Climate simulations and pollen data reveal the distribution and connectivity of temperate tree populations in eastern Asia during the Last Glacial Maximum

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ABSTRACT

Publications on temperate deciduous tree refugia in Europe are abundant, but little is known about the patterns of temperate tree refugia in eastern Asia, an area where biodiversity survived Quaternary glaciations and which has the world's most diverse temperate flora. Our goal is to compare climate model simulations with pollen data in order to establish the location of glacial refugia during the Last Glacial Maximum (LGM) period. Limits in which temperate deciduous trees can survive are taken from the literature. The model outputs are first tested for the present by comparing climate models with published modern pollen data. As this method turned out to be satisfactory for the present, the same approach was used for the LGM, Climate model simulations (ECHAM5 T106), statistically further down-scaled, are used to infer the temperate deciduous trees distribution during the LGM. These were compared with available fossil temperate tree pollen occurrences.

The impact of the LGM on the eastern Asia climate was much weaker than on the European climate. The area of possible tree growth shifts only by about 2° to the south between the present and the LGM. This contributes to explain the greater biodiversity of forests in eastern Asia compared to Europe. Climate simulations and the available, although fractional, fossil pollen data agree. Therefore, climate estimations can safely be used to fill areas without pollen data by mapping potential refugia distributions. The results show two important areas with population connectivity: The Yellow Sea emerged shelf and the southern Himalayas. These two areas were suitable for temperate deciduous tree growth, providing corridors for population migration and connectivity (i.e. less population fragmentation) in glacial periods. Many tree populations live in interglacial refugia; not glacial ones. The fact that the model simulation for the LGM fits so well with observed pollen distribution is another indication that the used model is good to simulate also the LGM period.

Key words

Eastern Asia, ECHAM5 model, Last Glacial Maximum, pollen, temperate deciduous trees, population connectivity

Supplementary information is added, discussing **Appendix S1: Monsoon progression in the model compared to observation**
and
Appendix S2: Uncertainty **of precipitation analysis**

Introduction Eastern Asia temperate deciduous forests boast the world's most diverse temperate deciduous forest flora (Donoghue and Smith, 2004; Qiu et al., 2011). They also contain the highest numbers of Tertiary relict taxa that have disappeared from Europe (Milne and Abbott, 2002; Svenning, 2003), such as *Carya* and *Parrotia* (Li and Del Tredici, 2008; Orain et al., 2013). The reason for this situation should be sought in the history of these forests through Quaternary glaciations and earlier. The last time when these forests had a considerable reduction of their population or underwent a shift of their distribution was during the Last Glacial Maximum (LGM), i.e. 21,000 years ago. On different continents, this happened in different ways due to the climate of the area, the topography (including the orientation of the main mountain ranges that may act as geographical corridors or barriers), the location and extent of icecaps and the extent of emerged coastal shelves. In Europe, during the LGM, the temperate deciduous forests, especially the warm-temperate tree species, died out in much of northern and central Europe and survived in refugia in the mountainous areas of the three southern peninsulas: Iberia, Italy and the Balkans, as well as in some smaller areas around the Black Sea and the southern Caspian Sea (Leroy and Arpe, 2007; Arpe et al., 2011).

Various methods have been used to establish the locations of glacial refugia of temperate deciduous trees during the LGM in Eastern Asia. For example, population distributions have been published based on phylogenetic data in Eastern Asia (Qian and Ricklefs, 2000) and based on biomisation using palaeo-data for the Japanese archipelago (Takahara et al., 2000; Gotanda and Yasuda, 2008) and for China (Harrison et al., 2001). A disagreement regarding the location of temperate tree refugia in China, especially at its northern limit, has appeared: Harrison et al. (2001) proposed the northern limit of the temperate deciduous forest biome to have retreated far south (south of 35° N) versus Qian and Ricklefs (2000) who suggested an extension of the temperate forest over the emerged continental shelf. Qian and Ricklefs (2000) highlighted the important role played by physiography heterogeneity, climatic change and sea-level changes in allopatric speciation. According to the results of their ecological analysis, a temperate tree population extended across the emerged shelf and linked populations in China, Korea and Japan during glacial times. This led to the concept of interglacial fragmentation and refugia.

Additional information from phylogenetics of temperate deciduous trees should also be considered for phylogeography purposes. But few trees/bushes belonging to the deciduous forest have been analysed so far. A temperate deciduous bush, *Ostryopsis davidiana*, indicates multiple LGM refugia both south and north of the Qin Mountains (Tian *et al.*, 2009).

To be complete, it should be mentioned that the distribution of key temperate tree biomes (discrete points) for the LGM can be found in Ni et al. (2014).

Our aim is to contribute to this debate on the northern limit of temperate deciduous trees by using another approach to ecology, to biomisation and to phylogeography: i.e one based on climate model simulations. The results from this approach are validated by pollen data, whose amount has increased spectacularly since 2010. Distribution maps are then produced.

2 MATERIAL AND METHODS

The climatic data, model and methods used in this study are described by Leroy and Arpe (2007) and Arpe *et al.* (2011) in more detail. Coupled ECHAM5-MPIOM atmosphere ocean model simulations were carried out, though with a very low horizontal resolution of T31 (i.e. a spectral representation which resolves waves down to 31 on any great circle on the earth corresponding to approx. 3.75°). In such a coupled model, the atmosphere as well as the ocean and the vegetation were simulated and interact with each other and generated their own Sea Surface Temperature (SST) and vegetation parameters. These SSTs and vegetation parameters were then used for uncoupled ECHAM5 T106 atmospheric simulations. The ECHAM models including the coupled ocean model were developed at the Max-Planck Institute for Meteorology in Hamburg (MPI).

The models were run on one hand with the present-day conditions concerning the orography, solar radiation, ice cover and CO_2 and on the other hand under LGM conditions concerning the same parameters (e.g. atmospheric CO_2 concentration at 185 ppm). The simulations for the present and the LGM with a T106 resolution (approx. 1.125° horizontal resolution) model with 39 atmospheric vertical levels were carried out with the ECHAM5 atmospheric model (Roeckner et al., 2003). The boundary data, e.g. the SST and vegetation parameters, were taken from the coupled ECHAM5-MPIOM atmosphere ocean dynamic vegetation model (Mikolajewicz et al., 2007) simulations, which have been made for the present and the LGM with a spectral resolution of T31 and 19 vertical levels. The experimental setup is largely consistent with the Paleoclimate Modelling Intercomparison Project phase 2 PMIP2 (Braconnot et al., 2007). These SSTs were corrected for systematic errors of the coupled run by adding the SST differences between observed SSTs and simulated ones for the present, the corrections are generally below 3°C.

In Arpe et al. (2011), comparisons of the model generated SSTs with other reconstructions, e.g. from the MARGO project (Kucera et al., 2005), were performed and good agreement was found. Differences to the CLIMAP (1981) reconstruction agree with findings by PMIP2 (Braconnot et al., 2007). Also, other information from the LGM gave further confidence in the performance of the model. In Arpe et al. (2011), the importance of a high resolution is stressed. Therefore, we use here again the T106 model. Intuitively one assumes that the model that provides good estimations for the present climate would also be best for simulating a climate with a different external forcing such as during the LGM. Indeed Arpe et al. (2011) found good correspondence between pollen findings for the LGM and the estimation of possible tree growth for Europe, which increased confidence in that model. As the climate of Eastern Asia is quite different to that of Europe, we try to find further evidence for the high performance of the model in Eastern Asia.

It is generally assumed that results from model simulations become more robust when using an ensemble of different model simulations; but we did not do that. As the ECHAM models have been shown by Reichler and Kim (2008) to belong to the best ones and by including other ones, we would only dilute our results because of very different results in different simulations (Tian and Jiang,(2016). Further, most of the available simulations are of much lower resolution than T106, that used here, and which we believe is essential for a region of diverse topography such as Eastern Asia. When combining the results of different models, an interpolation to a common grid is inevitable and that creates some smoothing with a further loss of resolution.

Nevertheless, even a T106 model resolution might not be sufficient for our investigation. Kim et al. (2008) demonstrate the importance of a high resolution with their model, among others, for the response of the Eastern Asian summer monsoon under LGM conditions. Therefore, we did a down-scaling to a 0.5° resolution. For that, the differences between the model simulations for the LGM and the present are added to a high-resolution present-day climatology. The climatology that seemed best for our investigation is that of Cramer and Leemans (Leemans, R. and Cramer (1991) ; Cramer, 1996), below abbreviated as “C&L”. With this method, the impact of possible systematic errors of the model is reduced. This method works only if the simulations are already reasonable; otherwise it might happen that e.g. negative precipitation amounts may occur. We could use this method only for the precipitation and 2m air temperature (T2m) while the winds had to be taken directly from the model simulations.

