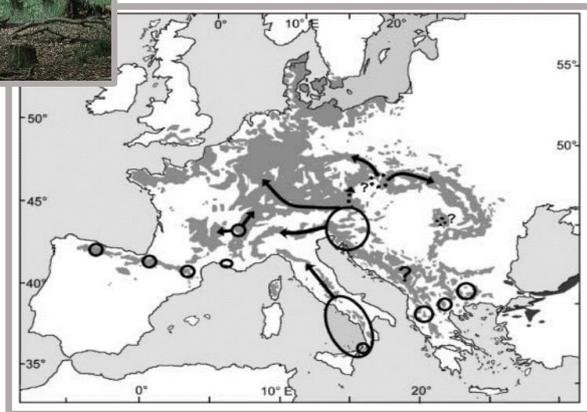
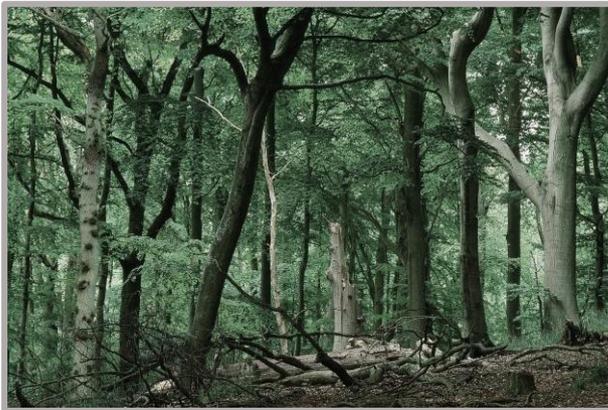


The influence of the autecology of *Fagus sylvatica* on its postglacial spread and population dynamics

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Laymen's summary

The European beech is currently one of the most dominant trees in Central Europe and is of great economic importance. Studies on the historical spread of this species are essential for developing an understanding of its response to climate and land use changes and for making accurate predictions of its future development.

Beech trees prefer a moist but not too wet environment and are sensitive to extreme frost, especially during the spring. Although they are very tolerant to shade, young beech trees seem to need light to actually grow larger.

The European beech survived the last ice age in mountainous areas in Southern Europe and has spread from these areas to Central and Northern Europe. In contrast to other tree species, beech populations did expand immediately when the climate got warmer (~12000 years ago) and beech only became an important tree in central Europe during the mid- Holocene (~5000 years ago) and in northern Europe during the late Holocene (~1500 years ago). Possible causes for this lag and triggers for its expansion have been the subject of many paleoecological studies that use pollen and macrofossils to infer the spread of species and through time. In these studies anthropogenic activities, soil development, disturbance by fire and slow migration rates are named as possible causes for late expansion of the European beech during the Holocene.

From the literature survey that was conducted in this thesis, it is concluded that slow migration as a cause for the late expansion of the beech in the Holocene is unlikely because populations seem to have been present at most locations long before they started to expand. Other factors that were assessed cannot be ruled out as they are either very difficult to untangle from each other or sufficient data is lacking. However, most evidence points to a combination of a favourable climate and anthropogenic disturbance as being sufficient to explain the time of the expansion of beech populations.

A spatial difference that can be noted from literature on the subject is the apparent stronger link to anthropogenic disturbance in Northern European lowlands. This could be an effect of there being more studies sensitive to these local disturbances in this area. Another possible explanation is that most locations that were researched in Central and Southern Europe are mountainous areas and that naturally provide more openings in the forest that are favourable for the growth of young beech trees than lowlands and thus additional disturbance may not be needed. In any case, it seems that both (local) climate and disturbance regime were important for the colonization of sites in Europe by the beech during the Holocene.

Abstract

The European beech, *Fagus sylvatica* is currently a very competitive species with a range that extends from the Cantabrian Mountains to the Carpathians longitudinally and the Balkan mountains latitudinally from Sicily to southern Sweden and Norway. Its current northerly distribution contrasts with its distribution of previous interglacial cycles, possibly indicating the importance of anthropogenic activities for its success. *Fagus* is a shade-tolerant tree and occurs on a wide range of soil types but it is very sensitive to drought and hypoxia, thus it avoids dry or waterlogged soils. Its spread during the Holocene has been a subject of extensive research given its economic importance and possible sensitivity to future climate change.

The pattern of low initial abundance in the pollen record followed by later expansion during the mid-late Holocene at most locations in central and northern Europe has been a subject of debate. The reason for this observed pattern is searched in light of *Fagus*' autecology in this thesis. Possible explanations for this observed pattern that are explored include the influence of changes in the climate during the Holocene, anthropogenic disturbance, changes in fire regimes, post-glacial soil development and genetic adaptation.

From the literature review conducted in this thesis it seems that the late expansion of *Fagus* during the Holocene cannot be explained by a single factor alone. Although anthropogenic disturbance has likely been a major cause of its establishment in northern Europe, this is less obvious for regions of Central, Southern and Eastern Europe, where climate may have been more important. Difficulties in assessing the underlying causes for expansion include the interconnectedness of most parameters and lack of sufficient data, especially for soil development and genetic adaptation throughout the Holocene. Nonetheless, available data strongly implies that favourable habitats have been created by combination of a favourable (intermediate) disturbance regime and sufficient moisture. A favourable disturbance regime, in line with the trees requirements for some light to mature but its competitive advantages in the shade, may be created by natural (fire, storm) or anthropogenic (land use, fire) causes. Sufficient moisture may arise from a favourable climate but also may be compensated for by soil properties.

