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The sunny side of the Ice Age: Solar insolation as a potential long-term pacemaker for demographic developments in Europe between 43 and 15 ka ago

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ABSTRACT

After a decade of research under the auspices of the project ‘Population dynamics: Land use patterns of populations between the Upper Pleistocene and Middle Holocene in Europe and the Middle East’, a consistent sequence of high-resolution palaeodemographic datasets has been compiled, spanning the entire Upper Paleolithic from roughly 43 to 15 ka ago. When viewed in a diachronic perspective, long-term trends of increasing and decreasing population sizes and densities, as well as expanding and contracting areas of settlement activities (Core Areas) become evident. An environmental parameter with potentially strong impact on hunter-gatherers societies is solar insolation. The sun’s energy available at a certain time and place is one of the main factors influencing plant growth. The amount of plant biomass, in turn, largely determines the amount of animal biomass in a landscape. The latter is the most important source of energy for European Upper Palaeolithic hunter-gatherers. Here, we aim to assess the potential influence of changes in solar insolation on palaeodemographic development in Western and Central Europe between 43 and 15 ka ago. To this end, we present estimates on the number, density and spatial distribution of hunter-gatherers for five consecutive Upper Paleolithic periods in Europe. Based on regional climate model data for the Last Glacial Maximum and solar insolation data, we calculate (1) differences in the amount of Megajoule per square meter (MJm^{-2}), (2) start, end, and length of the growing season, as well as (3) summed temperatures during the entire duration and during the first 30 days of the growing season. A comparison shows that a moderate, steady increase of population size and an extension of the Core Areas between 43 and 29 ka coincides with an increase in the summed temperature, particularly during the first 30 days of the growing season. The period between 29 and 25 ka shows a pronounced population decline, a strong contraction of Core Areas and a withdrawal from higher latitudes. This coincides with a markedly delayed growing season, a decrease in summed temperatures, and a marked reduction in solar insolation during the early part of the growing season. Between 25 and 20 ka, we see consolidation and renewed growth in both numbers and densities of people and an expansion and merging of Core Areas in Western Europe. There is a slight gain in the energy available during the first half of the year. The growing season starts earlier and is of increasingly longer duration, coupled with rising summed temperatures. Between 20 and 15 ka, the meta-population grows strongly, Core Areas expand and the higher latitudes become repopulated. This coincides with further increasing summed temperatures and an ever-earlier start to the growing season. Additionally, the gain in available solar energy during the early phase of the growing season is particularly pronounced. These findings indicate that solar insolation and its effects on an ecosystem’s phenological configuration over different trophic levels is indeed an important factor in the long-term demographic development of Paleolithic hunter-gatherers.

Key words: Palaeodemography, Upper Palaeolithic, Solar Insolation, Phenology, Growing Season, biomass production

1. INTRODUCTION

Over the last two decades, several innovative approaches to paleodemography (Bocquet-Appel and Demars 2000; Bocquet-Appel et al. 2005; French 2015; French and Collins 2015; Kretschmer 2015; Maier et al. 2016; Maier and Zimmermann 2017; Schmidt and Zimmermann 2019; Tallavaara et al. 2015) and population genetics (e.g. Fu et al. 2016; Posth et al. 2016) have advanced research on Upper Palaeolithic population dynamics. At the same time, a number of factors have been discussed with regard to their explanatory potential for the observed demographic developments; these include technological gain and loss, social organisation and norms, and environment (Boserup 1965; Bradtmöller et al. 2010; French 2018; Gamble 2002; Gamble et al 2004; Henderson and Loreau 2019; Roebroeks 2006). To be clear, social and technological factors certainly play an important role in human population dynamics and innovations or a loss of technological knowledge can affect population dynamics strongly. However, for large-scale studies such as this one, there are two major problems for exploring their impact on the number, density and distribution of humans in a landscape. The first problem is that social, technological, and demographic developments are interdependent, where social organisation may influence demographic developments and vice versa. Thus, it is extremely difficult to distinguish cause from effect. The second problem is that social organisation and technological repertoires depend on human decision making, which is observable at a different timescale than long-term developments. Long-term demographic developments over the period of several millennia are incompatible with human decision-making. Environmental change, on the other hand, can be meaningfully observed at small and large temporal scales. The impact of human societies on the environment during the Palaeolithic is subject to debates. Topics range from reflections on negative impacts on forest cover (Kaplan et al. 2016) to the involvement in the extinction of larger animals (e.g. Koch and Barnosky 2006; Sandom et al. 2014). However, during the entire period of observation between 43 and 15 ka, human influence on environment and particularly on climate seems to have been comparatively small, making it relatively easy to distinguish between cause and effect. Nonetheless, proving a causal relationship remains difficult, not least because of incompatible or insufficient temporal and spatial resolution in the archaeological data. The introduction of absolute numbers and densities of human populations as a new, quantified variable at a comparatively high spatial and temporal resolution is a first step in addressing this problem. While acknowledging the importance of social and technological factors for demographic developments, this paper will focus on environmental change and its explanatory potential for the changes we observe in the currently available palaeodemographic data.

The data for successive time-slices (Kretschmer 2015; Maier et al. 2016; Maier and Zimmermann 2017; Schmidt and Zimmermann 2019), has a temporal resolution of between 4 and 5 ka. Temperature change, as captured in the ice-core records, varies at a frequency much too high to be meaningfully compared to our data (**Figure 1**). Moreover, low temperatures alone are not a limiting factor for human settlement activities. To the contrary, it has been shown that some Palaeolithic hunter-gatherer communities preferred permafrost over equally accessible non-permafrost areas (Demidenko 2018; Maier et al. 2016). However, it would be overstated to assume that environmental thresholds were virtually meaningless for well-adapted Palaeolithic hunter-gatherers. Rather than temperature alone, the availability of animal biomass was probably a key factor to allow permanent settlement in a region (Kelly 1983; Mandryk 1993). The amount and diversity of animal biomass, in turn, is dependent on the amount and quality of primary plant biomass (Olff et al. 2002). A very important factor for the production of plant biomass is solar insolation (Monteith 1994). At the same time, this environmental parameter changes gradually and slowly, making it compatible to our demographic estimates (**Figure 1**). Solar insolation affects plant biomass production in two primary ways. Firstly, it drives air temperatures near the surface, one of the main factors determining the length of the growing season (Jiang et al. 2018). This correlation is so strong that temperature-based models to estimate insolation perform better than those based on sunshine, particularly when averaged to a monthly base (Hassan et al. 2016). Secondly, it provides the energy needed for photosynthesis and there is a linear relationship between

solar insolation and biomass production (Gosse et al. 1986). Therefore it seems to be an important factor in an ecosystem's phenological configuration, i.e. in the timing of periodic life cycle parameters of plants and animals (Gienapp et al. 2014; Parmesan and Hanley 2015; Liu et al. 2016, Huang et al. 2019). Phenological shifts may be effective over different trophic levels and lead to mismatches in resource availability and predator-prey relations (Burrows et al. 2011; Ohlberger et al. 2014). It has been shown for birds that these mismatches affect migrating species particularly strong when an expected food resource is not available upon arrival (Both et al. 2010; Mayor et al. 2017).
In the following, we will evaluate estimates of the number and density of people as well as the position and extent of Core Areas against insolation data for the period between 40 ka and 15 ka.

