Patterns and dynamics of European vegetation change over the last 15000 years

Thomas Giesecke¹, Simon Brewer², Walter Finsinger³, Michelle Leydet⁴, Richard H.W. Bradshaw⁵

1 Department of Palynology and Climate Dynamics, Albrecht-von-Haller-Institute for Plant Sciences, University of Göttingen, Untere Karspüle 2, 37073 Göttingen, Germany

2 Department of Geography, University of Utah, 260 S. Central Campus Drive, Salt Lake City, UT 84119, USA

3 Centre for Bioarcheology and EcologyPalaeoecology, ISEM (UMR 5059 5554 CNRS/UM2/EPHE), Place E. Bataillon, 34095 Montpellier, France

4 IMBE-CNRS, Aix-Marseille Université, IRD, Avignon Université, Technopôle Arbois-Méditerranée, Bât. Villemin – BP 80, F-13545 Aix-en-Provence cedex 04, France

5 School of Environmental Sciences, University of Liverpool, Liverpool L69 7ZT, United Kingdom

Corresponding author:

Thomas Giesecke
E-mail: thomas.giesecke@biologie.uni-goettingen.de
Phone: +49 (0) 551 39 10675
Fax: +49 (0) 551 39 8449

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Abstract

Aim Palaeoecological reconstructions document past vegetation change with estimates of rapid rates of changing species distribution limits that are often not matched by model simulations of climate-driven vegetation dynamics. Genetic surveys of extant plant populations have yielded new insight into continental vegetation histories, challenging traditional interpretations that had been based on pollen data. Our aim is to examine an updated continental pollen data set from Europe in the light of the new ideas about vegetation dynamics emerging from genetic research and vegetation modelling studies.

Location Europe

Methods We use pollen data from the European Pollen Database (EPD) to construct interpolated maps of pollen percentages documenting change in distribution and abundance of major plant genera and the grass family in Europe over the last 15,000 years.

Results Our analyses confirm high rates of postglacial spread with at least 1000 metres per year for Corylus, Ulmus and Alnus and average rates of 400 metres per year for Tilia, Quercus, Fagus and Carpinus. The late Holocene expansions of Picea and Fagus populations in many European regions cannot be explained by migrational lag. Both taxa shift their population centres towards the Atlantic coast suggesting that climate may have played a role in the timing of their expansions. The slowest rates of spread were reconstructed for Abies.

Main conclusions The calculated rates of postglacial plant spread are higher in Europe than those from North America, which may be due to more rapid shifts in climate mediated by the Gulf Stream and westerly winds. Late Holocene anthropogenic land use practices in Europe had major effects on individual taxa, which in combination with climate change contributed to shifts in areas of abundance and dominance. The high rates of spread calculated from the European pollen data are consistent with the common tree species rapidly tracking early Holocene climate change and contribute to the debate on the consequences of global warming for plant distributions.
Keywords: Europe, global warming, migrational lag, pollen, postglacial, spread of trees

Introduction

The pace of human-induced global warming is forecast to rival natural transitions from glacial to interglacial periods (Diffenbaugh & Field, 2013), with considerable consequences for plant distributions and diversity. The ability of plants to spread into new areas remains one of the greatest uncertainties in the debate on the impact of global warming on vegetation (e.g. Svenning & Sandel, 2013). Several studies on the rate of shifting bioclimatic envelopes suggest that plants may not spread fast enough and consequently will be threatened by extinction (Ohlemüller et al., 2006). The spread of plants after the last glaciation can provide guidance in this discussion on possible future change and evidence of past floristic change has been collected in Europe for more than 100 years (e.g von Post 1918). Reid (1899) pointed out that the distance covered by Quercus during postglacial recolonization of the British Isles was too large to be achieved by passive seed dispersal during the time available. Skellam (1951) used this paradox as an illustration for a diffusion model that connected population growth with the rate of spread, confirming the importance of long distance dispersal (LDD) to explain the postglacial spread of plants (Clark et al., 1998). LDD events are more frequent over shorter distances, while exceptional chance events over large distances do occur (Nathan, 2006), but even they need to have limits or there would be no difference between floras of regions with similar climates. The time required for trees and shrubs to produce seed and the number and size of propagules should also impose limits on the rate of spread. Consequently, there should be intrinsic species specific maximum rates of spread determining how fast plants can shift their ranges in response to climate change. Such potential limits for the postglacial spread of plants were already considered a century ago (see discussions in Firbas, 1949) and led to the interpretation that the intrinsic rate of spread and distance from Last Glacial Maximum (LGM) distributions could
explain the sequential appearance of taxa in Europe (Bertsch, 1940). The delayed arrival of a plant to a region with suitable climate was later described as ‘migrational lag’ (e.g. Huntley, 1989). The alternative dynamic equilibrium hypothesis explains the appearance of taxa and their population expansion as direct reactions to climate (von Post 1924; Rudolph, 1930; Godwin, 1975) with lags of less than 1.5 ka (Prentice et al., 1991). Numerous pollen based climate reconstructions during the last 25 years (e.g. Bartlein et al., 2011) have built on the dynamic equilibrium hypothesis. Nevertheless, the migrational lag hypothesis is often cited as the major factor explaining, for example, the late arrival of Fagus and its apparent continued spread to fill its climatic range (Lang, 1994). Svenning & Skov (2004) used species distribution models to show that most European trees had not yet filled their current potential ranges, suggesting that the postglacial northward spread of trees was still active and partly determining current tree distributions and diversity gradients (Svenning et al., 2008; Normand et al., 2011). This emphasises migrational lag as an important factor in past vegetation change and revives the debate about whether intrinsic, species-specific dispersal properties, can explain the sequential appearance and dominance of major trees in Europe. Pollen analysis is a blunt instrument for detecting the first appearance of a plant in a region, however, it is powerful at documenting regional abundance changes of anemophilous trees once they have reached densities larger than perhaps one tree per hectare (Bennett, 1986). Huntley & Birks (1983) mapped pollen data across Europe and using rather high abundance thresholds estimated rates of spread for common European trees with maximum values ranging between 300 and 2000 m yr⁻¹. These high rates of spread were difficult to reconcile with simulations using observed seed dispersal distances that result in much lower rates (e.g. Meier et al., 2012; Feurdean et al., 2013; Snell & Cowling, 2015). High rates of spread are obtained by assuming the spread originated from populations far to the south. Stewart & Lister (2001) suggested that plants may have survived in refugia much further north during the LGM than previously estimated. Willis & Andel (2004) demonstrated that many broadleaved trees occurred in central-eastern Europe just before the LGM, while Tzedakis et al. (2013) discussed that these may not have survived the coldest phase.
advocating for the absence of temperate trees in Europe north of 45°N. The time between the end of the coldest phase of the last glaciation and the onset of the Holocene may have allowed small outposts of temperate trees to establish far to the north of their LGM distributions as was first suggested by Rudolph (1930). Feurdean et al. (2013) considered the duration of the Lateglacial, as well as more northern LGM distributions and assumed that northward spread started in the Lateglacial and ended with arrival of trees at their current or maximum Holocene northern limit. These assumptions led to much lower overall rates of postglacial spread between 60 and 260 m yr⁻¹ and suggested that the earlier rates of Huntley & Birks (1983) could be overestimates.