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Introduction

European beech (*Fagus sylvatica*) is currently characterized by an extensive geographical distribution in Europe occurring longitudinally from the Cantabrian Mountains to the Carpathians and the Balkan mountains and latitudinally from Sicily to southern Sweden and Norway (Magri, 2008). The dominance of beech in especially Central European forests during this current interglacial contrasts with findings obtained from pollen records of past interglacials such as the Holstein and the Eem, where beech only played a minor role in regions north of the Alps (Pott, 1997). Developing an understanding of the drivers behind the spread and expansion of *Fagus* during the current interglacial may help to explain why its current success contrast with previous interglacials but is also of importance for future projections for this taxa as a response to climate change.

Data on the postglacial spread and population dynamics of *Fagus* consist mostly of palynological records and macrofossil finds (Magri et al., 2006). Palynological records from sedimentary environments such as peat bogs and lake beds allow for the assessment of long term vegetation changes as the quantity of pollen that is deposited in the sediment is related to the abundance of the parent plant at the time of deposition (Brewer et al., 2017; Matthias & Giesecke, 2014). The pollen content of these sedimentary cores can be extracted and individual taxa can be identified, counted and visualised by means of site specific pollen diagrams or pollen maps when assessing multiple sites at once (Brewer et al., 2017). From these data, both forest development and the spread and population expansion of individual taxa can be analysed through time.

Pollen data, macrofossil finds, and genetic marker analysis of current populations provide information on possible areas where beech populations survived during the last ice age (Ramil-Rego et al., 2000; Magri et al., 2006; López-Merino et al., 2008; Ruiz-Alonso et al., 2019; Tsipidou et al., 2021). These refuge areas, located mostly in southern Europe, are often humid, sheltered mountainous areas where small beech populations could survive when the climate started deteriorating (Magri et al., 2006). From here, *Fagus* spread out when the climate ameliorated after the Younger Dryas at the start of the Holocene to Central and Northern Europe. Interestingly, while other trees such as *Corylus*, *Quercus*, *Ulmus* and *Tilia* show rapid population growth soon after they have established in the region (Giesecke et al., 2017), *Fagus* pollen curves in Europe are often characterized by a long, regular but often discontinuous tale followed by a rise to high abundance of pollen grains, possibly indicating the occurrence of small, isolated populations before the tree became locally abundant. Therefore, it is suggested that the initial spread of beech during the Holocene occurred at low population densities (Giesecke et al., 2007).

The underlying causes for the late arrival and apparent delayed expansion after initial establishment of the European beech have been a topic of debate (Tinner and Lotter 2006, Giesecke 2007, Bradshaw et al., 2010). While some studies point to anthropogenic disturbance or changes in the fire regime as the main trigger for its expansion (eg. Björkman, 1997; Bradshaw & Lindbladh, 2005; Bradshaw et al., 2010) others are more suggestive of a climatic trigger (Tinner & Lotter, 2006; Valsecchi, 2008). An interesting notion for some of the main theories of the cause for *Fagus*' expansion, namely (anthropogenic) disturbance and fire disturbance (whether or not anthropogenically caused) is that *Fagus* is a tree that can grow

in intense shade, the need for openings in the forest to outcompete other trees therefore seems paradoxical (Bradley et al., 2013).

In this study, the literature on the subject of the postglacial spread and population expansion of *Fagus* will be reviewed to gain insight into the autecology of *Fagus sylvatica*, the pattern of its spread during the Holocene and the apparently paradoxical relation of the need for openings in the forest while its ability to grow in intense shade seems a competitive advantage. The question that will be answered in this regard is: *How has the autecology of Fagus sylvatica shaped its postglacial spread and population dynamics?* An answer to this question will help to understand past forest dynamics and the triggers for expansion of *Fagus* and is relevant for projections of future forest development that will undoubtedly be impacted by intensive land use and climatic change. Therefore, in addition, this type of study is relevant in a practical way for silvicultural practices and forest management strategies in the future.

1. Autecology of the European beech

When assessing the influence of the autecology of a tree species on its spread, several aspects are of importance. Firstly, the range of climatic parameters (temperature, precipitation) and soil parameters in which a species can survive and reproduce must be established. Secondly, the ability of a species to track its potential range as defined by these parameters depends on its ability to spread and thus depends on characteristics of its life cycle, seed production and dispersers. Thirdly, the impact of competition with other (tree) species and requirements for successful establishment are of importance.

1.1 Growth range

Fagus sylvatica is a tall, monoecious tree with a typical lifespan of about 300 years that can occupy a wide range of habitats with different soil types (Ellenberg, 1996). Its growth optimum is in the lower montane belt but it can also form communities on hilly, lowland areas and it forms the climatic treeline of southwestern Central European mountains. Mono-dominant stands are usually formed only in lower to mid-montane belts as its productivity and growth rate decreases more or less continuously with elevation in Central Europe (Leuschner & Ellenberg, 2017).

