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Trajectories of genetics, 150 years after Mendel/Trajectoires de la génétique, 150 ans après Mendel

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Microévolution des chênes européens en réponse aux changements environnementaux

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A B S T R A C T

This review reconstructs microevolutionary processes that allowed long-lived species as temperate oaks (*Quercus petraea* and *Q. robur*) to cope with climate change since the last glacial maximum, by assembling insights from complementary synchronic and allochronic approaches. Paleobotanical and genetic investigations show that oaks migrated at larger velocities than expected, thanks to long-distance rare events and most likely human interferences. Hybridization was a key mechanism accelerating migration and enhancing species succession. Common garden experiments and genome wide association studies demonstrated that diversifying selection across large environmental gradients contributed to rapid local adaptation. Finally the review explores how lessons taken from past evolutionary scenarios may help to predict future responses of oaks to ongoing climate change.

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R É S U M É

Cette revue fait une synthèse des trajectoires évolutives suivies par les chênes tempérés européens (*Quercus petraea* and *Q. robur*) durant les changements climatiques qui ont eu lieu depuis le dernier maximum glaciaire. Elle est basée sur des connaissances dérivant d'approches allochroniques et synchroniques. Les données phylogéographiques et paléobotaniques montrent que la migration postglaciaire a été très rapide, grâce notamment aux événements de dispersion rares et à longue distance, mais sans doute aussi grâce à l'intervention humaine. L'hybridation a joué un rôle très important, en accélérant la migration et en stimulant la succession d'espèces. Les résultats issus d'essais en jardin commun, et dérivant d'analyses de génétique d'association et de génétique des populations, suggèrent que la sélection divergente a contribué à une adaptation locale sur de longs gradients environnementaux. Enfin, ces enseignements du passé sont discutés en regard des réponses prévisibles des arbres aux changements climatiques en cours.

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1. Introduction

Oaks (Genus *Quercus*) are dominant woody species throughout the northern hemisphere and are key drivers of terrestrial biodiversity from tropical to boreal landscapes [1]. Their worldwide demographic success raises distinct questions regarding the evolutionary trajectories they adopted to cope with the drastic environmental crisis that occurred during the Pleistocene. The earth's climate has been dominated during the Pleistocene by the succession of more than fifteen glacial and interglacial periods. Glacial periods lasted on average from seventy thousand to hundred thousand years, while interglacial periods were much shorter (from ten to twenty thousand years). These repeated drastic environmental changes were followed by important alternating retractions and expansions of tree species distributions, placing them in different habitats over time and space. As for many other plant genera, some oak species got extinct at the onset of the first glacial periods [2], but remarkably several survived and some of them occupy today continental wide distributions (*Quer-cus robur* in Europe; *Q. macrocarpa* in North America; *Q. acutissima* in Asia). There has been no tree species extinction during the most recent glacial–interglacial periods, suggesting that extant tree species in Europe demonstrated an efficient ability to migrate and adapt to repeated climatic transitions. Quaternary evolutionary history suggests therefore that these species have developed mechanisms to help reduce the likelihood of extinction, despite the drastic environmental changes. This review aims at highlighting evolutionary mechanisms that triggered adaptive pathways of European temperate white oaks (*Q. petraea* and *Q. robur*) during major climatic transition since the Last Glacial Maximum (LGM). It builds on complementary insights provided by allochronic and synchronic approaches that were obtained during the past twenty years (Fig. 1). The review ultimately aims at suggesting hints for retracing the pace of microevolution under major environmental crisis, which is a timely concern in the context of ongoing climate change. It also explores how the lessons taken from past evolutionary scenarios may help to predict future responses of these long-lived tree species.

