

1 Patterns and dynamics of European vegetation change over the last  
2 15000 years

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24

25 **Abstract**

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

Comment [t1]: Deleted "Yet"

33 **Location** Europe

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

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

Comment [t2]: Got rid of first sentence.

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

50

51 **Keywords:** Europe, global warming, migrational lag, pollen, postglacial, spread of trees

52

## 53 Introduction

54 The pace of human-induced global warming is forecast to rival natural transitions from glacial to  
55 interglacial periods (Diffenbaugh & Field, 2013), with considerable consequences for plant  
56 distributions and diversity. The ability of plants to spread into new areas remains one of the greatest  
57 uncertainties in the debate on the impact of global warming on vegetation (e.g. Svenning & Sandel,  
58 2013). Several studies on the rate of shifting bioclimatic envelopes suggest that plants may not  
59 spread fast enough and consequently will be threatened by extinction (Ohlemüller *et al.*, 2006). The  
60 spread of plants after the last glaciation can provide guidance in this discussion on possible future  
61 change and evidence of past floristic change has been collected in Europe for more than 100 years  
62 (e.g von Post 1918). Reid (1899) pointed out that the distance covered by *Quercus* during postglacial  
63 recolonization of the British Isles was too large to be achieved by passive seed dispersal during the  
64 time available. Skellam (1951) used this paradox as an illustration for a diffusion model that  
65 connected population growth with the rate of spread, confirming the importance of long distance  
66 dispersal (LDD) to explain the postglacial spread of plants (Clark *et al.*, 1998). LDD events are more  
67 frequent over shorter distances, while exceptional chance events over large distances do occur  
68 (Nathan, 2006), but even they need to have limits or there would be no difference between floras of  
69 regions with similar climates. The time required for trees and shrubs to produce seed and the  
70 number and size of propagules should also impose limits on the rate of spread. Consequently, there  
71 should be intrinsic species specific maximum rates of spread determining how fast plants can shift  
72 their ranges in response to climate change. Such potential limits for the postglacial spread of plants  
73 were already considered a century ago (see discussions in Firbas, 1949) and led to the interpretation  
74 that the intrinsic rate of spread and distance from Last Glacial Maximum (LGM) distributions could

75 explain the sequential appearance of taxa in Europe (Bertsch, 1940). The delayed arrival of a plant to  
76 a region with suitable climate was later described as 'migrational lag' (e.g. Huntley, 1989). The  
77 alternative dynamic equilibrium hypothesis explains the appearance of taxa and their population  
78 expansion as direct reactions to climate (von Post 1924; Rudolph, 1930; Godwin, 1975) with lags of  
79 less than 1.5 ka (Prentice *et al.*, 1991). Numerous pollen based climate reconstructions during the  
80 last 25 years (e.g. Bartlein *et al.*, 2011) have built on the dynamic equilibrium hypothesis.  
81 Nevertheless, the migrational lag hypothesis is often cited as the major factor explaining, for  
82 example, the late arrival of *Fagus* and its apparent continued spread to fill its climatic range (Lang,  
83 1994). Svenning & Skov (2004) used species distribution models to show that most European trees  
84 had not yet filled their current potential ranges, suggesting that the postglacial northward spread of  
85 trees was still active and partly determining current tree distributions and diversity gradients  
86 (Svenning *et al.*, 2008; Normand *et al.*, 2011). This emphasises migrational lag as an important factor  
87 in past vegetation change and revives the debate about whether intrinsic, species-specific dispersal  
88 properties, can explain the sequential appearance and dominance of major trees in Europe.  
89 Pollen analysis is a blunt instrument for detecting the first appearance of a plant in a region,  
90 however, it is powerful at documenting regional abundance changes of anemophilous trees once  
91 they have reached densities larger than perhaps one tree per hectare (Bennett, 1986). Huntley &  
92 Birks (1983) mapped pollen data across Europe and using rather high abundance thresholds  
93 estimated rates of spread for common European trees with maximum values ranging between 300  
94 and 2000 m yr<sup>-1</sup>. These high rates of spread were difficult to reconcile with simulations using  
95 observed seed dispersal distances that result in much lower rates (e.g. Meier *et al.*, 2012; Feurdean  
96 *et al.*, 2013; Snell & Cowling, 2015). High rates of spread are obtained by assuming the spread  
97 originated from populations far to the south. Stewart & Lister (2001) suggested that plants may have  
98 survived in refugia much further north during the LGM than previously estimated. Willis & Andel  
99 (2004) demonstrated that many broadleaved trees occurred in central-eastern Europe just before  
100 the LGM, while Tzedakis *et al.* (2013) discussed that these may not have survived the coldest phase

101 advocating for the absence of temperate trees in Europe north of 45°N. The time between the end  
102 of the coldest phase of the last glaciation and the onset of the Holocene may have allowed small  
103 outposts of temperate trees to establish far to the north of their LGM distributions as was first  
104 suggested by Rudolph (1930). Feurdean *et al.* (2013) considered the duration of the Lateglacial, as  
105 well as more northern LGM distributions and assumed that northward spread started in the  
106 Lateglacial and ended with arrival of trees at their current or maximum Holocene northern limit.  
107 These assumptions led to much lower overall rates of postglacial spread between 60 and 260 m yr<sup>-1</sup>  
108 and suggested that the earlier rates of Huntley & Birks (1983) could be overestimates.

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

## 123 Methods

### 124 Study area

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

### 131 Data

132 We used all sites from the publicly available EPD with associated age information based on the  
133 calibrated chronologies (Giesecke *et al.*, 2014), of which about 790 are situated within the study area  
134 or sufficiently close so that they contributed to the interpolations. All ages are given as calibrated  
135 years before present (BP), where 0 BP equals the year 1950 Anno Domini. We selected samples with  
136 age uncertainties of less than  $\pm 500$  years and the minimum “1 star” uncertainty classification,  
137 limiting extrapolations to 2000 years beyond the oldest control point (Giesecke *et al.*, 2014). Pollen  
138 counts were converted to percentages based on the sum of all terrestrial pollen taxa, excluding  
139 pollen from Cyperaceae, other wetland and aquatic flowering plants as well as all fern and moss  
140 spores. Samples were collated into consecutive 500-year wide bins centred on full 500-year intervals  
141 between 0 and 15 ka. The values were averaged over all samples where more than one sample per  
142 site fell within one bin. The available information differs between time slices, due to sample  
143 selection and the length and resolution of individual pollen diagrams. Fewer sites are available prior  
144 to the Holocene (Giesecke *et al.*, 2014). The resulting dataset has been used for mapping abundance  
145 changes at individual sites (Brewer *et al.*, 2016), which may be used for comparison with the  
146 interpolated maps.

147

148 Interpolation and classification

149 Long distance transported pollen as well as pollen grains delivered to lakes from eroding older  
150 material biases the interpretation of small pollen proportions in terms of the regional occurrence of  
151 the parent tree. We applied threshold values (Lisitsyna *et al.*, 2011) to the pollen proportions ( $T_{int}$ ,  
152 Table 1) setting values below the threshold to zero prior to interpolation to reduce this bias. The  
153 resulting pollen proportions for each time slice were interpolated using the tricube distance-  
154 weighting function (Cleveland & Devlin, 1988, Huntley *et al.*, 1989) with a horizontal search limit of  
155 300 km radius and a vertical threshold of 500 m. Horizontal and elevation differences between grid  
156 cells and pollen diagrams are used as co-variables, making the procedure well suited for continental  
157 interpolations of pollen data (e.g. Williams *et al.* 2004), with an uneven spatial coverage. It is  
158 conceptually simpler than e.g. Universal Kriging and correctly displays outliers. The inclusion of  
159 elevation is important as it represents the change of vegetation with altitude, which is done by  
160 decreasing the weight of pollen diagrams at high elevations for adjacent grid cells with low elevation  
161 and vice versa. This limits the propagation of abundance information from a mountainous area into  
162 the neighbouring lowlands. Nevertheless, in the case of the *Fagus* distribution in the north of the  
163 Iberian Peninsula it was necessary to manually restrict the extrapolation towards the south, which  
164 was done by introducing pseudo-absences from non-existent sites with 0% *Fagus* pollen.