Beech survives on a wide range of soil PH and hummus types but it is often absent on waterlogged soils since it is very sensitive to hypoxia (Leuschner & Ellenberg, 2017). The tree is characterized by a full crown and a shallow root system, which makes it poorly resistant to strong winds and drought (Weeda, 1985). Drought sensitivity may not only be related to moisture deficits but may also be an effect of drought-related decreases in nitrogen uptake (Gessler et al., 2004). To reduce its sensitivity to drought, *Fagus* forms a ectomycorrhizal symbiosis that results in an improved uptake of water and nutrients, with 100% of mature trees roots being colonized by ectomycorrhizal fungi and 5-10% in young seedlings after two seasons in forest soil (Pena et al., 2013). Severe frosts with temperatures below -20 degrees during the winter as well as late frost may damage beech cambium, make it

more susceptible to fungal infection and lead to misshapen branches and large scale sapling death (Bolte et al., 2007)

In the northern part of its range, in southern Scandinavia, *Fagus* occurs at low elevations down to sea level and is limited in the north by a growing season that is shorter than 140 days. In Southern Europe, beech trees occur at higher elevations up to 2000 m and in humid mountain valleys as drought limits is growth in this region (Magri, 2008). At its eastern limits, lack of mild winters and moist summers are the main reasons that the tree is absent further to the east (Bolte et al., 2007)

It is difficult to establish critical limits for temperature ranges and precipitation as these limits also depend largely on local site conditions (Bolte et al., 2007). A study by Mellert et al. (2018) shows that soil parameters may compensate for climatic incompatibilities with tree requirements. For example, soil water storage may compensate for climate aridity.

1.2 Regeneration

According to Leuschner & Ellenberg (2017) “European beech is a shade-tolerant and shade-producing species that will eventually outcompete all other Central European tree species on soils that are not too dry, too nutrient-rich or too cold.”

However, regeneration time is usually relatively slow. Trees that grow in dense stands may take about 60-80 years to start flowering (Firbas, 1949). In addition, flowering does not occur every year but at irregular intervals of 3-10 years (Övergaard et al., 2007). Masting is thought to be triggered by high radiation temperatures during summer in the preceding year although nitrogen input may also play a role (Övergaard et al., 2007; Müller-Haubold et al. 2015). On poor soils and in colder environments, masting occurs even less frequently. In addition, flowers or fruits are often destroyed by late frosts or summer droughts. Therefore, it may take decades until reproduction occurs in continental areas where these conditions occur frequently (Leuschner & Ellenberg, 2017).

The heavy seeds of *F. sylvatica* trees have been suggested to be dispersed by mallards (*Anas platyrhynchos*), woodpigeon (*Columba palumbus*), Nuthatches (*Sitta europae*), marsh tits (*Poecile palustris*), Jays (*Garrulus glandarius*) nutcrackers (*Nucifraga caryocatactes*) and several rodents and other seed-eating vertebrates. The most effective long distance transport of beech seeds is most likely by jays. However, since jays prefer acorns to beech mast this effective long distance dispersal occurs only when acorns are not available, so when beech and oak mast years do not coincide (Nilsson, 1985).

Production of shade by beech trees occurs by the formation of dense branches that allow only very little amounts of light to reach the forest floor. Because of this, beech forests usually have very little growth of plants in the understory (Weeda, 1985). Research on the spatiotemporal dynamics of beech recruitment shows that that advanced beech recruits can grow to 4 cm diameter at breast height under a closed canopy, but to grow larger, they generally require a significant canopy disturbance (Janík et al., 2016). Regeneration of beech



Figure 1: Beech old growth forest in eastern Slovakia (Leuschner & Ellenberg, 2017)

is thus facilitated by gaps in the forest cover. In natural beech forests these are created by windthrow, smallscale fires or death of single trees due to fungal infection or old age (Leuschner & Ellenberg, 2017). *Fagus*' shallow root system makes the tree susceptible to strong winds, thus uprooting is a common feature of beech-dominated forests (Weeda, 1985). These small-scale disturbance events contribute to forest renewal and favour beech expansion as beech was seen to be most frequent gap-filler after small scale disturbance events (Petritan et al., 2013).

It has been shown that beech trees of all ages lack fire resistance traits although risk of mortality during wildfire increases with increasing fire intensity and decreasing diameter of the tree (Maringer et al., 2016). The frequency and severity of wildfires, however, is lower in beech stands and stands with other deciduous trees that possess leaves with a high moisture content compared to conifer stands, since the high resin content and low hanging branches in conifer trees promote wild fire intensity and frequency (Feurdean et al., 2017).

2. Drivers of postglacial spread and population expansion

Information on spread and population expansion of species comes mostly from palynological records and (to a lesser extent) from macrofossil evidence. These types of data can indicate the presence of taxa during the last glacial at a site, and thus reveal potential starting points of the expansion. Pollen maps, showing when and where *Fagus* established locally or regionally in combination with analysis of genetic markers reveal hints about the direction and timing of the spread. Additional information such as the abundance of microscopic charcoal particles, the presence of taxa indicative of agricultural activities in the local or regional surroundings or the prevailing climate, may provide insight into what triggered the population expansion.

