

# Oak tree symbolism in the light of genomics

Thibault Leroy<sup>1,2,\*</sup>, Antoine Kremer<sup>2</sup> & Christophe Plomion<sup>2</sup>

1. ISEM, Université de Montpellier, CNRS, IRD, EPHE, Place Eugène Bataillon, 34095 Montpellier, France

2. BIOGECO, INRA, Université de Bordeaux, 69 Route d'Arcachon, 33612 Cestas, France

\* thibault.leroy@umontpellier.fr

## Summary

**Oak wood is exceedingly strong, dense and durable, and these properties have long been attributed to living oak trees too, through a symbolism common to the peoples of the Northern Hemisphere, their political systems and religions. This symbolism has led to oaks being considered among the strongest and most resilient species on earth, despite the threats to oak forest health worldwide posed by global changes. Here, we will describe the nature and strength of oak symbolism across the Northern Hemisphere, before discussing how recent advances in oak genomics have already led to a reassessment of the relevance of some of these symbols. Given recent advances in oak genomics, we suggest that new research questions directly or indirectly related to the special symbolic importance of oaks will emerge.**

## I - Introduction

Oaks (genus *Quercus*) have inspired traditional symbolism in the Northern Hemisphere, in diverse settings, including political systems (Box 1). The pedunculate oak is one of the most ancient symbols of the English monarchy. It was also a widely used symbol of the monarchy in neighbouring France, and became a widespread icon of the republic soon after the French

Revolution. Many other Northern Hemisphere countries, including the United States of America, Poland, Portugal and Germany, have also adopted the mighty oak as a national symbol. The Nazis also made use of this tree in their propaganda.

The reasons for this universality of oak tree symbolism across all political systems cannot be understood without considering its roots, in the sanctity of oaks in monotheist and polytheist religions, in particular (cited as the most widely venerated tree species by Lehner & Lehner, 2003). In ancient Greece and Rome, and in the Celtic and Germanic cultures too, trees, especially oaks, were associated with the most important gods (e.g. Zeus, Jupiter and Thor) and were often used as images of the *axis mundi*, the centre of the world. The intricate relationship between humans and oaks probably emerged soon after humans migrated out of Africa. Archaeological evidence suggests that acorns were consumed in the Middle East, consistent with an early incorporation into the human diet during the northward migration (Chassé, 2015). Indeed, the consumption of acorns by humans probably contributed to the northward dispersion of oaks in Europe during the Upper Paleolithic (Kremer, 2015).

With this rich political and mythological history, a very strong symbolic image of oaks has developed, associating longevity, strength, stability, endurance, power, justice and honesty. We will evaluate some of these symbolic aspects

### Box 1

#### An illustrative example of oak symbolism: the Gernika tree

A historical example of the endorsement of oak trees as a symbol of human values, is the Gernika tree, a pedunculate oak standing in front of the parliament of the Biscay province of the Basque Country (Figure 1a). 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 (Figure 1b). 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 (Figure 1c). The French philosopher Jean Jacques Rousseau cited these assemblies as an early form of democracy in "Le contrat social" (1762).

The Gernika tree is still depicted on the coats of arms of many Basque towns (Figure 1d), and is used as an icon in social celebrations (Figure 1e). Offspring from the original tree have been planted in many places worldwide to which Basque people have emigrated, as a symbol of the cohesiveness of the Basque diaspora.



**Figure 1: Gernika oak symbolism.** a) A third-generation offspring of the original Gernika tree in front of la Casa de Juntas (House of Assemblies), Basque Country, Spain. 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. d) Biscay coat of arms from la Casa de Juntas, with its representation of the Gernika tree. e) Poster of the 650<sup>th</sup> anniversary of the establishment of Gernika.

below, in the light of recent findings at the intersection of ecology, genomics and population genetics.

## II - Longevity

Unlike animals, which are generally less long-lived than humans, tens of thousands of plant species can live for hundreds, or even thousands of years, including most of the 400-500 oak species. Majestic ancient living oaks in public squares, parks and forests are a strong element of Northern Hemisphere cultures. The observation of the same old oaks throughout a lifetime may trigger enduring positive memories, much like Proust's madeleine. Some famous specimens, such as the Major Oak of Sherwood Forest in England, are thought to be up to 1,000 years old.

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 to 1,000,000 new sessile oak seedlings per year and per hectare (Jarret, 2004). Ten years later, in the absence of silvicultural disturbance, the number of living individuals per hectare has been estimated at 57,000 to 63,000, suggesting that the vast majority (68-94%) of these new individuals die within ten years due to biotic and abiotic stresses (Jarret, 2004).

