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► **To cite this version:**

Thomas Caignard, Laura Truffaut, Sylvain Delzon, Benjamin Dencausse, Laura Lecacheux, et al..
Fluctuating selection and rapid evolution of oaks during recent climatic transitions. *Plants, People,
Planet*, 2024, 6 (1), pp.221-237. 10.1002/ppp3.10422 . hal-04213282

HAL Id: hal-04213282

<https://hal.inrae.fr/hal-04213282v1>

Submitted on 21 Sep 2023

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RESEARCH ARTICLE

Fluctuating selection and rapid evolution of oaks during recent climatic transitions

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Funding information

European Research Council, Grant/Award Number: FP7-339728; French Forest Service; ANR, Grant/Award Numbers: ANR-10-LABEX45, ANR-20-IDES-0001, ANR-19-CE32-0008

Societal Impact Statement

The rapidity of evolutionary changes in trees and whether this pace is sufficient to cope with ongoing climatic change are hotly debated issues in ecology today. Climate warming began in the mid-19th century, after the Little Ice Age (LIA). Monitoring temporal genetic changes during this climatic transition in multicentennial oak populations revealed evidence of fluctuating selection and rapid evolution. These findings suggest that rapid evolution is probably also currently underway. They may lead to management options for operational forestry aiming to stimulate evolutionary mechanisms during the renewal of oak stands and to decrease potential temporal gene flow.

Summary

- Retrospective studies of the evolutionary responses of tree populations to past documented climate change can provide insight into the adaptive responses of these organisms to ongoing environmental changes. We used a retrospective approach to monitor genetic changes over time in multicentennial sessile oak (*Quercus petraea* L.) forests.
- We compared the offspring of three age-structured cohorts (340, 170, and 60 years old, dating from about 1680, 1850, and 1960) spanning the late Little Ice Age and early Anthropocene. The experiment was repeated in three different forests in western France. The offspring were raised in a common garden experiment, with 30 to 53 open-pollinated families per cohort.
- We assessed 16 phenotypic traits in the common garden and observed significant shifts between cohorts for growth and phenology-related traits. These shifts were correlated with differences in the prevailing temperatures in the past and could be interpreted as temporal genetic changes. However, there was no temporal trend for genetic variation. The genetic changes between the cold (late Little Ice Age) and warm (early Anthropocene) periods were mostly opposite for growth and phenology-related traits.
- These findings highlight fluctuations of selection and a rapid evolutionary response of tree populations to climatic transitions in the past, suggesting that

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similar trends may be at work now. We discuss these results in terms of the mode and direction of evolution, and their potential implications for the adaptive management of oak forests.

KEYWORDS

Anthropocene, evolution, growth, Little Ice Age, phenology, *Quercus*

1 | INTRODUCTION

Lessons from the past can help us to understand the present and the future. Retrospective studies of the evolutionary responses of tree populations to past climate change can teach us about the adaptive capacities of these organisms and their responses to ongoing environmental changes. Climatic reconstructions of the last millennium based on various approaches (Anchukaitis et al., 2017; Corona et al., 2010; Luterbacher et al., 2016; Neukom et al., 2019; Wang et al., 2019) have revealed a consistent pattern of warmer climates during the Medieval period (950–1350) followed by a much cooler period between approximately 1450 and 1850. This 400-year-long period is known as the Little Ice Age (Matthes, 1939; Tkachuck, 1983). In the northern hemisphere, mean summer temperatures decreased by 0.5°C to 2°C between the Medieval Warm Period (MWP) and the Little Ice Age (LIA) and then increased again by more than 1.5°C to present times (Anchukaitis et al., 2017; Corona et al., 2010; Wanner et al., 2022). The causes of the LIA remain a matter of debate (Crowley, 2000; Nesje & Dahl, 2003; Owens et al., 2017; Palastanga et al., 2011; Ruddiman et al., 2016; van Oldenborgh et al., 2013; Wanner et al., 2022), but this period clearly had a major impact on agriculture and society (Fagan, 2002; Parker, 2013; Pfister, 1984a, 1984b). The LIA was dominated by cooler temperatures and a higher frequency of extreme winters and summers (Fagan, 2002; Le Roy Ladurie, 2004; Le Roy Ladurie, 2006; Pfister, 1984a) than in modern times (Cook et al., 2015; Rousseau, 2012; Van Engelen et al., 2001). Thus, climate warming during the Anthropocene is considered to have started in the mid-19th century, with an acceleration during the late 20th century. These climatic changes triggered latitudinal and elevational changes in the tree line (Camarero et al., 2015; Helama et al., 2020; Kullman, 2015; Kullman & Öberg, 2022). Historical records also report severe damage in forests, including the deaths of many trees following extreme winters (Avila & Avila, 1987; Hausendorff, 1940; Schnitzler, 2020) during the LIA. Retrospective studies of past phenotypic changes in trees have been a major area of research in dendroecology based on wood increment cores, but longitudinal observations of microevolutionary trajectories during past environmental changes remain scarce (Dauphin et al., 2021; Saleh et al., 2022) despite the recent interest in time-series approaches based on genomics (Garcia-Elfring et al., 2021; Saleh et al., 2022; Snead & Alda, 2022; Snead & Clark, 2022). However, multicentennial tree populations have experienced these major environmental changes during their lifetime, and these changes may have contributed to significant evolutionary changes (Garcia & Arroyo, 2020).

Explorations of historical trajectories can provide answers to key questions about the current and future adaptive responses of tree populations (Mitchell & Whitney, 2018; Neophytou et al., 2022). What is the mode and direction of evolution during climatic transition, such as the transition from a cold to a warm climate that occurred from the late LIA to the Anthropocene warming, and how fast does evolution occur in such conditions? Is the trend of continuous increase in growth in trees during the Anthropocene climate warming adaptive?

The experimental assessment of recent evolutionary change in forest trees remains challenging due to biological constraints and possible confounding sources of temporal variation in long-lived species. For example, resurrection experiments (Franks et al., 2018; Gomez et al., 2018) cannot be implemented over such long-time frames as the long-term storage of tree seeds, and of acorns in particular, is not possible. We used a retrospective *in situ* approach to assess temporal genetic changes in *Quercus petraea* (sessile oak), a long-lived oak species widespread in Europe. We made use of populations that have persisted over several centuries, from which we were able to sample age-structured cohorts dating back to the mid-17th century, in the LIA. The offspring of open-pollinated families collected in three cohorts (340, 170, and 60 years old) from three forests were raised and compared under common-garden conditions to estimate temporal genetic changes in multiple phenotypic traits. The time periods sampled encompass the climatic transition from the late LIA, a relatively cold period, to early Anthropocene warming. We previously addressed genomic changes in the same sampled material (Saleh et al., 2022). We found that the climatic transition between the LIA and modern times resulted in genome-wide imprints of natural selection during the LIA and Anthropocene warming (Saleh et al., 2022). These findings led us to explore the targets of natural selection at the phenotypic level. We investigated whether these climatic transitions had triggered shifts due to directional selection in sessile oak (*Q. petraea*) populations. Had selection fluctuated and generated different adaptational pathways, ultimately resulting in extant coexisting age-structured cohorts selected for different optimal phenotypes? We focused on multiple putatively adaptive juvenile traits likely to respond to strong selection during the early life of the tree, and we addressed the phenotypic targets of selection. Are the evolving traits currently displaying changes in phenotype in forests? Finally, by repeating our experiment in three different forests, we addressed the question as to whether genetic changes underlying shifts in phenotypic traits display parallel or contrasting evolution in different populations subjected to similar climatic transitions.

