To what extent has climate constrained the distribution of beech (*Fagus sylvatica*) 6000 years BP in Europe?

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Abstract

The question, why the distribution of beech (*Fagus sylvatica*) was slowed down during its immigration into the lowlands of Northern and Western Europe is still not answered satisfactorily.

Beech prefers oceanic humid conditions in summer as well as mild conditions in winter having sensitivity against late frosts. These attributes make it a typical representative of present day European forests.

Palaeoclimatology however shows a thermal maximum during the mid Holocene, 6000 years BP, with a more continental climate than present day what might have created climatic conditions for beech inferior to those of today. This allows the hypothesis that the migration flow of beech was detained by inappropriate bioclimatic factors for growth and reproduction and therefore was predominantly influenced by climate.

In this thesis, modelling techniques were used to compare the ecological situation prevailing for beech 6000 years BP with present day to check if there are shown significant changes between the two time-slices. For this purpose, the climate output of three Atmospheric General Circulation Models (AGCMs) out of PMIP (Paleoclimate Modelling Intercomparison Project) was chosen. But instead of relying only on correlations with standard climatic variables, the distribution limits of beech were characterized in terms of bioclimatic variables representing distinct physiological limiting mechanisms. These variables were calculated by the vegetation models LPJ and STASH.

The comparison of the mid Holocene maps calculated by using the three AGCMs with the present day data show however that all of the specific physiological factors were sufficient for beech growth. Therefore, based on the obtained results it seems that climate did not constrain the spreading of beech 6000 years BP.

Zusammenfassung

Im mittleren Holozän war die Einwanderungsgeschwindigkeit der Buche (*Fagus sylvatica*) in die Tiefländer von Nord- und West-Europa stark verlangsamt. Die Ursache für diese im Vergleich zu anderen Baumarten sehr langsame Ausbreitungsgeschwindigkeit ist immer noch nicht zufrieden stellend geklärt.

Die Buche bevorzugt ein ozeanisches Klima mit relativ feuchten Sommern und milden Wintern, da sie sehr anfällig gegenüber Spätfrösten ist. Diese Faktoren machen die Buche zu einem typischen Vertreter der heutigen Wälder in Mitteleuropa sowie Südschweden, Nordspanien, Norditalien und Teilen der Balkan Halbinsel.

Paläoklimatische Untersuchungen zeigen aber das Vorherrschen eines Wärmeoptimums während des mittleren Holozäns (6000 Jahre vor heute) welches zu einem höheren jahreszeitlichen Kontrast geführt hat. Diese klimatischen Bedingungen könnten aufgrund von kälteren Wintern die Wachstumsperiode der Buche verkürzt sowie im Sommer zu einem erhöhten Dürrerisiko und damit verbundenen Gefahr durch Brände geführt haben. Dies erlaubt die Vermutung, dass die Wanderungsbewegung der Buche aufgrund von ungünstigen bioklimatischen Bedingungen im Bezug auf Wachstum und Fortpflanzung verzögert und daher überwiegend von dem damals vorherrschenden Klima beeinflusst wurde.

Dieser Theorie stehen allerdings noch weitere gegenüber wie zum Beispiel das Aufkommen der Landwirtschaft und dem damit verbundenen stärkeren Eingriff des Menschen in das Ökosystem aber auch die Möglichkeit einer allgemein eingeschränkten Verbreitungsgeschwindigkeit der Buche im Vergleich zu anderen Baumarten.

Der Ansatz dieser Arbeit ist es, die klimatisch bedingten Abweichungen der ökologischen Voraussetzungen der Buche im mittleren Holozän mit Hilfe von Computermodellen zu simulieren und mit den heutigen Voraussetzungen zu vergleichen. Hierfür wurden die Ergebnisse von drei Klimamodellrechnungen des PMIP (Paleoclimate Modelling Intercomparison Project) verwendet. Um allerdings eine genauere Aussage über die Verbreitungsgrenzen der Buche treffen zu können als es alleine mit einfachen Korrelationen der Klimadaten möglich ist, wurden unter Verwendung der Vegetationsmodelle STASH und LPJ bioklimatische Faktoren berechnet, welche spezifische physiologische Grenzen für die Buche darstellen. Um diese bioklimatischen Faktoren zu visualisieren, wurden 19 Karten erstellt, welche die Ergebnisse der drei PMIP-Modelle sowohl untereinander als auch mit dem heutigen Klima vergleichen.

Der Vergleich der bioklimatischen Faktoren des heutigen Klimas mit denen, welche ausgehend von den drei Klimamodellen für das mittlere Holozän errechnet wurden zeigen jedoch, dass keine der spezifische physiologischen Grenzen der Buche in den Gebieten von Europa unterschritten wurde, in denen die Buche auch heute Auftritt. Daher scheint es, basierend auf den hier angewandten Methoden, dass das Klima im mittleren Holozän keinen dominanten Einfluss auf die Verbreitungsgeschwindigkeit der Buche hatte.

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List of Abbreviations

Abbreviation	Meaning	in Chapter
AET	Actual evapotranspiration	3.4.5
AGCM	Atmospheric General Circulation Model	3.1.1
CRU	Measured present day climate data-set. Climate Research Unit, University of East Anglia	3.1.2
DGVM	Dynamic Global Vegetation Model	3.2.2
GDD_5	Growing degree days above 5°C	3.4.4
LPJ	Vegetation model (DGVM). (Sitch et al. 2003)	3.2.2
P-E	relation of precipitation to evaporation	3.4.5
PET	Potential evapotranspiration	3.4.5
PFT	Plant Functional Type	3.2.2
PMIP	Paleoclimate Modelling Intercomparison Project	3.1.1
STASH	Bioclimatic model (Sykes et al. 1996)	3.2.1

Software used

Modelling and Programming:	Writing, Visualisation and Layout
Microsoft Visual C++ 6.0	Microsoft Word XP
Fortran 77	Adobe Illustrator CS2
ESRI ArcGIS 9.0	Adobe Photoshop CS2
Microsoft Excel XP	Adobe InDesign CS2

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1 Introduction

In the mid Holocene, the expansion rate of beech (*Fagus sylvatica*) was slowed down during its immigration into the lowlands of Northern and Western Europe (Huntley & Webb 1988b; Kral 1973; in Mayer 1992, p. 92). However, the question, why the distribution of beech was constrained in mid-Holocene is still not answered satisfactorily (Ellenberg 1996, p. 150f; Huntley & Webb 1988b, p. 370ff; Gliemeroth 1995, p. 60).
But answers that potentially lead to a solution of this open question may help towards an understanding of what determines the geographic distribution as well as the local abundance of different kinds of plants to extend the knowledge about their behaviour in consequence of 'global change' at present day and in the future (cf. Grubb 1989 in Prentice 1992).

Beech prefers oceanic humid conditions in summer as well as mild conditions in winter having sensitivity against late frosts (Lang 1994, p. 158ff). These factors make it a characteristic present day representative in forests of Central Europe as well as Southern Sweden, Northern Spain, Northern Italy, and parts of the Balkan Peninsula.
Palaeoclimatology however shows a thermal maximum during the mid Holocene with a more continental climate than present day that might have induced a shorter growing season due to colder winters as well as more droughts and a higher frequency of fire events in summer creating climatic conditions for beech inferior to those of today.
This allows the hypothesis that the migration flow of beech was detained by inappropriate bioclimatic factors for growth and reproduction and therefore was predominantly influenced by climate (Prentice 1991 in Prentice 1992; Huntley & Webb 1988b).
However, this 'Climate-Theory' is not accepted in all respects. Hence it is contrasted by other theories like the impacts by humans or a spreading limitation caused by the limited dispersal rate of beech.

The approach of this work was the modelling of the ecological situation prevailing for beech in mid-Holocene, 6000 yrs BP, forced by climate and to compare the results with present day data to check whether significant changes are visible. The investigation area includes whole Europe up to the longitude of the Black Sea in the east. The modelling was carried out by using the output of three different AGCMs (Atmospheric Global Circulation Models) provided by PMIP (Paleoclimate Modelling Intercomparison Project[1]). But instead of relying only on correlations with standard climatic variables such as minimum precipitation or temperature, the distribution limits of beech were characterized in terms of bioclimatic variables representing distinct physiological limiting mechanisms (Prentice et al. 1992; Sykes et al. 1996).

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[1] *http://www-lsce.cea.fr/pmip*

Therefore, the modelling was carried out by using the bioclimatic model 'STASH' (Sykes et al. 1996) and the vegetation model 'LPJ' (Sitch et al. 2003) in order to obtain information about ecological variables limiting the spreading of beech.

The following **chapter 2** provides a background about beech and introduces the major theories dealing with the mid Holocene constraint of beech namely the 'climate hypothesis', as well as the contrasting hypotheses about 'human land use', the hypothesis about a dispersal lag of beech and the absence of Megaherbivores. **Chapter 3** points out the materials and methods used to obtain the modelling output. It is followed by **chapter 4** showing 19 maps as result of the modelling and the discussion.

2 Background

2.1 Ecology of beech

Beech today extends from the tree-line forests of the Cordillera Cantabrica and the Appenines to the chalk and gravel areas of South-Eastern England, the mor-humus covered podsols of Denmark, and the mixed forests of Southern Sweden (*figure 1*).

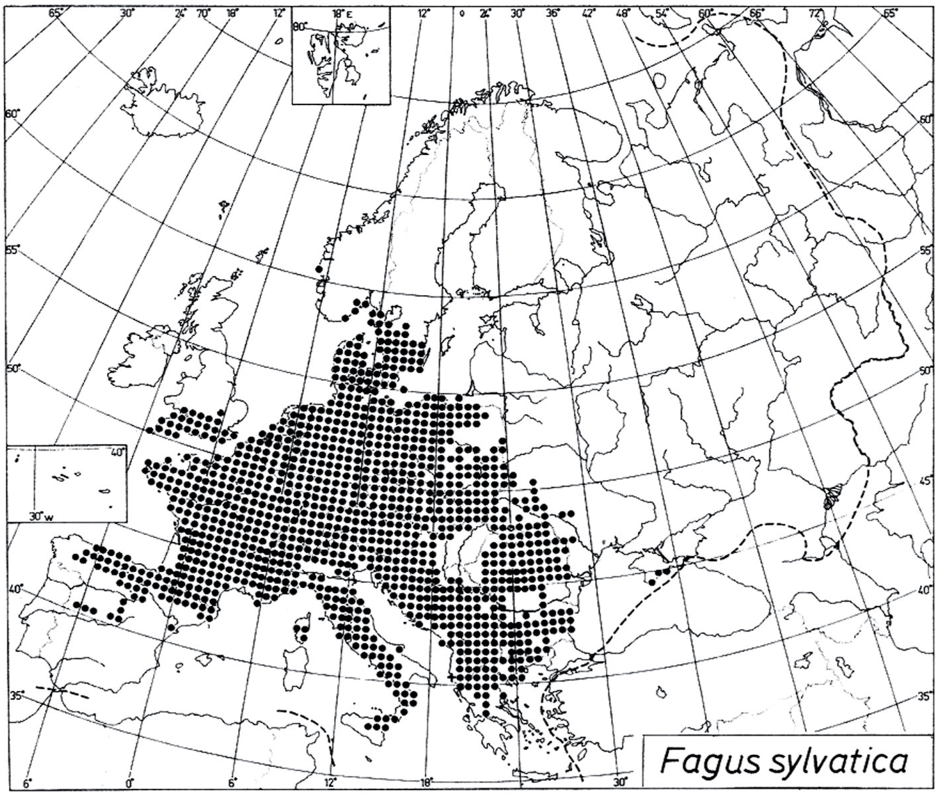


Figure 1: Present day distribution of *Fagus sylvatica*. Jalas & Suominen (1976): Atlas Florae Europaeae.

Beech does not spread far into the more continental east of Europe. This suggests intolerance against aspects of the continental climate like lower temperatures in winter as well as higher temperatures in summer that increase the risk of drought (Iversen 1973, Godwin 1975 in Huntley & Webb 1988b, p. 370ff). This sensitivity against drought is reflected also in the ecogramme in *figure 2*.

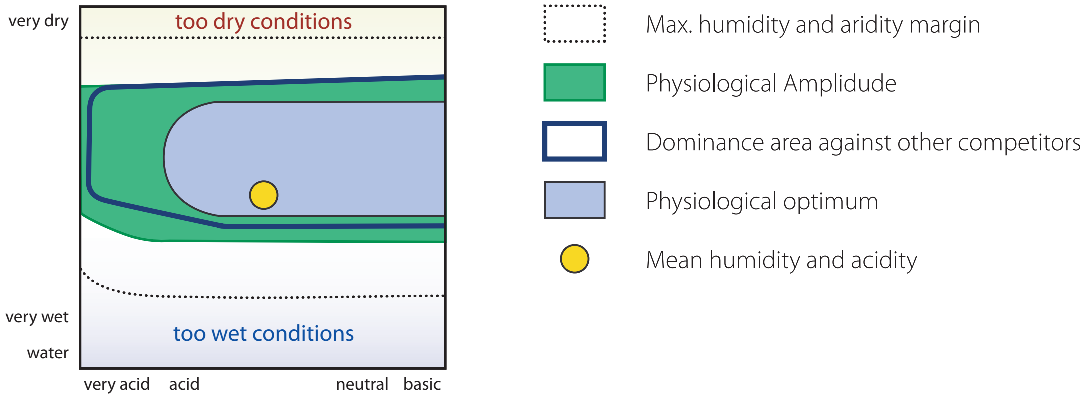


Figure 2: Natural humidity and acidity area of beech under temperate sub-oceanic climate and open competition between different species. After Ellenberg (1996, p. 118).

Though having the physiological optimum on neutral to basic, beech is tolerant of a wide range of soils (Ellenberg 1996, p. 118f; Huntley & Webb 1988b, p. 370). These soil types vary from shallow rankers and rendzinas over chalk and limestone to acid podsols, often with a mor-humus layer. This enables beech to occupy a wide dominance area (*figure 2*) where it outcompetes other tree species.

This dominant role is underlined also by *figure 3* below, showing beech in relation to its competitors.

The habit of beech trees varies from having large, single trunks in high forests to low coppice forms and even krummholz on southern European mountains. It casts a dense shade and often grows in almost pure stands, both near the tree-line and in the north European lowlands.

Beech is an asset-creator ('Bestandsbildner') in many European forests at present day (Mayer 1992, p. 93). Because beech is more shade-tolerant than any other of the most common deciduous European trees, it often comes to dominate the forest in the absence of disturbance. Due to that distinct presence, it is sometimes called 'the sovereign of the natural forest' (Ellenberg 1996, p. 149; Mayer 1992, p. 94). Therefore it is remarkable, that beech did not keep track with the other tree-species during Holocene spreading. Like mentioned before, the species has reached the present day extend of its geographic area only in a short geological period of time ago (Huntley & Webb 1988b, p. 369). At glacial maximum, this extend was limited to refugia at the Iberian, Apennine and Balkan Peninsula from where it commenced its spreading over Northern and Western Europe (*figure 4*).

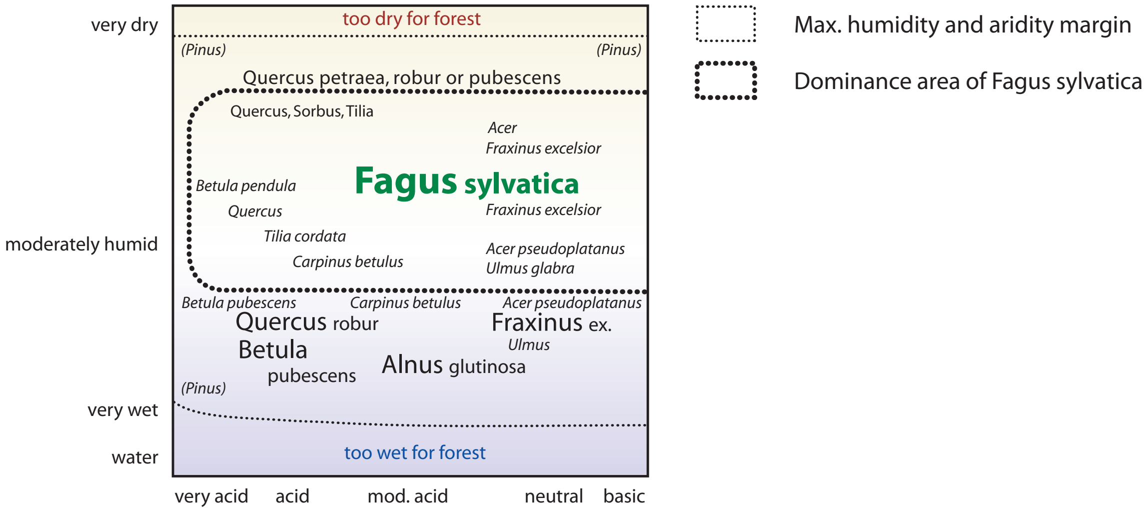


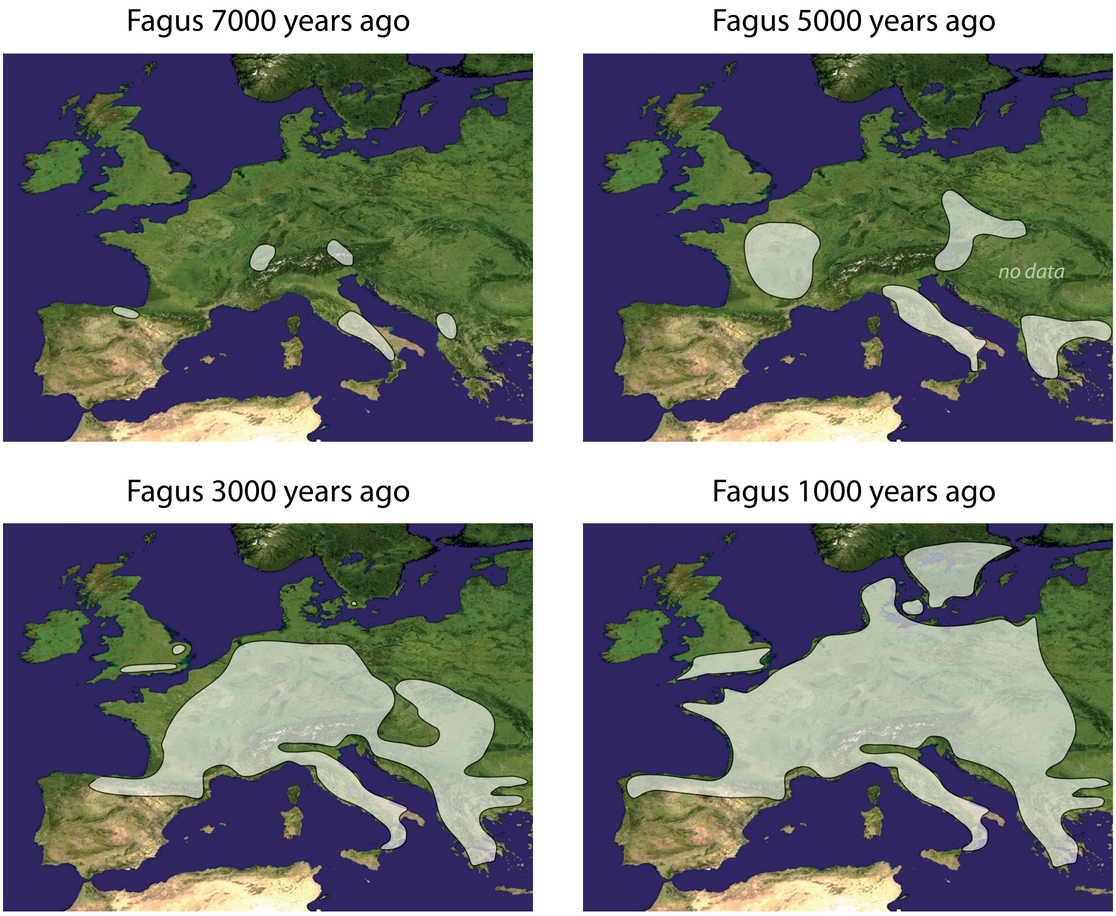
Figure 3: Ecogramme showing the dominance of beech in European forests at present day. After Ellenberg (1996, p. 120).

2.2 Beech spreading during the Holocene

An extensive body of literature referring to beech in Holocene is available (e.g. Ellenberg 1996, p. 144ff; Huntley et al. 1983, 1988, 1989; Mayer 1992; Woods & Davis 1989). Huntley & Webb (1988b, p. 371) as well as Kral (1973 in Mayer 1992, p. 92) have divided the Holocene spreading of beech in three stages (cf. *figure 4*):

- In the first phase there was a relatively slow initial expansion during the early Holocene.
- During the mid Holocene (Atlantic), the spreading speed of beech continues only within the alpine region of Central and Eastern Europe and the low mountain ranges of central Europe.
- The third stage is represented by the late-Holocene (Subboreal) expansion into and across the lowlands of Northern and Western Europe, where beech reached Britain, Denmark and Spain.