165 The resulting interpolations suggest an accuracy that is not inherent in the data. Pollen percentages  
166 suffer from the Fagerlind effect (Prentice & Webb, 1986), which arises from species specific pollen  
167 production and dispersal in combination with the closure effect of percentages. Therefore, the same  
168 pollen percentage at different sites may correspond to different abundances of the parent plants  
169 with a different dominant vegetation and/or site characteristics. A reduction of this bias is  
170 theoretically possible, however the required parameters of relative pollen productivity are not yet  
171 available for all of Europe. Other uncertainties adding to these interpolations stem from the uneven  
172 coverage of sites and the underrepresentation of dry environments. In order to acknowledge these  
173 uncertainties, we restrict the mapping and subsequent analysis to four abundance classes capturing

174 the main differences in the abundance of the parent plants (Table 1). The lowest class is designed to  
175 capture the regional presence of the taxon, while the highest abundance class was chosen to  
176 represent the area within which a species is regionally dominant or characteristic. In both cases we  
177 determined the threshold values in comparisons between interpolations of modern samples (1700-  
178 2010 A.D.) with species distribution maps and abundance information. The two remaining  
179 abundance classes were set to intermediate values with class two representing a more conservative  
180 threshold for presence and class three indicating increased abundance. The threshold for presence  
181 used on the interpolated surface (T1) was necessary to restrict distributions in data sparse areas  
182 where sites below and above the initial threshold for presence ( $T_{int}$ ) were far apart. No presence  
183 threshold was set for Poaceae as taxa of this family are presumed to occur everywhere in Europe  
184 and only changes in abundance through time and space are informative. *Pinus* and *Betula* are prolific  
185 pollen producers and their northern limit occurs in a landscape of low total pollen production. It is  
186 therefore impossible to find pollen percentage thresholds that would adequately describe their  
187 northern limits and thresholds were chosen to describe their southern boundaries (Lisitsyna *et al.*,  
188 2011). As a consequence, rates of spread cannot be obtained for these species based on this  
189 analysis. The results of the interpolations are presented as maps and numeric values for further  
190 analysis and data model comparison in the supplementary information to this publication (PANGAEA  
191 doi when accepted; currently at: [http://www.uni-goettingen.de/en/epd-interpolated-  
maps/538484.html](http://www.uni-goettingen.de/en/epd-interpolated-<br/>192 maps/538484.html) logon: epd, password: epd).

### 193 *Change in area and rate of spread*

194 In all area calculations we adjusted for the latitudinal reduction in area represented by grid cells.  
195 Area calculations of lower abundance classes include higher abundances. The general position of  
196 inferred distributions and abundance classes was compared with the distance to the Mediterranean  
197 and Atlantic coasts by computing the distance for all grid cells and summing all values from grid cells  
198 with the respective abundance class.



199 We restricted more detailed analysis of the dynamics of spread to the nine common arboreal taxa  
200 for which we can confidently estimate the northern distribution limit based on pollen. We limited  
201 the study area to north of 47°N latitude, which is outside the location of possible LGM distributions  
202 for the analysed tree taxa with the exception of *Picea* (Tzedakis et al., 2013). For this northern half of  
203 Europe, we fitted the logistic function to the increase in the area of presence with time and  
204 estimated the inflection point, the point at which the initial exponential increase in area starts to  
205 slow. Rates of overall spread and area doubling times were estimated for all abundance classes. We  
206 assumed a simple model of reaction diffusion describing the overall rate of spread  $V=2(kD)^{1/2}$  with  $k$   
207 as the intrinsic rate of population growth and  $D$  as the diffusion coefficient (Birks 1989). The slope of  
208 the square root of area increase over time is an estimate of  $(kD)^{1/2}$  and thus  $V$  can be obtained as an  
209 overall rate of spread, considering the time from the appearance of a taxon with the respective  
210 abundance class, until the time when maximum values were reached. The area-doubling time was  
211 estimated as  $\ln(2)/r$  based on a logistic model, where the growth rate  $r$  was determined as the slope  
212 of the regression between the decadal logarithm of  $(K-N)/N$  versus time  $t$ , with  $N$  as the area at time  
213  $t$ , and  $K$  as the carrying capacity set to the maximum area.

214 We used a more detailed estimate of the possible northern limit of thermophilous trees to estimate  
215 the rate of spread at 0.5 ka resolution (Figure 1). This configuration was used as a possible starting  
216 point for any spread. The limits were moved north in eastern Europe to avoid large initial dispersal  
217 jumps in data poor areas. Prior to calculations, we manually removed the appearance of isolated  
218 small occurrences that subsequently declined, while considering disjointed dispersal jumps growing  
219 into larger areas and/or higher abundance classes. This resulted in connected areas of distribution as  
220 the bases for analysis and this requirement is the reason why higher abundance classes, which often  
221 have disjoint areas, were not considered in this analysis. Rates were obtained as the shortest  
222 geographic distance between the centres of grid cells marking the distribution limits in two  
223 consecutive time slices and dividing the value by 0.5 ka. This yields rates of spread in all directions,  
224 however since the analysis was restricted to the area north of the Alps, changes of the southern

225 limits were not considered. We also computed the distance of the northward shift of the 95  
226 percentile of the distributions, with respect to distance to the Mediterranean Sea, using the initial  
227 set of taxa and based on the entire area represented by the maps.

### 228 *Difference maps and dynamics of change*

229 The initial interpolations, before the classifications described above, were used to calculate the  
230 difference in pollen proportions between consecutive time slices for each grid cell. The resulting  
231 values were classified into four classes of increase and decrease and one class of no change.  
232 Thresholds were obtained per taxon as the standard deviations (sd) of all values over all time slices,  
233 so that the value of zero was assigned to grid cells with less than one sd difference, while maximum  
234 and minimum values of 4 and -4 were assigned to differences larger than four sd. The resulting maps  
235 are provided as supplementary information (PANGAEA doi when accepted; currently at:

236 <http://www.uni-goettingen.de/en/epd-interpolated-maps/538484.html> logon: epd, password: epd).

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

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

### 244 *Results and Interpretations*

245 The Lateglacial vegetation in Europe was dominated by herbaceous vegetation types with abundant  
246 Poaceae and *Artemisia* as well as scrublands with *Juniperus* and *Betula nana* and boreal woodlands  
247 with *Pinus* and *Betula* trees. A continuous forest formed during the Lateglacial with a latitudinal  
248 treeline in central Europe (Theuerkauf & Joosten, 2012; Mortensen *et al.*, 2014). The treeline  
249 reached a more northerly position to the east of the Baltic Ice Lake (Amon *et al.*, 2014). However,

250 this treeline formed by the northern limits of *Pinus* and *Betula* is not adequately represented in the  
251 maps (see methods) resulting in biases in their Lateglacial distribution. This problem does not occur  
252 for *Picea*, which was most likely part of the latitudinal treeline east of the Baltic Ice Lake during the  
253 Younger Dryas (Heikkilä *et al.*, 2009) and elsewhere during the early Holocene (Giesecke & Bennett,  
254 2004).

255 The effect of the Bølling-Allerød warming and Younger Dryas cooling can be seen in the area of  
256 occurrence and/or abundance of some taxa (e.g. *Artemisia*, *Juniperus*, *Ulmus*), although the 500  
257 year-time slices adopted here can only weakly resolve the impact of these climate fluctuations (Fig.  
258 2, Appendix S1.1). The 12 ka time slice represents the situation just before the onset of Holocene  
259 warming at 11.7 ka (Rasmussen *et al.*, 2014), however, due to age uncertainty and the 500-year wide  
260 sampling window, some initial expansion may already be included. The onset of the Holocene  
261 warming sets the clear starting point for the expansion in area and abundance of many temperate  
262 woody taxa at the European scale. *Ulmus* and *Corylus* followed by *Quercus* and *Tilia* fill most of their  
263 current distribution area within 2 kyr from the onset of the Holocene (Fig. 2). *Fagus* and *Carpinus*  
264 represent the other extreme with hardly any response to the onset of the Holocene. They show a  
265 gradual increase in area almost until present that only starts after 9 ka. *Picea* and Ericaceae show  
266 similar trends of steady increase though the Holocene. *Alnus* and *Abies* show intermittent patterns  
267 with distribution expansions that start late, but stop during the mid-Holocene.

268 The increasing curves for the area of occurrence through time (Fig. 2) follow logistic models of  
269 population growth. This becomes particularly clear when limiting the area considered to central and  
270 northern Europe north of 47°N latitude (Fig. 3). The inflection point that was estimated for these  
271 logistic increases provides a parameter to describe the differences in the time required by the  
272 various species to fill their ranges. *Ulmus* and *Corylus* slowed their exponential increase less than 1  
273 ka after the onset of the Holocene at around 11.2 and 11.1 ka respectively. *Tilia* and *Quercus*  
274 followed at 10.3 ka and 10.1 ka, while *Alnus* started to spread late but rapidly reached the inflection

275 point at 9.5 ka. *Picea* survived the LGM north of 47°N latitude and its increase in apparent area of  
276 occurrence is gradual without a strong sigmoidal shape. Nevertheless, the age for the inflection  
277 point of 6.7 ka characterizes well its Holocene expansion in comparison to the other taxa. *Abies*  
278 started spreading north of the Alps around 9 ka and slowed its increase in area at around 5.9 ka.  
279 *Fagus* and *Carpinus* started to slow their spread at 4.9 ka and 4.8 ka, respectively.

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

296 The overall rates of spread presented in Fig. 5a assume the rate of spread to be constant through  
297 time, which we know was not the case. The highest rate of spread for the entire distribution is  
298 estimated for *Alnus* with 1000 m yr<sup>-1</sup>, while the estimates for most other taxa fall between 600 m yr<sup>-1</sup>  
299 for *Corylus* and 250 m yr<sup>-1</sup> for *Abies* and are thus comparable to the measures of the rate of spread in

300 Fig. 4. Only the gradual increase in the distribution of *Picea* results in a slow rate of 150 m yr<sup>-1</sup>. The  
301 fastest rate of spread recorded is for the highest abundance class of *Corylus*, caused by the rapid and  
302 often synchronous population increase of *Corylus avellana* across large areas of Europe (Giesecke *et*  
303 *al.*, 2011). The logistic growth model used in the calculation of the area doubling time (Fig. 5b)  
304 compensates for the saturation phase that reduces the slope in the overall estimate of spread in Fig.  
305 5a. This results in some interesting differences in the rank order, which are most pronounced for  
306 *Fagus* and *Carpinus*. The three higher abundance classes in *Carpinus* and the highest abundance  
307 class in *Fagus* have doubling times similar to early spreading taxa like *Tilia* and *Ulmus*.

