
427 and can evolve. However, despite significant differences among populations, the level of genetic
428 differentiation in plasticity among populations remains low and amounts to the magnitude observed
429 for neutral traits in the only known experiment where intra and inter population genetic variation of
430 plasticity were assessed (Soularue *et al.*, 2023). Maintenance of genetic variation and low genetic
431 differentiation among populations of the slope of the norms of reaction suggest that past evolution
432 has generated a «generalist» type response in trees maintained in all populations. Evolution towards
433 an optimum plastic response, where genotypes can reach optimal fitness in all environments, is also
434 predicted by theory for long-lived species experiencing large spatio-temporal environmental
435 heterogeneity and composed of populations connected by extensive gene flow (Scheiner, 2013;
436 Hendry, 2016). The «generalist» type of response increases the ability of populations to persist under

437 a wide range of environmental disturbances and thus contribute to their resilience (Ghalambor *et al.*,
438 2007).

439 Finally, empirical results suggest that plastic and genetic variation contribute synergistically to
440 phenotypic evolution of adaptive traits. Covariation of plastic and genetic effects in the same direction
441 is expected when plastic responses to environmental changes ultimately result in increased fitness
442 thus contributing to the persistence of the species under altered conditions (« Baldwin effect », Crispo,
443 2008). Under this scenario, plasticity first leads to phenotypic changes followed later by genetic
444 changes, but alternative scenarios may occur as well (Crispo, 2008). Whatever the evolutionary
445 sequence in trees, experimental results show that positive covariation of plastic and genetic effects of
446 adaptive traits are more frequent in extant tree populations than negative covariation (Kremer *et al.*,
447 2014, Box 3). Several contemporary studies of variation in tree growth illustrate the positive
448 covariation of plastic and genetic effects. Large scale surveys of tree growth using increment cores
449 conducted *in situ* indicated steady increase of growth during recent decades due to higher atmospheric
450 CO₂ concentration and nitrogen deposits (Maes *et al.*, 2019). Temporal genetic changes assessed in
451 age-structured oak cohorts spanning the last two centuries (Caignard *et al.*, 2024), and genetic changes
452 predicted over two successive generations (Alexandre *et al.*, 2020) showed similar trend for tree
453 growth. In this example phenotypic changes, combining plastic and genetic responses, and genetic
454 changes *per se* covary in the same direction. Monitoring of trait variation conducted *in situ* and in
455 genetic tests (common gardens) exhibit mostly positive covariation of plastic and genetic effects (Box
456 3). Thus, both sources of variation amplify synergistically phenotypic responses to environmental
457 changes and contribute more efficiently to persistence following perturbations.

458

459 **2.5. Sustained local adaptation despite widespread gene flow within species**

460 Most temperate forest trees are anemophilous and able to disperse pollen over long
461 distances. Documented extreme effective pollen dispersal –although rare- may reach
462 hundreds of kilometres and, in Europe, are of the same magnitude as predicted shifts of
463 climate during this century (Kremer *et al.*, 2012). In some species gene flow can also take place
464 by seed as well as via pollen, and in some tree species, e.g. *Sorbus aucuparia*, seed flow may
465 even be more important than pollen flow (Bacles *et al.* 2004). Under such circumstances,
466 whether gene flow would facilitate or constrain adaptation to ongoing climate change has
467 been a pressing issue that has been addressed recently by theoretical and experimental
468 approaches (Savolainen *et al.*, 2007). From a theoretical standpoint, gene flow generates

469 conflicting evolutionary trends (Lopez *et al.*, 2008). On the one hand, gene flow homogenizes
470 allele frequencies among populations across space and increases the lag between the extant
471 genetic value of populations and their expected optimal value, thus generating migration load.
472 On the other hand, gene flow increases the standing genetic variation within populations and
473 enhances their response to natural selection. Recent experimental results at a very local scale
474 suggest that the latter effects of gene flow are dominating in ecological settings of closely
475 located populations (Scotti *et al.*, 2023). Notably, adaptive divergence of nearby populations
476 at individual SNPs is not prevented by extensive gene flow that connects close populations. In
477 four conifers with contrasting life history traits, genomic differentiation correlated to local
478 adaptation was maintained between close populations growing under contrasting
479 environmental conditions. Fine scale comparisons of immigrant with local gene pools
480 indicated indeed that within population genetic variation was increased by gene flow and
481 enhanced adaptive differentiation (Gauzere *et al.*, 2020). In the same vein, the ratio π_0/π_4 ,
482 which measures the efficiency of selection in purging deleterious mutations did not vary
483 across populations in six European forest tree species (James *et al.*, 2023), contrary to
484 expectations that marginal populations would show a higher value than core populations.
485 Altogether these experimental results suggest that gene flow does not constrain adaptive
486 differentiation when divergent selection is strong. Note, however, that the strong short-term
487 response to selection observed at a very local scale may not necessarily translate into high
488 evolutionary rate when large time periods are considered (Messer *et al.*, 2016). A possible
489 explanation is pervasive fluctuating selection as recently suggested by Saleh *et al.* (2022) in
490 oaks and shown in *Mimulus* by (Kelly, 2022). In the latter, out of 1.8 M SNPs, 1796 SNP showed
491 significant fluctuating selection and 40 significant directional selection, the rest behaving
492 neutrally. Conversely, pollen flow may even amplify adaptation by introducing preadapted
493 genes from distant populations into target populations under a directional shifting climate.
494 Theory shows that in a heterogeneous environment changing linearly in space and time
495 mimicking climate change along a geographic gradient, pollen dispersal will shift the ecological
496 niche of a species to match the moving environmental change, and accelerate the shift for
497 species dispersing pollen at long distances (Aguilée *et al.*, 2016). Although we are lacking
498 experimental results supporting these predictions, beneficial effects of pollen flow are likely
499 to overcome negative effects, considering in addition that airborne pollen production of many
500 tree taxa is stimulated by climatic change (Ziello *et al.*, 2012).