To improve the understanding of limitations in the climate data, estimates of the present climatology with data from the Global Precipitation Climate Center (GPCC) (Schneider et al., 2011; Becker et al., 2013; GPCC, 2013) and with data from the ECMWF interim reanalyses (ERA) (Dee et al., 2011; ECMWF, 2014) are used.

Lower CO_2 concentration in the atmosphere during the LGM has caused a decline of pollen production. Therefore, low pollen concentrations or influxes may already be indicative of the presence of trees (Ziska and Caulfield, 2000; Leroy, 2007). It should be noted that we are here not working at the level of forests, nor of biomes. Hence it is considered that pollen sites will reliably indicate the survival of temperate deciduous trees (summer-green and broadleaf), if records have a sub-continuous curve of at least one temperate taxon such as deciduous *Quercus*, *Ulmus*, *Carpinus* or *Tilia*. The study focuses on the period of the LGM, hence on an age of 21± 2 cal ka BP (Mix et al., 2001). The geographical areas of China, Japan, SE Russia, Korea and the Himalayas are explored. The dataset includes terrestrial and marine sites. A literature review of pollen data was made. It was first based on the large compilations of Cao et al. (2013) mainly for China and of Gotanda and Yasuda (2008) for Japan. Then this was enlarged geographically and with an update including more recent publications.

Modern pollen assemblages were used to check the validity of the tree growth limits chosen. The following databases were used: Zheng et al. (2014) for China and Gotanda et al. (2002) for Japan.

This was complemented by local studies such as by Park (2011) and Park and Park (2015) for Korea and the Himalayas (Fuji and Sakai, 2002; Chung et al., 2010; Kotlia et al., 2010; Yi and Kim, 2010). It was not aimed to be exhaustive. From these databases, the occurrences of temperate deciduous trees (mainly deciduous *Quercus*, and *Ulmus*, but also others such as *Carya, Tilia, Carpinus*) of at least 0.5% were selected.

3 CLIMATE OF EASTERN ASIA

In our earlier investigations on glacial refugia of trees over Europe (Leroy and Arpe 2007; Arpe et al., 2011), limiting factors for possible tree growth were the precipitation during summer, the mean temperature of the coldest months and the growing degree days (number of days with temperatures >5°C) (GDD5), the latter is related to the summer temperatures. The climate of Eastern Asia is different to that of Europe and a short review of its climate is therefore needed in order to adapt the limits.

The climate of Eastern Asia is dominated by the monsoon (more information in Appendix S1 of Supporting Information) as well as by its very strong topographic variability. The latter makes it difficult to create a reliable climatology on a regular grid. This is demonstrated for air temperature T2m) during December to February (DJF) by comparing the C&L climatology with a long-term mean from the ECMWF interim reanalysis (Dee et al. 2011; ECMWF-ERA. 2019) (ERA), a simulation for the present (CTR) and LGM simulations (Fig. 1).

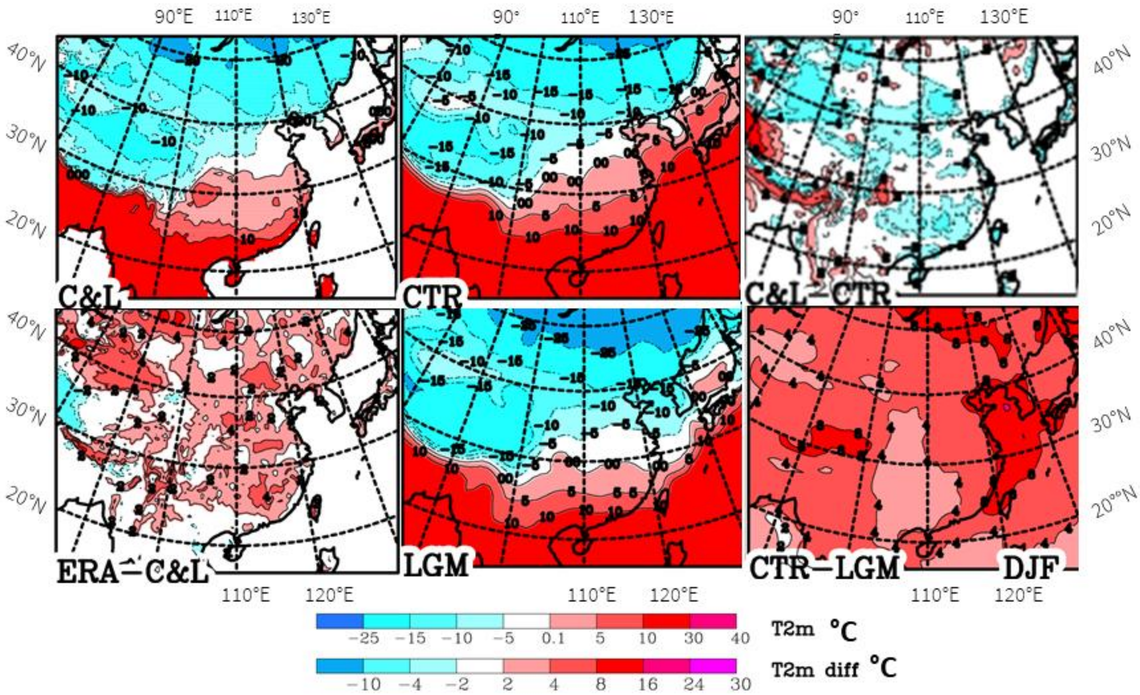

Fig. 1: Climatological mean distribution of T2m over Eastern Asia for December to February (DJF)

Values by Leemans, R. and Cramer (1991) (C&L), the ECMWF reanalysis (ERA) and model simulations (CTR and LGM), as well as some differences between them.

Much stronger structures in the C&L climatology compared to the other climatologies can be seen (Fig. 1). Moreover substantial differences are observed, e.g. the white band (-5 to 0°C) is positioned about 5° further north in eastern Asia in ERA compared to C&L with up to 4 °C warmer temperatures over a large part of Eastern Asia (Fig. 1, panel ERA- C&L). For the Caspian region, Molavi-Arabshahi et al. (2015) showed how biases of several °C in ERA can occur in mountainous areas when the topographic height in the ECMWF model and the real topography are different. So it is assumed that the warmer temperatures in ERA compared to C&L are due to this analysis system. The climate simulation for the present (Fig. 1, CTR) agrees similarly well with ERA and C&L, a little warmer than C&L and cooler than ERA (not shown).

A main purpose of different simulation periods (Fig. 1) is the display of changes from the LGM to the present (Fig. 1 lower right). Over the Yellow Sea, temperatures differ by up to 16 °C, as a large area of the ocean shelf emerged during the LGM, while the differences are much smaller for continental China, mainly 4 to 5 °C. These changes between the present and the LGM are overall much weaker than for Europe in winter (Fig. 2). Typical differences for continental central Europe are 8-15 ºC while they are only around 4-5 ºC for the Eastern Asian continent. One has to take into account that China is further south than central Europe, the central latitudes in the European map are 45 to 50 °N while for China they are 32 to 37 °N, which contributes to explain the large differences in the temperature change. Also, the proximity of the Fennoscandian ice sheet is of importance for the colder temperatures in Europe, as well the weakening of the Gulfstream, which presently supplies Europe with warmer temperature. The strong temperature change over the Yellow Sea is a consequence of the larger heat capacity of the ocean, which limits the winter-time cooling under present-day conditions. At the LGM, this area was emerged due to the lower sea level, which leads to much stronger winter-time cooling.

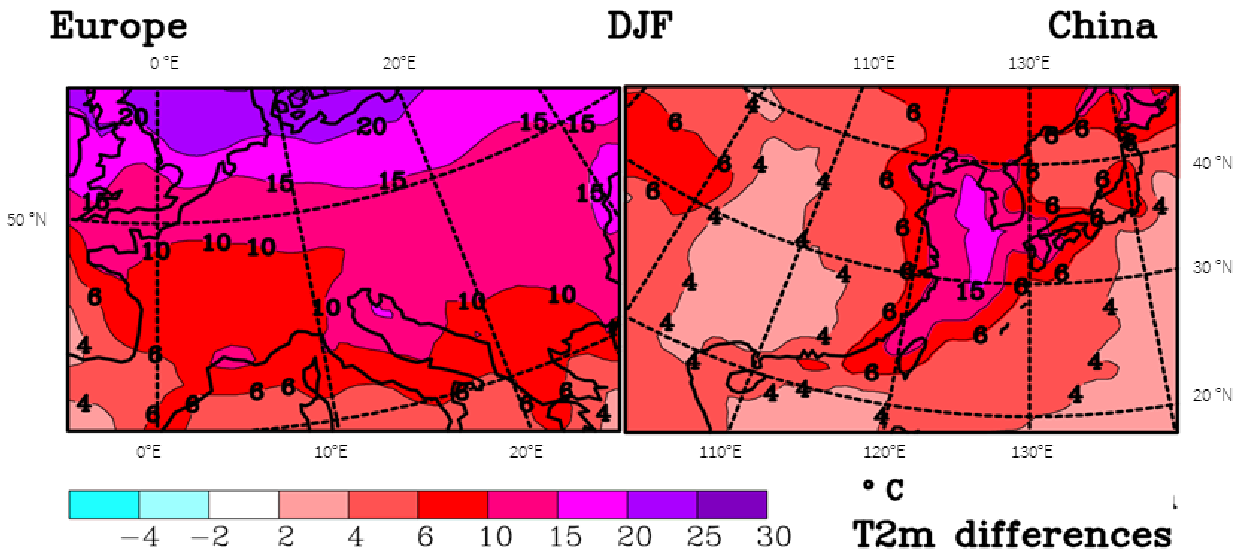

Fig. 2: Difference maps between simulated CTR and LGM T2m during winter (DJF) for Europe and Eastern Asia.

