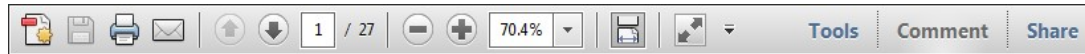
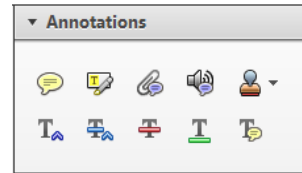


Once you have Acrobat Reader open on your computer, click on the [Comment](#) tab at the right of the toolbar:



This will open up a panel down the right side of the document. The majority of tools you will use for annotating your proof will be in the [Annotations](#) section, pictured opposite. We've picked out some of these tools below:



1. [Replace \(Ins\) Tool](#) – for replacing text

box where replacement text can be entered.

How to use it

- Highlight a word or sentence.
- Click on the [Replace \(Ins\)](#) icon in the Annotations section.
- Type the replacement text into the blue box that appears.

Standard framework for the analysis of mark-ups. Nevertheless, it also led to exogenous number of strategic competitors and the number of competitors is that the structure of the industry is mainly composed of large firms. At the industry level, are exogenous shocks important? (M henceforth) we open the 'black b

2. [Strikethrough \(Del\) Tool](#) – for deleting text

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How to use it

- Highlight a word or sentence.
- Click on the [Strikethrough \(Del\)](#) icon in the Annotations section.

there is no room for extra profits as mark-ups are zero and the number of firms (net) values are not determined by exogenous factors. Blanchard ~~and Kiyotaki~~ (1987), perfect competition in general equilibrium. The effects of aggregate demand and supply shocks in the classical framework assuming monopoly competition are an exogenous number of firms

3. [Add note to text Tool](#) – for highlighting a section to be changed to bold or italic.

Highlights text in yellow and opens up a text box where comments can be entered.

How to use it

- Highlight the relevant section of text.
- Click on the [Add note to text](#) icon in the Annotations section.
- Type instruction on what should be changed regarding the text into the yellow box that appears.

dynamic responses of mark-ups are consistent with the VAR evidence

4. [Add sticky note Tool](#) – for making notes at specific points in the text.

Marks a point in the proof where a comment needs to be highlighted.

How to use it

- Click on the [Add sticky note](#) icon in the Annotations section.
- Click at the point in the proof where the comment should be inserted.
- Type the comment into the yellow box that appears.

and supply shocks. Most of the evidence is consistent with the VAR evidence

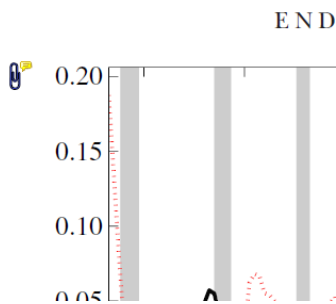
5. Attach File Tool – for inserting large amounts of text or replacement figures.



Inserts an icon linking to the attached file in the appropriate place in the text.

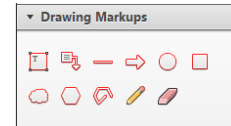
How to use it

- Click on the **Attach File** icon in the Annotations section.
- Click on the proof to where you'd like the attached file to be linked.
- Select the file to be attached from your computer or network.
- Select the colour and type of icon that will appear in the proof. Click OK.



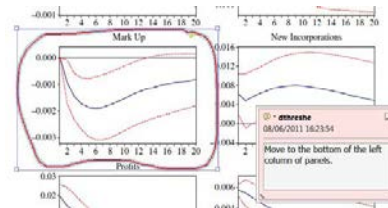
6. Drawing Markups Tools – for drawing shapes, lines and freeform annotations on proofs and commenting on these marks.

Allows shapes, lines and freeform annotations to be drawn on proofs and for comment to be made on these marks.



How to use it



- Click on one of the shapes in the Drawing Markups section.
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- To add a comment to the drawn shape, move the cursor over the shape until an arrowhead appears.
- Double click on the shape and type any text in the red box that appears.



SYNTHESIS



Patterns and dynamics of European vegetation change over the last 15,000 years

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ABSTRACT

Aim Palaeoecological reconstructions document past vegetation change, with estimates of fast shifts in species distributions. The resulting rates of plant spread are often not matched by model simulations of climate-driven vegetation dynamics. Genetic surveys of extant plant populations document directions of the post-glacial spread of trees, challenging traditional interpretations. 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 changes in the 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 post-glacial spread with at least 1000 m year⁻¹ for *Corylus*, *Ulmus* and *Alnus* and average rates of 400 m year⁻¹ 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 post-glacial 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 rapid tracking of early Holocene climate change by common tree species, documenting that plants can spread fast tracing their climate space, regardless of their dispersal strategy.

Keywords

Europe, global warming, migrational lag, pollen, post-glacial, spread of trees

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INTRODUCTION

The pace of human-induced global warming is forecast to rival the rates of change associated with natural transitions from glacial to interglacial periods (Diffenbaugh & Field, 2013) and the ability of plants to respond remains one of the greatest uncertainties about the impact of global warming on

vegetation (e.g. Svenning & Sandel, 2013). The rate of shifting bioclimatic envelopes may not be met by the spread of plants causing a risk for their extinction (Ohlemüller *et al.*, 2006).

The spread of plants after the last glaciation provides examples of how plants altered their ranges and abundance in response to climate change, which has been researched

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and discussed for more than a century. Reid (1899) showed that the distance covered by *Quercus* during post-glacial recolonization of the British Isles was too large to be achieved by passive seed dispersal alone. Skellam (1951) demonstrated this paradox using a diffusion model connecting population growth with the rate of spread, confirming the importance of long-distance dispersal (LDD; Clark, 1998). LDD events are more frequent over shorter distances, but exceptional chance events over large distances do occur (Nathan, 2006). 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.

