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Review

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Oaks: an evolutionary success story

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Summary

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The genus *Quercus* is among the most widespread and species-rich tree genera in the northern hemisphere. The extraordinary species diversity in America and Asia together with the continuous continental distribution of a limited number of European species raise questions about how macro- and microevolutionary processes made the genus *Quercus* an evolutionary success. Synthesizing conclusions reached during the past three decades by complementary approaches in phylogenetics, phylogeography, genomics, ecology, paleobotany, population biology and quantitative genetics, this review aims to illuminate evolutionary processes leading to the radiation and expansion of oaks. From opposing scales of time and geography, we converge on four overarching explanations of evolutionary success in oaks: accumulation of large reservoirs of diversity within populations and species; ability for rapid migration contributing to ecological priority effects on lineage diversification; high rates of evolutionary divergence within clades combined with convergent solutions to ecological problems across clades; and propensity for hybridization, contributing to adaptive introgression and facilitating migration. Finally, we explore potential future research avenues, emphasizing the integration of microevolutionary and macroevolutionary perspectives.

I. Introduction: oak evolution in context

Oaks arose an estimated 56 million years ago (Ma) and have radiated and expanded subsequently across the Northern Hemisphere (Manos & Stanford, 2001; Hipp *et al.*, 2020). Today they extend from the equator (Colombia and Indonesia) up to the boreal regions at a latitude of 60°N in Europe, and from sea level to 4000 m in the Yunnan province in China (Camus, 1936, 1938, 1952; Menitsky, 2005; De Beaulieu & Lamant, 2010). Oaks range in habitat from dense bottomland forests to open grasslands and

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savannas, and from alkaline to acidic soils (Abrams, 1992; Nixon, 1997). The genus has diversified into numerous species in America and Asia, with the highest diversity observed at 15–30°N in Mexico and east Asia (Valencia, 2004; Menitsky, 2005; Nixon, 2006). Europe exhibits lower species richness (up to 30 species), but the genus is nearly as widespread there as it is in North America and east Asia, as a limited number of European species have expanded across the continent (Camus, 1936). Most recent estimates place diversity of oaks at approximately 435 species (Denk *et al.*, 2017), though ongoing work in Mexico and Central America suggests that this number may be an underestimate. The genus is in any case among the most species-rich tree genera in the Northern Hemisphere, together with *Salix*, and the most important in terms of species and biomass in the Americas (Cavender-Bares *et al.*, 2016a, Cavender-Bares, 2019).

Oaks are, by at least these measures of diversity and distribution, an evolutionary success. Although there might be some arbitrariness and anthropomorphic overtone in defining ‘success,’ we sidestep for the moment the semantic embarrassment to investigate the evolutionary underpinnings of the increase in species abundance and geographic range of the genus *Quercus* from its origin to the current day. Our review complements the integrative review of the American oaks in Cavender-Bares (2019), which emphasizes the reciprocal effects of ecological and evolutionary processes on oak diversity. In our review, we focus on the question of how global patterns of oak diversity and abundance are shaped by the joint effects of microevolutionary processes – processes at or below the species level – and macroevolutionary processes – processes at the clade level. The extraordinary species diversity in America and Asia as well as the continuous continental distribution of a limited number of European species together plead for a joint consideration of macro- and microevolutionary processes that triggered and molded the radiation and expansion of oaks. Oaks have been scrutinized at both scales of inquiry over the last three decades, taking the North American, European, and East Asian settings as study cases (Manos *et al.*, 1999; Manos & Stanford, 2001; Petit *et al.*, 2002; Ohsawa *et al.*, 2007; Okaura *et al.*, 2007; Pearse & Hipp, 2009; Kremer *et al.*, 2010; Torres-Miranda *et al.*, 2011; Rodriguez-Correa *et al.*, 2017; Deng *et al.*, 2018; Jiang *et al.*, 2019). In North America, two oak clades arose simultaneously in the late Eocene to early Oligocene and radiated in sympatry, maintaining similar degrees of diversity and range (Cavender-Bares *et al.*, 2018; Hipp *et al.*, 2018; Cavender-Bares, 2019). Europe affords a contrasting evolutionary stage, where two species (*Quercus petraea* and *Quercus robur*) underwent repeated continental retraction and expansion during the late Pleistocene, generated by peculiar demographic and genetic processes (Brewer *et al.*, 2002; Petit *et al.*, 2003). We review major findings regarding radiation and expansion in oaks and extend our review beyond these emblematic cases by addressing more recent research in Asian species (e.g. Deng *et al.*, 2018; Jiang *et al.*, 2019).

Our review is not exhaustive, and many important papers will have been missed in it. This fact notwithstanding, our separate examinations of microevolution and macroevolution and consideration of their reciprocal effects on oak evolutionary success offer general insights into the success of the genus *Quercus* across the northern hemisphere. We believe our review demonstrates the power of integrating perspectives across diverse evolutionary scales for understanding the past and future of oak diversity.

II. Microevolution in oaks

Most studies of oak microevolution have either quantified the amount of evolutionary change within a given spatiotemporal interval or have investigated the pace and mechanism of evolutionary processes driving evolutionary change. These studies have made use of complementary approaches and disciplines, including paleobotany, ecology, phylogeography, population biology and quantitative genetics, as partially reviewed previously (Manos *et al.*, 1999; Kremer *et al.*, 2010; Barrón *et al.*, 2017; Cavender-Bares, 2019). In general, microevolutionary processes have been studied from synchronic monitoring of data for traits and gene markers in extant *in situ* natural populations or *ex situ* common gardens (provenance tests). Allochronic approaches based on ancient DNA have only recently been attempted to explore the persistence and/or replacement of temperate European oak populations during the Holocene (Wagner *et al.*, 2018). The overall time frame encompassed by allochronic and synchronic microevolutionary investigations spans the last 15 000 yr. Most microevolutionary studies have focused on oak species widely distributed in the northern temperate zone, the populations of which were established during the most recent postglacial warming (i.e. during the Holocene). The major evolutionary changes during this period were triggered by macroecological changes, comprising a general trend towards warming since the last glacial maximum, but also shorter alternating periods of cooling and warming known as the ‘Little Ice Ages’ (Jones & Mann, 2004). Impacts of climate change on forest ecosystems lasting only a few centuries are also well documented in northern latitudes (Kullman & Kjallgren, 2006; MacDonald *et al.*, 2008). In other parts of the world – in Mexico, for example, where oak species diversity is highest – climate change has been complemented by local orogeny (mountain formation) during the Holocene (Ferrari *et al.*, 2012). Climatic and orogenic changes have served as strong selective drivers in plant and animal species, triggering migration, the colonization of new habitats, adaptation, and introgression (Svennig *et al.*, 2015; Meng *et al.*, 2017; Muellner-Riehl, 2019).

1. Rapid migration limiting the erosion of diversity

Empirical reconstructions of post-glacial oak colonization in Europe based on fossilized pollen have indicated a mean migration velocity of 400–500 m yr^{-1} (Brewer *et al.*, 2002; Giesecke & Brewer, 2018), with maximum values as high as 1000 m yr^{-1} (Fig. 1) (Brewer *et al.*, 2005). These estimates outpace migration rates inferred from data on dispersal by jays or rodents (Bossema, 1979). This apparent discrepancy suggests that postglacial migration dynamics involved a composite mechanism combining diffusion at the migration front with rare long-distance dispersal events (Le Corre *et al.*, 1997). Computer simulations have shown that even very rare long-distance dispersal events can increase

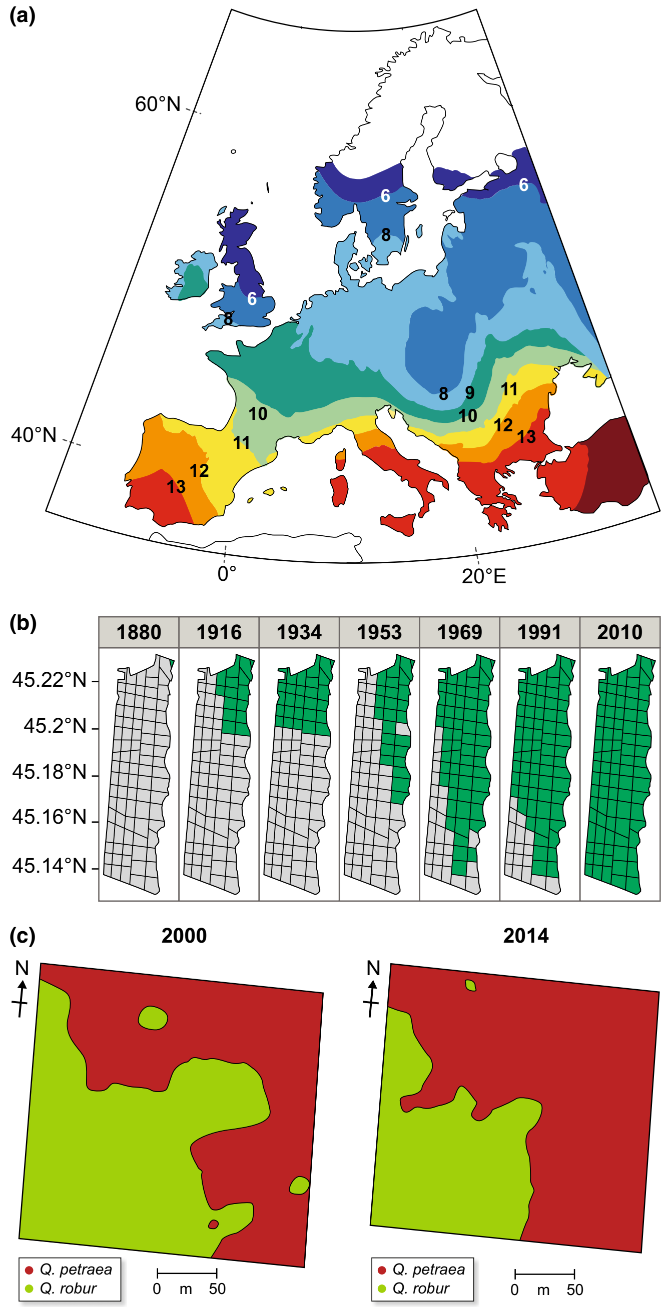


Fig. 1 Velocity of oak migration at different temporal and spatial scales. These assessments were made in very different ecological settings and using different methods. They are shown for illustration purposes and cannot be used for detailed quantitative comparisons. (a) Migration velocity of deciduous oaks retrieved from palynological records retracing postglacial colonization in Europe. This map shows isochrone maps at 1000-yr time slices from 13 000 BP to 6000 BP, representing arrival times of oaks as derived from the European Pollen Database (EPD) (Brewer *et al.*, 2002). Velocity varies over time and space, with average values amounting to 500 m yr^{-1}, with maximum values of up to 1000 m yr^{-1} (Brewer *et al.*, 2005). Although palynological records may overestimate migration effects due to the persistence of small refugial populations, these figures were recently confirmed by updating EPD data (Giesecke, 2016; Giesecke & Brewer, 2018). (b) Migration velocity of Holm oak (*Quercus ilex*) during the last century at the northern margin of its distribution (Delzon *et al.*, 2013). Holm oak is a Mediterranean evergreen species and its northern margin stretches along the Atlantic coast of France. These maps illustrate its distribution (in green) across a national forest located on the Atlantic coast at different times over the last century. Forest maps show compartment subdivisions (black lines). The maps are derived from floristic inventories conducted at the compartment level by the forest service every 10–20 yr when management plans of national forest are renewed. The migration velocity amounts, on average, to 20 m yr^{-1}, with maximum values up to 57 m yr^{-1}. These figures are likely underestimated, as Holm oak is considered locally to be a weed by foresters and is screened during thinning operations. (c) Expansion of *Quercus petraea* over two successive generations in La Petite Charnie Forest, located in the northwestern part of France (Truffaut *et al.*, 2017). The map shows the distribution of individual trees of each species (red area: *Q. petraea*; green area: *Q. robur*) in 2000 and 2014, before and after natural regeneration occurred. *Q. petraea* has expanded its distribution by up 50%, corresponding to maximum linear shifts of 20 m.

overall migration velocity, as new focal populations generated stochastically by these events ultimately merge through population growth (Le Corre *et al.*, 1997; Bialozyt *et al.*, 2006). A somewhat different picture has emerged from postglacial migration reconstructions in North America. East of the Rocky Mountains and in the Pacific Northwest, oak stands persisted closer to the Laurentide ice sheet during the glacial period and extended northward to lower latitudes than in Europe (Schlarbaum *et al.*, 1982; Magni *et al.*, 2005; Soltis *et al.*, 2006; Marsico *et al.*, 2009). West of the Rocky Mountains, in California, populations were maintained *in situ* during glacial periods, albeit at reduced sizes, and these populations subsequently expanded during postglacial warming, but over limited total distances (Grivet *et al.*, 2006). In China, postglacial colonisation occurred as in Europe over very large distances as oaks were restricted to tropical and subtropical areas at the Last Glacial Maximum and expanded up to the northeastern rim of the Tibetan Plateau (Cao *et al.*, 2015). Rapid migration seems to have been triggered by quaternary climatic oscillations (Svenning *et al.*, 2015), but at spatial scales that differed between continents. While in central Europe (Brewer *et al.*, 2002) and Asia (Cao *et al.*, 2015) postglacial colonization dynamics of temperate oaks were dominated by large scale expansion, in Mediterranean regions of Europe (de Heredia *et al.*, 2007) and California (Grivet *et al.*, 2006), oak species expanded at a limited scale from multiple refugial foci.