New insights into the direction and patterns of the postglacial spread of plants have recently come from mapping genetic markers in extant populations (Hu et al. 2009) and these phylogeographic studies are available for most European tree taxa. New independently dated pollen diagrams have also become available with the original count data stored in the European Pollen Database (EPD). Based on these sources of information we revisit the palaeoecological evidence from the European continent, 33 years after the summary by Huntley & Birks (1983). Pollen diagrams are rarely equally spaced across the landscape, but cluster due to the availability of suitable sites for investigation such as lakes and bogs. We therefore construct interpolated maps of the past distribution and abundance of widespread European plant genera and the grass family using pollen data stored in the EPD. The aim of this study is to analyse changes in spatial patterns of plant distribution and abundance during the last 15 kyr and interpret them in the light of the new insights emerging from genetic research and modelling studies. We compare the dynamics and rate of the postglacial spread and abundance changes of the dominant European tree genera. Our analyses provide a basis for comparative studies with vegetation model experiments.
Methods

Study area

We based the construction of interpolated maps on pollen data from the EPD. Sites from beyond the limits of the European continent included in the EPD were ignored for this study. European islands for which no data were publically available in the EPD were also excluded. Pollen data from European Russia are still sparse in the EPD, particularly for the steppe areas in the south. We limited the analysis in the east to a line from the Black to the White Sea to avoid large extrapolations. We used a 0.5° grid with the average elevation of each cell for interpolation within this area.

Data

We used all sites from the publicly available EPD with associated age information based on the calibrated chronologies (Giesecke et al., 2014), of which about 790 are situated within the study area or sufficiently close so that they contributed to the interpolations. All ages are given as calibrated years before present (BP), where 0 BP equals the year 1950 Anno Domini. We selected samples with age uncertainties of less than ±500 years and the minimum “1 star” uncertainty classification, limiting extrapolations to 2000 years beyond the oldest control point (Giesecke et al., 2014). Pollen counts were converted to percentages based on the sum of all terrestrial pollen taxa, excluding pollen from Cyperaceae, other wetland and aquatic flowering plants as well as all fern and moss spores. Samples were collated into consecutive 500-year wide bins centred on full 500-year intervals between 0 and 15 ka. The values were averaged over all samples where more than one sample per site fell within one bin. The available information differs between time slices, due to sample selection and the length and resolution of individual pollen diagrams. Fewer sites are available prior to the Holocene (Giesecke et al., 2014). The resulting dataset has been used for mapping abundance changes at individual sites (Brewer et al., 2016), which may be used for comparison with the interpolated maps.
Long distance transported pollen as well as pollen grains delivered to lakes from eroding older material biases the interpretation of small pollen proportions in terms of the regional occurrence of the parent tree. We applied threshold values (Lisitsyna et al., 2011) to the pollen proportions ($T_{in}$, Table 1) setting values below the threshold to zero prior to interpolation to reduce this bias. The resulting pollen proportions for each time slice were interpolated using the tricube distance-weighting function (Cleveland & Devlin, 1988, Huntley et al., 1989) with a horizontal search limit of 300 km radius and a vertical threshold of 500 m. Horizontal and elevation differences between grid cells and pollen diagrams are used as co-variables, making the procedure well suited for continental interpolations of pollen data (e.g. Williams et al. 2004), with an uneven spatial coverage. It is conceptually simpler than e.g. Universal Kriging and correctly displays outliers. The inclusion of elevation is important as it represents the change of vegetation with altitude, which is done by decreasing the weight of pollen diagrams at high elevations for adjacent grid cells with low elevation and vice versa. This limits the propagation of abundance information from a mountainous area into the neighbouring lowlands. Nevertheless, in the case of the Fagus distribution in the north of the Iberian Peninsula it was necessary to manually restrict the extrapolation towards the south, which was done by introducing pseudo-absences from non-existent sites with 0% Fagus pollen. The resulting interpolations suggest an accuracy that is not inherent in the data. Pollen percentages suffer from the Fagerlind effect (Prentice & Webb, 1986), which arises from species specific pollen production and dispersal in combination with the closure effect of percentages. Therefore, the same pollen percentage at different sites may correspond to different abundances of the parent plants with a different dominant vegetation and/or site characteristics. A reduction of this bias is theoretically possible, however the required parameters of relative pollen productivity are not yet available for all of Europe. Other uncertainties adding to these interpolations stem from the uneven coverage of sites and the underrepresentation of dry environments. In order to acknowledge these uncertainties, we restrict the mapping and subsequent analysis to four abundance classes capturing
the main differences in the abundance of the parent plants (Table 1). The lowest class is designed to
capture the regional presence of the taxon, while the highest abundance class was chosen to
represent the area within which a species is regionally dominant or characteristic. In both cases we
determined the threshold values in comparisons between interpolations of modern samples (1700-
2010 A.D.) with species distribution maps and abundance information. The two remaining
abundance classes were set to intermediate values with class two representing a more conservative
threshold for presence and class three indicating increased abundance. The threshold for presence
used on the interpolated surface (T1) was necessary to restrict distributions in data sparse areas
where sites below and above the initial threshold for presence (T0) were far apart. No presence
threshold was set for Poaceae as taxa of this family are presumed to occur everywhere in Europe
and only changes in abundance through time and space are informative. Pinus and Betula are prolific
pollen producers and their northern limit occurs in a landscape of low total pollen production. It is
therefore impossible to find pollen percentage thresholds that would adequately describe their
northern limits and thresholds were chosen to describe their southern boundaries (Lisitsyna et al.,
2011). As a consequence, rates of spread cannot be obtained for these species based on this
analysis. The results of the interpolations are presented as maps and numeric values for further
analysis and data model comparison in the supplementary information to this publication (PANGAEA
doi when accepted; currently at: http://www.uni-goettingen.de/en/epd-interpolated-
maps/538484.html) logon: epd, password: epd).

Change in area and rate of spread

In all area calculations we adjusted for the latitudinal reduction in area represented by grid cells.
Area calculations of lower abundance classes include higher abundances. The general position of
inferred distributions and abundance classes was compared with the distance to the Mediterranean
and Atlantic coasts by computing the distance for all grid cells and summing all values from grid cells
with the respective abundance class.
We restricted more detailed analysis of the dynamics of spread to the nine common arboreal taxa for which we can confidently estimate the northern distribution limit based on pollen. We limited the study area to north of 47°N latitude, which is outside the location of possible LGM distributions for the analysed tree taxa with the exception of Picea (Tzedakis et al., 2013). For this northern half of Europe, we fitted the logistic function to the increase in the area of presence with time and estimated the inflection point, the point at which the initial exponential increase in area starts to slow. Rates of overall spread and area doubling times were estimated for all abundance classes. We assumed a simple model of reaction diffusion describing the overall rate of spread \( V = 2(kD)^{1/2} \) with \( k \) as the intrinsic rate of population growth and \( D \) as the diffusion coefficient (Birks 1989). The slope of the square root of area increase over time is an estimate of \( (kD)^{1/2} \) and thus \( V \) can be obtained as an overall rate of spread, considering the time from the appearance of a taxon with the respective abundance class, until the time when maximum values were reached. The area-doubling time was estimated as \( \ln(2)/r \) based on a logistic model, where the growth rate \( r \) was determined as the slope of the regression between the decadal logarithm of \( (K-N)/N \) versus time \( t \), with \( N \) as the area at time \( t \), and \( K \) as the carrying capacity set to the maximum area.

We used a more detailed estimate of the possible northern limit of thermophilous trees to estimate the rate of spread at 0.5 ka resolution (Figure 1). This configuration was used as a possible starting point for any spread. The limits were moved north in eastern Europe to avoid large initial dispersal jumps in data poor areas. Prior to calculations, we manually removed the appearance of isolated small occurrences that subsequently declined, while considering disjointed dispersal jumps growing into larger areas and/or higher abundance classes. This resulted in connected areas of distribution as the bases for analysis and this requirement is the reason why higher abundance classes, which often have disjoint areas, were not considered in this analysis. Rates were obtained as the shortest geographic distance between the centres of grid cells marking the distribution limits in two consecutive time slices and dividing the value by 0.5 ka. This yields rates of spread in all directions, however since the analysis was restricted to the area north of the Alps, changes of the southern
limits were not considered. We also computed the distance of the northward shift of the 95th percentile of the distributions, with respect to distance to the Mediterranean Sea, using the initial set of taxa and based on the entire area represented by the maps.