After the third stage, the area occupied by beech is decreasing again due to natural and anthropogenic factors (KRAL 1973 in MAYER 1992, p. 92).


Fagus 7000 years ago

Fagus 5000 years ago

Fagus 3000 years ago

Fagus 1000 years ago

Figure 4: Spreading of beech. The first map from 7000 years BP shows possible refugia of the species where it could have outlasted the last Ice Age. After Bradshaw (2004, p. 8).

2.3 Potential causes for the reduced spreading speed during the mid Holocene

2.3.1 Climate change

The climate of the mid Holocene (6000 years BP) is well documented by proxy data (Hewitt & Mitchell 1996; de Noblet et al. 1996a, Vettoretti et al. 1998, Kutzbach et al. 1996 in Bonfils et al. 2004, p. 79; Joussaume et al. a; Ellenberg 1996; Ruddiman 2001). The mid Holocene is also called 'Atlantic' or 'Holocene climate optimum' having mean temperatures of 1 to 3 Kelvin higher in the mid-continent and far north than the mean Holocene temperature of 15°C (Budyko 1982, p. 145, Huntley & Prentice 1988, p. 687; Schönwiese 1995, p. 92). These changes are well visible in *figure 5* showing the variation of mean temperature during the Holocene.

At this time, the remains of continental glaciation disappeared in Europe and North America (Budyko 1982, p. 145). The seasonal contrast was larger on the northern hemispheric summer (Joussaume & Taylor, a) with more solar radiation in summertime (~ +5%) and less in wintertime (~ -5%) than present, creating a more continental climate than today (Bonfils et al. 2004, p. 79; Ruddiman 2005, p. 318ff).

Plausible mechanisms that may explain this climatic difference between 6000 yrs BP and today include the response of the general atmospheric circulation to orbitally induced changes in the seasonal and latitudinal distribution of insolation (Huntley & Prentice 1988, p. 687).

According to pollen based reconstructions, summers during mid Holocene were warmer-than-present in the north, and cooler-than-present in the south, while winters were colder-than-present in the southwest and milder-than-present in the northeast (Bonfils et al. 2004, p. 79).

In the southern areas however, the pollen-based climate reconstructions could be biased because humans already had a profound impact on vegetation patterns (Masson et al. 1999, p. 180).

This 'thermal maximum' is a general feature in Europe and is documented in Greenland, Scandinavia, Central Europe and the Atlantic summer sea surface temperatures (Negendank 2004, p. 100).

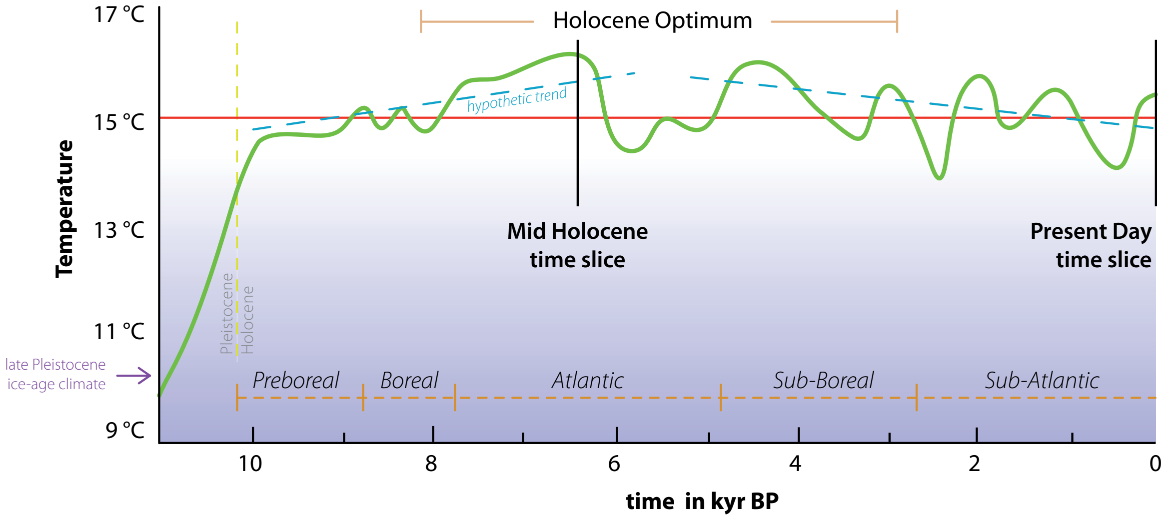


Figure 5: Reconstructed variations of mean temperature of the last 10 000 years (probably uncalibrated) on the northern hemisphere. The temperature curve is highly smoothened. After Schönwiese 1995, p. 92.

The following aspects of mid Holocene climate could have constrained beech range expansion during the mid Holocene:

Minimum temperature

Huntley et al. (1989) have quantified that beech does not extend far into the continental interior (cf. *figure 1*: Atlas Florae Europaeae) and that it is not found in places where the mean temperature of the coldest month is less than -3°C (Dahl 1980 in Huntley et al. 1989). This may be connected to its distinctive sensitivity against late frosts (Sykes et al. 1996). However, beech shows also to have a very steep response to the length of the chilling period (Murray et al. 1989 in Sykes et al. 1996; Crawford 2000, p. 271). Therefore these attributes suggest that beech definitely needs a chilling period triggering budburst which is though not too long to avoid the mentioned negative influence on budburst by late frosts (Sykes et al. 1996; Crawford 2000, p. 271).

Drought

An increased continentality which caused higher summer temperatures may probably also have increased drought, leading to severe damage especially on beech. Drought is a major cause of annual differences in crown density which has become accepted as the most useful single indicator of tree health[2]. The occurrence of severe drought and heat impact on beech could for example be observed in the extreme summer of 2003 in central Europe with decreased crown density accompanied by heavy seed production (very energy consuming mast years), and formation of small leaves followed by late leave shooting in the following year ('Waldzustandsbericht' 2004[3]). Drought stress increases also the sensitivity against infestation by harming insects like *Rynchaenus fagi* ('Buchenspringrüssler')

Fire

Drought also increases the likeliness of fire events showing higher intensity and frequency. As beech compared to most other European trees has only a thin bark that is easily damaged by fire, the tree could have been harmed severely or even been killed (Ellenberg 1996, p. 149f).

Mid Holocene charcoal samples show that fire frequency has generally increased since 6000 BP (cf. *figure 6*). Natural fires are ignited mostly by thunderbolts (James 1989 in Ellenberg 1996, p. 149f). However, the amount of naturally ignited fires was small compared to the increase of fires caused by humans especially with the increasingly applied slash-and-burn techniques (Carcaillet 2002, p. 851). This strong anthropogenic interference makes it therefore nearly impossible today to differentiate between anthropogenic and natural fires.

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[2] *http://www.nbu.ac.uk/iccuk/indicators/27.htm*

[3] *http://www.fva-bw.de*

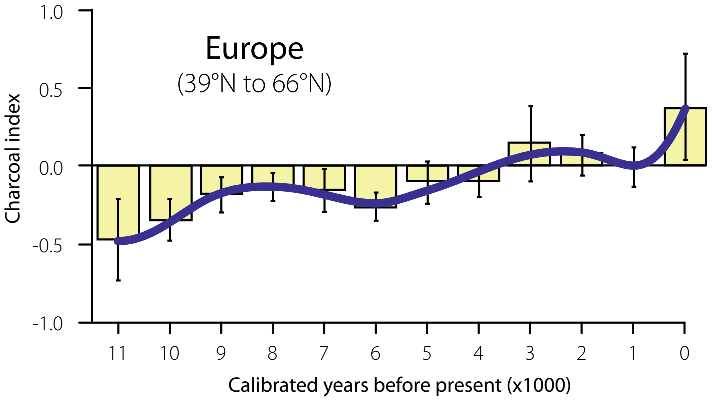

Figure 6: Biomass burning reconstruction in Europe from the Mediterranean to upper boreal ecosystems with charcoal index deduced from stratigraphic time series. The error bar corresponds to the standard error. Carcaillet et al. 2002, p. 853

But regardless of whether fires were caused anthropogenically or naturally, the increased possibility of summer-droughts caused by the continental mid Holocene climate supported fire spreading through increasing biomass flammability and a faster fire spreading speed (Carcaillet 2002, p. 855ff).

All these aspects allow the assumption that beech-spreading was constrained by the greater seasonal contrast of mid Holocene climate. This may not have been a direct consequence of climate. Likewise the climatic conditions 6000 years BP might have caused competition disadvantages for beech against other taxa like oak (*Quercus*) and lime (*Tilia*) in the Northern European lowlands limiting beech to alpine regions (Iversen 1973, Godwin 1975 in Huntley & Webb 1988b, p. 370f). Therefore a reason for the increasing spread of beech could be the decreasing continentality of climate after the mid Holocene, leading to a more oceanic climate in Europe with warmer winter conditions (Huntley & Webb 1988b, p. 371; Huntley et al. 1989).

2.3.2 Human land use

The correspondence in time between the late Holocene expansion of beech and the expansion of agriculture and Neolithic peoples has led to the theory that the tree used the opportunity to spread onto cleared and abandoned areas where competition was reduced and/or soil fertility was lowered (Andersen 1973 in Huntley & Webb 1988b; Frenzel 1992).

The spreading of this systematic anthropogenic interference started from the Near East which was the most important centre of domestication at the beginning of the Holocene and went on proceeding from South-Eastern to North-Western Europe (Bradshaw 2004; Ruddiman 2001, p. 391) along the Danube-Rhine axis (cf. *figure 7*) (Roberts 1998, p. 152). This development permitted a smooth but definite transition from a society of hunters and gatherers to farmers (Roberts 1998, p.129; Bell & Walker 2005, p. 150ff) affecting natural vegetation which has not been heavily influenced by anthropogenic factors until then.

By settling down, men started to clear forests to obtain wood for building and burning purposes and to use the thereby cleared land as agricultural area (Küster 1998, p. 68f). The non cleared forest was used as well by domesticated browsing animals like cattle, pigs, sheep and goats (Küster 1998, p. 74). These high human-managed livestock densities in the forest may have favoured beech, as other trees such as lime (*Tilia*) are more heavily browsed (Cowling et al. 2001)

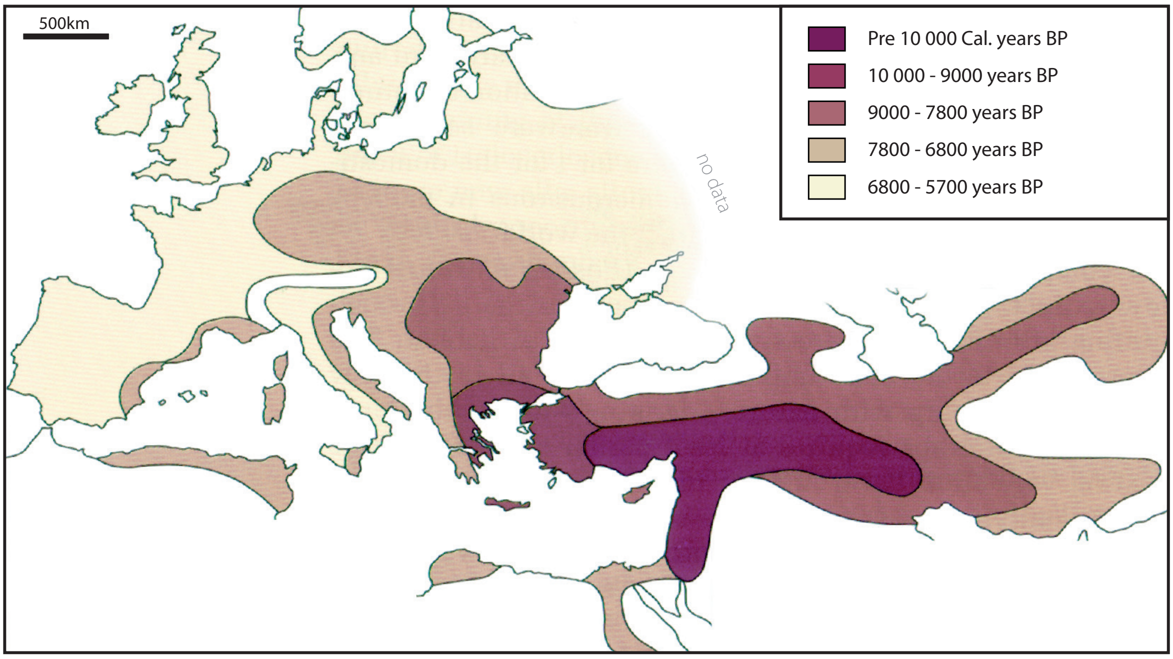

Figure 7: The spread of Neolithic farming across western Eurasia during the Holocene. After Roberts 1998, p. 152

Another indication is that the dominance of beech in the present day forest landscape evolved during the Holocene only as a final step of postglacial forest growth (Ellenberg 1996, p. 149). Beech pollen and macrofossils however have been identified from both Miocene and Pliocene deposits (24 to 1.6 Myr BP) in Europe (van der Hammen, Wijmstra & Zagwijn 1971 in Huntley et al. 1989, p. 551). This indicates that the species already existed during the interglacials preceding the Holocene but never reached the kind of distribution like today. So there must have been circumstances in our interglacial differing from those of earlier interglacials supporting this kind of dominant spread of beech like it occurred the last 5000 years (Ellenberg 1996, p. 149). And these circumstances could have been the further development of human society and the advent of agriculture.

However, the closer analysis of spreading dynamics and the relation with comparable spreading in the USA does not really support this theory satisfactorily because the anthropogenic impact on vegetation in the USA was not that affecting like in Europe during the mid Holocene (Huntley et al. 1989). Indeed, former modelling of the present and past range limits of forest trees have suggested, that climate change is the major driving force behind range changes (SYKES ET AL. 1996). The human-impact-theory ignores also the ability of beech to both occupy 'fertile' soils and, as a shade-tolerant, late-successional tree, to regenerate as part of a mixed canopy (HUNTLEY & WEBB 1988b), making the necessity to come upon cleared or abandoned land less important. Furthermore, the expansion of beech occurred more gradually and still continues today in Sweden (SYKES ET AL. 1996).

FRENZEL (1992, p. XI) argues that 'the human impact on the environment in the Early Neolithic had generally not been to grave. The areas cleared from forests will hardly have exceeded 10%'. Hence natural changes in the period 'Late Atlantic' to the middle of the Subboreal far outweigh the changes induced by man (GROENMAN-VAN WAATERINGE 1992, p. 13**).** There is only the correspondence in time between the late Holocene expansion of beech and the advent of agriculture supporting this theory of a beech constraint caused by human land use (HUNTLEY & WEBB 1988b).

3.3.3 Megaherbivores

The advancement of humans was not the single change in the environmental system in the Holocene in comparison with earlier interglacials. The absence of megaherbivores in the Holocene might have assisted also the spreading of beech (ELLENBERG 1996, p. 150).

Prior to their extinction, elephants (*Elephantidae*) may have killed juvenile trunks by eating, cracking or excoriating them. To some degree that applies also to rhinoceros (*Rhinocerotidae*), large ungulate and other larger herbivores living in Europe before the last ice age. One result of this behaviour is that Megaherbivores could have created clearings in forest cover.

There exist two theories about the extinction of Megaherbivores. One is that these mammals could not withstand the consequences of climatic change after the last ice age (RUDDIMAN 2001, p. 394). A second explanation is that human impact both directly by hunting kill-off or indirectly, through loss of habitat caused this major pulse of extinctions maybe in combination of the appearance of a new hunting technology (REMMERT 1984A, 1985 in ELLENBERG 1996, p. 151; RUDDIMAN 2001, p. 394f; ROBERTS 1998, p. 151; KÜSTER 1998, p. 68).

ELLENBERG (1996, p.151) therefore states that the interaction between the influence of Megaherbivores and major fires that may have already been set by humans constrained a spreading of beech before the Holocene. This impact (the most important was caused by the influence of elephants) was not active anymore in the Holocene allowing beech to constantly maintain or enlarge its dominancy.

However, neither the behaviour of European Forest Elephants, nor the mentioned frequent setting of major fires by Palaeo- or Mesolithic humans is proven and leaves many open questions (ELLENBERG 1996, p. 151).

2.3.4 Dispersal limitations

This hypothesis states, that rejuvenescence of beech was not fast enough to allow their range limits to keep track with climatic changes in the early Holocene. Their continued migration throughout the Holocene therefore merely represents a gradual adjustment to Holocene climate conditions (Huntley & Birks 1983).

The observed range shift of beech is about 150 to 300 m per year (Huntley & Birks 1983; Bennett 1985 in Huntley et al. 1989; Davis 1981 in Woods & Davis 1989).

Compared to other major European tree species, the dispersal rate of beech is limited by several factors like the following: Beech-nuts cannot fly and therefore fall to the ground perpendicularly being dispersed only when hitting leaves and branches (Ganz 2004, p. 122f). Dengler (1935 in Ganz 2004, p. 123) confirmed that there occurs also spreading by animals (squirrel, mice, pigeons, jay and brambling). In Northern America, Blue Jays (*Cyanocitta cristata*) have been observed carrying beechnuts up to 4 km and bury them (Johnson & Adkisson 1985 in Woods & Davis 1989). Rivers or streams cannot assist spreading either as beech is not able to establish under the wet conditions prevailing there (cf. *figure 2*) The rejuvenation process depends also on the terms of survival for the seedlings (Ganz 2004, p. 116f) and the danger for the juvenile plant by browsing animals (Ganz 2004, p. 123ff).

This chapter provided a general background about beech, the hypothesis of a ‘climate constraint’ as well as an outline of three other hypotheses which try to explain the reasons for a distribution constraint of beech.

Like mentioned before, the hypothesis underlying this thesis is the assumption that climate was the dominant factor constraining the distribution of beech 6000 years BP in Europe. Therefore the subject was to analyse to what extent the distribution of beech was constrained by the factor climate in this time-slice. Computer modelling techniques were used as method which are explained in the following chapter.

3 Material and Methods

This chapter describes the functionalities of and the links between the two computer models LPJ and STASH, and the climate data used as modelling input. In the following, the word 'model' is related always to 'computer models'.

3.1 Input data

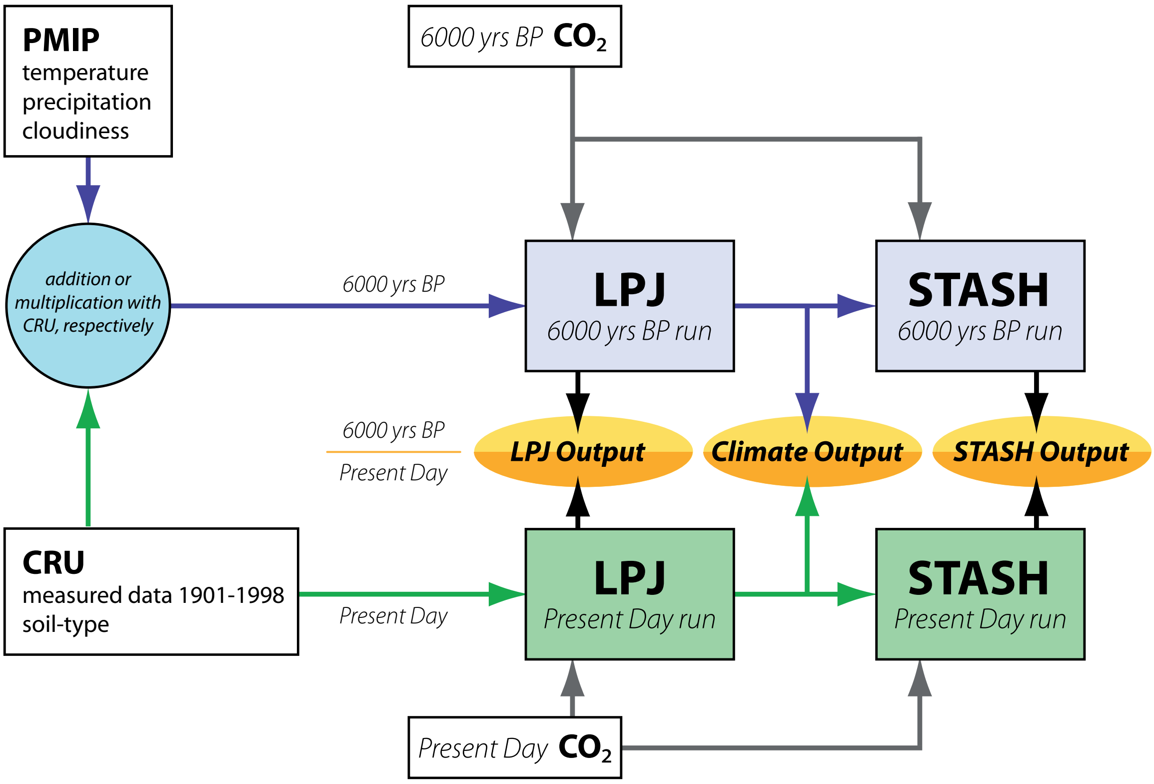

Figure 8: Input flow-chart for LPJ- and STASH-model

3.1.1 6000 years BP climate data

The modelling work is reliant on grid cell based climate data, providing the variables temperature, precipitation and sunshine**.** There are two options available to obtain this data: The use of proxy-data reconstructions or the output of climate models.

