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# Long-term demographic trends and spatio-temporal distribution of past human activity in Central Europe: Comparison of archaeological and palaeoecological proxies

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**Abstract**

Estimating past population dynamics has become a major research topic for archaeology, which uses several proxies for studying past demography. The Czech Republic represents a unique region with abundant digital archaeological and palynological datasets comprising tens of thousands of records covering the whole Holocene. We used these datasets to quantify long-term demographic trends and to delimit past human activity in space and time. Our results, based on large data from both disciplines, are one of the first quantitative results covering the whole Czech Republic. Through summed probability distributions of radiocarbon dates and spatio-temporal modelling of human activity based on archaeological sites, we identified four major demographic events and processes between 10,000 BCE and 1000 CE – the beginning of the Neolithic at 5400 BCE, the Eneolithic/Bronze Age transition in the 3rd millennium BCE, Bronze Age expansion after 1500 BCE, and mediaeval expansion after 500 CE. We identified two settlement cores in the lowlands, with additional inner and outer peripheries with different demographic histories. Our study clearly shows that prehistoric and early historic population dynamics were not a homogenised process and were regionalized according to local environmental and social conditions. The comparison of archaeological results with pollen-based vegetation proxies also showed regional aspects in human-vegetation interactions. Agro-pastoral communities dwelling in the lowlands mostly influenced the openness of the landscape, used for fields and pastures, whereas contemporary communities with a similar economic mode residing in a different region are more visible in pollen records through species and structural changes in woodlands. The agro-pastoral subsistence strategy did not start everywhere with the onset of the Neolithic: in some regions it failed after several centuries, in others, the foraging lifestyle persisted significantly longer, and farming became a major economic strategy much later. Our study shows that archaeological site-based and $^{14}C$-based demographic proxies cannot be utilized for all periods and regions due to several limitations. Only the combination of different quantitative and qualitative archaeological proxies for population does reveal important details.

**Keywords**

Palaeodemography; prehistory; radiocarbon summed probability; quantitative archaeology; palaeoecology; farming; woodland management; spatial archaeology; population dynamics; Czech Republic

## 1. Introduction

Prehistoric population dynamics is one of the main research topics for current archaeology (e.g., French et al., 2021; Nikulka, 2016; Shennan, 2018; Zimmermann et al., 2009). Population size and density, and demographic fluctuation, are among the most significant factors playing roles not only in social organisation but also human-environment interactions (e.g., Bevan et al., 2017; Kolář et al., 2018; Kuosmanen et al., 2016; Riris and Arroyo-Kalin, 2019; Tallavaara and Seppa, 2012; Whitehouse et al., 2014). However, producing realistic estimates of the size of prehistoric communities is still a major research challenge. Reliable population estimates on a large spatial scale (continental or global) combined with information on subsistence strategies would better inform us about the relationship between historical land use and land cover, and would enhance our knowledge on the impact of anthropogenic activity on global climate during the Holocene (de Noblet-Ducoudré et al., 2012; Gaillard et al., 2018; Pongratz et al., 2010; Ruddiman and Ellis, 2009). Although archaeology has been using digital databases for sites for decades and analysing large data has been integral to the paradigmatic shifts within the discipline (Kristiansen, 2014), the combined use of large-scale interdisciplinary datasets only started being acknowledged and spread recently (Bird et al., 2022; Ellis, 2015; Gaillard and LandCover6k Interim Steering Group members, 2015; Kintigh et al., 2014; Morrison et al., 2021; Palmisano et al., 2021; Racimo et al., 2020).