**Difference maps and dynamics of change**

The initial interpolations, before the classifications described above, were used to calculate the difference in pollen proportions between consecutive time slices for each grid cell. The resulting values were classified into four classes of increase and decrease and one class of no change. Thresholds were obtained per taxon as the standard deviations (sd) of all values over all time slices, so that the value of zero was assigned to grid cells with less than one sd difference, while maximum and minimum values of 4 and -4 were assigned to differences larger than four sd. The resulting maps are provided as supplementary information (PANGAEA doi when accepted; currently at: [http://www.uni-goettingen.de/en/epd-interpolated-maps/538484.html](http://www.uni-goettingen.de/en/epd-interpolated-maps/538484.html) logon: epd, password: epd).

To visualize these changes in abundance and distribution, the numeric value (4 to -4) of each class was multiplied by the area represented by grid cells assigned to this class. The resulting values were summed over all grid cells per time slice to obtain an index for the dynamics (area × amount) of change. This was carried out separately for northern and southern Europe with the division at 47°N latitude to compare the dynamics of change between northern and southern Europe through time.

All interpolations and analyses were carried out in R (R Core Team, 2016) using the packages ncdf (Pierce, 2014) and raster (Hijmans, 2015).

**Results and Interpretations**

The Lateglacial vegetation in Europe was dominated by herbaceous vegetation types with abundant Poaceae and Artemisia as well as scrublands with Juniperus and Betula nana and boreal woodlands with Pinus and Betula trees. A continuous forest formed during the Lateglacial with a latitudinal treeline in central Europe (Theuerkauf & Joosten, 2012; Mortensen et al., 2014). The treeline reached a more northerly position to the east of the Baltic Ice Lake (Amon et al., 2014). However,
this treeline formed by the northern limits of *Pinus* and *Betula* is not adequately represented in the maps (see methods) resulting in biases in their Lateglacial distribution. This problem does not occur for *Picea*, which was most likely part of the latitudinal treeline east of the Baltic Ice Lake during the Younger Dryas (Heikkila et al., 2009) and elsewhere during the early Holocene (Giesecke & Bennett, 2004).

The effect of the Bølling-Allerød warming and Younger Dryas cooling can be seen in the area of occurrence and/or abundance of some taxa (e.g. *Artemisia, Juniperus, Ulmus*), although the 500 year-time slices adopted here can only weakly resolve the impact of these climate fluctuations (Fig. 2, Appendix S1.1). The 12 ka time slice represents the situation just before the onset of Holocene warming at 11.7 ka (Rasmussen et al., 2014), however, due to age uncertainty and the 500-year wide sampling window, some initial expansion may already be included. The onset of the Holocene warming sets the clear starting point for the expansion in area and abundance of many temperate woody taxa at the European scale. *Ulmus* and *Corylus* followed by *Quercus* and *Tilia* fill most of their current distribution area within 2 kyr from the onset of the Holocene (Fig. 2). *Fagus* and *Carpinus* represent the other extreme with hardly any response to the onset of the Holocene. They show a gradual increase in area almost until present that only starts after 9 ka. *Picea* and Ericaceae show similar trends of steady increase though the Holocene. *Alnus* and *Abies* show intermittent patterns with distribution expansions that start late, but stop during the mid-Holocene.

The increasing curves for the area of occurrence through time (Fig. 2) follow logistic models of population growth. This becomes particularly clear when limiting the area considered to central and northern Europe north of 47°N latitude (Fig. 3). The inflection point that was estimated for these logistic increases provides a parameter to describe the differences in the time required by the various species to fill their ranges. *Ulmus* and *Corylus* slowed their exponential increase less than 1 ka after the onset of the Holocene at around 11.2 and 11.1 ka respectively. *Tilia* and *Quercus* followed at 10.3 ka and 10.1 ka, while *Alnus* started to spread late but rapidly reached the inflection point.
point at 9.5 ka. *Picea* survived the LGM north of 47°N latitude and its increase in apparent area of occurrence is gradual without a strong sigmoidal shape. Nevertheless, the age for the inflection point of 6.7 ka characterizes well its Holocene expansion in comparison to the other taxa. *Abies* started spreading north of the Alps around 9 ka and slowed its increase in area at around 5.9 ka. *Fagus* and *Carpinus* started to slow their spread at 4.9 ka and 4.8 ka, respectively.

The rate at which distributions shift in space at 0.5 ka time steps yields a range of values as some edges spread faster than others and we presented all values except zeros in boxplots where the width of the box indicates the number of values included (Fig. 4). We also computed the northward movement of the 95-percentile of distributions for the different abundance classes (Appendix S1.7). Both assessments show that the fastest rates of spread were reached during the early Holocene, with the maximum rate for *Ulmus*, with the uppermost quantile (Fig. 4 beyond plot margin) ranging between 3000 and 1600 m yr\(^{-1}\) for the time between 11.5 ka and 11 ka. The 95-percentile also shifted over this time period by about 1000 km for the first and second abundance classes, which converts to a rate of 2000 m yr\(^{-1}\). The northward shift in the distribution of *Ulmus* is concentrated in one 500-year interval, while the rapid spread of *Corylus*, *Tilia* and *Quercus* is stretched out over consecutive time bins, with average values around 400 m yr\(^{-1}\). Nevertheless, the uppermost quantile of the *Corylus* boxplot for 12-11.5 ka ranges between 1300 and 2800 m yr\(^{-1}\) (Fig. 4 beyond plot margin). The late spreading taxa *Fagus* and *Carpinus* start with an initial rapid increase in their distribution area resulting in an apparent rate of spread in the range of 400 m yr\(^{-1}\), while the later spread occurs generally at slower speed and only *Carpinus* shows a sudden increase in higher abundance classes around 2 ka.

The overall rates of spread presented in Fig. 5a assume the rate of spread to be constant through time, which we know was not the case. The highest rate of spread for the entire distribution is estimated for *Alnus* with 1000 m yr\(^{-1}\), while the estimates for most other taxa fall between 600 m yr\(^{-1}\) for *Corylus* and 250 m yr\(^{-1}\) for *Abies* and are thus comparable to the measures of the rate of spread in
Fig. 4. Only the gradual increase in the distribution of *Picea* results in a slow rate of 150 m yr\(^{-1}\). The fastest rate of spread recorded is for the highest abundance class of *Corylus*, caused by the rapid and often synchronous population increase of *Corylus avellana* across large areas of Europe (Giesecke et al., 2011). The logistic growth model used in the calculation of the area doubling time (Fig. 5b) compensates for the saturation phase that reduces the slope in the overall estimate of spread in Fig. 5a. This results in some interesting differences in the rank order, which are most pronounced for *Fagus* and *Carpinus*. The three higher abundance classes in *Carpinus* and the highest abundance class in *Fagus* have doubling times similar to early spreading taxa like *Tilia* and *Ulmus*.

The good agreement between the estimates of overall spread (Fig. 5a) based on different abundance classes is remarkable. Early Holocene rapidly spreading taxa *Alnus, Corylus, Ulmus* and *Tilia* show values above 400 m yr\(^{-1}\) for all abundance classes. *Quercus* takes an intermediate position. Its postglacial spread north starts early, while the expansion at the northern limits in Sweden lasted until about 3 ka (e.g. Giesecke, 2005b). *Picea* clearly is the slowest in its overall dynamics, which is partly due to the fact that this analysis focusses on its Holocene dynamics, while its area of occurrence was already large during the Lateglacial. The tree was likely widespread in Europe during the coldest stages of the last glacial (Ravazzi, 2002; Latalowa & van der Knaap, 2006) and its Lateglacial history remains a focus of study and debate (Birks et al. 2012). The position of *Abies* differs between the panels in Fig. 5, with the overall rate of spread for all abundance classes being similar to *Picea*, while the doubling time for the first abundance class is close to that for *Quercus*.

