



Tansley insight

Oak symbolism in the light of genomics

Author for correspondence:

Thibault Leroy

Tel: +33 5 35 38 53 65

Email: thibault.leroy@umontpellier.fr

Received: 11 April 2019

Accepted: 31 May 2019

Thibault Leroy^{1,2} , Christophe Plomion² and Antoine Kremer² 

¹ISEM, Université de Montpellier, CNRS, IRD, EPHE, Place Eugène Bataillon, 34095 Montpellier, France; ²BIOGECO, INRA,

Université de Bordeaux, 69 Route d'Arcachon, 33612 Cestas, France

Contents

Summary	1012	VI. Robustness	1015
I. Introduction	1012	VII. Conclusions	1016
II. From early ties between humans and oaks to symbolic representations	1012	Acknowledgements	1016
III. The symbolic load of oak in the humanities and science	1013	References	1016
IV. Longevity	1013		
V. Cohesiveness	1014		

New Phytologist (2020) **226**: 1012–1017
doi: 10.1111/nph.15987

Key words: interspecific gene flow, oak biodiversity, oak genomics, plant resistance, plant speciation, *Quercus*, tree longevity, tree mutation rates.

Summary

Throughout the Northern Hemisphere, human societies, political systems, and religions have appropriated oaks in symbolic representations. In this review, we explore the possible associations between recent genetic and genomic findings and the symbolic representations of oaks. We first consider the ways in which evolutionary history during the Holocene has tightened links between humans and oaks in Europe, and how this may have led to symbolic representations. We then show how recent findings concerning the structure and evolution of the oak genome have provided additional knowledge about symbolic representations, such as longevity, cohesiveness, and robustness.

I. Introduction

Throughout the Northern Hemisphere, human societies, political systems, and religions have appropriated oaks in symbolic representations. Oaks have been present in traditional rites and celebrations for many centuries, as far back in history as the early Proto-Indo-European cultures (Chassé, 2016). Oaks have been associated with longevity, strength, fertility, and robustness. Recent findings in genetics and genomics may shed new light on these symbolic representations of oaks. Intricate relationships between oaks and human populations developed following the migration of humans out of Africa, due to reciprocal benefits. Did the joint evolutionary trajectories of humans and oaks during the Holocene contribute to their 'shared' history, reinforcing ties between trees and people? This review is not designed to be an exhaustive

consideration of the many types of symbolism attached to oaks by humans. We address only a few symbolic elements (longevity, cohesiveness, robustness) for which the association with a genetic perspective is most marked, particularly in recent recorded European history (from Greek and Roman to Celtic societies). Our approach should be seen as a first step towards the assembly of knowledge from different fields (history, ecology, genomics, and social sciences) with a view to understanding symbolic representations of plants in human societies.

II. From early ties between humans and oaks to symbolic representations

Symbolism may have been attached to trees in early human societies on the basis of the very early ties linking people and trees and the

ways in which these ties developed historically. Oaks, more than any other tree species, paved the way for the colonization of the Middle East and Europe by *Homo sapiens* some 45 000–50 000 yr ago (Bar-Yosef & Belfer-Cohen, 2013). Oaks were an invaluable food resource for humans during the early settlement of Eurasia, as suggested by the remains of *Quercus ithaburensis* and *Quercus calliprinos* acorns in caves known to have been occupied by humans (Lev *et al.*, 2005). There is increasing evidence to suggest that acorns made an essential contribution to the staple diet of the first modern humans, based on ethnographic, archeological, and historical clues. Despite underestimations of acorn consumption due to the charring of remains and the decay of fossil remains (taphonomical issues), recent archeological investigations have highlighted the widespread use of acorns as a food source (Lev *et al.*, 2005; Humphrey *et al.*, 2014; Antolin & Jacomet, 2015; Morales, 2018) by various hominids, including Neanderthals (Villa & Roebroeks, 2014). This archeological element is supported by historical evidence from the writings of the earliest geographers (such as Pausanias and Strabon), philosophers (such as Platon), poets (such as Ovid), and naturalists (such as Pliny the Elder and Theophrastus) describing the regular consumption of acorns up to the Greek and Roman ages (reviewed by Chassé, 2016). Before the development of agriculture in Mesopotamia, human hunters and gatherers fed themselves with various seeds, including acorns from the oak forests of the Zagros Mountains or the oak–pistachio uplands of the Mesopotamian valley (Murphy, 2007; Scott, 2017). Ties between humans and oaks were reinforced as humans migrated to Europe and experienced the last glacial/interglacial transition *c.* 40 000 yr ago, and then during later migrations of human populations northwards. Kremer (2015) intriguingly highlighted similarities in the colonization dynamics of modern humans and oaks, in terms of velocity (500 m yr^{-1} : Brewer *et al.*, 2002, for oak; Henn *et al.*, 2012, for humans), processes (serial founder effects: Le Corre *et al.*, 1997, for oaks; Deshpande *et al.*, 2009, for humans), and colonization routes. These similarities are too wide ranging to be mere coincidence, suggesting that humans may have transported acorns as food reserves while migrating northwards as the climate warmed, thus contributing to rapid oak colonization (Kremer, 2015).