Archaeology differs from many palaeosciences by the character of the data it can provide. In most cases archaeologists are focused on a specific period, they excavate in detail a handful of sites in a particular region, or they are specialists in specific types of artefacts. Additionally, archaeological datasets are mostly dispersed in individual archives (Richards et al., 2021), despite the recent positive but slow development in international access and harmonisation (cf. Richards and Niccolucci, 2019). Producing a long-term and geographically large-scale perspective on demographic trends comparable with palaeoenvironmental proxies is, therefore, an extremely difficult task. Several approaches to the reconstruction of past population dynamics have been developed over recent decades and we can divide them into two groups – absolute and relative (Müller, 2013; Schmidt et al., 2021). Absolute population estimates (often given as population density, i.e. persons per $km^2$) are related to environmental factors such as carrying capacity (cf. Sayre, 2008), or analogies from ethnography. Relative values do not provide us with specific numbers of people living in an area or settlement, rather they are based on the assumption that the amount of archaeological evidence directly reflects the population size and density (Rick, 1987).

The most widespread technique in current demographic archaeology is the use of the summed probability distribution (SPD) of radiocarbon dates (e.g., Bevan et al., 2017; Chaput et al., 2015; Palmisano et al., 2021, 2017; Seidensticker et al., 2021; Shennan, 2018). Although the method itself has been criticised for several reasons – the divergent financial possibilities of individual countries, the radiocarbon dating traditions of different research communities, past mobility and subsistence strategies influencing the taphonomy of archaeological sites, the 'date-as-data' approach itself (e.g., Carleton and Groucutt, 2021; Contreras and Meadows, 2014; Crombé and Robinson, 2014; Torfing, 2015) – developments, upgrades, and interdisciplinary comparisons have proven its general usability (e.g., Crema and Bevan, 2021; Edinborough et al., 2017; Hinz, 2020). Nowadays, SPDs are used in multi-proxy demographic studies and the main challenge seems to be to explore the relationship between the proxy and absolute population numbers.

Central Europe is one of the archaeologically best-known regions in the world and seems to be an ideal place to demonstrate the data-driven approaches currently transforming the whole discipline (Huggett, 2020; Kristiansen, 2014). The area of the Czech Republic is endowed with tens of thousands of archaeological sites which have been excavated during the last 200 years. Basic information on them is currently stored, managed, and further collected in digital databases and maps (Kolář et al., 2016; Kuna et al., 2015). The unique availability of large digital datasets of archaeological sites and finds which have a potential for creating a long-term demographic perspective has already prompted several regional studies utilising quantitative techniques of population estimation or settlement dynamics (Demján and Dreslerová, 2016; Demján et al., 2022; Dreslerová and Demján, 2019; J. Kolář et al., 2016; Kolář et al., 2018; Kuna, 2015; Mertel et al., 2018). The available data come from different projects and research institutes, and were merged within the Archaeological Information System of the Czech Republic (https://www.aiscr.cz/) only recently. Moreover, Czechia is newly endowed with a database of radiocarbon dates from archaeological contexts covering most of the Holocene (Tkáč and Kolář, 2021a). Additionally, most of the available palynological archives are stored in a regularly updated database PALYCZ (Kuneš et al., 2009). This unique situation, characterised by data quantity, relatively homogeneous quality and availability, enables us to present the first country-wide (in Central Europe) compilation of site data, radiocarbon dates, and pollen data in a long-term perspective, analyse them together, and present a multi-proxy and regionally-specific demographic model. It enables us to ask several questions. Is there evidence of regionally specific demographic trajectories? What social or environmental processes might account for them? What was the spatial extent of human settlement in Czech territory during prehistory and the mediaeval period? Was the inhabited area in different periods stable or fluctuating? Are demographic patterns reflected in vegetation changes? How do models based on archaeological sites and radiocarbon dates differ? Does this difference limit their usability for some periods?

To answer these questions, we first use the SPD of archaeological radiocarbon dates as a population proxy and then employ spatio-temporal modelling to create a site-based demographic proxy. Secondly, we use an independent pollen dataset to capture possible changes in vegetation caused by the spread of humans and land use transformations. Lastly, we discuss the demographic fluctuations in the context of coinciding social and economic changes, consider the validity of the proxies, and suggest future research directions.