501 An extreme case of local adaptation in spite of gene flow is provided by Scots pine (*Pinus*
502 *sylvestris*). Scots pine has one of the largest natural ranges among forest trees extending from
503 Scotland in the west to Russian Pacific Coast in the east and from the Iberian and Balkans
504 mountain ranges in the south to the Barents Sea to the north. A recent rangewide genomic
505 survey showed that genetic differentiation is weak and genetic diversity high and strikingly
506 uniform across the range (Bruxaux *et al.*, 2024). Similarly, the ratio π_0/π_4 , was consistently high
507 and barely varied across populations. Nonetheless, decades of common garden studies (aka
508 provenance tests in the forestry literature) have repeatedly shown evidence of local
509 adaptation. However, in the case of Scots pine, different factors underly local adaptation in
510 different parts of the range, with temperature playing a major role in the central part of the
511 range, drought-related variables in Spain and photoperiod in Scandinavia (Leites and Benito
512 Garzon 2023). Those regional patterns of local adaptation may, at least in part, explain the
513 weak signal of genotype-environment association detected by Bruxaux *et al.* (2024) at the
514 range level and, importantly, together with extensive gene flow maintaining the connections
515 among populations, may have contributed to the maintenance of genetic diversity at the
516 species level.

517 **2.6. Frequent hybridization in trees enhances adaptive introgression**

518 Both hybridization and introgression have occurred frequently in forest trees and
519 hybridization was found to be positively correlated with perenniality (Mitchell *et al.*, 2019).
520 Hybridization between different species and ensuing generations of backcrossing, i.e.
521 introgression, is one of the most efficient genetic mechanisms to quickly introduce vast
522 amount of genetic variation into the genome of a given species (Soltis, 2013). While the
523 importance of hybridization and introgression in plant species has been recognized for nearly
524 a century, a systematic understanding of both processes in plants has only started over the
525 last decades. A first indication of the importance of hybridization and introgression in plant
526 species was revealed by frequent conflict between chloroplastic and nuclear DNA, and
527 between different nuclear genomic regions when reconstructing phylogenetic trees.
528 However, only recently did the development of large-scale genomic sequencing allowed us to
529 gain a global picture of the importance of historical gene flow on the evolution of whole group
530 of species, such as *Ficus* (Gardner *et al.*, 2023), *Fagaceae* (Zhou *et al.*, 2022), *Salix* and *Populus*
531 (*Sanderson et al.*, 2023), and *Picea* (Karunarathne *et al.*, 2024). Even rare introgressed alleles

532 can contribute to increase the number of adaptive mutations, that may be in short supply
533 because of small N_e or low mutation rate. Studies in *Quercus* (Leroy *et al.*, 2020; Fu *et al.*, 2022)
534 have revealed that adaptive introgressed alleles were common across the genome of widely-
535 distributed European and Asian oaks, and that their proportion was influenced by genetic drift
536 and environmental factors (Figure 3). Introgression was affected by genetic divergence
537 between pairs of populations and also by the similarity of the environments in which they
538 live—populations occupying similar ecological sites tended to share the same introgressed
539 regions. Fu *et al.* (2022) further pointed out that i) adaptive introgression did not affect the
540 genes themselves but instead the cis-regulatory elements regulating their expression leading
541 to similar expression profiles of closely related species in the same environment, and that ii)
542 although recombination facilitates the integration of introgressed alleles, suppression of
543 recombination is necessary for the maintenance of adaptive introgressed alleles. Suarez-
544 Gonzalez *et al.* (2016) also identified linked adaptive introgression signals near a telomeric
545 region in two *Populus* species. The suppressed recombination rate may help improve the
546 efficacy of natural selection or reduce the so called ‘segregating load’ by preventing breaking
547 down co-adapted parental alleles (Moran *et al.*, 2021). In summary, while the exact
548 mechanisms underlying adaptive introgression remain to be deciphered, introgression, by
549 increasing the level of genetic diversity and bringing new adaptive alleles, will contribute to
550 the resilience of forest trees.

551

552 **2.7. Demographic dynamics boost genetic rescue**

553 We have so far focused on genetic factors. As resilience was primarily viewed as an important
554 evolutionary property it made sense to focus on those. However, resilience is also intrinsically
555 a demographic property. And, while we have shown above that empirical genetic and
556 evolutionary evidence indicates that tree populations are prone to resilience, our
557 understanding of how resilience is ultimately achieved remains limited. We are still lacking
558 sufficient historical monitoring across generations to grasp the ecological and genetic
559 mechanisms that triggered the recovery of populations to extreme environmental changes.

560 The question arises of how tree populations are maintained after repeated sequences of
561 extreme climatic events that may have lethal consequences. The increased occurrence of

562 extreme climatic events has stimulated worldwide monitoring of tree mortalities (Allen *et al.*,
563 2015). These reviews concentrated mostly on the abiotic causal drivers of mortality, rather
564 than on the subsequent demographic changes in tree populations. Regional studies confirmed
565 that increasing mortalities followed severe drought episodes in Europe (Senf *et al.*, 2020;
566 George *et al.*, 2022). Reported mortality statistics described extreme spatial and temporal
567 variation. Extant observed mortalities are the consequence of the background mortality pre-
568 existing in the population and the die-off generated by the extreme event, which have
569 different temporal dynamics. Even die-off mortalities exhibit extreme spatio-temporal
570 variation due to tree diversity, and microecological variation. Thus, forest stands undergoing
571 dieback are characterized by the simultaneous persistence of dying and surviving trees, a
572 situation that may subsist over years or decades.