What were the evolutionary consequences of rapid migration? Long-distance dispersal imprinted strong phylogeographic structures, because such dispersal events were rare and gave rise to small populations, with founding events for chloroplast genomes (Le Corre & Kremer, 1998). While haplotype fixation within population is nearly complete in most oak species in Europe (Vitelli *et al.*, 2017; Petit *et al.*, 2002), North America (Whittemore & Schaal, 1991; Cavender-Bares *et al.*, 2015) and Asia (Yang *et al.*, 2017; Harada *et al.*, 2018), geographical haplotype distributions have also been shaped by postglacial movements: oak species that expanded over large distances usually exhibit widely distributed haplotypes, while species with regional expansion show locally distributed haplotypes (Pham *et al.*, 2017; Sork *et al.*, 2016a, c). Studies of ancient DNA retrieved from wood remains (Wagner *et al.*, 2018) have shown that chloroplast genomes have been maintained since the establishment of these populations. Thus, the extant phylogeographic structures were imprinted during postglacial migration

(Wagner *et al.*, 2018). A somewhat counterintuitive consequence of long-distance dispersal is the maintenance of diversity despite founding events during colonization. Computer simulations have shown that the multiple local populations created by long-distance dispersal maintain higher degrees of diversity than populations displaying mainstream diffusion during colonization (Bialozyt *et al.*, 2006).

However, founding events and the strong phylogeographic structures they generated have tended to persist only in organellar genomes, as subsequent gene flow mediated by pollen travelling among widely separated populations within species progressively erased nuclear differentiation among geographic regions (Kremer *et al.*, 2010). Contrasts between organellar and nuclear differentiation are widespread in most oak species studied to date, as a result of strong differences of seed vs pollen movement that is common in oak species (Petit *et al.*, 2005; Petit & Excoffier, 2009). Rapid migration associated with fast establishment may lead ultimately to priority effects, resulting from novel evolutionary and ecological opportunities favoring species that arrived first (Cavender-Bares *et al.*, 2016b; Cavender-Bares, 2019). Impacts of evolutionary priority effects may include demographic growth, expansion, ecological divergence and diversification. The most recent comparative data regarding postglacial expansion velocities in the three continents (Giesecke *et al.*, 2017 in Europe; Cao *et al.*, 2015 in Asia, and Harnik *et al.*, 2018 in North America) suggest that oaks benefited from priority effects in many circumstances.

2. Regional adaptation despite extensive gene flow

Evidence for adaptation during the Holocene has been provided by many common-garden experiments, demonstrating the occurrence of adaptive divergence between modern populations established after postglacial colonization. Range-wide population-level collections from species with continental distributions have revealed high degrees of population differentiation for adult growth-related traits in species representing three major clades of the genus: *Quercus rubra* (Kriebel *et al.*, 1976, 1988), representing section *Lobatae*; *Quercus macrocarpa* (Dicke & Bagley, 1980) and *Q. petraea* (Kremer *et al.*, 2010), representing section *Quercus*; and *Quercus suber* (Gandour *et al.*, 2007; Ramirez-Valiente *et al.*, 2014a,b), representing section *Cerris*. Reported *Qst* values (a metric of genetic population differentiation for traits) reach up to 0.8, greatly exceeding typical differentiation values for neutral genetic markers (Kremer *et al.*, 2010; Ramirez-Valiente *et al.*, 2018), suggesting that natural selection is the predominant driver of differentiation in phenotypic traits (Fig. 3d, see later). Similar results have been obtained for juvenile traits and in limited population samples from other species (e.g. *Quercus acutissima* (Zhang *et al.*, 2017) of sect. *Cerris*, *Quercus oleoides* (Ramirez-Valiente *et al.*, 2017, 2019; Koehler *et al.*, 2012) of sect. *Virentes*).

These studies also suggest that divergent selection has shaped genetic variation across species ranges. Clinal variation tracking geographic temperature-driven trends is often observed for growth and phenological traits (Fig. 2; Soularue & Kremer, 2014). However, the direction of the cline may differ between species or continents. Bud burst, for example, tends to occur later in spring for European oak populations from higher elevation or latitude than for more southerly populations (Ducousso *et al.*, 1996; Vitasse *et al.*, 2009), whereas the opposite pattern is observed for northern red oak (McGee, 1970, 1974; Kriebel *et al.*, 1976; Daubree & Kremer, 1993). This raises the question of whether the abiotic or biotic factors driving divergent selection for flushing date differ between the two continents or between different species. More recent studies have focused on physiological traits thought to contribute to adaptation to climate in *Q. petraea* (Torres-Ruiz *et al.*, 2019) and *Q. suber* (Ramirez-Valiente *et al.*, 2014a,b). Interestingly, in these two cases, population differentiation was less pronounced for leaf traits and traits relating to water metabolism, suggesting that divergent selection has disproportionately targeted more integrated traits, such as overall growth or bud phenology. The opposite trend was observed in *Q. oleoides*, in which leaf functional traits and water use efficiency varied according to populations' climate of origin (Cavender-Bares & Ramirez-Valiente, 2017; Ramirez-Valiente & Cavender-Bares, 2017. At a more local scale, local adaptation was demonstrated in reciprocal transplantations for leaf herbivore resistance in *Q. rubra* (Sork *et al.*, 1993).

High degrees of adaptive divergence for phenotypic traits have led to studies aiming to identify genomic footprints of diversifying selection based on two different approaches. In one approach, genome scans have been used to search for genome–environment associations (Rellstab *et al.*, 2016; Sork *et al.*, 2016b,c; Martins *et al.*, 2018). In the other, associations between genomic and trait variation have been explored in situations for which common-garden results were available (Alberto *et al.*, 2013). Significant statistical associations were detected in each case study, but there has been a lack of consistency across studies at the SNP, gene or function level (Alberto *et al.*, 2013). More recently, whole-genome sequencing in different populations has revealed the existence of thousands of SNPs significantly correlated with bud burst in *Q. petraea* and displaying clinal variation with temperature for allelic frequencies (Leroy *et al.*, 2020a). The genetic architecture of the traits contributing to climate adaptation is therefore highly polygenic. Under such circumstances, diversifying selection proceeds by first combining allelic effects at different genes rather than targeting single genes, an approach that can lead to rapid adaptive responses, occurring over a few tens of generations (Fig. 3; Kremer & Le Corre, 2012). Indeed, the existence of extensive genetic differentiation for integrated traits raises questions about the timing of divergence and adaptation (recently, during the Holocene) and whether divergence has reached optimal levels. In European temperate oaks, it is likely that the existing divergence developed gradually and exclusively during the Holocene, as evidenced by the lack of association between populations' trait values and their glacial refugial origins (Kremer *et al.*, 2002). Furthermore, based on theory, polygenetic architecture of traits enhances 'rapid divergence' (Kremer & Le Corre, 2012). However, just as divergence can be limited by the extensive pollen flow reported in oaks, adaptation also can be limited by pollen swamping. This fact notwithstanding, we argue that adaptation can develop from standing genetic variation despite gene swamping, especially for polygenic traits, for which the contributions of individual alleles are small. As predicted by simulations (Kremer &

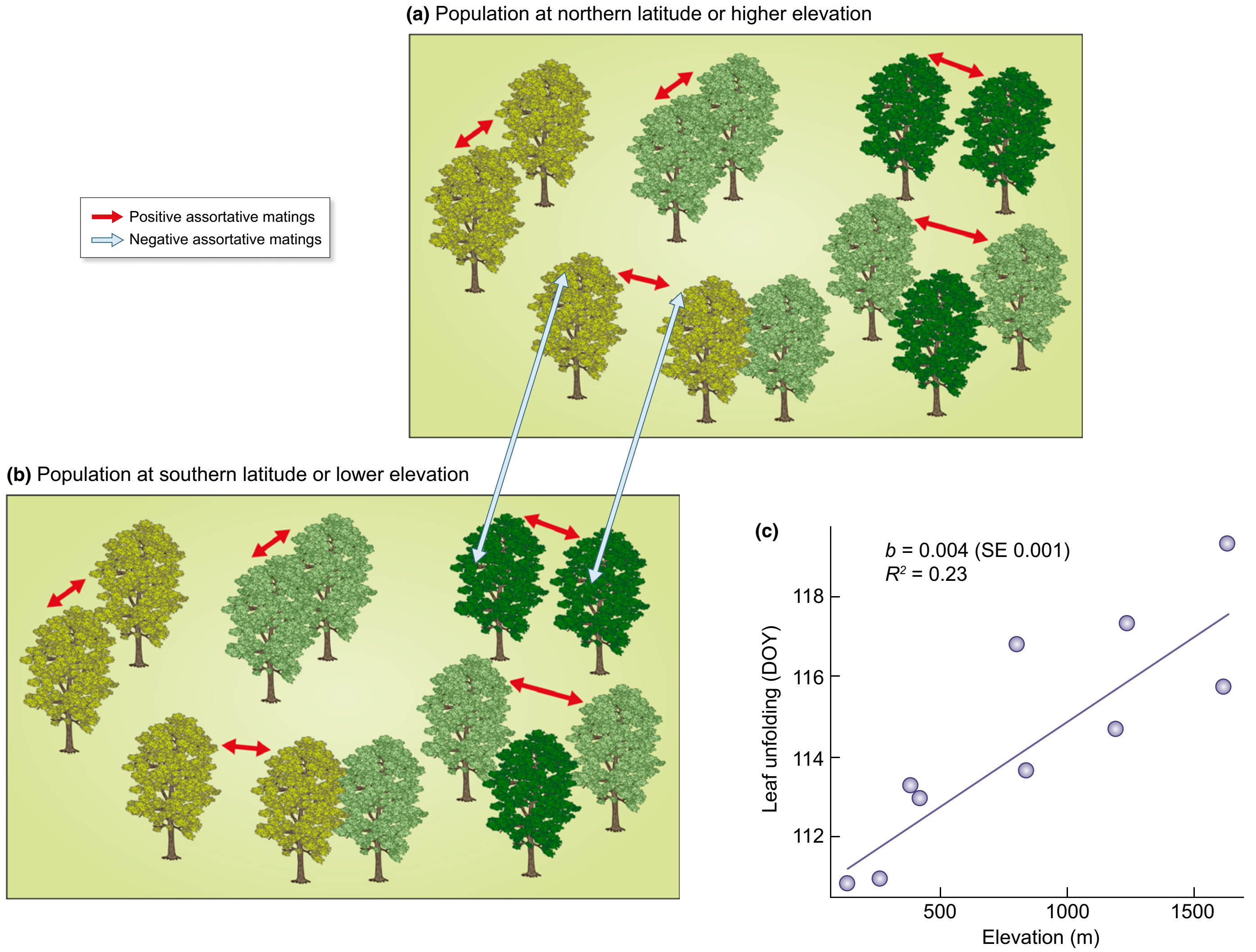
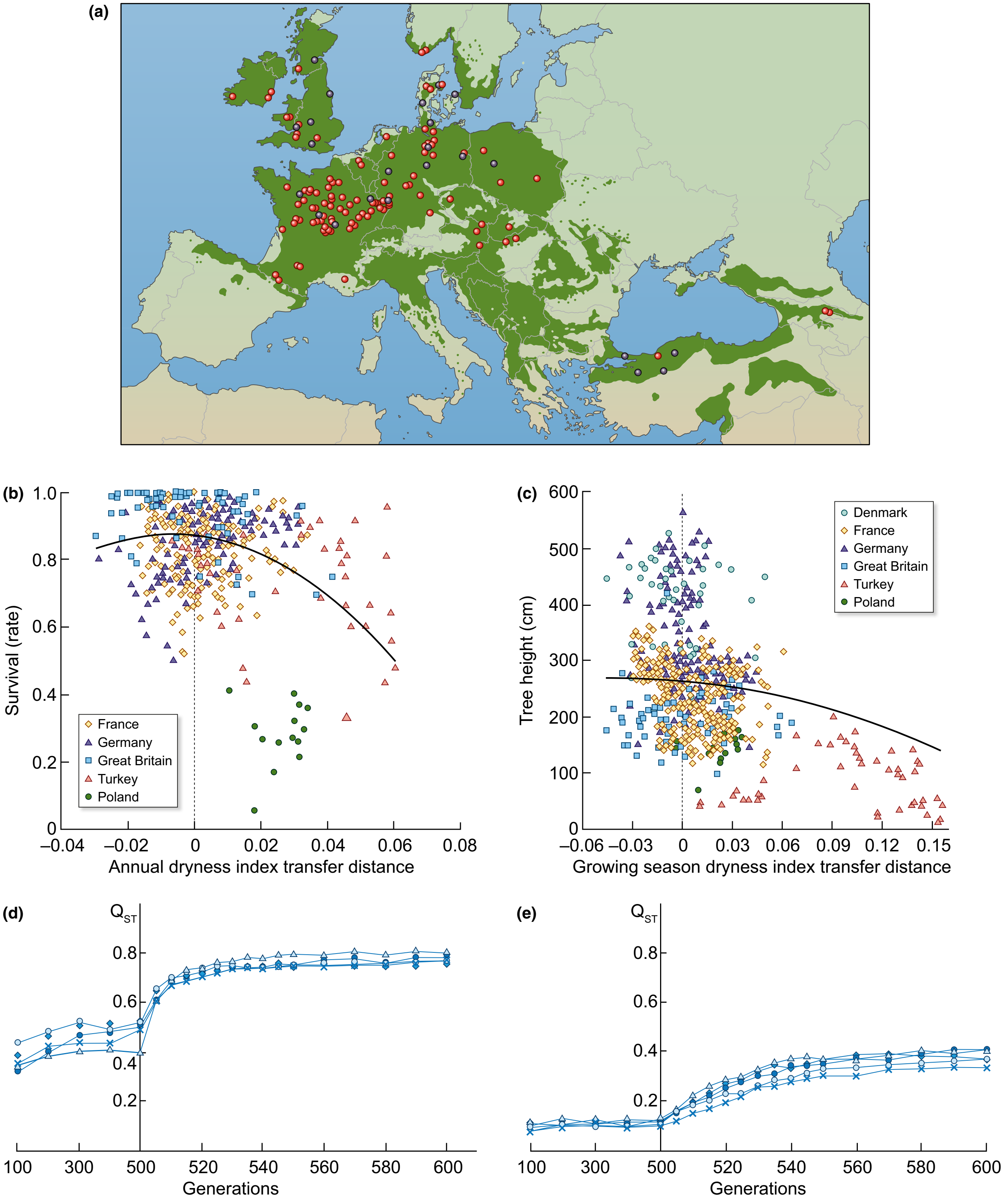