2 | MATERIALS AND METHODS

2.1 | Sampling of forests and cohorts

Three oak forests located in central and western France, comprising some of the oldest stands in the country were selected for this study (Bercé, Réno-Valdieu, and Tronçais, Figure S1, Table 1). These national forests have been managed under even-aged regimes since the 17th century and are, thus, subdivided into compartments of different ages, all trees within a compartment being of about the same age. Documentary records available from the successive management plans provide convincing clues to the natural origin of these three forests, which have been continually renewed by natural regeneration, resulting from open mating between mature trees. Further evidence of a natural origin is provided by the fixation of the same chloroplast haplotype within each forest (Petit et al., 2002). We sampled four compartments from each forest, corresponding to four age-class cohorts (340, 170, 60, and 12 years old, dating from about 1680, 1850, 1960, and 2008), but only the three oldest were analyzed in this study as the youngest did not produce any seed (Table 1). The ages of the cohorts were confirmed by the documentary records of each forest and dendrochronological data collected from increment cores from the sampled trees in each cohort (Table 1). Dendrochronological records provided information about the approximate time period for the recruitment of each cohort (Figure S2). The forests and cohorts were described in more detail in a previous article addressing genomic differentiation between the cohorts (Saleh et al., 2022). Under even-aged management, tree densities are greatly decreased during the juvenile phase (before the age of 10 years) by natural selection, competition for resources, and exposure to biotic pressures (Jarret, 2004). As a result, selection pressures on the cohorts sampled here would have been strongest in the early years of their establishment. This rationale supports our retrospective approach to investigating genetic changes over time. Here, we compared the offspring of the different cohorts in a common garden experiment. In the fall of 2014, open-

pollinated families from 30 to 53 trees (per cohort) were collected from the ground, for the three oldest cohorts (Table 1). The youngest cohort did not produce any seed as it was only 6 years old, and the seed crop was very poor in the Réno-Valdieu forest, which led us to postpone acorn collection from this forest until the fall of 2015. Pollination by trees located outside of the cohorts in neighboring compartments may have occurred. However previous studies on pollination distances in even-aged stands reported maximum observed and estimated distances lower than 300 m (Gerber et al., 2014), thus suggesting that external pollination, if it occurred, was limited to trees located at the edges of the cohort, as the area of cohorts varied between 10 and 30 ha (Table 1).

2.2 | Common garden experiment

Seeds from the Tronçais and Bercé forests were sown in the spring of 2015 in the nursery of the INRAE Pierroton research station in South West France (44°44'N, 00°46'W). The experimental layout was a complete block design with three replicates; open-pollinated families were randomly allocated to row plots in each block, regardless of the cohort or forest from which they originated. Each plot was sown with 40 seeds, at 5 cm intervals. The same layout was repeated in the spring of 2016 for the families collected from the Réno-Valdieu forest. In total, 294 open-pollinated families from the three forests and the three cohorts within each forest were sown in the experiment. During winter 2018–2019, the whole experiment, including the families of all three forests, was transplanted to another site in the same nursery, with a large spacing between plants (1.40 m between rows and 0.8 m between saplings in a row) and conservation of the same three complete-block experimental layout. Plot identity was maintained during transplantation. Families were replicated in linear plots of four offspring. Thus, the sample size per family was reduced by a factor of 10 during transplantation, between the seedling and sapling stages. Sampling of first-year seedlings to be transplanted was done

TABLE 1 Age-structured cohorts of oak taken from three French forests since 1680, with mean temperature for each cohort.

Forest (area, ha)	Cohort	Dates of establishment according to management documents	Dates of establishment according to dendrochronological data ^a	Area of compartments (ha)	Sample size (number of families)	Mean temperature during the recruitment period (°C)
Bercé (5,405 ha)	B2	1957	1954–1963 (3)	28	30	10.98
	B3	1855	1856–1858 (3)	28	30	10.30
	B4	1687	1675–1713 (18)	21	30	10.26
Réno-Valdieu (1645 ha)	R2	1959	1959–1973 (26)	10	32	10.12
	R3	1854	1820–1857 (3)	12	36	9.49
	R4	1704	1665–1731 (10)	13	38	9.49
Tronçais (10,600 ha)	T2	1961	1953–1962 (10)	19	53	11.01
	T3	1833	1841–1852 (3)	16	34	9.50
	T4	1671	1654–1677 (4)	28	33	9.86

^aEarliest and latest dates assessed based on the rings visible in the stump. The numbers in brackets indicate the number of trees felled for the assessment.

systematically by selecting the first four seedlings in a plot. Thus, families from Bercé and Tronçais were raised from the first to the fourth growing season as seedlings and were then transplanted as saplings for observations from growing seasons 5 to 7. For the families from Réno-Valdieu, the seedling stage lasted from the first to the third growing season and the sapling stage, during which observations were performed, lasted from the fourth to the sixth growing season.

2.3 | Historical and contemporary climatic data

High-resolution (1 km coarse resolution) temperature data were reconstructed from the late LIA onwards with Luterbacher's database (Luterbacher et al., 2004). These reconstructions were based on a combination of instrumental data, documentary records, and ice core and tree ring proxy data (Luterbacher et al., 2004). Mean monthly temperatures were retrieved for each forest back to 1660 (Figure S2). These reconstructions made it possible to extract the temperatures prevailing at the time of recruitment of each cohort.

Current temperature data were monitored hourly to account for microgeographic variations between the cohorts in each forest over a period of three complete years (2018, 2019, and 2020). Air temperature was recorded with data loggers (HOBO Pro RH/Temp, Onset Computer Corporation, Bourne, MA, USA) for each cohort and forest (nine locations/populations). All sensors were intercalibrated in the laboratory before installation. At each site, sensors were installed 1.5 m above the ground in an open area within the studied population. Sensors were protected by a white plastic shelter, to prevent exposure to rain or direct sunlight. Data were recorded hourly, from the beginning of 2018 to the end of 2020.

2.4 | Phenotypic assessments in the common garden

Numerous traits of adaptive and functional significance related to growth, phenology, and physiology were assessed in the common garden at the seedling or sapling stage (Table 2). Briefly, we monitored spring (leaf unfolding: LU), fall (leaf senescence: LS), and winter (marcescence: MA) phenology, growth-related traits (see Table 2), mean leaf area (MLA), specific leaf area (SLA), carbon and nitrogen content (C and N), and the isotopic composition ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for C and N, respectively) of leaves. These traits and the protocols for their measurement have been described elsewhere (Alexandre et al., 2019, 2020). We also included powdery mildew infection among the set of phenotypic traits measured, as powdery mildew (PW) was introduced into Europe during the time period studied and may have affected oak populations (Desprez-Loustau et al., 2019). Most assessments were made on single trees (offspring of the open-pollinated families), but physiological traits assessed on leaves were evaluated on bulk collections of leaves within plots or within open-pollinated families (Table 2). Phenological traits were monitored in successive years (Table 2).

2.5 | Differentiation of cohorts

2.5.1 | Single-trait differentiation

For all traits, we used linear mixed models to assess the genetic differentiation between cohorts within each forest. In ANOVA format, the linear mixed model used can be expressed as follows:

$$Y_{ijklm} = \mu + F_i + C_j + (F * C)_{ij} + f_{ijk} + b_l + \varepsilon_{ijklm} \quad (1)$$

where μ is the overall mean, Y_{ijklm} is the phenotypic value of tree m belonging to family k of cohort j located in forest i and growing in block l , F_i is the effect of forest i , C_j is the effect of cohort j , $(F * C)_{ij}$ is the interaction effect between forest i and cohort j , f_{ijk} is the effect of family k of cohort j located in forest i , b_l is the effect of block l , and ε_{ijklm} is the residual effect due to tree m .

Symbols in upper case (forest and cohort) correspond to fixed effects, whereas symbols in lower case correspond to random effects. We restricted our analysis of interactions to the forest*cohort interaction. For phenology (LU, LS, and GSL); we also added year as a random effect, as these traits were monitored in 2016, 2017, and 2019 for the Bercé and Tronçais forests and in 2017 and 2019 for the Réno-Valdieu forest. For growth traits (HT and DIA), seed weight was introduced into the model as a covariate to account for potential maternal effects. For count data, we ran a general linear model with a Poisson distribution (Table 3). General linear mixed effect models were fitted to model (1) using glmmTMB (Brooks et al., 2017) and residual distributions were checked with the DHARMA package (Hartig, 2022). All analyses were performed using R (version 4.2.2, R Development Core Team, 2022).

2.5.2 | Multitrait differentiation

Principal component analysis (PCA) was performed using family mean values for all traits, to determine the overall direction of cohort differentiation within each forest. PCA based on the mean values for open-pollinated families was performed separately for each forest using FactorMineR (Lê et al., 2008).

