Oak symbolism in the light of genomics

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Summary

Throughout the Northern Hemisphere, human societies, political systems and religions have appropriated oaks in symbolic representations. In this review, we question whether recent findings in genetics and genomics can be associated to symbolic representations of oaks. First we examine how evolutionary history during the Holocene has tightened links between humans and oaks in Europe, which may have ultimately contributed to generate symbolic representations. We then show how knowledge regarding the structure and evolution of the oak genome provide additional elements supporting or rebutting some of the most adopted symbolic representations as longevity, cohesiveness and robustness.

I - Introduction

Throughout the Northern Hemisphere, human societies, political systems and religions have appropriated oaks in symbolic representations. Starting with the very early cultures of the Proto-Indo-Europeans, oaks were already present in traditional rites and celebrations (Chassé, 2016). From then on, oaks were associated to various symbols as longevity, strength, fertility, robustness and many others. We question whether recent findings in genetics and genomics can shed a new light on symbolic representations of oaks. Beforehand we examine how symbolic representations may have developed. We contend that they are to be found in the intricate relationships that emerged between people and oaks when modern humans migrated out of Africa, as a result of reciprocal benefits. We thus explore how findings in the joint evolutionary trajectories of humans and oaks during the Holocene contributed to their "shared" history, reinforcing ties between trees and people. By no means, we attempt to be exhaustive by considering the countless symbols that humans have assigned to oaks. We address only a few (longevity, cohesiveness, robustness) for which associations with a genetic perspective are most conspicuous particularly in European history (from Greek, Roman to Celtic societies). Our approach should be seen as an introduction, a stepping stone to future investigations assembling knowledge from different fields (history, ecology, genomics and social sciences) and aiming at understanding symbolic representations of plants in human societies.

II From early ties between humans and oaks to symbolic representations

How symbolic meanings of trees have arisen in early human societies relates to the very early ties that linked people and trees, and how these ties developed historically. More than any other tree species, oaks have paved the way of *Homo sapiens* while colonizing the Middle East and Europe. Oaks provided unvaluable food resources to humans in their early days in Eurasia. Evidence about the essential contribution of acorns to the dietary staple of the first modern humans is steadily increasing as ethnographic, archeological and historical clues accumulate. Despite the taphonomical underestimation of acorns consumption due to charred remains, recent archeological investigation underpinned the widely use of acorns as food source (Lev *et al.*, 2005; Humphrey *et al.*, 2014, Antolin and Jacomet, 2015; Morales, 2018), including consumption by Neanderthals (Villa and Roebroeks, 2014). Archeological elements are reinforced by historical evidence that comes from the writings of the earliest geographers as Pausanias and Strabon, philosophers as Platon, poets as Ovid, naturalists as Pliny the Elder and Theophrastus highlighting regular acorn consumptions up to the greek and roman ages (reviewed by Chassé, 2016). Before agriculture developed in Mesopotamia, human hunters and gatherers feed themselves with a variety of seed including acorns from the nearby oak forests located in the Zagros Mountains or in 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 at about 40.000 years BP and later on when human populations migrated northwards. Kremer (2015) emphasized intriguing coincidences between human and oak colonization dynamics in terms of velocity (500m/year Brewer, 2002 for oak and Henn et al. 2012 for modern humans), processes (serial founder effects Le Corre et al., 1997 for oaks and Deshpande et al., 2012 for humans) and colonization routes, suggesting that humans may have transported oaks as food reserves while migrating northwards as the climate warmed, thus contributing to the rapid colonization of oaks.

III Oak symbolic charge in humanities and science

The same story as for food tells how oak served for various other purposes and uses. Besides acorns, any other part of the tree served either for food, medicine, fuel, shelter and arts. Oaks became the "tree of life" (Anderson, 2007) or the "frame of civilization" (Logan, 2006). For example, almost all prehistoric pile dwellings that were built during the Bronze Age along lake shores were made of oak logs (Menotti, 2004). Clearly oaks facilitated human establishment in Europe, while humans contributed to the widely expansion of oaks across the continent. Subsistence relationships turned into values and virtues associated to trees that ultimately became symbols in societies, or sacred beings assigned to trees in religions (Logan, 2006). In addition shared history between human and oaks generated cultural and emotional relationships that translated into symbols or become part of religious beliefs and mythology. Oaks were associated with the most important gods (e.g. Zeus, Jupiter and Thor) in the mythology of ancient Greece and Rome, and in the Celtic and Germanic cultures and were often used as images of the *axis mundi*, the centre of the world.