The summer temperatures are shown in Fig. 3. ERA temperatures are often warmer by around 2 °C than the ones in the C&L climatology (Fig. 3 lower left panel) the arguments for this difference given above for DJF apply here as well. The differences between the present and the LGM in the simulations increase from China's east coast of 2-3 °C to up to 6 °C over Tibet. This is similar to what Tian and Jiang (2016) found in PMIP3 simulations; they state that the temperature drop in the LGM is too low compared to proxy data. The summer temperatures are being used to calculate the GDD5. For the small changes shown here, we do not expect that GDD5 does impose much more limitation for the LGM than for the present for tree growth.

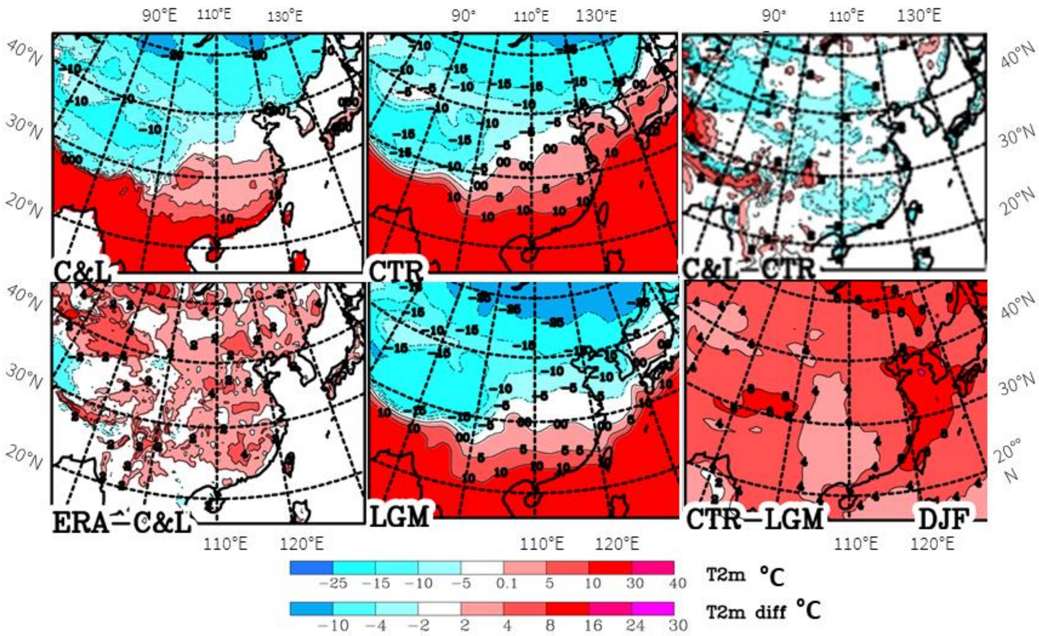

Fig. 3: Climatological mean distribution of temperature T2m (in °C) over Eastern Asia for June, July August (JJA)

Values by Leemans, R. and Cramer (1991) (C&L), the ECMWF reanalysis (ERA) and model simulations (CTR and LGM), as well as some differences between them.

The difference maps for CTR-LGM temperatures show values over the ocean (Figs. 1 to 3). These differences may have an important impact on continental temperatures. Therefore, it is interesting to compare these data with other estimates of the SST. For example, Annan and Hargreaves (2013) show annual means of SST differences of around 2°C for the South China Sea while our simulations have slightly larger values of 2.5 to 3°C, though this falls within the uncertainty range given by Annan and Hargreaves (2013). A main difference is less cooling during the LGM in our estimates at the Gulf and Kuroshio currents off the USA or Japan coast (not shown as they are too far outside the area of interest).

Summer precipitation is an important limiting factor for possible tree growth (Fig. 4). The sharp gradient of precipitation along the southern slopes of the Himalayas in the three sets of analyses (the climatology by C & L and the long-term means from ERA and GPCC) is clearly marked. The general patterns agree in the three sets, though with some biases. C&L and GPCC agree best, probably; because they are both based on precipitation observations at gauges. On the contrary, ERA is a model product forced by a very large range and more evenly distributed observations; moreover ERA does not use observed gauge precipitation. Differences between C&L and GPCC are mostly below 50 mm, especially in the northern areas where the precipitation is moderate. The differences between C&L and ERA are also small in northern areas; but can become quite large where the amounts of precipitation are large, mostly with ERA having larger precipitation amounts. The lower precipitation rates in ERA for Korea and southern Japan in contrast to C&L and GPCC are remarkable. Here the latter data are probably more accurate because this area is well-covered by observations (Fig. S2.3) and the ERA model may not be able to resolve the strong topographic structures. Many of the large uncertainties are probably due to the strong topographic structures over Eastern Asia, which makes an analysis difficult and which is enhanced by a low density of observational sites over western China (more information on precipitation accuracy in Appendix S2 of Supporting Information).

The systematic error of the model concerning China consists of the monsoon front being too far north by 2° of latitude (Fig. S1.2) and with a too early northward propagation in the season (Appendix S1 of Supporting Information). As we only use the differences between the present and LGM this systematic error is assumed to have only a minor impact on our results. Tian and Jiang (2016) found a general weakening of the summer monsoon in PMIP3 simulations, especially a decrease of precipitation in most of the simulations but they do not go into the details shown in Appendix S1 of Supporting Information, which makes a comparison difficult. However, they noticed a large variability within the models. For the area used in Fig. S1.2, they show a decrease of 10-20% of summer precipitation in the LGM compared to the Control which agrees with our simulation, strongest in June south of 32°N, though both CTR and LGM are too strong compared to ERA. In our simulation, the strengthening north of 32°N for March to August for precipitation and 850 hPa wind in the CTR and LGM simulations is stronger compared to ERA. This systematic error is assumed to have only a minor impact on our results. Indeed, most of the differences turn out to be less important for the further use in this study, except larger precipitation over western China at 37ºN on the northern slope of the Kunlun Shan in the C&L data set, which is investigated in more detail in Appendix S2 of Supporting Information. Also in the area 105°-110°E / 35°-40°N, the drop of precipitation during LGM may be important, as discussed below in section 6.

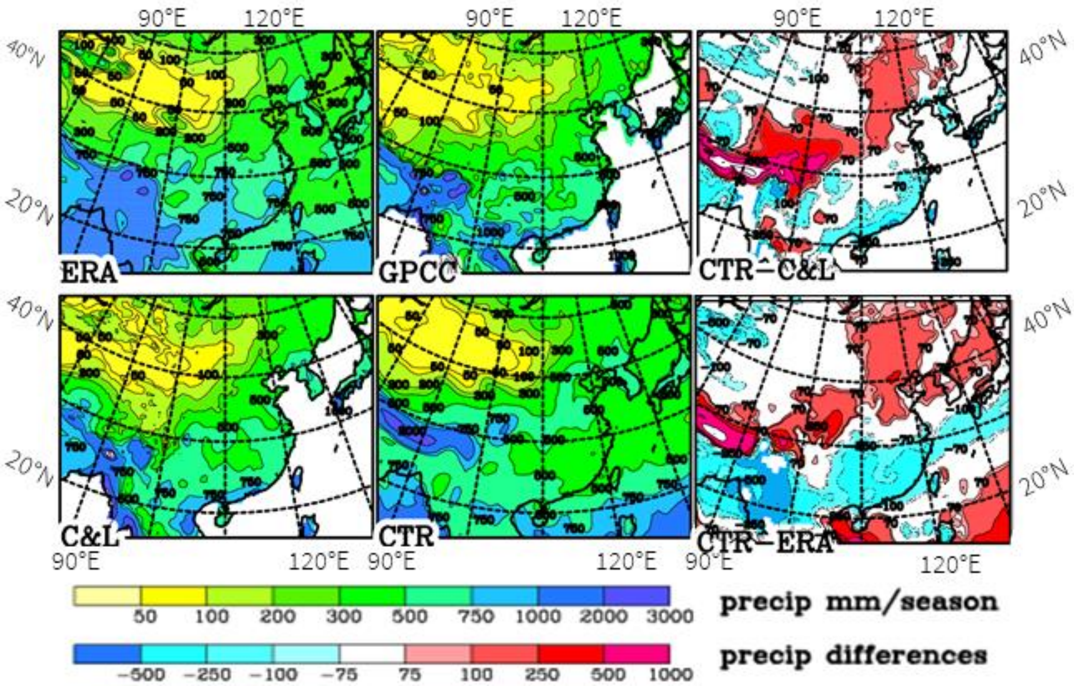

Fig. 4: Summer (JJA) precipitation over Eastern Asia as analyzed by Leemans, R. and Cramer (1991) (C&L), ERA and GPCC and as simulated for the present (CTR). Differences between the various fields are shown. Units: mm/season

