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Did Early Human Populations in Europe Facilitate the Dispersion of Oaks?

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ABSTRACT

This review contends that early human populations, while invading Europe during the Upper Paleolithic or while migrating in response to postglacial warming, contributed to the dispersion of oaks. Evidence suggests that humans, while migrating along the Danube route, facilitated acorn dispersal as they transported goods that could help them survive the local harsh climate. Some of the dispersed acorns very likely developed micro-populations, and may have finally resulted in cryptic northern populations, very far north of contemporary oak distribution. The human vector of acorn dispersal in Europe would have resulted in a scattered distribution of what we call today cryptic refugia. Such a scenario may explain why the Balkan genetic lineage is so widespread in Central and Eastern Europe (even in Western Europe) north of the Alps.

Keywords: acorn dispersal, oak migration in Europe

Introduction

Oak colonization of Europe during the postglacial period was extremely rapid. Rates of migration inferred from pollen deposit maps show a rate of more than 500 m/1,640 ft per year, exceeding by far the dispersion by jays, squirrels or rodents (Brewer et al. 2005). To explain this paradox, occurrences of rare long-distance dispersal events have been invoked. This mechanism has been tested by computer simulation and shows that dispersal events of a few dozen kilometers, even if very rare, would have substantially accelerated the overall migration rate (Le Corre et al. 1997). To date no conclusive evidence for a long-distance dispersion vector has been found. An alternative scenario has been proposed, suggesting that cryptic refugial populations persisted during the glacial period in more northern areas, and would have acted as source populations for recolonization (Stewart and Lister 2001). It is likely that both dispersal mechanisms can be advocated in the case of oaks. Currently however, clear evidence – based on genetic or fossil data – exists only for the northern refugia scenario. Archeological or historical evidence for long-distance dispersion is very scarce and there has been no specific research to determine what the possible vectors may have been.

We contend in this review that early human populations, while invading Europe during the Upper Paleolithic or while migrating in response to postglacial warming, contributed to the dispersion of oaks. It is suggested that early humans collected acorns for their food needs, probably storing them in pits before their consumption. Furthermore they brought part of their harvest along with them when they moved to new settlements. Any "lost" acorns dropped along the route, or any non-consumed acorns would constitute a dispersion event. This article mainly reviews evidence from different sources that support this scenario; indeed, recently there have been a number of contributions in human history, archeobiology and in population genetics that, when put all together, lead to such conclusions.

Acorns in the diet of early human populations

Acorns are a valuable food resource. Like cereals they are rich in carbohydrates, and fibers but also have a high fat content (Salkova et al. 2011). They contain tannins (responsible for their very bitter taste) that are soluble in water and can thus be removed through soaking. Acorns have always been a major component of human diets, and, quite interestingly, their potential human consumption in modern societies has recently been advocated in *Scientific American* as a possible means to overcome future food shortages (Starin 2014). There is ethnographic, archeological, and also historically documented evidence that humans have been consuming acorns since their presence in Europe and that in extant traditional tribes they continue to do so (McCorriston 1994; Mason and Nesbitt 2009). While this is well accepted (Aurenche 1997; Karg and Has 1996), more recent data suggests that acorns were used as a dietary staple (Zalkova 2011; Haws 2004; Liu et al. 2010) and not only when other resources became exhausted. Acorn-processing techniques do not always result in detectable remains or charred material, and have therefore been underestimated in archeological remains. It is known that preservation constraints of starch-rich seed hampers their detection. This has led to an underestimation of their presence and to the realization that acorn consumption has been overlooked (Deforce et al. 2009; Mason 1995). This picture has changed since other methods are now used that have confirmed the wide-spread use of acorns as a food source. These new methods include, for example, the analysis of dental caries or of food remains in teeth (Humphrey et al. 2014; Villa and Reybroeks 2014).