Limits on post-glacial spread considered a century ago (see discussions in Firbas, 1949) 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 taxa to a region with presumed suitable climate was later described as 'migrational lag' (e.g. Huntley & Webb, 1989). However, 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 < 1.5 ka (Prentice *et al.*, 1991). Pollen-based climate reconstructions (e.g. Bartlein *et al.*, 2011) imply the validity of 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 distributional models to show that most European trees had not yet filled their current potential ranges, suggesting that the post-glacial northward spread of trees was still active and partly determines current tree distributions and diversity gradients (Svenning *et al.*, 2008). 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 powerful for documenting regional abundance changes in anemophilous trees once they have reached densities higher than possibly one tree per hectare (Bennett, 1986). Huntley & Birks (1983) mapped pollen data across Europe using high abundance thresholds and estimated maximum rates of spread for common European trees between 300 and 2000 m year⁻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 *et al.*, 2014).

Lower rates of spread are obtained by assuming the spread originated from populations surviving the LGM further north than previously estimated (Stewart & Lister, 2001). This view is supported by finds indicating the occurrence of

temperate trees in central-eastern Europe just before the LGM (Willis & van Andel, 2004), whereas Tzedakis *et al.* (2013) discussed that these may not have survived the LGM, advocating 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 more northern LGM distributions, assumed that northward spread started with Lateglacial climate warming and ended with the arrival of trees at their current or maximum Holocene northern limit. These assumptions led to much lower overall rates of post-glacial spread between 60 and 260 m year⁻¹ and suggested that the earlier rates of Huntley & Birks (1983) could be overestimates.

New insights into the post-glacial spread of plants have come from mapping genetic markers in extant populations (Hu *et al.*, 2009). Independently dated pollen diagrams have increasingly become available with a large number 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). The uneven distribution of pollen diagrams hampers spatial analysis and we therefore construct interpolated maps of pollen deposition to infer past distribution and abundance of widespread European plant genera and the grass family. The aim of this study was 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 post-glacial spread and abundance changes in the dominant European tree genera. Our analyses provide a basis for comparative studies with vegetation model experiments.

MATERIALS AND METHODS

Study area

Interpolated maps were based on pollen data from the EPD. Sites beyond the European continent but included in the EPD were ignored. European islands without publicly available data were also excluded. Because the distribution of sites becomes increasingly sparse to the east, we limited the analysis to west of a line from the Black Sea to the White Sea. Pollen abundances were interpolated to a 0.5° grid.

Data

We used publicly available EPD sites with associated chronologies based on Giesecke *et al.* (2014), resulting in about 780 locations within or close to the study area contributing to the interpolations. All ages are given as calibrated years before present, where 'present' equals the year 1950 Anno Domini (AD). Sample selection is identical to the

set used for mapping abundance changes at individual sites (Brewer *et al.*, 2016) with age uncertainties of less than ± 500 years and extrapolations of < 2000 years (Giesecke *et al.*, 2014). Pollen counts were converted to percentages based on all terrestrial pollen taxa, excluding Cyperaceae, wetland and aquatic plants, fern and moss spores. Samples were collated into consecutive 500-year 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, with fewer sites available prior to the Holocene (Giesecke *et al.*, 2014).

Interpolation and classification

Long-distance transport, erosion and redeposition of pollen grains bias the interpretation of small pollen proportions regarding the regional occurrence of the parent tree. To reduce this bias we designed threshold values (T_{int} , Table 1) and interpolated percentages above the threshold 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 covariates, making the procedure well suited for continental interpolations of pollen data with an uneven spatial coverage (e.g. Williams *et al.*, 2004). The inclusion of elevation 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.

Acknowledging the many uncertainties in the resulting interpolation, 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 approximate the regional presence of the taxon, whereas the highest abundance class was chosen to represent the area within which a species is regionally dominant or characteristic. We determined the threshold values in comparisons between interpolations of modern samples (1700–2010 AD) with species distributional 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 on the interpolated surface (T1) was necessary to restrict distributions in data-sparse areas. No presence threshold was set for Poaceae because 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

Table 1 Pollen percentage thresholds. The threshold T_{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.

Taxon name	T_{int}	T1	T2	T3	T4
<i>Abies</i>	0.5	0.1	1	3	6
<i>Alnus</i>	2.5	2	4	8	12
<i>Artemisia</i>	0.5	0.1	1	2	5
<i>Betula</i>	0.5	2	6	15	25
<i>Carpinus</i>	0.5	0.1	1	2	5
<i>Corylus</i>	2	0.3	5	10	20
Ericaceae	0.5	0.3	1	4	10
<i>Fagus</i>	0.5	0.3	1	4	10
<i>Fraxinus</i>	0.5	0.1	0.5	2	4
Poaceae	NA	NA	4	8	15
<i>Juniperus</i> -type	0.5	0.1	0.5	2	4
<i>Picea</i>	0.5	0.5	2	5	10
<i>Pinus</i>	0.5	2	6	15	25
<i>Quercus</i>	1.5	0.3	4	8	14
<i>Tilia</i>	0.35	0.1	0.5	2	4
<i>Ulmus/Zelkova</i>	0.35	0.1	0.5	2	4

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 genera based on this analysis. The results of the interpolations are provided as supplementary information (<https://doi.pangaea.de/10.1594/PANGAEA.865121>).