The obtained doubling times describe the Holocene dynamics of distributions and their use to estimate the size of the LGM distributions by extrapolation may not be appropriate here (Magri 2008). However, they indicate that the taxa must have been widespread in the southern half of Europe during the LGM.

The Holocene vegetation history of Europe provides examples of both population expansions and declines in abundance. The overall area of occurrence contracted along the northern limits of
Corylus, Ulmus, Tilia and Quercus during the last 4 kyr. However, the decline in the area of occurrence is also due to a reduction in abundance below that which can be recognized using the applied percentage thresholds. This is mainly responsible for the strong decline in Tilia (Appendix S1.1), which is most likely influenced by forest clearance for agriculture (Turner 1962, Björse & Bradshaw 1998). The area curves for higher abundance classes document these shifts in the abundance of different species across Europe. The area curves for the highest abundance class show distinct peaks, some of which replace each other and thus characterize the different phases of European vegetation history (Fig. 6; see also Appendix S1.2). The 16 taxa considered here reach their largest area of the highest abundance class in the following order: Poaceae (15 ka), Juniperus-type (15 ka), Artemisia (12 ka), Betula (10.5 ka), Corylus (9.5 ka), Pinus (8.5 ka), Ulmus/Zelkova (7.5 ka), Fraxinus (7.5 ka), Tilia (6.5 ka), Quercus (6 ka), Abies (5.5 ka), Alnus (4 ka), Carpinus (3.5 ka), Fagus (3 ka), Picea (1.5 ka), Ericaceae (0.5 ka). These peaks mark in most cases the culmination of the expansion phase and are succeeded by a period of decline. The abundance of Ulmus and Tilia characterize many European forests between 9 ka and 6 ka. The pattern also clearly depicts the well described decline of Ulmus, which is followed by Tilia, while the area of abundance rises for Fagus and Carpinus. The deforestation of Europe over the last 3.5 kyr is also clearly depicted by the increase in the area for the highest abundance class of Poaceae, with an associated decline in the area for abundant cover of Fagus, Carpinus, Tilia and Quercus. The change in area and abundance for each taxon between two time slices is presented in the difference maps (PANGAEA doi) and these changes, summarized in one index (difference class multiplied by area) are presented in Fig. 7. This comparison shows large symmetry in population expansion and decline between north and south. Some species show more dynamics in the north (Picea) and others in the south (Abies), which is partly due to the centre of their distribution (Fig. 8). The genus Quercus is widespread in northern and southern Europe, while the lack of dynamics in northern Europe, except around 10 ka, is due to its increase and decline at low rates resulting in small differences over 500 year intervals. One would expect populations of temperate tree taxa that
survived the last ice age in southern Europe to begin expansions there. Once populations had grown in the south they would spread north and their expansion would continue there. This pattern is indeed visible for some taxa, in particular for Fraxinus and Abies where southern European dynamics clearly precede northern European changes. However, populations of Tilia and Ulmus expand almost in parallel in the south compared with the north, with a short lead in the south. On the other hand, for Corylus and Alnus the dynamics in the north appear to lead. Fagus populations have their highest rate of increase at the same time in the north and south around 5 ka. The dynamics of declining populations is mirrored for many taxa between north and south. Most symmetry in decline is visible for Corylus, while Ulmus declined earlier in the south compared with the north.

The asymmetry between northern and southern Europe in Fig. 7 already indicates where the main centres of distribution lie. To follow the change of the gravitational centre of the different taxa, we calculated the average distance of grid cells within the different abundance classes to the Mediterranean Sea and Atlantic Ocean (Appendix S1.3, S1.4 and Fig 8). In both cases the average distances for the different abundance classes are near each other for most taxa at most times, indicating that most distributions were symmetrical with higher abundance classes in the centre of the distribution. The abundance is skewed to the north for the boreal taxa Pinus and Betula, with higher abundance classes found successively further north, while the opposite trend is observed for Quercus with a southern affinity (Appendix S1.3). The symmetry of distributions often deteriorated when abundances declined. For example, the decline in the abundance of Corylus after its initial peak around 9.5 ka occurred mainly in the south and east without affecting the distribution area and consequently the gravitational centre of the abundant areas shifted north and west. The curves for Picea are striking. The distance to the Mediterranean describes the tree as a southern species during the early Holocene, when populations mainly expanded in the eastern Alps and Carpathians. In the Carpathians the dominance of Picea at mid-elevation is replaced by Fagus in the second half of the Holocene (Feurdean et al. 2010), while the tree expands in Fennoscandia during that time (Giesecke and Bennett 2004). As a consequence, the mean distance to the Mediterranean shifted for higher
abundance classes from southern dominance, as for *Quercus*, to northern dominance as for *Pinus* and *Betula*. At the same time the average distance to the Atlantic Ocean decreased steadily though the Holocene for all abundance classes. This westward shift was observed and reported for the two *Picea* distributions in central and northern Europe separately and it is interesting to see how both distributions shift simultaneously (van de Knaap et al. 2005, Giesecke and Bennett 2004). The two other latecomers *Fagus* and *Carpinus* follow the same trend, shifting the centres of their distributions from east to west with the general spread of the distribution in the same direction.

While the gravitational centres of distributions shift north together with the northern edges of the populations, the southern distribution limits do not move north with the early Holocene climate warming (Appendix S1.3, S1.4, S1.5, S1.6). *Betula* is the only taxon with a slight northward shift of its southern distribution limit, while higher abundance classes show a strong northward shift of the southern limits (Appendix S1.6).

**Discussion**

**Spread and population expansion**

Our analyses show that the rates of taxa spread slow before current northern distribution limits were reached, which is demonstrated by the logistic fits in Figure 3. This may not just be explained by range filling, but rather be an effect of slowed population growth rates near the northern limits, where growing season warmth often limits seed production. This interpretation is supported by findings of lower population growth at higher altitudes and latitudes (McLeod & MacDonald, 1997; Giesecke, 2005a) indicating a climatic control (Prentice, 1988). It is also consistent with a close link between population growth and rate of spread.

The observation that different abundance classes yield similar overall rates of spread (Fig. 5a) agrees with a simple diffusion model predicting that the speed of the wave can be obtained regardless of
the population threshold applied (Lubina & Levin, 1988). This would suggest that the wave is stable in space and even though the wave ‘front’ cannot be captured by palaeoecological methods (Bennett, 1986), the rate of spread may be obtained from higher abundance classes, where spread is followed by population expansion. A traveling wave of expanding populations has been described for Fagus in North America (Woods & Davis 1989) and Picea in Scandinavia (Giesecke, 2005a) and appears to be the rule rather than the exception, even where spread and population expansion may have been disconnected as in the case of Picea (Giesecke, 2013).

This disconnect is a feature of late expanding taxa and both Picea and Fagus provide some of the best examples for Europe. The mapping of genetic markers in extant Picea populations in Fennoscandia, Russia and the Baltic states documents strong links between the populations in Southern Sweden and in the Baltic states as well as between northern Sweden and northern Russia (Tollefsrud et al., 2008, 2009). Macrofossil evidence of Picea indicates that the tree occurred on the Scandinavian Peninsula soon after deglaciation (Kullman, 2008). On the other hand, pollen data documenting the time of population expansion shows a clear wave of expanding populations traveling northwest from southern Finland, crossing the northern extent of the Baltic Sea and then turning southwest into southern Sweden (Giesecke and Bennett 2004). Thus it seems that the expansion of populations, documented by rising pollen proportions, occurred independently of and in a different pattern to the initial spread of the species. The existence of a Picea haplotype occurring only on the Scandinavian Peninsula (Parducci et al., 2012) further complicates the matter. In any case, the initial spread, which left a genetic imprint in populations and the later population expansion are decoupled.