Archeological investigations have detected acorn remains in human settlements in different parts of Europe and at different periods. In the Middle East, the oldest remains found date from 60,000 to 40,000 BP (Lev et al. 2005). In Morocco, the substantial prevalence of dental caries analyzed from human remains (14,000 BP) has been attributed to starchy plant foods such as acorns (Humphrey et al. 2014). In Spain, acorn remains were discovered in the Nerja caves at the lake-dwelling site of La Draga from 14,000 BP up to 5,000 BP (see Haws 2010, for a review for Iberia; Antolin and Jacomet 2015). In more northern latitudes, prehistoric finds of acorn remains have been documented in France at 3,000 BP (Bouby 2000), in Belgium at 2,200 BP (Deforce et al. 2009), in Germany dating from the Bronze Age (Knörzer 1972), in Denmark from the Stone Age (Jorgensen 1977), and in Sweden at 8,000 BP (Regnell 2012). To illustrate some of these findings, the remains discovered by Deforce and coworkers (2009) were contained in an oval pit (2.3 m long, 1.75 m wide and 0.30 m deep/7.5 ft × 5.74 ft × 0.98 ft) almost completely filled with acorn samples. In total it has been estimated that this pit could have contained 69,000 acorns!! The authors discussed the various purposes for storing such a large quantity of acorns, and finally concluded that food provision (either for humans or animals) is the most likely interpretation. It has also been shown that acorn consumption was practiced since very early times by modern humans (Lev et al. 2005) and even earlier by Neanderthals (Villa and Roebroeks 2014). The recent and increasing number of reports on archaeological acorn remains as well as reviews on the presence of acorns in the human diet (Rosenberg 2008; Salkova et al. 2011; Rimavera and Fiorentino 2013) underpin the reconsideration of acorns as a dietary staple in early human populations.

Finally, acorn consumption has been well documented in more recent times in historical texts written by classical authors such as Strabon (the Greek geographer) or Pliny the Elder (the Roman historian) when they first discovered Iberia or France, and reported on the customs of the local people. Quoting Strabon (*Geografia 2*) “These people live in very austere settings: water is their only drink, they sleep on the ground. During most of the year, they eat acorns. First they dry them, then they grind them and bake a kind of bread that can be conserved over long time.” Pliny the Elder in *Naturalis Historia* reports very similar practices “When the cereals become rare, they dry the acorns, they shell them and grind them to make a flour and finally to produce bread. Today, even in the Hispanias, acorns are also part of desserts.” These excerpts stem from Arsuaga (1999); a more exhaustive review of historical writings, mostly by Greek authors, confirm these ethnographic observations (Aurenche 1997)

These archeological and historical reviews clearly suggest that human populations collected acorns, stored and further processed them (tannin removal and charring) for future consumption, and that this was probably largely practiced over the ages and across Europe.

Oak migration following environmental change

Oak migration in Europe has only been retraced since the last glacial maximum (LGM) based on pollen deposits (Brewer et al. 2002, 2005). At the end of the LGM, oak forests were largely restricted to the Iberian Peninsula, Italy, and the Balkan Peninsula