2. Tracking climate change by migration

The distribution of temperate white oaks in Europe has shifted repeatedly from the Mediterranean to the boreal regions and reciprocally during interglacial and glacial periods [3]. At the end of the Last Glacial Maximum, oak forests were restricted to the Iberian Peninsula, Italy, and the Balkan Peninsula (Greece and the western Coast of the Black Sea). A pan-European survey of oak pollen fossil remains showed that all refugial sites were located in mountainous areas (e.g., Sierra Nevada in Spain, the Southern Apennine chain in Italy, and the Pindos mountains in Greece) [4]. The extant distribution was approximately reached at 6000 BP (Fig. 1A). The velocity of oak migration during the post-glacial recolonization period (between 15,000 to 6000 BP) averaged 500 m/yr, reaching in some cases up to 1000 m/yr [4]. These figures

inferred from pollen deposits maps exceed by far the dispersion by jays, squirrels, or rodents. To explain this paradox, occurrences of rare long-distance dispersion events were invoked. This mechanism has been tested by computer simulation and shows that dispersion events of a few tens of kilometres, even if very rare, would substantially accelerate the overall migration rate [5]. But no long-distance dispersion vector has received so far conclusive evidence. An alternative scenario has been proposed, suggesting that cryptic refugial populations persisted during the glacial period in more northern areas, and would have acted as source populations for recoloni-zation [6]. It is likely that both dispersion mechanisms can be advocated in the case of oaks. A more recent intriguing hypothesis is that humans acted either as vector of long-distance dispersion, or contributed to the installation of northern cryptic refugia [7]. This hypothesis contends that early human populations, while invading Europe at the Upper Paleolithic period or while migrating in response to post-glacial warming, did actually contribute to the dispersion of oaks, as acorns were a major component of human diets. Acorns were not only used when other resources became exhausted, but also as dietary staple [8].

How much migration is actually going on at a contemporaneous times scale, due to global warming? There is scarce data available on the subject, as migration of trees by natural means is hardly tractable over of few decades. However, recent investigations based on past documentary description of forest composition at the north western margin of the *Q. ilex* distribution indicated that this Mediterranean oak species is indeed migrating at an average rate of less than 60 m/yr [9]. These figures however do not take into account the occurrences of large distance rare dispersion events that can hardly be detected today unless very detailed inventories are implemented. Finally migration by natural means may be severely constrained by land fragmentation and human impacts. Overall, one may conclude from these speculations that migration by natural means will not be sufficient to reach the shift of the oak distribution predicted by niche-based or process-based models [10].