2.5.3 | Temporal climate-driven differentiation

We investigated whether cohort differentiation was triggered by differences in the temperatures prevailing during the recruitment periods of the three cohorts, with the following model:

$$Y_{ijk} = \beta_0 + \beta_1 T_{ij} + \beta_2 S_{ij} + \beta_3 F_i + \beta_4 (F_i * T_{ij}) + \beta_5 C_j + \varepsilon_{ijk}, \quad (2)$$

where Y_{ijk} is the mean phenotypic trait value of family k belonging to cohort j in forest i , β_0 is the intercept, T_{ij} is the average historical temperature prevailing in forest i at the time when cohort j in forest i was established (Figure S2), S_{ij} is the temperature prevailing from 2018 to

TABLE 2 Description of the phenotypic traits for oak trees used to assess their temporal genetic responses to climate change.

Trait class	Trait abbreviation	Trait definition	Trait units	Growing season of assessment ^a	Unit of assessment	Sampling rules
Phenology	LU	Julian day of leaf unfolding	Number of days	2,3,5 (2,4)	Single tree	10 trees/plot at the seedling stage, 4 trees/plot at the sapling stage
	LS	Julian day of leaf senescence	Number of days	2,3,5 (2,4)	Single tree	10 trees/plot at the seedling stage, 4 trees/plot at the sapling stage
	GSL	Length of growing season	Number of days	2,3,5 (2,4)	Single tree	10 trees/plot at the seedling stage, 4 trees/plot at the sapling stage
	MAR	Marcescence	Score	7 (6)	Single tree	4 trees/plot
Growth	NF	Number of flushes	Count	2 (2)	Single tree	5 trees/plot
	MFL	Mean flush length	cm	2 (2)	Single tree	5 trees/plot
	HT	Total height	cm	7 (6)	Single tree	4 trees/plot
	DIA	Diameter at the collar	Mm	7 (6)	Single tree	4 trees/plot
Physiology	C	Carbon content of leaves	g/kg	2 (3)	Open-pollinated family	Bulk of 3 plots/family
	N	Nitrogen content of leaves	g/kg	2 (3)	Open-pollinated family	Bulk of 3 plots/family
	C/N	Carbon/nitrogen ratio	Ratio	2 (3)	Open-pollinated family	Bulk of 3 plots/family
	$\delta^{13}\text{C}$	Leaf carbon isotope (^{13}C) composition	‰	2 (3)	Open-pollinated family	Bulk of 3 plots family
	$\delta^{15}\text{N}$	Leaf nitrogen isotope (^{15}N) composition	‰	2 (3)	Open-pollinated family	Bulk of 3 plots family
	MLA	Mean leaf area	cm ²	2 (3)	Plot	Bulk of 5 trees/plot of 3 plots
	SLA	Specific leaf area	m ² /kg	2 (3)	Plot	Bulk of 5 trees/plot of 3 plots
Disease resistance	PW	Powdery mildew	Index	6 (5)	Single tree	

^aGrowing seasons within brackets correspond to the material collected in the Réno-Valdieu Forest.

2020 in the site where cohort j in forest i is growing, and S_{ij} accounts for microgeographic temperature differences between cohorts. F_i is the effect of forest i . $F_i * T_{ij}$ is the interaction effect of forest i and the historical temperature T_{ij} , c_{ij} is the effect of cohort j in forest i (random effect), and ε_{ijk} is the residual effect of family k (random effect).

In addition to the historical temperature (T_{ij}), we added in the model modern temperature (S_{ij}) assessed during the last 3 years (2018, 2019, and 2020) in the cohorts, which allowed us to estimate climate-driven genetic differentiation due to two different potential sources:

- temporal changes during the transition from the Little Ice Age to the Anthropocene
- microgeographical variations due to different locations, yet close, of the different cohorts

As traits were assessed at different levels (individual tree, plot, or family), the phenotypic value used for running model (2) (Y_{ijk}) was the

family mean value. Finally, the computation of model (2) was run on standardized data (reduced centered values of Y_{ijk}) so that comparisons of the β coefficients could be made among the different traits that were assessed with different metric units. General linear mixed effect models were fitted to model (2) using glmmTMB (Brooks et al., 2017) and residual distributions were checked with the DHARMA package (Hartig, 2022).

2.6 | Changes in genetic variation

We estimated the genetic variation of traits that were assessed at the single tree level (Table 1), using the subdivision of each cohort into open-pollinated families. We applied the following model separately within each cohort:

$$Y_{klm} = \mu + f_k + B_l + \varepsilon_{klm} \quad (3)$$

TABLE 3 Differences observed between forests and cohorts for the 16 traits assessed in the common garden experiment.

Trait class	Trait (GPD) ^a	Fixed effect	<i>p</i> value ^b	Mean values ^c		
Phenology	LU (G)	Forest	<.001	B: 100.3	R: 100.2	T: 105.3
		Cohort	<.001	C ₁₆₈₀ : 102.9	C ₁₈₅₀ : 101.9	C ₁₉₆₀ : 102.4
		Forest × cohort	<.001			
	LS (G)	Forest	<.001	B: 329.3	R: 324.8	T: 328.0
		Cohort	<.001	C ₁₆₈₀ : 327.6	C ₁₈₅₀ : 327.4	C ₁₉₆₀ : 328.1
		Forest × cohort	.006			
	GSL (G)	Forest	<.001	B: 229.0	R: 224.6	T: 222.7
		Cohort	.0612	C ₁₆₈₀ : 224.7	C ₁₈₅₀ : 225.5	C ₁₉₆₀ : 225.7
		Forest × cohort	<.001			
	MAR (P)	Forest	.013	B: 0.57	R: 0.58	T: 0.47
		Cohort	.011	C ₁₆₈₀ : 0.52	C ₁₈₅₀ : 0.49	C ₁₉₆₀ : 0.6
		Forest × cohort	.140			
Growth	NF (P)	Forest	<.001	B: 5.50	R: 6.60	T: 5.31
		Cohort	.246	C ₁₆₈₀ : 5.83	C ₁₈₅₀ : 5.81	C ₁₉₆₀ : 5.76
		Forest × cohort	.329			
	MFL (G)	Forest	.004	B: 327.5	R: 376.1	T: 335.7
		Cohort	.010	C ₁₆₈₀ : 338.9	C ₁₈₅₀ : 346.4	C ₁₉₆₀ : 355.3
		Forest × cohort	.472			
	HT (G)	Forest	.008	B: 66.0	R: 69.9	T: 61.4
		Cohort	.012	C ₁₆₈₀ : 64.6	C ₁₈₅₀ : 62.2	C ₁₉₆₀ : 70.0
		Forest × cohort	.167			
		Acorn weight	.814			
	DIA (G)	Forest	<.001	B: 14.8	R: 16.1	T: 13.3
		Cohort	.001	C ₁₆₈₀ : 14.7	C ₁₈₅₀ : 13.9	C ₁₉₆₀ : 15.4
Forest × cohort		.136				
Acorn weight		.039				
Physiology	C (G)	Forest	<.001	B: 459.0	R: 453.3	T: 459.3
		Cohort	.492	C ₁₆₈₀ : 458.0	C ₁₈₅₀ : 457.0	C ₁₉₆₀ : 456.4
		Forest × cohort	.013			
	N (G)	Forest	<.001	B: 20.	R: 19.2	T: 20.4
		Cohort	.065	C ₁₆₈₀ : 20.2	C ₁₈₅₀ : 19.9	C ₁₉₆₀ : 19.7
		Forest × cohort	.029			
	C/N (G)	Forest	<.001	B: 23.0	R: 23.8	T: 22.6
		Cohort	0.140	C ₁₆₈₀ : 22.8	C ₁₈₅₀ : 23.2	C ₁₉₆₀ : 23.4
		Forest × cohort	0.016			
	δ ¹³ C (G)	Forest	<.001	B: -27.6	R: -28.7	T: -27.0
		Cohort	0.200	C ₁₆₈₀ : -27.7	C ₁₈₅₀ : -27.7	C ₁₉₆₀ : -27.9
		Forest × cohort	0.002			
	δ ¹⁵ N (G)	Forest	<.001	B: 0.22	R: 0.87	T: 0.6
		Cohort	0.003	C ₁₆₈₀ : 0.58	C ₁₈₅₀ : 0.47	C ₁₉₆₀ : 0.67
		Forest × cohort	<.001			
	MLA (G)	Forest	0.076	B: 22.3	R: 23.3	T: 23.0
		Cohort	0.151	C ₁₆₈₀ : 23.1	C ₁₈₅₀ : 22.3	C ₁₉₆₀ : 23.2
		Forest × cohort	<.001			
SLA (G)	Forest	<.001	B: 131.4	R: 120.2	T: 131.4	
	Cohort	0.278	C ₁₆₈₀ : 128.6	C ₁₈₅₀ : 127.8	C ₁₉₆₀ : 126.6	

TABLE 3 (Continued)

Trait class	Trait (GPD) ^a	Fixed effect	p value ^b	Mean values ^c		
		Forest × cohort	0.131			
Disease resistance	PM (G)	Forest	0.005	B: 1.19	R: 1.42	T: 1.16
		Cohort	0.313	C ₁₆₈₀ : 1.22	C ₁₈₅₀ : 1.28	C ₁₉₆₀ : 1.26
		Forest × cohort	0.868			

Note: C₁₆₈₀, C₁₈₅₀, and C₁₉₆₀ stand for the three age-structured cohorts.