Fig. 2 Assortative mating, gene flow and diversifying selection drive clinal phenological responses in oaks. As bud phenology is correlated to the growth rhythm and to flowering in oaks, it is intensively studied in microevolution. The discovery of very large within- and between-population genetic variation has raised numerous questions about the mechanisms that maintain its evolutionary potential and its contribution to local adaptation. In addition to common evolutionary drivers such as gene flow and selection, assortative mating makes a significant contribution to phenological responses of oak populations. This figure illustrates how gene flow and assortative mating shape clinal genetic variation between populations of higher latitude/elevation (a) and lower latitude/elevation (b). (a, b) Within natural populations, early flushing trees tend to mate with early flushing trees, resulting in positive assortative mating. Trees with similar phenotypes regarding date of bud burst preferentially mate within populations. Positive assortative mating is indicated by red arrows between trees sharing similar colours in part (a) (colours indicate here the timing of bud burst). However, matings resulting from immigrant pollen flow are likely to result in negative assortative mating, especially if source populations are farther away in latitude or elevation. Populations at northern latitudes or higher altitude flush, on average, later than populations from more southern latitudes or from lower elevations because of temperature differences. Hence, successful matings resulting from pollen flow can only associate late flushing trees from the south (or low elevation) to early flushing trees in the north (or at higher elevation). Negative assortative mating is indicated by blue arrows in (b). As a result, assortative mating and gene flow contribute to a directional filtering of late flushing genes to the northern (or higher elevation) populations (Soularue & Kremer, 2012, 2014). (c) Within-population positive assortative mating generates higher within-population genetic variance, whereas negative assortative mating and gene flow create genetic clines along temperature gradients in the landscape, as shown here by the genetic divergence of the time of bud burst along an elevational gradient in sessile oak in the Pyrénées (Firmat *et al.*, 2017).

Le Corre, 2012) and by theory (Yeaman, 2015), greater genetic variation due to gene flow provides more opportunities for allelic combinations with favorable effects, facilitating adaptation.

3. Hybridization facilitating migration and reinforcing adaptation

Hybridization is widespread within sections of the *Quercus* genus and has received considerable attention during the last decade, as illustrated by examples in white oaks, sect. *Quercus* (Ishida *et al.*, 2003; Curtu *et al.*, 2007; Lepais & Gerber, 2011; Castillo-Mendoza *et al.*, 2019), southern live oaks, sect. *Virentes* (Cavender-Bares & Pahlich, 2009; Eaton *et al.*, 2015), red oaks, sect. *Lobatae* (Dodd & Afzal-Rafii, 2004; Peñaloza-Ramírez *et al.*, 2010; Moran *et al.*, 2012; Sullivan *et al.*, 2016), golden cup oaks, sect. *Protobalanus* (Ortego *et al.*, 2018), holly oaks, sect. *Ilex* (Neophytou *et al.*, 2007), and ring-cupped oaks, sect. *Cyclobalanopsis* (Song *et al.*, 2015; An *et al.*, 2017). Most of these studies focused on the



ecological, demographic and genetic factors shaping the rates and variation of hybridization in extant sympatric stands. Much less attention has been paid to the evolutionary implications of hybridization and introgression, which we explore here.

Recent studies based on whole-genome sequencing or reduced-representation genomic sequencing have shown that hybridization can occur without jeopardizing species integrity, even if only a limited part of the genome, comprising numerous widely

Fig. 3 Adaptive divergence, plasticity and local adaptation in oaks. Whether oak populations are locally adapted has been a recurrent concern in oak ecological genetics. Reciprocal transplantations are the experimental tool with which to test for local adaptation. Here an incomplete translocation experiment in *Quercus petraea* has been implemented at a European continental scale to assess whether natural divergent selection has resulted in locally adapted populations (Sáenz-Romero *et al.*, 2019, 2017). (a) Acorns were collected from 116 forest stands (populations, red dots) distributed across Europe; saplings were redistributed in 23 field tests (black dots) in six different countries following standard experimental designs. The monitoring of adaptive phenotypic traits was conducted from installation. (b, c) The response of two fitness related traits (survival and height growth at age 10 yr) are plotted for each population as a function of the climatic transfer distance between the climate of the origin of the populations and the climate of the test site. Populations are labelled according to the country in which the test site is located. Various climatic data were tested to account for the transfer distance. For survival and height, dryness-related indices explained the largest amount of variation in population responses. Both traits show an overall quadratic curve, with a maximum near the null transfer distance, suggesting that populations are nearly locally adapted. On average, populations grow under slightly dryer conditions than their optimum. (d, e) Local adaptation due to diversifying selection has resulted in adaptive divergence. The rate at which adaptive divergence builds is largely unknown, but simulations suggest that adaptive differentiation can be quite rapid. Two evolutionary scenarios calibrated to the oak case study (55 populations undergoing diversifying selection and connected by gene flow) with two extreme within-population selection intensities (strong, d; moderate, e) were simulated to give an idea of the pace of adaptive divergence, measured here as Qst (a metric of genetic population differentiation, varying between 0 and 1) following methods described in Kremer & Le Corre (2012). At generation 500, environmental changes were introduced to assess the response of adaptive divergence following environmental changes. In a few tens of generations following environmental changes, genetic differentiation again reached a plateau.

distributed small regions, is responsible for maintaining species barriers (Eaton *et al.*, 2015; Leroy *et al.*, 2017, 2020b). Genes under selection for drought-tolerance (Oney-Birol *et al.*, 2018) or involved in photoperiodic control of growth and development (Lind-Riehl *et al.*, 2014) may be disproportionately responsible for genetic divergence between species: selection in ecologically distinct species may suffice to explain divergence in the face of gene flow. Equally importantly, these observations are inconsistent with the notion that hybridization triggers speciation by creating new hybrid species (Abbott *et al.*, 2013), or favoring the assimilation of one species by another, although one cannot exclude the possibility that relictual hybrid populations might in rare cases behave as new species (Hauser *et al.*, 2017).

Instead, hybridization should be seen as a microevolutionary process reinforcing adaptation (Cavender-Bares, 2019; Leroy *et al.*, 2020a), and, more surprisingly, enhancing migration (Petit *et al.*, 2003), as shown by ecological and population genomics studies of various oak complexes. Evidence for a role of hybridization in facilitating colonization comes from the continent-wide sharing of chloroplast genomes by sympatric European or North American white oaks (Whittemore & Schaal, 1991; Petit *et al.*, 1997, 2002). In each case study, two species cohabiting the same forest have the same chloroplast haplotype, whereas the same species co-occurring in a nearby mixed stand may share a different chloroplast haplotype. These findings suggest that hybridization and subsequent backcrossing between two species can result in the chloroplast genome of one species being captured by the other. Furthermore, according to this scenario, the hybridization/backcrossing mechanism necessarily occurred recently (during the Holocene), at some time since post-glaciation establishment of the two species. Interestingly, in the European example, ABC simulations have supported these conclusions by showing that secondary contacts between white oak species began at the onset of the last glacial period, before recolonization (Leroy *et al.*, 2017, 2020b). In the particular context of the *Q. petraea* – *Q. robur* complex, in which backcrossing is preferentially unidirectional, from *Q. petraea* to hybrids, *Q. petraea* (the pollen ‘invader’ species) should be progressively ‘regenerated’ within *Q. robur* (the ‘resident’ species) stands as a result of recurrent backcrossing after the initial hybridization. A recent demographic and genetic study of the spatial distribution of pure species and admixed forms conducted over two successive generations confirmed the progressive invasion of *Q. robur* by *Q. petraea* as a result of hybridization (Truffaut *et al.*, 2017). To sum up, the pioneer species *Q. robur* is more readily dispersed long distance by jays (Bossema, 1979), while *Q. petraea* migrates more readily by long distance pollen movement. Ultimately *Q. petraea* invades *Q. robur* as a consequence of the recurrent backcrossing after initial hybridizition (Petit *et al.*, 2003). We conclude that this mechanism – introgression-driven migration – was active during post-glacial colonization in Europe and was probably selected to increase vagility during the repeated climatic oscillations that prevailed during the quaternary period (Dynesius & Jansson, 2000). Artificial directional backcrossing in chestnut breeding programs has shown that the pollen invader species can largely be regenerated in a relatively small number of generations, compatible with the post-glacial time frame (Diskin *et al.*, 2006; Steiner *et al.*, 2017). This directional introgression is still evident at the northern margins of the temperate European oak range, at which the frequency of introgressed forms is much higher than in the center of the distribution (Beatty *et al.*, 2016). According to this scenario, introgression occurs mostly from the resident to the invading species, as predicted by theory (Currat *et al.*, 2008) and observed in sympatric *Q. petraea* – *Q. robur* stands (Guichoux *et al.*, 2013).

While the direction of introgression has been elucidated, the genes actually transmitted, even the classes of genes, remain a matter of speculation. An early study based on a rangewide genome scan of four co-occurring California red oaks (Dodd & Afzal-Rafii, 2004) demonstrated that the amount and source of introgression in a landscape context is predictable by climatic conditions and that introgressed amplified fragment length polymorphisms (AFLPs) could be found well outside the natural range of their source species. This suggested that selective introgression could facilitate species migration. A more recent study (Leroy *et al.*, 2020a) builds on this finding, confirming expectations that introgression may facilitate adaptation of the invading population. In a broad collection of *Q. petraea* populations sampled along elevational and latitudinal gradients, whole genome sequencing detected signatures of introgression of temperature tolerance related genes from *Q. robur*, facilitating adaptation at higher latitudes and elevation of the invading species (Leroy *et al.*, 2020a). This appears to be the first reported case of adaptive introgression in oaks supported by genomic and phenotypic evidence.

4. Pace and targets of microevolutionary change

Synchronic approaches, in common-garden experiments or in extant natural populations, have been valuable for estimating the magnitude and direction of evolutionary change. However, because such approaches integrate divergence or differentiation estimates accumulating over time during the Holocene, including changes in opposing directions that effectively cancel each other out, they tend to underestimate the instantaneous rate of evolution, or evolution occurring over a very small number of generations (Gingerich, 2001). It is unclear, for example, whether observed divergence in bud-break phenology between red oak (*Q. rubra*) populations at two ends of the species range includes only the changes triggered by the minor environmental changes of the few centuries since the stabilization of overall climate in the northern hemisphere (6000 yr BP). Alternative explanations are either longer-term divergence between populations throughout the Holocene or, conversely, early equilibrium reached within a few generations after post-glacial establishment.

There are a few documented examples in oaks of evolutionary change occurring over a small number of generations, mostly in conditions of strong environmental change. Many North American oak species were introduced into Europe during the last three centuries. These species were initially established in botanical gardens, then in planted forests (Timbal *et al.*, 1994). Northern red oak, *Q. rubra*, was introduced into Europe in the eighteenth century and is now widely used in operational forestry across the continent. A genetic survey conducted in Europe and throughout the natural range of this species showed that a diverse germplasm had been introduced, probably from the northern part of the natural distribution (Merceron *et al.*, 2017). At the same time, a range-wide common garden of plants from introduced and native populations was established in Europe, and studies of this common garden showed that the introduced populations had diverged from the native gene pool in phenological and growth traits (Daubree & Kremer, 1993; Merceron, 2017). As there is evidence to suggest that founder effects were limited (Merceron *et al.*, 2017), the observed divergence between the two gene pools probably results from selection, due to the difference in environment between the two continents and the particular colonization dynamics of an exotic species (Fig. 4).

Another example is provided by the monitoring of genetic, phenotypic and demographic changes in two successive generations of *Q. petraea* and *Q. robur* (Truffaut *et al.*, 2017). Predicted and observed changes were detected for highly integrated traits, such as height and diameter growth, whereas physiological traits tended to be more static (Hermine Alexandre, unpublished). These rare examples suggest that evolutionary change may occur over short periods of time, even a single generation. We would argue that extensive and rapid change is possible because oaks harbor large reservoirs of diversity. Such rapid evolutionary changes may shape species coexistence in oaks through selection for divergent competitive abilities (Hart *et al.*, 2019) and thus shape oak diversity at scales ranging from single forests to entire continents.