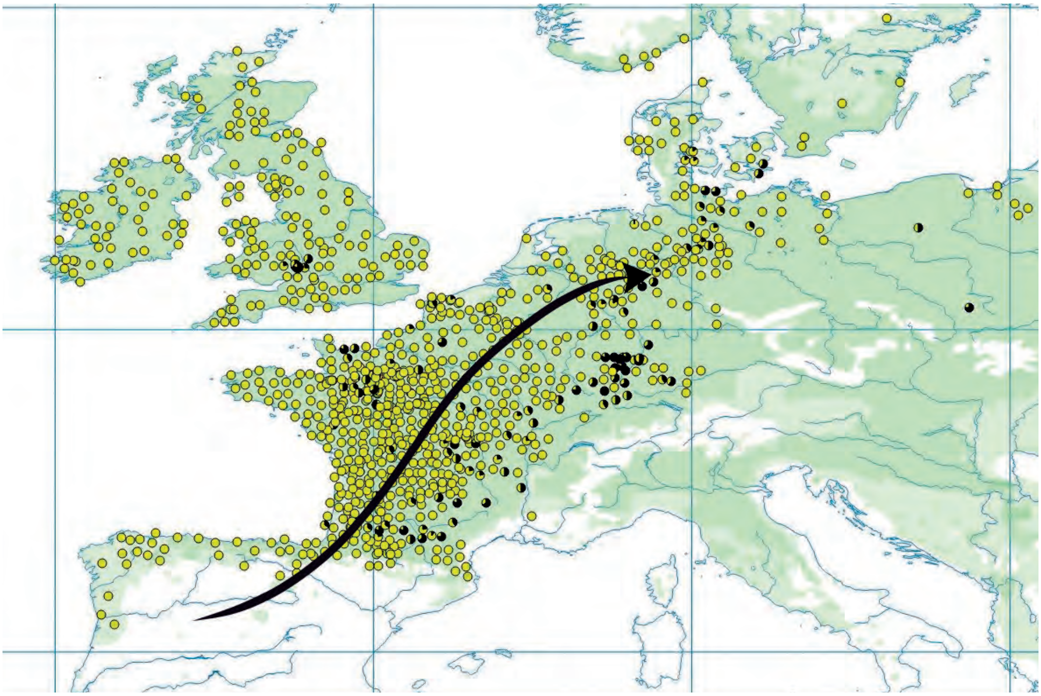

Figure 1a/ Distribution of oak stands belonging to the Atlantic lineage. The green shaded area corresponds to the joint extant distribution of *Quercus petraea* (Matt.) Liebl. and *Q. robur* L. Only populations bearing haplotypes 10, 11, 12 (according to Petit et al. (2002), belonging to the Atlantic lineage) are plotted here. The black arrow indicates the most likely postglacial migration route from the Iberian refugial area to Northern Europe. Data extracted from the GD2 database (Georeferenced Database of Genetic Diversity): https://w3.pierroton.inra.fr/QuercusPortal/index.php?p=gd2

(Greece and the western coast of the Black Sea). These refugial areas bear distinct genetic fingerprints in chloroplast DNA (Petit et al. 2002). Hence, migration from the three genetic refugial areas can be reconstructed based on the extant distribution of these fingerprints. As the climate warmed up, between 13,000 and 10,000 BP, oaks increased in abundance, attaining the Pyrenees, the Alps and the Carpathian Mountains. The cooling of temperatures from 11,000 BP to 10,000 BP temporarily stopped the expansion that accelerated again after 10,000 BP. Oaks reached their extant distribution at about 6,000 BP. This is the reconstructed scenario of the colonization waves inferred from fossil pollen deposits (Brewer et al. 2002). Locally, the colonization process was a mix of dispersion by biological vectors (jays, squirrels, etc.) and by rare long distance "jumps" (Le Corre et al. 1997).

As indicated earlier, migration routes can be inferred by the geographic distribution of the chloroplast genetic fingerprints (so called genetic lineages). We illustrate in Figure 1 the colonization route followed by the Atlantic lineage (Figure 1a), and by the Balkan lineage (Figure 1b). The Atlantic lineage went from southwest to northeast (Spain to Scandinavia) while the Balkan lineage most likely followed an east to west route, north of the Alps, and later a northern direction (Figure 1b). It is quite surprising that the eastern part of France is inhabited by the Balkan lineage rather than the Atlantic lineage. Somehow the former was present there before the latter arrived.