# 2. Materials and methods

## *2.1. Geographical settings*

The study area, defined by the extent of the Czech Republic (78,866 km$^2$), lies in the temperate zone of Central Europe and has a variety of environments (Figure 1). The altitudinal range spans from 115 to 1,603 m asl, but 50% of the area is located below 500 m asl. Two large lowland regions (area below 200 m asl) follow the two main rivers and their tributaries – the Elbe river in northern and central Bohemia (western part of the country), and the Morava river in Moravia (eastern part of the country). The Elbe river basin is surrounded by the higher mountain ranges, with islands of alpine grasslands and tundra-like habitats, where the highest peaks are between 1,300 and 1,603 m asl (Chytrý, 2017), and is separated from the Morava river basin by the Bohemian-Moravian Highlands, whose highest peaks are slightly over 800 m asl and hill passes at 440 m asl. The Moravian lowlands are framed by Sudeten Mountains to the north and Carpathians to the east, but are connected to the south to the Pannonian Plain. A minor lowland region can be found in Czech Silesia in the north-eastern part of the country, which is drained by the Oder river towards Poland (most of the lowland is situated beyond the national border).

Archaeologists traditionally study the prehistoric settlement of the Czech Republic independently within the boundaries of its historical lands (Bohemia, Moravia, and Czech Silesia), therefore this is one of the first attempts to analyse and interpret the existing nation-wide datasets. In our study, population history is the key element for defining regions, therefore, we did not use traditional regional divisions, which mostly reflect the administrative jurisdiction of archaeological institutions and heritage management units. The

200 year-long history of archaeological research in the current Czech Republic which led to the current large archaeological datasets was summarised by Kuna et al. (2015) and Kolář et al. (2016).