The most commonly used way to obtain information about climate and vegetation structure of 'pre-measured time' is the use of proxy-data (ROBERTS 1998, p. 30). Like mentioned in the last chapter, mid Holocene climate is well documented by proxy data, in particular through reconstructions based upon pollen data (HEWITT & MITCHELL 1996, DE NOBLET ET AL. 1996A, KUTZBACH ET AL. 1996, VETTORETTI ET AL, 1998, JOUSSEAUME ET AL. 1999 in BONFILS ET AL. 2004).

Palynology (the study of living and fossil pollen grains, spores, and certain macrofossils) is the most important proxy-method for the Holocene. The underlying basis assumption is that parts of plant pollen can be preserved under anaerobic conditions in lake mud, peat bogs or other sediments (Roberts 1998 p. 29). By counting the deposited pollen grains in a sample it is possible to draw conclusions about the distribution of the parent trees and therefore also about prevailing climatic conditions (Andersen 1973 in Roberts 1998, p.30).

However, gridded data reconstructions using pollen (or other proxies) have the disadvantage to be created by applying a spatial interpolation to unevenly distributed samples. Guiot et al. (1999, p. 570) for example state, that 'for paleoclimate studies, even with the most complete data set available, the data coverage is poor and not regularly spaced, and is characterised by different spatial scales of variability from local to synoptic' (cf. Prentice et al. 1996, figure 3, p. 192). This leads to a varying accuracy from gridcell to gridcell (cf. Huntley et al. 1989, p. 552f). Another source of error is that vegetation was already anthropogenicaly influenced at least in the Mediterranean area 6000 years BP so that pollen samples are biased by default (Masson et al. 1999, p. 180). Furthermore, there is only one gridded proxy-dataset (Davis et al. 2003) for the whole of Europe available at present and this data set provides only estimates of temperature.

The problems occurring with proxy data can be avoided by using the already gridcell based output of 'atmospheric general circulation models' (AGCMs). Therefore the 'Paleoclimate Modelling Intercomparison Project' (PMIP) (Joussaume & Taylor a) was chosen since no other AGCM-Dataset exists at present providing the full set of climatic variables that may have constrained the geographical range of beech 6000 years BP.

The PMIP-Project coordinated the systematically analysis of 18 AGCMs for their usability to predict two strong variations of the climate of the Quaternary: The last glacial maximum, 21 000 years BP and the mid-Holocene, 6000 years BP. The latter was used for this work.

The results of Bonfils et al. (2004) were used to decide which PMIP-model data is most suitable as climatic input for vegetation-modelling. Their approach is the systematic comparison of all 18 different '6000 years BP'-model-runs carried out by the PMIP-project with pollen and lake level data (Cheddadi et al. 1997) to draw a conclusion about their accuracy in simulating the climate that prevailed during the mid Holocene.

According to the results of Bonfils et al. (2004), only two out of the 18 available models are capable of simulating the complex attributes of the climate 6000 years BP rudimentarily, but because of being the most accurate climate models available at present, they were used.

These models are 'Genesis 2' (GEN2 - National Center for Atmospheric Research / Pennsylvania State University) and 'UKMO' (United Kingdom Meteorological Office 1997). As a third model, the 'ECHAM3'-model (Max Planck Institute for Meteorology Germany, run at Bremen

University) was chosen. This model simulates more warming than the others and is used as complement because the PMIP AGCMs may underestimate mid Holocene warming as they do not include vegetation feedbacks on the atmosphere (RUDDIMAN 2001, p. 318).
For this thesis, the calculations by LPJ or STASH were carried out once for each of the three mentioned AGCMs both for mid Holocene and present day to avoid exceeding a passable bias level. *Table 1* shows the three variables out of PMIP used to run Stash and LPJ. These are the surface air temperature (*TAS*), the precipitation (*PR*) and the cloudiness (*CLT*).

Table 1: PMIP-Variables used as input for LPJ amd STASH

Name	Variable-Name	Unit	Description
Surface Air Temperature	TAS	°C	2-meter screen temperature
Total Precipitation	PR	mm	include liquid & soild phase, convective & large scale precipitation
Total Cloudiness	CLT	%	percentage of atmospheric column covered by clouds

In context of PMIP, the three different AGCM were all run with the same preconditions, apart from the fact, that they are available only with differences in resolution (*table 2*). So in order to compute the variables with STASH or LPJ, they were resampled to a uniform gridcell size.

Table 2: Resolution of climate-variables.

Name	Variable	lon x lat *	°-steps lon x lat
ECHAM3	CLT	128 x 64	2.8 x 2.8
	PR	128 x 64	2.8 x 2.8
	TAS	128 x 64	2.8 x 2.8
GEN2	CLT	96 x 48	3.75 x 3.75
	PR	96 x 48	3.75 x 3.75
	TAS	180 x 90	2 x 2
UKMO	CLT	96 x 73	3.75 x 2.5
	PR	96 x 73	3.75 x 2.5
	TAS	96 x 73	3.75 x 2.5

* Represents the gridcells for the whole globe

3.1.2 Present day climate data

In order to get a reliable measured climate basis both for the calculations carried out to obtain the input data for LPJ and STASH as well as to generate the present day maps, the CRU climate data set was used. This climate data set is published by the 'Climate Research Unit' of the University of East Anglia, UK[4] providing measured climate data covering the last century (1901-1998) with a spatial resolution of 0.5° x 0.5°. However, a dataset adapted to the LPJ-model was used for his work (Sitch et al. 2003).

3.1.3 CO_2-level

The amount of carbon dioxide in the atmosphere was set to a constant level of 280ppm for the mid-Holocene representing a pre-industrialised value (the same value used by PMIP[5]). Due to anthropogenic influences, the CO_2-level has risen rapidly since industrialisation started. Atmospheric CO_2 concentrations for this period were therefore obtained from the Carbon Cycle Model Linkage Project (McGuire et al. 2001).

3.1.4 Soil data

Soil texture data was, as in Sitch et al. (2003), based on the FAO soil data set (Zobler 1986; FAO 1991).

3.2 Vegetation models

3.2.1 Bioclimatic Model: STASH

STASH is a bioclimatic model based on physiological constraints to plant growth and regeneration. It is used here in an empirical way to describe the potential distribution of beech (Sykes et al. 1996). It draws on techniques developed for global biome modelling by Prentice et al. (1992).

Sykes et al. (1996) and Prentice et al. (1992) have shown, that the accuracy in simulating present-day species ranges can be predicted from a small set of limits representing particular processes that are assumed to control species' range limits.

The Stash model was used to compute the potential distribution of beech without having competition by other plants. The model output is based only on bioclimatic limits and the ability of the simulated tree to regenerate.

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[4] *http://www.cru.uea.ac.uk*

[5] *http://www-lsce.cea.fr/pmip/docs/condidoc.htm*

The main climatic factors that influence the distribution and dominance of beech are **winter cold** (the tolerance of cold extremes versus chilling requirements to trigger dormancy), **growing-season warmth requirements**, and **drought tolerance** (Woodward 1988, in Prentice et al. 1996). As calculated in Prentice et al. (1992), these factors are quantified here in terms of bioclimatic variables:

- Mean temperature of the coldest month (T_C in °C).
- Length of chilling-period (temperature in °C)
- Annual 'growing-degree-days' above 5°C (GDD_5 in days.°C).
- The ratio of actual to equilibrium evapotranspiration (AET/PET or α) which serves as an index of moisture availability.

3.2.2 Vegetation Model: LPJ

The Lund-Potsdam-Jena Model (LPJ) is a 'Dynamic Global Vegetation Model' (DGVM) simulating the growth of plant populations inside of grid cells. LPJ was developed as a DGVM with a broad bandwidth of possible applications in the field of global challenges. Therefore three aspects served as a development guideline:

1. A process based coupling of land and atmosphere that is still computable efficiently.
2. The inclusion of main processes of vegetation dynamics including growth, competition and natural fire as well as demographic processes.
3. An emphasis on a broad evaluation of data both from Climatology and Ecology.

Multiple attributes were adopted from the BIOME model family (Sitch et al. 2003). Therefore plant species in LPJ are not represented individually but by their general attributes being explicit parameterizations of their growth and interactions (Smith et al. 2001, p. 621). These attributes are classified into so called 'Plant Functional Types' (PFT) because the prevailing assumption is that taxa sharing the same PFT group also share the same bioclimatic space (Peyron et al. in Davis et al 2003; Prentice et al. 1992, 1996).

Vegetation dynamics like being represented in this modelling context comprise the processes of competition for resources among the PFTs and their feedback on plant carbon assimilation and allocation, reproduction and survival (Smith et al. 2001, p. 621).

In addition to their physiology and dynamic, there are assigned bioclimatic limits to each PFT which determine whether a PFT is able to survive or to regenerate in a certain gridcell with a given climate at one point in time (cf. *figure 9*; Sitch et al. 2003). The simulation of vegetation processes by LPJ is therefore limited to the currently processed grid cell and does not simulate dispersal (Cramer et al. 2001 in Smith et al. 2001).

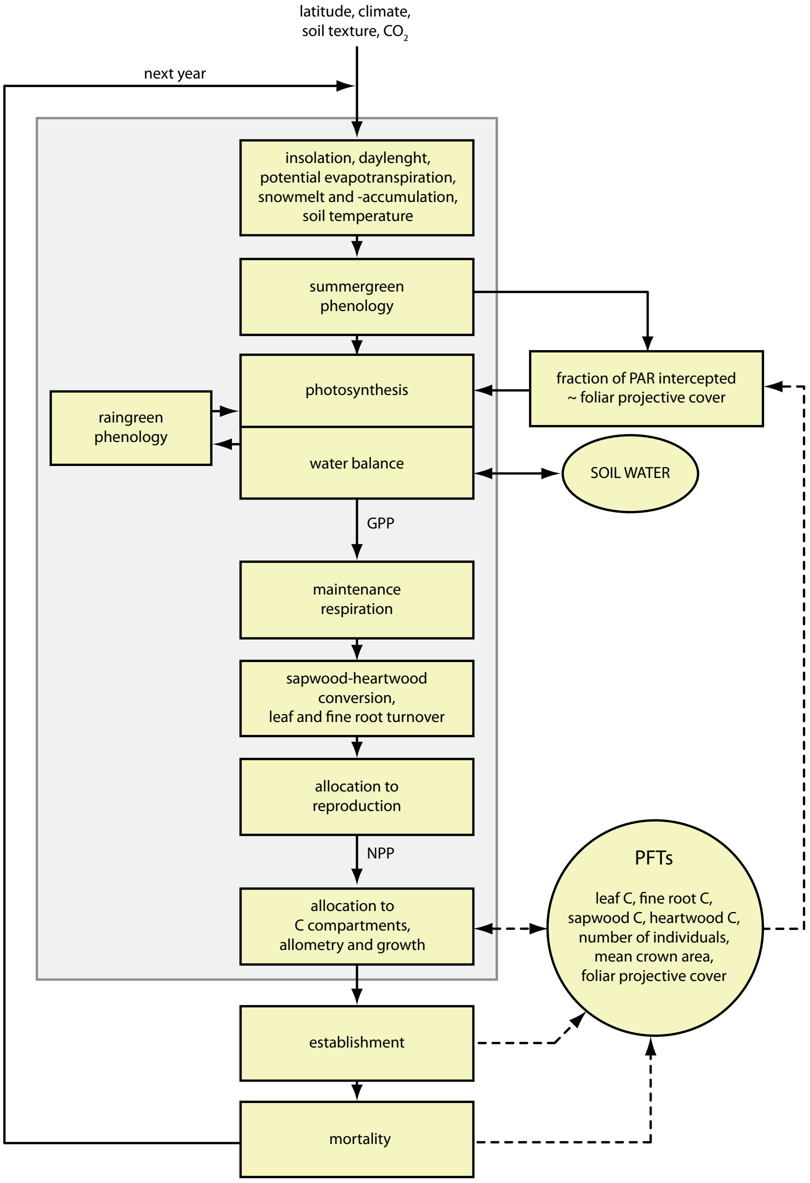

Figure 9: Flow-chart of LPJ functionality. SMITH ET AL. **2001**

The simulated PFT composition is translated into broad, generally-recognized vegetation types (*table 3*). This allows a better comparability to other maps.

Table 3: Vegetation types simulated by LPJ. The italicised type includes beech.

Vegetation type	Type
Warm grassland (C3 grass)	herbaceous
Temperate Forest	***woody***
Boreal Forest	woody
Tundra (C3 grass)	herbaceous

Two of the vegetation types are woody (temperate forest and boreal forest) and two are herbaceous (warm grassland and Tundra). The herbaceous types are however simulated only as ‘C3 grass’ by LPJ. Therefore, this vegetation type is divided into ‘warm grassland’ and Tundra whereas the border between the both is set at 45° latitude.

3.3 Modelling protocol

3.3.1 Processing climate data for model input

In order to use the PMIP-data, it has been necessary to extract it out of the PMIP-database and to pre-process it to make it utilisable by the STASH and LPJ models. However, it would be inaccurate to use both present day and mid Holocene data directly out of the AGCMs because AGCMs are already biased to some extent with respect to present day climate.

To avoid this systematic failures when simulating paleovegetation, the variations between the present day and the 6000 years BP AGCM runs were calculated as first step. This is done for the temperature (*TAS*) and the ‘Total Cloud Cover’ (*CLT*) by subtraction (6000 yr BP minus present day). The variance of precipitation (*PR*) is expressed by the quotient (6000 yr BP divided by present day) to avoid getting values below zero. In order to obtain corrected datasets for the mid-Holocene, the calculated varieties were added (*TAS* and *CLT*) or multiplied (*PR*) after an adjustment to the 0.5° x 0.5° resolution to each month of each gridcell of the CRU dataset for the 97 years included in the CRU data-set (cf. *figure 8*).

3.3.2 LPJ

LPJ was run both for present day (only with CRU data-set) and for 6000 years BP (CRU combined with AGCM data set) for the mentioned 97 years. Because LPJ starts simulating from ‘bare ground’ without having any plant biomass present, a spin-up period of 600 years was included.

In the course of postprocessing, for the present day time-slice, a thirty year interval from 1950 to 1980 was chosen out of the 97 years simulated by LPJ to avoid the bias caused by rapid warming especially in the 1990s which is not yet seen in the distribution of beech as seen in the data of the ‘Atlas Florae Europaeae’ (JALAS & SUOMINEN 1976). Analogue to present day, the interval for the mid Holocene time-slice was year 49 to 79.

3.3.3 STASH

The mean of the 30 years simulated by LPJ was calculated to obtain one single year for mapping and as input data for STASH. To simulate the potential distribution of beech out of the climate data, the STASH model needs a parameterisation for beech which was defined by the following limits: The mean minimum temperature of the coldest month (T_c) was set to -3.5°C and maximum T_c to 6.0°C (the latter parameter is necessary due to the relevance of a chilling period to beech). Furthermore, minimum temperature of the warmest month was set to 5.0°C and minimum GDD_5 required for beech to reach budburst with no chilling was set to 1150 days.°C (cf. Sykes et al. 1996). The maximum drought-index tolerated by beech is set to $\alpha = 0.35$. These limits were shown to accurately predict the current range of beech (Sykes et al. 1996).

Table 4: Parameterisation of beech for STASH use

Sapling establishment rate (ha per year)	10.0
Minimum tolerated drought-index during growing period (α-value)	0.35
Minimum effective GDD_5	0.35
Minimum temperature of coldest month	-3.5 °C
Maximum temperature of coldest month	+6.0 °C
GDD_5 required to reach budburst with no chilling	1150.0
GDD_5 requirement decay rate with increased chilling	0.0065

The higher the output growth indices, the better the growth conditions for beech in this gridcell (Sykes et al. 1996, p. 206; Prentice et al. 1992).

All steps mentioned in the modelling protocol were carried out for each of the three AGCMs (UKMO, GEN2, and ECHAM3), both for present day and mid Holocene.

3.4 Overview of processed variables

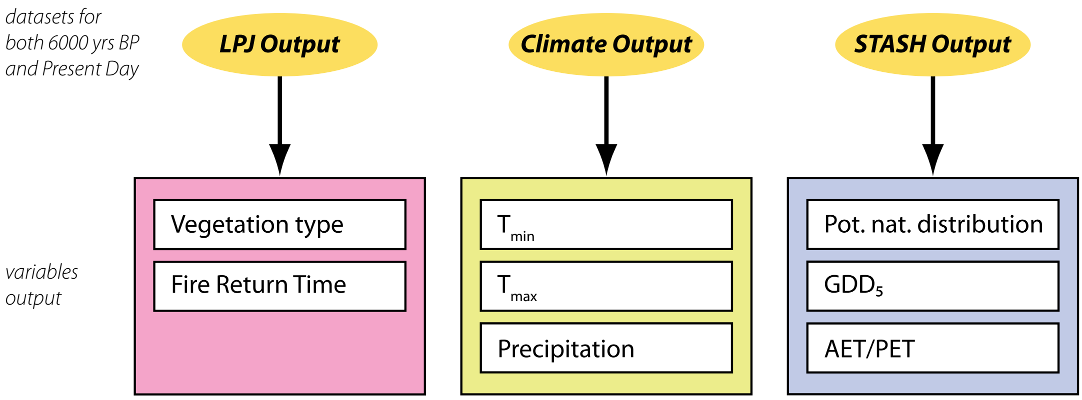

Figure 10: Output of bioclimatic factors and variables. Continued from *figure 8*

3.4.1 Mean temperature of coldest month

The first climatic factor that constrains the distribution of plants by setting its eastern limits (Sykes et al. 1996, p. 206) is the mean temperature of coldest month (T_C) represented by the tolerance of cold extremes versus chilling requirements to trigger dormancy (Woodward 1988 in Sykes et al. 1996). This factor is derived from the PMIP-variable *TAS* (cf. *chapter 3.1.1*).

3.4.2 Mean temperature of warmest month

This factor T_W is also derived from the PMIP-variable *TAS*.

3.4.3 Precipitation

The mean monthly precipitation was summarized for the growing season (April to October) to obtain the 'growing season precipitation'.

3.4.4 GDD$_5$

In central and northern Europe, the major factor limiting poleward spread (northern limit) of different woody plant types is not the maximum temperature but the temperature accumulation over the growing season. It shows the integrated sum of temperatures above 5°C (Masson et al. 1999, p. 166).

GDD$_5$ is defined by the following function:

$$GDD_5 = \sum_{j=1}^{365} \left\{ \; T(j) - 5, \;\; if \; T(j) \geq 5 \; \right\}$$

where j is the day and T the daily temperature interpolated from the climatological monthly means of the surface temperature. (cf. Masson et al. 1999, p. 166). The '5' is set as constant for the minimum temperature of 5°C required for growth.

Woody plants of temperate regions commonly require a winter chilling period with temperatures below 5°C for rapid budburst the following spring. Beech is especially sensitive to the length of the chilling period. This relationship is presumed to be an adaptation to weather variability causing that budburst is delayed long enough to minimize the risk that the emerging buds will be damaged by frost. The length of the chilling period is therefore defined and used in STASH as the period with temperatures below 5°C (Sykes et al. 1996, p. 204)

3.4.5 Ratio of actual to potential evapotranspiration (α = AET/PET)

The variable α (AET/PET) is an index of drought stress on vegetation (Prentice et al. 1992; Sykes et al. 1996; Cheddadi et al. 1997). The moisture available for plant growth is best expressed in terms of the seasonal course of soil water content. To obtain a good fit to the distribution of vegetation physiognomy in terms of available moisture, the climatic index of the ratio of precipitation to potential evapotranspiration (PET) is used (P-E). However, plants do not experience PET as such, but respond to the interaction of seasonal PET with soil moisture. Soil moisture in turn responds to the seasonal course of precipitation and PET, mediated by the water-storage capacity of the soil.

The seasonal distribution of precipitation can strongly affect the severity of drought experienced by beech. To get an index of the drought, the ratio of actual evapotranspiration to potential evapotranspiration (Priestley-Taylor coefficient: AET/PET = α) is calculated.

In contrast to Prentice et al. (1992) who evaluated α over the whole year, α is evaluated in this modelling over the growing period with temperatures >5°C (equivalent to 1-α* in Sykes et al. 1996). This gives a finer discrimination among environments with relatively slight summer drought stress (Sykes et al. 1996, p. 204).

α can be considered as an integrated measure of the annual amount of growth-limiting drought stress on beech (Prentice et al. 1992, Cheddadi et al. 1997).