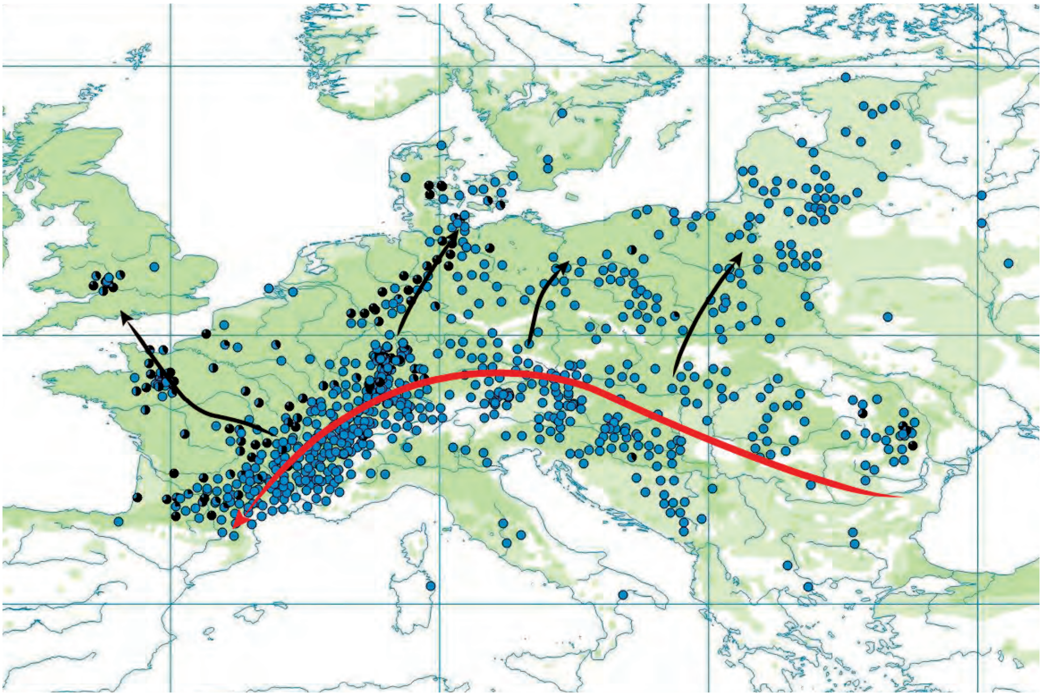

Figure 1b/ Distribution of oak stands belonging to the Balkan lineage and possible migration routes of oaks. The green shaded area corresponds to the joint extant distribution of *Quercus petraea* (Matt.) Liebl. and *Q. robur* L. Only populations bearing haplotypes 4, 6, 7, 26 and 30 (according to Petit et al. (2002), belonging to the Balkan lineage) are plotted here. The red arrow mirrors the possible early dispersion pathway of oaks due to the modern human migration (see text and Figure 2) that took place from 45,000 to 40,000 BP. Human presence along the Danube route may have facilitated the dispersion of oaks from 45,000 BP up to the LGM resulting in the possible installation of cryptic oak refugia north of the Alps (along the red arrow). Black arrows indicate the most likely migration route after the LGM, when the climate improved (18,000 BP and thereafter). Data extracted from the GD2 database (Georeferenced Database of Genetic Diversity): https://w3.pierroton.inra.fr/QuercusPortal/index.php?p=gd2

Human migrations in Europe during environmental changes

Humans were present in Eurasia since about 600,000 BP. While settlements as early as 1.4 Ma have been reported (Moncel et al. 2004), the expansion of *Homo heidelbergensis* Schoetensack takes place after 600 ka and contributed to the emergence of *H. neanderthalensis* King. From 230,000 BP to 40,000 BP Neanderthals inhabited most of Northwestern Eurasia (Stewart and Stringer 2012). Finally, modern humans (*H. sapiens* L.) colonized Europe at 45 to 40,000 BP and they have occupied the Old World ever since (Mellars 2004; Henn et al. 2012). It is generally accepted that *H. heidelbergensis* and *H. sapiens* migrated from Africa to Eurasia at different times while *H. neanderthalensis* emerged in Western Europe and subsequently migrated eastwards in Asia during the Upper Pleistocene (75,000 to 57,000 BP) (Bar-Yosef and Belfer-Cohen 2013).