573 Overall individual tree mortality, and tree population decline following extreme events is a
574 temporal gradual process (Changenet *et al.*, 2021). The Tree Decline Recovery Seesaw model
575 (Whyte *et al.*, 2016) nicely illustrates the long duration during which tree populations maintain
576 a decline status characterized by the coexistence of dying and surviving trees. One-off total
577 tree mortalities are thus exceptions that may occur after fire or gale events but are unlikely
578 the result of other biotic or abiotic events, including recent extreme droughts (as in 2003 or
579 2018-2019 (Senf *et al.*, 2020)). Canopy opening, resulting from the mortality of adult trees,
580 favors recruitment resulting from open crossing between surviving trees (Martínez-Vilalta &
581 Lloret, 2016). The time period during which partial mortalities will persist under steady state,
582 thus increases opportunities for genetic rescue to proceed by facilitating the renewal of the
583 population. Long distance pollen flow may prevent the break-down of genetic diversity in the
584 recruited seedlings, and thus maintain the adaptive potential in the new generation.
585 Ultimately, as the adult cohort may still be under a steady state decline, the juvenile cohort
586 originating from the surviving adult trees will develop and undergo selective screening under
587 natural selection. Two cohorts following different evolutionary dynamics may then inhabit the
588 same forest: the adult cohort undergoes steady decline while the juvenile cohort, given the
589 higher expected selection intensity in the higher density among the seedlings, undergoes
590 more rapid adaptive shifts to cope with the ongoing environmental changes. The coexistence
591 of both cohorts over longer periods will reinforce the self-replacement as the seedlings may
592 benefit from additional seeding years. In some cases, the two cohorts may be composed of

593 different species and lead to replacement of the pre-existing species (Cerioni *et al.*, 2024).
594 However, self-replacement dynamics have also been observed following severe droughts
595 (Margalef-Marrase *et al.*, 2022) but their genetic consequences remain poorly investigated.
596 Such scenarios combining early expansion of new recruits benefiting from pre-existing genetic
597 diversity will contribute to important adaptive shifts to the ongoing stress episode, while the
598 adult cohort may progressively disappear (“silver-lining” scenario, Coleman&Wernberg,
599 2020).

600 **3. Conclusion**

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

613 While we still have a far from complete understanding of the evolutionary mechanisms
614 contributing to forest tree resilience, some salient features have started to emerge. In
615 particular, one key attribute of forest trees contributing to resilience appears to be their ability
616 to combine large populations connected through extensive gene flow with pronounced local
617 adaptation. This combination of features may have, in turn, enabled forest tree species to
618 maintain high genetic diversity and survive their generally high genetic load. Even factors such
619 as long and overlapping generations time may not have only negative consequences on
620 resilience, and the “storage effect” observed under fluctuating selection could also have
621 contributed to the maintenance of genetic diversity. One practical implication of the present
622 review is that gene flow in forest trees is not something we need to worry about as it did not
623 erase local adaptation and may even have contributed to it (Le Corre and Kremer 2012). Finally

624 rapid adaptive responses to new selection pressures are indeed expected in populations
625 combining high levels of standing genetic variation and polygenic architecture of fitness, and
626 exposed to strong selection intensities (Kremer & Le Corre, 2012; Le Corre & Kremer, 2012).
627 As we highlighted in our review tree species share these attributes, and encounter severe
628 selection intensities during the juvenile phase, thus demonstrating their high evolutionary
629 potential (Box 4).

630 However, our review highlights the lack of understanding of the temporal frames at which
631 these mechanisms are operating in tree populations. As far as possible, we have distinguished
632 short term and long-term processes, as inferred from population genetics or synchronic
633 monitoring in common garden experiments. Temporal dynamics (allochronic approaches) are
634 needed to grasp the pace at which resilience builds up in comparison to the strength and
635 velocity of environmental changes. Yet, we illustrated in a case study that microevolutionary
636 changes could occur rapidly during the transition between the Little Ice Age and the
637 Anthropocene warming. Ancient DNA studies (a few millennia back in time) in trees may be a
638 new avenue to explore temporal dynamics at various time scales. While they are still in their
639 infancy technical breakthroughs will undoubtedly usher a new era in evolutionary biology of
640 forest trees as it did in humans. A second limitation of our review comes from the focus on
641 tree species sharing particular attributes, such as wide and continuous distribution, allogamy
642 and longevity. Because they also share economic importance, their genetics, genomics and
643 evolutionary biology have been more intensely studied, and were thus preferentially prone
644 for a review. It may well be that species with contrasting attributes (e.g., scattered vs narrow
645 distribution, autogamy vs obligate outcrossing, short vs very long lifespan) behave differently.
646 Comparative studies that span these life history traits and emergent attributes of species are
647 needed to gauge the generality of our conclusions. Finally, we have put a bit more emphasis
648 on genomic studies than on quantitative genetics simply because those allow easier historical
649 inferences, not because we believe that quantitative genetics is not relevant. On the contrary,
650 quantitative genetics is certainly going to play a central role in our efforts to understand the
651 resilience of forest trees. Decades-long breeding programs and provenance tests, national
652 forest surveys provide a vast trove of comparative data ready to be analysed. Responding to
653 the urgent conditions presented by ongoing climate change and environmental degradation