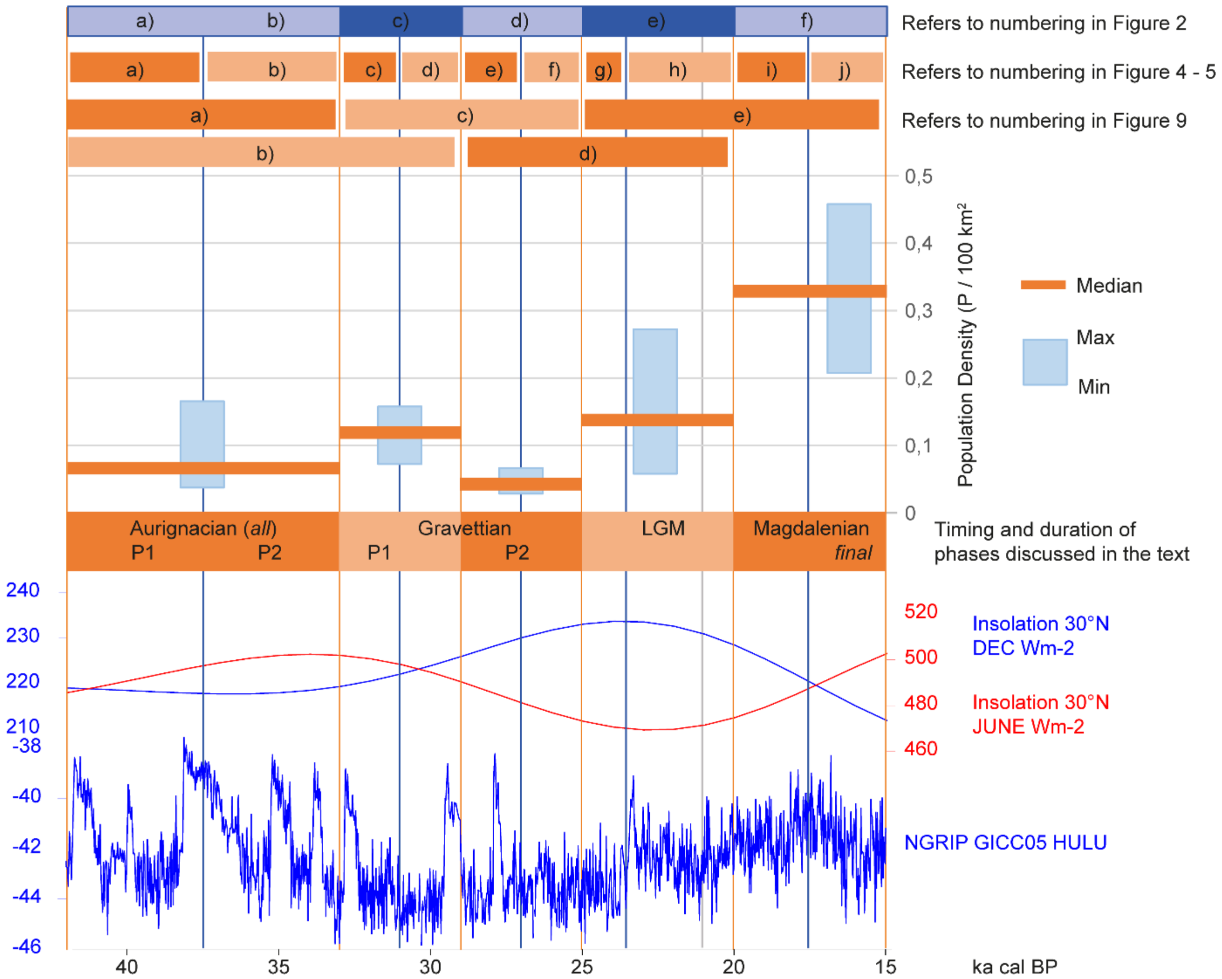


Figure 1: Overview on timeframe and temporal scales of data. Population density estimates are given for the generalised Total Area of Calculation (TAC) of 2.3 Million km^2 (see **Figure 2** for spatial extent), terminology for archaeological phases corresponds with **Table 1**. Note: estimates for the Magdalenian in total have not been calculated (see Kretschmer 2015), but would resemble those of the Final Magdalenian. Vertical lines indicate "insolation reference dates": Blue lines indicate Insolation values used for synchronic illustrations (**Figure 2**), orange lines for calculating differences in insolation for diachronic developments (**Figure 9**), grey line at 21ka indicates anchor point of the PMIP3 LGM climate model data. Timeframes covered in **Figure 2** and **9** are indicated and labelled accordingly. Insolation (30° N, June and December) and GISP 2 Delta18O/16O are taken from Climate Data CalPal (Weninger and Jöris 2008, accessed 27.06.2019).

2. MATERIAL AND METHODS

2.1 PALEODEMOGRAPHIC AND SPATIAL DATA

The study uses spatial information on site locations and raw material transport as well as derived demographic data for the periods of 42-33 ka (Aurignacian, Schmidt and Zimmermann 2019), 33-29 ka and 29-25 ka (Gravettian subdivided into an early phase 1 and later phase 2, Maier and Zimmermann 2017), 25-20 ka (LGM, Maier et al. 2016), and 20-14 ka (Magdalenian, Kretschmer 2015). The approach to estimate population sizes and densities, the "Cologne Protocol", was developed and described for Neolithic and younger periods (Zimmermann et al. 2009) and subsequently transferred to hunter-gatherer contexts (Kretschmer 2015). For details on the protocol, we refer the reader to Maier et al. (2016) and the supplementary material of Maier and Zimmermann (2017). Briefly, the protocol distinguishes areas of intensive use, so-called Core Areas, from areas which have been used either ephemerally, temporarily (e.g. during short phases of perceived climatic amelioration) or even not at all. Core Areas thus provide the minimum, but also the most robust evidence for human presence on a large spatial *and* temporal scale (e.g. Klein et al. In prep.). Core Areas are modelled within a defined map section, called Total Area of Calculation (TAC). The spatial distribution of Core Areas and the TAC used for the European Upper Palaeolithic is given in **Figure 2**. In a next step, spatial information on lithic raw material transport is used to estimate the number of groups within a Core Area. Using information on group sizes from the ethnographic literature, number and density of people within a Core Area and within the TAC are inferred. **Table 1** reviews the basic data for the paleodemographic estimates. For the Magdalenian we used data from the final Magdalenian period only, instead of averaging the higher resolution data provided by Kretschmer (2015). Similarly, for reasons of comparability, the demographic density estimates presented in **Table 1** are calculated based on a unified TAC, comprising 2,300,000 km^2 and illustrated in **Figure 2**, thus partially differing from previously published estimates. Core Areas for the final Magdalenian located outside the TAC (e.g. in Great Britain and Italy) were not considered for calculating spatial differences in Core Area distributions.

2.2 ENVIRONMENTAL DATA

Insolation data after Berger (1978) in Watt per square meter (Wm^{-2}) was obtained from the R package palinsol (Crucifix 2016) for twelve successive "insolation reference dates" at 42, 37.5, 33, 31, 29, 27, 25, 23.5, 21, 20, 17, and 15 ka cal BP (see **Figure 1**). These insolation reference dates were chosen to coincide with the boundaries and midpoints of the periods for the palaeodemographic estimates to provide an optimal fit of the data (**Figure 2**). The only exception is the LGM period, for which two internal insolation reference date are provided. This accounts for the observation of the transition between the Solutrean and Badegoulian in the archaeological record at around 23.5 ka as well as for the anchor point of our climatic data at 21ka, which is the focus time of the PMIP3 (Paleoclimate Modelling Intercomparison Project, Phase 3, Braconnot et al. 2012) LGM climate models (21 ka). Averaged daily temperatures (2 meters above ground level) were obtained from a 30 year long regional climate model simulation (horizontal grid spacing ~50km) with the WRF model (Weather Research and Forecasting, Skamarock et al. 2008) that was nested into the coarse gridded (~200 km horizontal grid spacing) MPI-ESM-P (Max Planck Institute for Meteorology Earth System Model in Paleo model, Giorgetta et al. 2013) LGM simulation. The regional WRF model has been adapted to LGM boundary conditions (e.g. ice sheets, lowered sea level, orbital parameters) and is forced by 6-hourly MPI-ESM-P data at its lateral boundaries (Ludwig et al. 2017). Additionally, an adjustment of sea surface temperatures based on the MARGO project (Multiproxy Approach for the Reconstruction of the Glacial Ocean surface, MARGO Project Members 2009) yield a better agreement of the WRF model results with the available proxy data (Ludwig et al. 2017). For comparison with the present-day, an additional WRF simulation has been performed that was forced by MPI-ESM-P data for present day climate simulation.

In order to transform these data into information meaningful for the production of primary biomass, we estimate for each insolation reference date the available energy per month at a given latitude in Megajoule per square meter (MJm^{-2}), as well as the start, end, length, and summed temperature of the growing season.