2.1 Glacial refugia and postglacial spread

Locations of the refuge areas of *Fagus sylvatica* during the last glacial are a topic of ongoing debate. An investigation by Magri et al. (2006) based on pollen records and macrofossils suggests several areas as beech refugia's during the last glacial from macrofossil finds and pollen occurrences during the glacial and during the early Holocene. An overview of the current evidence that points to these locations being refugia's for *Fagus* during the glacial is given in figure 2.

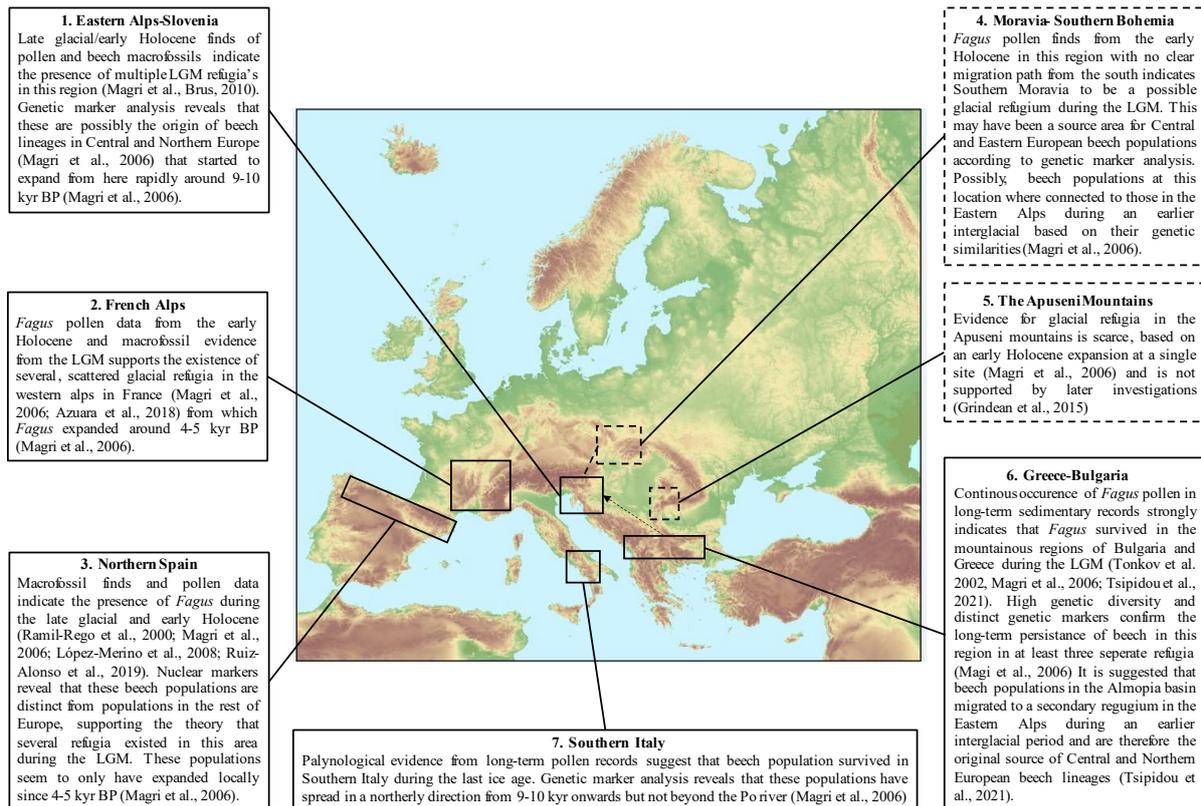


Figure 2: Available evidence for 7 areas that have been suggested to be LGM refugia's for the European beech by Magri et al. (2006). These locations, mostly in southern Europe, consist mostly of humid, sheltered mountainous areas where small beech populations could survive when the climate started deteriorating. The extent of elevation is expressed on the map (source: <https://www.eea.europa.eu/legal/copyright>) in green for lowland areas to brown for mountainous areas.

From these (tentative) locations, *Fagus* must have spread out when the climate started to ameliorate, with beech population showing exponential spread until about 3500 years BP, when growth rates tended towards an equilibrium value (Magri, 2008). The direction of spread from these refugia's as postulated by Magri et al. (2006) is shown in figure 3B. A refuge location that is believed to be the main source area of beech populations in the Italian alps, Northern France and eventually the British isles is located in the Eastern Alps. Possibly, this population could also have expanded southward to the Dineric alps, although evidence for this is lacking (Magri et al., 2006). Analysis of isozymes, chloroplasts and nuclear markers separates several distinct populations in the Balkans and Northern Iberia (Magri, 2008). In a recent paper by Tspidou et al. (2021) it is suggested that the Almopia basin is actually the main source area of postglacial beech lineages in central and northern Europe and that the eastern alps were a secondary refugia that beech populations from the Almopia basin reached during an earlier interglacial.

Not all populations in these refuges areas expanded considerably, as some show only moderate growth in pollen maps. Areas that show rapid expansion include Southern and Central Italy, the Eastern Alps, as depicted in figure 3A. Around 4-5 kyr BP, rapid expansion started from Central Europe. Only Slovenia, the eastern Alps, the French Alps and possibly Moravia are considered important source areas for this expansion. As mentioned, Interestingly, mountain ranges do not seem to form a barrier for the spread of beech during the Holocene, but even facilitated its survival and diffusion. Instead, river valleys and large, continental plains such as the Hungarian plain, the Po valley and the lower Danube valley seem to have acted as geographical barriers for the postglacial spread of beech (Magri et al.,

2006).