654 demand that we keep working with these data to understand tree adaptive capacity and
655 resilience even as we establish new experiments tailored to our evolving questions and needs.
656 Finally our conclusions open new avenues to be explored for operational adaptive
657 management in temperate forests. Among the various mechanisms and properties
658 contributing to resilience that we have highlighted, some are intrinsic to species or
659 evolutionary legacies and can hardly be shaped by human interventions, but others can be
660 refined or manipulated through silvicultural practices. For example, the efficiency of natural
661 selection could readily be improved by increasing the density of seedlings during natural
662 seeding by accumulating seedlings over multiple years of fruiting. Thinning operations
663 following early signals of mortalities due to extreme events should avoid clear cuttings or
664 replacement by new species, but, instead, should facilitate renewal by natural regeneration
665 of the declining species. It is out of the scope of this review to go through all potential
666 applications. Instead, the results presented here should be viewed as a modest stepping stone
667 towards more scientifically-based decisions in the management and conservation of tree
668 species.

669

670 **Acknowledgements:** We would like to thank Richard Ennos, Andrew Hipp, Rémy Petit and
671 Outi Savolainen for constructive comments and suggestions on an earlier version of the paper,
672 and Tongzhou Tao for help with drawing Figure 2. ML thanks FORMAS, the Swedish Research
673 Council for sustainable development (Grant Formas 2020-01456) and the Swedish Energy
674 Agency through the Project Tree for ME for support. This study was also supported by the
675 European Research Council through an Advanced Grant (project TREEPEACE # FP7-339728) to
676 AK.

677

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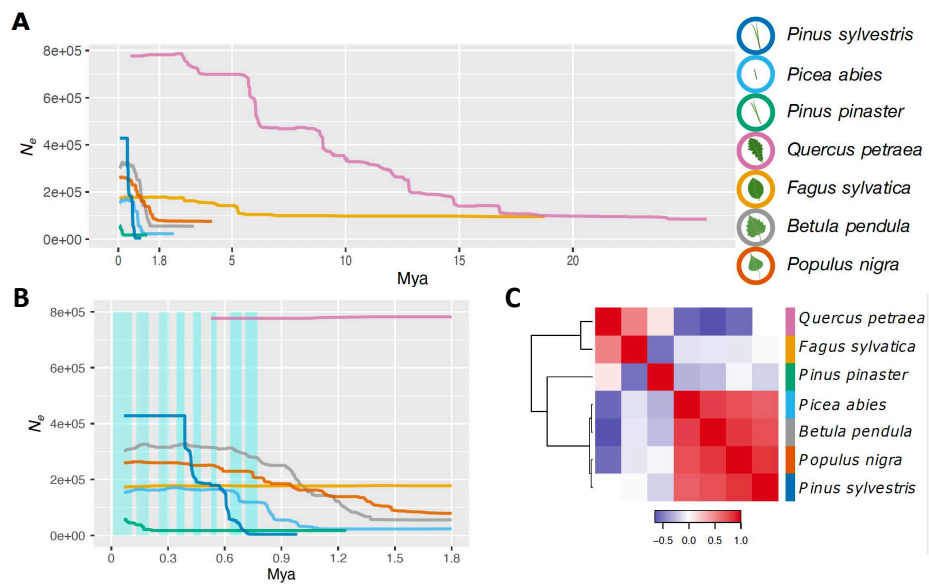
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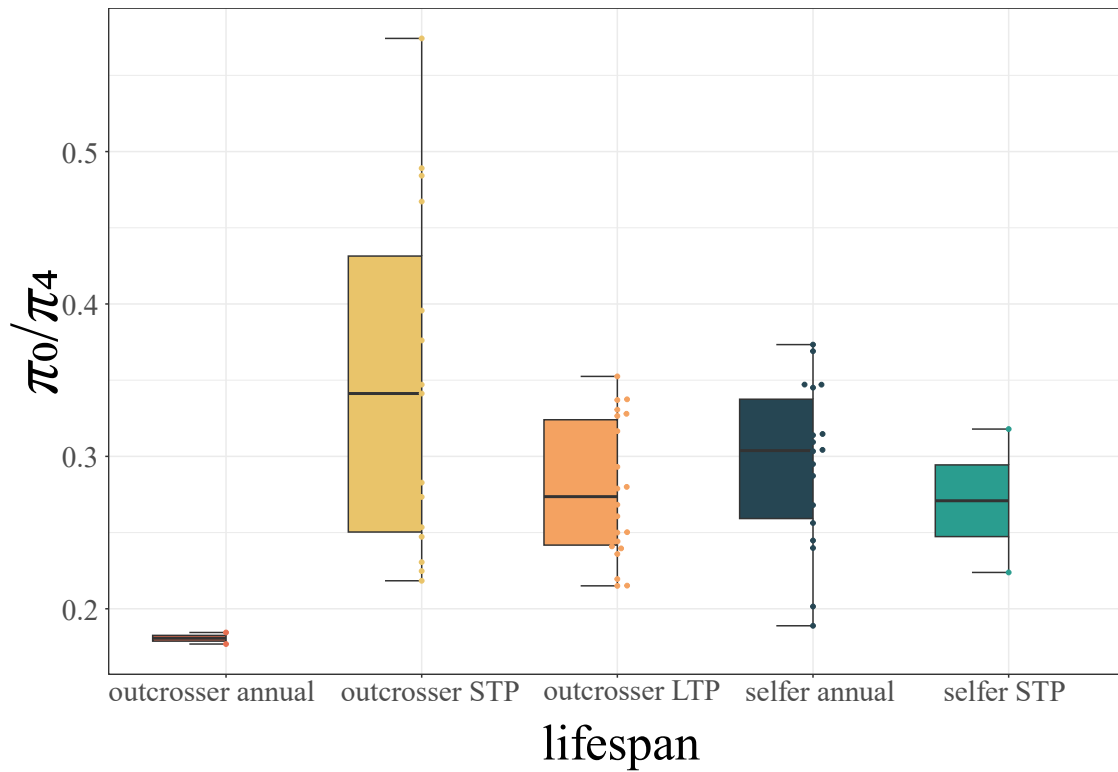
1060 **Figure 1.** Genetic resilience of seven common European tree species. (A) Change in effective
 1061 population size (N_e) through time (million years ago, Mya), inferred with Stairway Plot 2 (lines,
 1062 with one-sample-per-population). The median changes in N_e are reported. (B) A zoom-in of
 1063 (A) focusing on the 0–1.8 Mya period. Blue shaded rectangles delineate periods of glacial
 1064 advance. (C) Species can be grouped based on their N_e -trajectories. Heatmap based on
 1065 Kendall's correlation coefficients computed from changes in N_e through time between each
 1066 pair of species. The order of species along the x-axis is the same as that along the y-axis. Blue
 1067 and red colors represent negative and positive correlation values, respectively. Adapted from
 1068 Milesi et al. (2024).