To transfer monthly Wm^{-2} into monthly MJm^{-2} we use the following function

$$MJm^{-2}{}_{month} = \left(\frac{Wm^{-2}}{1000}\right) \times ld_{lat} \times nd \times 3.6$$

where ld_{lat} is the length of daylight at a given latitude under current orbital conditions, nd is the number of days per month and 3.6 is the factor to transform kWh into MJ. Given the large scale of this study, we ignore insolation distortions introduced by local topography or daily differences due to cloud cover.

By most definitions, the growing season starts with six consecutive days of a mean daily temperature near the surface above 5°C and ends with six consecutive days below 5 °C of mean daily temperature (Jiang et al. 2018). Since mean daily temperatures in the model data are averaged over 30 years, increases and decreases are rather steady and reversions are rare. In order to account for this increased steadiness, we calculated the length of the growing season as the number of days between the first of the first three consecutive days above 5°C and the last day before the first three consecutive days below 5°C.

In order to estimate the start, end, and length of the growing season at 50°N and 45°N for each of the twelve insolation reference dates, we used the finding by Van Meerbeeck et al. (2009: 44) that during MIS 3 an increase in 4 Wm^{-2} resulted in an increase of 1°C, based on the seasonal global mean July surface air temperature range difference between model data of stadial conditions during MIS3 and the LGM. We calculated the differences in Wm^{-2} per month for each pair of consecutive reference dates and divided it by 4 to estimate the differences in °C. We then added the difference per month to each day within that month. This of course leads to a slight overestimate of the early days and a slight underestimate of the late days in a month for the first half of the year and vice versa for the second half. However, given the scope of this study, we consider the differences negligible.
In doing so, we can estimate the start, end, length, and summed temperature of the growing season for each insolation reference date.

The following results are shown for single time slices, as the difference between two consecutive time slices and as an accumulated trend over all time slices. By comparing changes in the spatial distribution of Core Areas between two time slices, possibly relating to expansions or contractions of human occupation, with changes in insolation, we analyse the impact of these changes on hunter-gatherer populations.

Table 1: **Overview of timeframe and database for each phase.**

Archaeological Period	ka cal BP	Duration (ka)	Number of sites included	Number of nites / ky	Core Areas (km^2)	Population size			Population density estimate per 2.3 Mio km²		
						min	median	max	min	median	max
Aurignacian (all)	42 - 33	9	382	43	**103,686**	**880**	**1,550**	**3,800**	0.038	0.067	0.165
Aur P1 (Proto/Early)	*n.a.*	*5*	*117*	*23*	***81,900***	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*
Aur P2	*n.a.*	*4*	*317*	*79*	***128,600***	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*
Gravettian P1	33 - 29	4	347	87	**243,039**	**1,660**	**2,760**	**3,610**	0.072	0.120	0.157
Gravettian P2	29 - 25	4	163	41	**123,810**	**660**	**1,000**	**1,530**	0.029	0.044	0.067
Last Glacial Maximum	25 - 20	5	396	79	**275,413**	**1,330**	**3,240**	**6,260**	0.058	0.141	0.272
Magdalenian (final)	20 - 15	5	1,002	200	**332,949**	**4,820**	**7,600**	**10,520**	0.210	0.33	0.46

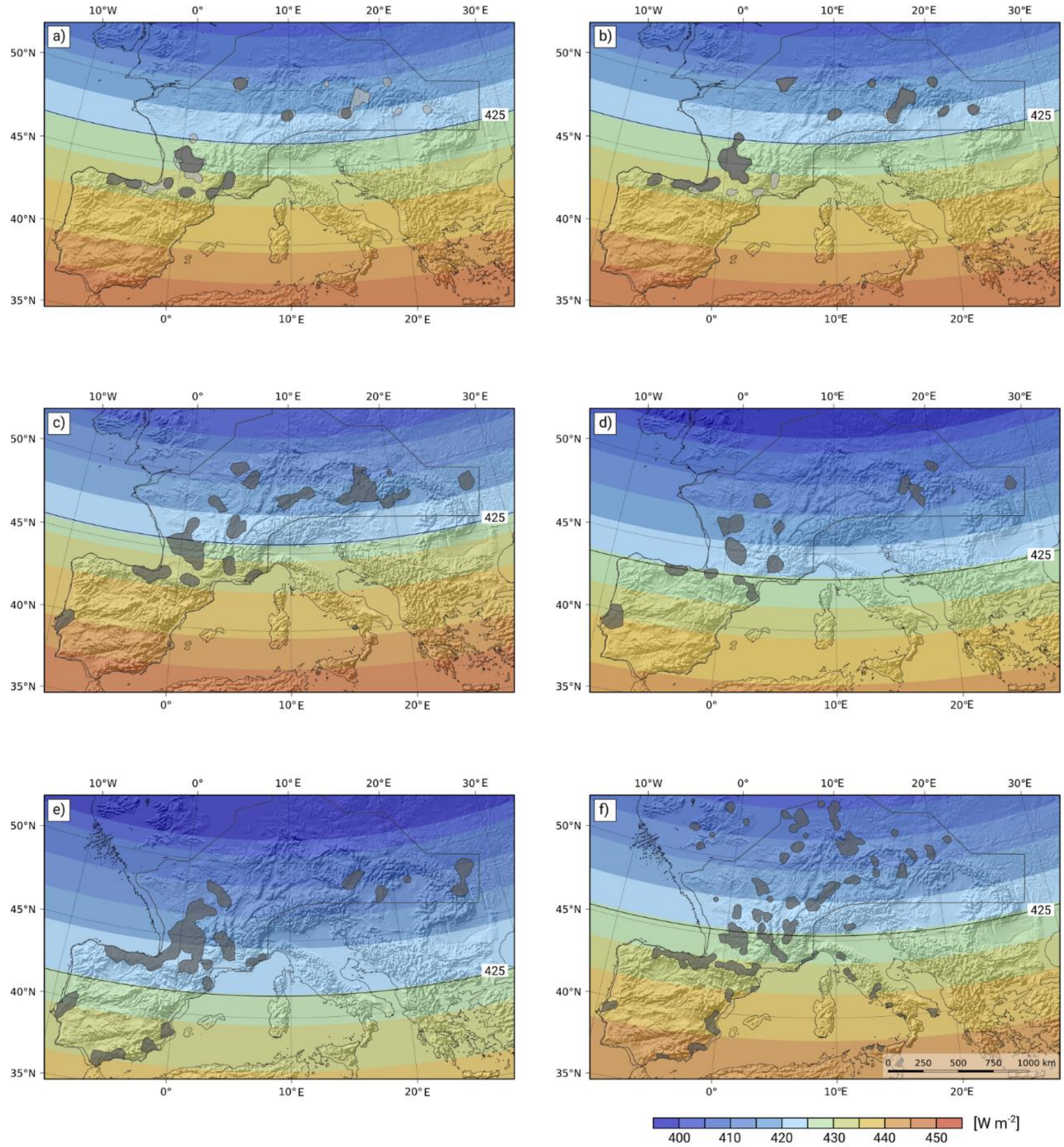


Figure 2: Distribution of Core Areas of the Upper Paleolithic plotted against insolation (Wm^{-2}) during growing season. For reasons of comparability, the growing season is set from April to September in this graph. Individual growing seasons are given in Figure 7 and Table 4**.** Latitudinal changes in insolation are highlighted by the 425 in Wm^{-2} isoline for visualisation. Core Areas falling within the Total Area of Calculation (TAC, grey line) are considered during further analysis. a) and b): 42-33 ka cal BP (Aurignacian P1 (a) and P2 (b) plotted in dark grey onto *Aurignacian all* Core Areas in light grey), insolation at 37.5; c) 33-29 ka (Gravettian P1), insolation at 31 ka; d) 29-25 ka (Gravettian P2) insolation at 27 ka; e) 25-20 ka (LGM), insolation at 23.5 ka; f) 20-15 ka (Magdalenian *final*), insolation at 17 ka. Coastline is -75 m b.c.s.l (a and b), -80 m b.c.s.l. (c and d), -120 m b.c.s.l. (e) and -115 m b.c.s.l. (f) (taken from: Zickel et al. 2016).