3. Accelerating migration and species succession via hybridization

A pan-European genetic survey of chloroplast DNA diversity indicated that the two temperate oak species (*Q. petraea* and *Q. robur*) share systematically the same haplotypes when they occupy the same forest. The almost complete sharing of chloroplast variants among the two species occupying the same stand was observed across the natural distribution of the oaks, suggesting that hybrid-ization was common and widespread during post-glacial colonization [11]. Hybridisation may have played an important role in the colonisation process, since repeated hybridization events accelerate species migration and succession rates. This scenario has been described in detail in the case of *Q. petraea* and *Q. robur* by Petit et al. [12]. Because *Q. robur* tends to be a more pioneering species than *Q. petraea*, it was most likely present at the northern edge of the oak migration front, while *Q. petraea* was
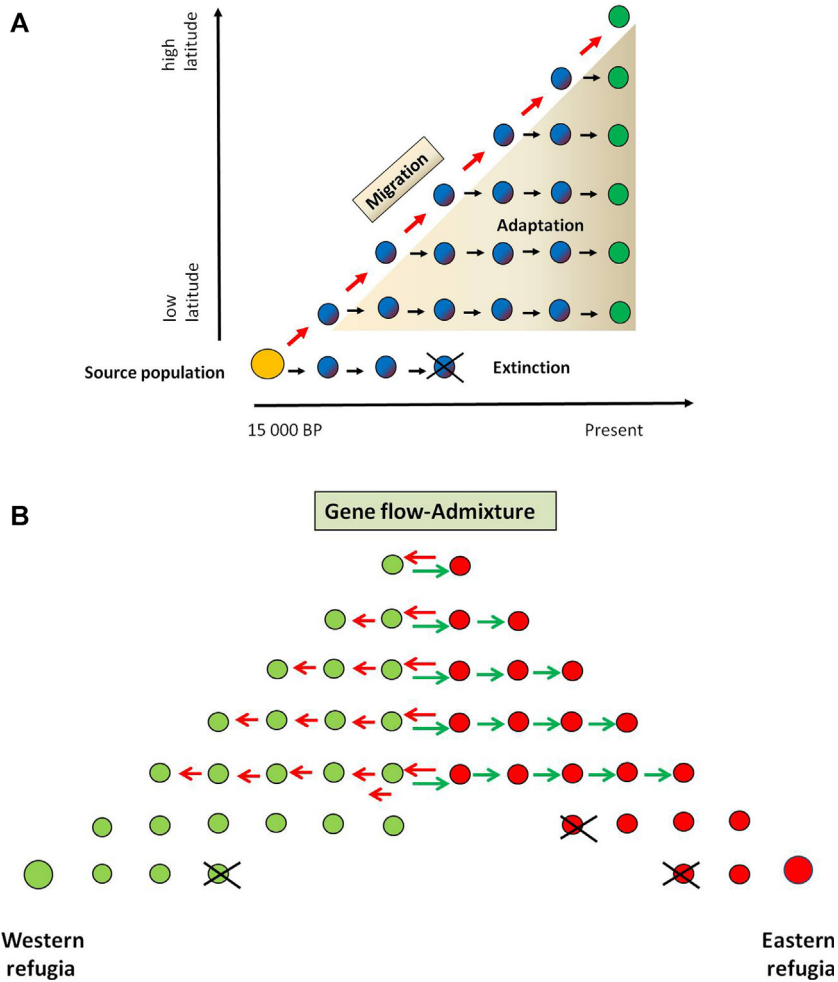
Fig. 1. Evolutionary trajectories of oaks during the Holocene. At the end of the last glacial maximum, oaks, as many other trees, were restricted to three main genetically separated refuge areas (Iberian Peninsula, Spain, and the Balkan Peninsula) [4]. A. Illustrates the likely evolutionary trajectory of populations stemming from one refugial area (for example, Spain, orange circle). As the climate warmed, oaks migrated northwards (red arrows). Whether the migrating populations just tracked the climate change, without major changes in their fitness, is unknown. At the southern edge, populations were facing new climates and natural selection resulted in the extreme south to population extinction, while in other places populations adapted to the new climate (black arrow). However, extinction was limited during the post-glacial warming as the two temperate oaks are still present in Spain Italy and the Balkans, although in scattered populations. Overall, the whole scenario is more comparable to an expansion, rather than an entire shift of the distribution of the species from the south to the north. In this review, we illustrate some of the findings regarding the velocity and dynamics of migration, and the mechanics of local adaptation. The reconstruction of this scenario is based on paleobotany, phylogeography, and evolutionary inferences drawn from synchronic analysis of molecular or phenotypic data of modern populations (green circles). These investigations are currently being completed by ancient DNA analysis retrieved from fossil or archeological remains collected throughout Europe from ancient populations (blue circles). However today's oak forest in central Europe were colonized by different lineages stemming from two or more refugial areas (B), here represented by green and red circles. As migration developed from both source populations, both lineages met in central and northern European forests, followed by gene flow between both lineages (red and green arrows), thus generating substantial admixture between lineages within today's populations.