III. The symbolic load of oak in the humanities and science

The use of oak for food was paralleled by its use for other purposes. Acorns were used for food, but other parts of the tree were used for medicine, fuel, shelter, and art, as oaks became the ‘tree of life’ (Anderson, 2007) or the ‘frame of civilization’ (Logan, 2006). For example, almost all prehistoric pile dwellings built along the shores of lakes during the Bronze Age were made of oak logs (Menotti, 2004). Oaks clearly facilitated the establishment of human populations in Europe, and humans returned the favor, contributing to the considerable expansion of oak populations across the continent. Subsistence relationships led to values and virtues being associated with trees, which ultimately became symbols in societies, or to the association of sacred beings with trees in religions (Logan, 2006). The shared history of humans and oaks also generated

cultural and emotional relationships that translated into symbols or were incorporated into religious beliefs and mythology. Oaks were associated with the most important gods (e.g. Zeus, Jupiter and Thor) in the mythology of ancient Greece, Rome and Germany, and were often used to represent the *axis mundi*, the center of the world, in Celtic and Germanic cultures.

Since the earliest ties between humans and oaks, a very strong symbolic image of oaks has developed in which these trees have become associated with longevity, strength, stability, endurance, fertility, power, justice, and honesty. These symbols have been widely studied in the humanities, in history (Logan, 2006), social sciences (Brosse, 1989; Mazoyer & Rey, 2003), literature (Corbin, 2015), and the arts (Farcas *et al.*, 2015). In natural sciences, the first insights into oak symbolism emerged from very early botanical writings by Theophrastus (*Historia Plantarum*, Book 3, *Wild Trees and Shrubs*) and Pliny the Elder (*Natural History*). Theophrastus provided the first taxonomic description of oaks in ancient Greece, but he also noted the longevity of these species in his scientific approach (Thanos, 2005). Pliny the Elder provided a detailed description of the ways in which druids celebrated mistletoe growing on scared oak trees and its use to prepare remedies to cure infertility (Brunaux, 2006). Much more recently, many Northern Hemisphere countries, such as the UK, Poland, Portugal, and Germany, and a number of regions have adopted the ‘mighty’ oak as an official national emblem (Fig. 1). In 2001, a nationwide popular vote took place, over a period of 4 months, to select the official national tree of the USA. The people of the USA selected oaks from a list of 20 tree species (International Oak Society, 2001), and Congress then recognized the oak as the national tree of the USA in 2004.

IV. Longevity

Unlike animals, which are generally less long-lived than humans (Bozek *et al.*, 2017), tens of thousands of plant species, including many oak species, can live for hundreds of years. Majestic ancient living oaks in public squares, parks, and forests are a strong element of Northern Hemisphere cultures (Farjon, 2017; Pater, 2017). Observations of the same old oaks enduring throughout a lifetime may trigger positive memories, much like Proust’s Madeleine (Proust, 1913). Some famous specimens, such as the Major Oak of Sherwood Forest in England, are thought to be up to 900 yr old (Farjon, 2017).

However, the widely held view that oaks have a long lifespan merits qualification. Anyone who has ever walked under a majestic oak tree will already have noticed the huge number of seedlings growing under its canopy. Total seed production and germination are difficult to evaluate, but it has been estimated that there may be 200 000–1000 000 new sessile oak seedlings per year and per hectare within sessile oak-dominated forests (Jarret, 2004). Ten years later, in the absence of silvicultural disturbance, the number of living individuals per hectare has been estimated at 57 000–63 000, suggesting that the vast majority (68–94%) of these new individuals die within 10 yr due to biotic and abiotic stresses (Jarret, 2004). Some individual oaks may be long lived, but the life expectancy of any given oak seedling is very short indeed.