3. RESULTS ON POPULATIONS SIZES, DISTRIBUTION AND INSOLATION

3.1 PALEODEMOGRAPHIC ESTIMATES

The paleodemographic estimates (**Figure 1**) show an increase in the number of people during the period from 42 to 33 ka (Aurignacian) and to the period between 33 and 29 ka (Early Gravettian). This population growth is followed by a strong decline during the period between 29 and 25 ka (Late Gravettian), with absolute numbers decreasing even below the initial “starting” population at 42 ka. This decline coincides with a withdrawal from the higher latitudes. The period between 25 and 20 ka (Solutrean, Badegoulian, Epigravettian) is a period of population consolidation and renewed growth in Western Europe, while the population in Central Europe remains at low levels. This only changed between 20 and 15 ka, when populations in both Western and Central Europe increased strongly and the higher latitudes were resettled (**Table 1**).

In calculating the amount of overlap and discontinuity between the expanding, contracting, newly emerging and vanishing Core Areas of consecutive time slices, it is possible to quantify the spatial population dynamics. Here, overlapping Core Areas are seen as indicative of continuity in human presence, whereas expanding or contracting ones are understood as indicating discontinuity. Interestingly, percentages of areas either contracting or expanding vary considerably through time, while spatial overlap of Core Areas for two consecutive phases is constant and covers around 30% (**Table** 2) of the entire summed area - except for the Magdalenian, where the rapid expansion of humans into northern latitudes and the missing data for eastern Central-European sites produces a different pattern with a reduced percentage of overlap. Generally, the percentage of overlapping Core Areas is surprisingly low, given the constant presence of hunter-gatherers in Western Europe and their quasi-constant presence in Central Europe (**Table** 2).

Table 2: Percentages of overlapping, expanding and contracting Core Area sizes for paired phases.

Comparison of two Phases	Map in **Figure** B	Sum of Core Areas of two phases (sq km)	% Overlapping areas	% Expanded areas	% Contracted areas
Aurignacian P 1 and P2	(a)	157,750	33	48	18
Aurignacian (all) and *Grav. P1*	(b)	257,875	34	60	6
Gravettian P1 and *P2*	(c)	272,069	35	11	54
Gravettian P2 and *LGM*	(d)	310,713	28	60	11
LGM and Magdalenian	(e)	494,062	26	38	36

Note that the percentage of overlapping areas is quite constant through time, with decreases towards the Magdalenian due to the overall expansion into northern latitudes.

Table 3: Quantification of diachronic changes in Core Area sizes.

		Continuity	**Discontinuities**		**Percentage of areas within a single phase**			
Phase	**Core Areas (km^2)**	**overlapping areas**	**expansion in comparison to previous phase**	**contraction in comparison to subsequent phase**	**overlapping in comparison to previous phase**	**expansion in comparison to previous phase**	**Sum**	**contraction in comparison to subsequent phase**
		(km^2)	**(km^2)**	**(km^2)**	**%**	**%**	**%**	**%**
Aurignacian	103,686	n.a.	n.a.	14,836	n.a.	n.a.	n.a.	14
Aur P1 (Proto/Early)	*81,900*	*n.a.*	*n.a.*	*29,150*	*n.a.*	*n.a.*	*n.a.*	*36*
Aur P2 (Late)	*128,600*	*52,750*	*75,850*	*n.a.*	*41*	*59*	*100*	*n.a.*
Gravettian P1	**243,039**	88,850	154,189	148,259	37	63	*100*	61
Gravettian P2	**123,810**	94,780	29,030	35,300	77	23	*100*	29
Last Glacial Maximum	**275,413**	88,510	186,903	161,113	32	68	*100*	58
Magdalenian	**332,949**	114,300	218,649	n.a.	40	60	*100*	n.a.

Size and percentage of overlapping, contracting and expanding Core Areas are compared for each phase to previous (areas of overlap and expansion) and subsequent phases (areas of contraction).

3.2 INSOLATION AND GROWING SEASON

An overview of the length, summed temperature and start of the growing season based on the regional climate model data for LGM and present day is given in **Figure** 3 and **Table 4**. The number of days with daily mean temperature above 5°C are obviously much lower for LGM climate conditions, which is in accordance to a much lower summed temperature during the growing season for LGM conditions. Likewise, there is a pronounced shift of the 1st day of the year when daily mean temperatures above 5°C were simulated. For present day climate, large parts of Western Europe already reach the first day with mean daily temperature above 5°C already in January. For LGM climate conditions, there is a shift of ~3 months into the year until mean daily temperatures reach values above 5°C.