308 The good agreement between the estimates of overall spread (Fig. 5a) based on different abundance  
309 classes is remarkable. Early Holocene rapidly spreading taxa *Alnus*, *Corylus*, *Ulmus* and *Tilia* show  
310 values above 400 m yr<sup>-1</sup> for all abundance classes. *Quercus* takes an intermediate position. Its  
311 postglacial spread north starts early, while the expansion at the northern limits in Sweden lasted  
312 until about 3 ka (e.g. Giesecke, 2005b). *Picea* clearly is the slowest in its overall dynamics, which is  
313 partly due to the fact that this analysis focusses on its Holocene dynamics, while its area of  
314 occurrence was already large during the Lateglacial. The tree was likely widespread in Europe during  
315 the coldest stages of the last glacial (Ravazzi, 2002; Latalowa & van der Knaap, 2006) and its  
316 Lateglacial history remains a focus of study and debate (Birks *et al.* 2012). The position of *Abies*  
317 differs between the panels in Fig. 5, with the overall rate of spread for all abundance classes being  
318 similar to *Picea*, while the doubling time for the first abundance class is close to that for *Quercus*.  
319 The obtained doubling times describe the Holocene dynamics of distributions and their use to  
320 estimate the size of the LGM distributions by extrapolation may not be appropriate here (Magri  
321 2008). However, they indicate that the taxa must have been widespread in the southern half of  
322 Europe during the LGM.

323 The Holocene vegetation history of Europe provides examples of both population expansions and  
324 declines in abundance. The overall area of occurrence contracted along the northern limits of

325 *Corylus*, *Ulmus*, *Tilia* and *Quercus* during the last 4 kyr. However, the decline in the area of  
326 occurrence is also due to a reduction in abundance below that which can be recognized using the  
327 applied percentage thresholds. This is mainly responsible for the strong decline in *Tilia* (Appendix  
328 S1.1), which is most likely influenced by forest clearance for agriculture (Turner 1962, Björse &  
329 Bradshaw 1998). The area curves for higher abundance classes document these shifts in the  
330 abundance of different species across Europe. The area curves for the highest abundance class show  
331 distinct peaks, some of which replace each other and thus characterize the different phases of  
332 European vegetation history (Fig. 6; see also Appendix S1.2). The 16 taxa considered here reach their  
333 largest area of the highest abundance class in the following order: Poaceae (15 ka), *Juniperus*-type  
334 (15 ka), *Artemisia* (12 ka), *Betula* (10.5 ka), *Corylus* (9.5 ka), *Pinus* (8.5 ka), *Ulmus/Zelkova* (7.5 ka),  
335 *Fraxinus* (7.5 ka), *Tilia* (6.5 ka), *Quercus* (6 ka), *Abies* (5.5 ka), *Alnus* (4 ka), *Carpinus* (3.5 ka), *Fagus* (3  
336 ka), *Picea* (1.5 ka), Ericaceae (0.5 ka). These peaks mark in most cases the culmination of the  
337 expansion phase and are succeeded by a period of decline. The abundance of *Ulmus* and *Tilia*  
338 characterize many European forests between 9 ka and 6 ka. The pattern also clearly depicts the well  
339 described decline of *Ulmus*, which is followed by *Tilia*, while the area of abundance rises for *Fagus*  
340 and *Carpinus*. The deforestation of Europe over the last 3.5 kyr is also clearly depicted by the  
341 increase in the area for the highest abundance class of Poaceae, with an associated decline in the  
342 area for abundant cover of *Fagus*, *Carpinus*, *Tilia* and *Quercus*.

343 The change in area and abundance for each taxon between two time slices is presented in the  
344 difference maps (PANGAEA doi) and these changes, summarized in one index (difference class  
345 multiplied by area) are presented in Fig. 7. This comparison shows large symmetry in population  
346 expansion and decline between north and south. Some species show more dynamics in the north  
347 (*Picea*) and others in the south (*Abies*), which is partly due to the centre of their distribution (Fig. 8).  
348 The genus *Quercus* is widespread in northern and southern Europe, while the lack of dynamics in  
349 northern Europe, except around 10 ka, is due to its increase and decline at low rates resulting in  
350 small differences over 500 year intervals. One would expect populations of temperate tree taxa that

351 survived the last ice age in southern Europe to begin expansions there. Once populations had grown  
352 in the south they would spread north and their expansion would continue there. This pattern is  
353 indeed visible for some taxa, in particular for *Fraxinus* and *Abies* where southern European dynamics  
354 clearly precede northern European changes. However, populations of *Tilia* and *Ulmus* expand almost  
355 in parallel in the south compared with the north, with a short lead in the south. On the other hand,  
356 for *Corylus* and *Alnus* the dynamics in the north appear to lead. *Fagus* populations have their highest  
357 rate of increase at the same time in the north and south around 5 ka. The dynamics of declining  
358 populations is mirrored for many taxa between north and south. Most symmetry in decline is visible  
359 for *Corylus*, while *Ulmus* declined earlier in the south compared with the north.

360 The asymmetry between northern and southern Europe in Fig. 7 already indicates where the main  
361 centres of distribution lie. To follow the change of the gravitational centre of the different taxa, we  
362 calculated the average distance of grid cells within the different abundance classes to the  
363 Mediterranean Sea and Atlantic Ocean (Appendix S1.3, S1.4 and Fig 8). In both cases the average  
364 distances for the different abundance classes are near each other for most taxa at most times,  
365 indicating that most distributions were symmetrical with higher abundance classes in the centre of  
366 the distribution. The abundance is skewed to the north for the boreal taxa *Pinus* and *Betula*, with  
367 higher abundance classes found successively further north, while the opposite trend is observed for  
368 *Quercus* with a southern affinity (Appendix S1.3). The symmetry of distributions often deteriorated  
369 when abundances declined. For example, the decline in the abundance of *Corylus* after its initial  
370 peak around 9.5 ka occurred mainly in the south and east without affecting the distribution area and  
371 consequently the gravitational centre of the abundant areas shifted north and west. The curves for  
372 *Picea* are striking. The distance to the Mediterranean describes the tree as a southern species during  
373 the early Holocene, when populations mainly expanded in the eastern Alps and Carpathians. In the  
374 Carpathians the dominance of *Picea* at mid-elevation is replaced by *Fagus* in the second half of the  
375 Holocene (Feurdean *et al.* 2010), while the tree expands in Fennoscandia during that time (Giesecke  
376 and Bennett 2004). As a consequence, the mean distance to the Mediterranean shifted for higher

377 abundance classes from southern dominance, as for *Quercus*, to northern dominance as for *Pinus*  
378 and *Betula*. At the same time the average distance to the Atlantic Ocean decreased steadily though  
379 the Holocene for all abundance classes. This westward shift was observed and reported for the two  
380 *Picea* distributions in central and northern Europe separately and it is interesting to see how both  
381 distributions shift simultaneously (van de Knaap *et al.* 2005, Giesecke and Bennett 2004). The two  
382 other latecomers *Fagus* and *Carpinus* follow the same trend, shifting the centres of their  
383 distributions from east to west with the general spread of the distribution in the same direction.

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

389

## 390 Discussion

### 391 Spread and population expansion

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

399 The observation that different abundance classes yield similar overall rates of spread (Fig. 5a) agrees  
400 with a simple diffusion model predicting that the speed of the wave can be obtained regardless of



401 the population threshold applied (Lubina & Levin, 1988). This would suggest that the wave is stable  
402 in space and even though the wave 'front' cannot be captured by palaeoecological methods  
403 (Bennett, 1986), the rate of spread may be obtained from higher abundance classes, where spread is  
404 followed by population expansion. A traveling wave of expanding populations has been described  
405 for *Fagus* in North America (Woods & Davis 1989) and *Picea* in Scandinavia (Giesecke, 2005a) and  
406 appears to be the rule rather than the exception, even where spread and population expansion may  
407 have been disconnected as in the case of *Picea* (Giesecke, 2013).