Fig. 1 An illustrative example of the endorsement of oak trees as a symbol of human values: the Gernika tree, a pedunculate oak standing in front of the parliament of the Biscay province of the Basque Country. (a) A third-generation offspring of the original Gernika tree in front of la Casa de Juntas (House of Assemblies), Basque Country, Spain. This tree became a symbol of liberty, as leaders of the Biscay province and, later, of the Basque people as a whole, swore an oath below the tree to safeguard the freedom of the Basque people. (b) The Gernika tree depicted in a stained-glass window in the ceiling of la Casa de Juntas showing a Lord of Biscay swearing an oath to safeguard the freedom of the Basque people. (c) Painting from la Casa de Juntas showing one of the first assemblies of representatives beneath the Gernika tree. General assemblies of people's representatives from villages and provinces subsequently met near the tree to pass laws, and the tree became a symbol of justice and the unity of the Basque people. The French philosopher Jean Jacques Rousseau cited these assemblies as an early form of democracy in 'Le contrat social' (1762). (d) Biscay coat of arms from la Casa de Juntas, with its representation of the Gernika tree. (e) Poster of the 650th anniversary of the establishment of Gernika.

But what are the genetic consequences of growing old? Several studies in primates have shown that aging has a strong impact on intergenerational heritable mutation rates, particularly due to the number of germline cell divisions in males (e.g. Jónsson *et al.*, 2017; Thomas *et al.*, 2018). In plants, the germline cell lineage is generally assumed to segregate and differentiate from somatic cells at the end of stems or branches (but see Lanfear, 2018). Consequently, *de novo* mutations would be expected to accumulate throughout plant growth, and might potentially be passed on to the progeny. Heritable mutations would, therefore, be expected to accumulate with age, particularly in long-lived species, such as oaks. Two recent independent studies tested this hypothesis by comparing whole-genome sequence data from oak leaves or buds collected at two or three locations on 236- and 100-yr-old trees (Schmid-Siebert *et al.*, 2017; Plomion *et al.*, 2018, respectively). They used very different methods and data, with potential implications for interpretation (Plomion *et al.*, 2018), but both reported only small numbers of mutations (17 and 46 single-nucleotide polymorphisms over a

genome of more than 750 million bases; Kremer *et al.*, 2007). These findings challenge the poetic vision of each tree as a forest in its own right (Hallé, 2005). After a detailed analysis at the interface between population genetics and philosophy, Gerber (2018) reached a similar conclusion. These findings suggest that taller plants may have low rates of mutation per unit time, consistent with the conclusions of Lanfear *et al.* (2013), based on comparisons of molecular evolution rates between herbs, shrubs, and trees (i.e. plants of different statures).

V. Cohesiveness

Since ancient times, oaks have been seen as cohesive species. In Celtic cultures, for example, *Dara*, which means *oak tree*, is a specific type of knot created from an endless cord forming interlaced patterns symbolizing eternity and unity. However, subtle morphological differences between closely related species have remained unrecognized even in recent times, as illustrated by the

use of the generic word ‘oak’ indifferently for *Quercus robur* or *Quercus petraea*. But beyond such symbolism, are oak species genetically cohesive units?

Over the last decade, several studies have tried to clarify oak taxonomy (Hubert *et al.*, 2014; Denk *et al.*, 2017; Hipp *et al.*, 2020). They have proposed a comprehensive backbone for the evolutionary history of the genus *Quercus*. The latest infrageneric classification clusters oak species into two subgenera (*Quercus* and *Cerris*) with eight sections (*Quercus*, *Ponticae*, *Virentes*, *Protobalanus*, *Lobatae*, *Ilex*, *Cerris* and *Cyclobalanopsis*). Hybridization between species from different sections is rare in nature, consistent with reproductive isolation (Hubert *et al.*, 2014), but hybridization within sections is widespread (Hipp, 2015). This phenomenon led Rieseberg *et al.* (2006) to include oaks in their shortlist of ‘botanical horror’ taxa. Darwin was aware of the complexity of oak species relationships (Darwin, 1859), which he considered a ‘thorny problem’: ‘[...] in this country the highest botanical authorities and practical men can be quoted to show that the sessile and pedunculated oaks are either good and distinct species or mere varieties’ (Darwin, 1859).