Abbreviations: B, Bercé; R, Réno Valdieu; T, Tronçais.

^aTrait abbreviations as defined in Table 2. GPD: GLM probability distribution (G: Gaussian; P: Poisson).

^bp value according to Chisq tests of the main effects (Forest and Cohort) and the interaction Forest × cohort.

^cUnits of mean values according to Table 1.

where Y_{klm} is the phenotypic value of tree m belonging to family k and located in block l , μ is the overall mean, f_k is the effect of family k (random effect), B_l is the effect of block l (fixed effect), ε_{klm} is the residual effect of the tree m .

Assuming that open-pollinated families consisted predominantly of half-sibs (Gerber et al., 2014), narrow sense heritability values (h^2) within each cohort were estimated as follows:

$$h^2 = \frac{4 * \sigma_f^2}{\sigma_f^2 + \sigma_e^2}, \quad (4)$$

where σ_f^2 and σ_e^2 are respectively the estimated variances of the family and residual effects.

As we estimated genetic components of variance in open-pollinated families, we ignored nonadditive gene effects. Earlier reports of the total genotypic variance in clonally propagated progeny tests, but in different traits and in *Quercus robur*, showed limited contribution of nonadditive effects (Caignard et al., 2019; Saintagne et al., 2004). However, our study ignores whether nonadditive effects could be triggered during climate-driven selection episodes. Variances components σ_f^2 and σ_e^2 were estimated with the general linear mixed model glmmTMB (Brooks et al., 2017) using R (version 4.2.2, R Development Core Team, 2022). The sampling variance of heritability values was calculated according to Visscher and Goddard (2015).

2.7 | Genetic changes over time

For each trait, we calculated the genetic change (ΔG) over successive time periods (t and t' , where t is the most recent time period) by assessing the difference in cohort mean values (X):

$$\Delta G_{t-t'} = \frac{X_t - X_{t'}}{\sigma}, \quad (5)$$

where σ is the mean within-cohort standard deviation of cohorts t and t' . ΔG is expressed here in standardized units. However, the time span ($t-t'$) cannot be translated into a number of generations, precluding the expression of ΔG as a rate of evolution as described by Haldane (Gingerich, 1993; Hendry & Kinnison, 1999). Indeed,

management under even-aged regimes implies mating between trees of various ages, from the first year of fruiting (age of about 30 to 40 years) onward, with regeneration only at rotation age (about 200 years in the three forests). This creates an overlap between generations, making it difficult to standardize genetic changes as described by Haldane.

We focused on comparing the sign and size of ΔG over two time periods (1680–1850) and (1850–1960). These comparisons were conducted for each trait separately, but overall comparisons should provide some indication as to whether the direction of selection was maintained or changed between the two time periods. Maintenance of the same sign for genetic change indicates continuous directional selection, whereas a change of sign indicates a change in the direction of selection and suggests fluctuating selection. This rationale is based on the following reasoning.

Let us assume that selection acts on two traits (X and Y) in a tree population evolving under directional selection and that the two traits are adaptive and contribute to the relative fitness w of a tree as follows:

$$w = b_x * X + b_y * Y, \quad (6)$$

where b_x and b_y correspond to the selection gradients and their signs indicate the direction of selection for the two traits.

Under directional selection, the genetic change over time, between t and t' , can be predicted by the second theorem of selection (Price, 1970; Robertson, 1966), as follows:

$$X_t - X_{t'} = Cov(w_{at}, X_{at}), \quad (7)$$

where X_t and $X_{t'}$ are the mean values for the population at times t and t' , respectively, and w_{at} and X_{at} are the additive (genetic) values of fitness and of the trait, respectively, at time t .

From (6) and (7), we can conclude that

$$X_t - X_{t'} = b_x * VarX_{at} + b_y * Cov(Y_{at}, X_{at}), \quad (8)$$

where $VarX_{at}$ is the additive variance of trait X at time t , and $Cov(Y_{at}, X_{at})$ is the covariance of the additive values of the different traits (G covariance matrix between traits at time t).

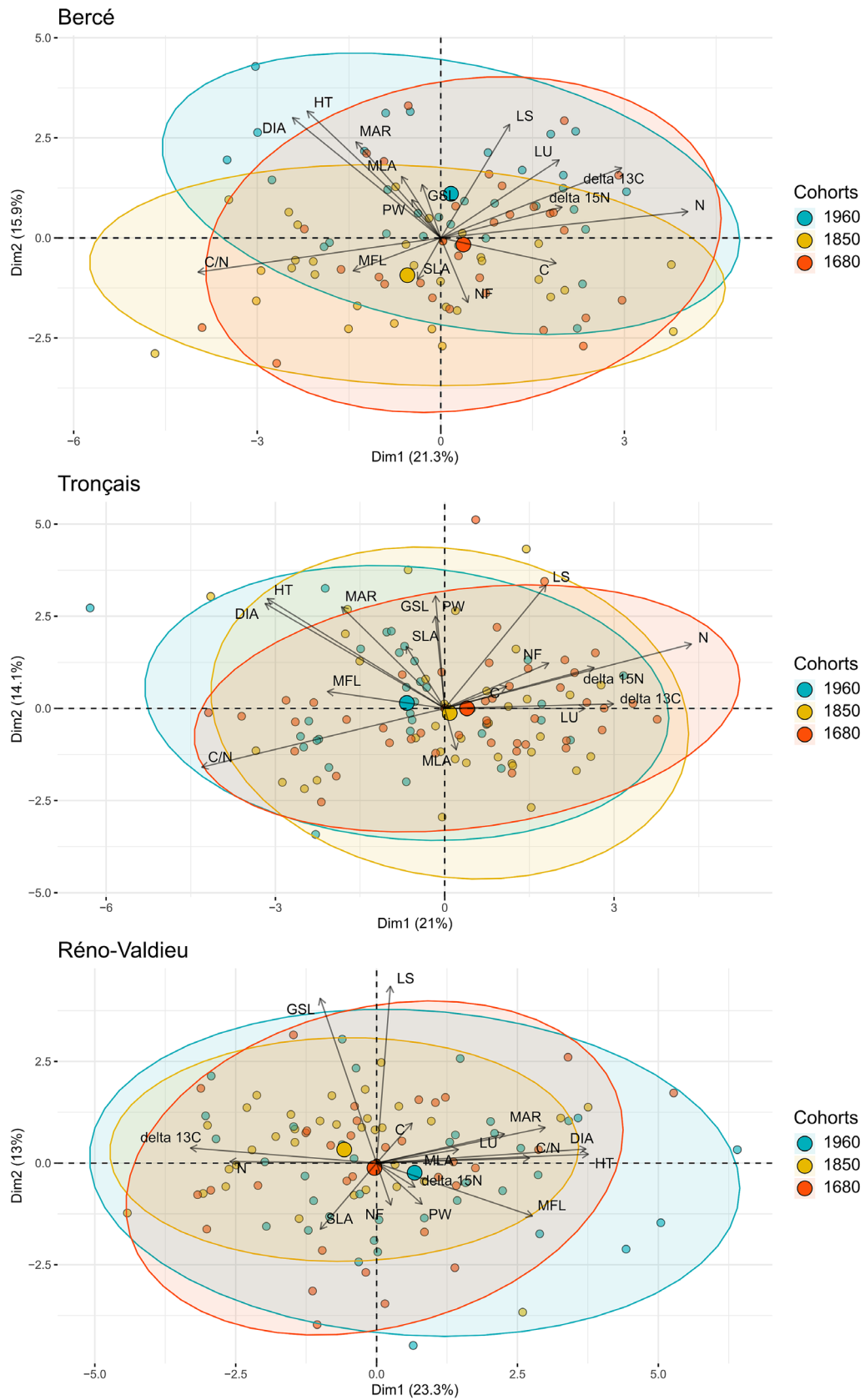


FIGURE 1 Legend on next page.