But what are the genetic consequences of growing old? Several studies in primates have shown that ageing has a strong impact on intergenerational heritable mutation rates, particularly the number of germline cell divisions in males (e.g. Jónsson *et al.*, 2017; Thomas *et al.*, 2018). In plants, 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, potentially, to pass 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 85-year-old trees (Schmid-Siegert *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 SNPs over a genome of more than 750 million bases; Kremer *et al.*, 2007). This challenges the poetic vision of each tree as a forest in its own right (Hallé, 2005). Instead, it suggests 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).

## III - 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 formed from an endless cord forming interlaced patterns symbolising eternity and unity. But beyond such symbolism, are oak species genetically cohesive units?

Over the last decade, several large studies of hundreds of oak species have tried to resolve the taxonomic classification of oaks (Hubert *et al.*, 2014; Denk *et al.*, 2017). They established a comprehensive backbone in the evolutionary

history of the genus *Quercus*. The latest infrageneric classification clusters oak species into two subgenera (*Quercus* and *Cerris*) with eight sections (sections *Quercus*, *Ponticae*, *Virentes*, *Protobalanus*, *Lobatae*, *Ilex*, *Cerris* and *Cyclobalanopsis*). Hybridisation between species from different sections is rare in nature and consistent with reproductive isolation (Hubert *et al.*, 2014), but hybridisation within sections is widespread (Hipp, 2015), a phenomenon leading Rieseberg and collaborators (2006) to include oaks in their shortlist of ‘botanical horror’ taxa. Darwin had already raised the issue of the complexity of oak species boundaries a century and a half earlier. In “On the Origin of Species”, he reveals that oak classification was a thorny problem for the botanists of his time: “[...] 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).

A large body of population genetics (e.g. Curtu *et al.*, 2007; Lepais *et al.*, 2009; Leroy *et al.*, 2017; Ortego *et al.*, 2014) and population genomics studies (Leroy *et al.*, 2018; Ortego *et al.*, 2018) have provided profound empirical support for ongoing admixture and gene flow between oak species, excluding the possibility that oak species are discrete entities evolving as independent evolutionary units. Instead, most oak species correspond to intermediate states on the speciation continuum, the so-called “grey zone”, for which species definition remain controversial (Roux *et al.* 2016). Studies using 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, in association with the advance and retreat of glaciation (e.g. Leroy *et al.*, 2017; 2018; Merceron *et al.*, 2017). 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; 2018). Barriers to mating dispersed throughout the genome may partially or totally prevent interspecific gene flow, ensuring that interspecific differences are essentially fixed, whereas interspecific gene flow rates are high elsewhere in the genome. Oaks may not evolve as cohesive units, but they are still ideal taxa for studies of the early stages of speciation or investigations of the flow of adaptive alleles across these porous species boundaries (i.e. adaptive introgression, Leroy *et al.* in preparation). Hybridisation, which fuels genetic variation in mixed oak stands, is a key evolutionary mechanism underlying adaptation, particularly for traits with low levels of intraspecific variability, such as embolism resistance (Lobo *et al.*, 2018).

#### IV - Robustness

Pedunculate oak (*Q. robur*) is the most abundant oak 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 United States and Germany. Based on the information provided by the oak genome, can we consider oaks to be robust enough to neutralise 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 catalogue) and a diversification of gene function driven by a long-standing co-evolutionary arms race between oaks and their natural enemies (viruses, bacteria, fungi, oomycetes, nematodes, 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 globalisation 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 powdery mildew into Europe at the start of the 20<sup>th</sup> century led, for example, to high rates of *Q. pyrenaica* mortality in Southwestern and Western France (Desprey-Loustau *et al.*, 2011). This pathogen still has a deleterious impact on tree growth in European forests (Bert *et al.*, 2016). Similarly, the recent emergence of *Phytophthora ramorum*, causing sudden oak death on the West Coast of the United States, is another main 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.

Aside from the extrinsic threats to oaks, publication of the pedunculate oak genome has shed light on the capacity of this species to accumulate deleterious mutations. Of all the plant and animal species investigated to date (Chen *et al.*, 2017), the pedunculate oak is the species found to accumulate the largest number of harmful mutations (Plomion *et al.*, 2018). The mutation load depends on local recombination rates and is very high in regions with low levels of recombination, suggesting that these mutations are purged only inefficiently by natural selection (T. Leroy, personal communication).

## VI - 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 worldwide 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 recent genomic findings to examine the relevance of some of these symbols. We are firmly convinced that recent academic findings, such as the importance of archaeological 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 too. We anticipate that the increase in genomic resource availability for oaks (Plomion *et al.*, 2016; 2018; Sork *et al.*, 2016; Ramos *et al.*, 2018, and this issue) will reveal a myriad of other surprises, provided that analyses are data-driven and assumption-free. It should also be stressed that the long-term trajectory of intra- and interspecific biodiversity in oaks is highly dependent on public policies and preventive strategies for countering the effects of climate change and globalisation, as in many other plant species perceived as more susceptible.

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