Change in area and rate of spread

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 the analysis of the dynamics of spread to the nine common arboreal taxa for which the northern distributional limits may be approximated by the pollen percentage thresholds adopted here. 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. We estimated rates of overall spread (V) and area-doubling times for all abundance classes, using a simple model of reaction diffusion $V = 2(kD)^{1/2}$, where k is the intrinsic rate of population growth and D the diffusion coefficient (Birks, 1989). The slope of the square root of area increase over time is an estimate of $(kD)^{1/2}$ yielding V for 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 configuration as a starting point for assessing the dynamics of post-glacial spread (Fig. 1). 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, whereas considering disjointed dispersal jumps growing into larger areas and/or higher abundance classes. This resulted in connected areas of distribution as the basis for analysis and this requirement is the reason why higher abundance classes, which often have disjoint areas, were not considered. Rates were obtained as the shortest geographical distance between the centres of grid cells marking the distributional limits in two consecutive time slices and dividing the value by 0.5 ka. This yields rates of spread in all directions, however, as the analysis was restricted to the area north of the Alps, changes in the southern limits were not considered. We also computed the distance of the northward shift of the 95 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

For each grid-cell, we calculated the differences in interpolated pollen proportions between two consecutive time slices and classified the results into four classes of increase and decrease, with one class of no change. Thresholds were obtained per taxon as the standard deviations (SD) of all values over all time slices. The value of zero was assigned to

grid cells with <1 SD difference, whereas maximum and minimum values of 4 and -4 were assigned to differences larger than 4 SD. The resulting maps are provided as supplementary information (https://doi.pangaea.de/10.1594/PAN_GAEA.865119).

We visualized these changes by multiplying the numeric value (4 to -4) of each class with 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 \times amount of change). This was carried out separately for northern and southern Europe with the division at 47° N latitude.

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. During the Lateglacial the latitudinal tree line formed in central Europe (Theuerkauf & Joosten, 2012; Mortensen *et al.*, 2014), and reached a more northerly position to the east of the Baltic Ice Lake (Amon *et al.*, 2014). However, this tree line consisting 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 tree line east of the Baltic Ice Lake during the Younger Dryas (Heikkilä *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

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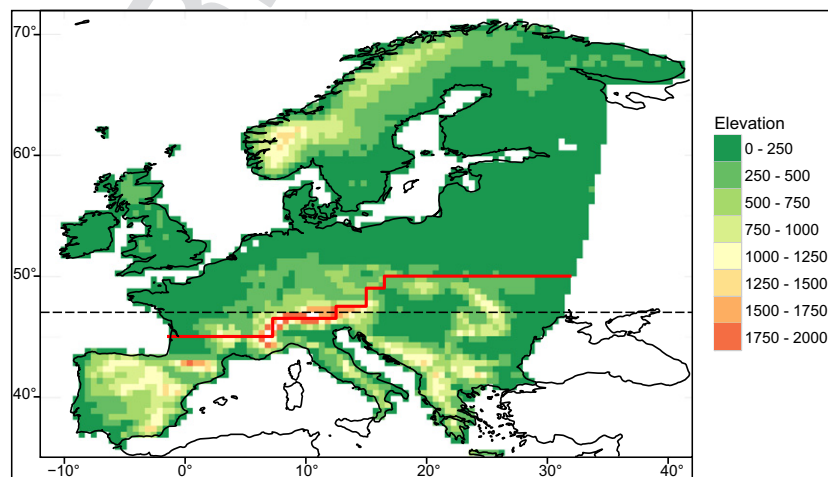


Figure 1 Study area of Europe restricted towards the east in a line from the Black to the White Sea. The red line marks the starting point for the evaluation of the rate of spread ignoring the regions to the south as here species may have survived the last ice age so that patterns are more difficult 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.

abundance of some taxa (e.g. *Artemisia*, *Juniperus*, *Ulmus*), although the 500-year time slices can only weakly resolve the impact of these climate fluctuations (Fig. 2, see Appendix S1.1 in Supporting Information). 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 set 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* filled most of their current distributional area within 2 kyr from the onset of the Holocene (Fig. 2). Conversely, *Fagus* and *Carpinus* had hardly any response to the onset of the Holocene. They showed a gradual increase in area that only starts after 9 ka and which continues almost to the present. *Picea* and Ericaceae had similar trends of steady increase though the Holocene. *Alnus* and *Abies* showed intermediate patterns with late starting area expansions that stopped in the mid-Holocene.

The areas of occurrence increased through time (Fig. 2) and followed logistic models of population growth. This becomes particularly clear when limiting the analysis to Europe north of 47° N latitude (Fig. 3). The inflection point that was estimated for these logistic increases provides a description for the timing of spread and range filling. *Ulmus* and *Corylus* slowed their exponential increase < 1 ka after the onset of the Holocene at around 11.2 and 11.1 ka respectively. *Tilia* and *Quercus* followed at 10.3 and 10.1 ka, whereas *Alnus* started to spread late but rapidly reached the inflection point at 9.5 ka. *Picea* survived the LGM north of 47° N latitude and its increase in apparent area of occurrence was gradual without a strong sigmoidal shape. The age of inflection point at 6.7 ka characterizes its mid-Holocene expansion. *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 and 4.8 ka respectively.