Pollen records illustrate an occurrence of small populations of *Fagus sylvatica* in most locations preceding actual population growth by thousands of years, indicating that although beech had spread, it was not yet able to increase its role in forest communities. Findings of wood and other macrofossils during this time at some locations with low pollen percentages confirms that these pollen originate from small populations present at these localities, rather than a long-distance origin (Magri et al., 2006).

Other than the need for available long-term records without hiatuses and good chronological control, identification of refuge areas is hampered when relict beech populations are small. Local presence is often established with pollen threshold values since low pollen percentages may be a result of long-distance influx. However, these threshold values may not always accurately reflect local presence, especially when populations are small. Macrofossil finds that are more indicative of local presence can help. However these finds are scarce thus although macrofossil finds may indicate local presence, the absence of macrofossil finds does not reject local presence (Magri et al., 2006).

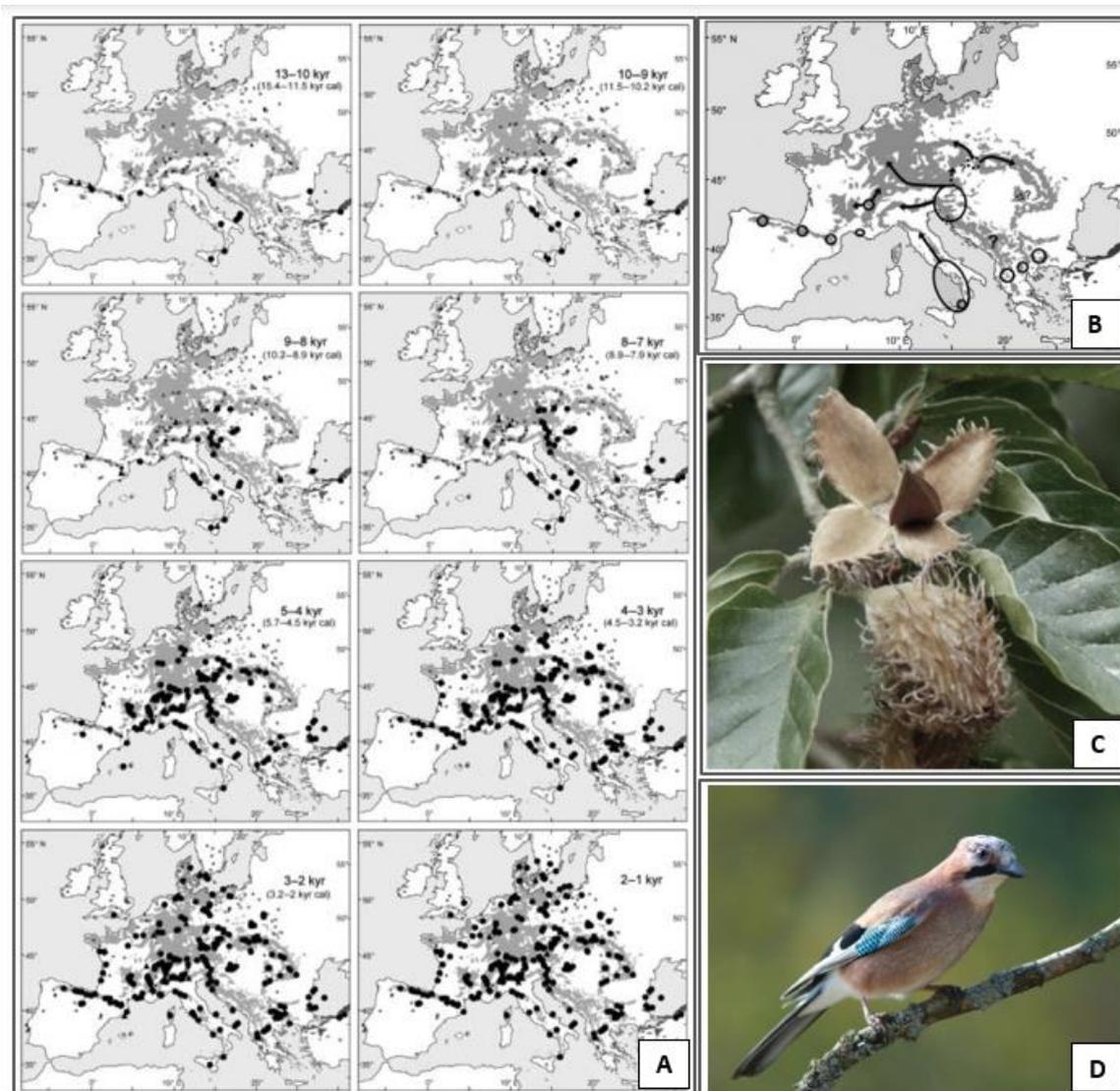


Figure 3: A) Geographical distribution of the late glacial and postglacial records of *Fagus sylvatica* in Europe. The modern beech distribution is depicted by the shaded grey area (Magri et al., 2006); B) Direction of spread for postglacial beech populations. The modern beech distribution is depicted by the shaded grey area (Magri et al., 2006); C) *Fagus sylvatica* fruits. (Photograph by Jason Ingram) D) Eurasian Jay (*Garrulus glandarius*), an important contributor to *Fagus*' long distance dispersal (Photograph by Luc Viatour).