Many population genetics studies (e.g. Curtu *et al.*, 2007; Lepais *et al.*, 2009; Ortego *et al.*, 2014; Leroy *et al.*, 2017) and population genomics studies (Leroy *et al.*, 2020b; Ortego *et al.*, 2018) have provided empirical support for ongoing admixture and gene flow between phylogenetically related oak species, raising the possibility that oak species evolve as independent evolutionary units. Whole-genome sequencing has shown that hybridization can occur without disrupting species integrity, which is restricted to a limited part of the genome, maintaining species barriers (Leroy *et al.*, 2020b). Studies based on the methodology of Roux *et al.* (2016) have shown that the intensity of interspecific gene flow between divergent oak populations or species may have varied over time, with the advance and retreat of glaciation (e.g. Leroy *et al.*, 2017, 2020b; Merceron *et al.*, 2017). Genetic inferences and genome scans for differentiation have suggested that gene flow is heterogeneous over time, space, and genomic regions (Lang *et al.*, 2018; Leroy *et al.*, 2017, 2020b). Barriers to mating dispersed throughout the genome may partially prevent interspecific gene flow, ensuring that interspecific differences are essentially fixed, whereas interspecific gene flow rates are high elsewhere in the genome. These recent results tell us that cohesiveness should be viewed at the level of the gene – at which species barriers are maintained – rather than at the genome level, which is largely permeable to gene flow in these outcrossing species. However, such interspecific exchanges should not be disregarded, because they can contribute to local adaptation in populations living in marginal habitats (Leroy *et al.*, 2020a). Further population genomic studies will be required to improve our understanding of current evolutionary trajectories, and of the adaptive potential of oaks in a changing environment.

VI. Robustness

Pedunculate oak (*Q. robur*) is the most abundant oak species in Europe. The properties of its wood probably explain the Latin meaning of its name: ‘strength’. Figurative representations of oaks

are common on military medals and decorations, including current awards for distinguished service and bravery in the USA and Germany. Artistic representations of oak trees have also been used to symbolize the strength and robustness of ideas (Fig. 2). Based on the information provided by the oak genome, can we consider oaks to be robust enough to neutralize attacking enemies?

The Pedunculate Oak Genome Consortium recently revealed patterns of immune system diversification in this species (Plomion *et al.*, 2018). Their analyses support both an expansion of resistance (R) genes (accounting for 9% of the gene catalog) and a diversification of gene function driven by a long-standing coevolutionary arms race between oaks and their natural enemies (viruses, bacteria, fungi, oomycetes, nematodes, and insects). However, oaks are far from invulnerable. On the contrary, several plant pathogens are currently a major source of concern, including the causal agent of acute oak decline, which has recently spread in the UK (Brown *et al.*, 2016). The globalization of world trade has increased the dissemination of alien pests and pathogens that have not coevolved with native species, creating new threats to oaks. The accidental introduction of a powdery mildew (*Erysiphe alphitoides*) into Europe at the start of the 20th century led, for example, to high rates of mortality in Pyrenean oak (*Quercus pyrenaica*) in southwestern and western France (Desprez-Loustau *et al.*, 2011). This pathogen is still having a deleterious impact on tree growth in European forests (Bert *et al.*, 2016). The recent emergence of *Phytophthora ramorum*, causing sudden oak death on the US West Coast, is



Fig. 2 Oak tree artwork as symbol of robustness of ideas (Bloomfield, 2012). An illustrative symbolic oak representation linking art and science was the choice for a longitudinal oak tree section as artwork for the ceiling of the Natural History Museum of London in 2009. The artwork was planned to celebrate the 200th anniversary of Darwin. A panel of art experts, museum experts, and scientists selected the oak project from 10 proposals made by different artists. The work TREE proposed by artist Tania Kovats was chosen by unanimous decision. Her proposal was to embed in the ceiling a longitudinal 3–5 mm thick section of a 200 yr old entire oak tree, from the ground to the canopy. The tree was 21 m high and came from a managed forest of Longleat Estate in Wiltshire. The artwork was meant as a replicate of the iconic drawing of the ‘Tree of life’ by Darwin, which echoes in this contribution the ‘Tree of life’ revered by early human populations (Anderson, 2007). As described by Bloomfield (2012) ‘Rendered in stalwart English oak, the artwork is a metaphor of the endurance of Darwin’s ideas, as well as Darwin’s own bravery and commitment to them’. Photo credit: <https://mikesmithstudio.com/projects/tree-natural-history-museum/>.

another major cause for concern (Cunniffe *et al.*, 2016). Given the vulnerability of oaks to these pathogens and the intrinsic difficulties of managing invasive forest pathogens, greater attention should be paid to preventing new introductions, thereby limiting the risk of devastating new outbreaks.