Below we will concentrate on summer precipitation because that is the time when plants need water most. Other scientists use the annual mean precipitation as a limiting factor (e.g. Tian et al., 2016). When comparing the analyses with the model simulations for the present (CTR), one finds that the model fits better to GPCC and least to ERA (Fig. 4) away from the high mountain ranges where the agreements between the different precipitation climatologies is very low. The amounts of precipitation in ERA is on a large scale higher than the other ones. For most of China south of 35°N the precipitation in ERA is much lower than in the other climatologies. The belt with stronger precipitation at 25 to 35°N in CTR is assigned in Appendix S1 of Supporting Information to an earlier northward propagation of the monsoon front in CTR compared to ERA, that is weakened from the CTR to LGM, which results in a belt of largest differences between the present and the LGM of up to 150 mm (Fig. 5). Kim et al. (2008) found similar differences in their higher resolution simulation, though spreading further north. In Appendix S1 of Supporting Information, it is shown that the monsoon, as represented by the wind direction, does not change much over the continent between the present and the LGM, and with the monsoon front propagating northward already in June the wind speeds increase. This is somewhat in contrast to results by Jiang and Lang (2010) who showed for the ensemble mean of model simulations (all with a much lower horizontal resolution than the one used here) a reduction of the JJA wind speeds. The lower JJA precipitation during LGM may also result from lower temperatures during LGM, when the atmosphere can carry only a lower amount of water vapour.

While Tian and Jiang (2016) found in PMIP3 simulations a general decrease of precipitation, we find it only for a belt at 29-36° N where the model shows already too large values for the present (CTR-C&L in Fig. 4).

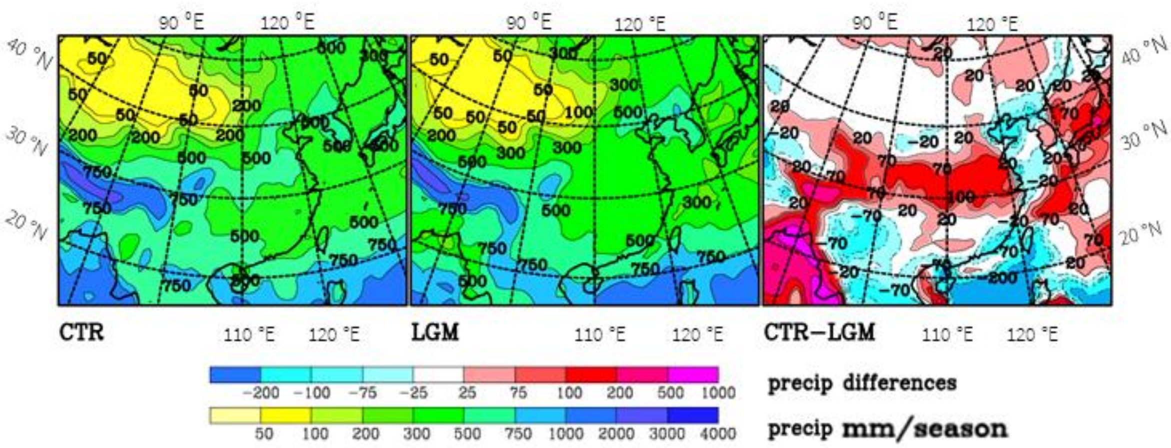

Fig. 5: Summer (JJA) precipitation simulated for Eastern Asia and differences. Between CTR and LGM. Units: mm/season.

4 COMPARING POLLEN INFORMATION WITH CLIMATIC DATA

In Leroy and Arpe (2007) and Arpe et al. (2011), climatic data were combined to find the areas where temperate deciduous trees could survive due to limiting criteria and then compared that with palaeo-data of such trees for Europe. The same method is now applied for Eastern Asia. Europe is limited to the south by steppe and by the Mediterranean Sea. However, in E. Asia, a vast subtropical area with deciduous temperate trees mixed with conifers and broadleaved evergreens (i.e. between biomes TEDE and WTEM of Ni et al., 2010) lies south of the temperate deciduous forest (Qiu et al., 2011). It was therefore essential to add a climatic limit to separate these two main vegetation types. In addition to the limits used for Europe, we add also a maximal winter temperature (Tmax) which the climatological temperature must fall below to allow deciduous tree to grow but not the evergreens tree, suggested by Sitch et al. (2003) and Roche et al. (2007) (Table 1). Sitch et al. (2003) require a less strong limit of -17 ºC minimum temperature and +15.5 ºC maximum temperature of coldest month for temperate deciduous trees but only for very few sites such a relaxation of limits would decrease the number of sites that fail the comparison with the climatological estimate. Roche et al. (2007) used for temperate broadleaf forest Tmin=-2 ºC and Tmax of +5 ºC. We regard a Tmin limit of -2 ºC only valid for warm-loving deciduous trees.

Table 1: Limiting factors for temperate deciduous tree growth used in this study.
Tmin = minimum temperature of the coldest month, Tmax = maximum temperature of the coldest month, GDD5 = growing degree days for which the excess over 5°C is accumulated for each day, JJA precipitation =accumulated summer precipitation.

Tmin	Tmax in winter	GDD5	JJA precipitation
-15°C	+5°C	800	50 mm/summer

When combining these limits with the climate data we arrive at the distribution shown in Fig. 6.