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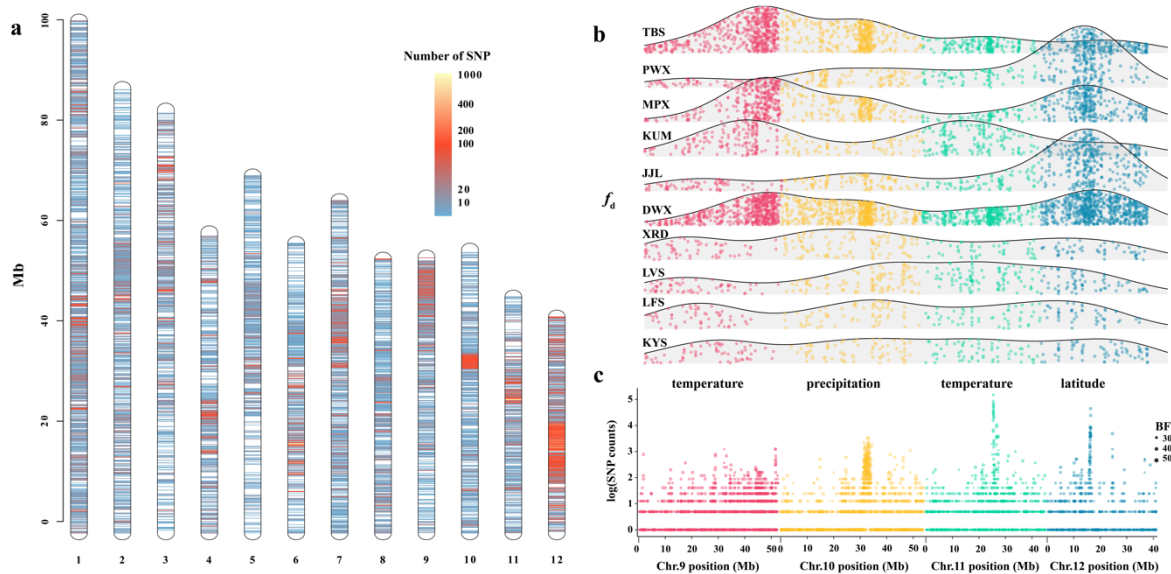
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1075 **Figure 2.** The ratio π_0/π_4 , where π_0 is nucleotide diversity at 0-fold sites (non synonymous) and
1076 π_4 is nucleotide diversity at 4-fold sites (synonymous), differs between combinations of mating
1077 system and lifespan. Each dot corresponds to a species. Box limits indicate the range of the
1078 central 50% of the data, and the central line marks the median value. The ratio π_0/π_4 is as
1079 high in long-term perennials as in annual selfers, suggesting that they accumulate deleterious
1080 mutations at the same rate. STP, short-term perennial; LTP, long-term perennial. The list of
1081 the species used to draw the Figure is given in additional file piNpiS.xlsx .

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1086 **Figure 3.** Distribution of adaptive introgressed SNPs across the genome and their association
 1087 with environmental factors.

1088 **a.** Distribution of the number of SNPs under diversifying selection in windows of introgression
 1089 for *Q. acutissima* 12 chromosomes. The y axis represents the coordinates of chromosomes
 1090 and the x axis represents the 12 chromosomes.

1091 **b.** Density distribution of introgression windows with significant evidence of introgression on
 1092 Chr.9–12. The x axis shows the coordinates of each chromosome that was equally divided into
 1093 512 bins and the y axis gives the number of 10 kb sliding windows with significant evidence of
 1094 introgression. Introgression is estimated by f_d , which quantifies the proportion of genomic
 1095 regions affected by introgression (Martin *et al.* 2005). Each distribution curve corresponds to
 1096 a population whose name is given at the start of the curve.

1097 **c.** All four main introgressed regions in Chr.9–12 are enriched with SNPs with frequency
 1098 significantly associated with environmental/geographical factors (written in bold-face, aligned
 1099 vertically with each major introgression peak represented in panel b and c). The size of the
 1100 dots represents mean Bayesian Factor (BF) across all significant SNPs in the window.