VII. Conclusions

Symbols are common literary elements transforming the complexity of reality into something easier to understand, thereby enabling writers to impart significant meaning and emotion. Some oak symbols are so ancient and powerful that they actually distort reality, influencing our lives and our way of thinking. In recent years, this gap between the symbol and reality has been widened by pseudoscientific literary essays and movies deeply rooted in this symbolism that have received considerable media and public attention, to the point of becoming world-wide bestsellers (e.g. *The Hidden Life of Trees*; Wohlleben, 2016). Our objective in this brief excursion into oak symbolism was to call for more thorough scientific assessments and the use of scientific findings to examine the relevance of some of these symbols. We are convinced that recent academic discoveries, such as the importance of archeological diving prospections for studies of oak evolution through the sequencing of ancient waterlogged remains (Wagner *et al.*, 2018), will be of interest to the general public. We anticipate that the increase in genomic resources for oaks (Plomion *et al.*, 2016, 2018; Sork *et al.*, 2016; Ramos *et al.*, 2018; this issue) will reveal a myriad of surprises, provided that analyses are data driven and free from cultural assumptions.


This review argues for future investigations of genetic properties relating to the three symbolic representations of oaks discussed here. For longevity, future research could refine the relationship between tree aging and mutation rates, accounting for meiotic and somatic mutations. Ultimately, age-related mutation rates in different long-lived animal and plants would provide clues as to whether there is a 'generation-time effect' (Moorjani *et al.*, 2016); for example, with a lower yearly mutation rate in woody species. For cohesiveness, our conclusions are, for the time being, mostly driven by emblematic examples, such as European white oaks (but see Hipp *et al.*, 2020). The cohesiveness at genome level of species traditionally considered to be taxonomic nightmares supports recent proposals for taxonomic standardization based on genomic data (see Galtier, 2018). Taxonomic decisions could be made less arbitrary by analyzing the population structure of a large set of populations from diverse geographic regions and assuming a threshold for the net amount of differentiation or divergence for oaks. Such an approach would contribute to a scientifically more rigorous definition of oak species. For robustness, we are beginning to establish an inventory of the oak leaf microbiome and rhizosphere. Combined metagenomic and expression studies would show whether the expanded R-genes in the oak genome contribute to an extended microbial phenotype and, ultimately, to greater resilience of oaks to emerging biotic and abiotic threats.

Acknowledgements

This research was funded by the French ANR (GENOAK project, 11-BSV6-009-021), *France Génomique* national infrastructure (Oakadapt project), funded as part of the *Investissements d'Avenir* program managed by the ANR (ANR-10-INBS-09) and by the European Research Council under the European Union's Seventh Framework Programme (TREEPEACE project, FP/2014-2019; ERC Grand Agreement no. 339728). TL also thanks the ANR BirdIslandGenomic (ANR-14-CE02-0002) project, including the project co-ordinator Benoit Nabholz, for support and feedback.