5. Accumulation of fuel for evolutionary change

Expected evolutionary change increases with the degree of diversity residing within populations, regardless of whether drift or natural selection dominates. Studies of genetic diversity in natural oak populations date to the advent of tools for monitoring diversity. Initially, such studies focused on isozymes or morphology (Baranski, 1975), but they now consider whole-genome sequences. The diversity statistics compiled in an earlier review based on isozymes (Kremer & Petit, 1993) were subsequently confirmed by a myriad of studies encompassing species from three continents, which highlighted the very high degree of genetic diversity residing within populations. If we restrict the analysis to diversity inventories based on microsatellites, then a general picture of high heterozygosity (> 0.7) with numerous rare alleles emerges. This is the case not only for species with a broad distribution (*Q. macrocarpa* (Craft & Ashley, 2007); *Q. rubra* (Lind-Riehl & Gailing, 2015; Alexander & Woeste, 2017); *Quercus candicans, Quercus castanea* and *Quercus crassifolia* (Oyama *et al.*, 2018); *Q. petraea* and *Q. robur* (Mariette *et al.*, 2002; Neophytou *et al.*, 2010); *Q. acutissima* (Zhang *et al.*, 2013); and *Quercus mongolica* (Zeng *et al.*, 2015)), but also for species with much narrower ranges (*Quercus hinckelyi* (Backs *et al.*, 2015); *Quercus engelmannii* (Ortego *et al.*, 2012); *Quercus tomentella* (Ashley *et al.*, 2018); *Quercus alnifolia* (Neophytou *et al.*, 2011); and *Quercus austrocochinchinensis* (An *et al.*, 2017)). Whole-genome sequencing results have recently confirmed marker estimates, highlighting a strikingly high degree of nucleotide diversity (π values of 0.0114 (Plomion *et al.*, 2018), and one SNP every 23 bp (Leroy *et al.*, 2020b). Despite potential constraints due to either natural vegetative reproduction (Ainsworth *et al.*, 2003; Valbuena-Carabana *et al.*, 2008; Backs *et al.*, 2015; Ashley *et al.*, 2018) or scattered distributions at the edges of the main range (Ohsawa *et al.*, 2008; Marsico *et al.*, 2009; Ortego *et al.*, 2015), the erosion of diversity has been limited.

The high degree of within-population polymorphism that appears to characterize almost all oaks raises the question of whether properties intrinsic to *Quercus* might enhance the accumulation of genetic diversity. Diversity is mechanistically driven by population size, which is itself determined by population history and life history traits (Ellegren & Galtier, 2016). According to neutral theory, new mutations are more likely to remain within a population, and for longer periods of time before fixation, in large populations. Thus species with large population sizes tend to accumulate diversity simply because they do not lose new mutations. It could be argued that oak species, despite their different evolutionary histories, have several life history traits in common that collectively contribute to the establishment and maintenance of large populations and high degrees of diversity. Longevity increases the opportunity for somatic mutations, which may ultimately enter the germline, increasing overall diversity (Plomion *et al.*, 2018). Longevity, and the long juvenile period in particular, facilitate the replenishment of population density through colonization, allowing migrants to enter the recipient population before reproduction takes place (Austerlitz *et al.*, 2000; Austerlitz & Garnier-Gere, 2003). Polyandry similarly increases with longevity, contributing to greater diversity (Nakanishi *et al.*, 2005; Craft *et al.*, 2009). Long-distance pollination has now been repeatedly demonstrated by paternity analysis in various oak species (in *Q. macrocarpa* (Dow & Ashley, 1996, 1998; Craft & Ashley, 2010); and *Q. robur* (Buschbom *et al.*, 2011)), suggesting that oaks maintain large effective population sizes even if their populations are spatially isolated (Oyama *et al.*, 2017). Perhaps equally important in oaks is the role of interspecific gene exchange as a mechanism for enriching within-population diversity. Multispecies oak communities are common, and genetic diversity of the widespread *Quercus castanea* has been shown to increase with the number of co-occurring oak species in the species-rich Transmexican Volcanic Belt (Valencia-Cuevas *et al.*, 2014).

In addition to neutral diversity, oaks also retain variation that is potentially adaptive (Ramirez-Valiente *et al.*, 2014a,b). Empirical estimates of within-population heritability and evolvability show that oaks possess large within-population aphenotypic variance encompassing a number of functional traits. Historically, estimates of genetic variance were limited to species and traits of economic relevance, mostly growth and wood-related traits. Previous reviews of North American oaks (mainly *Q. alba*, *Q. rubra*, *Q. falcata* and *Q. pagoda*) (Kriebel, 1993) and European oaks (mainly *Q. petraea*

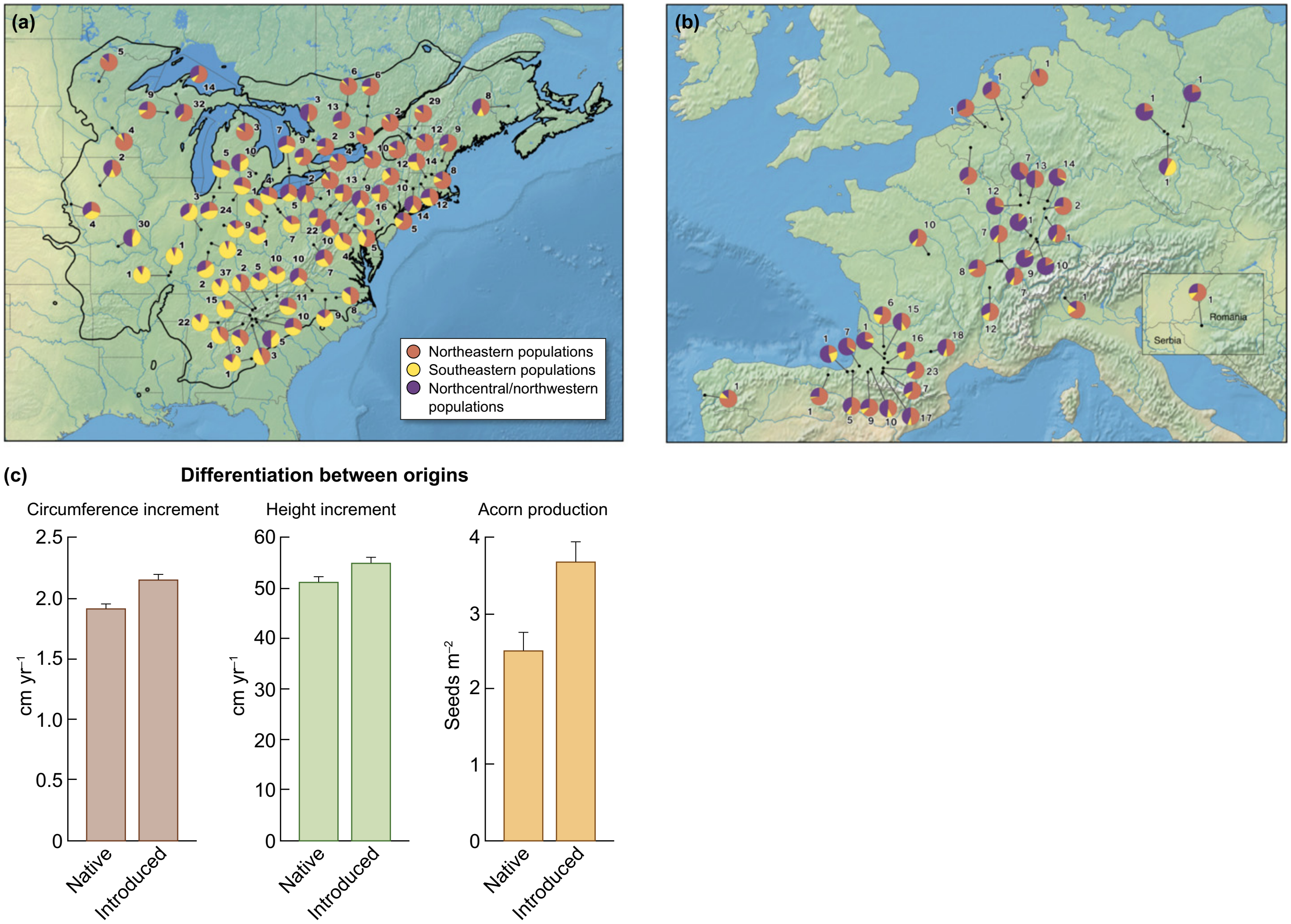


Fig. 4 Evolutionary change assessed in transferred populations. Historically well-documented transfers of populations allow for the tracking of evolutionary changes. Oaks have been transplanted from North America to Europe. Northern red oak (*Quercus rubra*) is an emblematic example of a widely introduced species in Europe that is currently used in operational forestry. In the early 1980s common-garden experiments were raised in Europe comprising descendants of introduced populations (of unknown origin) and descendants collected in the 1980s in native stands in North America. This experiment enables the estimation of genetic changes in northern red oak since its introduction in Europe. A comprehensive genetic survey and spatially explicit Bayesian clustering method using SNP markers was implemented in both sets of populations and showed that genetic diversity was not eroded following the introduction, and that the European introduced population likely originated from the northeastern part of the distribution. The native and introduced populations were planted in common-garden experiments installed in the southwest of France. Height and circumference increments (after maternal effects have vanished in oaks) and seed production were assessed (between age 20 and 30 yr) and compared between the two origins, taking into account the common ancestry based on the SNP markers. The results show increased growth and reproduction in introduced populations, suggesting that detectable evolutionary changes had occurred over a low number of generations (Merceron *et al.*, 2017). (a) Distribution of the native populations included in the genetic survey. The colours in the pie chart correspond to the genetic clusters assigned by the genetic clustering analysis (orange: northeastern populations, yellow: southeastern; purple: north-central/northwestern). (b) Distribution of the introduced populations included in the genetic survey. (c) Comparison between native and introduced populations in terms of height increment (cm yr^{-1}), circumference increment (cm yr^{-1}) and seed production (seed m^{-2}).

and *Q. robur*) (Kleinschmit, 1993) highlighted the existence of already extremely variable phenotypes within and between progenies raised in common gardens in terms of height and diameter growth, crown form and phenology. Similar outcomes were also observed more recently in Asian species for growth (in *Q. acutissima* (Na *et al.*, 2015) and *Q. serrata* (Kang *et al.*, 2007)). Within the context of environmental change, attention has shifted towards fitness-related traits, such as phenology, resistance to biotic and abiotic stresses, and reproduction (Ramirez-Valiente *et al.*, 2019; Brendel *et al.*, 2008). Strikingly, the heritability of spring phenology is very high (>0.8) in various oak species (*Q. robur* (Baliuckas & Pliura, 2003); *Q. petraea* (Alberto *et al.*, 2011; Firmat *et al.*, 2017); *Q. suber* (Ramirez-Valiente *et al.*, 2014a,b)), probably due to assortative mating, with preferential mating between extreme flushing phenotypes (Soularue & Kremer, 2012, 2014). Artificial cloning by cuttings has made it possible to assess the wide genotypic variation in water use efficiency (Brendel *et al.*, 2008; Roussel *et al.*, 2009), resistance to waterlogging (Parelle *et al.*, 2007) and fecundity (Caignard *et al.*, 2019). Estimates of genetic variation are highly variable among species where traits have been studied, but there is on average inflated genetic variance within natural populations for a number of traits, including fitness-related traits such as growth and fecundity (Alexandre *et al.*, 2019).

Convergent assessments of within-population diversity regardless of the species and traits considered raise questions about the inherent mechanisms responsible for the maintenance of this variation. In addition to generic processes, such as extensive gene flow, spatially and temporally fluctuating selection may act over long time periods, during which environmental or climatic changes may alter natural selection in contrasting ways or opposite directions. Stabilizing selection, favoring intermediate phenotypes, and the polygenic architecture of most of the traits studied in oaks to date probably also contribute to the maintenance of genetic variation in natural populations.

III. Macroevolution in oaks

Macroevolutionary studies in oaks trace the history of lineage diversification from the birth of the genus *c.* 56 Ma to the present day. Phylogenetic research in oaks initially proceeded from synthetic inferences based on morphology and biogeography (Trelease, 1924; Camus, 1936, 1938, 1952; Axelrod, 1983) to morphological cladistics (Nixon, 1985, 1993b) (reviewed in Manos *et al.*, 1999; Manos, 2016). These first studies make evident the importance of molecular data for distinguishing between hypotheses that emphasize morphology vs biogeography. The first molecular phylogenetic studies analyzed relatively small numbers of genes (Whittemore & Schaal, 1991; Manos *et al.*, 1999, 2008; Oh & Manos, 2008; Hubert *et al.*, 2014; Deng *et al.*, 2013) and were successful at recovering many broad relationships, but not robust species-level relationships near the tips of the phylogeny. DNA fingerprinting techniques (Pearse & Hipp, 2009) and phylogenomic approaches of the past five years based primarily on RAD-seq reduced-representation genomic sequencing (Hipp *et al.*, 2014; Cavender-Bares *et al.*, 2015; Fitz-Gibbon *et al.*, 2017; Deng *et al.*, 2018) succeeded in recovering fine-scale phylogenetic relationships and lay the groundwork for this review.

1. Biogeographic transitions and trait evolution shape oak-dominated ecosystems

The stem age of *Quercus* dates to at least the Paleocene/Eocene boundary, 56 Ma, based on fossilized pollen records (Hofmann, 2010; Hofmann *et al.*, 2011). At that time, global temperatures were *c.* 10°C warmer than current conditions (Zachos *et al.*, 2001). Oaks underwent a basal vicariance between Eurasia and North America (Manos and Stanford, 2001; Hipp *et al.*, 2019). Fossil data suggest that several of the major lineages that we now recognize as sections (Denk *et al.*, 2017) – *viz.* sections *Cyclobalanopsis* (Manchester, 1994; Manchester, 2011), *Lobatae* (Greenwood *et al.*, 2016; Grimsson *et al.*, 2016), *Quercus* (McIntyre, 1991; Eberle & Greenwood, 2012), and possibly section *Ilex* (Hofmann, 2010) – originated within about 10 million yr (Myr) following the early Eocene climatic optimum. The early diversification of *Quercus* thus rapidly divided the genus into geographically structured clades (Fig. 5). As temperatures cooled over the past 40 Myr, they diversified largely *in situ* (Axelrod, 1983; Manos & Stanford, 2001), diversifying ecologically within each region.