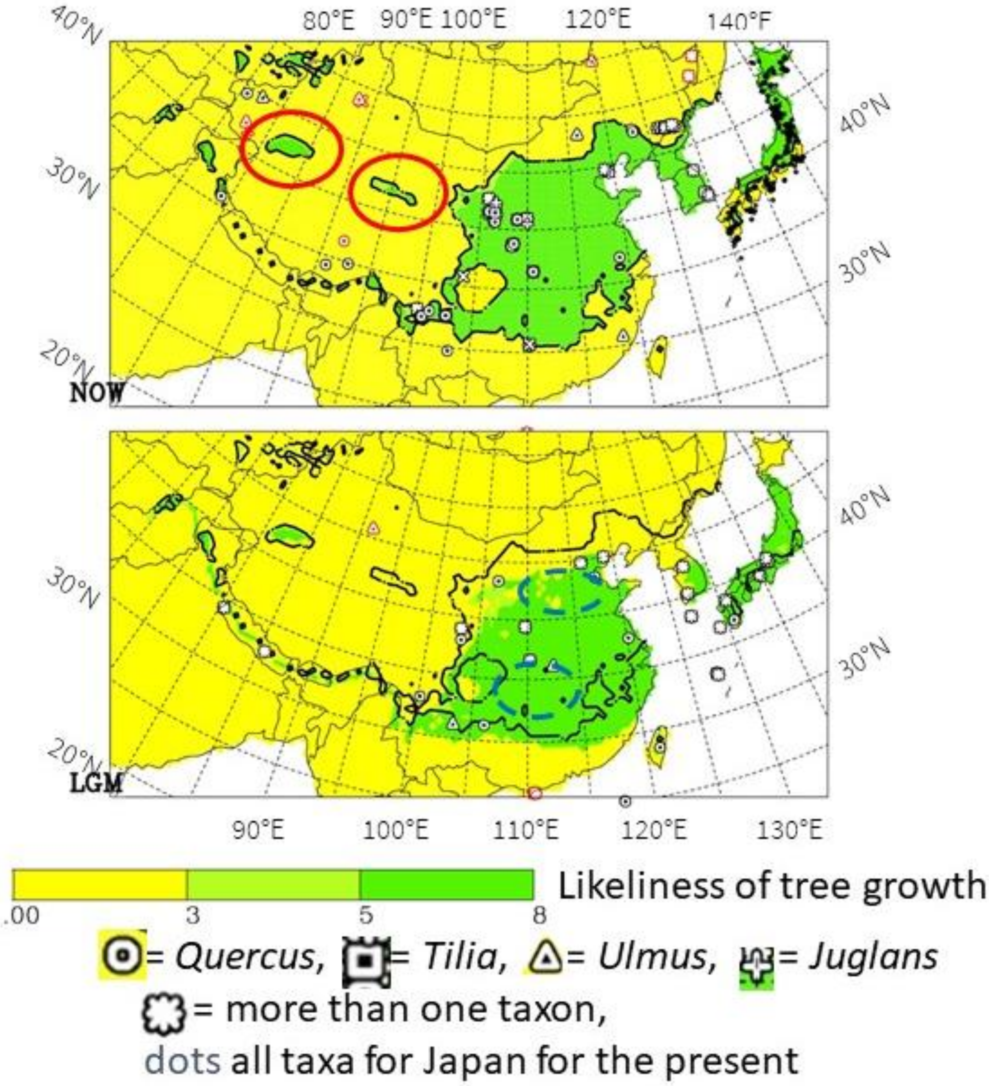

Fig. 6: Possible tree growth according to our limitations given in Table 1. Darker colours (green) mean that the climate data suggest possible tree growth. For easier comparison between the present (upper panel) and the LGM (lower panel), the limits for the present are copied as a solid line into the LGM panel. Markers indicate where and which tree pollen of deciduous trees are found. Markers: circles = *Quercus*, squares = *Tilia*, triangles= *Ulmus*, plus = *Juglans* and stars = more than one taxon. For modern-day sites in Japan only dots are used for clarity of the plot. Open markers = at least within a distance of ± 3 grid points (~150 km radius) the climate data suggest

possible tree growth; otherwise filled (red) markers. Red and blue (dashed) ovals show areas of interest mentioned in the text.

Only very few stations with observed pollen are outside (not within a distance of ± 3 grid points, i.e. about ~150 km radius) the area of possible tree growth according to our criteria (filled markers see also Tables 2 a and b for the LGM). For the present, 13 out of 380 stations with observed deciduous tree pollen do not fit to the climate data of the present, most of them because of too cold winter temperatures (-20 to -23 °C), one at 91°E, 31°N because of a too short summer (GDD5 < 600), two (both at 109 °E, 18 °N) because of too warm winter temperatures (>17 °C) and one (77 °E, 37 °N) because of lack of summer precipitation and too cold winter temperatures, though these are both near given limits. South-eastern Japan is often too warm in winter for deciduous trees though there are many observations in that area. These stations are, however, within 3 grid points to areas that are marked as suitable for their growth.

In Fig. 6 for the present, two areas marked by red ovals in western China at latitude 37 ºN indicate possible tree growth according to the climatic data where the precipitation in the C&L climatology (Fig. 4) exceeds the ones of ERA and GPCC considerably. Also ERA and GPCC show relative maxima at 37 ºN in that area but shifted by 5 º to the east. We believe that the precipitation by C&L is deficient here, as explained in Appendix S2 of Supporting Information.

In the southern China Sea around 120°E,28°N only one marker with observed tree pollen for the LGM is shown in fig. 6 although around that position four cores are available (see Table 2 for details). All four observations agree with the possibility of trees according to the climate estimate. Because of the use of marine sediment, pollen must have been transported from the land, which is further discussed in the next section.

In Eastern Asia, some species might have evolved which are hardier than those of the same genus present in Europe. Fang et al. (2009) show *Ulmus pumila* over large areas of northern China and SE Siberia, a species that can withstand extremely cold temperatures in winter and drought (Solla et al., 2005). *Ulmus* has the most failures in our comparison with model data. Fang et al. (2009) show a wide spread of *Tilia amurensis* in NE China, SE Siberia and N Korea, which is also absent from Europe. This tree, like the elm, is extremely frost hardy (Piggott, 2012).

5 POSSIBLE TREE GROWTH DURING THE LGM

Thirty-five pollen sites for the LGM were used (Table 2). A good overall fit occurs between the climate data and the LGM pollen data. In Fig. 6 lower panel, only two filled markers, not agreeing with climate data, are found on the continent. The site of Huguangyan in the south has winter temperatures higher than 10° C, which are too high for deciduous trees. In the north-west China in the Tarim basin is another filled marker. The observation consists of only 1% pollen for *Ulmus*. There the winter temperatures are -17 °C, just outside the limit used here (Table 1) but within the limits suggested by Sitch et al. (2003). On Hokaido a filled marker indicates a disagreement between climate and pollen observation but it is only slightly too cold in winter (-15.7 °C).

Four cores in the deep ocean in the S. China Sea are marked in Table 2 and Fig. 6 as not agreeing with our given limits when using the down-scaled climate data, but because of the deep sea the pollen must have been transported there. From Fig. 7, it can be concluded that the pollen could only have come with the north-easterly 10m wind from Taiwan where also *Quercus* was found during the LGM (Table 2). As the present blooming period for *Quercus variabilis*, a widespread species of the deciduous forest, is January to March in Taiwan (Liao, 1996), the winds during March are shown in Fig. 7, assuming a little later blooming period during the cooler LGM than presently, though the wind fields for March and February are hardly different. When taking the wind at a higher level (850 hPa or around 1500m), the wind is blowing more from the east in accordance with the Ekman spiral in the atmospheric boundary layer. Therefore, pollen must have travelled near the surface when coming from Taiwan or if it arrived at higher levels it may have come from the Philippines (Luzon) that however seems to be too far south for deciduous oak and, moreover, this area is not suggested in our estimate of having possible deciduous tree growth (Fig. 6).

Thus, the area boundaries for the present and for the LGM are only slightly different with a shift for the LGM by 2 to 3° to the south of both the northern and southern limits, and an eastwards shift of the western boundary. In northern China, Korea and north Japan (Hokkaido), differences result mainly from the winter minimum temperatures, as can be seen from Fig. 1 in which winter temperatures drop by more than 6°C from the present to the LGM.

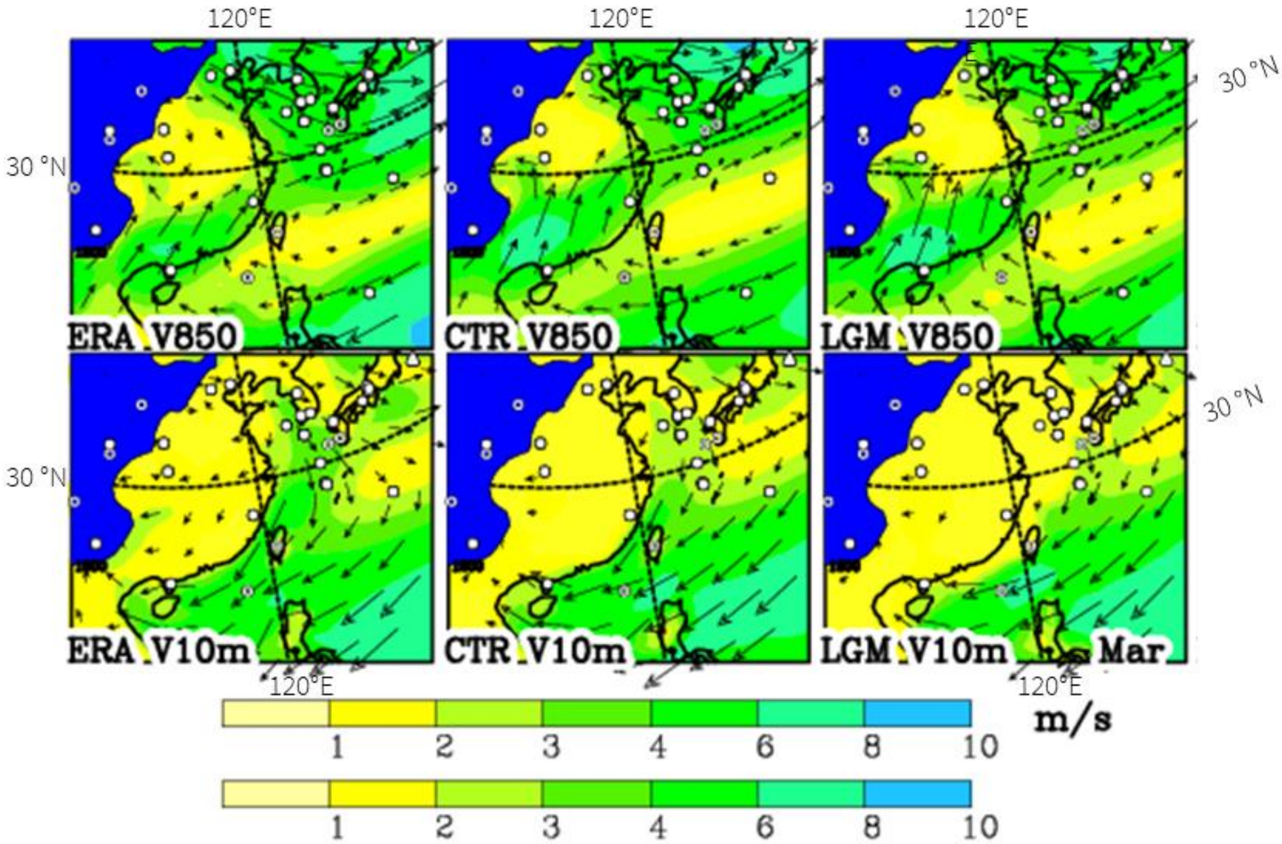

Fig. 7: Winds at 10m (V10m) and at 850hPa (V850) for March as analysed (ERA) and simulated for the present (CTR) and LGM. All panels are showing the prevailing north easterlies. Areas with topography above the 850hPa level are erased and blue coloured. Observational sites for the LGM are indicated by markers

Table 2: Selected sites with observed pollen during the LGM. "*Quercus*" include deciduous *Quercus* and *Lepidobalanus*, "*Ulmus*" includes *Ulmus-Zelkova*, and "others" include: *Carya, Tilia, Carpinus*.