These historical perspectives clearly suggest that hominid populations faced at least four interglacial/glacial periods while modern human populations experienced the most recent glacial/interglacial transition. How did they respond to the recurrent major environmental changes that occurred during the Pleistocene? Much as for other organisms (Taberlet et al. 1998; Hewitt 2000) there is evidence that human presence expanded and

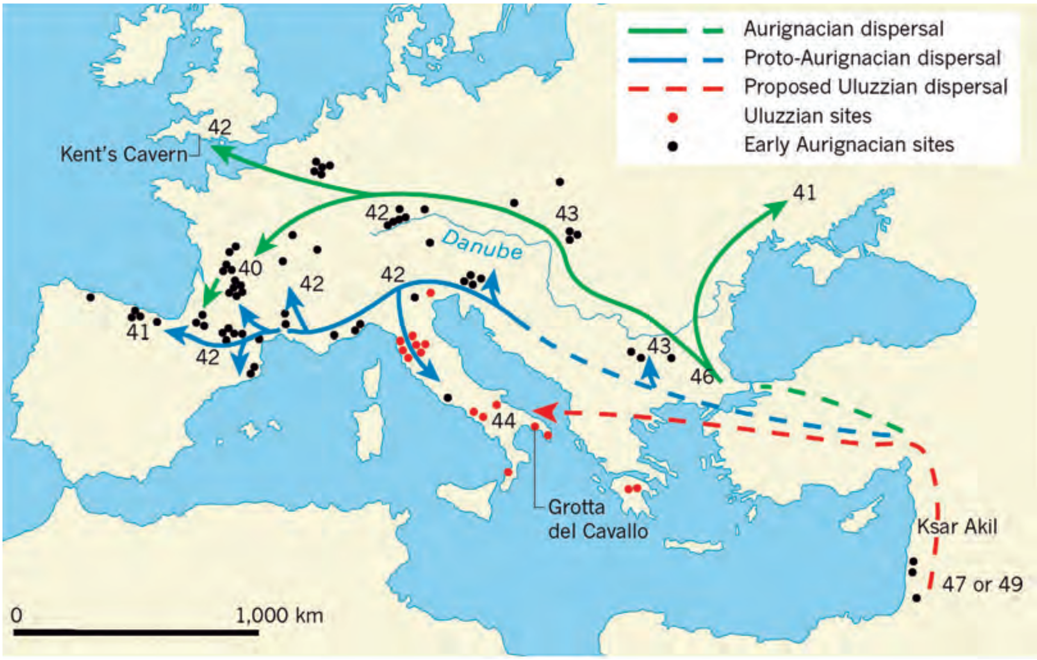

Figure 2/ Dispersal routes of modern humans in Europe (Mellars 2011). Numbers indicate k years BP.

retracted in response to climatic oscillations, and these migration routes or refugial areas have been retraced (Stewart and Stringer 2012). Such periods of contraction or expansion have been reported to be a result of climate changes (Gamble et al. 2004). For example, the Gravettian industry disappeared from Northwestern Europe about 23,000 years ago, with recolonization of that area dating from after the LGM (Gamble et al. 2004). Extreme rapid cooling during the Heinrich events H4 and H5 have been invoked as possible drivers of the Neanderthal extinction (Bradtmöller et al. 2012).

Northward expansion, albeit documented, is not as strongly linked to climate change as is contraction because dispersal usually occurred within wide climatic tolerances (Gamble et al. 2004). This latter review, that retraces past population distribution based on radiocarbon dating in Western Europe, shows that Iberia appears as a southern refugium of human populations. Less documentation is available on the impact of earlier interglacial/glacial periods for Neanderthals. Indeed Neanderthals witnessed the last interglacial period (Eemian) that occurred 125 to 127 ka ago and the subsequent cooling that led to the LGM. At what rate did human populations migrate? Based on archeological records and genetic data, Henn et al. (2012) estimated that human populations expanded at a minimum rate of 0.5 km/1.6 ft year during the out-of-Africa expansion. Furthermore these figures are also consistent with the spatial distribution of genetic diversity and correspond to a colonization process with repeated serial founder effects (Despande et al. 2012).