Each of the eight sections of *Quercus* overlaps with one or more others in ecological and geographic space (Cavender-Bares *et al.*, 2015; Eaton *et al.*, 2015; Fitz-Gibbon *et al.*, 2017; Hauser *et al.*, 2017; Leroy *et al.*, 2017; McVay *et al.*, 2017b; Ortego *et al.*, 2017). This has been explored in depth in the Americas, where the white and red oaks (sections *Quercus* and *Lobatae* respectively) arose from a northern ancestor, then diversified southward as temperatures warmed from the early Eocene climatic optimum until the mid-Oligocene (Zachos *et al.*, 2001), radiating in parallel in the western US, eastern North America, and Mexico and the southwestern US (Hipp *et al.*, 2018; Cavender-Bares, 2019). In both the red and white oaks, the move into Mexico resulted in an abrupt uptick in net diversification rate in the topographically diverse Mexican mountains (Hipp *et al.*, 2018). A similar history played out in Europe, where the *Cerris* and *Ilex* clades radiated to cover a broadly overlapping geographic range, ecologically diversifying within clades (Hipp *et al.*, 2019). As in North America, increases in diversification rate in the Eurasian oaks were driven by ecological opportunity in two clades, but not in sympatry as we find in the Americas. One of the Eurasian oak clades, the Roburoid white oaks, arrived in Eurasia from an eastern North American ancestor somewhere between 10 and 20 Ma (McVay *et al.* 2017b). Arriving to a continent lacking in closely related oaks, the Roburoid white oaks diversified at a higher rate than the *Ilex* and *Cerris* clades present in Europe when they arrived. By way of comparison, the Roburoid net diversification rate, at 0.174 (0.07–0.29, 95% CI) spp Myr^{-1}, is 2.8× the net diversification rate of sections *Cerris* and *Ilex* – both 0.063 (0.05–0.08) spp Myr^{-1} – the only other oak clades present in Europe when the Roburoids arrived, and 2.0× the net diversification rate of *Quercus alba* and allies, the sister clade that it left behind in eastern North America, at 0.085 (0.05–0.20) spp Myr^{-1} (Hipp *et al.*, 2020).

While the Roburoids were diversifying in Europe and east Asia, a portion of section *Cyclobalanopsis*, comprising the Glauca, Acuta, and Semiserrata clades (Deng *et al.*, 2018), was radiating in southeast Asia, reaching a net diversification rate of 0.31 (0.14–0.47) spp Myr^{-1} (Hipp *et al.*, 2020). Section *Cyclobalanopsis* – by far the largest of the Old World clades, with *c.* 90 species – originated with uplift of the Himalayas at the Oligocene/Miocene boundary (Deng *et al.*, 2018). As in the oaks of Mexico, increased topographic heterogeneity is implicated in the initial diversification of the section as well as an uptick in diversification *c.* 8 Ma, coinciding with the uplift of the eastern Tibetan plateau (Deng *et al.*, 2018). Initiation of the Asian summer monsoons in the late Oligocene may have contributed to spread of the section, which is a dominant of evergreen broadleaf forests. Global oak diversification is thus a story of repeated diversification into the same areas of geographic and ecological space by different lineages, with occupation of new territory facilitating diversification.

2. Adaptation has shaped macroevolution of oak traits

Oaks adapted to new climatic conditions throughout their radiation. The Ornstein–Uhlenbeck (O–U) adaptation model adaptive half-

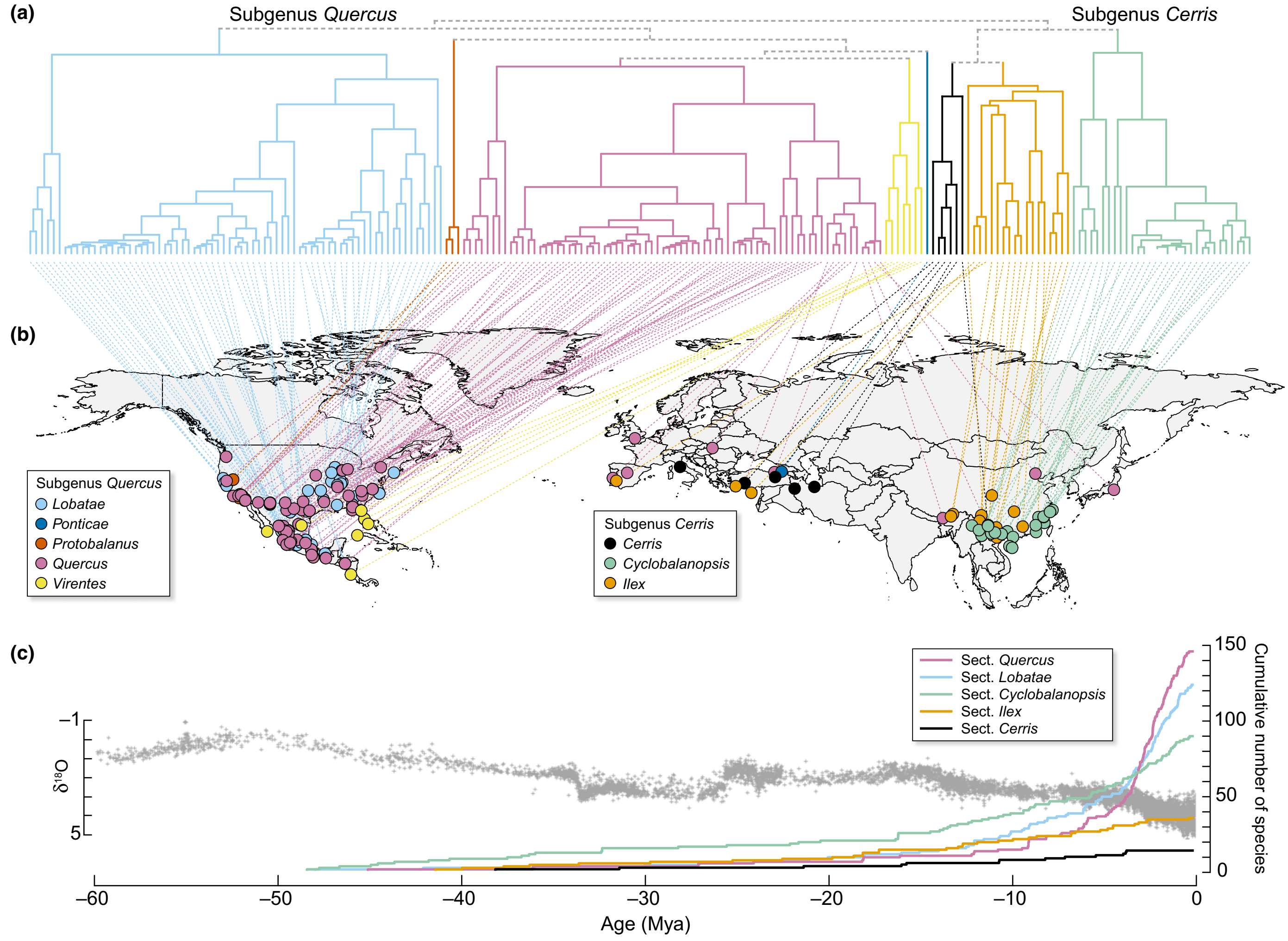


Fig. 5 Phylogeny shapes global oak biodiversity. (a) Oak diversification has been a history of replicated region-specific diversifications of multiple lineages, each of which diversified ecologically within the region. Within each of the eight sections recognized today, species have diversified ecologically, converging on similar habitats between sections, so that most geographic regions have representatives of at least two sections. The diversity we observe today is in part due to the fact that divergent lineages have evolved convergent ecologies. (b) In the Americas, the white and red oaks dominate (sections *Quercus* and *Lobatae*), followed by sections *Virentes* and *Protobalanus*. Red and white oaks radiated in sympatry in western and eastern North America, and subsequently in Mexico and Central America. In Europe, sections *Ilex*, *Cerris*, and *Quercus* overlap in distribution, whereas in southeast Asia, the highly diverse section *Cyclobalanopsis* is a dominant clade of broad-leaved evergreen forests, accompanied by sections *Ilex* and *Quercus* in part. (c) Oaks arose at northern latitudes *c.* 56 Ma, at around the time of the early Eocene climatic optimum. Temperatures at this time were *c.* 10°C warmer than they are today, as evidenced by global deep-sea oxygen isotope ($\delta^{18}O$) records (represented here by gray '+' signs), which serve as ocean temperature proxies (Zachos *et al.*, 2001). The eight major lineages now named as sections all appear to have originated within the first *c.* 10 Myr of oak evolution and have subsequently diversified largely on the continents where they arose. Standing diversity, however, has mostly arisen in the past 10 Myr. All figures are adapted from Hipp *et al.* (2020), with infrageneric taxonomy following Denk *et al.* (2017). Sources: (a) phylogeny pruned to one tip per species, including only tips with a georeferenced collection; (b) georeferenced specimens sequenced to make the phylogeny, colored by section; (c) lineage-through-time (LTT) plot with unsampled species added at random positions within the clades where they occur to recover the contemporary standing diversity of the genus.

time ($t_{1/2}$) – the expected time for a trait to evolve halfway from its ancestral state to its optimum (Hansen, 1997; Hansen *et al.*, 2008) – has been estimated at 7.53 Ma for adaptation of oak clades to transitions in climate (Hipp *et al.*, 2018). The model-averaged $t_{1/2}$ of an index of herbivore resistance evolving toward an optimum predicted by the multivariate climate has been estimated at 12.8 Ma (Pearse & Hipp, 2012). These significant but relatively slow estimated rates of adaptation seem to stand at odds with the high variation of phenological traits among populations within oak species (Firmat *et al.*, 2017; Cavender-Bares, 2019). This mirrors the contrast between high rates of adaptation for individual populations and low rates of macroevolutionary change observed for trees as a whole (Petit & Hampe, 2006). While the phylogenetic O–U model may be thought of as a framework for translating microevolutionary dynamics into phylogenetic expectations (Martins, 1995), aggregating traits up to species means masks variation within species that underlies local and regional adaptation; thus, the particular value of $t_{1/2}$ should not be taken as an estimate of the rate at which species will adapt to future climate change.

Convergence between the red and white oak clades and divergence within those clades, combined most likely with niche differentiation between clades along resource-acquisition axes that we are only beginning to understand (González-Rodríguez *et al.*, 2019), allowed oaks to pack niche space more densely (Cavender-Bares *et al.*, 2004; Cavender-Bares *et al.*, 2006; Pearse & Hipp, 2012; Kaproth & Cavender-Bares, 2016, 2019; Cavender-Bares *et al.*, 2018; Hipp *et al.*, 2018). The high diversity of Mexican oaks is thus a consequence of both increased diversification rates within Mexico, likely due to increased topographic heterogeneity as oaks entered the mountains on their way south (Nixon, 1993a, b; Valencia, 2004; Torres-Miranda *et al.*, 2011; Rodriguez-Correa *et al.*, 2017; Hipp *et al.*, 2018), and the fact that white oaks and red oaks were able to radiate simultaneously across the region.