- α = 1 actual evapotranspiration is in equilibrium with potential evapotranspiration.
- α < 1 actual evapotranspiration is lower than potential evapotranspiration. The lower this value, the higher is the possibility of drought stress for plants (varies between plants) (cf. *chapter 3.3.3*).

3.4.6 Fire Return Time

The conditions causing a fire to ignite and to continue spreading inside a grid cell are determined by the litter moisture and fuel load. The longer these burning condition persist, the longer the fire size can grow. Given the length of the fire season, which is the relative sum of the fire probabilities over the year, the fraction of the grid cell burnt in a particular year can be calculated (Thonike[6]). LPJ was adjusted to put out the area burned for each gridcell and year in percent (‘Fractional Area Burned’). As it is not common to use this definition, the ‘Fire Return Time’ (the time in years between the occurrences of two events of fire) is used instead, which is calculated as follows:

$$\text{Fire Return Time} = \frac{1}{\text{Fractional Area Burned}}$$

where the value of the ‘FireReturnTime’ is set to 2000, when the value of the ‘Fractional Area

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[6] *http://www.pik-potsdam.de/~kirsten/web_page_lpj.htm*

Burned‘ is zero (to avoid division by zero) or the ‘Fire Return Time’ would be greater than 2000 years (to avoid absurd large numbers). So the minimum is > 0 years and the maximum ≤ 2000 years.

The lower the value for the ‘Fire Return Time’, the higher the frequency of events of fire.

3.4.7 Potential distribution of beech

This by STASH calculated variable shows the potential spread of beech without having competition. So only the bioclimatic factors (see *chapter 3.2.1*) are of importance making the maps of the mid Holocene and present day time slices comparable as the potential spread of beech is not directly ‘measurable’ in both time-slices. There is no measured data available for the mid Holocene whereas the present day forests are heavily influenced by anthropogenic factors. The temperature, precipitation and sunshine serve as climate input. STASH is then run with the parameterisation for beech.

3.4.8 Simulated Vegetation

This variable shows the vegetation type for each gridcell and is simulated by the LPJ DGVM. The map gives an idea about the magnitude of change in general vegetation composition that would be expected as a result of differences in climate between 6000 BP and today.

The simulations can also be compared to the results of BIOME6000 (Prentice et al. 1996) allowing an indirect validation of the climate input.

4 Results and Discussion

A total of 19 maps were created representing general climate conditions, bioclimatic factors and the vegetation structure (*figure 13 to 19*). Except the maps showing the vegetation types and the natural distribution of beech, all maps are composed by the following scheme:

The upper map shows the degree of variation of the Mid Holocene from the present day variable (mid Holocene *minus* present day). The lower two maps point out the absolute values calculated by the models for the mid Holocene (left) and present day (right). Furthermore, the base resolution of all maps is set to 0.5 x 0.5 decimal degrees per gridcell as a result of the native resolution of the CRU-dataset.

In the following, model calculations carried out by LPJ or STASH by using one of the three climate-models are solely called by the AGCM name (e.g. 'GEN2' for the map calculated by using the output of the GEN2 model as input for STASH or LPJ). Moreover, the names of the present day countries and regions were used both for present day and mid Holocene maps to make spatial classification easier.

The legends of the three maps (a: UKMO, b: GEN2 and c: ECHAM3) representing the same bioclimatic factor are consistently the same either for all the maps showing absolute values or the ones showing the variation between 6000 years BP and present day. This decreases the available classes and colours if one AGCM simulates more extreme values than the others, but allows a better comparability.

4.1 Climatic and bioclimatic factors

Like mentioned in the last chapter, the northern and north-western range limits of beech are determined by minimum values of GDD_5, the eastern limits by T_C and the southern and south-eastern limits towards the Mediterranean by minimum values of α (SYKES ET AL. 1996, p. 206). Furthermore the 'mean temperature of warmest month', the precipitation and the 'Fire Return Time'-map are analysed.

4.1.1 Mean temperature of coldest month - T_C

Figure 13a,b,c; page 31ff

UKMO simulates a predominantly cooler 'mean temperature of coldest month' of up to 2K lower than today for the mid Holocene with the exception of Iceland, Northern Scandinavia and South-Eastern Europe (up to 1K higher than today).

GEN2 shows both higher minimum temperatures for southern and the western part of Europe with a peak of up to 4K higher T_C at the Balkan region as well as a slightly lower T_C in Scandinavia, Great Britain and the Low Countries.

ECHAM3 simulates an overall warmer T_C for the mid Holocene being up to 2K higher in the western half of Europe and up to 6K higher in eastern half and northern Scandinavia. There are only some spots showing a lower T_C for the mid Holocene time-slice in Iceland, Scotland, Southern France and Southern Spain.

All calculated T_C variance maps show a good correlation with the PMIP-maps calculated by Masson et Al. (1999). Compared to pollen data (Cheddadi 1997, p. 7), only UKMO approximates showing a cooler T_C in South-Western Europe and a warmer T_C in North-Eastern Europe. This approximation is still visible in ECHAM3 whereas GEN2 simulates T_C the other way round showing a warmer T_C in South-Western Europe and a cooler T_C in North-Eastern Europe.

The area of T_C below the defined beech-minimum of -3.5°C (see *chapter 3.3.3*) is visible on all three mid Holocene and the present day maps in areas with higher altitude or latitude and in Eastern Europe. When comparing the present day map with the 'Atlas Florae Europapaeae' (Jalas & Suominen 1976) there is a good correlation between a T_C below -3.5°C and the eastern margin of beech supporting the statement, that the eastern margin of beech is limited by T_C (cf. Sykes et al. 1996).

Due to the simulated positive mid Holocene T_C variation of up to 6K in Eastern Europe, a distinctive feature of ECHAM3 is that T_C does not fall below the beech minimum of -3.5°C in this area up to the eastern margin of the investigation area that would allow the eastern spread of beech at least by this factor.

4.1.2 Mean temperature of warmest month - T_W

Figure 14a,b,c; page 34ff

With the exception of Southern Corsica, **UKMO** shows an overall warmer mean temperature of warmest month (T_W) for 6000 years BP. There are two peak-areas with the centre in South-Eastern Spain and Eastern Europe showing an up to 3.5K higher T_W. The T_W of rest of Europe lies around 1 to 2K higher.

GEN2 also simulates an overall higher mid-Holocene T_W with peak-areas in Northern Scandinavia, the Baltic States and the Western Mediterranean area (up to 3K higher than present day).

The highest T_W is simulated by **ECHAM3**. It shows higher temperatures of up to 4K for most of Europe. Only Southern Italy, Ireland and Scotland as well as Scandinavia show a more moderate warmer T_W. However, the north of the latter area as well as Iceland show some spots having a slightly lower temperature (circa 0.9K).

Like argued by Bonfils et al. (2004, p. 79), none of the mid Holocene runs of the three AGCMs simulate completely the by pollen reconstructions shown warmer than present summers in the north and cooler than present summers in the south as well as colder-than-present winters in the southwest and milder-than-present winters in the northeast.

But a higher seasonal contrast is shown by all AGCMs supporting the by pollen-reconstructions shown more continental climate of 6000 years BP. However, the mid Holocene time-slice is also called 'climate-optimum' having mean temperatures of 1 to 3 Kelvin higher in the mid-continent and far north than the mean Holocene temperature of 15°C (Budyko 1982, p. 145, Huntley & Prentice 1988, p. 687; Schönwiese 1995, p. 92. See *chapter 2.3.1*). This warming in combination with a higher seasonal contrast compared to present day climate is only shown by ECHAM3.

4.1.3 Precipitation

Figure 15a,b,c; page 37ff

All three AGCMs simulate a higher precipitation in Southern Spain and the central parts of Europe for the mid Holocene.

UKMO simulates less precipitation 6000 years BP in the north-eastern part of Europe (up to circa 100mm less at the west coast of Norway, the Baltic States, the Balkan Peninsula and Central Italy). In contrast, the model simulates more precipitation in North-Western Europe (up to 127mm more 6000 years BP).

GEN2 shows a higher mid Holocene precipitation in Western, Central and Eastern Europe (up to 127mm more in Spain, Germany, Balkan). Great Britain and almost whole Northern Europe as well as Italy and the South-Eastern Balkan simulate less precipitation 6000 years BP (circa 10 up to 100mm less than today).

ECHAM3 is the AGCM showing the largest negative variation of precipitation (mostly close to about 100mm less than today). Only Iceland, Central and Northern Scandinavia and Southern Spain as well as latitude-parallel strip continuing from Germany eastwards have a higher precipitation rate in mid Holocene.

4.1.4 GDD_5

The simulations of GDD_5 represent the temperature accumulation over the growing season (*results not shown*). The comparison with the PMIP-maps of Masson et al. (1999, p. 170ff) shows again a good correlation.

Expectedly, all the absolute values for GDD_5 in both time slices are high in the lower latitudes up to the northern borders of France, Benelux and Germany, excluding the mountain areas (Alps, Pyrenees, and Massif Central). Lower GDD_5-values appear in the higher latitudes of Europe.

When interpreting the GDD_5 variation-maps, the AGCMs show neither strong variations between the two time-slices nor insufficient GDD_5 for the mid Holocene in the regions where beech occurs today.

Due to the little variation between the two time-slices, one can conclude, that the absolute GDD_5-levels were high enough for beech growth in the same areas of Europe during the mid Holocene like they are at present day. Therefore the bioclimatic factor of GDD_5 does not seem to have constrained beech spreading in the mid Holocene.

4.1.5 AET/PET

Figure 16a,b,c; page 40ff

UKMO shows few variations between the two time-slices. A lower α occurs in Northern Spain, Southern Italy, the Balkan Peninsula, Southern Scandinavia and Eastern Europe. A positive variation of α is visible in contrast in the south-western part of Spain and the western most part of France and Hungary.

GEN2 simulates lower α-values in Western France and Southern Italy as well as around the Baltic Sea whereas whole Spain, Turkey, the Balkan and parts of Eastern Germany show a higher α-value.

The by **ECHAM3** simulated lower precipitation (see *chapter 3.1.3*) is reflected also to a certain degree in the AET/PET-map. Most of Central Europe (excluding the mountain ranges and the Low Countries with no change) show a drier situation for mid Holocene compared to present day (negative variation of α-value of up to 52.7%). Only South-Eastern Spain shows a positive variation of α.

To be able to compare the model output of this variable with proxy-data (model-data comparison), the work of Yu & Harrison (1996) and Harrison et al. (1996) was used providing a comparison of lake-levels (6000 yrs BP minus present day.

All three AGCMs show a good correlation when being compared to the lake-level data (*figure 11*) in Southern Spain, the Apennine Peninsula, the alpine region, northern Germany and Poland, Denmark and the area of southern Scandinavia. The positive variation at the Balkan Peninsula or the Baltic States is however not correctly simulated.

A limitation of this model-data comparison is however, that the same limitations occur like mentioned for other proxy-data (see *chapter 3.1*): The lake-level sample sites in the work of Yu & Harrison (1996) are not evenly distributed. There are missing sample-points nearly for the whole area of France, Eastern Spain, Germany, Norway and Eastern Europe. Another source of error is that lake levels only show the relation of precipitation to evaporation (P-E) which does not reveal, if the higher amount of available water due to the rise of a lake-level is also completely available for plant growth. Lake-levels are therefore only an indicator for AET/PET.

However, none of the gridcells where beech occurs today falls below an α-value of 0.35 (represented by the yellow classes) in the mid Holocene showing that this bioclimatic factor was again not constraining beech spread.

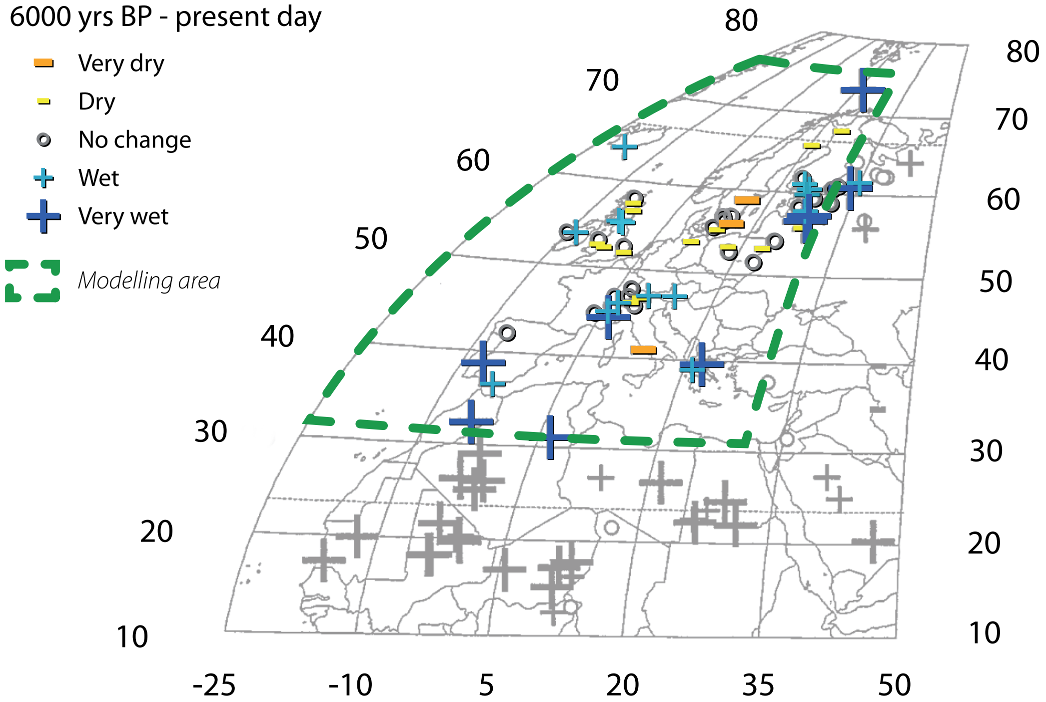


Figure 11: The change in lake status between 6000 yrs BP and present day. After Yu & Harrison 1996, p. 727.

4.1.6 Fire Return Time

Figure 17a,b,c; page 43ff

UKMO simulates a higher fire frequency in Central, Eastern and Northern Europe for the mid Holocene time-slice (peaks are around the Alps, Massif Central, Scandinavia, Ireland and the Baltic States. A lower 'Fire Return Time' is simulated for the Mediterranean countries and islands like Spain, Sardinia and Italy as well as Western and Southern France, Great Britain and Romania.

GEN2 shows for the mid Holocene a higher frequency of returning fires in Scandinavia, southern Great Britain, the Pyrenees and the Massif Central and western Alps. Most of Central and Southern Europe instead have a lower frequency. The fires are less frequent in mid Holocene than present day especially in the Eastern Alps, the Central European lowlands, the Balkan and Ireland.

ECHAM3 simulates more frequent fire events than the other two AGCMs over whole Europe especially in Great Britain, around the Alps and the Baltic States. Only Spain, Central Scandinavia and the Ukraine are having a lower fire frequency.

Both the absolute present day map (calculated out of measured data) and the mid Holocene map represent well the climatic connections between latitude and European orography. Southern Spain and the most southern parts of the Mediterranean Countries (as well as North Africa) show for example a high 'Fire Return Time' having an up to annual intervals whereas Scotland, Norway and the higher altitudes of the Alps approximate to the lower margin of 2000 years.

The single area where beech occurs today and where an increase in frequency of fire events during the mid Holocene is shown are the northern plains of Central Europe simulated by UKMO and ECHAM3 (GEN2 indeed shows less fire).

It needs to be accentuated however, that the LPJ-model may only simulate natural fires. Anthropogenically ignited fires (see *chapter 2.3.2*) therefore cannot be included although it seems that they had an increasing impact on vegetation during the Holocene (cf. Carcaillet et al. 2002, p. 850f).

4.2 Potential distribution of beech

Figure 18a,b,c; page 46ff

Basing upon the used bioclimatic factors and having no competition, beech would spread over most parts of Europe avoiding the higher altitude regions (e.g. Alps, Pyrenees and Carpathians) which seem to be limited by T_C like the eastern margin of beech.

The southern part of the Iberian, Apennine and Balkan Peninsula create the southern margin of beech spread. This margin is after Sykes et al. (1996, p. 206) connected solely to the AET/PET-value (α). However, the AET/PET-variable shows a high enough α in the Southern Mediterranean area. Therefore it seems to be connected also to other factors like maximum temperature or a not long enough chilling-period to trigger budburst (cf. Sykes et al. 1996, p. 204).

The northern margins are located in Central Great Britain (excluding Ireland) and southern Scandinavia and seem to be connected to a too short growing period (GDD_5) (Sykes et al. 1996, p. 206). The Bohemian Forest and the Massif Central, however, are excluded on all maps though only being low mountain ranges.

UKMO is the only model showing a slightly smaller potential growth area for beech which is situated around the mountain areas.

GEN2 however simulates nearly the same potential growth area for both time slices (apart from a small area with potential mid Holocene beech growth on the eastern side of the Carpathian Mountains).

Only **ECHAM3** shows a wider spreading of beech into the area of Eastern Europe and a bit northward in southern Sweden. Compared to present day, also the gaps of the low mountain ranges are closed (Bohemian Forest) or at least narrowed (Massif Central). This 'gap reduction' is also visible at the Alps or the Carpathian Mountains allowing the assumption, that the overall higher temperature (in this case probably a higher T_C) simulated by this AGCM favours the potential spread of beech.

4.3 Simulated Vegetation Types

Figure 19; page 49

The map shows a comparison of the simulated distribution of the vegetation types for all three AGCMs (mid Holocene) as well as for present day calculated out of the CRU-dataset.

All maps show a broad dominance area of the beech including *'temperate forest'* in Western and Central Europe up to the Atlantic Ocean and the North Sea coastlines including most parts of Great Britain and Ireland, parts of the northern and western coastline of Spain and Northern Italy. The Southern Mediterranean areas are predominantly occupied by *'warm grassland'*. The model does not reproduce the observed sclerophyllous woody vegetation in this area because the applied LPJ version does not include a Mediterranean PFT that would correspond to the species occurring there.

UKMO and **GEN2** show only small variations in the distribution of the vegetation types and are therefore similar to the present day map. The higher altitude regions (e.g. the Alps) as well as Eastern Europe show a transition from *'temperate forest'* to *'boreal forest'* including patches of *Tundra*. The same occurs for Scandinavia, where only a small strip of *'temperate forest'* is simulated in southern Sweden.

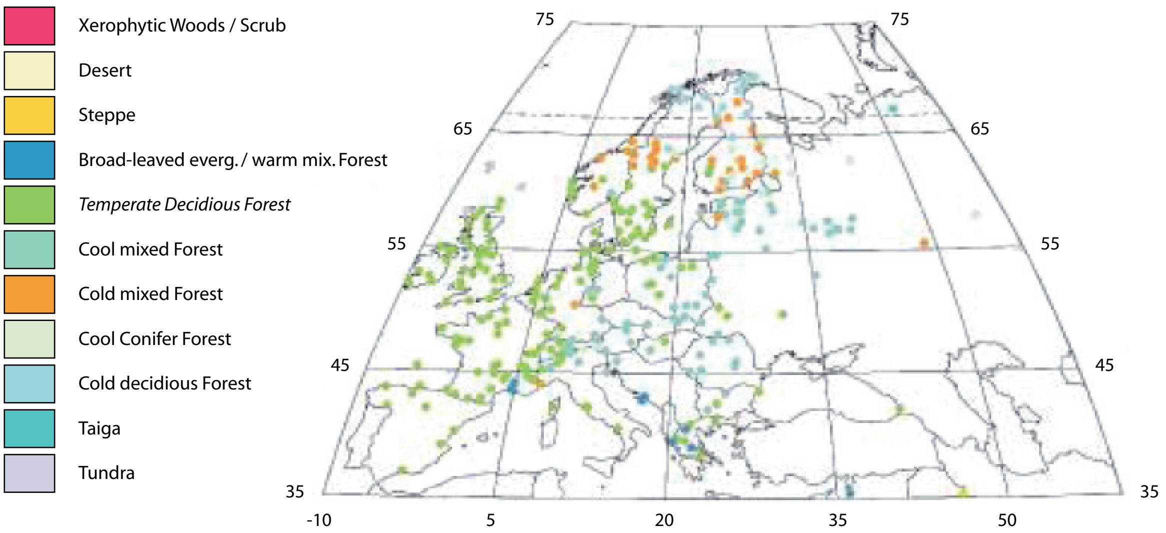
LPJ run with **ECHAM3** climate-input simulates however a strong eastward shift of *'temperate forest'* up to the Baltic States and Romania for 6000 BP replacing most of the for present day simulated *'boreal forest'* in Eastern Europe. There is also more *Tundra* simulated in Eastern Europe and *'warm grassland'* simulated in South-Eastern Europe.

It is astonishing that the vegetation type maps simulated by UKMO and GEN2 do not show a significant change between the two time-slices even though the prevailing thermal optimum in mid Holocene (see *chapter 2.3.1*).