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

422 *Fagus* genetic markers in extant populations have also yielded new insights into the understanding  
423 of its postglacial history. They confirm earlier claims (e.g. Pott, 2000) that *Fagus* survived the LGM on  
424 the Iberian Peninsula (Magri *et al.*, 2006) and possibly also in south-western France (de Lafontaine *et*  
425 *al.* 2013), yet these areas contributed little to the postglacial colonization of Europe. Similarly, the

426 populations on the Apennine and Balkan peninsulas did not contribute to the postglacial spread of  
427 the tree. Central and north western Europe are dominated by a single chloroplast haplotype, which  
428 is in sharp contrast with the high diversity of the southern edge of the distribution in northern  
429 Greece, where eight different chloroplast haplotypes are present on a small solitary mountain  
430 (Papageorgiou *et al.*, 2014). The simulations by Saltré *et al.* (2013) illustrate how the expansion from  
431 a more northerly population may block the northward spread from populations in the south.  
432 However, the dynamics of postglacial population expansion as depicted in the maps compiled here  
433 show that the *Fagus* populations on the Balkan and Iberian Peninsulas remained small until the mid-  
434 Holocene and grew in parallel with the populations in central Europe (Fig. 7; Giesecke *et al.*, 2007).  
435 Thus the LGM distribution of the tree does not inform on the time of population expansion in central  
436 and north-western Europe as has often been postulated (e.g. Lang 1994). Using the proposed LGM  
437 distributions as starting points to simulate the postglacial spread of *Fagus* as well as *Picea* (Saltré *et al.*  
438 *al.* 2013, Lehsten *et al.* 2014) does therefore not help develop understanding of the postglacial  
439 history of either species. In both cases similarities between simulated and reconstructed patterns  
440 may be accidental and although we have not yet understood why these two species spread late, the  
441 observations summarized here do not indicate that the time of population expansion can be  
442 explained by migrational lag. Vegetation models that can describe the spread of plants  
443 mechanistically are useful as they can test the importance of particular components like internal  
444 variability (Nabel *et al.*, 2013), but the models need further improvement before they can provide  
445 convincing estimates of the consequence of global warming for vegetation (Snell *et al.*, 2014). The  
446 patterns and rates presented here can be used to test these models, but care is needed in the  
447 selection of suitable taxa. Without a better understanding of early Holocene limitations for *Picea* and  
448 *Fagus* Modelling the postglacial colonisation of Europe may be useful for *Quercus*, but is of less  
449 value for *Picea* and *Fagus* without a better understanding of their early Holocene controls. Genetic  
450 markers in *Quercus* document that many different populations from around the Mediterranean  
451 Basin have spread north with postglacial warming (Petit *et al.*, 2002), yet these different immigration

452 routes find no reflection in a differentiated time of initial population expansion (Brewer *et al.*, 2002,  
453 Giesecke 2016). High resolution mapping of haplotypes in extant white oak populations in western  
454 France highlights the importance of frequent LDD events, which could explain the observed  
455 patchwork of distinct haplotypes of chloroplast DNA markers (Petit *et al.* 1997, Bialozyt *et al.* 2006).  
456 Simulations using this example also link the frequency of LDD to population density (Bialozyt *et al.*  
457 2006).

458

#### 459 [Notes on postglacial history and apparent rates of spread for common European trees](#)

460 The highest apparent rates of postglacial spread in Europe are found for *Ulmus* and *Corylus*, ignoring  
461 *Pinus* and *Betula*. *Corylus* has a short generation time of only 10 years. *Ulmus* needs more years to  
462 set seed (30-40), while its light seeds may be easily picked up by strong winds and transported over  
463 long distances. In northern Europe we have to consider three different species of *Ulmus* that may  
464 have contributed to the rapid spread of the genus. It is conceivable that the early Holocene spread in  
465 central and northern Europe started for both *Ulmus* and *Corylus* from outposts north of the Alps,  
466 although this presumption is currently not supported by evidence (Giesecke, 2016). Pollen  
467 proportions indicative of the regional presence of both taxa appear within a few hundred years after  
468 the onset of the Holocene in Scandinavian pollen diagrams and the taxa may even have been part of  
469 the initial colonization of bare ground after the retreat of the ice in north central Sweden during the  
470 early Holocene (e.g. Giesecke, 2005b). Thus rates of spread for these two taxa in the order of 1000 m  
471  $\text{yr}^{-1}$  do seem likely. However, the rapid expansion of *Corylus* around 10.5 ka is probably not a  
472 consequence of its spread. The timing of this expansion is similar for populations in south and  
473 central Europe (Giesecke *et al.*, 2011) regardless of the time the species arrived at the site. This  
474 would suggest at least partial climatic control of the final expansion of *Corylus* and the high apparent  
475 rate of spread for the highest abundance class in Fig. 5a is consequently not informative with respect  
476 to the rate of spread.

477 *Tilia cordata* and *Tilia platyphyllos* are the most widespread species of the genus in Europe. *T.*  
478 *platyphyllos*-type can be separated morphologically (Beug, 2004), but this has not been applied  
479 consistently and we therefore combined identifications to the genus level. *Tilia* spreads quickly in  
480 central Europe favoured by a short generation time (10-30 years) and wind dispersed seeds,  
481 although its rate of spread slows down towards its northern distribution limits. The control of  
482 summer temperature and growing season length on seed maturation in *Tilia cordata* has been well  
483 documented (Pigott & Huntley, 1981; Pigott, 1981) and these climatic factors may have slowed the  
484 rate of population growth near its northern limits. While the maximum rate of spread is lower than  
485 for *Corylus* and *Ulmus*, the average rates are similar. Huntley & Birks (1983) and Birks (1989) report  
486 500 m yr<sup>-1</sup> as the fastest observed rate, which agrees with our average values. The current evidence  
487 gives no reason to reduce the early Holocene rates of spread below this value.

488 The deciduous *Quercus* species in Europe share the same chloroplast haplotypes through  
489 hybridization. Moreover, Petit *et al.* (2004) suggest that *Quercus petraea* spreads by pollen dispersal  
490 through hybridization with *Quercus robur*, whose acorns are preferred by jays and thus dispersed  
491 over long distances. *Quercus* pollen disperse well so that it is difficult to distinguish between  
492 presence and absence based on pollen proportions (Lisitsyna *et al.* 2011) and the pollen type is  
493 found in small abundances in sediments of Lateglacial and early Holocene age over much of Europe.  
494 Macrofossil finds are rare and the first definite evidence for the occurrence of *Quercus* north of the  
495 Alps is the base of the oak dendrochronology, with the oldest ring dated to 10,430 cal. BP (Friedrich  
496 *et al.*, 2004). Of all taxa with a clear early Holocene spread in northern Europe, *Quercus* needs the  
497 longest time to reach maturity (30-60 years), which explains the slowly increasing pollen values at  
498 individual sites. The curves rise faster in the west which give a visual impression of an eastward  
499 direction of spread, but genetic evidence documents the parallel south to north spread of *Quercus*  
500 populations (Petit *et al.*, 2002). *Quercus* populations had already expanded during the warm phases  
501 of the Lateglacial south and west of the Alps (Finsinger *et al.*, 2006, 2011). Although there is no  
502 evidence documenting its Lateglacial occurrence north of the Alps, small outposts might have

503 become established and survived the Younger Dryas (Giesecke, 2016). The slow rates of population  
504 growth in eastern Europe and near the northern borders reduce the overall rate of spread. Even if  
505 we assume that outposts were present in central Europe before the onset of the Holocene,  
506 spreading rates of the order of 500 m yr<sup>-1</sup> need to be considered to explain all patterns, including the  
507 British Isles (Birks, 1989).

508 Three **Alnus** species are included in the genus analysed here. Although, pollen of *A. viridis* can be  
509 separated (Beug, 2004), this differentiation has not been consistently made. The differentiation  
510 between *Alnus incana* and *Alnus glutinosa* is more difficult and only rarely attempted (e.g. Bos *et al.*,  
511 2012). *Alnus viridis* is a shrub occurring mainly in the upper montane forest in central and southern  
512 Europe including the Alps, the Carpathians and Corsica. It is missing in Scandinavia, while it has  
513 occurrences in northern Russia. *A. incana* has an eastern and montane distribution including most of  
514 Scandinavia and the Alps, but is absent in the west. *A. glutinosa* has the widest distribution in  
515 Europe, while it does not grow as far north as *A. incana* in Scandinavia. The current distribution of *A.*  
516 *incana* and *A. viridis* would suggest that these species may have occurred in central Europe during  
517 the LGM and Lateglacial and pollen of *A. viridis* is occasionally identified in Lateglacial sediments  
518 from central Europe (e.g. Wolters, 1999). However, *Alnus* pollen is abundant in older sediments and  
519 enters basins with catchment erosion during the Lateglacial. Consequently, information on the  
520 Lateglacial occurrence of *A. incana* and *A. glutinosa* is often difficult to interpret (Douda *et al.*, 2014).  
521 The identification of *A. incana* fruits in early Holocene sediments from the western Netherlands  
522 dating to around 11400 cal. BP (Bos *et al.*, 2005) is most interesting as the location is west of the  
523 current distribution of *A. incana* and the timing is prior to the general increase of the pollen type.  
524 Pollen morphological identifications also indicate the occurrence of *A. incana* in the northern Upper  
525 Rhine Graben during the early Holocene (Bos *et al.*, 2012). We chose a rather high threshold for  
526 mapping the presence of *Alnus* to avoid the inclusion of redeposited pollen, inevitably ignoring this  
527 early Holocene history. The threshold captures the establishment of *A. glutinosa* near the site and  
528 the data may therefore primarily represent the expansion of this species. In eastern Europe the data

529 depict a clear east to west direction of spread. Around the Baltic Sea basin, the spread culminated in  
530 a rapid expansion, which occurred synchronously over a large region (Giesecke *et al.* 2011). At least  
531 in northern Scandinavia the spread and expansion of *A. glutinosa* occurred together with *A. incana*  
532 (Giesecke, 2005c). Further west, the expansion is regionally asynchronous with a gradual or rapid  
533 increase and may be described as patchy and erratic, particularly for the British Isles (Bennett and  
534 Birks 1990). Thus there is a sharp contrast in the behaviour of *A. glutinosa* between eastern and  
535 western Europe. The delay in initial population expansion of approximately 1500 years after the  
536 onset of the Holocene is difficult to explain. *Alnus* fruits, especially *A. glutinosa*, are well adapted to  
537 dispersal by water and with many European rivers having a south to north direction, fruits could  
538 traverse central Europe in weeks rather than millennia. The high overall rates of spread and area  
539 doubling time show this, placing *Alnus* in a group with *Corylus* and *Ulmus* with respect to realized  
540 rates of spread. Huntley and Birks (1983) also consider *Alnus* to be the fastest spreading taxon, while  
541 the estimate of only 100-250 m yr<sup>-1</sup> by Feurdean *et al.* (2013) disagrees with the rapid spread and  
542 expansion in Scandinavia.