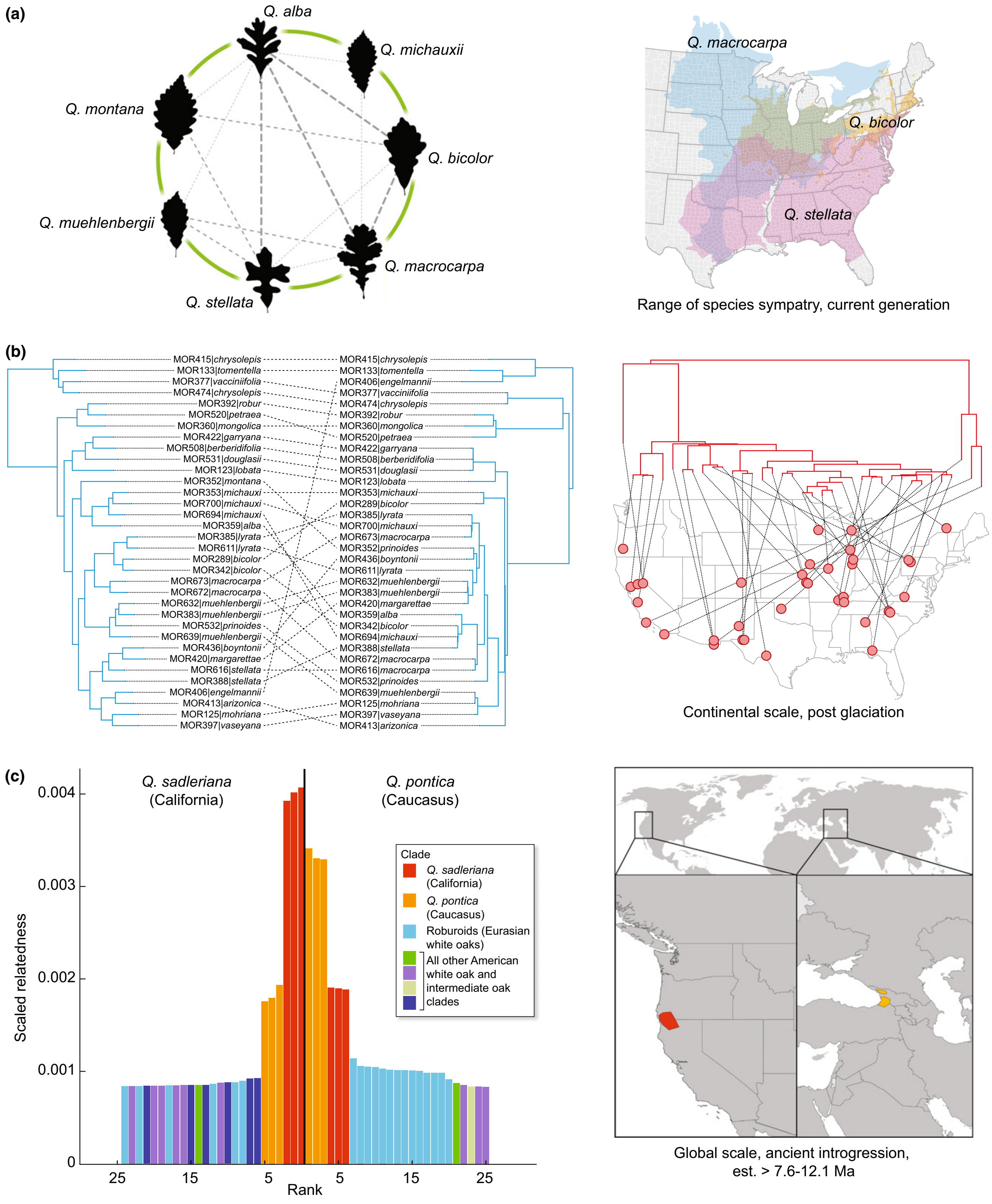
As discussed in the previous section, diversification of oaks in Eurasia parallels the American oak diversification. Eurasian oaks comprise four major clades, three constituting subgenus *Cerris*, which diversified exclusively in the Old World – sections *Ilex* and *Cerris*, together sister to section *Cyclobalanopsis* – and a clade of *c.* 25 white oaks of section *Quercus* (Manos & Stanford, 2001; Hipp *et al.*, 2018), the ancestor of which arrived from the Americas presumably via the North Atlantic Land Bridge between 15 and 18 Ma (Axelrod, 1983; Manos & Stanford, 2001; but see Denk *et al.*, 2010 who argue for a late Miocene origin of the Eurasian white oaks, also from an eastern North American progenitor). The uplift of the Himalayas is implicated in diversification of the holly oaks, section *Ilex*, and in the diversification of the ring-cupped oaks, section *Cyclobalanopsis*. Phylogenomic data, combined with morphometric analysis of fossil and living taxa (Jiang *et al.*, 2019), suggest that the European holly oaks arose from an East Asian ancestor via migration along the southern foothills of the Himalayas. This connection had been suggested previously (Denk & Grimm, 2010), but without phylogenetic evidence in support of the direction of migration. The authors also demonstrate a morphological transition in the two fossil section *Ilex* species of Europe, suggesting rapid ecological and morphological differentiation of European section *Ilex* species during the early diversification of the clade (Jiang *et al.*, 2019).

In aggregate, these studies suggest the following: ecological opportunity drives oak diversification; convergent patterns of diversification within co-occurring clades results in high regional oak diversity in the Americas and Europe; and plant traits exhibit both adaptation and phylogenetic niche conservatism in their macroevolutionary responses to novel climates (as also argued by Cavender-Bares, 2019). Oaks' ability to take advantage of novel ecological conditions has shaped the global distribution of oak biodiversity.

Fig. 6 Contemporary introgression becomes ancient introgression. (a) Contemporary introgression among the eastern North American white oaks has been a case study of interest in the oak syngameon since the mid-1970s (Burger, 1975; Hardin, 1975; Van Valen, 1976) and was the focus of the first chloroplast phylogenetic study in oaks (Whittemore & Schaal, 1991). Introgression at this scale occurs primarily within the range of species sympatry and reflects recent generations of gene flow. The figure illustrates observed gene flow between seven eastern North American white oaks based on analysis of 80 SNPs that map back to all 12 *Quercus* linkage groups, with distances between uniquely mapped loci an average of 7.47 million bp (± 8.74 million bp, SD). The figure replicates the 16-species figure of Hardin (1975; Fig. 1 therein), including only the subset of species investigated in Hipp *et al.* (2019), with lines indicating hybridizations that Hardin inferred from morphological study. Thin dashed lines indicate hybridizations identified by Hardin but not by the SNP genotyping; medium dashed lines were identified by both Hardin and SNP genotyping, at an admixture level of 0.10–0.19 for at least one specimen; and thick dashed lines indicate SNP admixture levels of 0.20 or higher for at least one specimen. (Hipp *et al.* 2019). (b) As species ranges change in response to climatic transitions, species that were once sympatric may become allopatric. Gene flow between them may still be detected by, for example, incongruence between chloroplast and nuclear topologies (Whittemore & Schaal, 1991; Manos *et al.*, 1999). Here, a RAD-seq (nuclear) phylogeny for predominantly North American white oaks (left side) shows strong species cohesion, whereas the phylogeny of whole chloroplasts for the same samples sorts better by geography than by species (Pham *et al.*, 2017). Such events may also be detected by phylogenomic incongruence in nuclear loci (McVay *et al.*, 2017a; e.g. Kim *et al.*, 2018). (c) With enough generations, ancient introgression events that were sufficiently pervasive may remain detectable. A fascinating case involves the sister species *Q. pontica* of the Caucasus, *Q. sadleriana* of California, and the Eurasian white oaks, or Roburoids. Because *Q. pontica* and *Q. sadleriana* are sister species, they are perforce equally closely related to all other oaks. With careful study, McVay *et al.* (2017b) and colleagues found that there are loci shared among the Roburoid white oaks that ally them much more closely to the Eurasian *Q. pontica* than to the American *Q. sadleriana*. The image shows genomic evidence for introgressive hybridization between wild *Q. pontica* samples and the Roburoid oaks: scaled locus similarity on the y-axis between *Q. pontica* and the Roburoids is significantly stronger than expected when data are simulated under incomplete lineage sorting alone ($P < 0.002$). Observed rankings of Roburoids relative to *Q. sadleriana* (left panel) did not differ significantly from rankings of loci simulated under incomplete lineage sorting alone, without gene flow. The fact that these loci are shared among the Roburoids in spite of the fact that most are not sympatric with *Q. pontica* suggests a history of ancient introgression between the lineage that contains *Q. pontica* but not *Q. sadleriana* (allowing for extinction, there may have been other species) and an ancestral Roburoid. This finding is borne out with analysis of a separate phylogenomic dataset using species-tree methods that account for hybridization. Thus a microevolutionary process, inferred to have preceded the crown divergence of the Roburoids an estimated 7.6–12.1 Ma (Hipp *et al.* 2020), became frozen in the genome, like a fly in amber.

3. Deep genomic incongruence shapes oak macroevolution

Early efforts at molecular phylogenetic reconstruction in oaks demonstrated that the chloroplast tracks phylogeographic history rather than population and species level divergences (Whittemore & Schaal, 1991; Dumolin-Lapègue *et al.*, 1997; Manos *et al.*, 1999). As has been shown in microevolutionary studies in the European white oaks (reviewed in Section 2.3), chloroplast DNA



markers are more informative about local and historical gene flow at regional scales than about species relationships. Within the North American white oaks alone, for example, phylogenetic history as inferred from multilocus nuclear (RAD-seq) DNA explains very little chloroplast variation, while geography explains 11%–21% of chloroplast phylogenetic variance (Pham *et al.*, 2017). In practical terms, chloroplast data are of little use in addressing fine-scale phylogenetic questions, and they fail to recover monophyly of even some very deep divergences in the tree. A particularly remarkable example of nuclear/chloroplast discordance is found in section *Protobalanus*, which segregates into two chloroplast types (Manos *et al.*, 1999; Pham *et al.*, 2017; Fig. 6b), in spite of the strong nuclear coherence of the section (Ortego *et al.*, 2018). In this case, microevolutionary dynamics of introgression and/or inheritance of ancestral allele polymorphisms near the base of the oak phylogeny appear to be frozen in the chloroplast phylogeny.

The first study to investigate broad phylogenetic patterns in oaks using a combination of cpDNA and the nuclear ribosomal internal transcribed spacer (ITS) + 5.8S region recovered the monophyly of the American oak clade (subgenus *Quercus*) and the among-section topology within that clade (Manos *et al.*, 1999). Addition of seven low-copy nuclear genes + ITS provided some support for clades and species monophyly, but with extensive incongruence and low statistical support (Hubert *et al.*, 2014). High among-locus incongruence in oaks demands large numbers of loci to reconstruct population divergence history: even AFLP markers, which are relatively difficult to model probabilistically (Luo *et al.*, 2007), yield more strongly supported phylogenies (Pearse & Hipp, 2009) than the longest multigene alignments to date (Hubert *et al.*, 2014). Extending the genome-wide sampling of AFLPs to nucleotide-level data from more readily characterized regions of the genome (Leroy *et al.*, 2017; Hipp *et al.*, 2014; Crowl *et al.*, 2020) provides highly resolved trees that track biogeography, morphology, and species boundaries. Study of the genomic architecture of the phylogenetic signal in RAD-seq markers demonstrates why such large numbers of loci are needed to reconstruct the history of population divergence in oaks: different regions of the genome resolve different portions of the oak tree of life, and the high variation in among-population relationships encoded along the length of the mosaic oak genome demands a large sample of loci to clearly pick out the dominant phylogenetic history (Hipp *et al.*, 2020).

As has been argued previously (Hipp, 2015) and demonstrated in recent multilocus papers (e.g. Pearse & Hipp, 2009; Hubert *et al.*, 2014; Leroy *et al.*, 2017; Hipp *et al.*, 2018, 2020), a consensus phylogenetic signal arises from the oak genome in spite of genomic mosaicism. This consensus divergence history has been the target of most phylogenetic work in the genus to date (though the phylogenetic network has been investigated for some groups; e.g. McVay *et al.*, 2017a,b; Crowl *et al.*, 2020; Ortego *et al.*, 2018). It remains to be seen, however, how gene trees that track alternatives to the primary population divergence history may record the history of trait transfers among lineages (Bastide *et al.*, 2018). Integrating our understanding of phylogenetic network inference, genomic mosaicism, and phylogenetic comparative methods that account for both will be a major challenge to the study of forest tree macroevolution in the genomic era.

4. Ancient introgression events are encoded in the genome

Because introgression is common across the tree of life (Arnold, 2016; Vargas *et al.*, 2017), we expect different genes to track different histories of adaptation to shifting climates, population divergence, and gene flow in sympatry. Microevolutionary studies, reviewed in the first half of this article, have focused on contemporary and often localized hybridization in oaks (Fig. 6a). Phylogenetic studies allow us to distinguish ongoing recent hybridization from ancient introgression in a multispecies system. Four dominant European white oaks, for example, show evidence of early divergence with gene flow only following secondary contact (Leroy *et al.*, 2017). In the California white oaks, a species of Mexican origin (*Q. engelmanii*) exhibits a signature of introgression with the ancestor of a distantly-related clade comprising *Q. durata* and *Q. berberidifolia*, suggesting that weaker reproductive isolation between this species and the white oaks of Californian origin may be a consequence of more secondary contact (Kim *et al.*, 2018). Even more dramatically, populations of *Q. engelmanii* (section *Quercus*) harbor a section *Protobalanus* chloroplast (Manos *et al.*, 1999; Pham *et al.*, 2017). There is no evidence of ongoing gene flow between these two, as attempts to make crosses between the sections have been unsuccessful (Cottam *et al.*, 1982), and we know of no other cases of interbreeding between white oaks and intermediate oaks. Thus this is the residue of hybridizations or lineage sorting long past.

Macroevolutionary studies also allow us to identify how hybridization shapes the tree of life. The European white oaks, for example, carry alleles received by ancient introgression from *Quercus pontica* into the ancestor of the European white oak clade (McVay *et al.*, 2017b, Crowl *et al.*, 2020; Fig. 6c). The western North American *Quercus gambelii* similarly appears to be a genetic conduit between the white oaks of California and the eastern North American *Q. macrocarpa* and allies (McVay *et al.*, 2017a, Crowl *et al.*, 2020). While many species-level studies using nuclear markers recover the history of species divergence (Muir *et al.*, 2000), they are usually conducted at the level of species pairs. Because oaks occur in multispecies communities and have undergone *in situ* radiation, introgression may be complex, involving numerous species and long time periods. Phylogenetic studies like the ones discussed here allow us to reconstruct ancient events that, at the time, had we been able to sequence, would have been microevolutionary processes. It remains to be seen whether the genes that fail to introgress at microevolutionary scales are also those that preserve phylogenetic history across the tree.