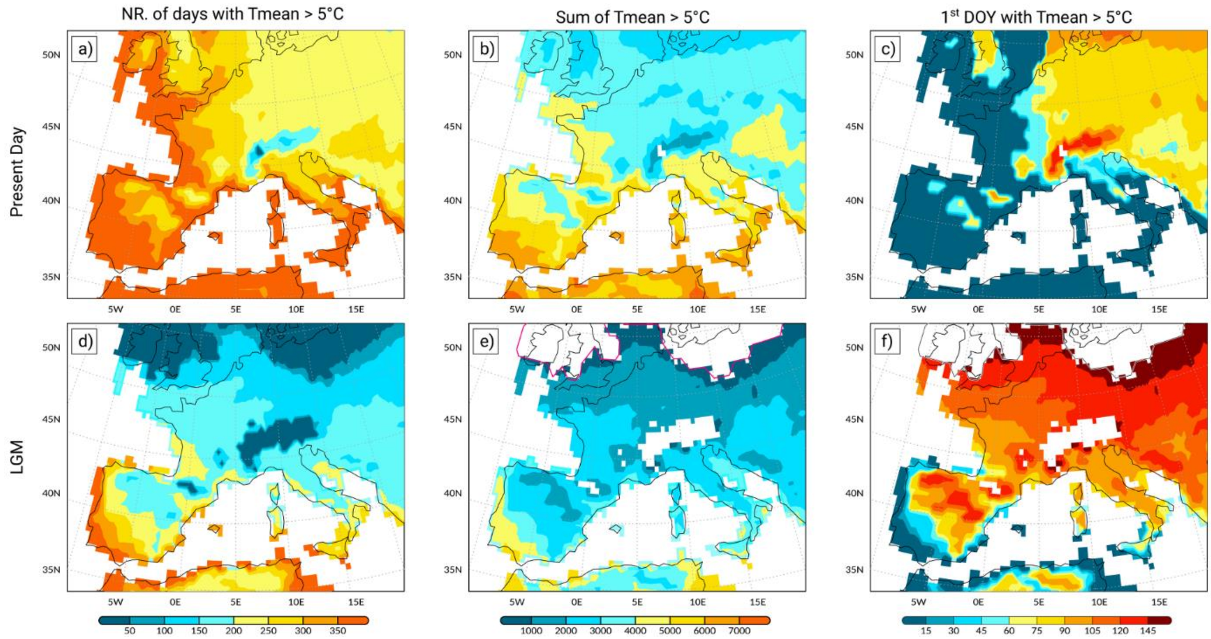


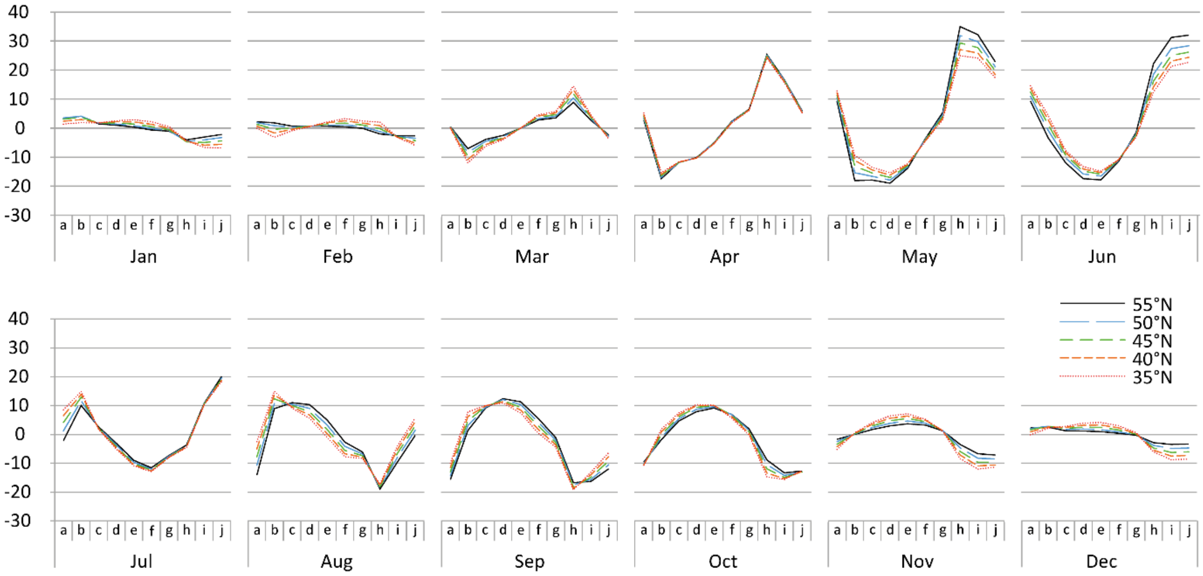
Figure 3: Parameters relevant for the growing season based on WRF model output for present day climate: (a) number of days with a mean daily temperature > 5°C; (b) temperature sum of all days within the growing season and (c) the first day of the year with a mean daily temperature > 5°C. (d)-(f) same as (a)-(c) but for LGM climate conditions.

When looking at the changes in MJm^{-2} for each month through the succession of the insolation reference dates as differences between consecutive reference dates (**Figure** 4), it becomes clear that the strongest differences throughout the period of observation occur during the months from April to October with differences of up to 60 MJm^{-2} in May and June, while the insolation from December to February remained rather stable.

The accumulated differences throughout the entire period of observation (**Figure** 5) show that highest losses in solar energy occur during the month of May and June between 29 and 25 ka, whereas the highest gains can be observed for September and October of the same period.

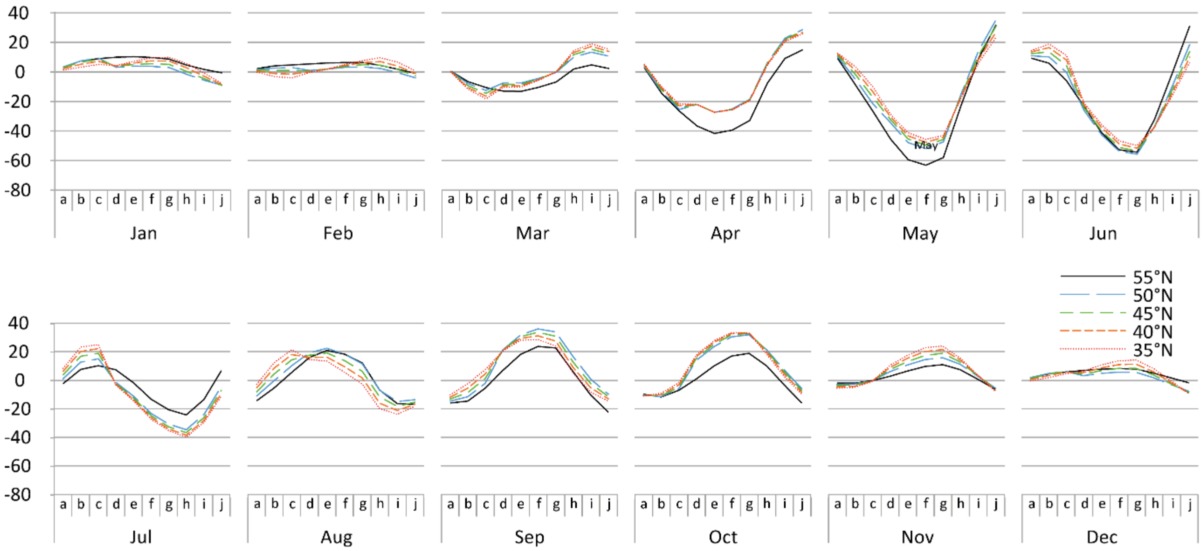
Figure 6 shows changes in MJm^{-2} throughout the year as differences between two consecutive insolation reference dates. After an initial gain in insolation in the first part of the year and a loss in the second from 42 to 37.5 ka, each of the following four units (37.5 to 27 ka) show the opposite trend with losses in the first half and gains in the second half. From 27 to 25 ka, the loss shifts to the middle of the year, while both the early and late parts of the year gaining energy. From 23.5 ka onwards, the system shifts back to the first pattern, with gains during the first half and losses during the second, but with a much higher amplitude. At 15 ka, a shift of energy gain towards the middle of the year is again observable.

Considering the accumulated differences with regard to the position and length of the growing season at 45°N (**Figure** 7, 8, **Table** 4) is very informative and reveals long-term changes. Three things are particularly remarkable. First, the shift from a gain of insolation during the first half to a pronounced loss and back to a strong gain with a complementary development during the second half becomes much clearer. Second, more or less in accordance with this shift, is a delay in the start of the growing season from mid-April between 42 and 37.5 ka to mid-May between 27 and 25 ka. The end of the growing season also shifts backwards. Third, is the particularly conspicuous loss of solar energy during the start of the growing season between 29 and 21 ka. Between 27 and 25.5 ka, plants have about 60 MJm^{-2} less for their photosynthesis during the crucial early part of the growing season.



a: 42-37.5ka b: 37.5-33ka c: 33-31ka d: 31-29ka e: 29-27ka f: 27-25ka g: 25-23.5ka h: 23.5-20ka i: 20-17,5ka j: 17.5-15ka

Figure 4: Differences in MJm^{-2} for each month through the succession of the insolation reference dates as differences between two consecutive reference dates.



a: 42-37.5ka b: 37.5-33ka c: 33-31ka d: 31-29ka e: 29-27ka f: 27-25ka g: 25-23.5ka h: 23.5-20ka i: 20-17,5ka j: 17.5-15ka

Figure 5: Differences in MJm^{-2} for each month through the succession of the insolation reference dates as accumulated differences throughout all reference dates. For legend see Figure 4.

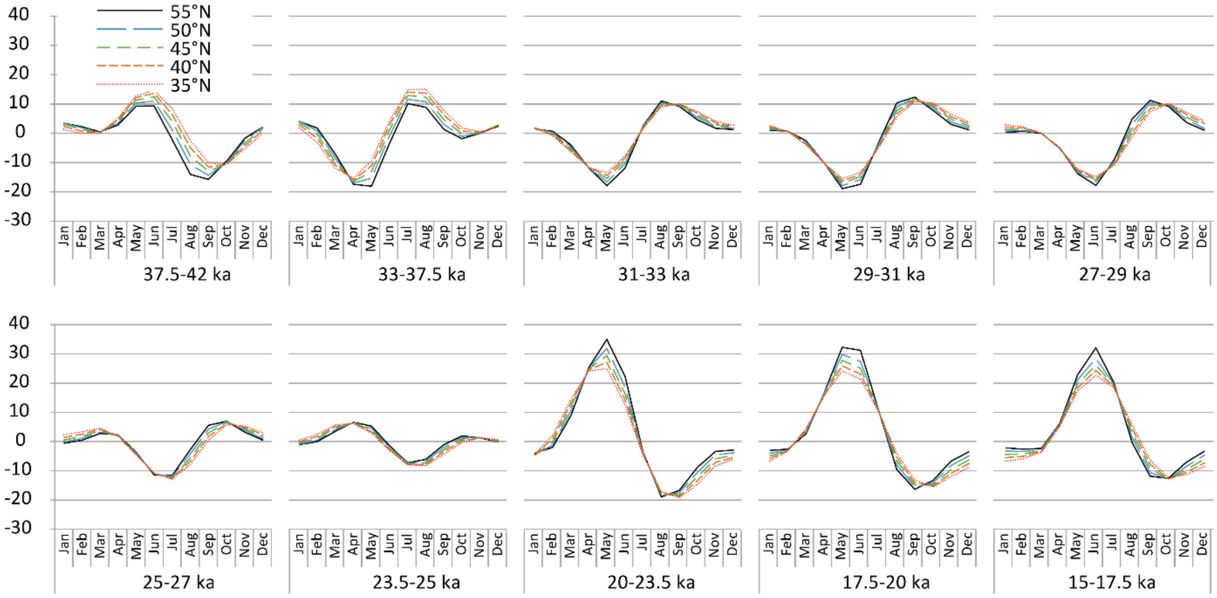


Figure 6. Changes in MJm^{-2} throughout the year as differences between two consecutive insolation reference dates. For legend see Figure 4.