1101 Figure adapted from Fu *et al.* (2022).

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1108 **Box 1 Estimating effective population size**

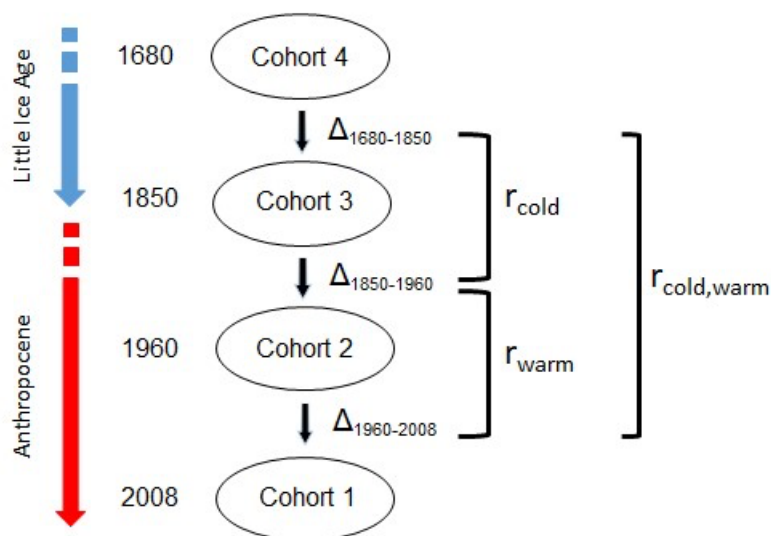
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1110 Classically, the effective size of a population, N_e , is defined as the size of an idealized
1111 population, typically a so-called Wright-Fisher population, that would produce the same rate
1112 of genetic drift as the population of interest (Wakeley 2009). As pointed out by (Waples, 2022)
1113 this definition is technically correct but its rather abstract nature hides the simpler
1114 dependency of N_e on three main demographic parameters: the number of potential parents,
1115 and the mean and variance in the number of offspring per parent (see also (Caballero, 2020)
1116 ch. 5). These three main parameters will, in turn, be influenced by population structure and
1117 selection. The effective population size will rarely be equal to the census number and it is
1118 therefore important to be aware that estimates of N_e only provide indirect information on
1119 past changes in census number. However, N_e is directly related to genetic variation and to the
1120 efficacy of selection, and is therefore indicative of the evolutionary potential of a species.
1121 There are various approaches to reconstruct changes in N_e over time. They differ primarily in
1122 the source of information they are using and this, in turn, determines the time scale on which
1123 inference can be made. Methods based on linkage disequilibrium will retrieve information on
1124 past N_e over a few hundred generations (GONE, Santiago et al. 2020), while methods based
1125 on the site frequency spectrum (StairwayPlot2 (Liu & Fu, 2020), Fitcoal (Hu et al. 2023)), or on
1126 the distribution of heterozygosity along the genome (PSMC (Li & Durbin, 2011), MSMC2,
1127 Schiffels and Wang 2020, SMC++ (Terhorst et al. 2017) will retrieve N_e trajectories across much
1128 deeper times but will have a low resolution for more recent ones. Finally, it is worth stressing
1129 that all these methods do not explicitly consider population structure. Nor do they consider
1130 introgression from other species. So, while the resulting estimates of N_e are good estimates
1131 of the evolutionary potential of the species at a given point in time they should be interpreted
1132 cautiously in term of demography.

1133

1134 **Box 2 Microevolutionary changes during climate transitions**

1135 Assessments of temporal genetic changes in forest trees over successive generations are very
 1136 rare given the time constraints imposed by long-lived species. In a recent study, genome wide
 1137 allelic frequency changes (Δ) were assessed in four different age structured cohorts in sessile
 1138 oak (*Quercus petraea*) even-aged managed forests to track temporal changes during the
 1139 transition from the cold period of the Little Ice Age to the warming Anthropocene (from 1680
 1140 to 2008). The experiment was repeated in three different forests (Saleh *et al.*, 2022). Under
 1141 even-aged silvicultural regimes, natural selection is strongest at the juvenile stage, when more
 1142 than 95% of seedlings are eliminated. These age-driven demographic dynamics were the
 1143 rationale for using a retrospective monitoring of evolutionary changes based on age
 1144 structured cohorts, despite the lack of access to discrete separate generations. To separate
 1145 stochastic genetic changes from one cohort to the next (due to genetic drift or other
 1146 demographic causes) from systematic changes due to natural selection, covariations of Δ
 1147 values were examined over different time periods (for example between $\Delta_{1680-1850}$ and $\Delta_{1850-1960}$).
 1148 Under stochastic sources of variation, the covariations (r) are expected to be zero, while
 1149 similar systematic sources as natural selection will raise positive values, and opposing sources
 1150 will generate negative values (Buffalo & Coop, 2019). The results showed temporal genome-
 1151 wide allelic frequency changes of the same sign during the cold period (r_{cold} positive) and in
 1152 the warm period (r_{warm} positive), the two periods being considered separately (Saleh *et al.*,
 1153 2022). Conversely covariations were negative when comparing Δ values between cold and
 1154 warm periods ($r_{\text{cold,warm}}$ negative). These results were further confirmed at the phenotypic level
 1155 in common garden experiments in which open pollinated progenies originating from the
 1156 different age structured cohorts were compared. In particular genetic changes of height
 1157 growth and phenology related traits were reoriented between the cold and warm period
 1158 (Caignard *et al.*, 2024). Overall, these results show that microevolutionary changes can occur
 1159 over ecological time frames in trees, and that the direction of evolution can change with
 1160 climate change.