At the same time, phylogenetic studies based on relatively small numbers of samples for large numbers of species allow us to test for species coherence across large numbers of loci and the origins of alleles with respect to species boundaries. The overwhelming evidence is that there are at least enough genes *not* shared locally among species to permit species coherence across wide geographic ranges. In the largest species sample to date, 97 out of 147 species for which multiple samples were sequenced were monophyletic (Hipp *et al.*, 2020). A study of 221 individuals representing 13 species of section *Cerris* (Simeone *et al.*, 2018) found that the 5S-IGS region is effective at both delineating clades and identifying

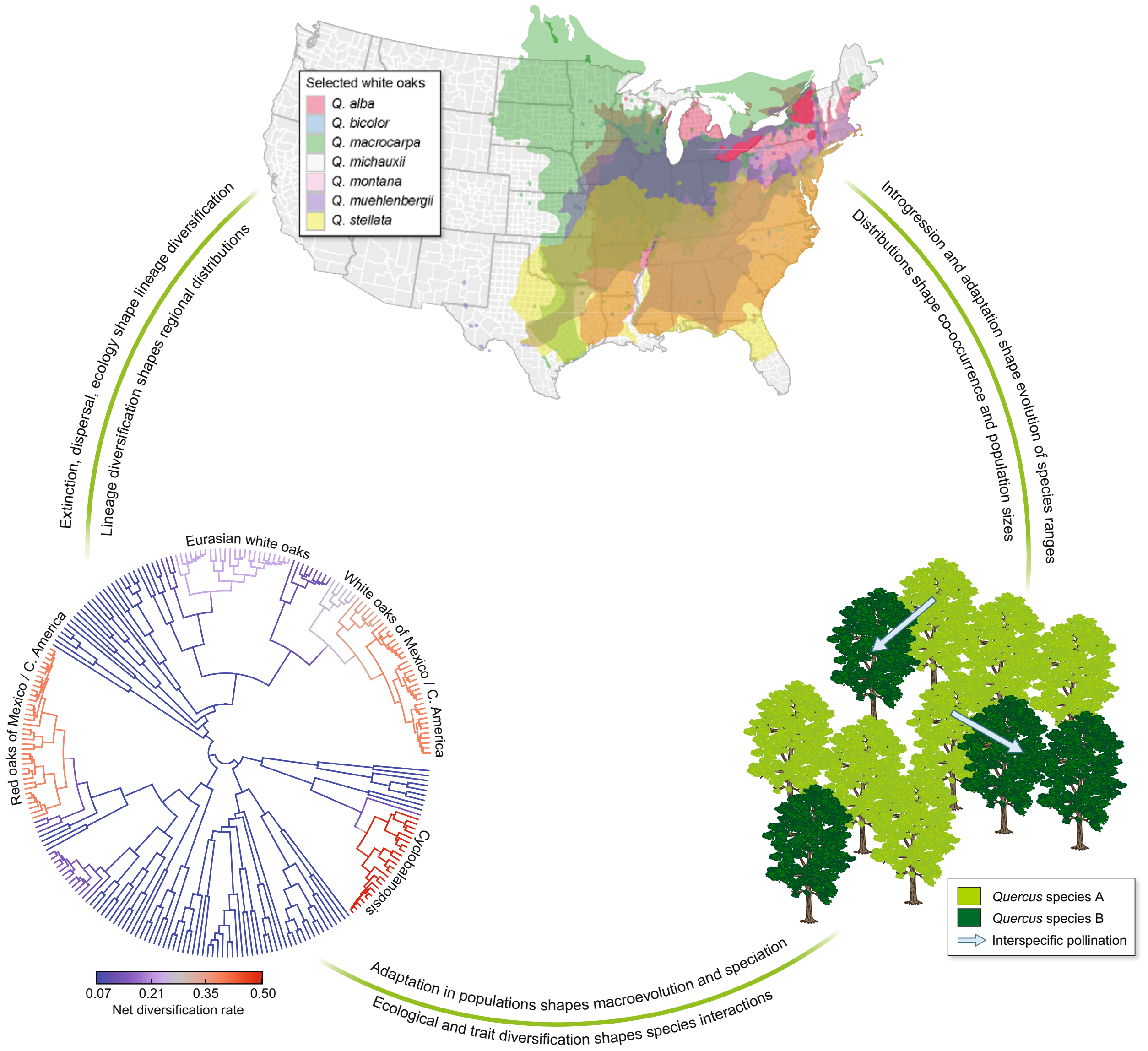


Fig. 7 Microevolution and macroevolution shape one another and the success of the oaks. The story of oak diversification and success rests on the interplay between microevolution and macroevolution. In this review, we have identified four attributes that combine in oaks to shape their diversity and abundance. Here we summarize some of the ways in which these attributes – in italics in this caption – shape interactions between microevolutionary and macroevolutionary processes in oaks, and how these in turn affect oak diversity, distributions, and abundance. *High rates of evolutionary divergence within clades* (lower left panel) shape the global and regional distributions of oak diversity. Radiations within the red oaks and white oaks of America, for example, have shaped regional diversity and distributions (upper panel). These distributions in turn affect *genetic diversity within populations and species*, and coexistence at the site level that influence rates of *hybridization and introgression* (lower right panel). Species distributions are further modified by *migration combined with the ability to adapt to new conditions*. Introgression and natural selection at these site scales then feedback to shape species migration and adaptation to climate, which drive extinction and ecological opportunity for the establishment of new populations. These forces shape diversification rates. In this way, microevolutionary dynamics shape the tree of life, and the tree of life creates the opportunity for microevolution. The figure depicts the phylogeny of the world's oaks (Hipp *et al.*, 2020), based on RAD-seq data, with net diversification rates by branch estimated using reversible-jump Markov chain Monte Carlo; four major increases in diversification rate are labeled (lower left panel). A hypothetical forest stand of two species, with arrows indicating the potential for hybridization between species (lower panel). Range map for co-occuring eastern North American white oaks from Little (1971, 1979) (upper panel). Text along the inside of the circle connecting panels indicates processes operating clockwise around circle; text along the outside indicates processes operating counterclockwise.

species boundaries, while providing some evidence against the putative hybrid-species status of *Quercus afares* (Welter *et al.*, 2012). The same general finding results from analysis of larger numbers of individuals in closely related species groups, for example the oaks of section *Virentes* (Cavender-Bares *et al.*, 2015; Eaton *et al.*, 2015), section *Protobalanus* (Ortego *et al.*, 2017), the eastern North American white oaks (Hipp *et al.*, 2019), and the California scrub white oaks (Fitz-Gibbon *et al.*, 2017) and red oaks (Hauser *et al.*, 2017). Macroevolutionary studies demonstrate with broad species sampling that regional assemblages of related oak species are true syngameons, 'good species' in spite of a long history of introgression (Hardin 1975; Cannon & Petit, 2020).

IV. Microevolution and macroevolution interact to shape oak success

In this review, we have somewhat artificially separated evolutionary processes within species from evolution above the species level. In fact, microevolutionary processes intergrade with and shape macroevolution (Fig. 7). Hybridization among co-occurring species within populations, for example, results in introgression of adaptive alleles among species (Leroy *et al.*, 2020a), facilitating recolonization of habitats following displacement by climate change (Petit *et al.*, 2003) or range extensions (Dodd & Afzal-Rafii, 2004). These migrations in turn afford oaks access to novel areas of niche space that may enable lineage diversification (Abbott *et al.*, 2013). At the population level, high genetic and phenotypic variation within species allows for niche complementarity and high species diversity within stands even when species are not highly divergent on average (Clark, 2010; Clark *et al.*, 2011; Hausch *et al.*, 2018). The capacity for rapid adaptation within populations (Petit & Hampe, 2006) may in addition allow for rapid divergence between species in competitive abilities, promoting differentiation and coexistence of species at both ecological and evolutionary scales (Hart *et al.*, 2019), as has been demonstrated previously in the American oaks (Cavender-Bares, 2019) and as we have argued here for the Eurasian oak clades (Hipp *et al.*, 2020).

By the same token, macroevolution shapes microevolution, providing the backdrop of lineage diversity against which introgression, maintenance of genetic variation within species, adaptation, genetic drift and other population-level processes play out. The high lineage diversity of oaks allows them to benefit from potentially adaptive multispecies introgression (Baranski, 1975; Hardin, 1975; Curtu *et al.*, 2007; Peñaloza-Ramírez *et al.*, 2010; Lepais & Gerber, 2011; Eaton *et al.*, 2015; Cannon & Petit, 2020). At the same time, trait divergence among species within clades enables close relatives to diverge ecologically and occupy a wide range of habitats, enabling high regional diversity among habitats (Cavender-Bares *et al.*, 2004, 2006), while among-clade convergence in habitat and climatic niche (Cavender-Bares *et al.*, 2018; Hipp *et al.*, 2018) and differentiation in ecosystem functions among clades (González-Rodríguez *et al.*, 2019) allow distantly related oaks to co-occur, enabling high local diversity. These processes have played out in parallel in the Americas among red and white oaks, in particular, and in Eurasia among sections *Ilex*, *Cerris* and *Cyclobalanopsis*, and the Eurasian white oaks of section *Quercus*. The diversity we observe in local oak communities is thus a product of regional diversity resulting from diversification history, filtered by ecological interactions (Ricklefs, 2004; Cavender-Bares *et al.*, 2004).

In both the Americas and Eurasia, lineage extinctions and migrations have laid the groundwork for subsequent cladogenesis and microevolution in oaks, while cladogenesis has placed populations into novel habitats that exerted strong natural selection. The rapid crown diversification of oaks, with origin of the major *Quercus* clades in the first 10 Myr following the origin of the genus (Hipp *et al.*, 2020) records the southward movement of oaks following the early Eocene climactic optimum, where their diversification was facilitated by reduced competition in the lee of receding tropical lineages (Graham, 2011; Cavender-Bares *et al.*, 2018). Following what appears to have been a relatively even pace of diversification until the late Miocene, oaks underwent a second pulse of diversification in four young clades *c.* 10 Ma: the white oaks of Mexico, the red oaks of Mexico, the white oaks of Europe, and a clade of ring-cupped oaks (sect. *Cyclobalanopsis*) (Fig. 7). The first three of these three diversification events reflect migrations into novel territory, either topographically heterogeneous (in the case of Mexico) or altogether lacking closely related oaks (in the case of Europe, where only sections *Ilex* and *Cerris*, with possibly some red oaks (Barrón *et al.*, 2017), were to be found when the white oaks arrived). In the fourth, section *Cyclobalanopsis*, diversification appears to have been driven by climatic changes associated with the Himalayan orogeny (Deng *et al.*, 2018). Thus cladogenesis was driven by population extinction and migrations, then drove ecological diversification among populations.

On more recent time-frames, tree species extinction at the Pliocene–Pleistocene transition had profound impacts on microevolution of Pleistocene tree populations. Extinction of tree species was severe up to the Middle Pleistocene, then dramatically reduced during more recent periods (Svenning, 2003; Magri *et al.*, 2017). As is the case for other woody genera (Latham & Ricklefs, 1993), the fossil record indicates widespread European oak extinction beginning at the Pliocene (Barrón *et al.*, 2017). While there are no solid figures on oak species numbers at the beginning of the Quaternary, there are today about eight times as many species in Asia and in the Americas as in Europe. Late Cenozoic extinction most likely contributed to this disparity in species richness (Hubert *et al.*, 2014). Across trees, more cold-tolerant genera, as judged by the temperature requirements of their living relatives in Europe, persisted into the Pleistocene in Europe (Svenning, 2003). While the early Pleistocene extinctions may have severely constrained expansion of *Quercus* and other tree genera in Europe, oaks rapidly became the dominant genus across the continent in the late Pleistocene (Magri *et al.*, 2017; Goni *et al.*, 2018), during both glacial and interglacial periods (Tzedakis, 1994; Tzedakis *et al.*, 2006). This appears not to have been a macroevolutionary (speciation) process, as the Eurasian species mostly predate the Pleistocene. Rather, it was a consequence of population dynamics and microevolution within the few remaining species both during the period of rapid extinctions and afterward.

Today's European white oak species exhibit a unique integration over macroevolutionary and microevolutionary history. Their crown diversification began an estimated 10–15 Ma from an Eastern North American ancestor presumably well adapted to cold, as it wended its way across the North Atlantic Landbridge. A subset of its European descendants escaped extinction during the early glacial–interglacial cycles. As severe cold constricted populations, maintenance of fecundity, genetic variation, and connectivity among populations by pollen flow would have been essential to the success of surviving oak species (Gomulkiewicz & Holt, 1995). Glacial extinctions were followed by interglacial range extensions, selecting for high migration rates and optimal exploitation of local resources. Priority effects would have been equally important. Large climatic oscillations over short evolutionary times scales, inducing alternating expansion and contraction of species ranges, would have had strong microevolutionary consequences (Dynesius & Jansson, 2000), selecting for clinal variation in dispersal ability and plasticity. Both processes have the potential to reduce speciation rates while mitigating extinction risk by increasing the rate of intraspecific gene flow and facilitating wide distributions. Whether the widely reported gene flow and plasticity in oaks was selected for by climate oscillation is unknown, but this might be tested by comparing these properties between European and North American species, where Pleistocene extinctions were reduced, and species underwent more limited expansion–contraction cycles. In either case, the Eurasian white oaks are a case history in the joint effects of macroevolution and microevolution on oak success that complements the history of American oak diversification (Hipp *et al.*, 2018; Cavender-Bares 2019).

At the finest scales, much has been made of the role of hybridization in oak evolution, but with possible very rare exceptions – for example, *Quercus gambelii*, which may be a species of hybrid origin (McVay *et al.*, 2017a) – hybrid speciation *per se* (Abbott *et al.*, 2013) has not been a source of new *Quercus* species and lineages. Rather, introgression of alleles from one species into another has been the predominant outcome of hybridization in oaks. The current review has pointed to evidence that interspecific gene flow in oaks, which was once viewed to be a potentially rampant force, does not seem to be homogenizing oak species (though see Ortego *et al.*, 2018), but may facilitate adaptive gene flow at selected loci. What is less clear is how introgression affects trait evolution among species – shuttling ecologically relevant traits among close relatives, for example. Understanding how and to what degree gene flow impacts oak adaptation and diversity is a potentially fruitful area for future research.