When comparing the obtained results to the pollen reconstructions by the BIOME 6000 project (PRENTICE ET AL. 1996, p. 192), the ECHAM3 model is the only one that shows well correlated areas between the AGCM and the pollen-reconstruction. There is for instance a good correlation between the mid Holocene proxy-reconstruction and the simulation in Southern Sweden, where a northward shift of '*temperate forest*' is simulated probably caused by the overall warmer climate in mid Holocene (*figure 12*). This shift is also shown in north-eastern Europe.

This correlation might indicate that UKMO and GEN2 underestimate the mid Holocene warming, possibly because vegetation feedbacks on climate were not included in the PMIP runs (RUDDIMAN 2001, p. 318).

a.) Pollen-derived biomes at 6000 yrs BP



b.) Pollen-derived biomes at present day

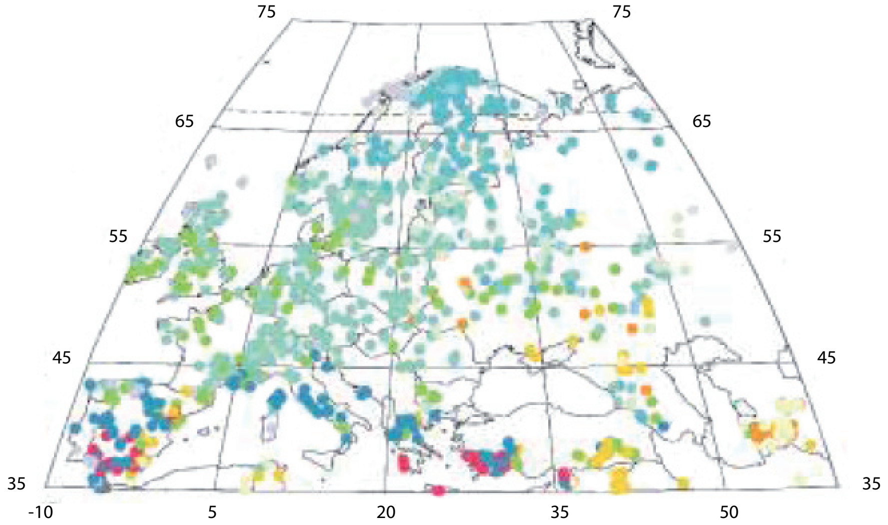


Figure 12: European Biomes (a) 6000 yrs BP and (b) present day reconstructed from pollen samples. After PRENTICE ET AL. (1996).