2.2 Migration rate

The spread of *Fagus* during the Holocene and the spread of other (tree) taxa can be regarded in several ways. First, they can be regarded as a direct response to the climatic change that occurred during the transition from the Younger Dryas to the Early Holocene while other possible explanatory factors such as time needed to spread and soil development are regarded of secondary importance (Von Post, 1946). Other authors (Saltré et al., 2013; Svenning et al., 2008) underline the importance of migrational lag and state that species are not able to closely track climate change as their migration speed is limited. This limitation is imposed on migration speed by the time required to produce seed, the number and size of propagules and the frequency of long distance dispersal events (Giesecke et al., 2017).

The use of migrational lag as an explanation for the late postglacial spread of the European beech is often referred to as the migrational lag theory. Although some authors argue against this theory (Tinner & Lotter, 2006; Giesecke et al., 2017) as an important explanatory cause for the late expansion of *Fagus*, others argue this might have been an important contributor to its delayed expansion the Holocene (Saltré et al., 2013). In this regard, it has been postulated that the heavy seeds of the European beech (figure 3C) might impose limits on its migration rate and therefore could explain the late expansion of the beech during the Holocene. However, other taxa like *Quercus* and *Corylus* also possess large heavy seeds and these taxa do not show any lag as their range immediately expanded as the climate ameliorated after the last glacial period. Furthermore, long distance dispersal of beech nut by rivers streams and dispersal agents such as jays (figure 3D) contradict this argument (Bradshaw et al., 2010).

To determine the importance of migrational lag in explaining the late expansion of *Fagus*, several attempts have been made to estimate its migration rate. This rate would give an indication of how well *Fagus* was able to track its growing potential range as a result of the changing climate during the Holocene (Saltré et al., 2013; Giesecke et al., 2017). Calculations of spread rates are based on assumptions on Last Glacial Maximum (LGM) refugia of a species and first establishment in pollen records, where establishment is assumed when pollen percentages reach a certain threshold value (Saltré et al., 2013; Giesecke et al., 2017). The timing of localities reaching pollen percentages for *Fagus* above 2% according to a review of European pollen records by Magri et al. (2006) is shown in figure 3A. Differences in assumptions on both the location of refugia and used threshold values may lead to different results for calculations of the spread rate.

Saltré et al. (2013) estimate a mean migration rate of 270-280 m yr⁻¹ from which they conclude that the Holocene spread of *Fagus* at the north-western leading edge of its distribution was limited by migration. The threshold value used by Saltré et al. (2013) of 2%, as used by Magri et al. 2006 may have been too high, thus leading to an underestimation of local presence and therefore an underestimation of spread rates as Lisitsyna et al (2011) have shown that a less conservative threshold value of 0.5% is more indicative of the local presence of the tree. This is supported by findings of beech macrofossils of beech at sites with a discontinuous tale of pollen values below 2%, indicating local presence of the tree at low pollen percentages (Magri et al., 2006). In contrast, Giesecke et al (2017) estimate a rate of spread of 400 m yr⁻¹ which would indicate that the role of migrational lag was not as important as other factors such as climate change and disturbance events.

Although large uncertainties of spread rate calculations prevent conclusions of possible role of migrational lag in explaining the observed late expansion of *Fagus* during the Holocene, the theory seems unlikely based on other grounds. Most pollen diagrams from Central Europe indicate a presence of the tree in small stands long before populations started to expand (Tinner & Lotter, 2006; Giesecke et al., 2007). In addition, *Fagus* populations expand very late even at some locations that are very likely to have been refugia's during the LGM (Magri et al., 2006).

If populations were present at these locations but expanded much later, not migration lag but other factors must have prevented the tree from expanding at here.

2.3 Soil parameters

The process of soil maturation after glacial periods is thought to impact the ability of plants to colonize new areas of land, resulting in lags of from 500-1500 years in response to climate amelioration (Pennington, 1986). This process is characterized by the development of fertile mature soils from skeletal mineral soils and later impoverishment and acidification during an interglacial. (Iversen, 1958) It is suggested that the impact of soil maturation on the availability of phosphorous has influenced the timing of tree expansion during the Holocene. Since phosphorus leached from early Holocene soil, availability of the nutrient was more limited during the mid-Holocene and thus tree taxa with phosphorous-mining mycorrhiza such as *Fagus*, *Carpinus* and *Picea* may have been favoured during these later stage of forest development (Kunes et al., 2011). Furthermore, since properties such as soil water storage may compensate for climate aridity (Mellert et al., 2018), soil maturation may have been needed for *Fagus* to be able to establish on European soils during the Holocene.

Willis (1994) argues that soil deterioration may have been the most important trigger for beech population expansion in the Balkans at some sites as *Fagus* and other taxa with relatively high tolerances for nutrient poor, acidic soils expanded at the same time. However, other factors such as anthropogenic activities and climatic change seem to have been more important in other sites in the Balkans.

Although soil parameters have may impact beech establishment, assessing their role in beech distribution and expansion during the Holocene is very difficult since detailed data on soil development for particular sites is scarce. In addition, soil parameters are influenced by other factors that possibly trigger beech spread and expansion during the Holocene such as anthropogenic activities and fire regime, making the assessment of causal relations seemingly impossible.