543 The genus ***Abies*** includes several species in Europe with distributions in the Mediterranean of which  
544 only *Abies alba* occurs north of the Alps. *Abies sibirica* grows in Russia outside the area considered  
545 here, while occasional finds of *Abies* pollen in northern Russia and Fennoscandia may originate from  
546 this species. *Abies* pollen is found in diagrams from the Mediterranean during the Lateglacial and  
547 clearly spreads in the northern Apennines during that time, from where it expanded rapidly with the  
548 onset of the Holocene (Vescovi *et al.*, 2010). The comparison of pollen diagrams from the Alps by  
549 van der Knaap *et al.* (2005) gives the impression that the tree crossed the mountains. Tinner & Lotter  
550 (2006) find this to be a conceivable scenario. The EPD point maps (Brewer *et al.*, 2016) document  
551 that population expansion occurred earlier in the western compared to the northern Alps,  
552 suggesting that the tree may also have spread along the western flanks of the mountains. The onset  
553 of rising *Abies* curves north of the Alps dates to 8.5 ka and 8.2 ka and the climatic disturbance of the  
554 8.2 event may have favoured this initial expansion (Tinner & Lotter, 2006). Apart from the more

555 rapid expansion in the western Alps between 9 ka and 8.5 ka, the spread of *Abies* in central Europe  
556 occurs at low rates of around 100 m yr<sup>-1</sup> (Fig. 4). The overall estimate of spread (Fig. 5) for the  
557 different abundance classes yields around 200 m yr<sup>-1</sup> and agrees with Huntley and Birks (1983) as  
558 well as Feurdean *et al.* (2013). *Abies* did not spread far north of possible LGM distributions and no  
559 accounts of large dispersal jumps have so far been published, so this may be an example of a slow  
560 rate of spread. Tinner *et al.* (2013) argue that the spread of *Abies* was suppressed by human activity  
561 over the past 5 kyr, explaining the observed slower rate of spread and incomplete range filling.

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

580 (2013) of less than 150 m yr<sup>-1</sup> are surely too low and the overall estimates in Fig. 5 of 350-450 m yr<sup>-1</sup>  
581 for the first two abundance classes may be more robust.

582 The data for *Fagus* mainly represent the single species *Fagus sylvatica*. While *Fagus orientalis* pollen  
583 cannot be separated, this species only occurs in the Balkans where it hybridizes with *F. sylvatica*. As  
584 described above, mapping of genetic markers in extant populations confirmed the LGM survival of  
585 the tree around the Mediterranean. Pollen diagrams document how central Italian populations  
586 expanded during the Lateglacial, while we know from genetic studies that this expansion did not  
587 lead to a spread out of the Iberian Peninsula (Magri *et al.*, 2006). By around 8 ka the tree had spread  
588 north of the Alps (Tinner & Lotter, 2006) and this may be the best region and time to estimate  
589 spreading rates for this tree, as later expansions in central and northern Europe are often connected  
590 with human activity (Giesecke *et al.*, 2007). The average rate of spread of 400 m yr<sup>-1</sup> for this time  
591 may be a guide. However, the overall Holocene estimate of at least 300 m yr<sup>-1</sup> from Fig. 5 is still  
592 twice the maximum rate from Feurdean *et al.* (2013). *F. sylvatica* produces seed at an age of about  
593 50 years, partly explaining the slow population growth rates and comparably low spreading rates .  
594 After its initial appearance north of the Alps, the further spread of the tree slowed as documented in  
595 Fig. 4. As with *Carpinus*, many central European pollen diagrams show a long tail of *Fagus* pollen  
596 before its final expansion that is often connected to human activity in the northern lowlands of  
597 central Europe as well as in Scandinavia (Ralska-Jasiewiczowa *et al.*, 2003; Bradshaw & Lindbladh,  
598 2005; Bradley *et al.*, 2013). The population dynamics of *Fagus* in the Balkans parallels some of the  
599 central European patterns with initial expansion around 8.5 ka and a further expansion after 5 ka,  
600 which is also seen in the Carpathians. However, in these regions the dynamics of *Fagus* expansion  
601 seem unrelated to human activity. *Fagus* persisted during the LGM on the northern Iberian Peninsula,  
602 while populations generally only expanded during the late Holocene with an east to west gradient in  
603 timing and abundance. Human activity may have led to a further expansion at some Iberian sites,  
604 although it cannot explain the overall regional patterns (López-Merino *et al.*, 2008, Muñoz Sobrino *et*  
605 *al.*, 2009). Thus the postglacial history of *Fagus* across Europe is complex with different drivers



606 operating at different times in different regions. A slow spread of the species may only be one factor  
607 with a contribution in some regions and cannot explain the patterns on the European scale.

608 The postglacial history of *Picea* has probably received the most attention of all the European trees.  
609 We can link the pollen type primarily to the single species of *Picea abies* since *Picea omorika*, with  
610 the same pollen type, is restricted to a small area in eastern Bosnia and Herzegovina and western  
611 Serbia. *Picea obovata* is restricted to Siberia as documented by genetic evidence (Tollefsrud *et al.*  
612 2015). Hybridization with *P. abies* occurs mainly around the Urals, but gene flow via pollen can be  
613 detected as far west as Scandinavia (Tsudea *et al.* 2016). *Picea*'s winged seeds can disperse over  
614 large distances and claims that the tree established on mountaintops in Scandinavia as early as the  
615 Lateglacial (Kullman, 2008) imply effective LDD that is in sharp contrast to the slow spread of denser  
616 populations. Unlike *Fagus* and *Carpinus*, its late Holocene expansion in southern Scandinavia cannot  
617 be linked to human activity (Bradshaw & Lindbladh 2005, Giesecke, 2004). Of all the late expanding  
618 species, it shows the clearest trend of an east-west shift in the centre of its distribution and since  
619 this cannot be explained by slow migration or human impact, we suggest that climate is a good  
620 candidate explaining its Holocene vegetation history.

621

## 622 Comparisons between Europe and North America

623 Estimated rates of postglacial spread of woody taxa in eastern North America are nearly always  
624 lower compared to the rates discussed here, regardless of the method used to obtain them. Davis  
625 (1976) published the first rates of spread based on independently dated pollen diagrams and used  
626 the increase in pollen accumulation rates as indication for the local arrival of a taxon. Based on a  
627 limited set of sites, she obtained rates between 350-500 m yr<sup>-1</sup> for *Pinus banksiana/resinosa* and 100  
628 m yr<sup>-1</sup> for *Castanea* (Davis, 1976). Delcourt & Delcourt (1987) used a modern dataset to interpret the  
629 regional arrival of a taxon to produce isochrone maps and evaluate the spread of woody plants along  
630 five different north-south tracks. They obtained average rates of spread between 287 m yr<sup>-1</sup> for *Salix*

631 and 70 m yr<sup>-1</sup> for *Nyssa*, including individual maximal dispersal jumps of 1044 m yr<sup>-1</sup> for *Tsuga* and  
632 753 m yr<sup>-1</sup> for *Tilia*. Highest rates of spread were observed for the Lateglacial between 17 ka and  
633 13.8 ka and thus much earlier compared to Europe, although also at lower latitudes. Ritchie and  
634 MacDonald (1986) presented a study with the highest rates of spread in North America namely for  
635 the spread of *Picea glauca* from south-central Alberta to the Mackenzie Delta with rates of 2000 m  
636 yr<sup>-1</sup>, while they reported rates of 2-300 m yr<sup>-1</sup> in other regions. The apparently high rates in the  
637 western interior may, however, result from an eastward spread of populations that survived the ice  
638 age in Alaska (Anderson *et al.*, 2006). Ordonez & Williams (2013) used well-dated pollen diagrams to  
639 model past species distributions using simulated past climate. Core distributions moved northwards  
640 at maximal mean velocities of 188 m yr<sup>-1</sup> for *Abies* and 153 m yr<sup>-1</sup> for *Alnus* during 12-10 ka and shifts  
641 of the southern boundaries occurred at similar or even higher rates. In Europe, the position of most  
642 rear-edge distributions has not changed significantly during the last 15 kyr, except perhaps for  
643 *Betula* which declined in abundance at its southern distribution limits in Italy during the early  
644 Holocene (Magri *et al.*, 2015). All other boreal and temperate trees and shrubs remain present in  
645 southern European mountains. *Pinus sylvestris* for example dominates the northern boreal forest in  
646 Scandinavia and grows at or near the tree-line on mountains in Spain, Greece and northern Italy.  
647 Bennett *et al.* (1991) speculate that the southern edge of the distributions of the European woody  
648 flora was maintained in these southern European mountains through glacial-interglacial cycles. It  
649 may also be argued for North America that the southern distribution limits for temperate species  
650 have not significantly moved north (Bennett *et al.* 1991), however here temperate trees may have  
651 survived close to the ice margin that extended much further south (McLachlan *et al.*, 2005).  
652 Consequently, studies estimating rates of postglacial spread in eastern North America have  
653 considered a wide latitudinal range where the trees in question may have occurred during the LGM.  
654 In this analysis we have focused on rates of spread north of 45°N in Europe, which in eastern North  
655 America corresponds to north of the Canadian border. The northern limits of several temperate  
656 species in Europe reach 60°N, and these high northern limits are due to the Gulf Stream pumping