Fagus genetic markers in extant populations have also yielded new insights into the understanding of its postglacial history. They confirm earlier claims (e.g. Pott, 2000) that Fagus survived the LGM on the Iberian Peninsula (Magri et al., 2006) and possibly also in south-western France (de Lafontaine et al. 2013), yet these areas contributed little to the postglacial colonization of Europe. Similarly, the
populations on the Apennine and Balkan peninsulas did not contribute to the postglacial spread of
the tree. Central and north western Europe are dominated by a single chloroplast haplotype, which
is in sharp contrast with the high diversity of the southern edge of the distribution in northern
Greece, where eight different chloroplast haplotypes are present on a small solitary mountain
(Papageorgiou et al., 2014). The simulations by Saltré et al. (2013) illustrate how the expansion from
a more northerly population may block the northward spread from populations in the south.
However, the dynamics of postglacial population expansion as depicted in the maps compiled here
show that the Fagus populations on the Balkan and Iberian Peninsulas remained small until the mid-
Holocene and grew in parallel with the populations in central Europe (Fig. 7; Giesecke et al., 2007).
Thus the LGM distribution of the tree does not inform on the time of population expansion in central
and north-western Europe as has often been postulated (e.g. Lang 1994). Using the proposed LGM
distributions as starting points to simulate the postglacial spread of Fagus as well as Picea (Saltré et
al. 2013, Lehsten et al. 2014) does therefore not help develop understanding of the postglacial
history of either species. In both cases similarities between simulated and reconstructed patterns
may be accidental and although we have not yet understood why these two species spread late, the
observations summarized here do not indicate that the time of population expansion can be
explained by migrational lag. Vegetation models that can describe the spread of plants
mechanistically are useful as they can test the importance of particular components like internal
variability (Nabel et al., 2013), but the models need further improvement before they can provide
convincing estimates of the consequence of global warming for vegetation (Snell et al., 2014). The
patterns and rates presented here can be used to test these models, but care is needed in the
selection of suitable taxa. Without a better understanding of early Holocene limitations for Picea and
Fagus Modelling the postglacial colonisation of Europe may be useful for Quercus, but is of less
value for Picea and Fagus without a better understanding of their early Holocene controls. Genetic
markers in Quercus document that many different populations from around the Mediterranean
Basin have spread north with postglacial warming (Petit et al., 2002), yet these different immigration
routes find no reflection in a differentiated time of initial population expansion (Brewer et al., 2002, Giesecke 2016). High resolution mapping of haplotypes in extant white oak populations in western France highlights the importance of frequent LDD events, which could explain the observed patchwork of distinct haplotypes of chloroplast DNA markers (Petit et al. 1997, Bialozyt et al. 2006).

Simulations using this example also link the frequency of LDD to population density (Bialozyt et al. 2006).

Notes on postglacial history and apparent rates of spread for common European trees

The highest apparent rates of postglacial spread in Europe are found for Ulmus and Corylus, ignoring Pinus and Betula. Corylus has a short generation time of only 10 years. Ulmus needs more years to set seed (30-40), while its light seeds may be easily picked up by strong winds and transported over long distances. In northern Europe we have to consider three different species of Ulmus that may have contributed to the rapid spread of the genus. It is conceivable that the early Holocene spread in central and northern Europe started for both Ulmus and Corylus from outposts north of the Alps, although this presumption is currently not supported by evidence (Giesecke, 2016). Pollen proportions indicative of the regional presence of both taxa appear within a few hundred years after the onset of the Holocene in Scandinavian pollen diagrams and the taxa may even have been part of the initial colonization of bare ground after the retreat of the ice in north central Sweden during the early Holocene (e.g. Giesecke, 2005b). Thus rates of spread for these two taxa in the order of 1000 m yr\(^{-1}\) do seem likely. However, the rapid expansion of Corylus around 10.5 ka is probably not a consequence of its spread. The timing of this expansion is similar for populations in south and central Europe (Giesecke et al., 2011) regardless of the time the species arrived at the site. This would suggest at least partial climatic control of the final expansion of Corylus and the high apparent rate of spread for the highest abundance class in Fig. 5a is consequently not informative with respect to the rate of spread.
Tilia cordata and Tilia platyphyllos are the most widespread species of the genus in Europe. T. platyphyllos-type can be separated morphologically (Beug, 2004), but this has not been applied consistently and we therefore combined identifications to the genus level. Tilia spreads quickly in central Europe favoured by a short generation time (10-30 years) and wind dispersed seeds, although its rate of spread slows down towards its northern distribution limits. The control of summer temperature and growing season length on seed maturation in Tilia cordata has been well documented (Pigott & Huntley, 1981; Pigott, 1981) and these climatic factors may have slowed the rate of population growth near its northern limits. While the maximum rate of spread is lower than for Corylus and Ulmus, the average rates are similar. Huntley & Birks (1983) and Birks (1989) report 500 m yr⁻¹ as the fastest observed rate, which agrees with our average values. The current evidence gives no reason to reduce the early Holocene rates of spread below this value.

The deciduous Quercus species in Europe share the same chloroplast haplotypes through hybridization. Moreover, Petit et al. (2004) suggest that Quercus petraea spreads by pollen dispersal through hybridization with Quercus robur, whose acorns are preferred by jays and thus dispersed over long distances. Quercus pollen disperse well so that it is difficult to distinguish between presence and absence based on pollen proportions (Lisitsyna et al. 2011) and the pollen type is found in small abundances in sediments of Lateglacial and early Holocene age over much of Europe. Macrofossil finds are rare and the first definite evidence for the occurrence of Quercus north of the Alps is the base of the oak dendrochronology, with the oldest ring dated to 10,430 cal. BP (Friedrich et al., 2004). Of all taxa with a clear early Holocene spread in northern Europe, Quercus needs the longest time to reach maturity (30-60 years), which explains the slowly increasing pollen values at individual sites. The curves rise faster in the west which give a visual impression of an eastward direction of spread, but genetic evidence documents the parallel south to north spread of Quercus populations (Petit et al., 2002). Quercus populations had already expanded during the warm phases of the Lateglacial south and west of the Alps (Finsinger et al., 2006, 2011). Although there is no evidence documenting its Lateglacial occurrence north of the Alps, small outposts might have
become established and survived the Younger Dryas (Giesecke, 2016). The slow rates of population
growth in eastern Europe and near the northern borders reduce the overall rate of spread. Even if
we assume that outposts were present in central Europe before the onset of the Holocene,
spreading rates of the order of 500 m yr\(^{-1}\) need to be considered to explain all patterns, including the
British Isles (Birks, 1989).