somewhat behind it, but still capable of hybridising with *Q. robur* through pollen flow. If the first generation hybridization is followed by later backcrosses (e.g., between hybrids and parents) with *Q. petraea* as male parent, then successive introgression will lead to the restoration of *Q. petraea* trees within the *Q. robur* stand. The end result is that *Q. petraea* becomes established within the *Q. robur* stand, consequently enhancing species succession [12]. The peculiar role of hybridization shows that colonization of newly available territories by oaks (for instance following successive ice ages) is facilitated by interspecific gene exchanges, allowing some species to

bypass colonization by seed to rapidly invade new sites. Incidently, continuous recent interspecific gene flow was confirmed by evolutionary investigations using ABC (Approximate Bayesian Computation) simulations (Leroy et al., unpublished results) based on genome wide SNP polymorphism in *Q. petraea* and *Q. robur*. Indeed genomic differentiation among the two species has been scanned by complete genome sequencing, thus allowing one to test different evolutionary scenarios resulting in such divergence patterns. Comparison of different contrasting speciation scenarios (strict isolation, ancient migration, constant migration, and secondary contact) showed that

posterior probabilities for secondary and recent contacts were much larger than for any other scenario. We may further extrapolate these results in the context of present ongoing shifts of species distribution. Range overlaps between Mediterranean and temperate white oaks can be anticipated more frequently, hence triggering hybridization and facilitating species migration via introgression, in a similar manner as during the post-glacial.

4. Local adaptation during past climate change

The comparison of today's distribution of temperate oaks with their past post-glacial distribution surprisingly indicates a clear overlap of their past and present range at the southern extant margin [4]. This observation clearly suggests that local adaptation has occurred, as some populations stayed in place over the past 15,000 years (Fig. 1A). These considerations are supported by experimental results obtained in large-scale common garden plantations of *Q. petraea* established along large-scale geographical gradients. There is now evidence that the genetic divergence among extant populations resulted from adaptive evolution due to local selection from the time of establishment of populations on new sites [13]. Assuming that the Spanish and Italian-Balkan refugial populations were genetically separated for more than 100,000 years during the last glacial period, genetic differentiation may have accumulated between these two source populations and may be partly responsible for the differentiation between extant populations in central Northern Europe that originated from different refugial origin. Genetic variation of phenotypic traits assessed in common garden experiments did however not support the persistence of a footprint due to the maternal origin of today's populations. Indeed most phenotypic traits show large population differentiation, with clinal patterns of variation that differ from historical patterns [13] (Fig. 2). A demonstrative example comes from phenological traits that exhibited consistent continuous variation across temperature gradients. Interestingly, some of the underlying genes that exhibit genetic associations with phenological traits exhibit also clinal variation along the same gradient [14]. There is little evidence in current populations of any phenotypic or adaptive trait differentiation relating to the refugial origin, even in neighbouring central European populations that are known to have originated (through migration) from different refugia. This is interpreted as the result of extensive gene flow during admixture followed by local adaptation [13] (Fig. 1B). One may conclude from these analyses that most variation in provenance tests is the result of recent adaptive evolution. Theoretical approaches have however shown that the interaction of extensive gene flow and strong diversifying selection will accelerate the divergence of complex multilocus traits [15] and achieve adaptation in less than 20 generations. The rapid process is generated by allelic associations among different loci that increase population differentiation of adaptive traits in response to diversifying selection. The mechanism is enhanced by gene flow that provides the diversity needed to create different allelic associations. The overall process
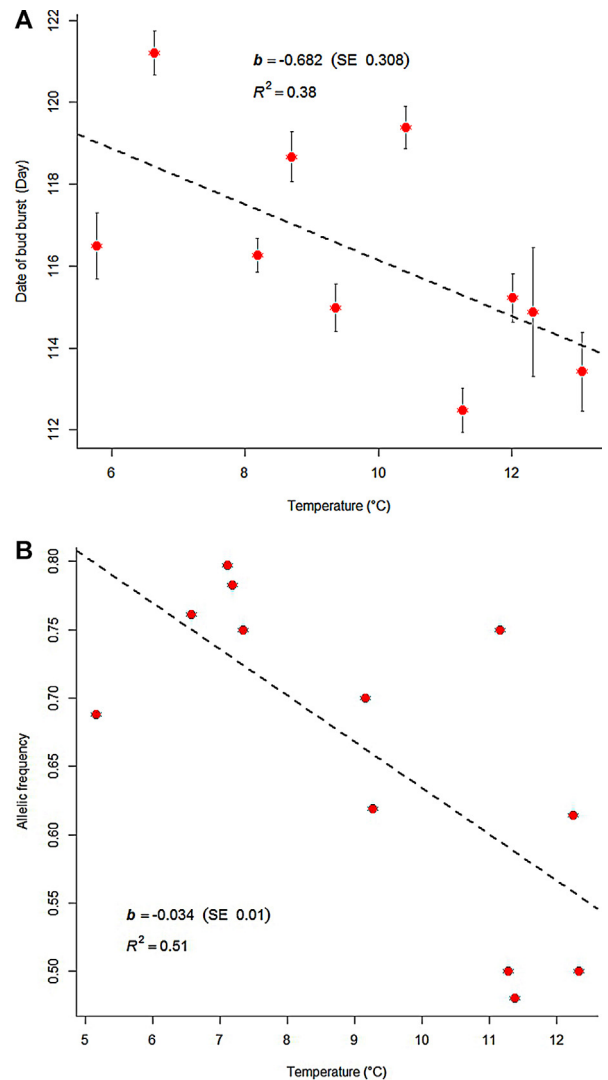
Fig. 2. Illustration of local adaptation of bud burst in Oaks. The time when oaks flush in the spring is highly dependent on the local temperature. Under warm spring temperatures, trees will flush earlier, and when the climate is cooler trees will flush later. These *in situ* patterns can also be observed in common garden experiments, where trees originating from different geographic origins start flushing according to the temperature at their origin. Under common garden conditions, trees from lower elevation and altitude will flush earlier than trees from higher elevation. This is illustrated in (A), where the date of flushing (number of days since 21 January) is plotted versus the spring temperature at the place of origin of the trees [13]. The populations were sampled along altitude within two Pyrenean valleys. Similar patterns were observed when the trees were collected along latitudinal gradients, suggesting that temperature is the driving environmental factor of population differentiation. Similar clinal variation was also observed in candidate genes [13], as illustrated here by linear variation of allele frequencies of one SNP within gene APS (5′-adenylylsulfate reductase) along the temperature gradient (B). The evolutionary driving force may either be biotic as defoliating insect pressure or abiotic as freezing damage due to late frost. On a wide-range scale, the latitudinal clinal pattern of bud burst is orthogonal to the historical distribution of variation (East-West pattern) that was generated by the different post-glacial migration routes. Thus, the extant bud burst genetic variation is likely to result from selection pressures and local adaptation that occurred during the Holocene.