Mean temperature of coldest month - UKMO

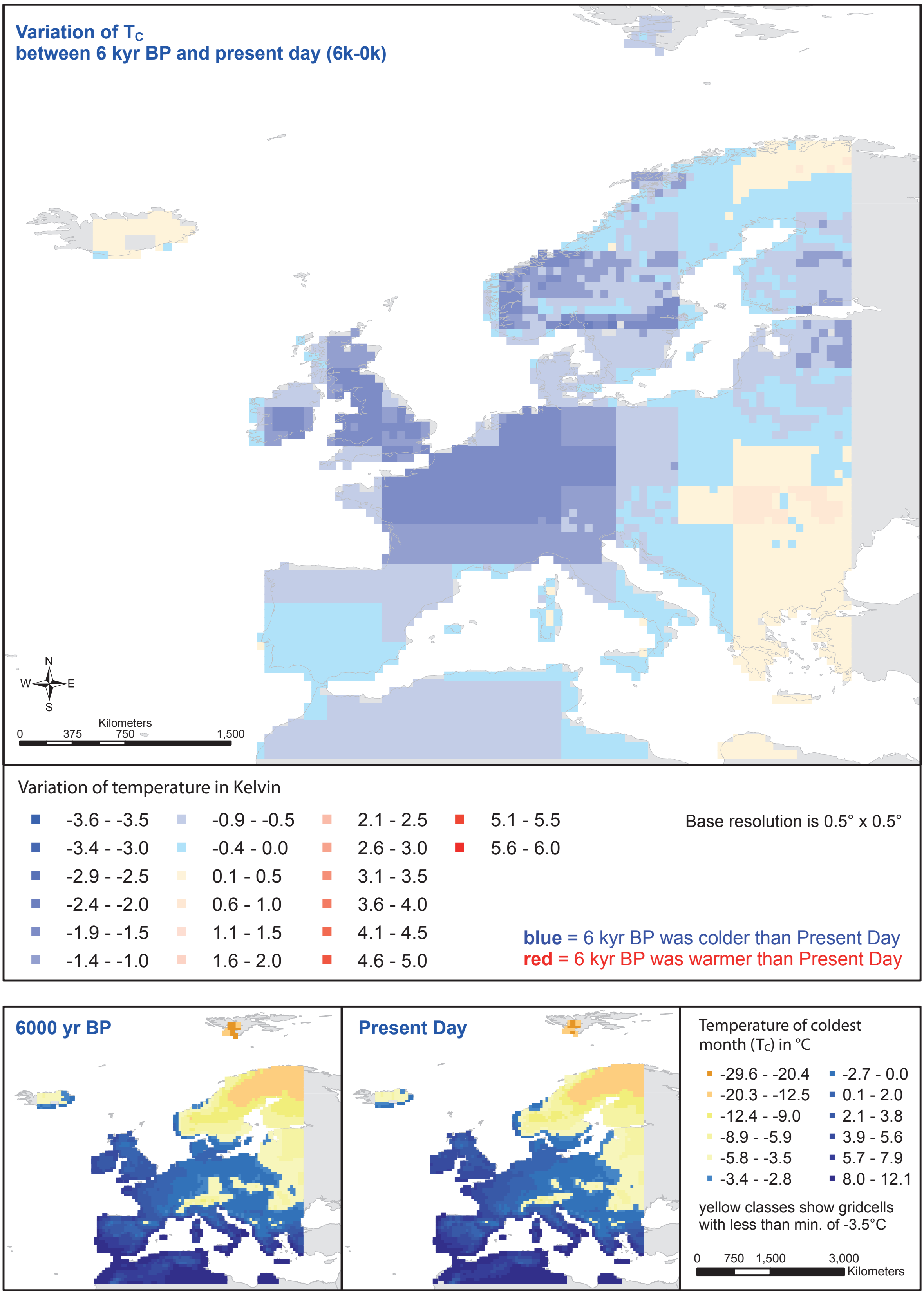


Figure 13a

Mean temperature of coldest month - GEN2

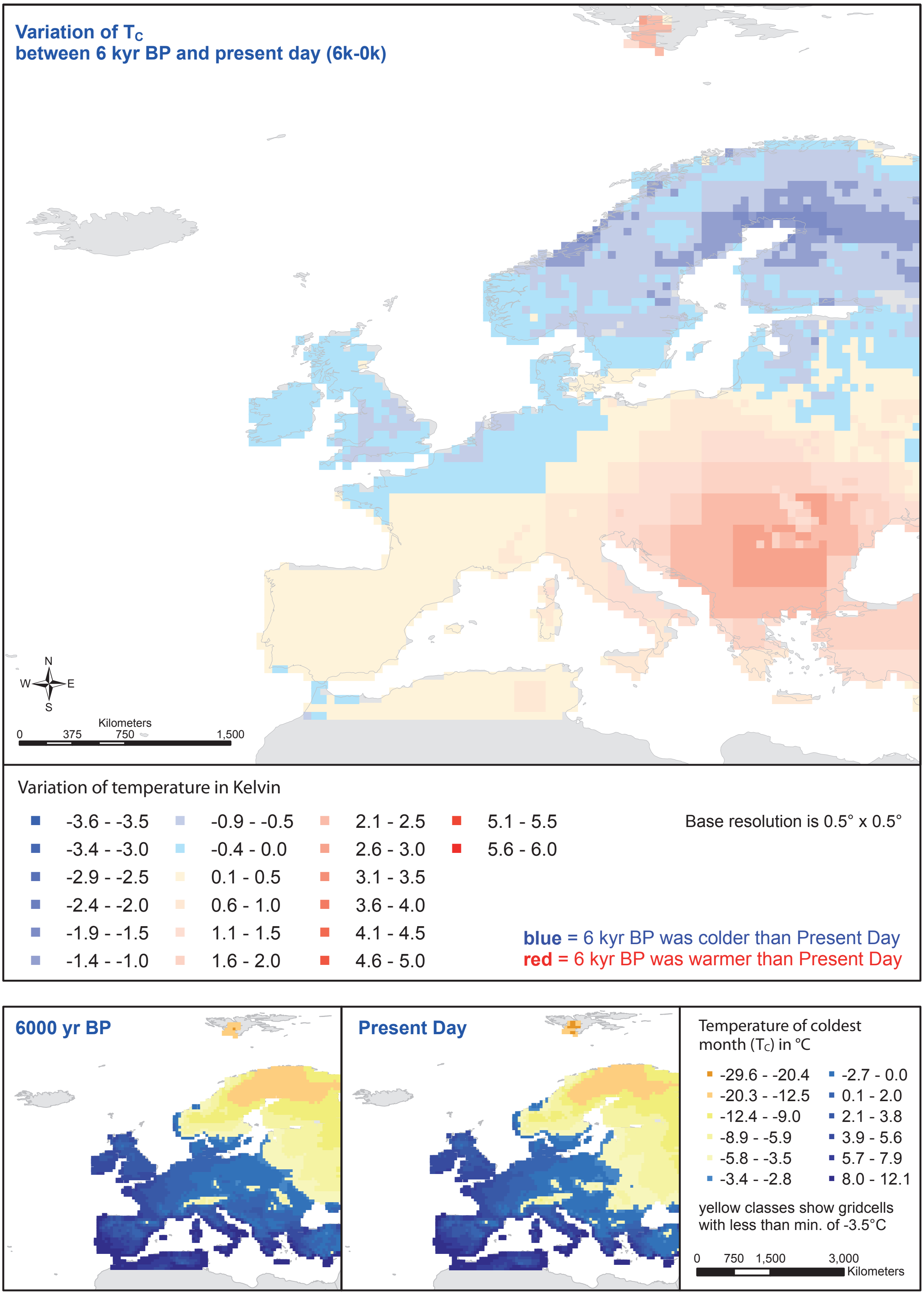


Figure 13b

Mean temperature of coldest month - ECHAM3

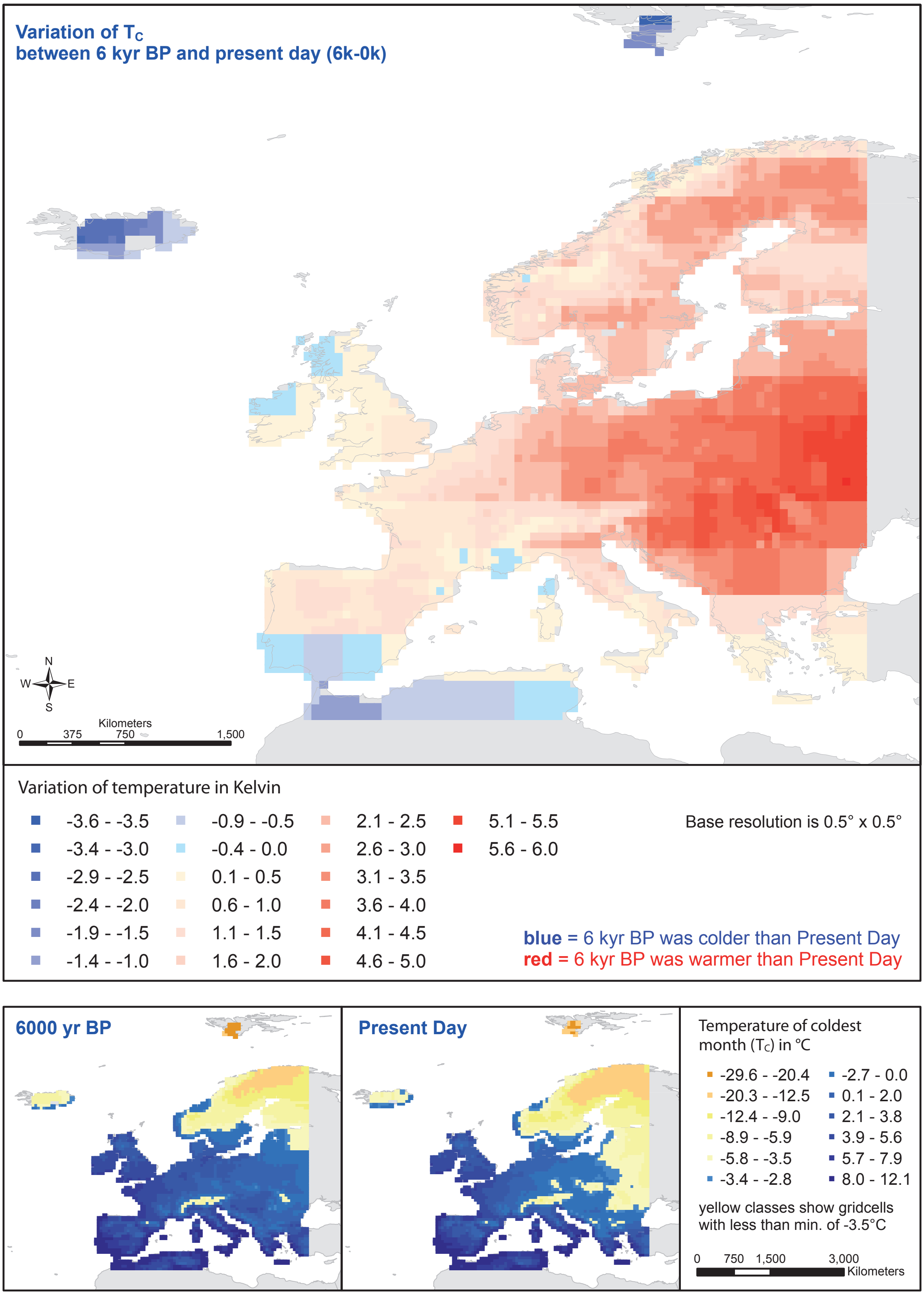


Figure 13c

Mean temperature of warmest month - UKMO

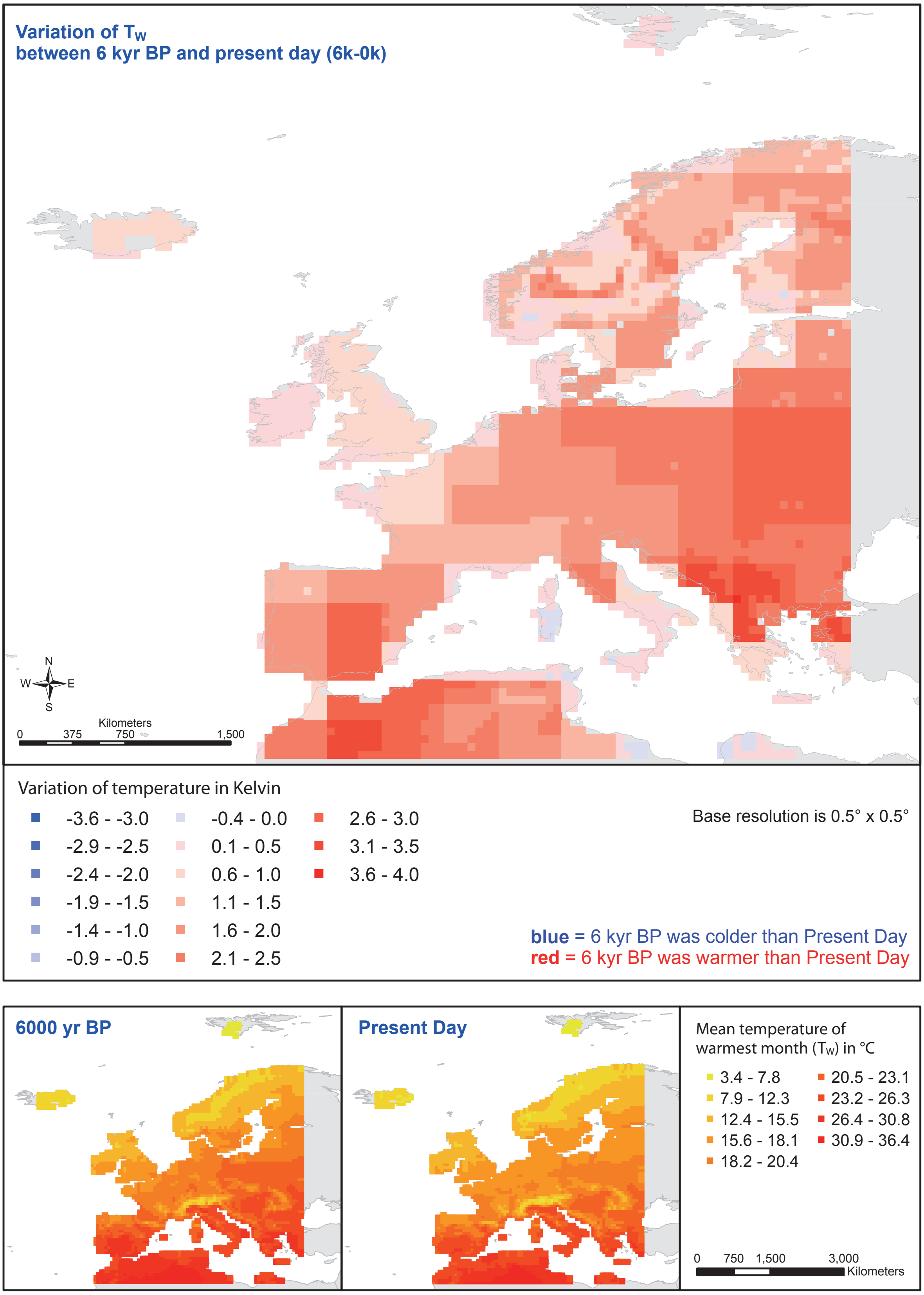


Figure 14a

Mean temperature of warmest month - GEN2

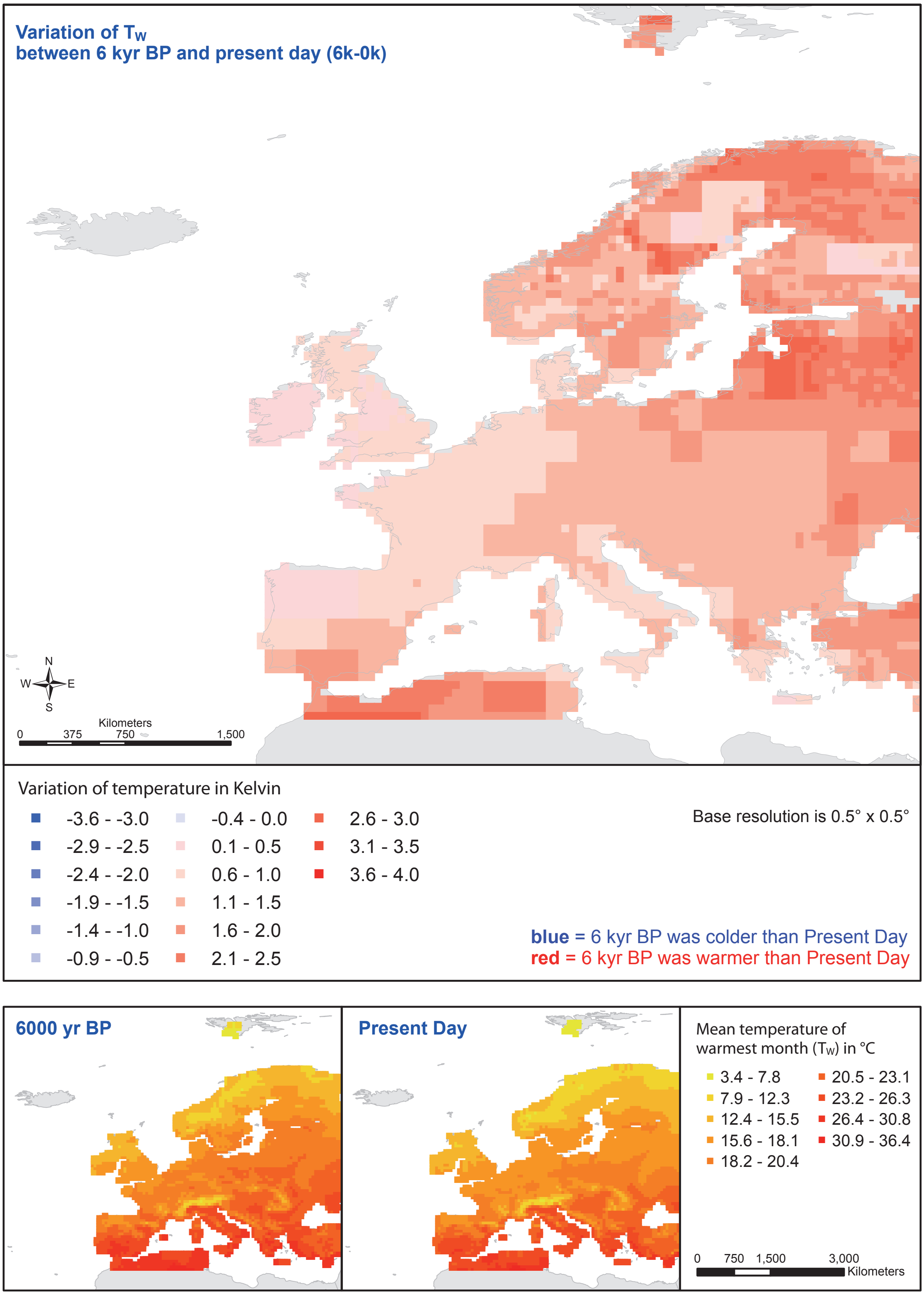


Figure 14b

Mean temperature of warmest month - ECHAM3

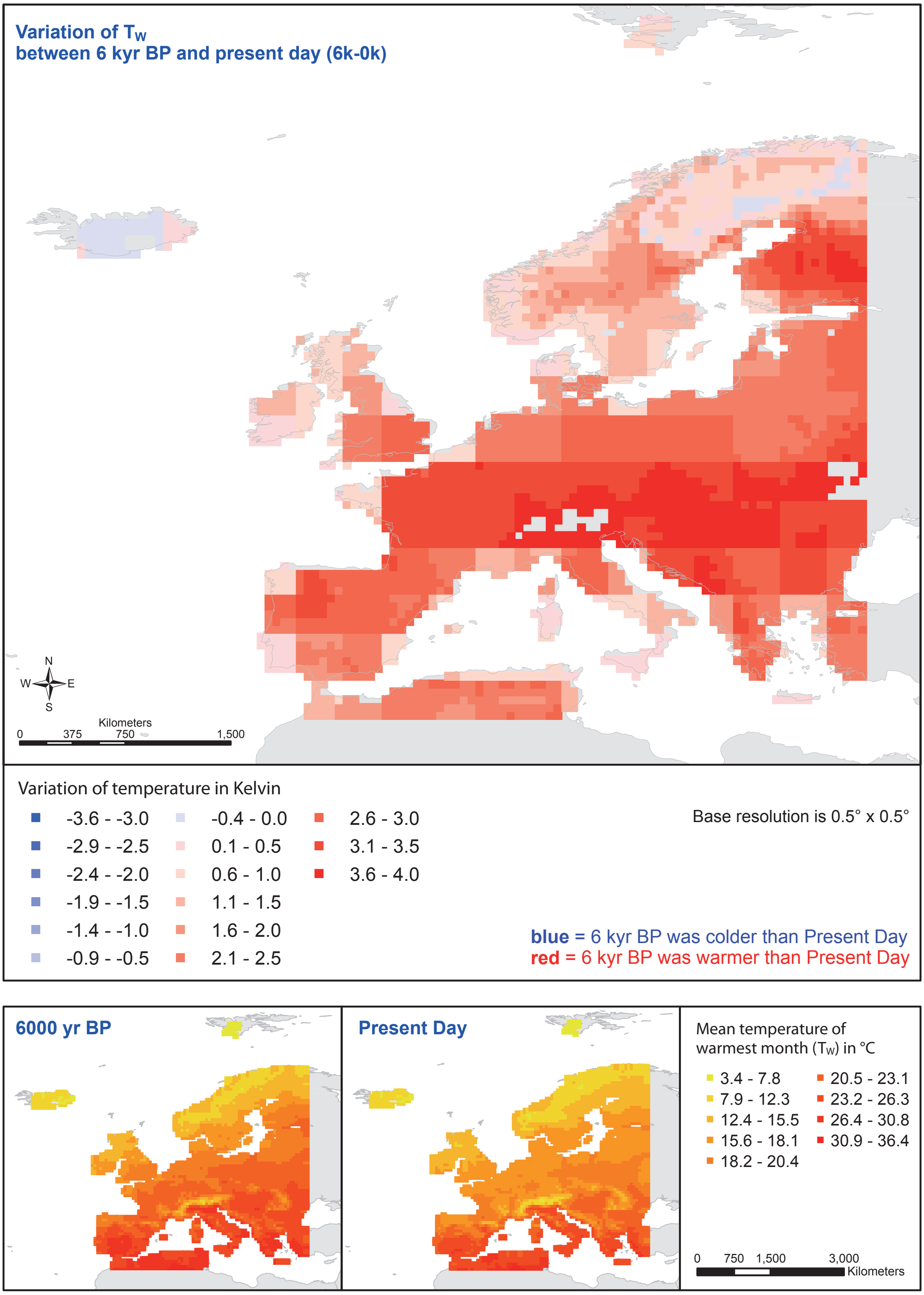


Figure 14c

Precipitation summarized over growing season - UKMO

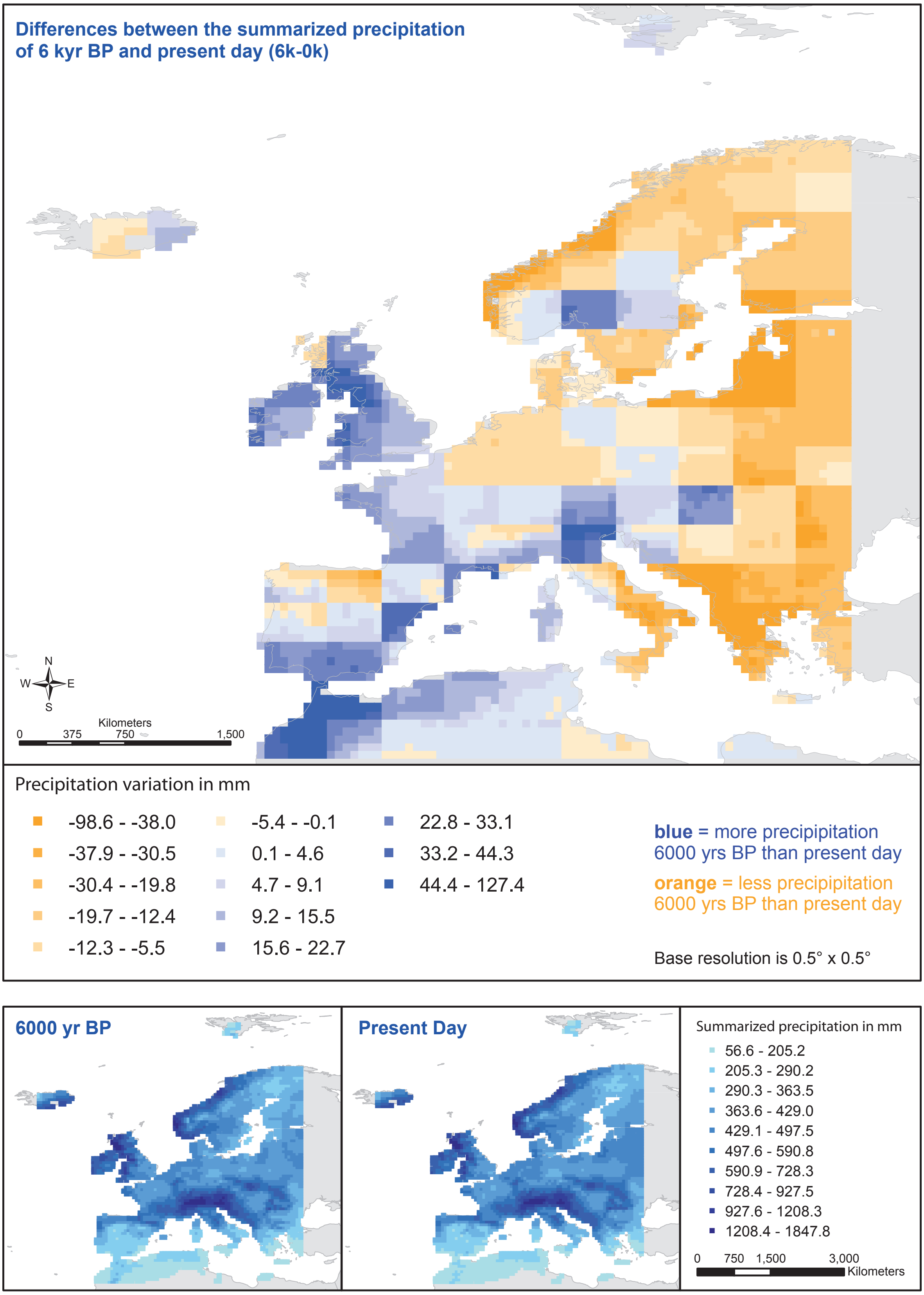


Figure 15a