Distributions did not shift evenly, but some edges spread faster than others resulting in a range of values (Fig. 4). The box plots and the northward movement of the 95-percentile of distributions for the different abundance classes (see Appendix S1.7) show that the fastest rates of spread were reached during the early Holocene. For *Ulmus* the uppermost quantile (Fig. 4 beyond plot margin) ranges between 3000 and 1600 m year⁻¹ for the time between 11.5 and 11 ka and the 95-percentile shifted over this time by about 1000 km for the first and second abundance classes, which converts to a velocity of 2000 m year⁻¹. The northward range shift of *Ulmus* was concentrated in one 500-year interval, whereas the rapid spread of *Corylus*, *Tilia* and *Quercus* had a longer duration, with average values around 400 m year⁻¹. Nevertheless, the uppermost quantile of the *Corylus* boxplot for 12–11.5 ka ranges between 1300 and 2800 m year⁻¹ (Fig. 4 beyond plot margin). The late-spreading taxa *Fagus* and *Carpinus* started with an initial rapid spread with apparent rates around 400 m year⁻¹, whereas the later spread occurred 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. 5(a) assume the rate of spread to be constant through time, which was not the case. The highest rate of spread for the entire distribution is estimated for *Alnus* with 1000 m year⁻¹, whereas the estimates for most other taxa fall between 600 m year⁻¹ for *Corylus* and 250 m year⁻¹ for *Abies* and are thus comparable to average rates in Fig. 4. Only the gradual increase in the distribution of *Picea* resulted in a slow rate of 150 m year⁻¹. The fastest rate of spread recorded is for the highest abundance class of *Corylus*, caused by the rapid and often synchronous population increase in *Corylus* 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. 5(a). This results in differences in the rank order, which are most pronounced for *Fagus* and *Carpinus*. The three higher

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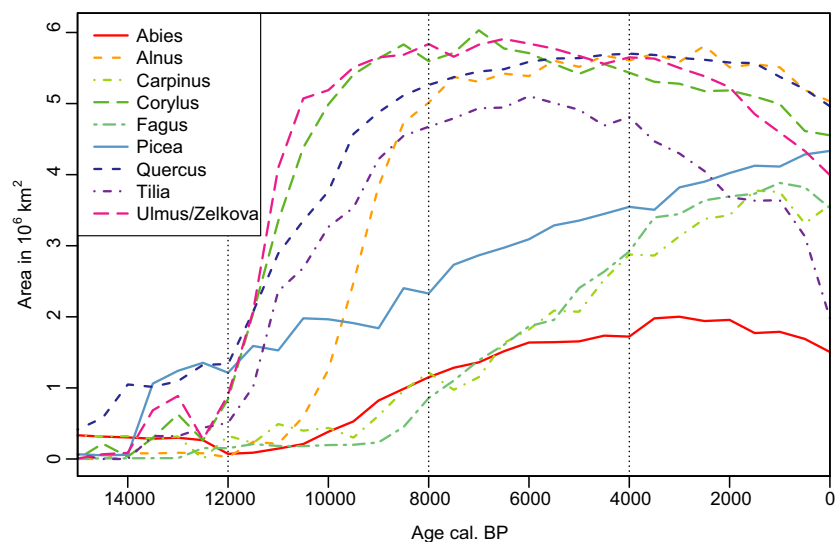


Figure 2 Post-glacial changes in area of occurrence for the most common European tree taxa based on interpolation and classification of pollen percentages.