Three *Alnus* species are included in the genus analysed here. Although, pollen of *A. viridis* can be
separated (Beug, 2004), this differentiation has not been consistently made. The differentiation
between *Alnus incana* and *Alnus glutinosa* is more difficult and only rarely attempted (e.g. Bos et al.,
2012). *Alnus viridis* is a shrub occurring mainly in the upper montane forest in central and southern
Europe including the Alps, the Carpathians and Corsica. It is missing in Scandinavia, while it has
occurrences in northern Russia. *A. incana* has an eastern and montane distribution including most of
Scandinavia and the Alps, but is absent in the west. *A. glutinosa* has the widest distribution in
Europe, while it does not grow as far north as *A. incana* in Scandinavia. The current distribution of *A.
incana* and *A. viridis* would suggest that these species may have occurred in central Europe during
the LGM and Lateglacial and pollen of *A. viridis* is occasionally identified in Lateglacial sediments
from central Europe (e.g. Wolters, 1999). However, *Alnus* pollen is abundant in older sediments and
enters basins with catchment erosion during the Lateglacial. Consequently, information on the
Lateglacial occurrence of *A. incana* and *A. glutinosa* is often difficult to interpret (Douda et al., 2014).
The identification of *A. incana* fruits in early Holocene sediments from the western Netherlands
dating to around 11400 cal. BP (Bos et al., 2005) is most interesting as the location is west of the
current distribution of *A. incana* and the timing is prior to the general increase of the pollen type.
Pollen morphological identifications also indicate the occurrence of *A. incana* in the northern Upper
Rhine Graben during the early Holocene (Bos et al., 2012). We chose a rather high threshold for
mapping the presence of *Alnus* to avoid the inclusion of redeposited pollen, inevitably ignoring this
early Holocene history. The threshold captures the establishment of *A. glutinosa* near the site and
the data may therefore primarily represent the expansion of this species. In eastern Europe the data
depict a clear east to west direction of spread. Around the Baltic Sea basin, the spread culminated in a rapid expansion, which occurred synchronously over a large region (Giesecke et al. 2011). At least in northern Scandinavia the spread and expansion of *A. glutinosa* occurred together with *A. incana* (Giesecke, 2005c). Further west, the expansion is regionally asynchronous with a gradual or rapid increase and may be described as patchy and erratic, particularly for the British Isles (Bennett and Birks 1990). Thus there is a sharp contrast in the behaviour of *A. glutinosa* between eastern and western Europe. The delay in initial population expansion of approximately 1500 years after the onset of the Holocene is difficult to explain. *Alnus* fruits, especially *A. glutinosa*, are well adapted to dispersal by water and with many European rivers having a south to north direction, fruits could traverse central Europe in weeks rather than millennia. The high overall rates of spread and area doubling time show this, placing *Alnus* in a group with *Corylus* and *Ulmus* with respect to realized rates of spread. Huntley and Birks (1983) also consider *Alnus* to be the fastest spreading taxon, while the estimate of only 100-250 m yr$^{-1}$ by Feurdean et al. (2013) disagrees with the rapid spread and expansion in Scandinavia.

The genus *Abies* includes several species in Europe with distributions in the Mediterranean of which only *Abies alba* occurs north of the Alps. *Abies sibirica* grows in Russia outside the area considered here, while occasional finds of *Abies* pollen in northern Russia and Fennoscandia may originate from this species. *Abies* pollen is found in diagrams from the Mediterranean during the Lateglacial and clearly spreads in the northern Apennines during that time, from where it expanded rapidly with the onset of the Holocene (Vescovi et al., 2010). The comparison of pollen diagrams from the Alps by van der Knaap et al. (2005) gives the impression that the tree crossed the mountains. Tinner & Lotter (2006) find this to be a conceivable scenario. The EPD point maps (Brewer et al., 2016) document that population expansion occurred earlier in the western compared to the northern Alps, suggesting that the tree may also have spread along the western flanks of the mountains. The onset of rising *Abies* curves north of the Alps dates to 8.5 ka and 8.2 ka and the climatic disturbance of the 8.2 event may have favoured this initial expansion (Tinner & Lotter, 2006). Apart from the more
rap expansion in the western Alps between 9 ka and 8.5 ka, the spread of Abies in central Europe occurs at low rates of around 100 m yr$^{-1}$ (Fig. 4). The overall estimate of spread (Fig. 5) for the different abundance classes yields around 200 m yr$^{-1}$ and agrees with Huntley and Birks (1983) as well as Feurdean et al. (2013). Abies did not spread far north of possible LGM distributions and no accounts of large dispersal jumps have so far been published, so this may be an example of a slow rate of spread. Tinner et al. (2013) argue that the spread of Abies was suppressed by human activity over the past 5 kyr, explaining the observed slower rate of spread and incomplete range filling.

The analysis for the genus Carpinus represents primarily Carpinus betulus, as its pollen can be separated from Carpinus orientalis, which occurs on the Apennine and Balkan Peninsulas. C. betulus is widespread in Europe, but absent from the Iberian Peninsula (Jalas & Suominen, 1972-1999). However, Carpinus pollen is present in Holocene pollen diagrams from the Iberian Peninsula attesting its former occurrence and recent decline (Abel-Schaad et al., 2014). Although, it is generally assumed that the tree did not survive the LGM on the Iberian Peninsula the absence of evidence is not firm evidence for absence. The fluctuating values of the pollen type in pollen diagrams from Spain and France result in erratic appearances and disappearances of distributions in these regions. The patterns are different in eastern Europe where populations built up in the south during the middle Holocene, then spread north around 6.5 ka and west at 4.5 ka, marking two periods of apparent rapid spread (Fig. 4). The long tails of Carpinus pollen curves in most central European pollen diagrams indicate that initial immigration and later population expansion were disconnected. The late Holocene expansion was most impressive in Poland, where the tree reached dominance in some areas around 3.5 ka. This expansion, and particularly later declines and renewed expansions often coincide with settlement phases at individual sites and the late Holocene history of the tree in the northern lowlands of central Europe is strongly connected to human activity (Ralska-Jasiewiczowa et al., 2003). Any rate of spread for this tree with wind dispersed seeds and a reproductive age of about 30 years is therefore tentative, but the estimates by Feurdean et al.
(2013) of less than 150 m yr\(^{-1}\) are surely too low and the overall estimates in Fig. 5 of 350-450 m yr\(^{-1}\) for the first two abundance classes may be more robust.

The data for *Fagus* mainly represent the single species *Fagus sylvatica*. While *Fagus orientalis* pollen cannot be separated, this species only occurs in the Balkans where it hybridizes with *F. sylvatica*. As described above, mapping of genetic markers in extant populations confirmed the LGM survival of the tree around the Mediterranean. Pollen diagrams document how central Italian populations expanded during the Lateglacial, while we know from genetic studies that this expansion did not lead to a spread out of the Iberian Peninsula (Magri et al., 2006). By around 8 ka the tree had spread north of the Alps (Tinner & Lotter, 2006) and this may be the best region and time to estimate spreading rates for this tree, as later expansions in central and northern Europe are often connected with human activity (Giesecke et al., 2007). The average rate of spread of 400 m yr\(^{-1}\) for this time may be a guide. However, the overall Holocene estimate of at least 300 m yr\(^{-1}\) from Fig. 5 is still twice the maximum rate from Feurdean et al. (2013). *F. sylvatica* produces seed at an age of about 50 years, partly explaining the slow population growth rates and comparably low spreading rates.

After its initial appearance north of the Alps, the further spread of the tree slowed as documented in Fig. 4. As with *Carpinus*, many central European pollen diagrams show a long tail of *Fagus* pollen before its final expansion that is often connected to human activity in the northern lowlands of central Europe as well as in Scandinavia (Ralska-Jasiewiczowa et al., 2003; Bradshaw & Lindbladh, 2005; Bradley et al., 2013). The population dynamics of *Fagus* in the Balkans parallels some of the central European patterns with initial expansion around 8.5 ka and a further expansion after 5 ka, which is also seen in the Carpathians. However, in these regions the dynamics of *Fagus* expansion seem unrelated to human activity. *Fagus* persisted during the LGM on the northern Iberian Peninsula, while populations generally only expanded during the late Holocene with an east to west gradient in timing and abundance. Human activity may have led to a further expansion at some Iberian sites, although it cannot explain the overall regional patterns (López-Merino et al., 2008, Muñoz Sobrino et al., 2009). Thus the postglacial history of *Fagus* across Europe is complex with different drivers.
operating at different times in different regions. A slow spread of the species may only be one factor with a contribution in some regions and cannot explain the patterns on the European scale.