Similarly, for time period ($t' - t''$):

$$X_{t'} - X_{t''} = b_x * VarX_{at'} + b_y * Cov(Y_{at'}, X_{at'}). \quad (9)$$

Assuming that the additive variances of the traits and the covariances between traits are maintained, which is likely for highly polygenic traits (Walsh & Lynch, 2018) and is confirmed by our dataset as shown by the heritability values of the cohorts (see results), then genetic changes over the different time periods should be similar, and at least of the same sign, if selection acts in the same direction, or if the fitness function of (6) is maintained over time periods. By contrast, changes in the sign of ΔG would indicate changes in fitness function, and thus, a change in the orientation of directional selection, suggesting fluctuating selection. We estimated ΔG in standardized units (Formula [5]) over the two time periods (1680–1850) and (1850–1960) and compared its values and signs between the two time periods.

3 | RESULTS

3.1 | Genetic differentiation between forests and cohorts

All phenotypic traits except MLA differed significantly between the three forests (Table 3). However, less difference was observed between the cohorts within each forest (Table 3). Growth (HT, DIA, and MFL) and phenology-related traits (LU, LS, and MAR) differed between the cohorts within the three forests (Table 3). The only other trait for which significant differences between cohorts were observed was $\delta^{15}\text{N}$ (Table 3). A non-significant forest*cohort interaction was observed for growth-related traits, suggesting parallel differentiation between cohorts in the three forests. However, cohort differences followed contrasting patterns in the three forests, particularly for phenology-related traits, as suggested by the significant forest*cohort interaction. For example, leaf unfolding occurred significantly later in the youngest cohort (1960) in Bercé, but in the oldest cohort (Cohort 1680) in the Tronçais forest.

We performed PCA for each forest, to evaluate the differentiation between cohorts within the forest concerned (Figure 1). Age-structured cohorts are delineated by ellipses in the figure. Interestingly, in each forest, the youngest cohort is oriented along an axis corresponding to the growth variables (DIA and HT), indicating a trend toward increasing growth during recent periods in which the climate has been becoming warmer.

The level of genetic variation did not differ between cohorts, as shown by the heritability values of the traits assessed at the single-

tree level (Figure 2). In general, for a given trait, with very few exceptions, heritability values were maintained at similar levels between cohorts within forests (Table S1). However, heritability values were slightly lower in the Bercé cohorts than in the cohorts from the other two forests (Figure S3).

3.2 | Effect of past climate on phenotypic variability

Having found genetic differences between cohorts, we then investigated whether these differences were correlated with the temperature prevailing during the recruitment period. As expected, temperature differed between the recruitment periods in the three forests, with warmer conditions for the most recent cohort (Table 1 and Figures S2A, S2B, and S2C). On average, the mean temperature was about 0.6°C higher during the recruitment period for the most recent cohort (Table 1) than during the recruitment periods for the other two cohorts. The temperature difference was smaller between the two oldest cohorts, with slightly cooler conditions for the intermediate cohort (during the mid-19th century). On average, temperatures were warmer in Bercé than in the other two forests, regardless of the cohort considered. We introduced the temperatures prevailing during the recruitment period into a linear model to account for differences between cohorts (model [2]). In the same model, we also considered current-day temperatures recorded in recent years for the three cohorts as covariates to account for potential microgeographic sources of variation. All trait values were standardized (reduced centered values) to allow comparisons between traits. We found significant responses of cohorts to historical temperature for eight traits, for growth traits (height, diameter, and number of flushes), phenological traits (leaf unfolding, leaf senescence, and marcescence), leaf $\delta^{15}\text{N}$ isotope composition, and specific leaf area (Figure 3). Temperature responses were positive for growth traits and phenological dates, implying greater growth, later flushing and senescence, greater marcescence, and a higher isotope $\delta^{15}\text{N}$ composition during warmer recruitment periods. Conversely, the response was negative for specific leaf areas and the number of flushes. Among these eight traits, three (LU, HT, and $\delta^{15}\text{N}$) exhibited significant Temperature*Forest interactions (Table S2). This was particularly the case for LU and $\delta^{15}\text{N}$ which showed opposite responses between forests; however, HT exhibited positive trends with temperature in all three forests (Figure S4). For the remaining eight traits, no significant effect of the temperature prevailing during the recruitment period was detected. Finally, no trait responded to microgeographic temperature differences (Table S2).

FIGURE 1 Multivariate analysis illustrating the overall temporal genetic changes between cohorts since 1680. PCA was performed for each cohort from the three forests (Bercé, Réno-Valdieu, and Tronçais). Correlation plot and projection of the family mean values along the axes corresponding to the first three components. Forests and cohorts within forests are indicated in different colors. The length and direction of the arrows indicate the contribution of each trait (see Table 2 for the meaning of the trait); 95% confidence ellipses are delineated for each cohort within forests. Ellipses corresponding to the different cohorts are shaded in blue (most recent cohort, 1960), yellow (cohort 1850), and red (oldest cohort, 1680).

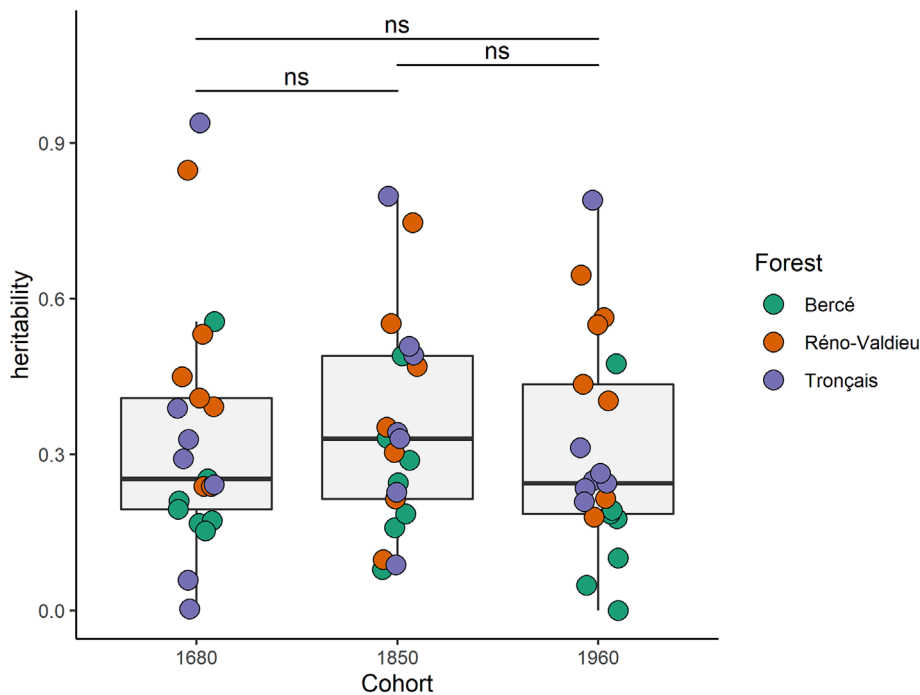


FIGURE 2 Changes of genetic variation within cohorts since 1680. Narrow sense heritability values within the age-structured cohorts. Heritability values estimated for traits assessed at the single-tree level (Table 1), assuming that open-pollinated families consisted of half-sibs. The bold horizontal line in the box indicates the median value of heritability, and the bottom and top of the box correspond to the first and third quartiles, respectively.

3.3 | Genetic changes over time

We compared genetic changes over time (ΔG values, Equation [5]) between the two time periods (1680–1850) and (1850–1960), which correspond roughly to cold (late Little Ice Age) and warm (Anthropocene) periods. We first calculated the Pearson correlation coefficients between $\Delta G_{1960-1850}$ and $\Delta G_{1850-1680}$ for all 16 traits (Table 2) and within each forest. We obtained significant negative values for Bercé (-0.70 , $p = .002$) and Réno-Valdieu (-0.74 , $p < .001$) but non-significant positive values for Tronçais (0.27 , $p = .302$). However, correlations between $\Delta G_{1960-1850}$ and $\Delta G_{1850-1680}$ for the same forest may be biased, as the two variables used for the calculation of the correlation are not independent because X_{1850} (mean value of a trait for cohort 1850) is used in the calculation of both $\Delta G_{1960-1850}$ and $\Delta G_{1850-1680}$.