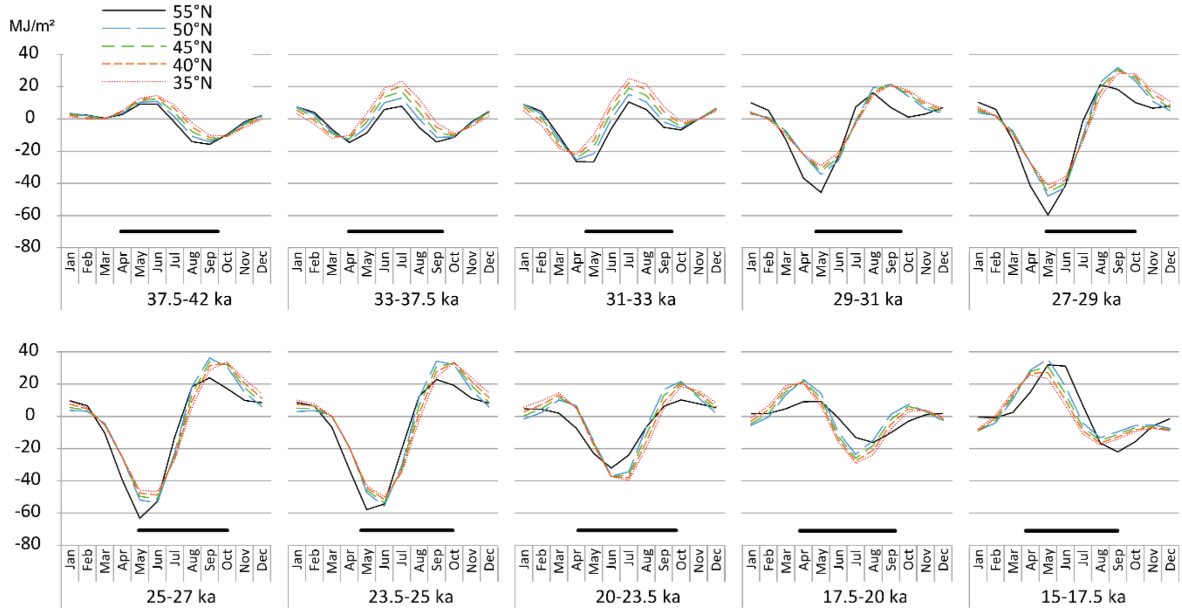


Figure 7. Changes in MJm^{-2} throughout the year as accumulated differences between consecutive insolation reference dates. Solid bars indicate position and length of the growing season at 45°N (see **Table** 4). For legend see Figure 4.

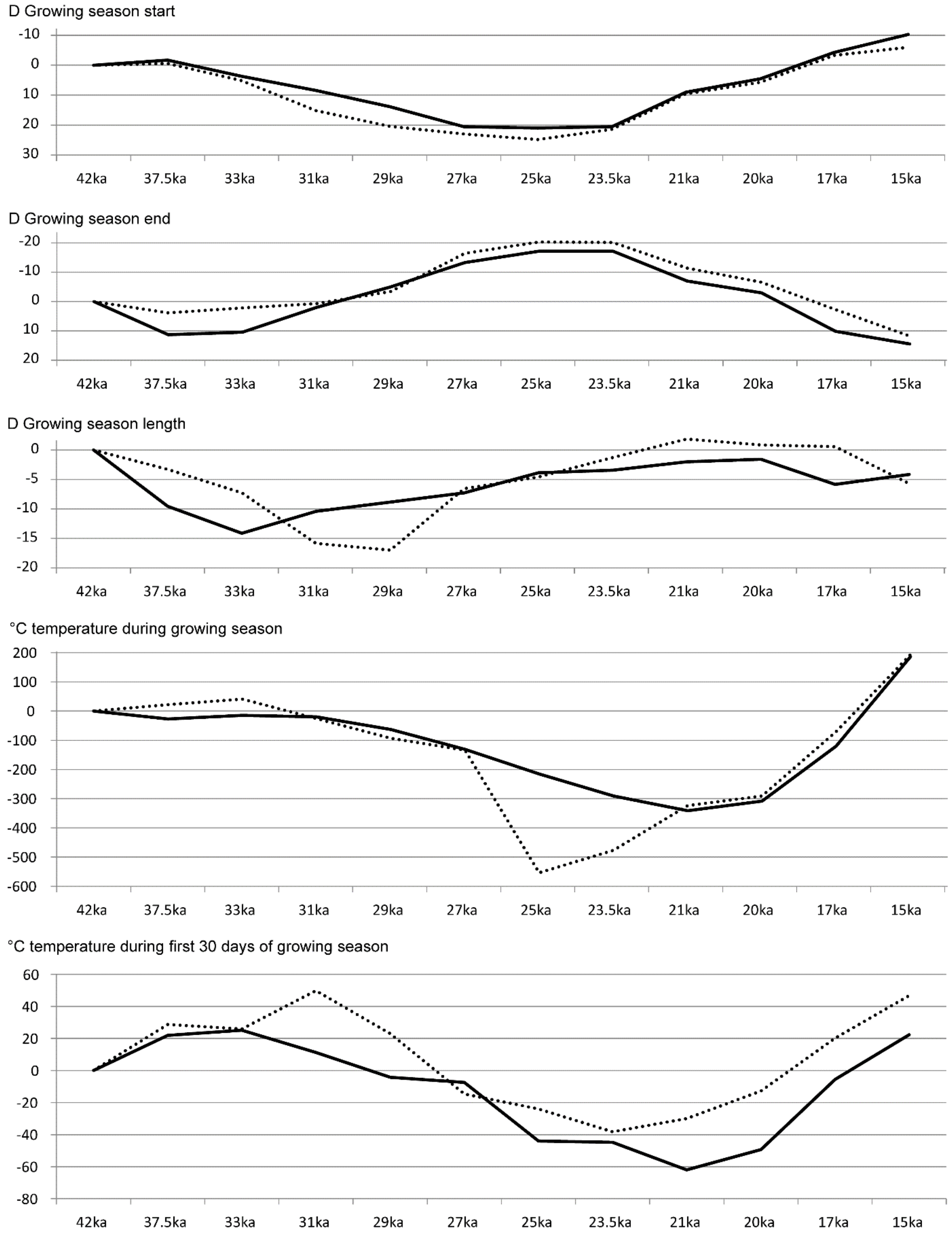


Figure 8. Changes in start, end, length, summed temperatures and summed temperatures during the first 30 days of the growing season at 45°N (dotted line) and 50°N (solid line).

Table 4. Parameters of the growing season.

		42ka	37.5ka	33ka	31ka	29ka	27ka	25ka	23.5ka	21ka	20ka	17ka	15ka
50°N	Σ T in°C*	1,772	1,745	1,757	1,753	1,710	1,641	1,557	1,481	1,431	1,464	1,652	1,958
	Start in calender day*	127	125	131	135	141	148	148	148	136	132	123	117
	End in calender day*	261	250	251	259	266	275	279	279	268	264	251	247
	Length in calender days*	135	126	121	125	127	128	132	132	133	134	130	131
45°N	Σ T in°C*	2,572	2,594	2,613	2,546	2,479	2,438	2,018	2,095	2,248	2,282	2,502	2,766
	Start in calender day*	169	166	162	153	152	163	165	168	171	170	170	163
	End in calender day*	107	106	112	122	127	130	132	128	116	113	104	101
	Length in calender days*	275	271	273	274	278	291	295	295	286	282	272	263
	Σ T in C° of first 30 days	291	320	317	341	314	277	267	253	261	279	312	338

All values represent averages from 7 longitudes at -1°, 3.5°, 8°, 12.5°, 17°, 21.5°, and 26° E.