is accelerated if the number of loci contributing to the trait of interest increases. To sum up, congruent results stemming from experimental results of trait and gene variation and from simulations suggest that evolutionary change can be substantial over a few generations leading to local adaptation. Recent sequencing of oak genomes showed indeed that standing genetic variation in oak population is extremely large, thus providing the necessary resource for adaptation over successive generations [16].

5. Conclusion

This brief review outlines peculiar microevolutionary strategies of long-lived tree species as oaks during past climatic transitions, and provides clues for understanding their current demographic success in terrestrial ecosystems. Inherent resources and capacities to oaks that facilitated migration and adaptation stem from generic life history and demographic features of trees as large population size, extensive gene flow, and high levels of genetic diversity. In addition, hybridization, which is usually considered as a nightmare in oak taxonomy, is seen here as a key evolutionary mechanism enhancing migration and succession, and contributing to adaptation by feeding standing genetic variation in mixed oak stands. Finally, this review suggests that human interferences may as well have contributed to the evolutionary success of oaks. While strong convincing evidence is still lacking, comparative archeobiological and genetic investigations indicate that post-glacial migration dynamics may have been accelerated by humans while feeding with acorns. It may well be that human interference may be again needed for transferring populations through assisted migration to cope with the rapid ongoing climate change.

Disclosure of interest

The author declares that he has no competing interest.

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