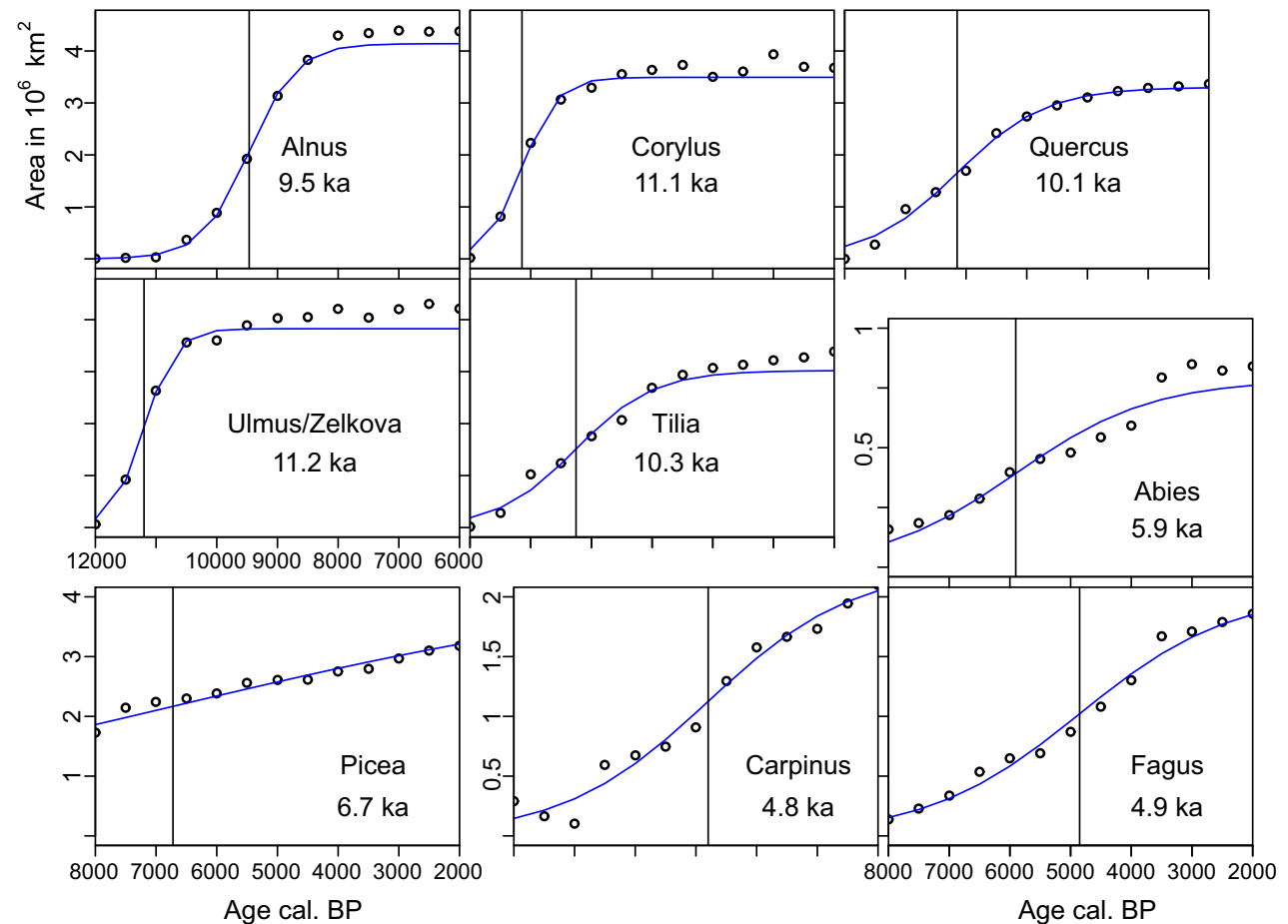


Figure 3 Fitted logistic functions to the increase in area of occurrence in Europe north of 47° N latitude as estimated from interpolation and interpretation of pollen percentages. The inflection point, where the exponential increase starts slowing down, is marked by the vertical line and its age given below the taxon name. Taxa are grouped according to the timing of the area expansion and differences in overall area.

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* showed values above 400 m year⁻¹ for all abundance classes. *Quercus* takes an intermediate position. Its post-glacial spread north started early, whereas 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 focuses on its Holocene dynamics, whereas 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) 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*, whereas 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 also provides examples of declines in distribution and 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 what can be recognized using the applied percentage thresholds. This is the main reason for the strong decline in *Tilia* (see Appendix S1.1). The area curves for higher abundance classes document these shifts in the abundance of different species across Europe. 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

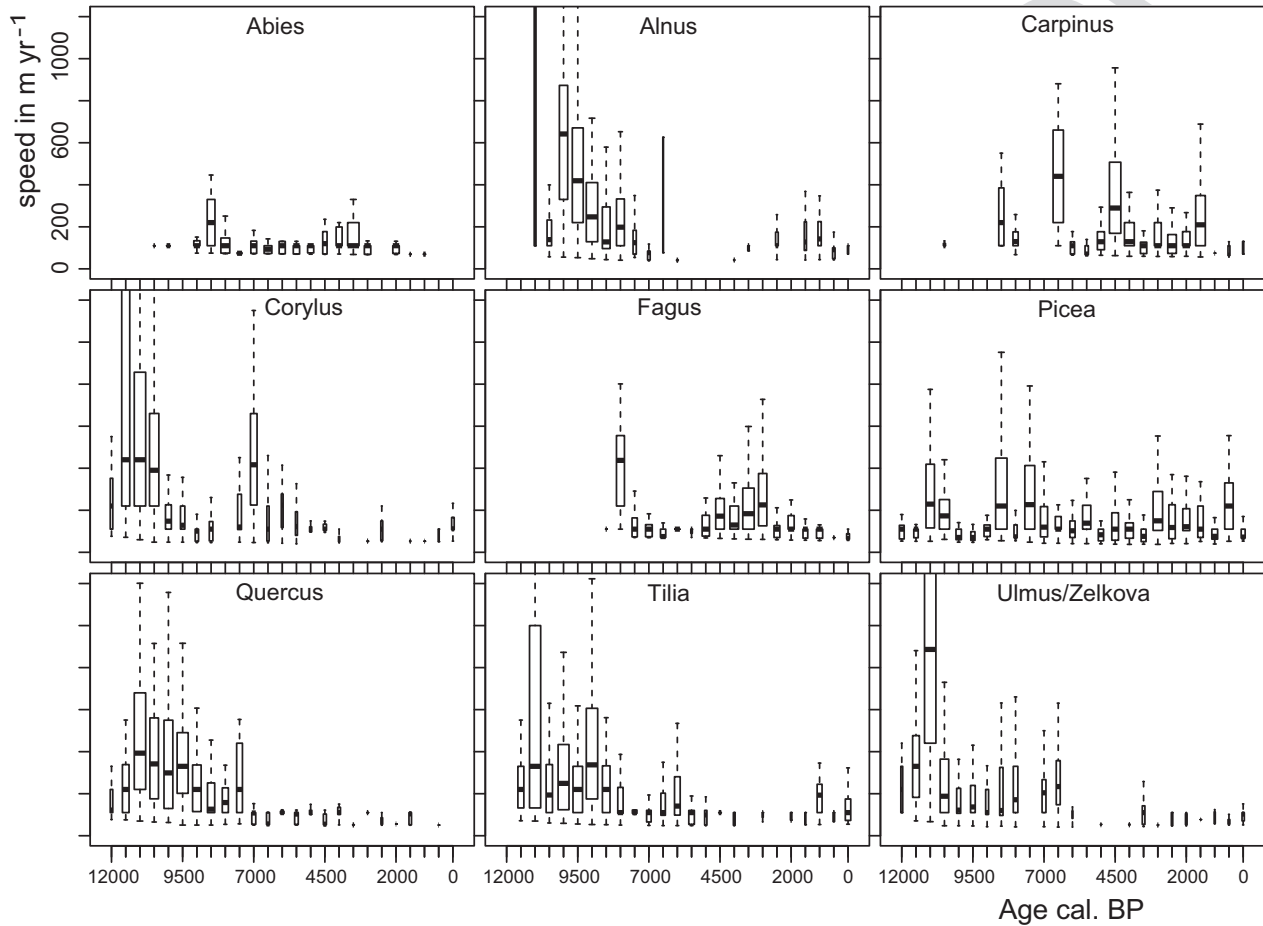
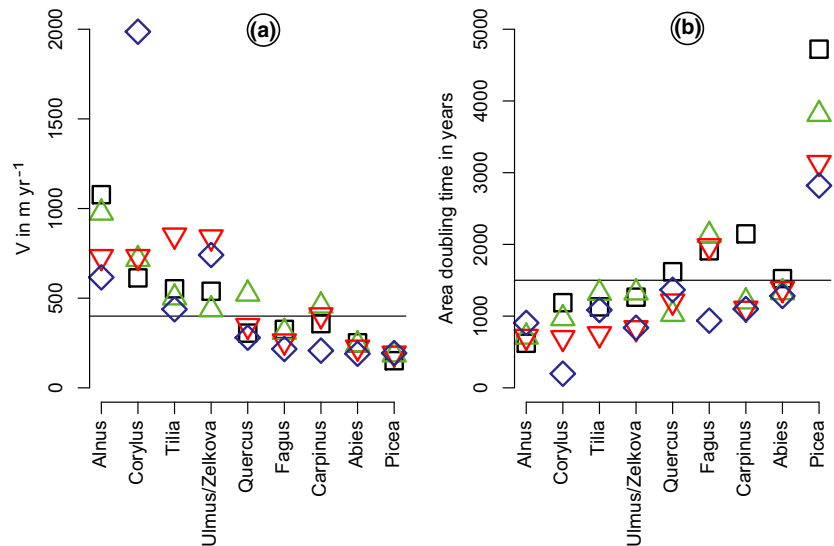