2.4 Climate

Given *Fagus*' sensitivity to drought and late frost, changes in (local) climatic conditions as a trigger for invasion and/or expansion of *Fagus* populations is an obvious possibility. Although the Holocene is generally characterized by a relatively constant mean temperature, reconstructions of precipitation show strong variations. Furthermore, a cooler and wetter climate towards the second half of the Holocene and some distinct climate events such as the 8.2 kyr event, when European temperatures decreased 2-3 degrees for several decades and heat distribution throughout the year become more constant, can be recognized (Tinner & Lotter, 2006, Borzenkova et al., 2015).

8.2 kyr- type events have been attributed as a cause for rising percentages of *Fagus* pollen in Switzerland and southern Germany (Tinner & Lotter, 2006). Similarly, in North-western Iberia, a rise in *Fagus* pollen percentages around 6400 cal BP has been coupled with

higher rainfall levels due to Atlantic influence from the Cantabrian sea and the Foehn effect (López-Merino et al., 2008). *Fagus* expansion as a response to climate changes is also supported by pollen data from a peat bog in the Pirin mountains in Bulgaria Tonkov (2003). Other studies also support a climatic cause for *Fagus* population growth in Italy (Valsecchi et al., 2008) and southeast France (Azuara et al., 2018) but additionally highlight other potentially important causes such as disturbance by fires and anthropogenic presence. In contrast, the lack of regional coherence in the establishment of *Fagus* in southern Sweden indicates that climate was not the limiting factor in its establishment here (Björkman, 1999).

On a broader scale, Giesecke et al. (2007) have tried to simulate the spread of beech using changes in climate parameters during the Holocene based on atmospheric circulation models. From their research, climate could not be established as the main factor influencing *Fagus*' spread. However, due to uncertainties of the model, this could also not be rejected.

Estimating the extent of the impact of the climate on beech spread and population expansion is hampered by difficulties in deriving seasonal distribution of temperature and precipitation from climate proxies, their incorporation in models and difficulties in estimating distribution ranges based on climate parameters alone. Furthermore, since the climate interacts with other factors that could possibly impact *Fagus*' postglacial spread such as anthropogenic activities, soil development and fire regime, its direct effects are not easy to deduce.

2.5 Genetic adaptation

It has been suggested that beech stands are capable of genetic adaptive changes in response to climate change. Microgeographic genetic differentiation of individuals with respect to climate suggests that some populations may adapt to changing temperatures through changes in gene frequency (Jump et al., 2006). In line with these findings, beeches in Greece showed less of an ecophysiological response (Fotelli et al., 2009) than Central European beech populations to similar drought circumstances (Leuzinger et al., 2005, Löw et al., 2006). An experiment comparing the drought response of beech seedlings from the centre of its distribution (Germany) and at the margin of its distribution (Poland), also reveals that marginal beech populations may be better adapted to drought (Rose et al., 2009).

The lag between the initial establishment and population expansion of the European beech may be explained by the time that is required for tree stands to adapt to local conditions, given the ability of beech population to adapt to climate conditions according to several studies. However, lack of genetic data on beech populations throughout the Holocene hampers this theory from being confirmed or disproven.

2.6 Fire frequency

Numerous papers have focussed on the role of fire frequency on the establishment and population expansion of *Fagus*, especially in Scandinavia (eg. Björkman, 1999; Bradshaw et al., 2010; Feurdean et al., 2017). The frequency of fires increases in warm periods due to two main factors. First, since biomass increases in warm periods due to higher forest productivity, higher fuel accumulation drives an increase in the extent of forest fires. Second, longer dry

seasons during warm periods increase the probability of fire occurrence as a result of lightning of human-caused ignitions (Bobek et al., 2018). Furthermore, changes in forest composition can superimpose on this trend as the frequency of forest fires is generally higher in a conifer forest relative to a deciduous forest. Therefore, regional synchronous changes in fire frequency caused by climate as well as local differences can be observed in fire-frequency studies (Feurdean et al., 2017). Other than these natural causes of changes in fire regimes, fires since the mid-Holocene are often related to anthropogenic (agricultural) activities (Tinner et al., 2005).

In the Carpathian mountains, low fire frequency and intensity was reconstructed during the expansion of *Fagus sylvatica* 4800-2800 BP (Feurdean et al., 2017). Seemingly contradictory, fire induced deforestations possibly induced *Fagus* expansion in the Western Carpathians in Poland (Kolaczek et al., 2020) and Norway (Ohlson et al., 2016). These results are in line with other findings from Scandinavia (Bradshaw & Lindbladh 2005; Bradshaw et al., 2010) that generally record establishment of *Fagus* after fire disturbance while the tree is disadvantaged by fire after establishment.

The role of fire for beech establishment and population expansion is suggested by a number of studies, especially in Northern Europe. Beech seedlings may benefit from openings created by small scale fires, but since grown beech trees lack fire-resistance traits they are disadvantaged by fires. On the other hand, beech forests are less prone to fires than most coniferous forests. Therefore fire frequency is expected to be relatively low in beech forests. This implies that less frequent fires *after* beech establishment may be a cause as well as a consequence of beech population expansion.