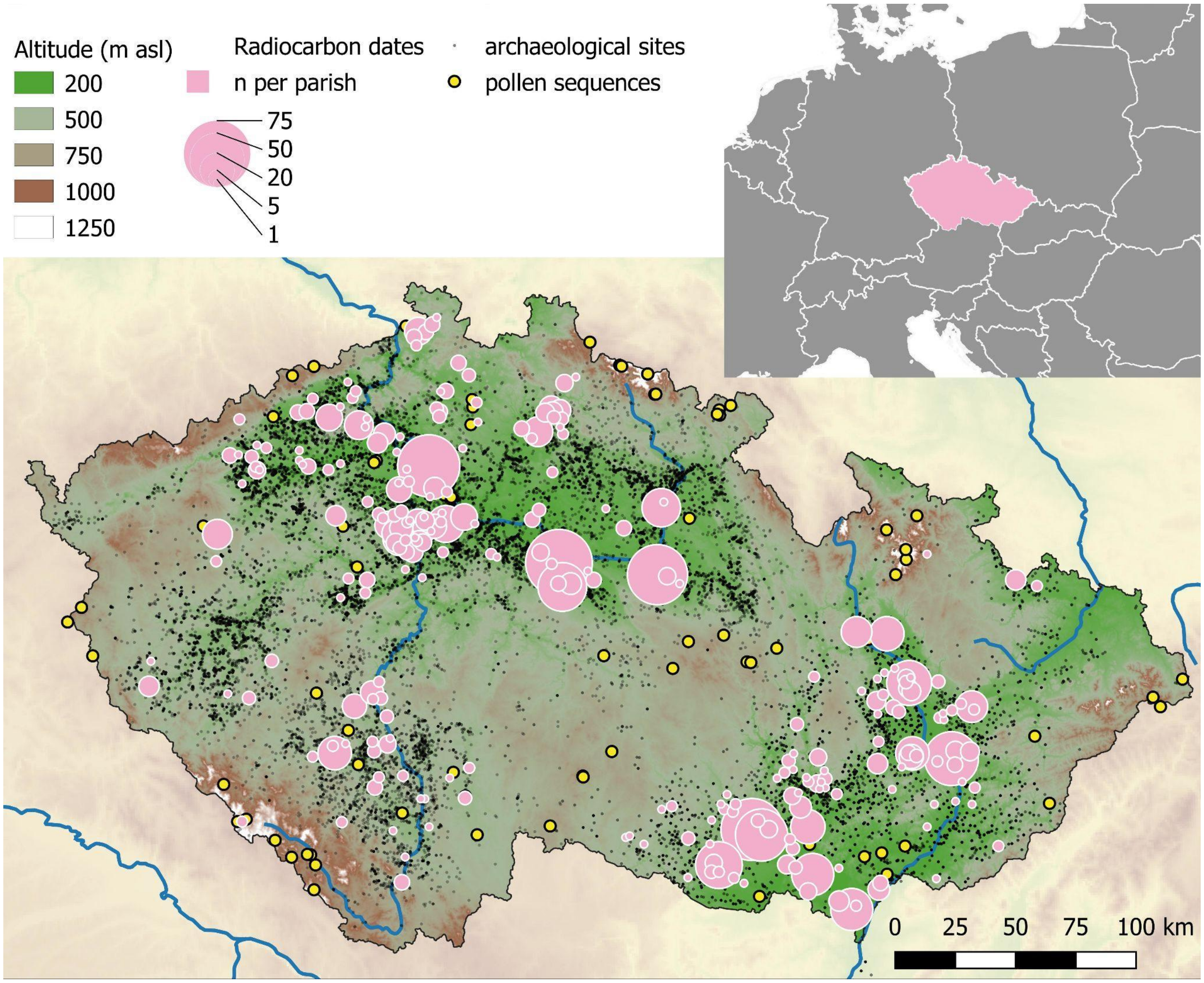


Figure 1. Spatial coverage of the Czech Republic by the archaeological and palaeoecological datasets used in the paper.

### *2.2. Archaeological radiocarbon dates and summed probability distributions*

Radiocarbon dates from archaeological contexts and SPDs are routinely used for relative estimates of human population, therefore we collected for this purpose a database covering the Holocene for the entire

Czech Republic (Tkáč and Kolář, 2021b). For this paper, we used mostly samples from short-lived organisms (humans, animals, non-woody plants). However, after exploring that the samples from long-lived organisms (e.g. wood samples or charcoal) do not introduce a significant bias into the SPDs, we used them as well.

When filtering data for suitability, we omitted radiocarbon dates without necessary information (BP date, standard deviation), dates originating in contaminated archaeological contexts or from contexts with unclear field situations, and stratigraphies already reported in the primary sources. Furthermore, we excluded sample duplicates and freshwater samples, owing to possible error caused by the reservoir effect. We included radiocarbon dates with unexpected dating when compared to the traditional typo-chronological dating according to primary sources. The contrast between absolute and relative dating is often caused by using non-revised chronologies of material culture without any kind of external evidence of their temporal position, therefore we used these radiocarbon dates as well, since, after all, they still date human activity. Altogether, 1520 radiocarbon dates from 340 archaeological sites entered the analyses.

The radiocarbon dataset was used for calculating SPDs. For calibration, summing the probability distribution, and binning, we used the functions *calibrate*, *spd,* and *binMed* from the *rcarbon* package in R (Crema and Bevan, 2021; R Core Team, 2021). From our previous analyses of the Czech radiocarbon dataset, we know that some sites and their phases were sampled more intensively. Therefore, we reduced this oversampling bias through binning. We aggregated the dates by site within 100-year bins. In case of using all dates (1520) from 340 sites, they were aggregated into 710 bins whose medians were visualised as barcodes (Figure 2: A). Because of the occurrence of artificial peaks at steep parts of the calibration curve (Weninger et al., 2015), we decided to use unnormalised sum distributions (for details, see Crema and Bevan, 2021). All dates were calibrated by the latest calibration curve IntCal20 (Reimer et al., 2020).