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1163 **Box 3 Positive covariation of plastic and genetic effects in trees**

1164 Covariation of plastic and genetic effects can be assessed in trees by comparing genetic and phenotypic
1165 clines in common gardens and *in natura*. When different populations stemming from different
1166 geographic origins are compared under common garden conditions, most adaptive traits exhibit
1167 continuous population variation along some ecological gradient of their origins (Morgenstern, 1996;
1168 Leites & Benito Garzon, 2023). This pattern, called genetic cline, is the consequence of past divergent
1169 selection along the ecological gradient. Genetic clines can be compared to phenotypic clines, resulting
1170 from observations of the same traits made *in natura* along the same ecological gradient, and which
1171 are mostly shaped by plastic responses (Conover & Schultz, 1995; Conover *et al.*, 2009). When both
1172 clines are oriented along the same direction, cogradient variation ensues (Conover *et al.*, 2009) and
1173 plastic effects amplify adaptive genetic variation. However, when the two clines are in opposite
1174 directions, countergradient variation occurs (Conover *et al.*, 2009) and plastic effects then offset
1175 genetic effects. We illustrate co- and counter-gradient variation for growth (panel a and b) and seed
1176 weight (panel c and d) in sessile oak (Caignard *et al.*, 2021) along an elevational gradient in the French
1177 Pyrénées. Height growth and seed weight were assessed in oak stands at various altitudes (panel a and
1178 c). The same traits were measured on offsprings collected on the same trees and raised in a common
1179 experiment (panel b and d). Both traits show clinal genetic and phenotypic variation, but positive
1180 covariation (cogradient) for height growth, and negative covariation (countergradient variation) for
1181 seed weight. The comparison of genetic and phenotypic clines for various adaptive traits (including
1182 growth, phenology, physiology and morphology) in oaks and eucalyptus showed that co-gradient
1183 variation was over-represented (Kremer *et al.*, 2014) in comparison to counter gradient variation.
1184 Reported examples of counter gradient variation were interpreted as the consequence of
1185 compensation between environmental and genetic sources of variation (Caignard *et al.*, 2021).

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1188 Figure adapted from Caignard *et al.*, 2021