“Agree” means that the observations agree with our estimates of possible tree growth as shown in Fig. 6 or 8 respectively.

Table 2a: east of 120°E

Lon E	Lat N	Site	Region	Alt/ depth in m	*Quercus*	*Ulmus*	Other	Agree	Author
126°32′	33°14′	HN-1, Hanon maar	Jeju Island	53			Y	**Y**	4
126°33′	33°15′	BH-4B	Jeju Island	53	Y	Y	Y	**Y**	5
126°52′	35°12′	Yeonjaedong Trench	Gwangju	20?	Y	Y		**Y**	6
127°13′	33°15′	UD-2	Hanam	19	Y	Y		**Y**	7
128°04′	35°10′	Pyonggeodong	Jinju	30			Y	**Y**	8
128°57′	38°33′	MD982195	N of E. China Sea	-746	Y			**Y**	9
130°23′	31°49′	Imutaike Pond	Southern Kyushu	330	Y			**Y**	10
130°23′	33°36′	Tenjin	Tenjin Fukuoka city, N Kyushu	0		Y	Y	**Y**	11
134°36′	34°24′	Ohnuma	Chugoku Mts	610	Y		Y	**Y**	12
135°48′	35°12′	Hatchodaira	Kyoto	810	Y	Y	Y	**Y**	13
135°53′	35°32′	Iwaya	Fukui	20		Y	Y	**Y**	14
135°53′	35°33′	Lake Mikata	C Japan	0		Y	Y	**Y**	15
138°53′	36°49’	Lake Nojiri	C Japan	250	Y	Y	Y	**Y**	16
140°10′	36°03′	Hanamuro River HS1	C Japan	5	Y	Y	Y	**Y**	17
139°40′	36°41′	Nakazato	C Japan	183	Y	Y	Y	**Y**	18
141°47′	36°04′	MD01-2421	off Kashima	-2224	Y	Y	Y	**Y**	21c
130° 42’	35°56′	KCES-1	Sea of Japan	-1464	Y	Y		**Y**	19
142 12.08	41 10.64	C9001C	NE Japan	-1180	Y	Y	Y	**?**	20
136°03	35°15′	BIW 95-4	Lake Biwa	85	Y	Y		**Y**	21a
142°28′	44°03′	Kenbuchi	Hokaido	137	Y	Y	Y	**N**	21b

Authors: 4: Park and Park 2015; 5: Chung 2007; 6 :Chung et al. 2010; 7 Yi and Kim 2010; 8: Chung et al. 2006; 9: Kawahata and Ohshima 2004; 10: Shimada et al. 2014; 11: Kuroda and Ota, 1978; 12: Miyoshi and Yano, 1986; 13: Takahara and Takeoka, 1986; 14: Takahara and Takeoka, 1992; 15: Nakagawa et al. 2002; 16: Kumon et al. 2003; 17: Momohara et al. 2016; 18: Nishiuchi et al. 2017; 19:: Chen et al. 2016; 20: Sugaya et al. 2016; 21a: Hayashi et al. 2010; 21b: Igaraachi and Zarov 2011; 21c Igarachi 2009

Table 2b: west of 120°E

Lon E	Lat N	Site	Region	Alt/ depth in m	*Quercus*	*Ulmus*	Other	Agree	Author
80°08′	29°20′	Phulara palaeolake	Kumaun Himalaya	1500?	Y	Y	Y	**Y**	1
85°18′	27°14′	JW-3	Kathmandu valley	1300	Y		Y	**Y**	2
93°49′	27°32′	Ziro valley	Arunachal Pradesh	1570	Y		Y	**Y**	3
91°03′	40°47′	CK2	Tarim basin	780	Y			**N**	22
99°57′	27°55′	06SD, lake Shudu	Yunnan	3630	Y			**N**	23
102°47′	24°20′	XY08A, Xingyun Lake	C Yunnan	1772	Y		Y	**Y**	24
102°57′	33°57′	RM Ruoergai	Zoige basin	3400	Y	Y		**Y**	26
103°30′	32°55′	Wasong	NE Tibetan Plateau	3490	Y			**Y**	27
106°30′	38°17′	Shuidonggou locality 2	Yinchuan，Ningxia	1200	Y	Y		**Y**	28
109°30′	34°24′	Weinan	Loess Plateau	650	Y	Y	Y	**Y**	29
110°00′	31°29′	DJH1, Dajiuhu	Shennongjia Mountains	1751	Y	Y	Y	**Y**	30
110°17′	21°09′	Huguangyan maar	southern China	23	Y	Y	Y	**Y**	31
115°57′	39°45′	East part	Yan Shan	150?	Y	Y	Y	**Y**	32
117°23′	20°07′	17940	S China Sea	-1727	Y			**N**	33
117°25′	20°03′	ODP 1144	S China Sea	-2037	Y			**N**	34
117°21’	20°08’	MD05-2906	S China Sea	-1636	Y	Y	Y	**N**	35
119°02′	26°46′	SZY peat bog	Fujian	1007	Y			**Y**	36
120°53′	23°49′	Toushe Basin	Taiwan	650	Y		Y	Y	37
127°16′	28°09′	DG9603	China Sea	-1100	Y			Y	38
127°22′	28°07′	MD982194	Okinawa Trough	-989	Y	Y		**Y**	39
118°16′	20°20′	STD235	S China Sea	-2630	Y	Y	Y	**N**	40

Authors: 1: Kotlia et al. 2010; 2: Fuji and Sakai 2002; 3: Bhattacharyya et al., 2014; 22: Yang et al., 2013; 23: Cook et al. 2011; 24: Chen et al. 2014 and Chen XM et al. 2015 IPS abstract; 26: Shen et al. 2005; 27: Yan et al. 1999; 28: Liu et al. 2011; 29: Sun et al. 1996; 30: Li et al. 2013; 31: Wang et al., 2012, Lu et al., 2003; 32: Xu et al. 2002; 33: Sun & Li 1999; Sun et al. 2000; 34: Sun et al. 2003; 35: Dai et al. 2015; 36: Yue et al. 2012; 37: Liew et al. 2006;
38: Xu et al. 2010; 39: Zheng et al. 2013; 40: Yu et al. 2017.

The down-scaling method used here does not allow us to present values over the emerged shelf of the Yellow Sea during the LGM, when the mean sea level was 120 m below the present one (Lambeck et al., 2014). Therefore, in Fig. 8, the possible tree distribution is shown using model data without down-scaling, when the high spatial resolution is lost and more impacts from systematic errors of the model may be expected. However, fortunately, such impacts can hardly be seen when comparing Fig. 6 with Fig. 8, except for the present along the southern slopes of the Himalayas and the southern border of possible tree growth, where T2m by C&L is lower than that of CTR (also than that by ERA), leading to a better fit with pollen data when using T2m by C&L.