Figure 4 Boxplots for rates of spread as obtained by the shortest distance between two grid cells marking the area of inferred occurrence in consecutive time slices. Note that the width of a box indicates the number of observations, with thin boxes indicating that distributional shifts occurred along a small section of the mapped limit. Negative shifts were ignored.

COLOR

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.



expansion phase and are succeeded by a period of decline. The abundance of *Ulmus* and *Tilia* characterized many European forests between 9 and 6 ka. The pattern also clearly depicts the well described decline of *Ulmus*, which is followed by *Tilia*, whereas 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 (<https://doi.pangaea.de/10.1594/PANGAEA.865119>) 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 change in the north (*Picea*) and others in the south (*Abies*), which is partly due to the centre of their distribution (Fig. 8). The lack of change for *Quercus* 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.

Assuming temperate tree taxa survived the LGM in southern Europe, one would expect populations to start expanding there and subsequently spread northwards where population expansion would be delayed. This pattern is indeed visible for some taxa, particularly 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 and north, with a short lead in the south. For *Corylus* and *Alnus* the change in the north appears 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*, whereas *Ulmus* declined earlier in the south compared to the north.

To follow the change in 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 (see 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. Abundance distributions are skewed to the north for the boreal taxa *Pinus* and *Betula*, with higher abundance classes found successively further north, whereas the opposite trend is observed for *Quercus* with a southern affinity (see 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 distributional 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 was replaced by *Fagus* in the second half of the Holocene (Feurdean *et al.*, 2010), whereas the tree expanded in Fennoscandia during that time (Giesecke & 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 shifted simultaneously (Giesecke & Bennett, 2004; van der Knaap *et al.*, 2005). The two other latecomers *Fagus* and *Carpinus* followed the same trend, shifting the centres of their

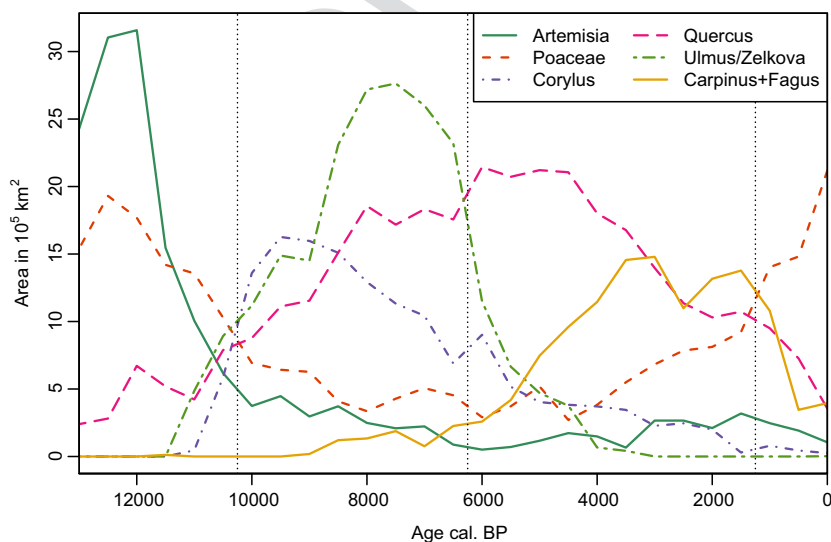


Figure 6 Post-glacial changes in area of highest abundance or dominance for the most common European tree taxa, *Artemisia* and *Poaceae* based on interpolation and classification of pollen percentages. Vertical dashed lines make times of change.