657 heat to high latitudes and the westerly winds pushing it into the continent. As a consequence,  
658 January isotherms in Europe have a strong N-S component while they run predominantly east west  
659 in eastern North America. The prevailing westerlies would also propagate rapid shifts in sea surface  
660 temperature in the north Atlantic connected to the mode of the North Atlantic Deep Water  
661 formation, such as its “off” mode during the Younger Dryas (Rahmstorf, 2002). Compared to eastern  
662 North America, the rate of climate change with the onset of the Holocene was therefore most likely  
663 much higher in Europe with highest rates near the Atlantic coast (Heiri *et al.*, 2014). Higher rates of  
664 climatic changes in Europe might explain the comparably faster apparent rates of spread and higher  
665 rates of vegetation change. The slower meltdown of the larger Laurentide ice sheet may have set a  
666 slower pace for North American climate and vegetation change during the Lateglacial and early  
667 Holocene (Shuman *et al.*, 2002). However, Delcourt & Delcourt (1987) note that in eastern North  
668 America the spread of trees along the Atlantic coast was initially delayed and subsequently achieved  
669 the highest rates.

670 Human influence has rarely been discussed in the spreading of tree taxa in North America, although  
671 humans were present in the postglacial landscape and probably influenced fire regimes and  
672 cultivated crops by 3.8 ka (Smith & Yarnell, 2009). Indians may have affected regional distribution  
673 limits of fire-sensitive hardwoods at the prairie-forest transition zone for a long time (Grimm, 1984).  
674 By contrast in Europe, there has been considerable discussion about potential human impact on the  
675 distribution and abundance change of several trees, particularly *Abies* (Tinner *et al.*, 2013), *Carpinus*  
676 (Ralska-Jasiewiczowa *et al.*, 2003), *Fagus* (Küster, 1997) and *Tilia* (Turner, 1962). The effect of  
677 humans on European vegetation was particularly pronounced during the second half of the  
678 Holocene (Molinari *et al.* 2013) and the conversion of forest to agricultural land is clearly visible in  
679 the increase of area dominated by grasses since 4 ka (Fig. 6). The late Holocene spread of *Fagus* in  
680 northern Europe has almost certainly been catalysed by anthropogenic activities (Bradshaw, 2004)  
681 which cannot be separated from a potential response to climate and we may never know for certain  
682 if the tree would have been able to reach its current northern limits in Sweden, western Norway,

683 Scotland and Ireland without human assistance. Genetic markers have provided supporting evidence  
684 for likely human translocation of trees such as *Castanea sativa* and *Pinus pinea*, whose  
685 Mediterranean distributions lack normal genetic structure (Fineschi *et al.*, 2000, Vendramin *et al.*,  
686 2008) and whose ranges have been significantly increased through millennia of cultivation  
687 (Conedera, 2004). Two types of dynamic possibly mediated by human activities emerge from our  
688 analyses. Firstly, disturbance-mediated population increases, either short-lived as seen with  
689 *Carpinus* in north-eastern Europe (Ralska-Jasiewiczowa *et al.*, 2003) or more sustained as shown by  
690 *Fagus* in northern Europe (Giesecke *et al.*, 2007). Secondly declines in abundance that are not  
691 necessarily linked to range contractions, best demonstrated for *Tilia* population declines in  
692 connection with forest clearance for agriculture (Turner, 1962), but also described for *Abies* linked to  
693 domestic grazing and use of fire (Tinner *et al.*, 2013). Human activities have therefore had a far  
694 greater influence on taxon spread and distributional limits in the Holocene of Europe than in North  
695 America, yet the pollen record for forest trees has been dominated by natural population dynamics  
696 until recent centuries (Bradshaw, 2004). Today very little 'natural' forest remains and the current  
697 population size of European trees is largely an outcome of recent land-use (Bradshaw *et al.*, 2015).

#### 698 Explanations for Holocene shifts in tree abundance

699 The vegetation cover of Europe has changed profoundly over the course of the Holocene with  
700 changing dominance of different woody taxa. Their time of dominance corresponds to their time of  
701 spread, but it was probably not the species specific rate of spread that determined the time of  
702 dominance in most cases. The late-arriving species *Fagus* and *Carpinus* do not show a constant slow  
703 spread northward that would explain their late arrival at their northern limits. The expansion of  
704 *Fagus* populations in the Balkan and Iberian peninsulas, where the species occurred during the LGM,  
705 was as late as in central Europe where the tree was previously absent. *Picea* presumably reached  
706 mountain tops in Scandinavia during the Lateglacial and early Holocene, but populations did not  
707 expand until at least 5 ka later. Thus the late expansion of particularly *Fagus*, *Carpinus* and *Picea*

708 cannot be explained by “migrational lag”, while a number of taxa that have not filled their potential  
709 distribution and are restricted to southern Europe (Svenning *et al.*, 2008) show a “lack of migration”.

710 The glacial/interglacial cycle first proposed by Iversen (1958) may have some power explaining the  
711 late expansion of some trees (Birks & Birks, 2004, Kuneš *et al.*, 2011). Glacials reset soil formation  
712 particularly in high latitude areas and the young soils gradually leach phosphorus (Boyle *et al.*, 2013).  
713 Thus while phosphorus may be readily available in young soils during the initial phase of an  
714 interglacial, with time this nutrient becomes increasingly limiting to plant growth. Kuneš *et al.* (2011)  
715 suggest that plants with phosphorus -mining ectomycorrhiza would therefore be favoured during  
716 the later stages of interglacials and lists *Fagus*, *Capinus* and *Picea* among those. The constant  
717 increase in area with various abundance classes of Ericaceae pollen over the last 8 kyr also attests to  
718 gradual changes in soils, namely paludification increasing the amount of peatland as well as  
719 podsolization reducing soil fertility. However, *Corylus* also possesses ectomycorrhiza and decreases  
720 in abundance particularly in more continental areas during the second half of the Holocene, which is  
721 unlikely to simply be due to the species being out-shaded by the expansion of *Fagus*. There is a  
722 simultaneous westward shift of *Picea* towards the Atlantic coast. *Corylus* benefits from mild winters  
723 while they seem to limit the natural distribution of *Picea* in Europe. Thus a decline of *Corylus* in more  
724 continental areas and a spread of *Picea* towards more oceanic regions may be interpreted as caused  
725 by decreasing winter temperatures in continental areas due to a reduction in the strength of the  
726 westerly winds (Giesecke *et al.*, 2008).

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

731 **Conclusions**

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

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

751

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758

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#### 1061 DATA ACCESSIBILITY

1062 All pollen data used for the maps are available from the European Pollen Database (EPD;  
1063 <http://www.europeanpollendatabase.net/>). The maps generated for this study are available as PDFs  
1064 as well as numerical values from the Pangaea database: <http://doi.pangaea.de/PANGAEA> when  
1065 accepted and can be currently viewed at: [http://www.uni-goettingen.de/en/epd-interpolated-](http://www.uni-goettingen.de/en/epd-interpolated-maps/538484.html)  
1066 [maps/538484.html](http://www.uni-goettingen.de/en/epd-interpolated-maps/538484.html) logon: epd, password: epd.

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1068 [Supporting Information](#)

1069 Additional Supporting Information may be found in the online version of this article:

1070 [Appendix S1 Additional Figures.](#)

1071 [Biosketches](#)

1072 Thomas Giesecke is a palaeoecologist interested in ecosystem dynamics on scales from decades to  
1073 glacial interglacial cycles, trying to tease apart internal vegetation drivers such as plant spread from  
1074 external forcing like climate change. Together with M.L., S.B., W.F. and R.B. he is working with the  
1075 EPD aiming to increase its usefulness as a resource for the immediate and wider scientific  
1076 community. The group also uses this resource to address continental scale questions of past  
1077 vegetation change.

1078 Author contributions: T.G., SB, WF and RB had the original idea and M.L. compiled the data. S.B.  
1079 constructed the maps; T.G. and S.B. performed analyses; T.G. wrote the paper with the substantial  
1080 contributions from M.L., S.B., W.F. and R.B.