Starting with the early ties between humans and oaks, a very strong symbolic image of oaks has developed, associating longevity, strength, stability, endurance, fertility, power, justice and honesty. In humanities, these symbols received a wide attention in history (Logan, 2006), social sciences (Mazoyer and Rey, 2003; Brosse, 1989), literature (Corbin, 2005) and arts (Farcas *et al.*, 2015). In natural sciences, first insights about oak symbols emerged in the very early writings in botany by Theophrastus (*Historia Plantarum, Book 3, Wild trees and schrubs*) or by Pliny the Elder (*Natural History)*. While Theophrastus provided the first taxonomical description of oaks in ancient Greece, he also underpinned longevity of the species in his scientific approach (Thanos, 2005). Pliny the Elder provided detailed description on how druids celebrated mistletoe growing on scared oak trees and prepared remedies to cure infertility (Brunaux, 2006). Jumping into more recent times, many Northern Hemisphere countries have adopted the mighty oak as an official national emblem, including the United Kingdom, Poland, Portugal and Germany, as well as regional ones (Figure 1). In 2001, a four-month-long and nationwide popular vote led the authority to choose the United States of America's national tree. The people of the USA selected oaks among 20 other tree species (International Oak Society, 2001) and oaks then became formally recognized as the USA's national tree by the Congress in 2004.

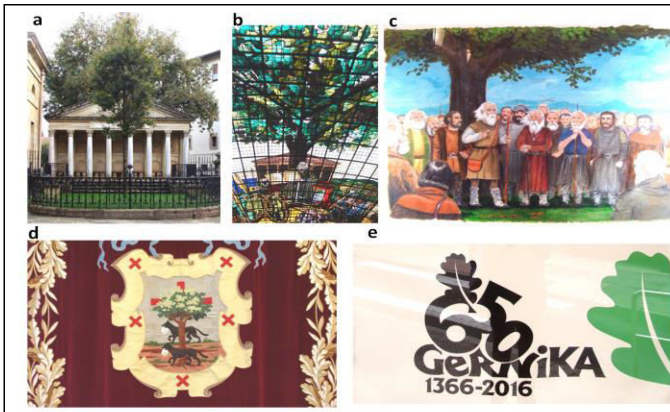

Figure 1: An illustrative example of the endorsement of oak trees as a symbol of human values, is the Gernika tree, a pedunculate oak standing in front of the parliament of the Biscay province of the Basque Country. *a) A third-generation offspring of the original Gernika tree in front of* la Casa de 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 winding 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* 650^{th} *anniversary of the establishment of Gernika.*

IV - Longevity

Unlike animals, which are generally less long-lived than humans (Bozek *et al.,* 2017), tens of thousands of plant species can live for hundreds of years, including many oak species. Majestic ancient living oaks in public squares, parks and forests are a strong element of Northern Hemisphere cultures (Farjon, 2017; Pater, 2017). 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 900 years 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 near 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 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 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). Some individual oaks may be long-lived, but the life expectancy of any given oak seedling is very short indeed.

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 100 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). After providing a detailed analysis at the interface between population genetics and philosophy, Gerber (2018) reached a similar conclusion. This finding 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).

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 formed from an endless cord forming interlaced patterns symbolising eternity and unity. However subtle morphological species differences between closely related species were not recognized even in recent times, as illustrated by the use of the generic word "oak" to assign irrespectively *Q. robur* or *Q. petraea*. But beyond such symbolism, are oak species genetically cohesive units?

Over the last decade, several studies have tried to resolve the taxonomic classification of oaks (Hubert *et al.*, 2014; Denk *et al.*, 2017; Hipp *et al.*, 2019). 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 (*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 was aware of the complexity of the oak species relationships (Darwin 1859) describing it as 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).