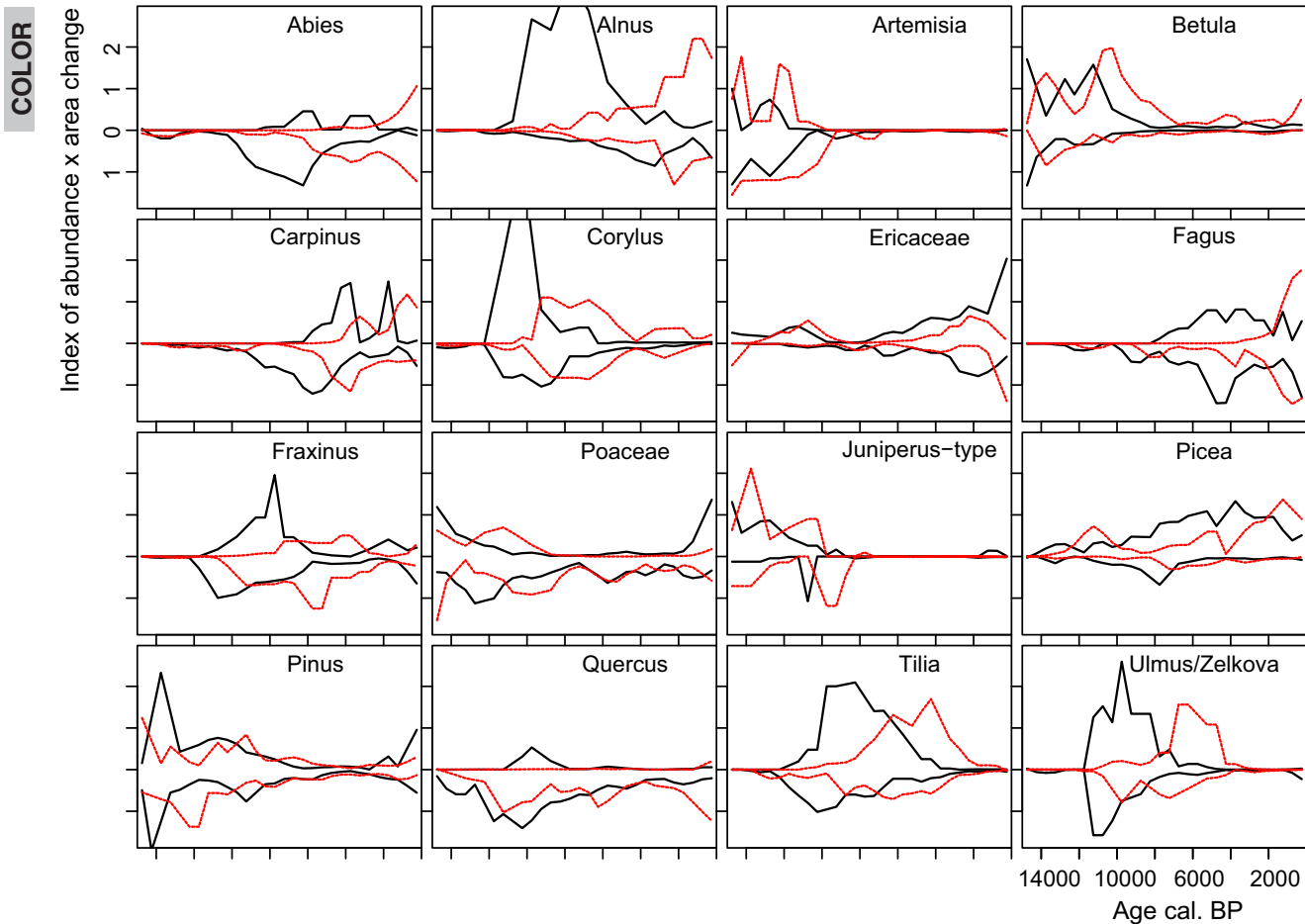


Figure 7 Dynamics of abundance change comparing Europe north and south of 47° N latitude depicted as upper and lower values from a central zero line. Solid lines indicate an increase, and dashed lines indicate a decline in area abundance.

distributions from east to west with the general spread of the distribution in the same direction.

While the gravitational centres of distributions shifted north together with the northern edges of the populations, the southern distributional limits did not move north with the early Holocene climate warming (see Appendix S1.3–S1.6). *Betula* is the only taxon with a slight northward shift of its southern distributional limit and higher abundance classes showed a strong northward shift of the southern limits (see Appendix S1.6).

DISCUSSION

Spread and population expansion

We found that the rates of taxon spread slowed before northern distributional limits were reached, which is demonstrated by the logistic fits in Fig. 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 travelling 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