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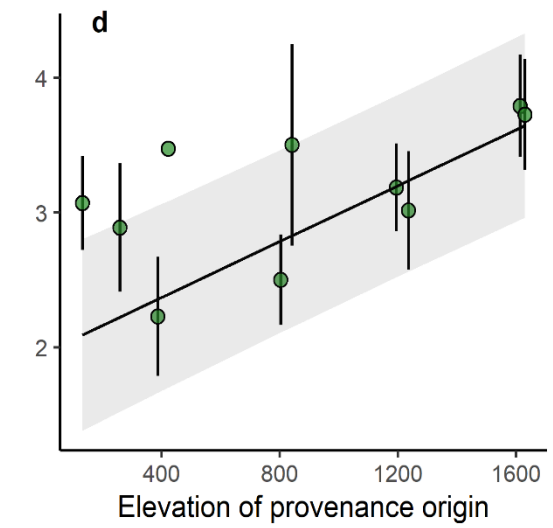
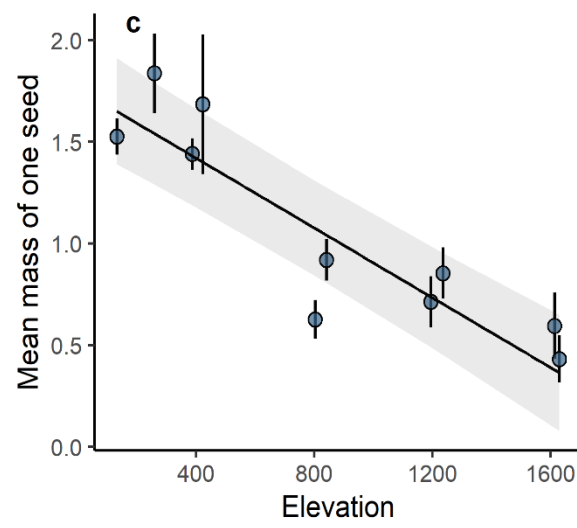
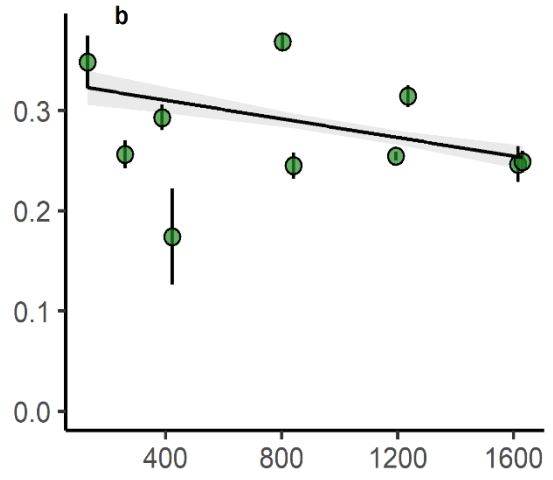
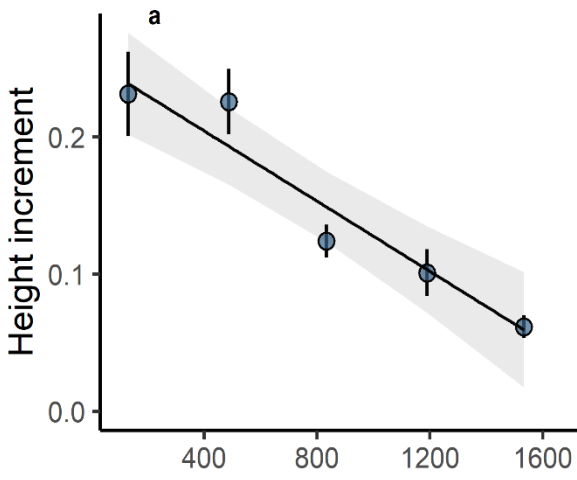
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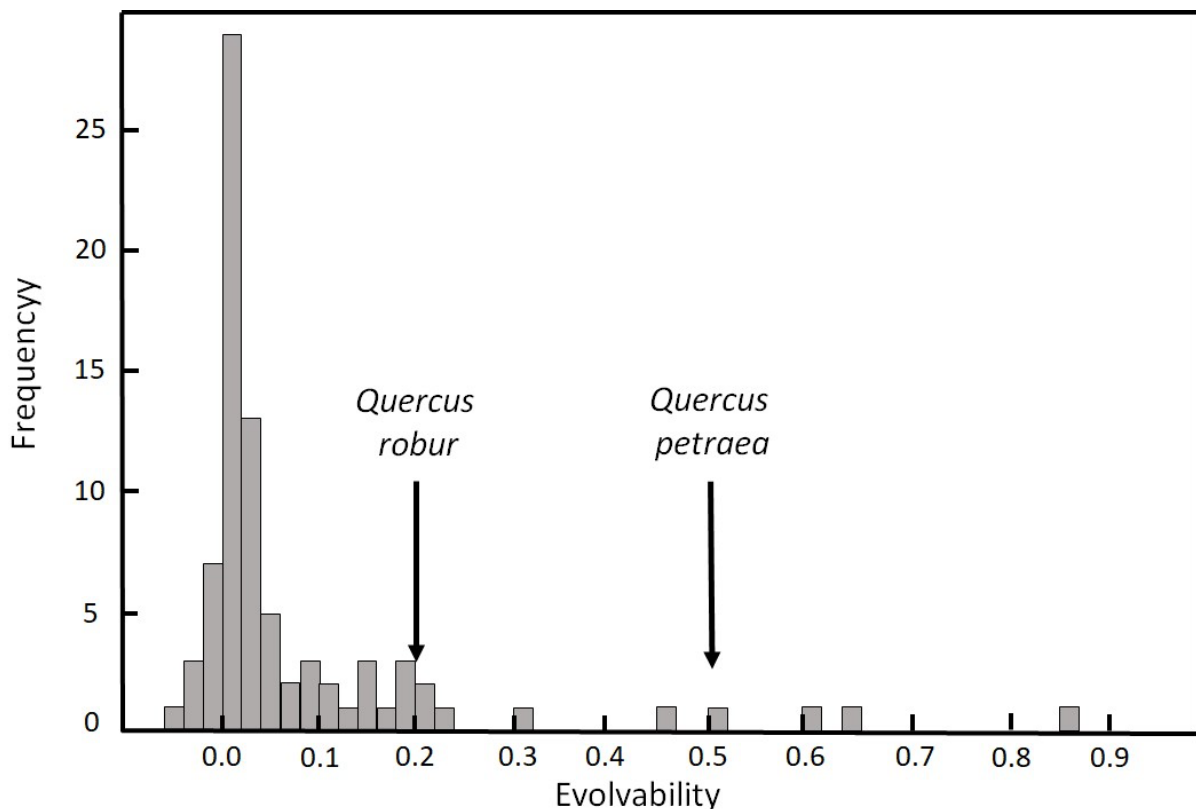
1206 **Box 4 Evolvability and evolutionary potential of oaks**

1207 Fitness of an adult tree can be assessed by the number of surviving descendants it produces
1208 (as a male or female parent) in the next generation and having reached the same age as the
1209 parent tree. Its estimation *in situ* therefore requires access to two successive generations in
1210 the same population, and the reconstruction of the genetic relatedness between the trees of
1211 the two generations based on parentage analysis. Its measurement in the forest is therefore
1212 laborious and handicapped by the experimental constraints linked to the forest context. The
1213 mean standardized genetic variance of fitness within a population provides an estimate of the
1214 evolvability of this population, which corresponds to its evolutionary potential (Hansen *et al.*,
1215 2011; Hansen *et al.*, 2019). It measures the expected increase in fitness resulting from the
1216 response to selection on all adaptive traits, which can be interpreted as a component of
1217 resilience. Recently, fitness assessments of adult trees in a mixed forest of pedunculate oak
1218 (*Q. robur*) and sessile oak (*Q. petraea*) were carried out (Alexandre *et al.*, 2020) and their
1219 evolvabilities compared to measurements available in other plant and animal species that
1220 were compiled in a review (i.e. 82 estimates, (Hendry *et al.*, 2018)). The attached graph,
1221 adapted from Hendry *et al.*, 2018, positions the values obtained for the two oaks (arrows)
1222 as compared to the distribution observed for the 82 values in plants and animals (distribution in
1223 grey). This example illustrates the remarkable evolutionary capacities of trees in comparison
1224 to other animal or plant species, suggesting that they are prone to resilience.

1225

1226 Figure adapted from (Hendry *et al.*, 2018) and (Alexandre *et al.*, 2020)

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