How may human populations have facilitated the migration of oaks?

To answer this question we need to compare the migration pathways and dynamics of both organisms. This comparison can only be made for the periods for which the best records of migration are available for both. Although oaks and humans can be found

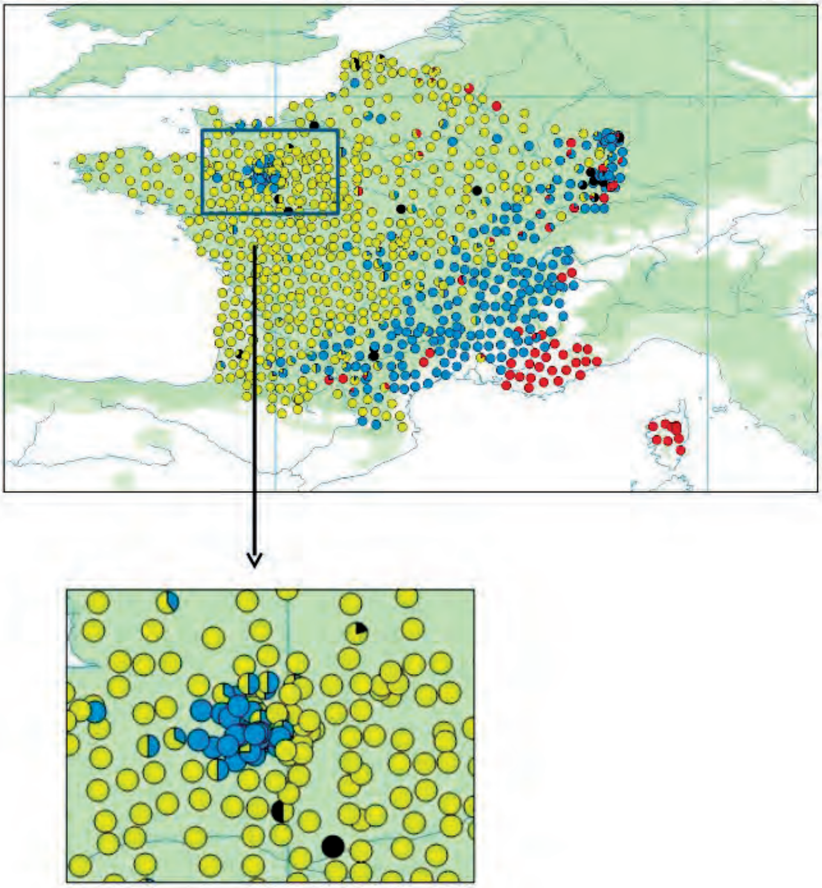

Figure 3/ Distribution of the oak genetic lineages in France and illustration of a long-distance dispersal event. Blue dots indicate oak stands belonging to the Balkan lineage (similar to Figure 1b). Yellow dots indicate oak stands belonging to the Atlantic lineage (similar to Figure 1a). Red dots indicate populations belonging to the Italian lineage (haplotype 1 according to Petit et al. 2002). A close up illustrates the « blue island » within the Atlantic lineage, witnessing a long-distance dispersion possibly due to a human mediated transfer (see text). Data extracted from the GD2 database (Georeferenced Database of Genetic Diversity): https://w3.pierroton.inra.fr/QuercusPortal/index.php?p=gd2

together much earlier, our comparison will therefore be restricted to the last 50,000 years (Upper Paleolithic), i.e., since the presence of modern humans (*Homo sapiens*) in Europe. This was actually the time (45,000-40,000 BP) when the very first modern humans coming from the Middle East colonized Europe (Mellars 2011). This spread is well-documented and followed basically two routes (Figure 2): the northern along the Danube River, and the southern (south of the Alps) along the Balkans, Slovenia, Italy and the south of France (Mellars 2011; Hoffecker 2009). During these periods, human populations were hunter-gatherers, and the climate in Central Europe (along the Danube river) dry and cold (tundra-like).