Precipitation summarized over growing season - GEN2

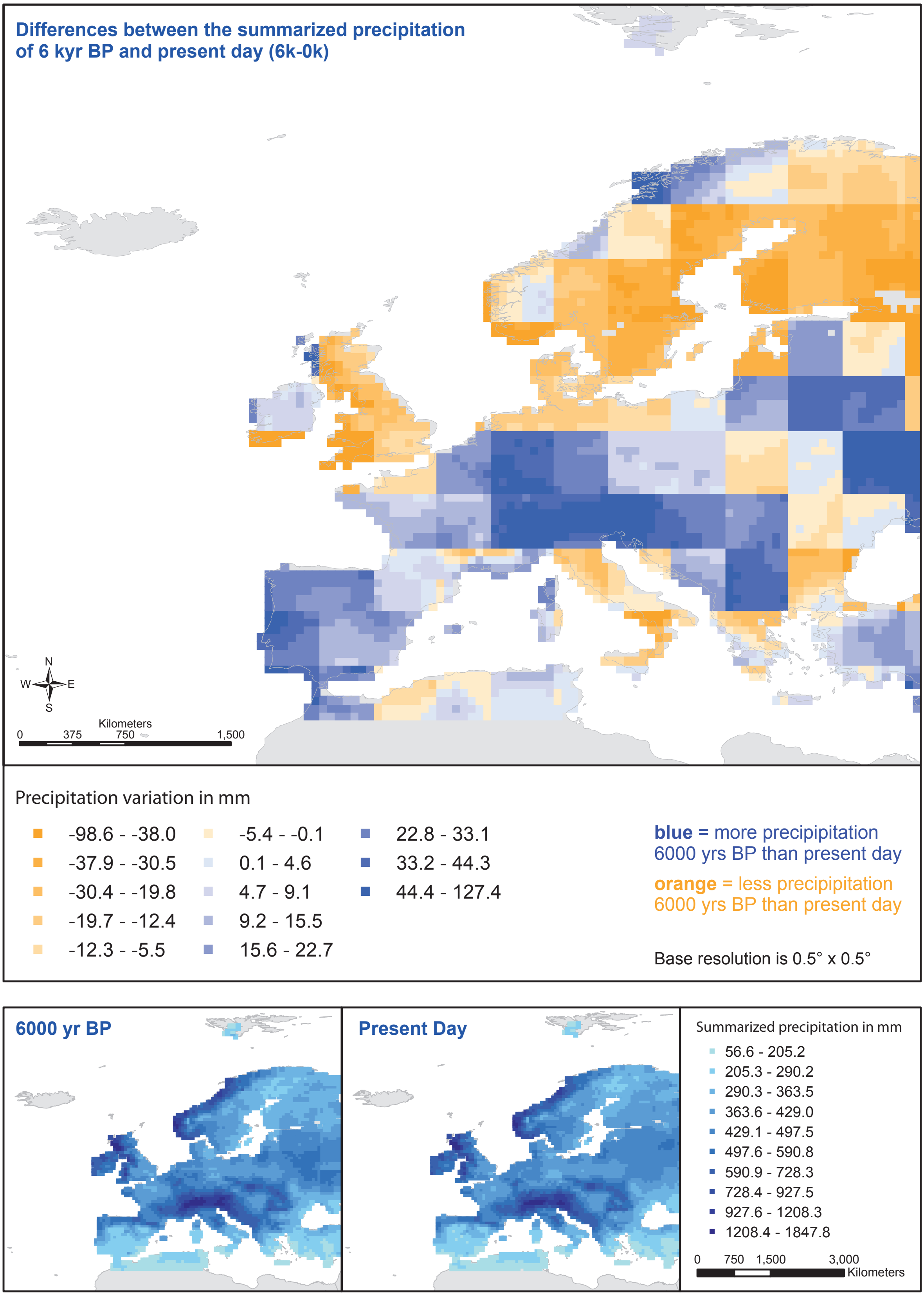


Figure 15b

Precipitation summarized over growing season - ECHAM3

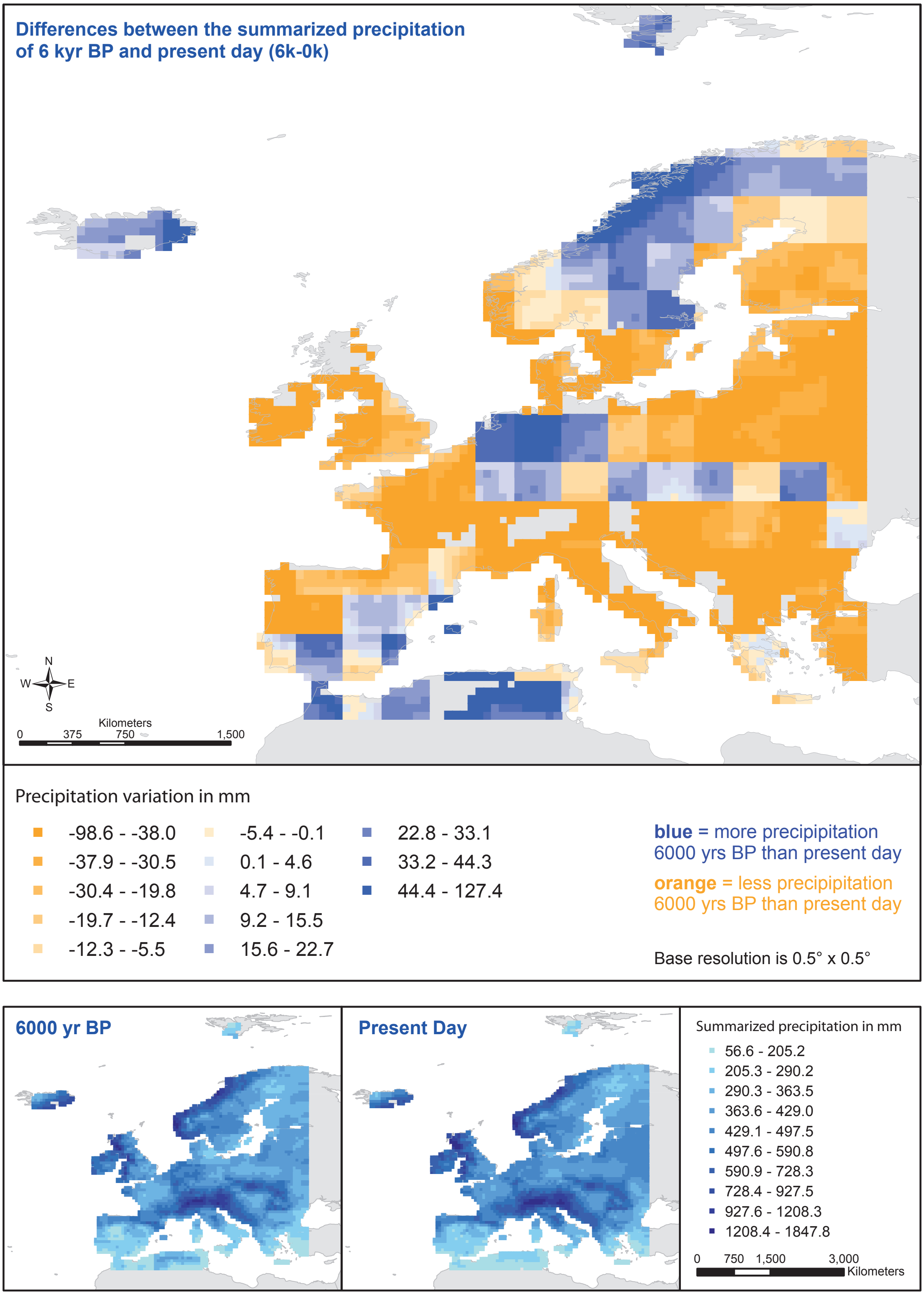


Figure 15c

AET/PET - UKMO

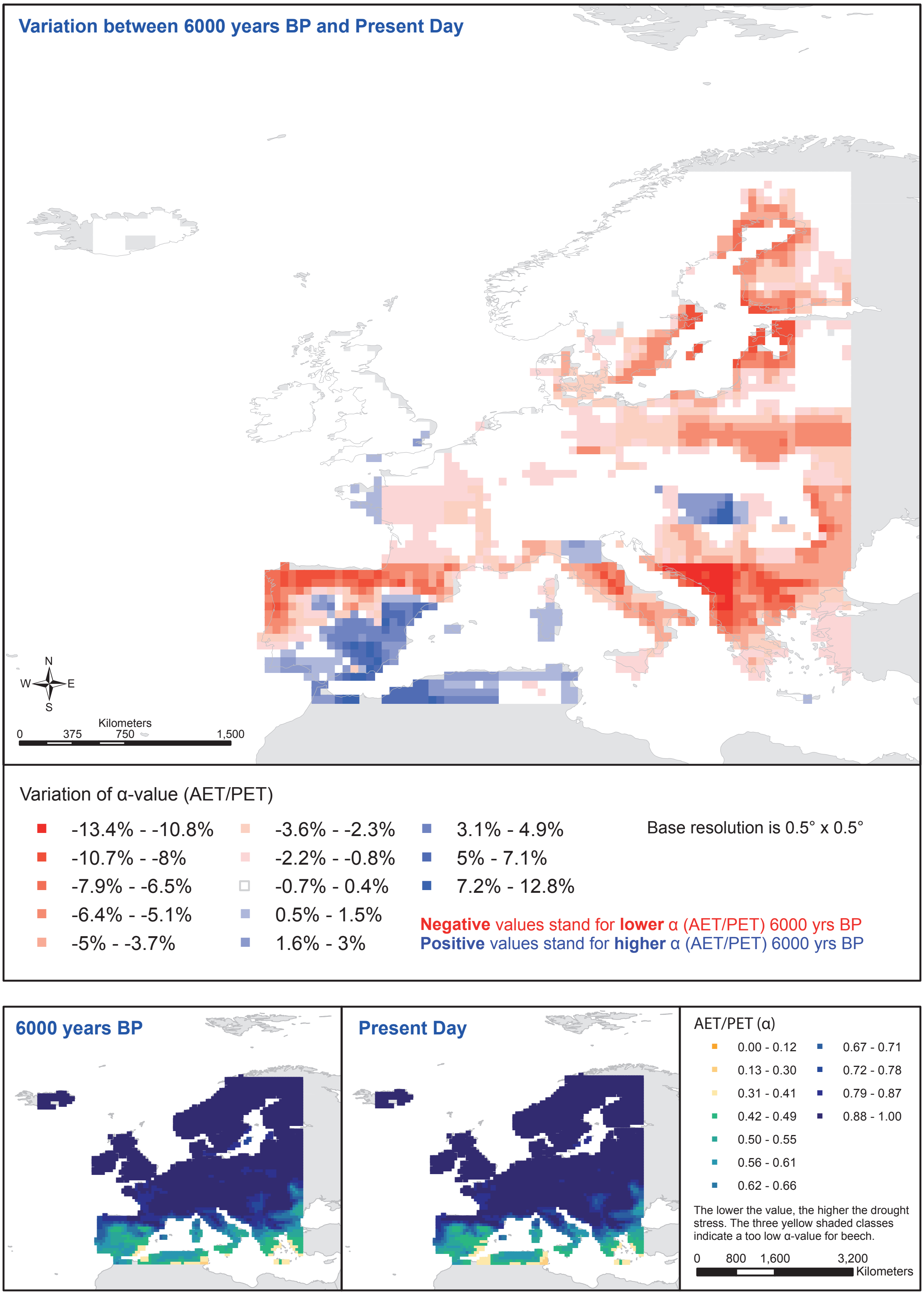


Figure 16a

AET/PET - GEN2

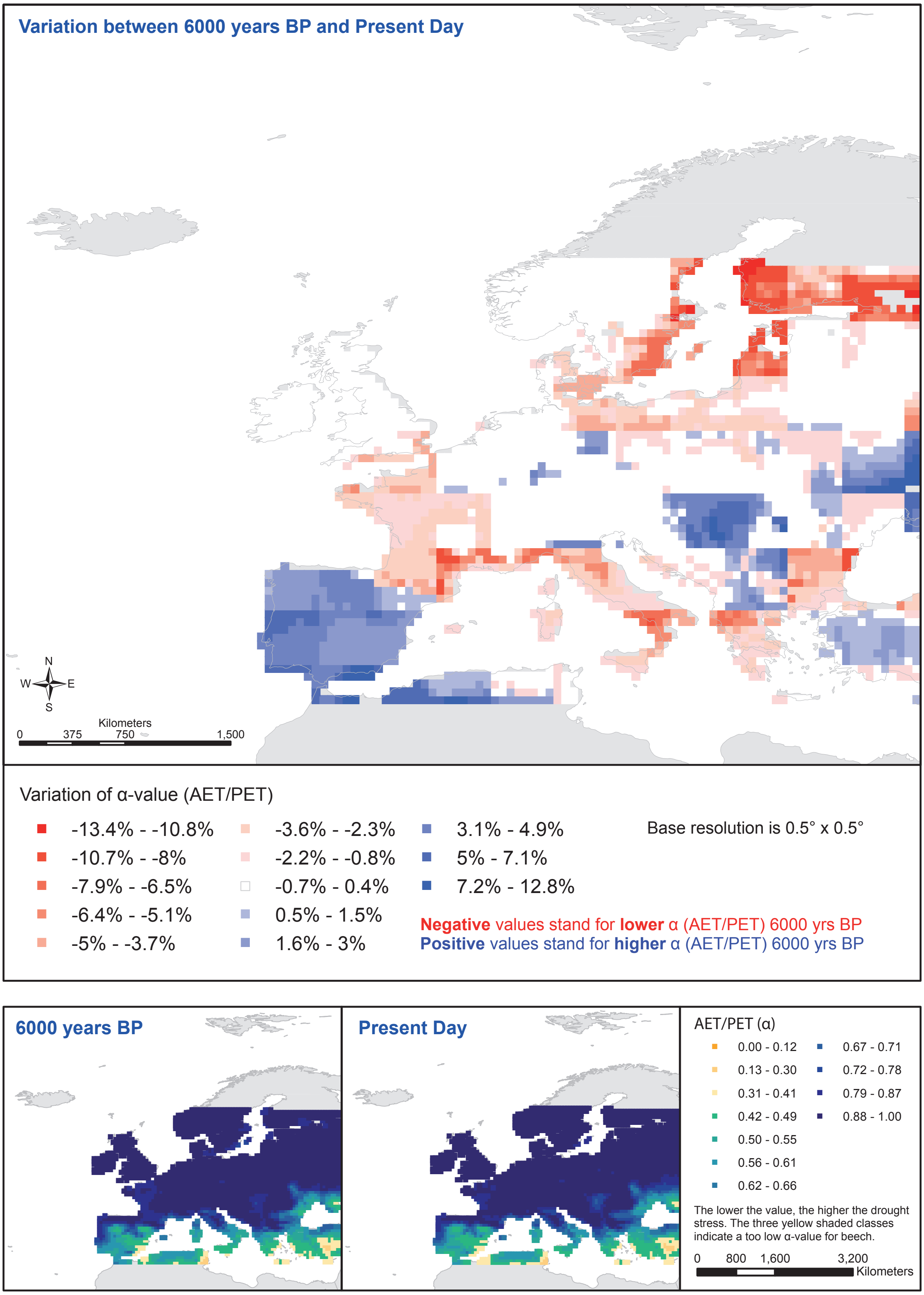


Figure 16b

AET/PET - ECHAM3

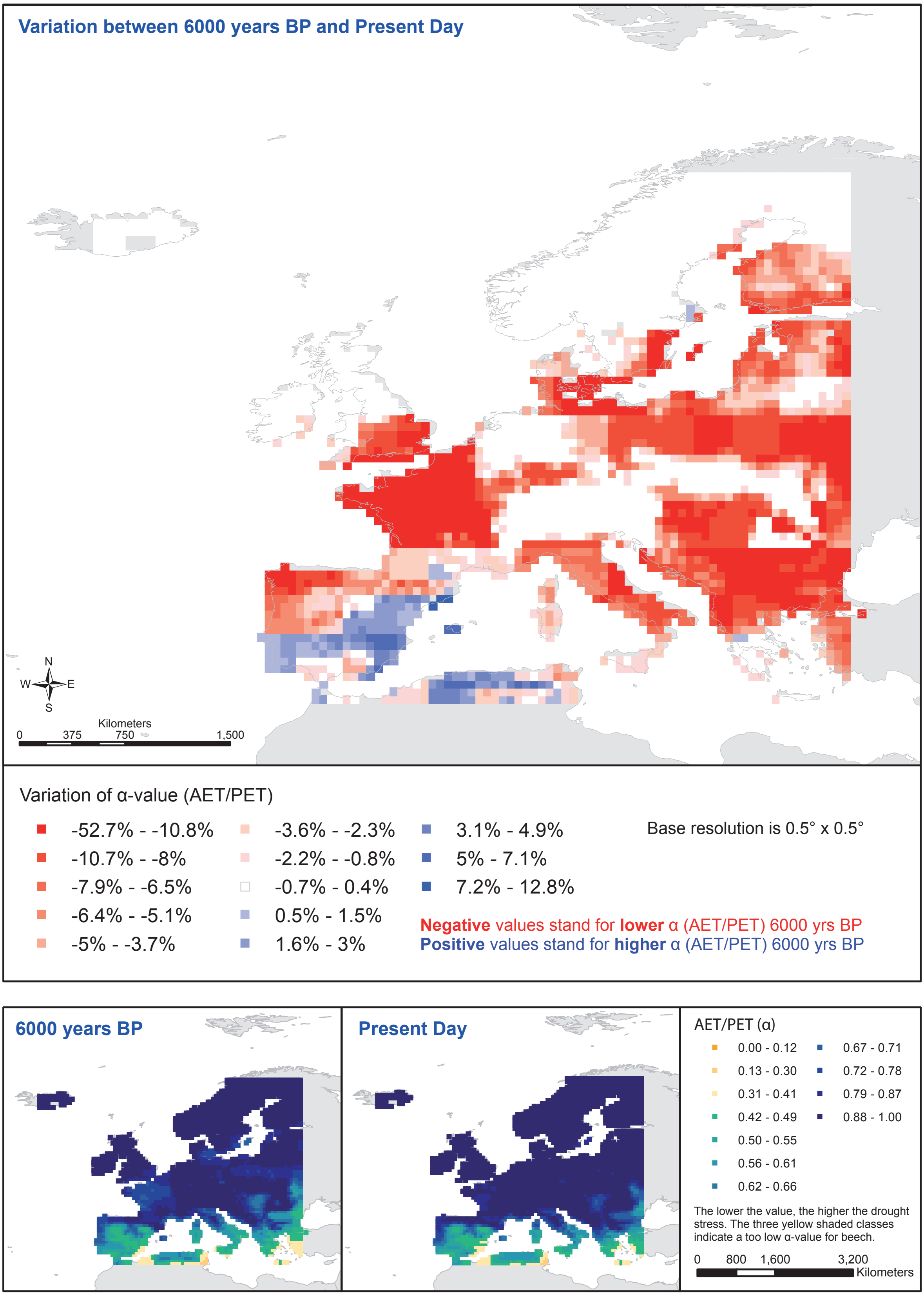
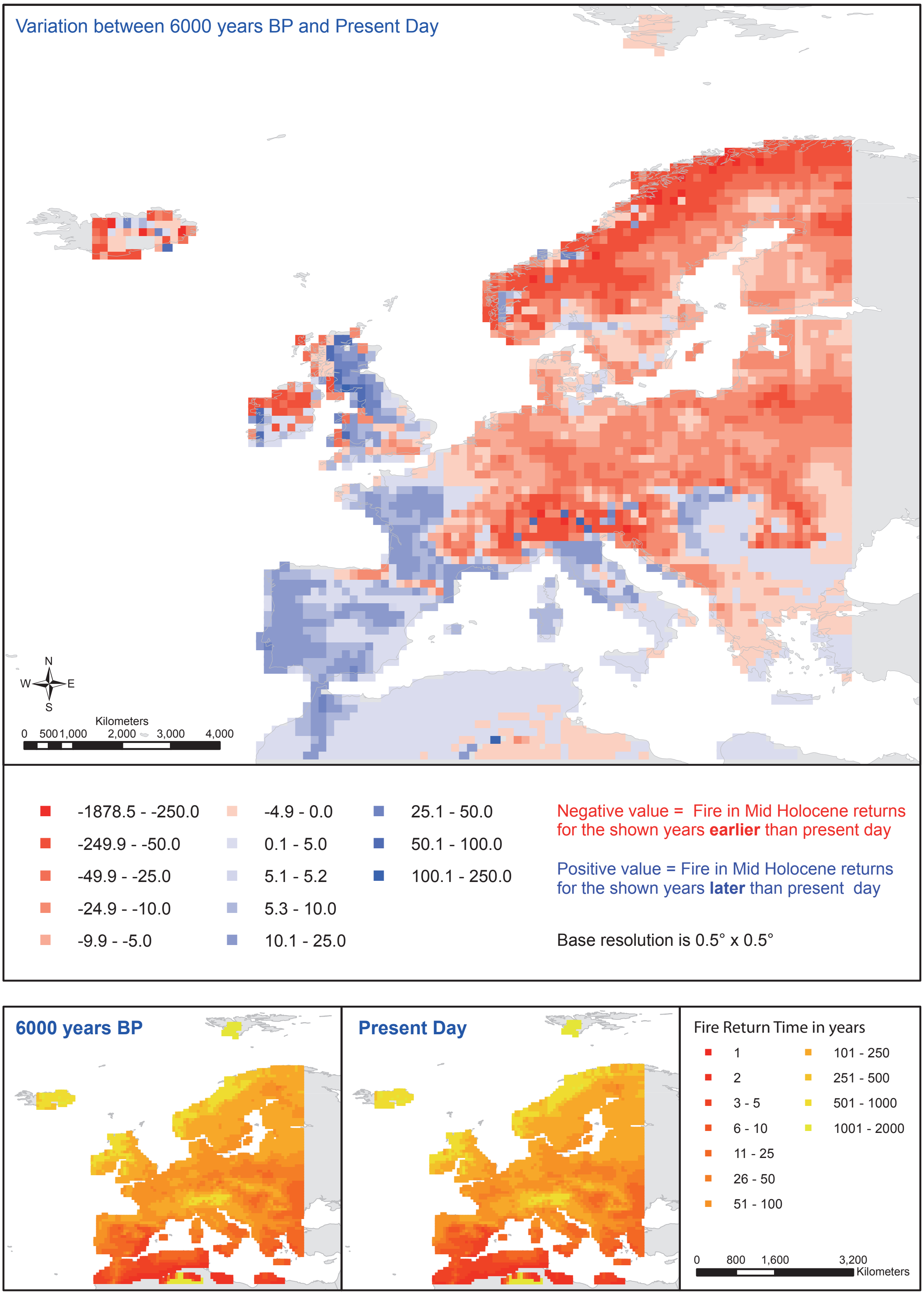


Figure 16c

Fire Return Time - UKMO



Negative value = Fire in Mid Holocene returns for the shown years **earlier** than present day

Positive value = Fire in Mid Holocene returns for the shown years **later** than present day