We overcame this limitation by including comparisons of Δ values for different forests (for example, $\Delta G_{1960-1850}$ for Bercé with $\Delta G_{1850-1680}$ for Tronçais) in our comparative analysis. Thus, comparisons of ΔG values between the two time periods were made across all pairwise combinations, within and between forests. As a result, for a given trait, the entire range of genetic change encompasses nine different comparisons (three within-forest, and six between-forest comparisons, Figure 4). These comparisons were restricted to traits displaying significant trends in variation over time (Figure 3). Comparisons were made graphically and separately for each trait as biplot graphs (Figure 4), representing the range of genetic change between the two time periods.

For growth traits (height and diameter), the range of genetic change over time encompassed positive values for $\Delta G_{1960-1850}$ and negative values for $\Delta G_{1850-1680}$. For phenological traits (leaf unfolding, marcescence), it also encompassed predominantly positive values

during the warm period with negative (or slightly positive values) during the cold period. Leaf $\delta^{15}\text{N}$ isotope composition followed a similar pattern, whereas the two remaining traits (specific leaf area and the number of flushes) followed no consistent contrasting pattern between the two time periods. Overall, separate comparisons of temporal changes for each trait were consistent with the negative correlation of changes between the two successive time periods observed in Bercé and Réno-Valdieu.

4 | DISCUSSION

We used a retrospective approach to monitor genetic changes over time in multicentennial oak forests. We compared the offspring of age-structured cohorts in a common garden and found genetic shifts during the transition between the late Little Ice Age (a cold period) and the early Anthropocene (a warm period). We acknowledge that genetic differentiation between age-structured cohorts may also result from microecological variation (other than climate, which was accounted for in our study), as the cohorts were sampled from different plots within the same forests. Although microecological variation cannot be entirely excluded, it is unlikely that it would act as a confounding source of variation, as the age-structured cohorts were not spatially distributed along any ecological gradient in the three forests. Microecological variation would just have increased the noise on the temporal signal. Furthermore, recent comparisons of population variation within and between oak forests concluded that there was very little within-forest genetic differentiation (Girard et al., 2022). Thus, differentiation between the age-structured cohorts was the main factor accounting for the genetic changes that have accumulated over different time periods during the last three centuries. We assessed

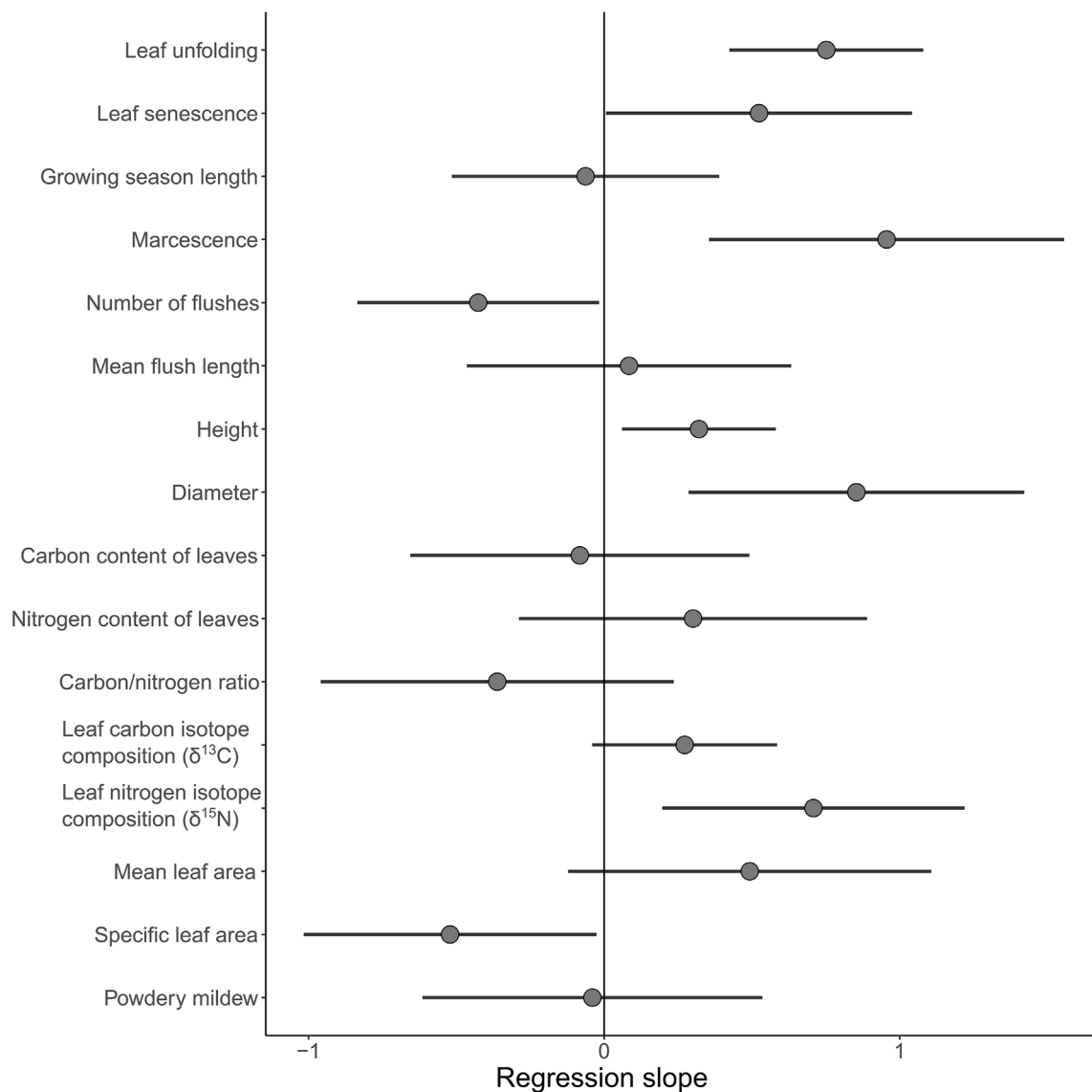


FIGURE 3 Response of the 16 phenotypic traits to temperature changes since 1680. Slopes of the regression lines between each phenotypic trait and the mean temperature prevailing during the period of cohort recruitment. Data for the various traits were standardized to allow comparisons of the slopes (β_1 values of model [2]) and their 95% confidence interval between traits represented as bars. Mean monthly temperatures during the recruitment period were extracted from Luterbacher's database (Luterbacher et al., 2004) (Figure S2).

16 phenotypic traits in the common garden (Table 2). We observed significant shifts principally for growth and phenology-related traits (Table 3), which were correlated with past differences in temperature and could be interpreted as temporal genetic changes (Figure 3). However, mean temperature changes between the recruitment periods of the cohorts were low, and these gradual small changes are unlikely to have caused the genetic shifts we observed. In an earlier published paper, we discussed the potential selective effects of extreme events occurring during cold and warm periods (Saleh et al., 2022). We investigated past occurrences of extreme events (such as extreme frosts and droughts) and searched for historical reports of the ecological consequences of these events in forests. We found that extreme events occurred more frequently during the late LIA and decreased during the Anthropocene warming. Interestingly, we found historical

reports of mortalities and forest decline following these events. Here, we discuss the implications of the genetic shifts in terms of the mode and direction of selection and for the adaptive management of oak forests.