Our suggested scenario is that humans, while migrating along the Danube route, facilitated acorn dispersal as they transported goods that could help them survive the local harsh climate. Some of the dispersed acorns very likely developed micro-populations and may have finally resulted in cryptic northern populations very far north of contemporary oak distribution. At this time, 20,000 years before a period of climate warming, these micro-populations would have had enough time to develop in stands that may have then acted as source populations for recolonization later on. However, these populations may have been too small to produce enough pollen deposits that would be detectable today. The human vector of acorn dispersal in Europe along the two routes would therefore have resulted in a scattered distribution of what we call today cryptic refugia. Such a scenario may explain why the Balkan genetic lineage is so widespread in Central and Eastern Europe (even in Western Europe), north of the Alps (see Figure 1b).

Humans may have also facilitated oak dispersion during the northward migration from the southern refugia and from the cryptic more northern refugia, following the LGM (18,000 BP). As mentioned earlier, humans (Gamble et al., 2014) and plants expanded northwards as the climate warmed. Interestingly the migration rate of man and oaks was very similar (Brewer et al. 2002; Henn et al. 2012). Both migrated in the same direction and at similar speed, thus suggesting that man may have acted as the vector of the rare long-distance dispersal events of oaks. An imprint of the human contribution is shown by the peculiar extant distribution of oak chloroplast haplotypes. For example, in Brittany, in a region that is entirely inhabited by oaks belonging to the Atlantic lineage, an “island” of Balkan origin (representing a circle with a 50 km/31 mi radius) can easily be shown. This feature is most likely the imprint of a long-distance dispersal event of acorns belonging to the Balkan lineage, some 8 to 10,000 years ago (Figure 3). Incidentally, the small blue “islands” in Figure 3 also exist in the British Isles (Cottrell et al. 2002). This may represent the western outcome of the original northern migration of *Homo sapiens* along the Danube River (Figure 3).

Conclusion

Referring to our introductory hypothesis, this review suggests that humans may have actually contributed to the installation of very early populations (late cryptic refugia) north of the Alps along the Danube migration pathway (43 to 42,000 BP). In addition they may have facilitated the northward migration along the postglacial colonization routes (15 to 6,000 BP). Our conclusions are at this time supported by only coincidental migration pathways and dynamics. More evidence is needed to confirm or dismiss them.

One possibility would be to conduct a detailed genetic spatial analysis based on fossil remains of humans and oaks collected in the same region. Similar mitochondrial (for man) and chloroplast (for oak) narrow-scale distribution would be a strong argument of human involvement in oak migration. Should such a scenario be confirmed, one could ask if intentional sowing or some kind of proto-silviculture for establishing new oak stands was not implemented. Beyond the consumption of acorns, oaks were indeed used for a variety of purposes including for firewood, construction, charcoal, and tannins. This then raises the issue of attempts of domestication. Haws (2004) suggested that hunter-gatherers probably used rudimentary techniques such as pruning to increase acorn production. Mason (2000) also raises the possibility that fire management may have improved seed crop. Finally, some sort of phenotypic selection of trees bearing sweet acorns has been mentioned by Haws (2004) for Mediterranean oaks (*Quercus suber* L.) as well as by Mason and Nesbitt (2009). These attempts further reinforce the general contention of this review that early human populations contributed to the dispersion of oaks in Europe

Photographers. Title page: Michel Timacheff (*Quercus petraea* (Matt.) Liebl.).

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