1081

1082 **Table**

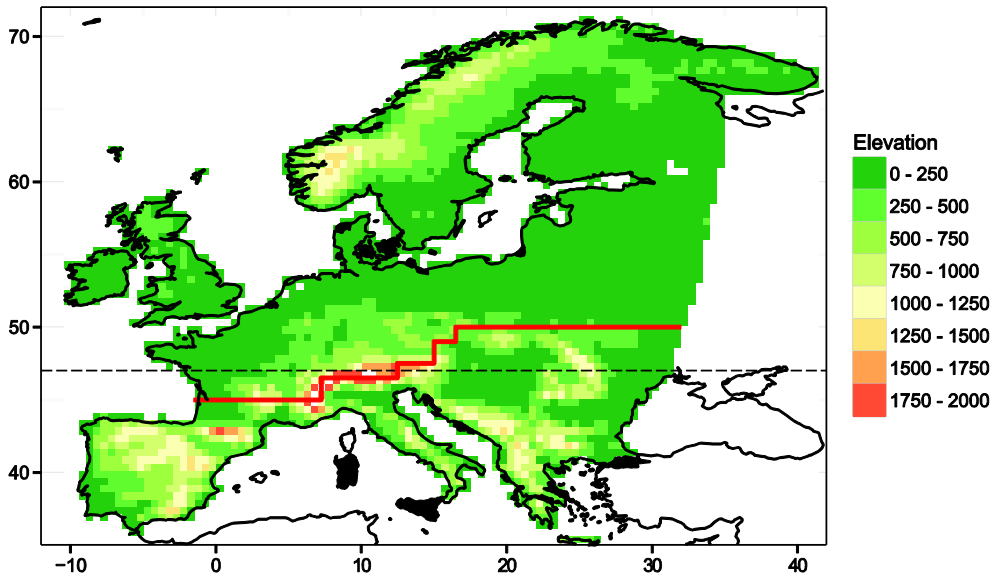
1083 Table 1. Pollen percentage thresholds. The threshold  $T_{int}$  is applied before the interpolation  
1084 procedure. Thresholds T1 to T4 are the lower limit of the four abundance classes applied to the  
1085 results of the interpolation.

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

1086

1087 **Figures**

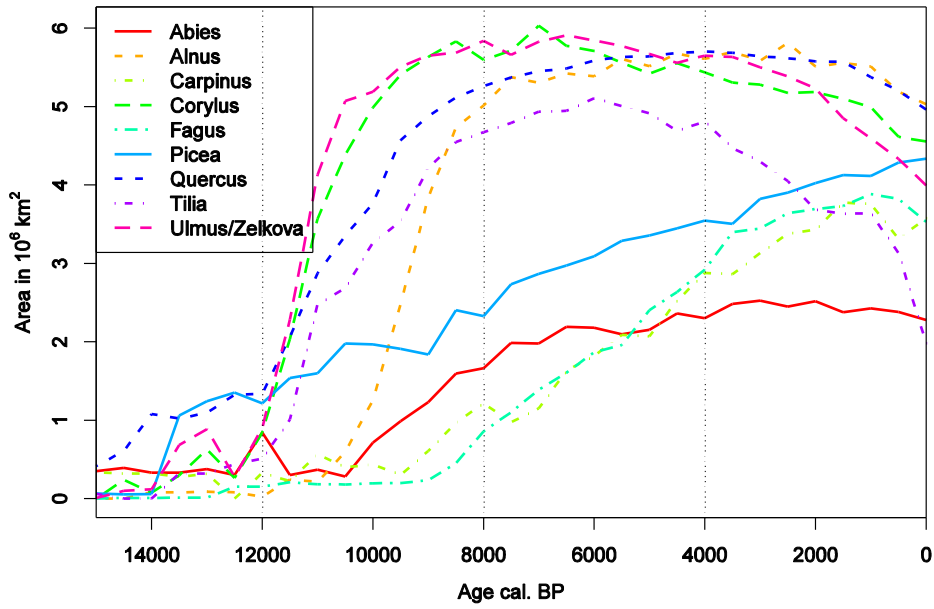
1088 **Figure 1** Study area of Europe restricted towards the east in a line from the Black to the White Sea.  
1089 The red line marks the starting point for the evaluation of the rate of spread ignoring the regions to  
1090 the south as here species may have survived the last ice age so that patterns are more difficult to  
1091 interpret and site density is lower, leading to additional biases. The broken line marks 47°N latitude,  
1092 which was used as a limit to contrast the dynamics of change between northern and southern  
1093 Europe.



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1096 **Figure 2** Postglacial changes in area of occurrence for the most common European tree taxa based  
1097 on interpolation and classification of pollen percentages.

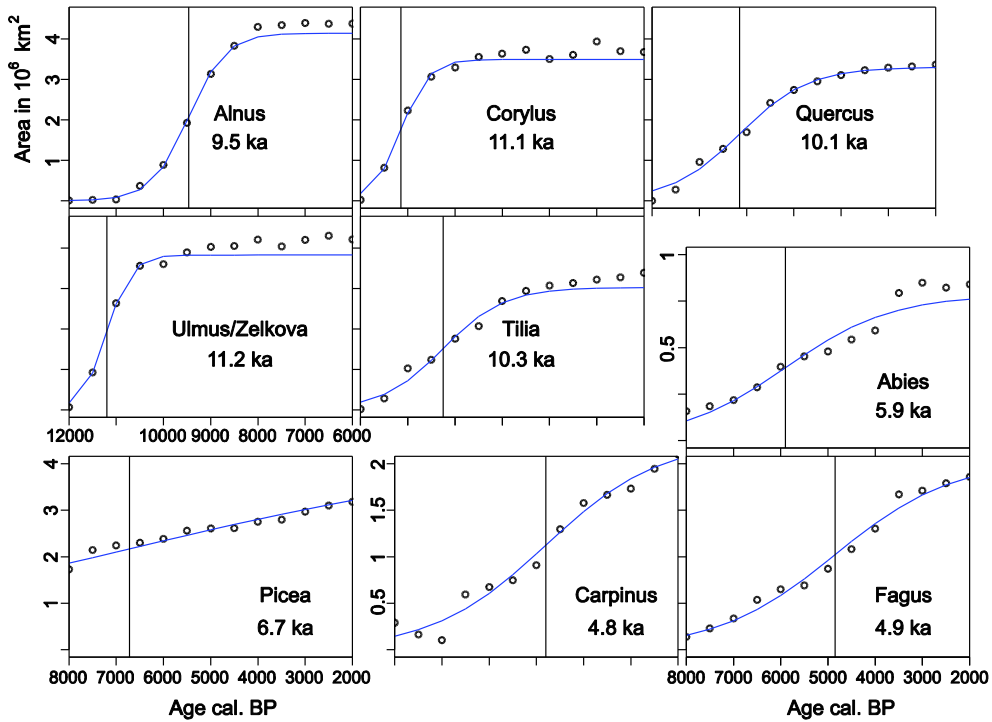


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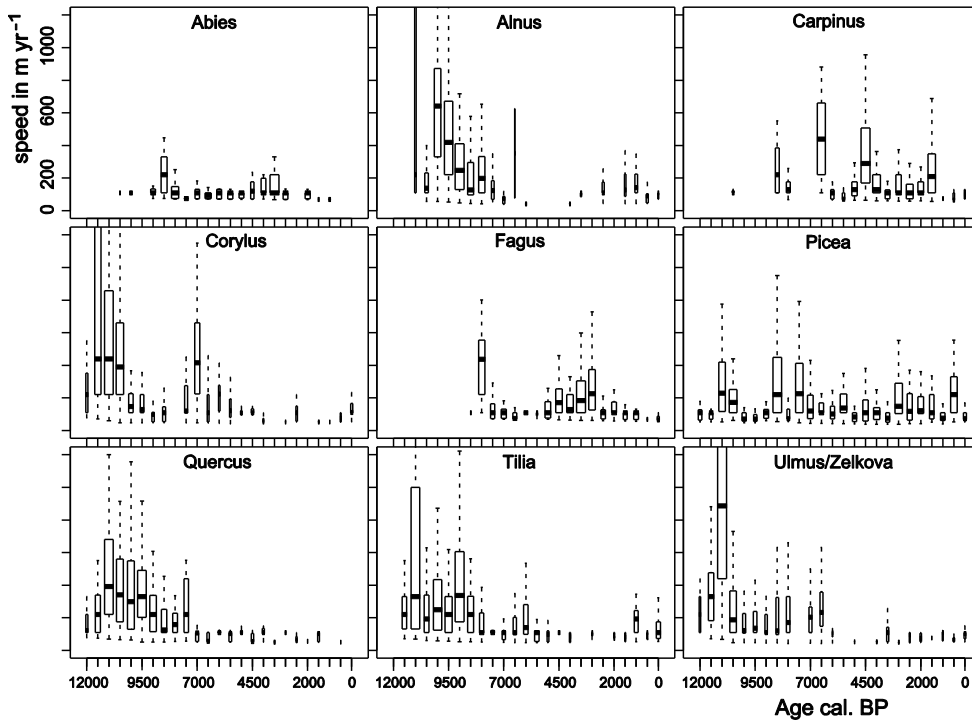


1100 **Figure 3** Fitted logistic functions to the increase in area of occurrence in Europe north of 47°N  
 1101 latitude as estimated from interpolation and interpretation of pollen percentages. The inflection  
 1102 point, where the exponential increase starts slowing down, is marked by the vertical line and its age  
 1103 given below the taxon name. Taxa are grouped according to the timing of the area expansion and  
 1104 differences in overall area.