Base resolution is 0.5° x 0.5°

Figure 17a

Fire Return Time - GEN2

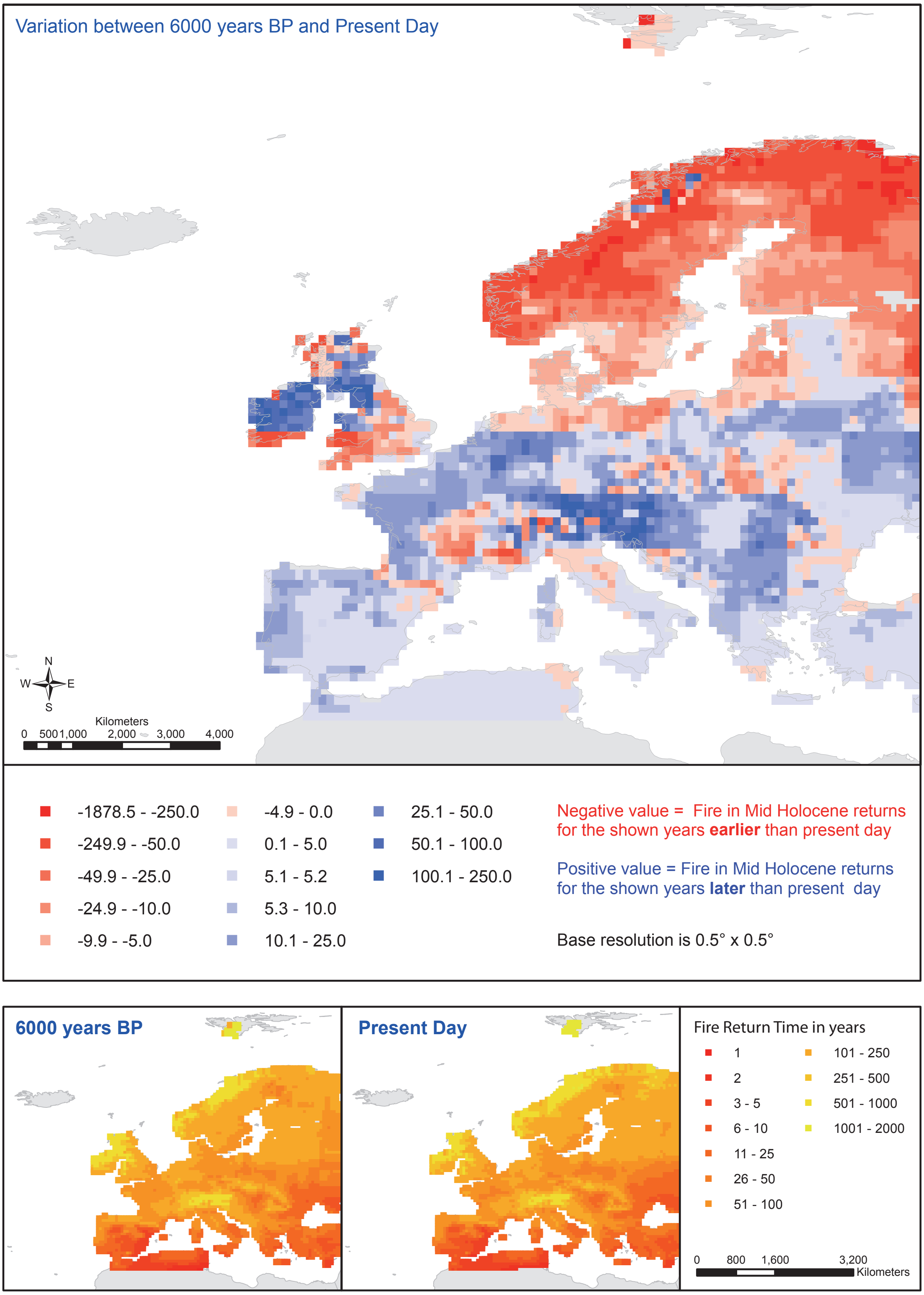


Figure 17b

Fire Return Time - ECHAM3

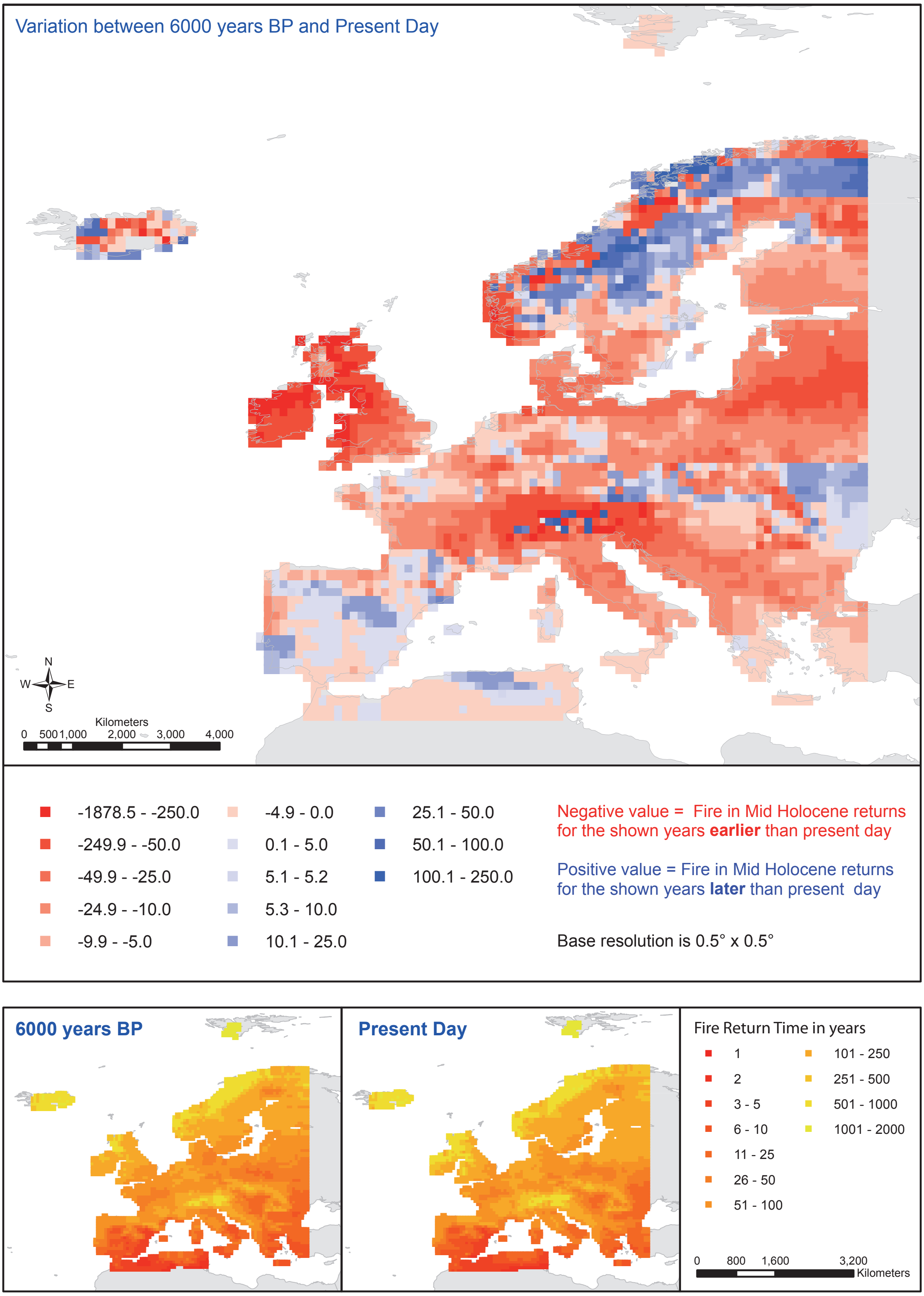


Figure 17c

Potential distribution of beech - UKMO

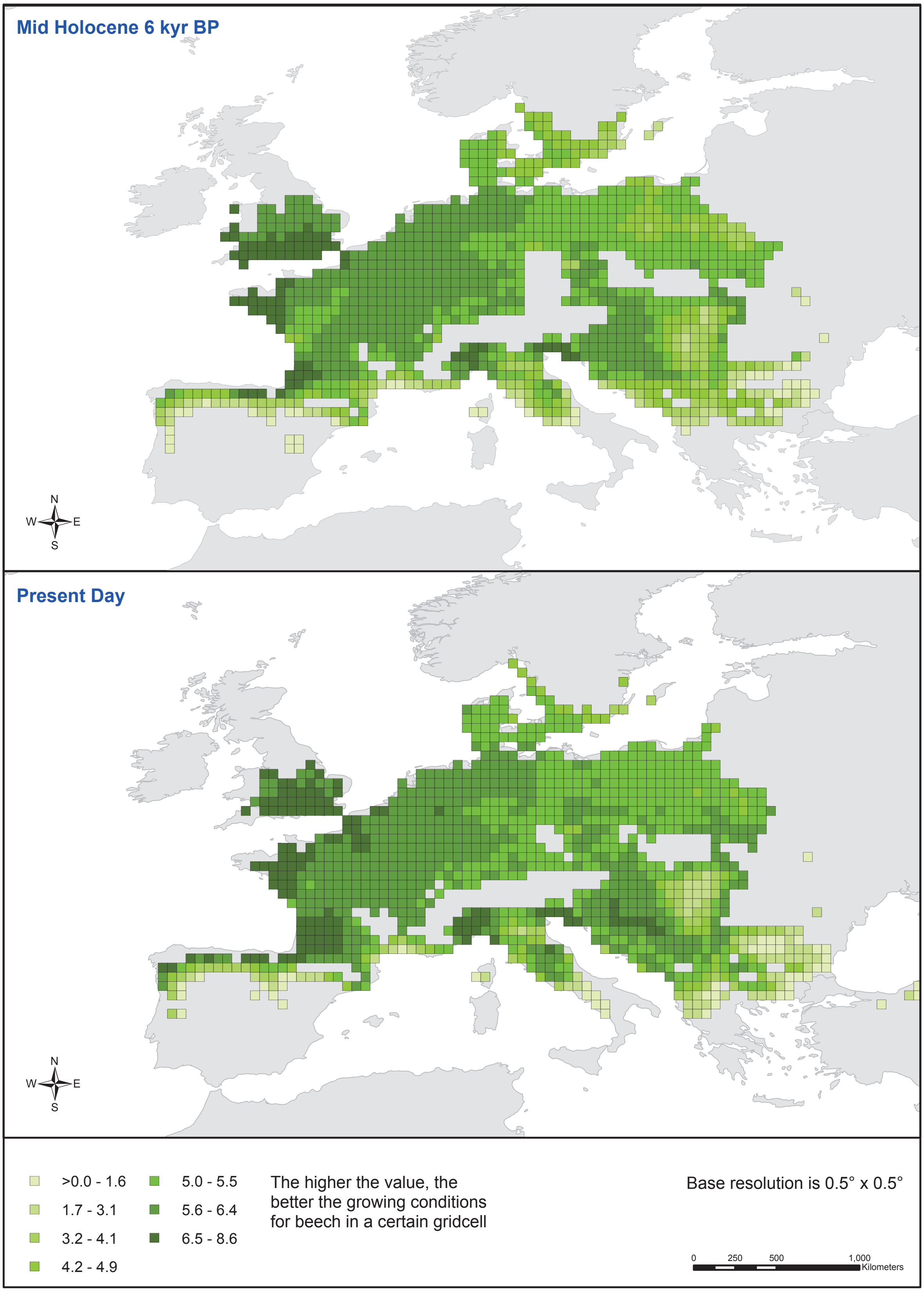


Figure 18a

Potential distribution of beech - GEN2

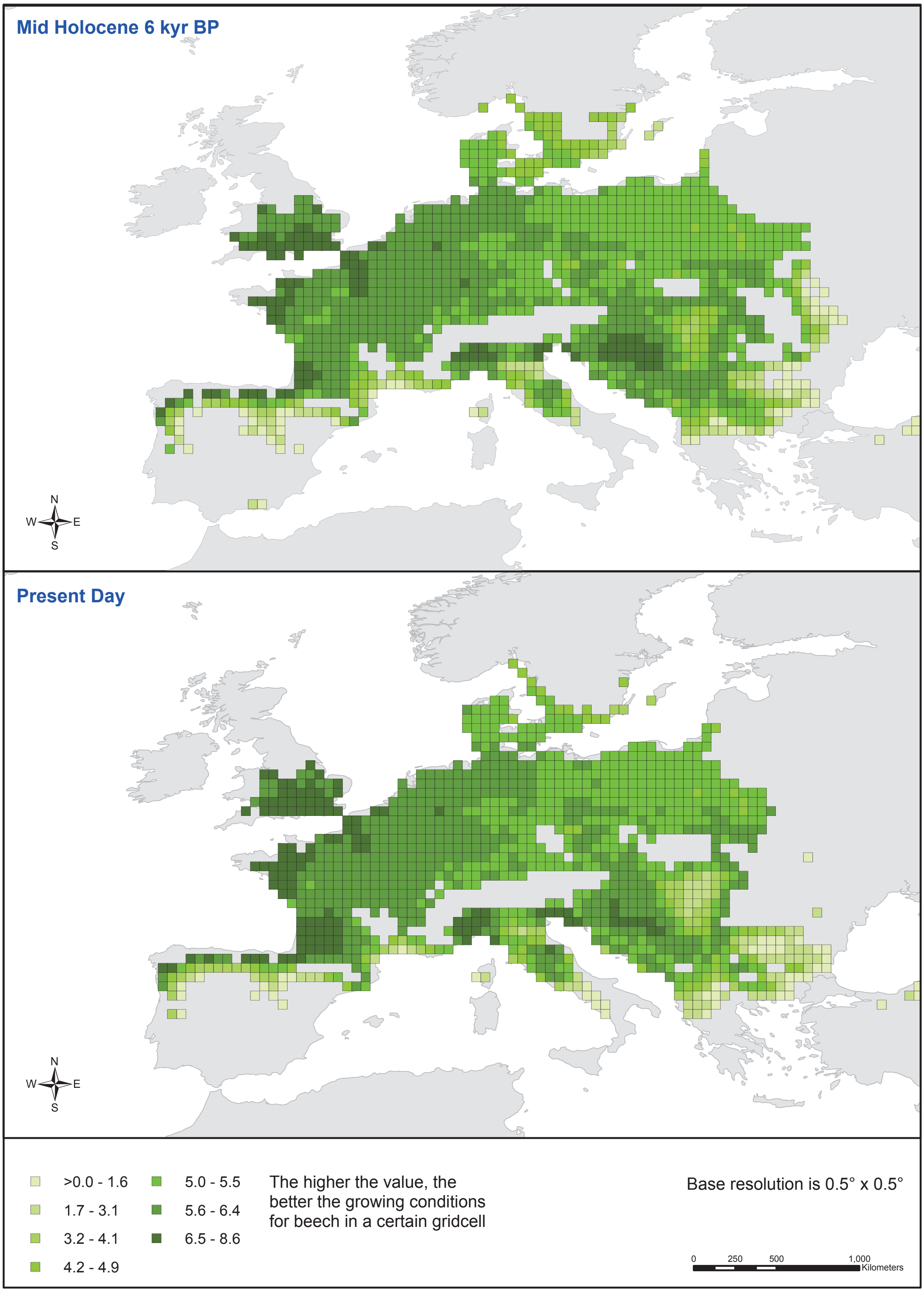
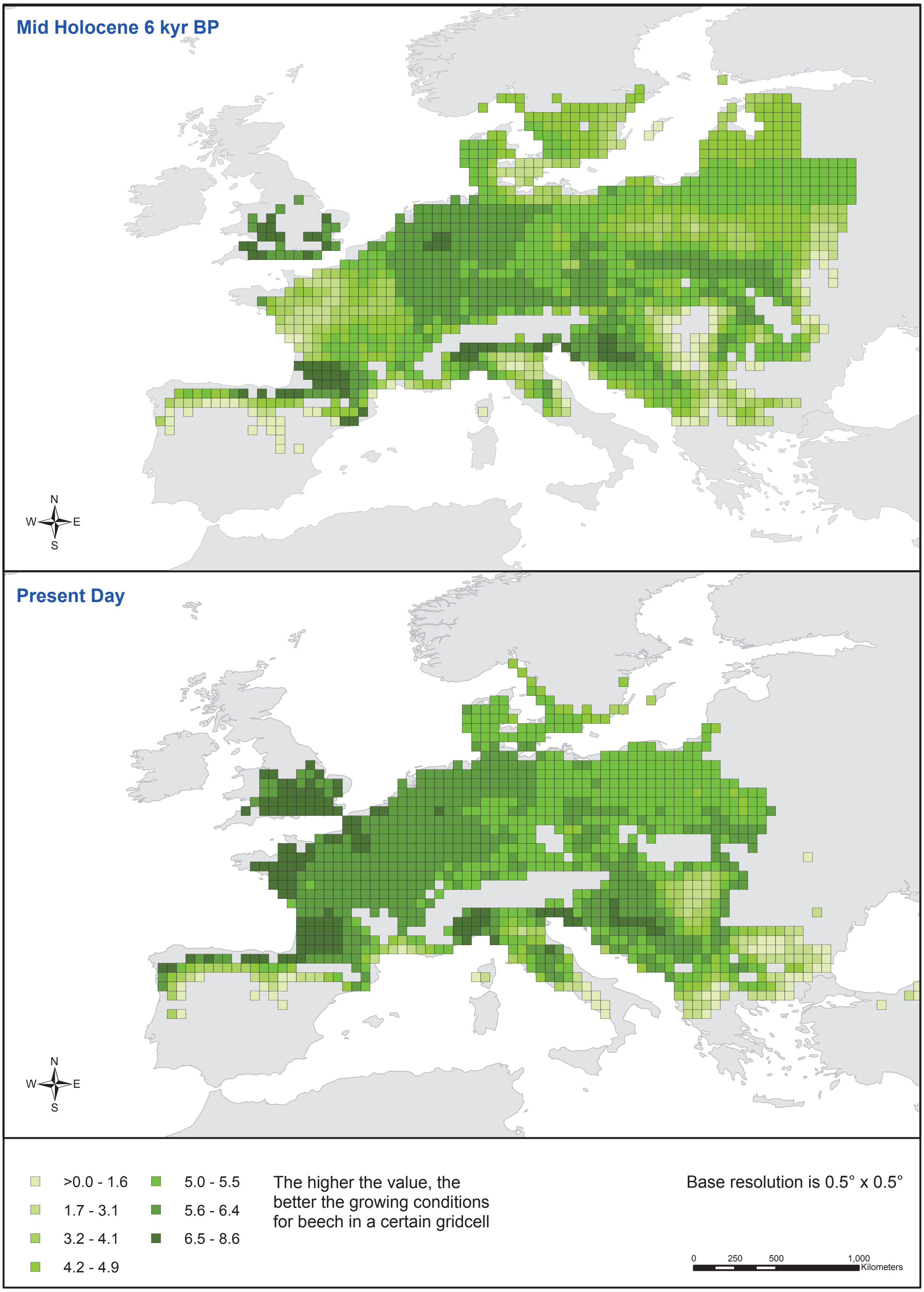


Figure 18b

Potential distribution of beech - ECHAM3



The higher the value, the better the growing conditions for beech in a certain gridcell

Base resolution is 0.5° x 0.5°

Figure 18c

Vegetation Types

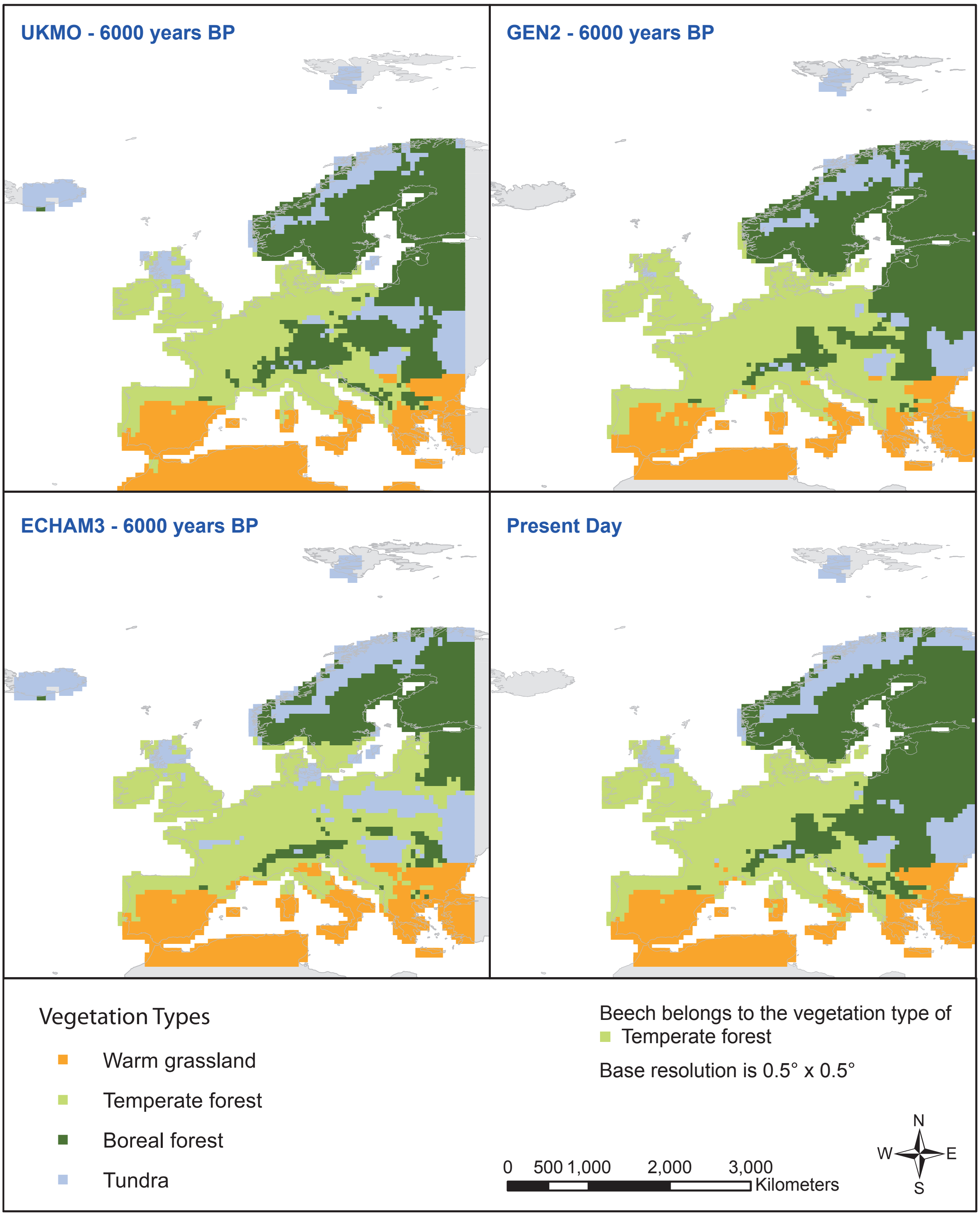


Figure 19

4.4 Summary of modelling results

One fact that is clearly visible is that, based on the modelling carried out, beech was not constrained by climate. ECHAM3 even shows better conditions for beech 6000 years BP than present day. So it seems that the climatic factors that entered into the modelling calculations did not negatively influence the spread of beech much. All three 'potential distribution of beech'-maps simulated by STASH emphasise this very well by showing no significant differences of the beech distribution in mid Holocene compared to present day.

4.5 Uncertainties

The maps, calculated by using the three AGCMs as climate input for LPJ and STASH, show unsteady variations when being compared to each other (model-model comparison) as well as to proxy-data. This appears because 'UKMO', 'GEN2' and 'ECHAM3' are based on different approaches how to simulate climate (Harrison) leading to variations in their accuracy when simulating climatological events and conditions. This leads to visible variations on the maps when comparing the model output with each other.

Like already mentioned in *chapter 3*, Bonfils et al. (2004) have shown, that the AGCMs have problems in simulating the by proxy-data indicated warmer-than-present winters in north-eastern Europe and the cooler-than-present summers in Southern Europe. These limitations were known (cf. Guiot et al. 1999; Bonfils et al. 2004), but better input data was not available at present.

Furthermore, the used method to increase the resolution of the AGCM output data causes inaccuracies leading to artefacts in the maps showing the difference between the mid Holocene and present day. There is a blocky looking overlay pattern visible creating steep gradients between values. This is well visible for example on the maps showing the direct output variables of the AGCMs like the temperature and precipitation maps. But they appear as well on maps being processed for instance by LPJ. The 'Fire Return Time'-map (GEN2) for example shows a steep gradient between Central Germany (fires return later) and Northern Germany (fires return earlier). This phenomenon can lead to misinterpretations. This could be resolved by applying a smoothing algorithm to the climate input data but would suggest a non existing higher resolution of the climate input dataset.

So a reasonable argumentation would be to use an AGCM having a higher native resolution, which are not available yet. Although Masson et al. (1999, p. 177f) could not confirm the statement that a higher resolution of the AGCMs would increase automatically the accuracy of the available climate-data, a higher native model resolution seems likely to increase the description of local orography leading to a better simulation of for instance precipitation patterns or climatological processes like stationary eddies in the mid-latitudes (Masson et al. 1999, p. 170).

Models are a simplification of nature and therefore limited to the image of nature represented by their algorithms and parameterisation. But there is no evidence, that phenomena being simulated by the AGCMs are automatically wrong when they can not be documented directly by proxy data. If such discrepancies exist in the simulations, it is also possible that either the AGCMs have simulated a climatic change that was not recorded by palaeoclimatic proxy-data from 6000 years BP, or that the data coverage used for model-data comparison is not sufficient to detect these signals (Bonfils et al. 2004, p. 86). It is for example known that the available data coverage for the mid Holocene time-slice is biased especially in the Mediterranean region (see *chapter 3.1.1*). The understanding of the mid Holocene climatic change in southern Europe and northern Africa remains for example still open because the pollen data distribution used for climatic reconstructions of this region is uneven and has a weak spatial resolution (Masson et al. 1999, p. 180). The possible sources of error in pollen-data in the Mediterranean area are increased also by the fact, that human impact was already present 6000 years BP. More precise proxy-data available for model-data comparisons could therefore lead to more accurate results.

4.6 Aspects of the climate system not considered in PMIP simulations

4.6.1 Microclimates

The resolution of the modelling carried out is 0.5° x 0.5° per gridcell. This resolution does not allow including the influence of microclimates into the modelling process.

These microclimates are influenced for instance by orography. The inclination, orientation, and steepness of slopes have a great effect on climatic factors in their vicinity, especially in the daytime, as the capture of solar radiation may vary to a considerable degree (Guyot 1998, p. 329f, 353f). Cold air, being accumulated in valley bases and terrain depressions can cause, beside the lower temperatures, frequent radiation fog (Glawion 2002, p. 141; Guyot 1998, p. 362). Late frosts can occur in spring and early frosts in autumn which reduce the growing season in these areas even more and may cause damage to beech (Mayer 1992, p. 94; Sykes et al. 1996, p. 204) and other plants. Further effects on local climate are a decrease of precipitation in areas lying in the rain shadow of mountains ranges, changes in radiation balance, dynamic actions of valleys (cone effects, formation of eddies), local mountain winds or effects caused by water bodies (e.g. lakes) (Guyot 1998, p. 357ff; Ruddiman 2001, p. 217).

4.6.2 Sea surface temperatures

Another factor is that the European climate is also under the influence of components of the climatic system like the sea surface temperatures (SST) that are for example driven by the North Atlantic current. The SSTs are not taken into account by the used PMIP-models (Joussaume & Taylor, b), creating another source of error. Masson et al. (1999, p. 178f) for example state, that 'changes in the Atlantic SST appear to be a key factor for winter temperature patterns over Europe'.

4.6.3 Vegetation feedbacks

Like mentioned before, the PMIP AGCMs may underestimate mid Holocene warming as they all do not include vegetation feedbacks into their calculations on the atmosphere like for instance changes of the surface albedo (Ruddiman 2001, p. 318f). This might be an explanation why UKMO and GEN2 do not simulate the mid Holocene temperature increase of 1 to 3 Kelvin in the mid-continent and far north shown by pollen reconstructions (Budyko 1982, p. 145; Huntley & Prentice 1988, p. 687; Schönwiese 1995, p. 92). Assuming the importance of these vegetation feedbacks it seems that the mid Holocene climate simulation by ECHAM3, showing higher temperatures, may be closer to the climate prevailing in mid Holocene than the two AGCMs UKMO and GEN2 designated by Bonfils et al. (2004) to be the most accurate PMIP-models.

5. Conclusion

This thesis analysed the question if climate constrained the spreading of beech during mid Holocene by using modelling techniques. For this purpose the time-slice of 6000 years BP was chosen because of the climatic optimum prevailing at this time showing a significant climatic variation compared to present day.

The modelling was carried out by using the simulated climate data of three PMIP-model runs in combination with vegetation modelling. This approach allowed the creation and analysis of maps of for beech spread important bioclimatic factors as well as maps of the potential beech distribution and the vegetation types.

On the basis of the obtained results it seems that the spreading of beech was not constrained by the climate of the mid Holocene. The AGCMs show varieties between the time-slices of 6000 years BP and present day but nevertheless there is no indication that any of the bioclimatic factors calculated out of one of the three AGCMs was insufficient for beech growth 6000 years BP. Therefore none of the model runs carried out for this work could show a significant correlation between climate 6000 years BP and the distribution of beech. Therefore it possible to draw two different consequences:

Either climate really did not constrain the spreading of beech or the used AGCMs are not accurate enough to answer this question satisfactorily. However, this thesis could not identify the matter having a larger influence on the obtained results. So it is likely that the results are a mixture of both of these options.

The obtained results allow also the assumption that, beside a still possible climate constraint, numerous other factors like changed human activities, dispersal limitations or the absence of Megaherbivores may have constrained the distribution of beech (see *chapter 2.3*). These other factors were however not subject of this thesis and could not be analysed. Therefore no statement about these factors can be made. Further research is required to be able to give a more precise statement about an impact of climate on beech.

For future projects using LPJ and STASH with palaeodata, it would be advantageous to use more accurate data like for instance the database that is created at the moment by PMIP II[7].

The development of a DGVM incorporating the influence of the fauna as well as the one of humans (as far as they are modelable) in addition to vegetation may bring modelling also closer to reality.

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[7] *http://www-lsce.cea.fr/pmip2*

Simulating vegetation dynamics on the regional scale at the level of tree species (instead of PFTs), including realistic representations of competition could be a step forward in the near future (HICKLER ET AL. 2004).

Furthermore, to obtain more accurate results it would probably be a benefit to use a higher resolution than the used 0.5° x 0.5° per gridcell both for the LPJ, STASH and the AGCMs to minimize the risk of loosing details.

However, up to date the highest resolution present day climate data set on a regional scale has a resolution of 0.167° (MITCHELL ET AL. 2002), which is still not detailed enough to account for variations in microclimate.

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