ORCID

Antoine Kremer  <https://orcid.org/0000-0002-3372-3235>

Thibault Leroy  <https://orcid.org/0000-0003-2259-9723>

References

- Anderson MK. 2007. *Indigenous uses, management and restoration of oaks of the far western United States*. Technical Note no. 2. Washington, DC, USA: USDA–Natural Resources Conservation Service.
- Antolin F, Jacomet S. 2015. Wild fruit use among early farmers in the Neolithic (5400–2300 cal BC) in the north-east of the Iberian Peninsula: an intensive practice? *Vegetation History and Archaeobotany* 24: 19–33.
- Bar-Yosef O, Belfer-Cohen A. 2013. Following Pleistocene road signs of human dispersals across Eurasia. *Quaternary International* 285: 30–43.
- Bert D, Lasnier J-B, Capdevielle X, Dugravot A, Desprez-Loustau M-L. 2016. Powdery mildew decreases the radial growth of oak trees with cumulative and delayed effects over years. *PLoS ONE* 11: e0155344.
- Bloomfield RM. 2012. Placing Darwin in the heart of the Natural History Museum. *Evolution: Education & Outreach* 5: 38–42.
- Bozek K, Khrameeva EE, Reznick J, Omerbašić D, Bennett NC, Lewin GR, Azpurua J, Gorbunova V, Seluanov A, Regnard P *et al.* 2017. Lipidome determinants of maximal lifespan in mammals. *Scientific Reports* 7: e5.
- Brewer S, Cheddadi R, De Beaulieu JL, Reille M. 2002. The spread of deciduous *Quercus* throughout Europe since the last glacial period. *Forest Ecology and Management* 156: 27–48.
- Brosse J. 1989. *Mythologie des arbres*. Paris, France: Editions Plon.
- Brown N, Jeger M, Kirk S, Xu X, Denman S. 2016. Spatial and temporal patterns in symptom expression within eight woodlands affected by acute oak decline. *Forest Ecology and Management* 360: 97–109.
- Brunaux JL. 2006. *Les druides: des philosophes chez les barbares*. Paris, France: Seuil.
- Chassé B. 2016. Eating acorns: what story do the distant, far, and near past tell us, and why? *International Oaks* 27: 107–136.
- Corbin A. 2015. *La douceur de l'ombre. L'arbre source d'émotions de l'antiquité à nos jours*. Paris, France: Editions Fayard.
- Cunniffe NJ, Cobb RC, Meentemeyer RK, Rizzo DM, Gilligan CA. 2016. Modeling when, where, and how to manage a forest epidemic, motivated by sudden oak death in California. *Proceedings of the National Academy of Sciences, USA* 113: 5640–5645.
- Curtu AL, Gailing O, Finkeldey R. 2007. Evidence for hybridization and introgression within a species-rich oak (*Quercus* spp.) community. *BMC Evolutionary Biology* 7: e218.
- Darwin C. 1859. *On the origin of species by means of natural selection, or preservation of favoured races in the struggle for life*. London, UK: John Murray.
- Denk T, Grimm GW, Manos PS, Deng M, Hipp AL. 2017. An updated infrageneric classification of the oaks: review of previous taxonomic schemes and synthesis of evolutionary patterns. In: Gil-Pelegrín E, Peguero-Pina JJ, Sancho-Knapik D, eds. *Oaks physiological ecology. Exploring the functional diversity of genus Quercus L.* Cham, Switzerland: Springer International, 13–38.