In the next step, we compared SPDs based on short-lived samples (bone, tooth, excrement, grain, nut shell, other plant material, seed, textile) and samples originating from woody plants (wood samples and charcoal). To estimate the influence of both sample categories on the SPD based on all radiocarbon dates, we run two correlation tests (Pearson's product moment correlation coefficient, function *cor.test* in R) between the SPDs based on all samples and short-lived samples, and all samples and wood samples.

Lastly, we compared the unnormalized SPD based on all radiocarbon dates with a theoretical null model of demographic change. This helped us to determine whether the fluctuations in SPD are statistically significant for demographic inferences. Due to the long-term perspective of more than four millennia we chose the exponential null model. Comparing the SPD with this theoretical model can be justified by a similar pattern of settlement growth during the prehistory observed by other authors in Bohemia (Demján and Dreslerová 2016) and by our demographic analysis based on archaeological sites (see below). We compared the SPD with the exponential null model only for periods with enough radiocarbon dates (6000-1500 BCE).

### *2.3. Archaeological site data and human activity model*

The archaeological dataset covering the whole Czech Republic originates in two large databases of archaeological sites and finds. The first database, currently managed by the Institute of Botany of the Czech Academy of Sciences, was created 2012–2016, revised recently, and collates all available records from the eastern part of the country (Kolář et al., 2016). The second database, covering representatively the western part of the country (Bohemia), was created over the last 30 years during long-term digitization efforts of the Institute of Archaeology of the Czech Academy of Sciences in Prague, and is currently managed as the Archaeological Map of Czech Republic (AMCR; Kuna et al., 2015). The AMCR is a living system, with data being supplemented daily; the dataset used for this study was harvested in August 2019 and contains data on fieldwork events reported up to this date.

Temporal coverage was set for the period between 10,000 BCE and 1000 CE and therefore covers most of the Holocene. Records without sufficient chronological accuracy (e.g., dated only to agricultural prehistory) were omitted from further analyses. As the structure of both databases is theoretically based on the ‘community area theory’ (Kuna and Dreslerová, 2007; Neustupný, 1991), the basic analytical unit was set for archaeological components. Archaeological components are defined by their function (e.g., settlement, hillfort, hoard), chronological assignment to a specific period, phase or archaeological culture, and spatially limited to an archaeological site or its specific part (as documented by any type of archaeological fieldwork – even repeatedly during particular fieldwork events; cf. Kuna et al., 2015). However, not all archaeological sites can be localised precisely, therefore for data collation purposes a basic spatial unit common for all archaeological components was set up at the level of the civil parish. Altogether 65,691 archaeological components entered the statistical and spatial analyses.

To estimate the human presence probability in the landscape at different times we partially followed previously elaborated procedures (Kolář et al., 2016). Firstly, we aggregated archaeological components to 2,552 regular geographic grid cells defined by geographic meridians and parallels (5 x 3 minutes, approx. 33.3 $km^2$).

In the next step, we randomly assigned the calendar year to each component within the temporal range of a specific period, phase, or archaeological culture (Tkáč and Kolář, 2021b), assuming a uniform probability of component dating within period limits. A grid cell was considered as occupied in a particular 500-year period if at least one component was assigned to the given period and grid cell. We repeated this procedure 1000 times and, finally, we calculated occupancy probability as the proportion of simulation runs where the grid cell was considered as occupied in a particular period. The 500-year period length was arbitrarily chosen, compromising between amount of generalisation, random noise (median uncertainty in component dating was 450 years), dimensionality of data with finer temporal resolution and comparability of archaeological and palynological proxies.

Lastly, we calculated the average occupancy probability of each grid cell over the entire study time-span and its temporal variability as the cumulative sum of absolute changes in occupancy probabilities between consecutive periods.

Further, we calculated the weighted sums of archaeological components in each period, categorised by the component type, using the proportions of the component's temporal range falling within the target 500-year periods as the weights.

To describe environmental conditions for each grid, we extracted minimum, median and maximum elevation as the main proxy for temperature gradient in this region from the DMR4G digital elevation model (State Administration of Land Surveying and Cadastre, www.cuzk.cz).