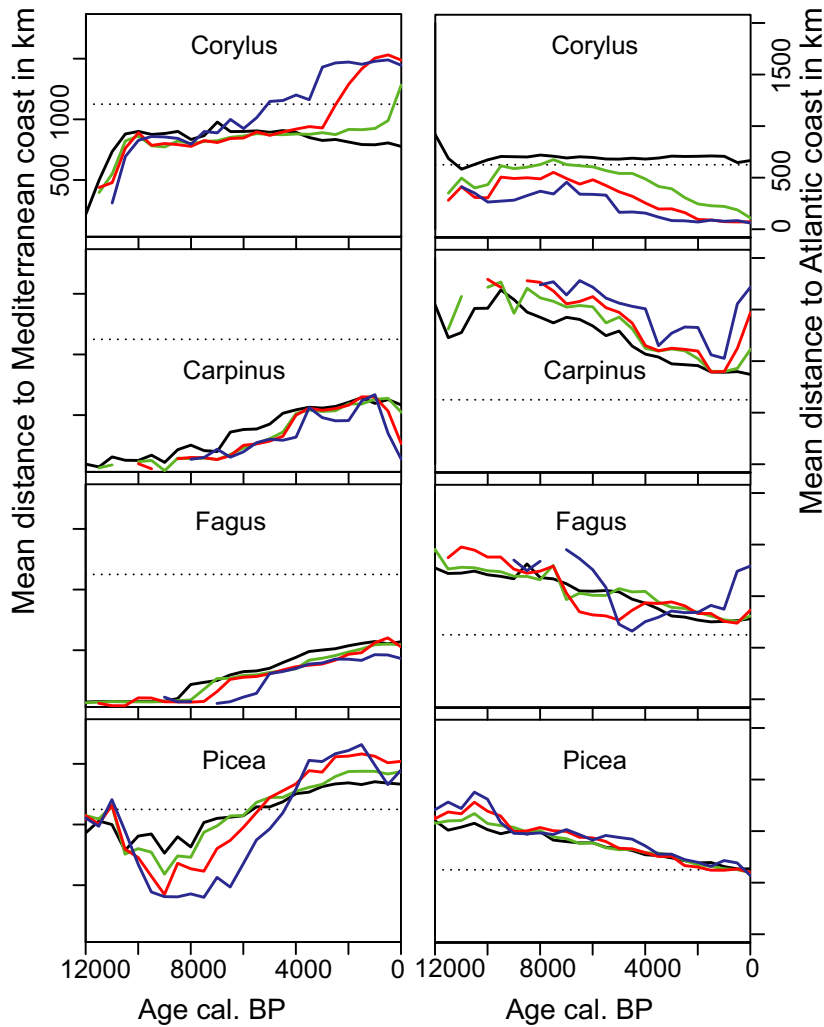


Figure 8 The average distance of areas assigned to different abundance classes to the modern coast of the Mediterranean and the Atlantic respectively. Lower abundance classes include the area of higher abundance classes. The dotted line represents the average for the analysed area. Colour codes: black = class 1, green = class 2, red = class 3, blue = class 4.

Sweden and in the Baltic states as well as between northern Sweden and northern Russia (Tollefsrud *et al.*, 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 travelling north-west from southern Finland, crossing the northern extent of the Baltic Sea and then turning south-west into southern Sweden (Giesecke & 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) supports this interpretation, documenting that the initial spread, which left a genetic imprint in populations, and the later population expansion are decoupled.

Genetic markers in extant populations confirm earlier claims that *Fagus* survived the LGM on the Iberian Peninsula (Magri *et al.*, 2006) and possibly also in south-western France (de Lafontaine *et al.*, 2014), yet these areas contributed little to the post-glacial colonization of Europe.

Similarly, the populations on the Apennine and Balkan peninsulas did not contribute to the post-glacial spread of the tree. The dominance of central and north-western Europe by a single chloroplast haplotype is in sharp contrast with the high haplotype diversity of the southern edge of the distribution in northern Greece (Magri *et al.*, 2006). 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, we found that *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 *Fagus* is not related to 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 post-glacial spread of *Fagus* as well as *Picea* (Saltré *et al.*, 2013; Lehsten *et al.*, 2014) does therefore not help develop understanding of the post-glacial 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, our findings 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. Modelling the post-glacial colonization of Europe would certainly 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 populations from around the Mediterranean Basin have spread north with post-glacial warming (Petit *et al.*, 2002), yet these 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). Simulations using this example also link the frequency of LDD to population density (Bialozyt *et al.*, 2006).

Comparisons between Europe and North America

Estimated rates of post-glacial spread of woody taxa in eastern North America are nearly always lower than the rates discussed here, regardless of the method. 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 year⁻¹ for *Pinus banksiana/resinosa* and 100 m year⁻¹ for *Castanea* (Davis, 1976). Delcourt & Delcourt (1987) used a modern data set 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 year⁻¹ for *Salix* and 70 m year⁻¹ for *Nyssa*, including individual maximal dispersal jumps of 1044 m year⁻¹ for *Tsuga* and 753 m year⁻¹ for *Tilia*. Highest rates of spread were observed between 17 and 13.8 ka and thus much earlier compared to Europe, although also at lower latitudes. Ritchie & MacDonald (1986) presented a study with the highest rates of spread in North America, for the spread of *Picea glauca* from south-central Alberta to the Mackenzie Delta with rates of 2000 m year⁻¹, whereas they reported rates of 2–300 m year⁻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 year⁻¹ for *Abies* and 153 m year⁻¹ for *Alnus* during 12–10 ka.

In North America the distributional shifts of the southern boundaries occurred at similar rates (Ordonez & Williams, 2013). In Europe, the position of most rear-edge distributions had not changed significantly during the last 15 kyr, except perhaps for *Betula* which declined in abundance at its southern distributional 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) speculated 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 distributional 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 post-glacial spread in eastern North America have considered a wide latitudinal range where the trees in question may have occurred during the LGM.

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).

Human influence has rarely been discussed in the spreading of tree taxa in North America, although humans were present in the post-glacial landscape and probably influenced fire regimes and cultivated crops by 3.8 ka (Smith & Yarnell, 2009). Indians may have affected regional distributional limits of fire-sensitive hardwoods at the prairie–forest transition zone for a long time (Grimm, 1984). In contrast in Europe,

there has been considerable discussion about potential human impact on the distribution and abundance change in 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 in 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. It may never be known 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 *et al.*, 2004).

Two types of change possibly mediated by human activities emerge from our analyses. First, 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). Second, 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', whereas 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 leached 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*, *Carpinus* and *Picea* among those. The constant increase in area with various abundance classes of Ericaceae pollen over the last 8 kyr (see Fig. S1.1) also attests to gradual changes in soils, namely paludification increasing the amount of peatland as well as podsolization reducing soil fertility. *Corylus* also possesses ectomycorrhiza, but decreased in abundance during the second half of the Holocene. Its decline, particularly in more continental areas, was unlikely to be due simply to the species being shaded out by more shade-tolerant taxa. There is a simultaneous westward shift of *Picea* distributions 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, population growth rates and other plant traits were surely important in shaping the early Holocene dynamics, but cannot explain many patterns.

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26 SUPPORTING INFORMATION

27
28 Additional Supporting Information may be found in the
29 online version of this article:

30 **14** Appendix S1 Additional figures.

DATA ACCESSIBILITY

All pollen data used for the maps are available from the European Pollen Database (EPD; <http://www.europeanpollen.ndatabase.net/>). The maps generated for this study are available as PDFs as well as numerical values from <https://doi.pangaea.de/10.1594/PANGAEA.865121>.

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 substantial contributions from M.L., S.B., W.F. and R.B.

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