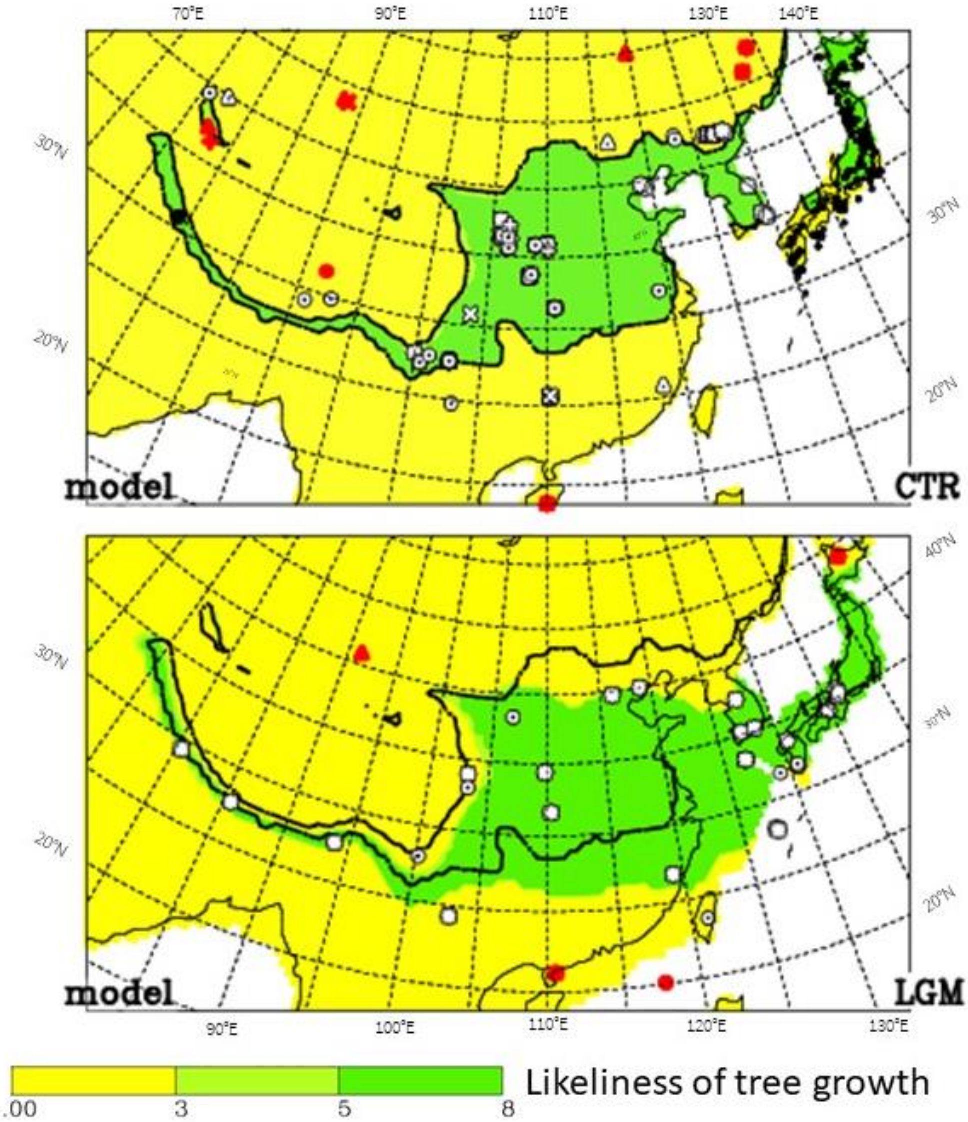

Fig. 8: same as Fig. 6 using model data without down-scaling. The Yellow Sea is shown as land in the LGM.

6 LGM CONNECTIVITY AND DISTRIBUTION MAPPING

The results show two worth-discussing areas with population connectivity: one is over the Yellow Sea emerged shelf and one along the south of the Himalayan Range.

The northern limit of the temperate deciduous trees assumed by previous research (Harrison et al., 2001, their figure 1) is much further south (30 - 35 ºN) than what is found here. Therefore, population connectivity over the shelf was rejected by Harrison et al. (2001). It should be mentioned that the results by Harrison et al. (2001) were based on the model available at that time which had a lower resolution and also was based on observational data available at that time, which have improved considerably since then. Indeed 80% of the sites used in the current investigation were published post-2001. Moreover, the Harrison et al. (2001) study is based on biomes, not tree occurrences. Three arguments can be presented now to support this connectivity.

Firstly, the model results clearly show the connectivity of tree populations between China, Korea and Japan during the LGM over the emerged shelf. This connectivity takes place because the limit of the possible tree growth of our investigation (darker areas in Fig. 8 as well as in Fig. 6) reaches still quite far north (40 °N), which is in accordance with pollen data.

A second argument is the presence of deciduous trees in sites located around the shelf in amounts suggesting larger than simple tree presence, even perhaps woodlands or forests. In several places around the emerged shelf the percentages of temperate deciduous trees indeed exceed 10%, e.g. in the Yeonjaedong swamp in Korea with 20-30% of deciduous *Quercus*, 7-20 % of *Ulmus-Zelkova* (Chung et al., 2010), the two sites on the Jeju island maar lake (Chung, 2007; Park and Park, 2015), Tenjin peatland in Japan with 12% deciduous *Quercus*, 8% *Carpinus*, 2.5% *Tilia* (Kuroda and Ota, 1978), and the marine cores DG9603 and MD982194 with 15% of deciduous *Quercus* (Xu et al., 2010).

Thirdly, information derived from recent phylogenetic investigations is supportive of the occurrence of deciduous trees on the emerged shelf. For example, the phylogeography of one of the most widely distributed deciduous species in eastern Asia, the oak, *Quercus variabilis*, clearly suggests the occurrence of land bridges over the East China Sea (Chen et al., 2012). Around the E. China Sea, other phylogenetic data indicate both mixing and absence of mixing between populations depending on plant type (Qi et al., 2014). The occurrence of mixing indicates that contacts were possible across the emerged shelf (e.g. Tian et al., 2016); while the absence of mixing for other species indicate that not all species mixed, but certainly does not suggest total absence of migration for other species. It appears therefore that the E. China Sea acted as a filter, letting some through, others not (Qi et al., 2014).

The eastern Asian case is very different from Europe, where fragmentation is the rule in the LGM. In Europe (Fig. 2), the temperatures were much lower than presently (8 to 15 ºC) compared to Eastern Asia (3 to 5 ºC) and therefore the shift of possible temperate deciduous tree growth is much smaller in E. Asia than in Europe. Phylogenetic results in E. Asia are indeed in favour of the hypothesis of species surviving both in the north and the south of China (Qian and Ricklefs, 2000) and not of species surviving only in the south (Harrison et al., 2001). The basic expansion-contraction model of vegetation belts in Europe was much less important in Eastern Asia (Qiu et al., 2011), due to the smaller Asian ice cap and a different topography (López-Pujol et al., 2011). Eastern Asia biodiversity was therefore preserved across the Ice Ages, owing to not only the more moderate lowering of temperatures but also to the better connectivity between populations

One question, was if the pollen, found in the emerged shelf of the Yellow Sea is produced locally or remotely. According to the Harrison et al. (2001) study, these pollen grains must have come from the southern part of China. Yu et al. (2004) have tried to calculate such long-distance transports. For *Quercus* and *Ulmus* they found transports of up to 6 ° latitude/longitude in any direction. This would be too short for a transport from China south of 30 °S. Also the high pollen percentages at the observed sites speak against such a long-distance transport.

We are not convinced that Yu et al. (2004) calculations are robust enough for using their results in our investigation, especially as their figure 3 does not agree with plant distributions by Fang et al. (2009). Therefore, the wind fields for the present as analysed by ECMWF (ERA) and as simulated by our model for the LGM were investigated. In Appendix S1 of Supporting Information as well as in Fig. 7, it is shown that ERA and the simulation for the present agree quite well, at least for the wind directions, which makes us confident that we can use the model simulations for the LGM straight away.

The winds at 10m and 850 hPa for March, a central month for the blooming of *Quercus variabilis*, are shown in Fig. 7 for the present (ERA), the CTR and the LGM. Over the emerged shelf of the Yellow Sea, the 10m winds are very light from the north-west during the LGM (much stronger in ERA because of the lower surface friction over the sea). For the higher level of 850 hPa, all data sets show very similar distributions all with north-westerlies. Long-distance transport of deciduous tree pollen would have come from NE China, an area that Harrison et al. (2001) assume to be void of deciduous trees, though some recent studies (including the present one) indicate the opposite (Yu et al., 2004). Further on in the year, the 850 hPa winds are blowing from the south-west, starting in April and fully crossing the 30 °N latitude in May (similar to CTR in Fig. S1.1), i.e. a transport from mainland China would have been possible, though a little late for the main blooming of the deciduous oak. In Appendix S1 of Supporting Information, it is shown for the present that the simulations suffer from a too early progression of the monsoon front, which suggests that the turn of the wind to south-westerlies may have occurred also later for the LGM, thus leading to a less likely transport from mainland China.

The source for the pollen found in the emerged Yellow Sea is not completely clear but May is late for the blooming season in central China (for Taiwan it is January to March). Therefore, a local production or transport from northern China is more likely, supporting our argument that the emerged Yellow Sea was occupied by deciduous trees during the LGM, as indicated by Fig. 8. Another important population connectivity result is that the Himalayas were more favourable to temperate deciduous trees in the LGM and provided the possibility of a quasi-continuous band of temperate forest at its southern slope, beneficial for the spreading and diffusion of genes (e.g. for Chinese mole shrew, He et al., 2016), more so than in the present (Fig. 6). Three observational sites, that are currently available, support this chain of possible tree growth during the LGM. For the present, this link does not exist because of too warm winter temperatures (warmer than 5 ºC in the C&L climatology). Along the slopes of the high Himalayas it is most likely that there would be a level at which the temperature will be below 5 ºC (an issue which needs further investigation).