4.1 | Direction of genetic changes

Height and diameter growth decreased during the cold period, the late Little Ice Age, and then increased during Anthropocene warming (Figures 3 and 4). More precisely, height and diameter were lower in the cohort recruited during the LIA compared to those recruited pre- and post-LIA. Interestingly, these genetic changes matched the trend in phenotypic growth changes observed over time in oaks. Long-term

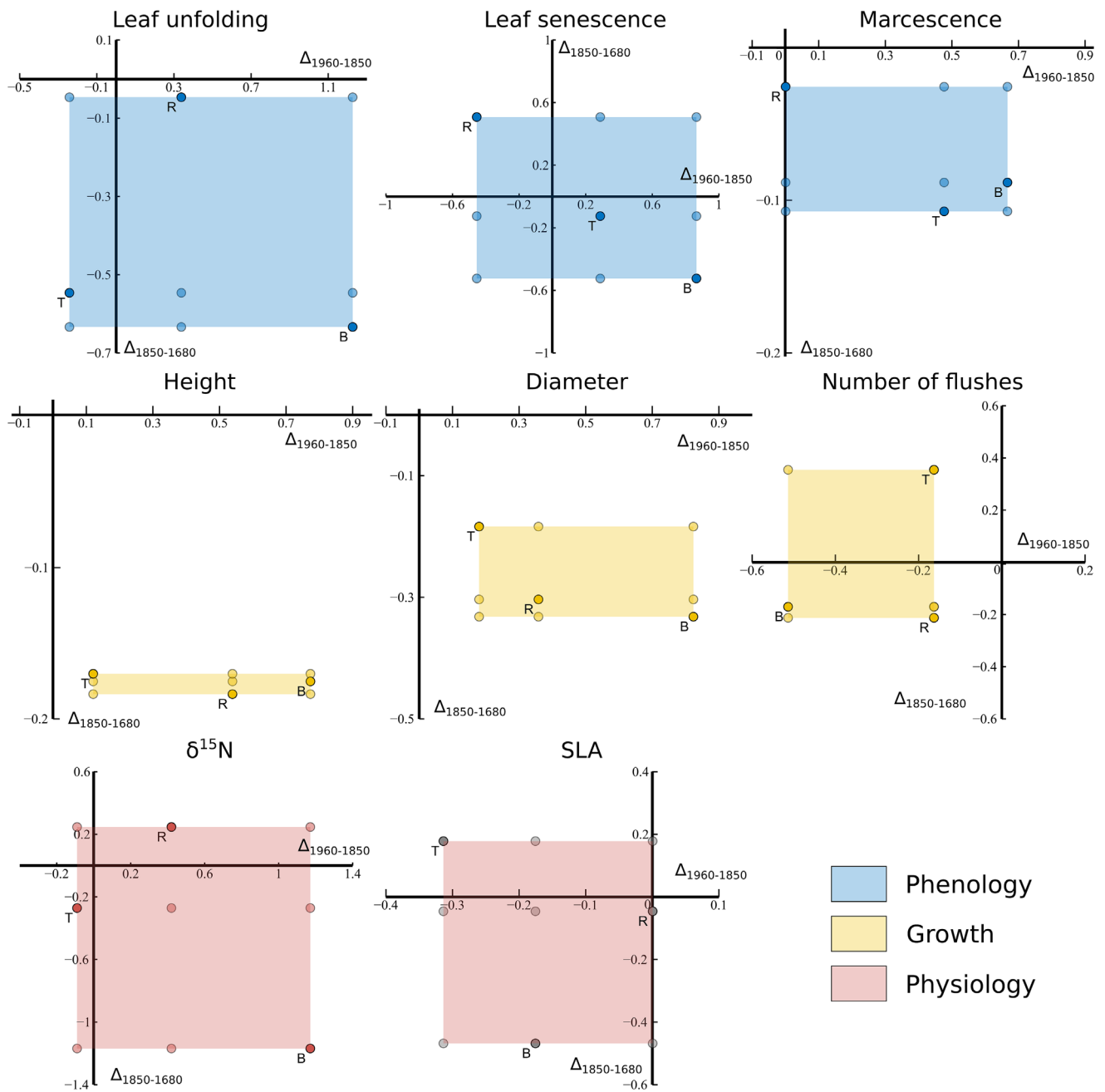


FIGURE 4 Range of genetic changes in multiple phenotypic traits between the cold ($\Delta G_{1850-1680}$) and warm ($\Delta G_{1960-1850}$) periods. Genetic changes are expressed as standardized values (Formula [5]). The range of genetic changes encompasses nine different comparisons (three within-forest, and six between-forest comparisons; see text). Bold dots correspond to comparisons within forests (B, Bercé; R, Réno-Valdieu; T, Tronçais). Pale dots correspond to comparisons between forests. $\delta^{15}\text{N}$, leaf nitrogen isotope (^{15}N) composition. SLA, specific leaf area.

observational plots and dendrochronological records revealed lower levels of growth during the LIA (Buntgen et al., 2011) and a continuous increase in growth during Anthropocene warming in oaks (Charru et al., 2017; Pretzsch, 2020; Pretzsch et al., 2014; Stimm et al., 2022). The acceleration of growth in the oak stands in the recent past was attributed to the combined effects of CO_2 and temperature increases and a lengthening of the growing season. The temporal genetic shifts that we observed between cohorts are parallel to the plastic or phenotypic trends observed in dendrochronological

records. We showed in another recent study that the increase in growth is also correlated with reproductive success and fitness (Alexandre et al., 2020), highlighting the adaptive significance of this tendency. However, our investigations were conducted in oak stands subject to even-aged management, in which strong natural selection occurs during the juvenile stage, thus favoring rapidly growing genotypes. Under such circumstances, provided that ongoing climate change does not limit growth, faster growth may, indeed, increase fitness.

Changes in phenological traits over time were different when phenotypic trends assessed *in natura* were compared with the genetic trends derived from our common garden experiments. *In natura* observations in the present day have indicated that bud burst occurs earlier with increasing temperature in sessile oak (Firmat et al., 2017; Vitasse et al., 2009, 2011), whereas our results suggest a genetic shift over time towards later bud burst with increasing temperature. The temporal genetic shifts also conflict with the spatial genetic divergence observed in common garden experiments containing trees from extant populations (Alberto et al., 2011; Girard et al., 2022), in which leaf unfolding occurs earlier in populations from warmer climates. The co-gradient variation of bud burst is generally interpreted as indicating that the date of bud burst is driven by cumulative temperatures in the spring (Dantec et al., 2014; Vitasse et al., 2011). Assuming this to be the case, under warmer conditions, natural selection would favor early-flushing trees, which would benefit from a longer growing season. However, extreme events, such as late frosts, could potentially disrupt this pattern by killing early-flushing trees. This situation provides an illustration of the two facets of climate change (gradual increases in temperature and the occurrence of extreme events) having opposite evolutionary consequences. On the one hand, continuously increasing temperatures favor early-flushing genotypes in the absence of limiting factors but, on the other, the occurrence of late frosts increases the fitness of late-flushing trees. Indeed, as shown in Figures S2A, S2B, and S2C, 1, the most recent cohorts were established during periods with unusually low spring temperatures (1956 and 1962).

The parallel variation of *in situ* observations from published reviews (Poorter et al., 2009) and the genetic changes along a temporal gradient reported here were also seen for specific leaf areas (Figures 3 and 4). Both sets of results converge to indicate that SLA decreases with increasing temperature. Similarly, $\delta^{15}\text{N}$ increased with temperature (Figure 3), as previously reported for non- N_2 -fixing species at a global scale *in natura* (Craine et al., 2018). Leaf nitrogen content did not vary with temperature or between cohorts, so the variation of $\delta^{15}\text{N}$ between cohorts essentially reflects a change in the dominant mode of N uptake by oaks, with the degree of symbiotic N_2 fixation and mycorrhizal associations making the largest contribution to the variation of ^{15}N abundance (Craine et al., 2009). Overall, our results suggest that the global phenotypic variations of growth traits, specific leaf area, and $\delta^{15}\text{N}$ reported in published reviews are partly driven by directional selection in response to temperature variation.

4.2 | Fluctuating selection

The genetic shifts observed for growth and phenology may appear small relative to the genetic differentiation between modern populations observed in common gardens (Girard et al., 2022). However, these shifts have occurred over a very short evolutionary time frame, corresponding to the last three hundred years. Interestingly, our results show a reorientation of genetic changes during the climatic

transition from the LIA to Anthropocene warming, with a switch in the sign of ΔG during this transition (Figure 4). This almost “instantaneous” reversal of genetic changes in response to new climatic conditions highlights the rapidity of evolution following the establishment of new selection pressures. With our time-based sampling scheme, we were able to detect fluctuating evolutionary changes. Had we sampled only populations established in 1680 and 1960, we would have missed this fluctuation of responses. The pace of evolution may be even more rapid, but undetectable here due to the sampling of only a few populations established at different times. Taken together, our results suggest that the rate of change is probably correlated with the sampling time scale, to such a point that lower resolution sampling would blur the evolutionary signal (Gingerich, 2001). Fluctuating selection acted in the same direction in all three forests, for growth traits (height and diameter) and marcescence but was variable for the other two phenological traits (leaf unfolding, and leaf senescence) (Figure S4). These results contrast with responses monitored in evolution experiments set up under controlled environments, in which parallel evolution is more frequently reported (Rudman et al., 2022). As mentioned above, our observations were conducted *in situ*, in conditions in which microecological differentiation between cohorts and gene flow could potentially obscure the temporal evolution signal (Bolnick et al., 2018). Non-parallel evolution may also be favored by the complex architecture of fitness, and the contribution of different traits to fitness varies from population to population. Interestingly, we previously identified a positive genetic correlation with fitness for growth-related traits, which displayed parallel evolution in this study (Alexandre et al., 2020).