4. DISCUSSION

4.1 A DIACHRONIC COMPARISON OF POPULATION DYNAMICS AND CHANGES IN SOLAR INSOLATION

In order to assess the possible impact of changes in insolation on the demographic developments of the Upper Palaeolithic in Europe, we compare the results of both analyses diachronically. Here, shifts in Core Areas are taken as indicators for spatial population dynamics.

4.1.1 42-33 ka – Aurignacian

For this period connected with the first extensive spread of anatomically modern humans into Central and Western Europe, we estimate a mean population size of 1,500 persons (max.1,800 / min. 700; Schmidt and Zimmermann 2019). Core Areas were calculated for an early phase (Proto and Early Aurignacian; Aur P1) and later phases (Aur P2; **Figure 2: a, b**), although paleodemographic estimates for these two sub-phases were not possible and are therefore given for the entire Aurignacian (Aurignacian *all*, see **Table 1**) (ibid.). It becomes clear that both phases show regional differences in their spatial pattern and several indicators (e.g. number of sites per 1,000 years, size of the Core Areas) support a population increase from the early to the late phase, particularly in the eastern part of the investigated area. Continuity through both phases can be attested for regions where viable populations have been estimated for the entire Aurignacian (ibid.: **Figure** 2 and **Table** 3). However, almost 60 % of the area covered during the later phase relates to newly emerging and expanding Core Areas (**Table 3**), occurring mainly in Northern Iberia, SW-France and the Middle Danube/Moravian Region (**Figure 9: a**).

With regard to the environmental data, we observe some changes. While there is a slight trend towards a later start and shortening of the growing season (**Figure** 8), the summed temperature during the entire growing season and during the first 30 days are both rising with a first peak of the latter at 37.5 ka and of the former at 33 ka (**Table 4**). This gain seems to be more pronounced in Central than in Western Europe. Between 42 and 37.5 we see a rise in solar energy during the early growing season followed by a shift of maximum insolation to the middle part of the year between 37.5 and 33 ka (**Figure** 7).

4.1.2 33-29 ka – Early Gravettian

The demographic trend continues during the first half of the Gravettian and the overall estimate of people rises to a median of 2,800 (+900 / -1,100; Maier and Zimmermann 2017). Core Areas with viable populations during the Aurignacian expand, especially in the Upper and Middle Danube/Moravian Regions and new ones emerge across the entire TAC, extending to the East and Southwest of Europe (**Figure 9: b**). Again, the areal increase ranges around 60%, with an exceptionally low "loss" of regions covered by Core Areas during the Aurignacian (only 14%). Estimated population density within the Core Areas, however, varies considerably from 2.7 to 0.3 persons per 100 km² (median often around 1.4, ibid).

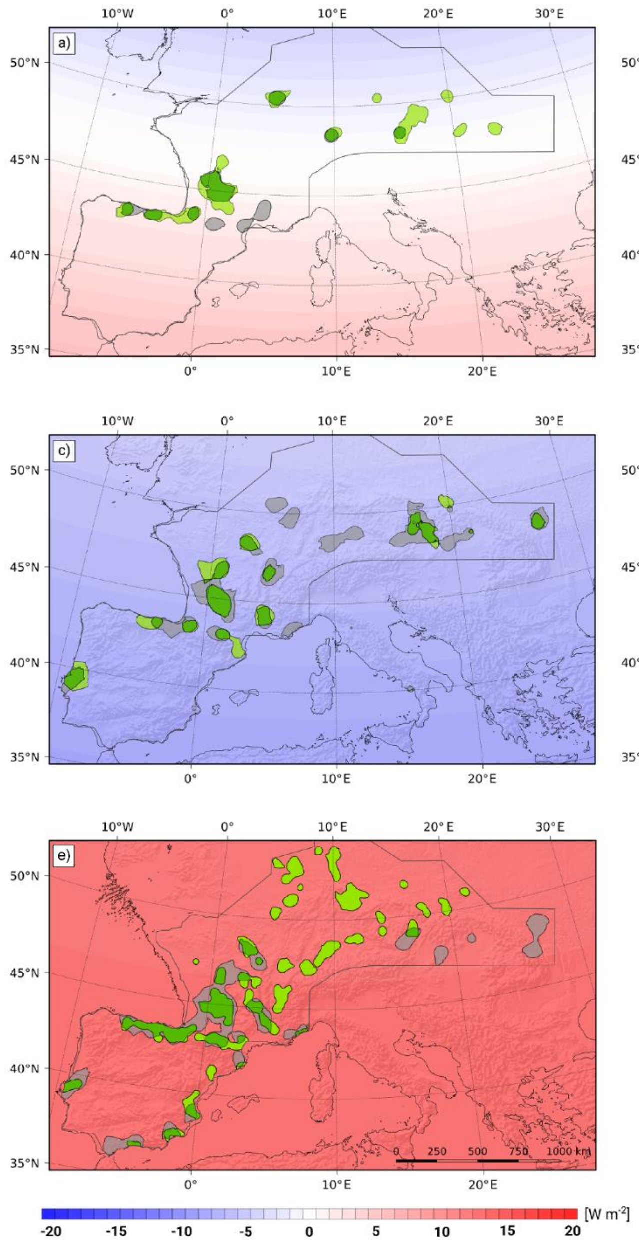


Figure 9: Diachronic changes of Insolation and Core Areas during the Upper Palaeolithic. Core Areas are displayed for two successive periods. Colours indicating continuity (dark green), expansion (light green) and contraction (grey areas) of Core Areas. Changes in insolation (W/m^2, see legend) during the respective phases are given as the difference between insolation at the end of each phase. a) Difference of insolation between 37.5 and 33 ka (Aurignacian P1 and P2); b) between 33 and 29 ka (Aurignacian all and Gravettian P1); c) between 29 and 25 ka (Gravettian P1 and P2); d) between 25 and 20 ka (Gravettian P2 and LGM); e) between 20 and 15 ka (LGM and Magdalenian). For reconstructed coastlines and TAC see **Figure 2**.

A look at the environmental data shows that this phase is characterised by a continuation of the moderate decline during the first half of the year, coinciding with a slight delay in the onset of the growing season in comparison to previous periods (**Figure** 7 and 8). This trend is counteracted, however, by a strong gain in temperatures during the first 30 days of the growing season with the highest values of the entire period of observation at 31 ka (**Figure** 8).

4.1.3 29-25 ka Late Gravettian

The most exceptional and marked decrease in population size and distribution during the entire Upper Palaeolithic of Europe has been detected for the later phase of the Gravettian (**Figure 9: c**), with estimates dropping to a median value of 1,000 (+500 / -300; Maier and Zimmermann 2017). Core Areas disappear in Western Central Europe and experience considerable contraction and fragmentation in all other regions of Europe, except for central Portugal. In comparison with the first half of the Gravettian, the spatial loss amounts to 61% (**Table** 3, see also **Table** 2). Only a few Late Gravettian Core Areas actually show evidence of an expansion (23%) and thus it is not surprising that the Core Areas of the Late Gravettian overlap – also to an exceptionally high percentage of 77% - within the areas already occupied previously.

Interestingly, the strong demographic decline coincides with the maximum delay in the start of the growing season coupled with the maximum loss of solar energy during its early phase (**Figure** 7). At the same time, the sum of temperatures during the growing season drops sharply towards 25 ka to the lowest values in the entire period of observation (**Figure** 8). The renewed prolongation of the length of the growing season back to the level of 33 ka apparently does not counteract these effects. In this context it is interesting to note the cave bear, a species that was apparently reliant on high-quality plant food which made it vulnerable to decreasing vegetational productivity, goes extinct in Central Europe at around 28 ka (Pacher and Stuart 2008).