The postglacial history of *Picea* has probably received the most attention of all the European trees. We can link the pollen type primarily to the single species of *Picea abies* since *Picea omorika*, with the same pollen type, is restricted to a small area in eastern Bosnia and Herzegovina and western Serbia. *Picea obovata* is restricted to Siberia as documented by genetic evidence (Tollefsrud et al. 2015). Hybridization with *P. abies* occurs mainly around the Urals, but gene flow via pollen can be detected as far west as Scandinavia (Tsudea et al. 2016). *Picea*’s winged seeds can disperse over large distances and claims that the tree established on mountaintops in Scandinavia as early as the Lateglacial (Kullman, 2008) imply effective LDD that is in sharp contrast to the slow spread of denser populations. Unlike *Fagus* and *Carpinus*, its late Holocene expansion in southern Scandinavia cannot be linked to human activity (Bradshaw & Lindbladh 2005, Giesecke, 2004). Of all the late expanding species, it shows the clearest trend of an east-west shift in the centre of its distribution and since this cannot be explained by slow migration or human impact, we suggest that climate is a good candidate explaining its Holocene vegetation history.

Comparisons between Europe and North America

Estimated rates of postglacial spread of woody taxa in eastern North America are nearly always lower compared to the rates discussed here, regardless of the method used to obtain them. Davis (1976) published the first rates of spread based on independently dated pollen diagrams and used the increase in pollen accumulation rates as indication for the local arrival of a taxon. Based on a limited set of sites, she obtained rates between 350-500 m yr^{-1} for *Pinus banksiana/resinosa* and 100 m yr^{-1} for *Castanea* (Davis, 1976). Delcourt & Delcourt (1987) used a modern dataset to interpret the regional arrival of a taxon to produce isochrone maps and evaluate the spread of woody plants along five different north-south tracks. They obtained average rates of spread between 287 m yr^{-1} for *Salix*...
70 m yr\(^{-1}\) for *Nyssa*, including individual maximal dispersal jumps of 1044 m yr\(^{-1}\) for *Tsuga* and 753 m yr\(^{-1}\) for *Tilia*. Highest rates of spread were observed for the Lateglacial between 17 ka and 13.8 ka and thus much earlier compared to Europe, although also at lower latitudes. Ritchie and MacDonald (1986) presented a study with the highest rates of spread in North America namely for the spread of *Picea glauca* from south-central Alberta to the Mackenzie Delta with rates of 2000 m yr\(^{-1}\), while they reported rates of 2-300 m yr\(^{-1}\) in other regions. The apparently high rates in the western interior may, however, result from an eastward spread of populations that survived the ice age in Alaska (Anderson et al., 2006). Ordonez & Williams (2013) used well-dated pollen diagrams to model past species distributions using simulated past climate. Core distributions moved northwards at maximal mean velocities of 188 m yr\(^{-1}\) for *Abies* and 153 m yr\(^{-1}\) for *Alnus* during 12-10 ka and shifts of the southern boundaries occurred at similar or even higher rates. In Europe, the position of most rear-edge distributions has not changed significantly during the last 15 kyr, except perhaps for *Betula* which declined in abundance at its southern distribution limits in Italy during the early Holocene (Magri et al., 2015). All other boreal and temperate trees and shrubs remain present in southern European mountains. *Pinus sylvestris* for example dominates the northern boreal forest in Scandinavia and grows at or near the tree-line on mountains in Spain, Greece and northern Italy. Bennett et al. (1991) speculate that the southern edge of the distributions of the European woody flora was maintained in these southern European mountains through glacial-interglacial cycles. It may also be argued for North America that the southern distribution limits for temperate species have not significantly moved north (Bennett et al. 1991), however here temperate trees may have survived close to the ice margin that extended much further south (McLachlan et al., 2005). Consequently, studies estimating rates of postglacial spread in eastern North America have considered a wide latitudinal range where the trees in question may have occurred during the LGM. In this analysis we have focused on rates of spread north of 45°N in Europe, which in eastern North America corresponds to north of the Canadian border. The northern limits of several temperate species in Europe reach 60°N, and these high northern limits are due to the Gulf Stream pumping
heat to high latitudes and the westerly winds pushing it into the continent. As a consequence,
January isotherms in Europe have a strong N-S component while they run predominantly east west
in eastern North America. The prevailing westerlies would also propagate rapid shifts in sea surface
temperature in the north Atlantic connected to the mode of the North Atlantic Deep Water
formation, such as its “off” mode during the Younger Dryas (Rahmstorf, 2002). Compared to eastern
North America, the rate of climate change with the onset of the Holocene was therefore most likely
much higher in Europe with highest rates near the Atlantic coast (Heiri et al., 2014). Higher rates of
climatic changes in Europe might explain the comparably faster apparent rates of spread and higher
rates of vegetation change. The slower meltdown of the larger Laurentide ice sheet may have set a
slower pace for North American climate and vegetation change during the Lateglacial and early
Holocene (Shuman et al., 2002). However, Delcourt & Delcourt (1987) note that in eastern North
America the spread of trees along the Atlantic coast was initially delayed and subsequently achieved
the highest rates.

Human influence has rarely been discussed in the spreading of tree taxa in North America, although
humans were present in the postglacial landscape and probably influenced fire regimes and
cultivated crops by 3.8 ka (Smith & Yarnell, 2009). Indians may have affected regional distribution
limits of fire-sensitive hardwoods at the prairie-forest transition zone for a long time (Grimm, 1984).
By contrast in Europe, there has been considerable discussion about potential human impact on the
distribution and abundance change of several trees, particularly Abies (Tinner et al., 2013), Carpinus
(Ralska-Jasiewiczowa et al., 2003), Fagus (Küster, 1997) and Tilia (Turner, 1962). The effect of
humans on European vegetation was particularly pronounced during the second half of the
Holocene (Molinari et al. 2013) and the conversion of forest to agricultural land is clearly visible in
the increase of area dominated by grasses since 4 ka (Fig. 6). The late Holocene spread of Fagus in
northern Europe has almost certainly been catalysed by anthropogenic activities (Bradshaw, 2004)
which cannot be separated from a potential response to climate and we may never know for certain
if the tree would have been able to reach its current northern limits in Sweden, western Norway,
Scotland and Ireland without human assistance. Genetic markers have provided supporting evidence for likely human translocation of trees such as *Castanea sativa* and *Pinus pinea*, whose Mediterranean distributions lack normal genetic structure (Fineschi et al., 2000, Vendramin et al., 2008) and whose ranges have been significantly increased through millennia of cultivation (Conedera, 2004). Two types of dynamic possibly mediated by human activities emerge from our analyses. Firstly, disturbance-mediated population increases, either short-lived as seen with *Carpinus* in north-eastern Europe (Ralska-Jasiewiczowa et al., 2003) or more sustained as shown by *Fagus* in northern Europe (Giesecke et al., 2007). Secondly declines in abundance that are not necessarily linked to range contractions, best demonstrated for *Tilia* population declines in connection with forest clearance for agriculture (Turner, 1962), but also described for *Abies* linked to domestic grazing and use of fire (Tinner et al., 2013). Human activities have therefore had a far greater influence on taxon spread and distributional limits in the Holocene of Europe than in North America, yet the pollen record for forest trees has been dominated by natural population dynamics until recent centuries (Bradshaw, 2004). Today very little ‘natural’ forest remains and the current population size of European trees is largely an outcome of recent land-use (Bradshaw *et al.*, 2015).