These fluctuating selection responses during the LIA–Anthropocene transition point to the underlying mechanisms likely to generate such “immediate” genetic shifts. We suspect that the combination of a high level of standing genetic variation and the very large density of seedlings within oak stands substantially increased the selection differential under episodes of strong selection caused by extreme events during the LIA (Le Roy Ladurie, 2006; Pfister & Wanner, 2021; Rousseau, 2012). Indeed, under natural regeneration, the density of stems during the renewal of oak stands decreases strongly during the early years of stand establishment (from more than 100,000/ha to approximately 4000/ha at 10 years) due to natural selection (Jarret, 2004). Simulations have shown that it may take only a few generations for populations to respond to episodes of strong selection when fitness depends on a large number of genes (Kremer & Le Corre, 2012). The response is almost immediate and builds on the multiple associations of genes that can arise in a population with a high level of standing genetic diversity. We recently provided evidence for the existence of a high degree of genetic variation for fitness in sessile oak (Alexandre et al., 2020). Our findings here also indicate that the phenotypic components of fitness display substantial variation (Figure 2). A high degree of genetic variation, a high intensity of selection, and a highly polygenic architecture of fitness together contributed to rapid changes in response to the selection episodes occurring during the LIA.

The genetic changes over time detected for phenotypic traits in this study follow the same trend as genome-wide allelic frequency

changes assessed on the same study material (Saleh et al., 2022). In both these studies, the changes act in opposite directions during successive cold and warm periods, as shown by their negative correlation, providing strong evidence for the occurrence of fluctuating selection. However, these trends are not synchronous. Negative correlations between genetic changes for phenotypic traits were detected between the two successive periods (1680–1850) and (1850–1960), whereas there was a slight time lag to the negative correlation between allelic frequencies, which emerged during a later time period (1680–1850) and (1960–2008). Unfortunately, it was not possible to raise offspring from the most recent cohort (2008) in the common garden, which precluded the calculation of correlations for genetic changes between the 1680–1850 and 1960–2008 periods. Nevertheless, unanswered questions remain concerning this lack of synchronicity of the negative correlation. Is it related to differences in statistical power for the detection of correlation? Or to differences in the genetic material used to estimate correlation (parental trees for the genomic correlation, the offspring of parental trees for phenotypic traits analyzed here)?

4.3 | Temporal migration

Fluctuating selection in oak stands raises questions about the temporal gene flow occurring between cohorts subject to different selection pressures in the past. Like most forests, oak forests consist of age-structured stands, in which conspecific trees of different ages coexist either in tree-by-tree mixtures or as spatially subdivided cohorts of different ages. Depending on the life history and longevity of the trees, age-structured tree populations are thus prone to overlaps between generations, potentially leading to gene flow between trees from different age classes. The combination of this generation overlap with temporal gene flow (i.e., gene flow between different age-structured cohorts) may ultimately lead to two evolutionary consequences (Yamamichi et al., 2019). On the one hand, generation overlap increases generation time, thereby slowing evolution (Yamamichi et al., 2019). On the other, temporal migration may generate a migration load if the selection pressures to which older cohorts were exposed differ from those acting on younger cohorts. Placing this notion in context, under continuous directional selection, pollen flow from the trees in 200-year-old cohorts is likely to decrease the fitness of current-day stands to a much greater extent than pollen originating from stands only 50 years old. As selection is at its strongest when the trees are at the juvenile stage, trees that are 200 years old today would have undergone the strongest selection during the early 19th century. For multicentennial trees, such as oaks, it is, thus, important to consider time trends in selection pressure over the lifetime of the tree, to evaluate the potential maladaptive consequences of temporal migration from the past. Here and in an earlier study (Saleh et al., 2022), we have shown that selection fluctuated during the LIA and Anthropocene. Theoretically, under environmental change, such as the climatic transition between the LIA and modern times, populations experience an adaptational lag when they track the shift in

optimal phenotype induced by the change in selection pressures (Lynch et al., 1991; Van Dooren, 2019). Orive et al. (2017) showed that this adaptational lag is amplified by the migration load from the past if age-structured cohorts coexist. To sum up, the consequences of temporal gene flow depend on the environmental conditions that prevailed when the cohorts were recruited in comparison to today's conditions. If the climatic conditions under which the oldest generation was recruited more closely match those of the contemporary period, then there may be an adaptive gain from the gene flow among generations. However, the climatic changes documented over the last two centuries indicate clear environmental shifts and thus raise some concerns about the maintenance of age-structured stands of multi-centennial trees.

5 | CONCLUSION

Experimentally monitoring evolutionary changes in situ remains challenging in trees, due to obvious biological constraints and the lack of genetic traceability over different time periods. However, we show here that it is possible to assess temporal genetic changes in present-day standing populations with age-structured cohorts maintained under even-aged management regimes. By comparing different age-structured cohorts of multicentennial oak trees, we found opposing temporal trends in genetic changes between the late Little Ice Age (a cold period) and the early Anthropocene (a warmer period). Our results echo earlier findings highlighting a negative correlation of genome-wide allelic frequency changes between cold and warm periods in the same experimental design (Saleh et al., 2022). Taken together, these findings suggest that there has been a rapid evolutionary response to the fluctuating selection generated by sharp climatic transitions in the past and that such trends may be continuing. The in situ tracking of temporal genetic changes may, thus, provide a new avenue of research for anticipating future ecological and evolutionary dynamics.

AUTHOR CONTRIBUTIONS

Conception and coordination of the study: Antoine Kremer. *Sampling of forests and cohorts:* Antoine Kremer and Sylvain Delzon. *Collection of open-pollinated families and common garden experiment installation:* Laura Truffaut, Benjamin Dencausse, Laura Lecacheux, and Antoine Kremer. *Monitoring of phenotypic traits and data analysis:* Thomas Caignard, Laura Truffaut, Benjamin Dencausse, Laura Lecacheux, Antoine Kremer, and José M. Torres-Ruiz. *Writing of the manuscript:* Antoine Kremer, Thomas Caignard, and Sylvain Delzon. All the authors reviewed the manuscript.

ACKNOWLEDGMENTS

This research was supported by the European Research Council through an advanced grant (project TREEPEACE # FP7-339728), and by the French Forest Service (ONF) (INRAE-ONF TREEPEACE contract), the ANR project FOREPRO (ANR-19-CE32-0008), and the ANR *Forêt Expérimentale* project (ANR-20-IDES-0001). We thank

the ONF staff at the National Forests of Bercé, Réno-Valdieu and Tronçais (Anthony Jeanneau, Vincent Breton, Benjamin Laurendeau, Loïc Nicolas, and Alexandre Durin), for technical assistance during the sampling of cohorts and trees and for acorn collection. We thank Leo Arnoux, Armel Thoni, Thibault Leroy, and Cyril Firmat for their assistance with acorn collections. We are also grateful for the support and assistance of the staff of the *Unité expérimentale Forêt-Pierrotton* during the nursery operations (sowing and replanting) for these cohorts. UMR BIOGECO is supported by a grant overseen by ANR as part of the “Investissements d’Avenir” program Labex COTE (ANR-10-LABEX45).

CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to report.

DATA AVAILABILITY STATEMENT

The datasets generated and/or analyzed during the current study are available in the Data INRAE repository: <https://doi.org/10.57745/2YKUTC>.

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How to cite this article: Caignard, T., Truffaut, L., Delzon, S., Dencausse, B., Lecacheux, L., Torres-Ruiz, J. M., & Kremer, A. (2023). Fluctuating selection and rapid evolution of oaks during recent climatic transitions. *Plants, People, Planet*, 1–17. <https://doi.org/10.1002/ppp3.10422>