- Deshpande O, Batzoglou S, Feldman MW, Cavalli-Sforza LL. 2009. A serial founder effect model for human settlement out of Africa. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 276: 291–300.
- Desprez-Loustau M-L, Feau N, Mougou-Hamdane A, Dutech C. 2011. Interspecific and intraspecific diversity in oak powdery mildews in Europe: coevolution history and adaptation to their hosts. *Mycoscience* 52: 165–173.
- Farcas CP, Cristea V, Farcas S, Ursu TM, Roman A. 2015. The symbolism of garden and orchard plants and their representation in paintings. *Contributii Botanice* 50: 189–200.
- Farjon A. 2017. *Ancient oaks in the English landscape*. Kew, UK: Kew Publishing.
- Galtier N. 2018. Delineating species in the speciation continuum: a proposal. *Evolutionary Applications* 12: 657–663.
- Gerber S. 2018. An herbiary of plant individuality. *Philosophy, Theory, and Practice in Biology* 10: e5.
- Hallé F. 2005. *Plaidoyer pour l'arbre*. Paris, France: Actes Sud.
- Henn BM, Cavalli-Sforza LL, Feldman MW. 2012. The great human expansion. *Proceedings of the National Academy of Sciences, USA* 10: 17758–17764.
- Hipp A. 2015. Should hybridization make us skeptical of the oak phylogeny? *International Oaks* 26: 9–18.
- Hipp AL, Manos PS, Hahn M, Avishai M, Bodénès C, Cavender-Bares J, Crowl A, Deng M, Denk T, Gailing O *et al.* 2020. The genomic landscape of the global oak phylogeny. *New Phytologist* 226: 1198–1212.
- Hubert F, Grimm GW, Jousset E, Berry V, Franc A, Kremer A. 2014. Multiple nuclear genes stabilize the phylogenetic backbone of the genus *Quercus*. *Systematics and Biodiversity* 12: 405–423.
- Humphrey LT, De Groote I, Morales J, Barton N, Colclutt S, Ramsey CB, Bouzouggar A. 2014. Earliest evidence for caries and exploitation of starchy plant foods in Pleistocene hunter-gatherers from Morocco. *Proceedings of the National Academy of Sciences, USA* 111: 954–959.
- International Oak Society. 2001. Oak voted national tree in the US. The newsletter of the International Oak Society 5: 1–4.
- Jarret P. 2004. *Guide des sylvicultures – chênaie atlantique*. Paris, France: Lavoisier.
- Jónsson H, Sulem P, Kehr B, Kristmundsdóttir S, Zink F, Hjartarson E, Hardarson MT, Hjorleifsson KE, Eggertsson HP, Gudjonsson SA *et al.* 2017. Parental influence on human germline *de novo* mutations in 1,548 trios from Iceland. *Nature* 549: 519–522.
- Kremer A. 2015. Did early human populations in Europe facilitate the dispersion of oaks? *International Oaks* 26: 19–28.
- Kremer A, Casasoli M, Barreneche T, Bodénès C, Sisco P, Kubisiak T, Scalfi M, Leonardi S, Bakker E, Builteveld J *et al.* 2007. Fagaceae trees. In: Kole C, ed. *Forest trees. Genome mapping and molecular breeding in plants, vol. 7*. Heidelberg, Germany: Springer, 161–187.
- Lanfer R. 2018. Do plants have a segregated germline? *PLoS Biology* 16: e2005439.
- Lanfer R, Ho SYW, Jonathan Davies T, Moles AT, Aarssen L, Swenson NG, Warman L, Zanne AE, Allen AP. 2013. Taller plants have lower rates of molecular evolution. *Nature Communications* 4: e1879.
- Lang T, Abadie P, Léger V, Decourcelle T, Frigerio J-M, Burban C, Bodénès C, Guichoux E, Le Provost G, Robin C *et al.* 2018. High-quality SNPs from genic regions highlight introgression patterns among European white oaks (*Quercus petraea* and *Q. robur*). *bioRxiv* 388447.
- Le Corre V, Machon N, Petit RJ, Kremer A. 1997. Colonization with long-distance seed dispersal and genetic structure of maternally inherited genes in forest trees: a simulation study. *Genetical Research* 69: 117–125.
- Lepais O, Petit RJ, Guichoux E, Lavabre JE, Alberto F, Kremer A, Gerber S. 2009. Species relative abundance and direction of introgression in oaks. *Molecular Ecology* 18: 2228–2242.
- Leroy T, Louvet JM, Lalanne C, Le Provost G, Labadie K, Aury JM, Delzon S, Plomion C, Kremer A. 2020a. Adaptive introgression as a driver of local adaptation to climate in European white oaks. *New Phytologist* 226: 1171–1182.
- Leroy T, Rougemont Q, Dupouey J-L, Bodénès C, Lalanne C, Belser C, Labadie K, Le Provost G, Aury J-M, Kremer A *et al.* 2020b. Massive postglacial gene flow between European white oaks uncovered genes underlying species barriers. *New Phytologist* 226: 1183–1197.
- Leroy T, Roux C, Villate L, Bodénès C, Romiguier J, Paiva JAP, Dossat C, Aury J-M, Plomion C, Kremer A. 2017. Extensive recent secondary contacts between four European white oak species. *New Phytologist* 214: 865–878.