2.7 Anthropogenic activities

Iversen (1973) has argued that anthropogenic activities were a requirement for *Fagus* to establish, since the dense forest of the Mid-Holocene were difficult to invade otherwise. Anthropogenic activities that contribute to a more open landscape include hunting activities, landuse leading to erosion, altering forest fire regime, (selective) wood logging and the use of leaf fodder.

The practice of collecting leaves and twigs has played a significant role in livestock feeding at least since the Late Neolithic. Different species were used for leaf-hay in different regions. In the Alps *Fraxinus*, *Tilia*, *Corylus* and *Abies* were mostly exploited while exploitation of *Alnus*, *Betula* and *Poplar* was more common in northern Europe and *Ulmus* was widely exploited across Europe. It has been suggested that this may have contributed to the widely observed Elm-decline across Europe (Hejcmanová et al., 2013). Interestingly *Fagus*, *Carpinus* and *Quercus* are considered to have lower forage quality and were thus less exploited than the aforementioned taxa. It is suggested by Hejcmanová et al. (2013) that this difference in leaf fodder quality and the resulting advantage of *Fagus* and *Carpinus* over taxa like *Ulmus*, *Tilia* and *Betula* may have attributed to their increase since the Bronze age.

Grazing pressure by ungulates is demonstrated to create openings in the forest and favours light-demanding species such as *Corylus* as they prevent regeneration of trees in the forest and thus possibly inhibit the succession towards a dominance by shade tolerant species such as *Fagus* (Vera et al., 2006). During the Mesolithic, hunting activities have resulted in declining populations of grazers (Kunes et al., 2011). Given the relation of grazing pressure on forest development, this may have resulted in a shift from a more open forest, to a closed canopy forest although this effect may be more prevalent in river valleys than in upland ecosystems

(Svenning, 2002). However, as previously established, disturbance is required for *Fagus* seedlings to establish so the presence of animals in forests may be essential for establishment and population growth of *Fagus* stands (Björkman, 1999).

Many studies from Northern Europe indicate that *Fagus* established in the area around the time when anthropogenic activities started to shape the landscape (Björkman, 1997; Bradshaw & Lindbladh, 2005; Bradshaw et al., 2010). From these studies it seems that a semi-open cultural landscape favoured beech establishment and therefore, *Fagus* initially benefitted from anthropogenic disturbances of forest. Recent industrial forest use and potash production, however, has been disadvantageous (Bradshaw & Lindbladh, 2005).

Although strong links are suggested between the spread of *Fagus* in Scandinavia and Northern Germany, similar observations were not made throughout its range, possibly because data from high-resolution stand scale sites is not available here. In Hungary, for example, signs of anthropogenic activities were present long before *Fagus* started to spread. In this light, Bradshaw et al. (2010) argue that although human impact may have been important locally, and may have helped *Fagus* from appearance to dominance, it cannot explain its pattern of population expansion on a European scale. A theory that was proposed by Küster (1997) to explain possible differences in triggers for population expansion between mountainous areas in Central Europe and lowlands of Northern Europe is that a higher biodiversity in mountainous areas relative to lowlands naturally leads to a higher occurrence of natural openings in these regions and thus additional disturbance may be less essential for *Fagus* to establish here.

3. Conclusion

In conclusion, *Fagus* has spread out from LGM refugia's when the climate ameliorated. These refugia's consist mostly of humid, sheltered mountainous areas in Southern Europe although not all refugia locations are supported by conclusive evidence. Its spread was further facilitated by these mountainous areas but obstructed by large plains and river valleys. Although *Fagus* expanded rapidly from some of these refugia during the Early Holocene such as in Italy and the Eastern alps, expansion only started thousands of years later in others.

The calculation of spread rates during the Holocene from pollen records during the Holocene is hampered when initial population size is low, and by the uncertainties in the exact locations of LGM refugia's and the direction of spread. Nonetheless the shape of the pollen curves, being characterized by a long, discontinuous tale of pollen occurrence before population expansion that together with macrofossil evidence suggest initial presence of *Fagus* at low population densities, argues against migrational lag as being an explanatory factor for the late expansion of beech during the Holocene.

Comparison of *Fagus* pollen curves to charcoal records, pollen curves of human impact indicator species and sedimentary indicators of regional or local changes point to disturbance by fire and anthropogenic land use triggering beech establishment especially in northern regions. On the other hand, more intensive land use and fires after establishment seems to affect beech populations negatively. Other factors that may have impacted the postglacial spread and delayed population expansion of *Fagus* in Europe include genetic adaptation and soil development. Insufficient data on the development of soils and beech gene pools throughout the Holocene, however, prevent these theories from being supported or disproven.

It appears that *Fagus* can outcompete other trees if the climate is favourable (not too

wet, not too dry) or if this is compensated for by soil properties, and if there is sufficient turnover that generates openings in the forest where seedlings can develop into mature trees but are also at times favoured over other trees by shade. In this sense, a moderate disturbance regime seems favourable for beech trees. Disturbance may be caused by anthropogenic activities but also by a fire regime characterized by small fires with sufficient recovery time in between or by grazing activity. This multifactorial trigger would explain why climate appears to be the trigger for population expansion in some regions (where the climate may already have been favourable) while disturbance seems to be the trigger in others (where sufficient turnover may already be present).

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