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.*, 2019a; Ortego *et al.*, 2018) have provided empirical support for ongoing admixture and gene flow between phylogenetically related oak species, questioning the possibility that oak species are discrete entities evolving as independent evolutionary units. However recent findings based on whole-genome sequencing showed that hybridization can occur without disrupting species integrity, which is restricted to a limited part of the genome, maintaining species barriers (Leroy et al. 2019a). 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; 2019a; 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; 2019a). 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 gene level –where species barriers are maintained– rather than at the genome level, which -in its largest part- is permeable to gene flow in these outcrossing species. However, such interspecific exchanges should not be disregarded since they can contribute to local adaptation in populations living in marginal habitats (Leroy et al. 2019b). Further population genomic studies will be crucial to better understand the current evolutionary trajectories, as well as 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 United States and Germany. Artistic representations of oak trees were also used to symbolize strength and robustness of ideas (Figure 2). 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

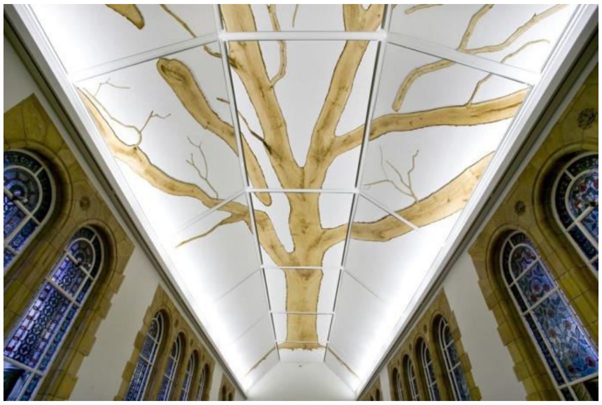

Figure 2: Oak tree artwork as symbol of robustness of ideas (Bloomfield, 2012). *An illustrative oak symbolic representation linking art and science was the choice for a longitudinal oak tree section as artwork for the ceiling of the Natural History Museum of London in 2009. The artwork was planned to celebrate the 200th anniversary of Darwin. A panel of art experts, museum experts and scientist selected the oak project among 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 to 5 mm thick section of a 200 year old entire oak tree, from the ground to the canopy). The tree was 21 metres high and came from a managed forest of Longleat Estate in Wiltshire. The art work 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" praised by early human populations (Andersson, 2007). As mentioned by R.M. 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/

have not coevolved new threats to oaks. The accidental introduction of powdery mildew into Europe at the start of the 20th century led, for example, to high rates of *Q. pyrenaica* mortality in Southwestern and Western France (Desprez-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.

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 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 discoveries, 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) will reveal a myriad of other surprises, provided that analyses are data-driven and assumption-free.

This review pleads for future investigations along the genetic properties related to the three symbolic representations of oaks that we discussed here. Concerning longevity, our results pave the way for future research aiming at refining the relationship between tree ageingand mutation rates, implicitly accounting for meiotic and somatic mutations. Ultimately, age-related mutation rates in different long-lived animal and plants would allow elucidating whether there is a "generation-time effect" (Moorjani *et al.*, 2016), *e.g.* with a systematic shift to lower yearly mutation rates in woody species. Concerning cohesiveness, our conclusions are for the time being mostly driven by emblematic examples, such as European white oaks, but see Hipp *et al.* (2019). That species that were traditionally recognised as taxonomic nightmares, remained largely cohesive at the genome level, support recent proposals for taxonomic standardization based on genomic data (see Galtier, 2018). After analysing the population structure of a large set of populations from diverse geographical regions and assuming a threshold for the net amount of differentiation or divergence for oaks, taxonomic decisions could be made less arbitrary. Such an approach will contribute to a scientifically refined definition of oak species. Concerning robustness, we are at the onset of the inventory of the oak leaf microbiome. Combined metagenomic and expression studies will help to confirm whether the expanded R-genes in the oak genome contributes to extended microbial phenotype and ultimately to increase the resilience of oaks to emerging threats.

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