- Lev E, Kislev ME, Bar-Yosef O. 2005. Mousterian vegetal food in Kebara Cave, Mt. Carmel. *Journal of Archaeological Science* 32: 475–484.
- Logan WB. 2006. *Oak. The frame of civilization*. New York, NY, USA: W.W. Norton & Co.
- Mazoyer M, Rey JP. 2003. *L'arbre, symbole et réalité*. Paris, France: L'harmattan Editions.
- Menotti F. 2004. *Living on a lake in prehistoric Europe. 150 years of lake dwellings research*. Abingdon, UK: Routledge.
- Merceron NR, Leroy T, Chanceler E, Romero-Severson J, Borkowski DS, Ducousso A, Monty A, Porté AJ, Kremer A. 2017. Back to America: tracking the origin of European introduced populations of *Quercus rubra* L. *Genome* 60: 778–790.
- Moorjani P, Gao Z, Przeworski M. 2016. Human germline mutation and the erratic evolutionary clock. *PLoS Biology* 14: e2000744.
- Morales J. 2018. The contribution of botanical macro-remains to the study of wild plant consumption during the Later Stone Age and the Neolithic of north-western Africa. *Journal of Archaeological Science: Reports* 22: 401–412.
- Murphy DJ. 2007. *People, plants and genes*. Oxford, UK: Oxford University Press.
- Ortego J, Gugger PF, Riordan EC, Sork VL. 2014. Influence of climatic niche suitability and geographical overlap on hybridization patterns among southern Californian oaks. *Journal of Biogeography* 41: 1895–1908.
- Ortego J, Gugger PF, Sork VL. 2018. Genomic data reveal cryptic lineage diversification and introgression in Californian golden cup oaks (section *Protobalanus*). *New Phytologist* 218: 804–818.
- Pater J. 2017. *Riesige Eichen*. Stuttgart, Germany: Frankh Kosmos, 380 p.
- Plomion C, Aury J-M, Amselem J, Alacitabar T, Barbe V, Belser C, Bergès H, Bodénès C, Boudet N, Boury C *et al.* 2016. Decoding the oak genome: public release of sequence data, assembly, annotation and publication strategies. *Molecular Ecology Resources* 16: 254–265.
- Plomion C, Aury J-M, Amselem J, Leroy T, Murat F, Duplessis S, Faye S, Francillon N, Labadie K, Le Provost G *et al.* 2018. Oak genome reveals facets of long lifespan. *Nature Plants* 4: 440–452.
- Proust L. 1913. *In search of lost time, Swann's Way*. Paris, France: Grasset.
- Ramos AM, Usié A, Barbosa P, Barros PM, Capote T, Chaves I, Simões F, Abreu I, Carrasquinho I, Faro C *et al.* 2018. The draft genome sequence of cork oak. *Scientific Data* 5: e180069.
- Rieseberg LH, Wood TE, Baack EJ. 2006. The nature of plant species. *Nature* 440: 524–527.
- Rousseau J. 1762. *Du contrat social ou principes du droit politique*. Amsterdam, the Netherlands: Marc-Michel Rey.
- Roux C, Fraisse C, Romiguier J, Anciaux Y, Galtier N, Bierne N. 2016. Shedding light on the grey zone of speciation along a continuum of genomic divergence. *PLoS Biology* 14: e2000234.
- Schmid-Siebert E, Sarkar N, Iseli C, Calderon S, Gouhier-Darimont C, Chrast J, Cattaneo P, Schütz F, Farinelli L, Pagni M *et al.* 2017. Low number of fixed somatic mutations in a long-lived oak tree. *Nature Plants* 3: 926–929.
- Scott JC. 2017. *Against the grain: a deep history of the earliest states*. New Haven, CT, USA: Yale University Press.
- Sork VL, Fitz-Gibbon ST, Puiu D, Crepeau M, Gugger PF, Sherman R, Stevens K, Langley CH, Pellegrini M, Salzberg SL. 2016. First draft assembly and annotation of the genome of a California endemic oak *Quercus lobata* Née (Fagaceae). *G3: Genes, Genomes, Genetics* 6: 3485–3495.
- Thanos CA. 2005. Theophrastus on oaks. *Botanika Chronika* 18: 29–36.
- Thomas GWC, Wang RJ, Puri A, Harris RA, Raveendran M, Hughes D, Murali S, Williams L, Doddapaneni H, Muzny D *et al.* 2018. Reproductive longevity predicts mutation rates in primates. *Current Biology* 28: 3193–3197.
- Villa P, Roebroeks W. 2014. Neanderthal demise: an archaeological analysis of the modern human superiority complex. *PLoS ONE* 9: e96424.
- Wagner S, Lagane F, Seguin-Orlando A, Schubert M, Leroy T, Guichoux E, Chanceler E, Bech-Hebelstrup I, Bernard V, Billard C *et al.* 2018. High-throughput DNA sequencing of ancient wood. *Molecular Ecology* 27: 1138–1154.
- Wohlleben P. 2016. *The hidden life of trees: what they feel, how they communicate – discoveries from a secret world*. Vancouver, BC, Canada: Greystone Books.

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