Two significant cases occur where population connectivity was higher, indicating less population fragmentation, in glacial than in interglacial periods. So, it appears that many tree populations live nowadays in interglacial refugia.

During LGM the precipitation and the temperature were lower than at the present. Which of both was more important for the tree growth cannot be said with certainty. Tian et al. (2016) stated: “annual precipitation is considered as the most important determinant”, and in our study we have some indication to agree with that. In Fig. 6 and 8, there is a cluster of pollen findings over central China (105-110°E/35-40°N) for the present but not for LGM. In this area the temperature does not change much (Fig. 2 and 3) but the summer precipitation decreases substantially (Fig. 5). This change is only slightly reflected by the boundaries of possible tree growth in Fig. 6 (north of 40°N. The lack of observational sites with pollen of tree pollen is not a proof, because it could be due to many reasons, but the massive change in occurrence is suggestive that we should have perhaps increased summer precipitation requirements for tree growth (Table 1). This can, however, also indicate the reduced water use efficiency of the trees at LGM due to lower atmospheric CO_2. Finally, this investigation shows that the model simulations suggest possible tree growth where pollen grains of such trees are found. This leads to the possibility of using the model data to fill gaps between observational sites by way of maps. Such gaps especially occur around 30-37 °N / 105-120 °E and 25-30 °N / 110-115 °E, i.e. the provinces Hupeh to Kiangsu and Hunan (ovals in Fig. 6 lower panel).

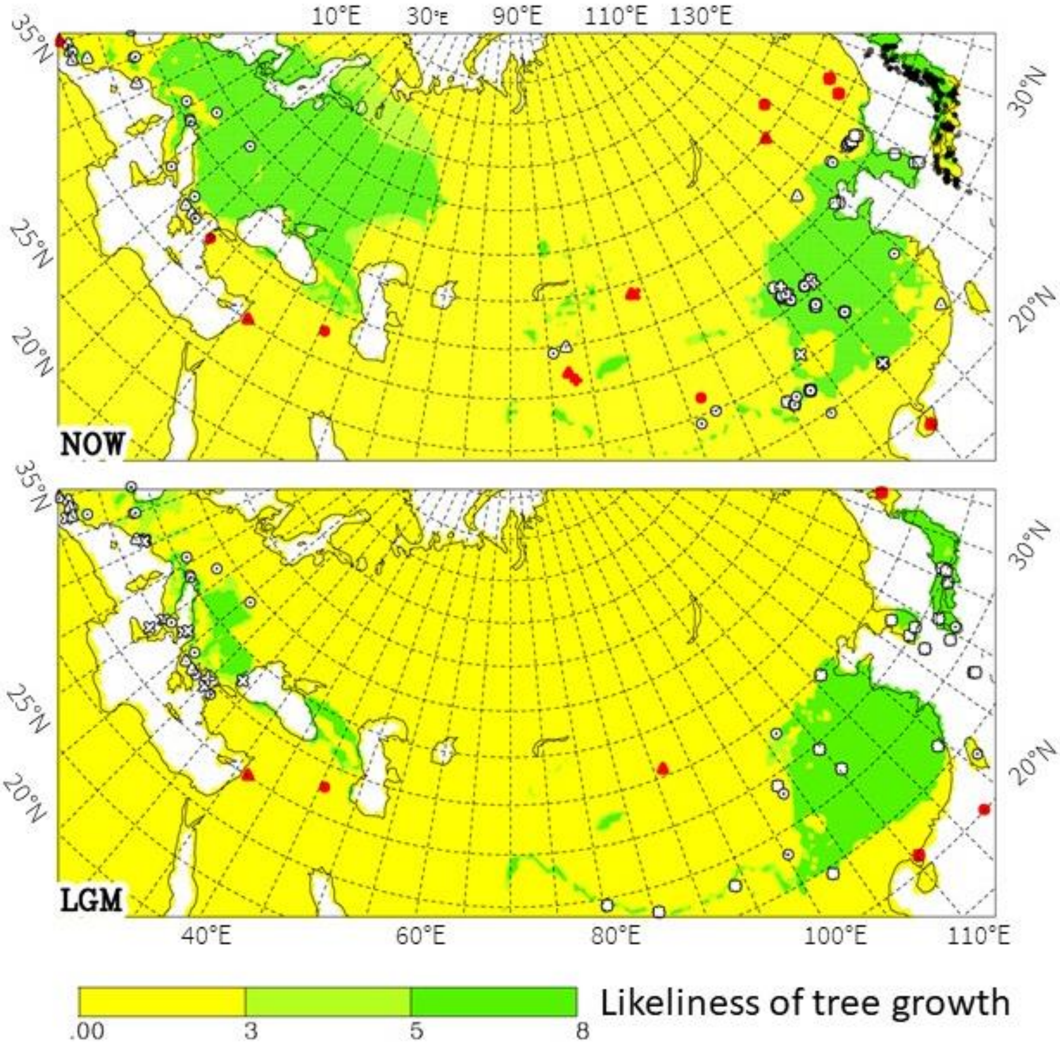

Fig. 9: same as Fig. 6 for the whole of Eurasia. Pollen data for Europe have been described by Arpe et al. (2011). Darker colours (green) are areas in which trees are able to grow according to model data. Lighter green are areas where not all criteria are completely fulfilled

By extending the view of our investigation for the whole of Eurasia (Fig. 9), a stronger link between China and Europe is shown during the LGM than presently. Along the foot of the Himalayas, a continuum existed; but westwards of it, still a gap north of Afghanistan (probably going back to the Tertiary) is maintained, inhibiting a total link across Eurasia. This continuum is broken for the present climate by model results because winter temperatures exceed 7 ºC, hence being too warm for temperate deciduous trees.

7 CONCLUSIONS

Generally, the estimates of possible temperate deciduous tree growth in the LGM in eastern Asia by model simulation agree with fossil pollen observations. Therefore, the model estimates can fill the areas without observations. The results in the form of LGM distribution maps are considered robust enough as model simulations for the present are within the range of climate estimates. Nevertheless, we are aware of some uncertainties in the climate of Eastern Asia and we can safely say they are not a limitation of this study.

During the LGM, major connectivities between populations are found, which is in agreement with observation, i.e. less tree population fragmentation. This is especially visible in two places. Firstly, the link between China, Korea and Japan is clear. Sufficient new pollen studies around and on the emerged Yellow Sea shelf are now available, confirming the results of the model. They suggest the presence of temperate deciduous trees, perhaps even woodlands, in the area.

Secondly, connectivity during the glacial period occurred at the southern slope of the Himalayan chain favouring genetic flow in interglacial refugia. Currently this link does not exist because of too warm winter temperatures there. Our simulations cannot be taken as a proof of this hypothesis, as one cannot imagine that along the Himalayan chain there would not be a level at which the winter temperatures do not exceed 5 ºC also for the present day, a higher resolution data set would be able to show how wide and continuous such a corridor of possible tree growth would be at the present.

Another outcome of this research is the contribution to the conservation agenda (López-Pujol et al., 2001). The areas of LGM refugia often match areas of present hotspots of biodiversity. Hence the distribution of temperate forest obtained in our investigation can serve as a guide to establish nature parks for plants and animals. Moreover the difference between LGM and present distribution contribute to the understanding of rate of distribution change (as well genetic flow), which is important to monitor in light of possible climatic change.

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AUTHORS CONTRIBUTION

S.A.G. Leroy

Looking after conceptual issues, collecting the data, writing the manuscript

K. Arpe

Writing most of the manuscript, preparing the figures and responsible for meteorological and climatological issues

U. Mikolajewicz

Providing the model simulations

J. Wu

providing observational tree pollen data

The authors declare that they have no conflict of interest

Code availability

The model version is already widely known and available. We have clearly described what has been done and the follow up programs are written in FORTRAN This can be requested from Klaus Arpe if wanted

Data availability

Table 2 provides a list of all observational sites and observational tree pollen data. Most of the other data are referred to by giving the website .Tt does not seem feasable to provide the model simulation data in a simple way. They can be obtained from Klaus Arpe in GRIB format.

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BIOSKETCH

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Author contributions: S.L. is responsible for the overall research and collected the pollen data with help by J.W., K.A. is responsible for the meteorology and climatology aspects as well as did most of the programming and writing of the manuscript, U.M. provided the climate model simulations and J.W. contributed to the data search and typical Chinese aspects.