Our review illustrates how macroevolution and microevolution feed one another and jointly affect diversity and abundance of oaks. In some cases, constraints on macroevolution (for example extinctions) have been compensated for by microevolutionary dynamics (adaptation and migration). In others, microevolution is driven by lineage diversity and macroevolutionary legacy effects. We highlight also the peculiar role of hybridization, which is typically considered in the context of microevolution, but which renders the macroevolutionary history of oaks a mosaic of individual gene histories bearing different traits along different evolutionary routes. While we have based our inferences on the most strongly studied systems, we believe our conclusions generalize well to oaks as a whole (Box 1). In the end, understanding oak diversity, abundance, and distributions demands a synthetic approach in which macroevolutionary and microevolutionary forces are considered in close relation to one another.

V. Conclusion

And so we return to the question with which we started: what makes the genus *Quercus* an evolutionary success? In this review, at both microevolutionary and macroevolutionary scales, we find at least four overarching explanations for the evolutionary success of oaks:

(1) **High diversity within populations and species** Genetic and phenotypic diversity within species increase the adaptive potential of species and facilitate coexistence of species.

(2) **Rapid migration combined with the ability to adapt to new conditions** As documented by palynological reconstruction during the late Pleistocene, rapid migration was essential for oak expansion during interglacial periods. It was likely as important during periods of oak diversification, during the late Miocene.

(3) **High rates of ecological divergence within clades, combined with convergent solutions to ecological problems across clades** Exceptionally well documented in the Americas, the combination of divergence within and convergence among clades appears to be characteristic of the European oak radiations as well and may be key to the high diversity of oaks across the three continents.

(4) **Hybridization and introgression** Gene flow in oaks is a largely creative force, increasing diversity, moving adaptive alleles between species, and serving as a migratory mechanism. While phylogenetic reconstruction has shown how introgression contributed to the diversification of oak genomes across species, this review also demonstrates how introgression has enhanced adaptation and stimulated migration.

While these attributes are individually shared with other tree genera, their combined effects together in oaks uniquely explain the evolutionary success of *Quercus* (Box 2). These explanations are presented here as drivers of evolution, but they may also be understood as evolutionary outcomes. Whether genetic diversity, migration rate, evolvability, and capacity for introgressive hybridization have actually been selected for remains to be investigated. There may be other emergent or aggregate species attributes that contribute equally to lineage diversification rates and form linkages between microevolutionary and macroevolutionary dynamics: population size, geographic range, plasticity, and ecological range all have the potential to influence species coexistence and the degree to which species can exchange genes, and thus shape patterns of lineage diversification. Demonstrating that such attributes may be driven by macroevolution would require that they respond to selection at a species level, suggesting investigations aimed at estimating phylogenetic heritability and effects on diversification rates, or fitness expressed at the species level (Rabosky & McCune, 2010). Range size, for example, appears to be phylogenetically heritable in the American oaks (Hipp, 2017), suggesting that the diversification of the clade shapes a key demographic attribute that governs patterns of sympatry and consequently may shape rates of hybridization and speciation. More nuanced investigations of species selection in oaks have the potential to demonstrate how macroevolution and microevolution operate jointly to shape diversification.

Our review also points to the potential insights to be gained from comparative analysis of intraspecific selection patterns across clades, investigating parallel microevolutionary dynamics in different species, habitats, and continents. Candidate traits for comparative analysis include phenology, growth rates, and leaf morphology, traits that have already been investigated in separate studies in different species. An immediate application would be to test whether gradients of selection are of similar magnitude and direction in species distributed along similar environmental clines.

Box 1 Generality of oak study systems, and research gaps.

Our review of microevolutionary processes is dominated by results and conclusions from the two European white oaks (*Quercus petraea* and *Quercus robur*), as they have been investigated longer than any other species, and insights into these two species have done much to inform our understanding of temperate tree speciation and population dynamics. Conversely, macroevolution in oaks has until quite recently received more attention in North America than in Asia or Europe, though recent work (e.g. Deng *et al.*, 2018; Jiang *et al.*, 2019), including a paper in the current volume (Hipp *et al.*, 2020), does much to amend this. What can we learn from these case studies regarding other congeneric species? What research gaps should be addressed in the future, and what new research avenues have become available?

The European story has demonstrated the impact of postglacial colonization on the distribution and pace of adaptive diversity and divergence. However, with recent phylogeographical and palynological investigations in an increasing number of oak species (Vitelli *et al.*, 2017; Sork *et al.*, 2016b,c; Muellner-Riehl, 2019), it is becoming clear that the clean relationship between postglacial migration and genetic diversity seen in the European white oaks is not universal. In the widespread temperate European and Asian species, postglacial migration occurred over very large distances, starting from a reduced number of refugial areas, resulting in a relatively tight correlation between geography and chloroplast diversity, as reviewed in part one of this review. In the North Eastern American and Mexican species case, however, refugial populations were more diffuse and some persisted closer to the glacial margin (McLachlan *et al.*, 2005). As a consequence, chloroplast variation in North American white oaks is structured geographically, but apparently only at very large scales, entailing separation between the western and eastern species but not obviously among regions within eastern North America (Pham *et al.*, 2017). This suggests that the scale of migration was smaller and mixing among refugial populations larger in eastern North American than in Europe. Migration range was also limited in Californian (Sork *et al.*, 2016b,c) and Mediterranean species (Vitelli *et al.*, 2017). It remains to be seen what evolutionary legacies persist from the European and American migration histories regarding ecological divergence and adaptation. It is also not yet clear whether the history of recent secondary contact between European species (Leroy *et al.*, 2017, 2020a) played out the same way in the Americas. More multispecies, geographically widespread samples will be needed in America, paralleling the work done in Europe, to test whether these alternative histories led to different timings in species contacts. Recent and ongoing work in the eastern North American sections *Virentes* (Cavender-Bares *et al.*, 2015) and *Quercus* (Hipp *et al.*, 2019; Garner *et al.*, 2019), the western North American sections *Quercus* and *Protobalanus* (Sork *et al.*, 2016b,c), and widespread Mexican oaks of sections *Quercus* and *Lobatae* (Rodriguez-Correa *et al.*, 2017) are particularly promising in this regard.

The effects of introgression on both migration (Petit *et al.*, 2003) and adaptation (Leroy *et al.*, 2020a) in the European white oaks are probably echoed in other clades and areas. Indirect evidence of large scale introgression comes from the chloroplast genome sharing that has been shown in many sympatric oaks (Whittemore & Schaal, 1991; Pham *et al.*, 2017), which, in combination with coherence at nuclear loci, demonstrates that introgression is strong and likely a long-term phenomenon in oaks, but that selection is strong enough to counterbalance introgression and maintain species genetically. A strong argument for introgression-driven migration requires a demonstration also of asymmetric gene flow (as has been shown, for example, in section *Virentes*; Eaton *et al.*, 2015) and different colonization dynamics between the species crossing, with one species dispersing and establishing better by seed than the other (i.e. being more of a pioneer species). Regarding adaptive introgression, the availability of reference genomes in the white oaks (Sork *et al.*, 2016b,c; Plomion *et al.*, 2018) and the existence of common-garden experiments for the same species should facilitate the detection of adaptive introgression, complementing landscape genomic approaches that have already demonstrated differential levels of introgression across loci associated with ecological variation (Dodd & Afzal-Rafii, 2004) and gene function (Oney-Birol *et al.*, 2018). A challenging and stimulating avenue of research would be a global comparative study of which portions of the genome of sympatric species introgress, in a climatic and ecological context (cf. Hipp *et al.*, 2020). Such a synthetic study is within grasp with new genomic and analytical tools.

Finally, a striking feature in European oaks is the large genetic variation in phenological responses to latitudinal or altitudinal temperature gradients shared among species. Equally striking is the opposing genetic cline found in common-garden studies between European white oaks, in which populations originating from higher latitudes or elevation flush later than populations from lower latitude or elevation (Firmat *et al.*, 2017), and North American red oaks, in which northern populations flush earlier in the common garden (McGee, 1974; Kriebel *et al.*, 1976). The timing of bud burst is a highly integrated trait that is closely correlated to reproduction and growth and consequently to fitness and response to temperature variation. These contrasting patterns observed in a limited number of species should stimulate extended investigations of a larger number of species and populations encompassing contrasting temperature gradients. Such comparative research would ultimately help clarify the role of genetic variation in phenological traits for adaptation to ongoing climate change.

At the same time, these comparative studies, paired with macroevolutionary studies of selection at the clade level, may cast light on the biological underpinnings of variation in evolutionary rates at different scales of inquiry, on different continents, and among clades.

Finally, this review provides insights into contemporary evolutionary challenges that oaks face in the context of environmental changes. What lessons did we gain from the past that may enlighten ongoing processes sustaining the evolutionary success of oaks? Migration triggered by climatic variation has already been reported for Mediterranean species, and it is likely that this trend will continue despite constraints generated by land management (Delzon *et al.*, 2013). Species shifts are expected to increase sympatry between Mediterranean and temperate oaks, potentially triggering hybridization and most likely adaptive introgression as well. But what will happen at the extreme southern margin? This and related questions will require long term monitoring and research. Ongoing climate change thus offers a unique opportunity to disentangle evolutionary processes in action at contemporary time scales.

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Box 2 Oaks: unique among tree genera?

We point to four non-mutually exclusive potential causes of oak evolutionary success: high genetic diversity, rapid migration rates, high rates of ecological divergence, and propensity for hybridization and introgression. Are these attributes peculiar to oaks or are they shared with other woody genera? High genetic diversity is common in trees and has been argued to be a major cause of their rapid microevolution (Petit & Hampe, 2006), but recent results based on whole genome sequences suggest that *Quercus* has accumulated even larger levels than is typical of forest trees generally (Plomion *et al.*, 2018). Maintenance of high genetic diversity is likely an outcome of life history traits that convergently manifest in large population sizes in unrelated woody plant lineages, as discussed in the main text. Regarding rapid migration, comparative analysis of postglacial spread of woody species in Europe suggests that oak migration rates were similar to and sometimes exceeded rates of such pioneer genera as *Alnus* and *Corylus* (alders and hazelnuts; Brewer *et al.*, 2005; Giesecke *et al.*, 2017). Similar comparative analysis in North American species is less convincing (Harnik *et al.*, 2018), although Davis (1983), in her earlier work on the late Pleistocene spread of trees, underpins the rapid migration of oaks: 'Oak range expansion was rapid, more rapid than any of the deciduous trees that today grow in major forests' (Davis, 1983, p. 558). The Asian picture also emphasizes 'the remarkably fast spread of *Quercus* from Southern China to the North East rim of the Tibetan Plateau' in comparison to other species (Cao *et al.*, 2015, p. 89).

Across a number of forest tree genera, ecological shifts may contribute to biodiversity and biomass. *Bursera* for example exhibits convergent transitions from seasonal dry tropical forest to xerophytic scrub and oak forest (De-Nova *et al.*, 2012) that may explain some degree of the diversity of the clade across biomes. *Inga* exhibits high species diversity within sites that has been shown to be associated with exceptionally high diversification in antiherbivore defenses (Kursar *et al.*, 2009). The temperate shrub genus *Viburnum* exhibits increases in diversification rate in association with increased rates of transition among forest types and colonization of mountainous regions (Spriggs *et al.*, 2015). The effect of ecological diversification on diversity of oaks, however, is exceptional among tree genera, as are the effects of biogeographic transitions and convergence on rates of lineage diversification (Hipp *et al.*, 2018, 2020) and species coexistence over long periods (Cavender-Bares *et al.*, 2004, 2018). The closest analogue to *Quercus* in the temperate Americas, *Pinus* – the tree genus with the second highest biodiversity in the US and the second highest biomass in both the US and Mexico, after *Quercus* (Cavender-Bares *et al.*, 2016a; Cavender-Bares, 2019) – exhibits differentiation of clades by fire tolerance, but not the simultaneous parallel diversification that shaped the diversity of *Quercus* (He *et al.*, 2012; Keeley, 2012).

Similarly, the contribution of introgression to adaptation (Suarez-Gonzalez *et al.*, 2018) has been demonstrated in *Populus* (Chhatre *et al.*, 2018) and *Cupressus* (Ma *et al.*, 2019), and the role of hybridization in species expansion was earlier shown in *Eucalyptus* (Potts & Reid, 1990). Introgression has also been demonstrated to lead to transgressive segregation in *Picea* (spruce), allowing for adaptive gene flow that is expressed in the second generation and potentially later (Hamilton & Miller, 2016). Increasingly, introgression appears to be widespread among forest trees, especially in the tropics (Cannon & Lerdau, 2015; Caron *et al.*, 2019). It is, however, the widespread hybridization within each of the different oak clades recognized as sections (Denk *et al.*, 2017), supported by widespread choroplast capture and nuclear population-level studies reported in the main text, that suggests that introgression may have significantly contributed to migration and coexistence of oak species.

While some of the micro- and macroevolutionary explanations we have offered for the global success of oaks might individually be shared with other genera, it appears that oaks possess a unique suite of attributes. Additionally, and not mentioned previously in this review, one cannot dismiss the minor but locally and temporally significant role of early human populations on the maintenance and spread of oak forests (Kremer, 2015; Chassé, 2016). Anthropogenic fire alone has greatly shaped the forest composition of North America, favoring oaks throughout the vast prairie province and bordering regions (Kline, 1997; Abrams, 1992). More generally, the exceptional diversity of services oaks provide for food, shelter, medicine, and culture make it highly likely that human activities have in many contexts favored oaks (Logan 2006) and shaped their evolutionary trajectories (Toumi & Lumaret, 1998).

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See also the Editorial on this article by Plomion & Martin, **226**: 943–946.