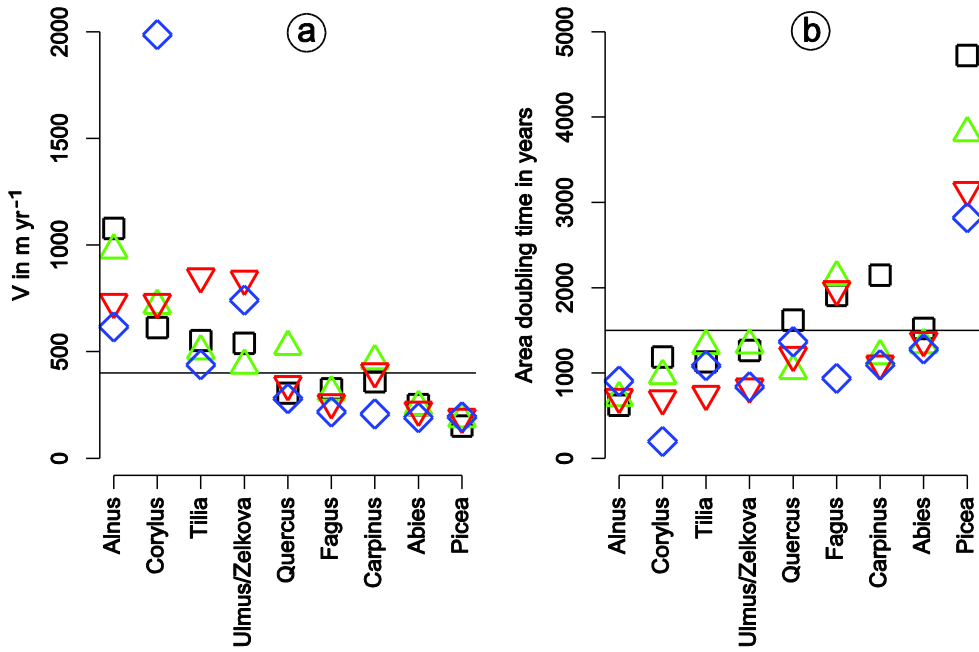
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1107 **Figure 4** Boxplots for rates of spread as obtained by the shortest distance between two grid cells  
 1108 marking the area of inferred occurrence in consecutive time slices. Note that the width of a box  
 1109 indicates the number of observations, with thin boxes indicating that distribution shifts occurred  
 1110 along a small section of the mapped limit. Negative shifts were ignored.



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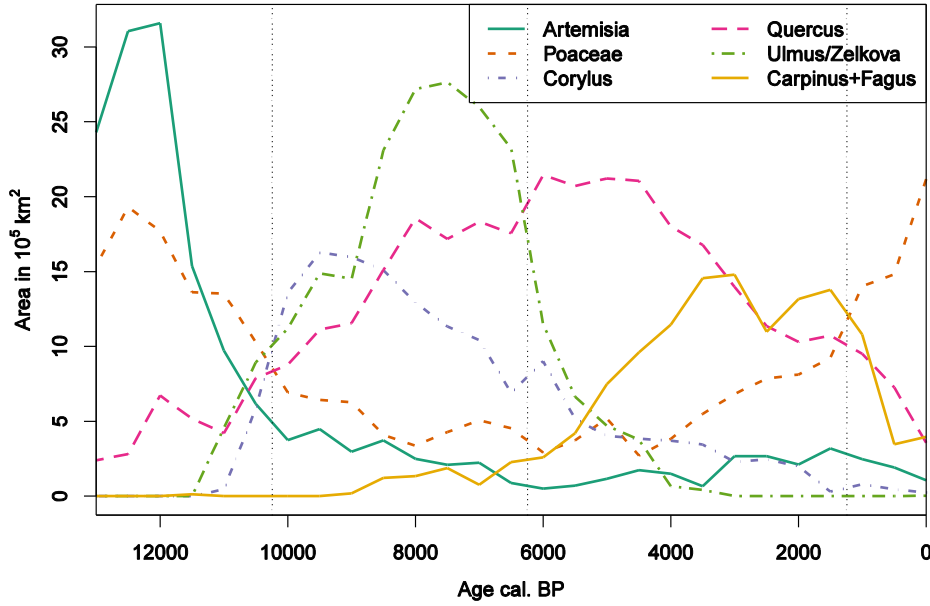
1113 **Figure 5** Assessments of the dynamics of area increase: a) Rate of overall spread estimated from the  
 1114 slope of the increase in square root of the area versus time, b) area doubling time obtained from the  
 1115 logistic growth model. Symbols: black square = class 1, green triangle = class 2, red triangle point  
 1116 down = class 3, blue diamond = class 4. Taxa are ordered according to their overall rates of spread  
 1117 and doubling time. Horizontal lines separate rapidly expanding taxa.



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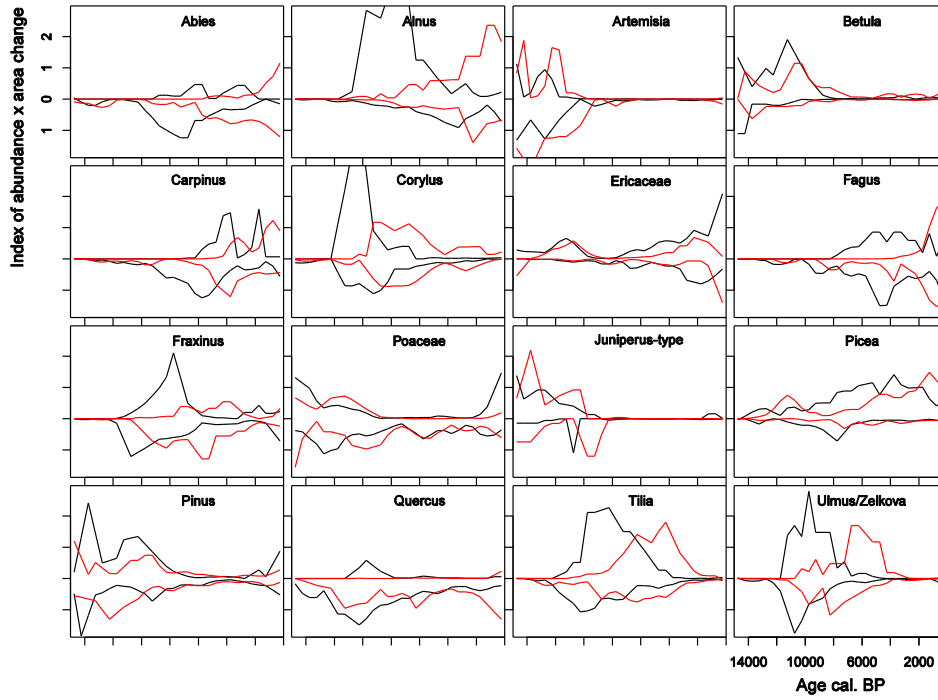
1120 **Figure 6** Postglacial changes in area of highest abundance or dominance for the most common  
 1121 European tree taxa, *Artemisia* and Poaceae based on interpolation and classification of pollen  
 1122 percentages. Vertical dashed lines make times of change.



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1126 **Figure 7** Dynamics of abundance change comparing Europe north and south of 47°N latitude  
1127 depicted as upper and lower values from a central zero line. Black lines indicate an increase, and red  
1128 a decline in area abundance.

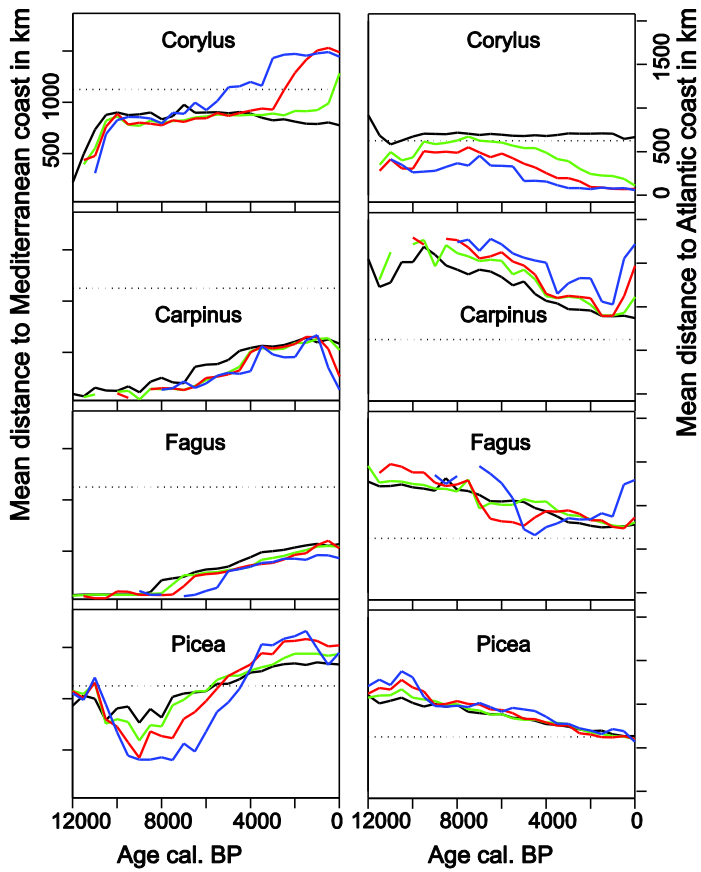


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1131 **Figure 8** The average distance of areas assigned to different abundance classes to the modern coast  
 1132 of the Mediterranean and the Atlantic respectively. Lower abundance classes include the area of  
 1133 higher abundance classes. The dotted line represents the average for the analysed area. Colour  
 1134 codes: black = class 1, green = class 2, red = class 3, blue = class 4.

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