4.1.4 25-20 ka – The Last Glacial Maximum – Solutrean, Badegoulian, Early Epigravettian

During the Last Glacial Maximum, we see a turnaround in the demographic downward trend. Mean population estimates of 3,100 (+3,200 / - 1,800) show renewed population growth (Maier et al. 2016). However, it is only in Western Europe that this growth is apparent, whereas populations in Central Europe remain at a low level. Furthermore, increasing the temporal resolution within this period of 5 ka, it seems that roughly between 22 and 21 ka, there is no evidence of hunter-gatherer north of 47°N. Previous tendencies towards fragmentation of Core Areas disappear in southwestern / northern Iberia and turn into expansion and even merging of Core areas (**Figure 9: d**). In southern Iberia, the Cologne Protocol detects Core Areas along the Mediterranean coast for the first time.
Environmentally, we again see an increasingly early start of the growing season, and the growing season length even peaks at 21ka. After a minimum at 23.5 ka, the summed temperatures of the first 30 days of the growing season rise again as does the sum of temperature during the entire growing season. In addition, we see a slight increase in solar energy during the first half of the year between 25 and 23.5 ka becoming a bit more pronounced between 23.5 and 20 ka. However, Verpoorte (2009) notes a marked decline in the diversity of the faunal assemblages of Central Europe occurring at around 24 ka. A similar pattern is reported by Jochim (1987) for south-western France. This might be related to a delay in the faunal response because of a certain inertia of population dynamics with regard to change in the environmental system.

4.1.5 20-15 ka – Magdalenian

Between 20 and 15 ka, the estimated number of people rises markedly to a mean of 7,700 (+3,000 / - 2,800), while the density in Core Areas ranges between 1.6 and 3.6 persons per 100 km² (Kretschmer 2015). With regard to spatial dynamics, it has to be stated that Core Areas are only available for Western Europe and the western part of Central Europe, since Epigravettian sites, located further East, have not been considered in the estimates. This does, to some extent, explain the relatively high percentages (58%) of contracting areas compared to the period of the LGM given in **Table** 3. Other contractions can be observed in south-western Europe (**Figure 9: e**). However, the general trend of continuity (40%) and expansion (60%) in the spatial distribution of final Magdalenian Core Areas already observed during the LGM does continue: together with the increasing population and the resettlement of the higher latitudes, we see an increasingly early start of the growing season (the earliest of the entire study at 15 ka) coupled with increasing summed temperatures for both the entire growing season (highest in the entire study at 15ka) and the first 30 days (second highest after 31 ka; **Figure** 8). In addition, there is a strong increase in solar energy during the first half of the year and thus also during the beginning of the growing season (**Figure** 7).

4.2 INSOLATION AS A PACEMAKER FOR LONG-TERM DEMOGRAPHIC DEVELOPMENTS?

For Palaeolithic hunter-gatherers, who extracted all their energy directly from their environment without further manipulation, the availability and diversity of animal biomass is probably a key-factor allowing their continued presence in a region (Tallavaara et al. 2018). For Western and Central Europe, terrestrial herbivores were the most important game. In addition to their role in human nutrition, they also provided useful raw materials, such as antler, bone or ivory, making them crucial in the entire subsistence system (Soulier 2014; Soulier et al. 2014). The abundance and diversity of herbivores in a landscape depends essentially on the availability and quality of plant food in a region (Olff et al. 2002).

Usually when thinking about availability of (plant) food, quantity and quality are the factors being considered. However, timing also seems to be of major importance. After long glacial winters, herbivorous animals depend on the availability of sufficient high-quality plant food in spring. Not only do they have to replenish their reserves, but this is also the period when their offspring are born. Spring is thus a crucial period for herbivorous animals and one during which they are rather vulnerable to shifts in plant phenology and environmental stress (Debeffe et al. 2019). The green-up of the landscape is also a key-factor for the timing and movements of ungulates for spring migration (Merkle 2016). Shifts, delays, and unforeseen changes in the migration patterns of their most important prey species, in turn, have a high potential to cause problems for hunter-gatherers (Krupnik 2018; Mandryke 1993; Smith 1978). As shown above, spring is the period affected the most by the changes in solar insolation between 43 and 15 ka. Between 25 and 23.5 ka, the growing season was delayed by about a month. Moreover, when it started, the available solar energy and temperatures were very low. Low temperatures also have negative influence on seed germination and seedling establishment (Trugdill et al. 2000; Zhang et al. 2018). The cooling effect of permafrost on soil temperature likely further hampered germination at 25ka, impeding the start of the growing season and thus biomass production even more strongly than estimated from insolation alone. Additionally, a lower CO_2 level (Van Meerbeeck et al. 2009) probably reduced the growth of at least C3-plants (Bartlein et al. 2010) and waterlogging in the active layer of permafrost soils likely further handicapped plant growth. Impeded germination eventually leads to fewer mature plants and less seeds for the following year, leading to a self-reinforcing reduction of the vegetation. It can thus be surmised that between 25 and 23.5 ka plant food was available only considerably later during the year, and when it appeared, overall biomass production was rather low. This likely caused substantial problems and environmental stress for herbivorous populations, especially in higher latitudes (Belovsky 1988; Mandryk 1993: 56). Such a shift in seasonality with a prolongation of the winter-period and a severely delayed start of the growing season might also explain the peculiar finding of virtual absence of mammoth during the LGM in large parts of Europe (Stuart 2005). With their high demand for plant food, the carrying capacity during springtime may have been too low to support a viable mammoth population.

The changes in solar insolation and the dependent vegetational system probably led to a loss of animal diversity, delayed spring migrations and eventually a strong reduction and/or withdrawal of larger herbivores from higher latitudes. In combination, these factors probably made the northern areas also inhospitable for hunter-gatherers, who apparently vanished from these regions. However, the lower latitudes were also affected by decreasing spring insolation with presumably negative effects on the net production of primary biomass; this is congruent with a general population decline at around 25 ka in Western and Central Europe. It is only with a renewed increase in spring insolation and an ever-earlier start to the growing season after 20ka, that populations in Western and Central Europe showed a considerable increase in numbers and densities and an expansion of their Core Areas into the higher latitudes.

Ultimately, it can be stated that this parallel development in palaeodemography and solar insolation is unlikely to be merely coincidental. It seems that for the spatially large-scale and long-term development of hunter-gatherer populations, in terms of both their numbers and distribution, solar insolation is an important driver.

5. CONCLUSION

It seems that ecosystems in Europe between 43 and 15 ka reacted very sensitively to gains and losses in solar energy and potentially resulting changes in plant and animal phenology. This effect seems to be particularly pronounced in the higher latitudes (cf. Feurdean et al. 2014), but affected the lower ones as well. Stronger reactions in the north are likely a consequence of generally lower temperatures and insolation values. Hence, while a reduction in the lower latitudes still left enough energy for a timely start of the growing season, a reduction at higher latitudes may have quite noticeable and rather severe consequences. For hunter-gatherers depending on the resources provided by their environment, it is not the total amount of annual insolation that is important. Rather it is the available energy during the growing season that, via plant biomass and herbivorous animals, affects the basis of existence of Palaeolithic hunter-gatherers. Interestingly, a late onset of the growing season seems to have more severe consequences for the ecosystem than a shorter duration.

Anatomically modern humans arrived in Europe during a period of medium intensity solar insolation. Subsequently, a moderate gain in insolation during the growing season was accompanied by moderate population growth and spatial extension of the Core Areas. Over the following millennia, the coupled effects of a late start to the growing season, a reduced amount of energy during its early phase, and a low overall temperature throughout its duration likely led to a considerable reduction in plant biomass availability until around 23.5 ka. It is highly likely that this development led to a reduction of the diversity and abundance of herbivorous animals in the landscape and might be part of the explanation for the virtual absence of mammoth during the LGM. We hence argue for assuming an indirect causal relationship, mediated by changes in animal abundance, between the decline of solar insolation and the pronounced decline of hunter-gatherer populations in Western and Central Europe between 29 and 25 ka. The same causal relationship can be assumed between the increase in spring insolation, an ever-earlier starting growing season and the demographic growth and spatial expansion of hunter-gatherer groups after 23.5 ka ago.

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