**Explanations for Holocene shifts in tree abundance**

The vegetation cover of Europe has changed profoundly over the course of the Holocene with changing dominance of different woody taxa. Their time of dominance corresponds to their time of spread, but it was probably not the species specific rate of spread that determined the time of dominance in most cases. The late-arriving species *Fagus* and *Carpinus* do not show a constant slow spread northward that would explain their late arrival at their northern limits. The expansion of *Fagus* populations in the Balkan and Iberian peninsulas, where the species occurred during the LGM, was as late as in central Europe where the tree was previously absent. *Picea* presumably reached mountain tops in Scandinavia during the Lateglacial and early Holocene, but populations did not expand until at least 5 ka later. Thus the late expansion of particularly *Fagus, Carpinus* and *Picea*
cannot be explained by “migrational lag”, while a number of taxa that have not filled their potential
distribution and are restricted to southern Europe (Svenning et al., 2008) show a “lack of migration”.

The glacial/interglacial cycle first proposed by Iversen (1958) may have some power explaining the
late expansion of some trees (Birks & Birks, 2004, Kuneš et al., 2011). Glacials reset soil formation
particularly in high latitude areas and the young soils gradually leach phosphorus (Boyle et al., 2013).

Thus while phosphorus may be readily available in young soils during the initial phase of an
interglacial, with time this nutrient becomes increasingly limiting to plant growth. Kuneš et al. (2011)
suggest that plants with phosphorus -mining ectomycorrhiza would therefore be favoured during
the later stages of interglacials and lists Fagus, Capinus and Picea among those. The constant
increase in area with various abundance classes of Ericaceae pollen over the last 8 kyr also attests to
gradual changes in soils, namely paludification increasing the amount of peatland as well as
podsolization reducing soil fertility. However, Corylus also possesses ectomycorrhiza and decreases
in abundance particularly in more continental areas during the second half of the Holocene, which is
unlikely to simply be due to the species being out-shadowed by the expansion of Fagus. There is a
simultaneous westward shift of Picea towards the Atlantic coast. Corylus benefits from mild winters
while they seem to limit the natural distribution of Picea in Europe. Thus a decline of Corylus in more
continental areas and a spread of Picea towards more oceanic regions may be interpreted as caused
by decreasing winter temperatures in continental areas due to a reduction in the strength of the
westerly winds (Giesecke et al., 2008).

Thus while migrational lag has little power to explain the shifts in Holocene plant abundance, the
combination of climate and soil changes may explain some patterns. Seed dispersal and population
growth rates and other plant traits were surely important in shaping the early Holocene dynamics,
but cannot explain many patterns.
Conclusions

Postglacial vegetation change in Europe exhibits high rates of change with apparent rates of spread being at least twice as high as in Eastern North America. The initial estimates of apparent spreading rates for Europe by Huntley & Birks (1983) were confirmed by this analysis. How much of the high apparent rates during the early Holocene are due to a Lateglacial establishments of outpost populations is difficult to assess. However, thermophilous species were most certainly absent from southern Scandinavia during the Lateglacial and their early appearance after the onset of the Holocene calls for high rates of spread in the order of 500 m yr\(^{-1}\) or more. Nevertheless, some of these rates may have been achieved in the absence of competition as the temperatures rose so quickly that a formerly treeless landscape became climatically suitable for the growth of thermophilous trees within a few hundred years.

The late population expansion of some taxa, in particular Fagus and Picea cannot be explained by a slow spread from their LGM distributions. Finding the true reasons for the late expansion of their populations may help understand why some species did not significantly spread north from their LGM distributions. While data-model comparisons are providing important insights to understand processes of past vegetation dynamics, using the taxa with late population expansions in model comparisons using simulations of their spread may not add to our understanding. Comparing past realised rates of vegetation change between North America and Europe suggests that the realised change in vegetation may be determined by the rate of climate change, indicating that Europe’s vegetation history was little influenced by intrinsic rates of spread.

Acknowledgements

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References


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DATA ACCESSIBILITY

All pollen data used for the maps are available from the European Pollen Database (EPD; [http://www.europeanpollendatabase.net/](http://www.europeanpollendatabase.net/)). The maps generated for this study are available as PDFs as well as numerical values from the Pangaea database: [http://doi.pangaea.de/PANGAEA when accepted and can be currently viewed at: [http://www.uni-goettingen.de/en/epd-interpolated-maps/538484.html](http://www.uni-goettingen.de/en/epd-interpolated-maps/538484.html)] logon: epd, password: epd.
Supporting Information
Additional Supporting Information may be found in the online version of this article:

Appendix S1 Additional Figures.

Biosketches
Thomas Giesecke is a palaeoecologist interested in ecosystem dynamics on scales from decades to glacial interglacial cycles, trying to tease apart internal vegetation drivers such as plant spread from external forcing like climate change. Together with M.L., S.B., W.F. and R.B. he is working with the EPD aiming to increase its usefulness as a resource for the immediate and wider scientific community. The group also uses this resource to address continental scale questions of past vegetation change.

Author contributions: T.G., S.B, W.F and R.B had the original idea and M.L. compiled the data. S.B. constructed the maps; T.G. and S.B. performed analyses; T.G. wrote the paper with the substantial contributions from M.L., S.B., W.F. and R.B.
Table 1. Pollen percentage thresholds. The threshold $T_{\text{int}}$ is applied before the interpolation procedure. Thresholds T1 to T4 are the lower limit of the four abundance classes applied to the results of the interpolation.

<table>
<thead>
<tr>
<th>Taxon name</th>
<th>$T_{\text{int}}$</th>
<th>T1</th>
<th>T2</th>
<th>T3</th>
<th>T4</th>
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<tr>
<td>Abies</td>
<td>0.5</td>
<td>0.1</td>
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Figures

Figure 1 Study area of Europe restricted towards the east in a line from the Black to the White Sea. The red line marks the starting point for the evaluation of the rate of spread ignoring the regions to the south as here species may have survived the last ice age so that patterns are more difficult to interpret and site density is lower, leading to additional biases. The broken line marks 47°N latitude, which was used as a limit to contrast the dynamics of change between northern and southern Europe.
Figure 2 Postglacial changes in area of occurrence for the most common European tree taxa based on interpolation and classification of pollen percentages.
Figure 3 Fitted logistic functions to the increase in area of occurrence in Europe north of 47°N latitude as estimated from interpolation and interpretation of pollen percentages. The inflection point, where the exponential increase starts slowing down, is marked by the vertical line and its age given below the taxon name. Taxa are grouped according to the timing of the area expansion and differences in overall area.
Figure 4 Boxplots for rates of spread as obtained by the shortest distance between two grid cells marking the area of inferred occurrence in consecutive time slices. Note that the width of a box indicates the number of observations, with thin boxes indicating that distribution shifts occurred along a small section of the mapped limit. Negative shifts were ignored.
Figure 5 Assessments of the dynamics of area increase: a) Rate of overall spread estimated from the slope of the increase in square root of the area versus time, b) area doubling time obtained from the logistic growth model. Symbols: black square = class 1, green triangle = class 2, red triangle point down = class 3, blue diamond = class 4. Taxa are ordered according to their overall rates of spread and doubling time. Horizontal lines separate rapidly expanding taxa.
Figure 6 Postglacial changes in area of highest abundance or dominance for the most common European tree taxa, *Artemisia* and Poaceae based on interpolation and classification of pollen percentages. Vertical dashed lines make times of change.
Figure 7 Dynamics of abundance change comparing Europe north and south of 47°N latitude depicted as upper and lower values from a central zero line. Black lines indicate an increase, and red a decline in area abundance.
Figure 8 The average distance of areas assigned to different abundance classes to the modern coast of the Mediterranean and the Atlantic respectively. Lower abundance classes include the area of higher abundance classes. The dotted line represents the average for the analysed area. Colour codes: black = class 1, green = class 2, red = class 3, blue = class 4.