### *2.4 Regionalization*

To delimit regions with characteristic settlement history and demographic trends, we employed numerical classification methods. We applied two approaches for classification: spatially unconstrained agglomerative clustering and spatially constrained agglomerative clustering. Spatially unconstrained classification aggregates observations (grid cells) exclusively according to the similarity of their temporal patterns in occupancy probability, while the spatially constrained classification also considers their spatial relationships. In both cases, we used the *manhattan* distance dissimilarity matrix and Ward clustering criterion. Because of the very low levels of occupancy in the pre-Neolithic era, with reduced temporal variability and higher uncertainty in dating, we restricted the time-span used for classification from 6000 BCE to 1000 CE. For spatially unconstrained classification, we used the *hclust* function from the *stats* package in R 4.0.4 (R Core Team, 2021). For spatially constrained agglomerative clustering, we used a multivariate dissimilarity matrix based on the temporal occupancy probabilities estimated for regular grid cells using the *const.hclust* R package (Legendre and Guénard, 2019). Clusters were spatially constrained to aggregate only the neighbouring cells. Finally, we cut the resulting dendrogram into ten clusters.

To evaluate resulting classification and to explore relations between classes we tested the significance of clustering with permutational multivariate analysis of variance (PERMANOVA) using distance matrices with 999 permutations from *vegan* package (Oksanen et al. 2020). Hierarchy and dissimilarity of classes was visualised using dendrogram representation of classification tree with the use of *gplots* package (Warnes et al. 2020) and the class centroids and their separability was inspected through nonmetric multidimensional scaling (NMDS) on dissimilarity matrix in *vegan* package (Oksanen et al. 2020).

### *2.5. Pollen assemblages and vegetation reconstructions*

Human population is known to have a major impact on vegetation. We examined the relationship between the archaeological proxy of the human population (see Section 2.3) and the proxy for regional vegetation cover – the fossil pollen spectra. To characterise changes in vegetation in different regions, we compared average occupancy with pollen-based vegetation development. We extracted all unrestricted pollen sequences with reliable chronologies from the PALYCZ database (https://botany.natur.cuni.cz/palycz/, Kuneš et al., 2009) by intersection with the polygons of archaeological regions delimited by spatially constrained clustering in this study, and calculated mean proportions of pollen for selected taxa in the same 500-year time-blocks as were used to aggregate the archaeological data. Taxa selected for analysis represented the most common trees (*Pinus, Betula, Corylus, Picea, Quercus, Ulmus, Fraxinus, Tilia, Abies, Fagus, Carpinus*) and anthropogenic indicators (wild grasses, cerealia, *Secale, Plantago lanceolata*, Chenopodiaceae, *Artemisia*, Cichorioideae, *Polygonum aviculare, Centaurea cyanus* and *Urtica*). Firstly, to summarise patterns of vegetation development and to visualise similarity between mean pollen compositions in archaeological regions and time windows, we clustered them in 6 groups using hierarchical ward.D method in the function *hclust* on the dissimilarity matrix of SQchord distance from the package *analogue* (Simpson et al., 2021). Secondly, we measured how the vegetation changes in individual archaeological regions influence the overall pattern. For this purpose, we calculated total variance in all time layers using chord distance in the *adespatial* package (Dray et al., 2021). The *beta.div* function provides the total variance and the contributions of individual areas to the total variance, which were kept for the results. Finally, we tested the relation between spatial variability in the intensity of human occupancy in the regions and spatial variability in vegetation represented by the total variance of pollen spectra by Pearson correlation test.

## 3. Results

### *3.1. Summed probability distribution (SPD) of radiocarbon dates*

The SPD presented here is one of the first attempts to quantify the past human population in a long-term perspective through this proxy for the area of the Czech Republic. Right at the outset, it has to be said that the total number of available radiocarbon dates is rather low in comparison with other regions (e.g., United Kingdom, Ireland, Levant, and Greece; Bevan et al., 2017; Palmisano et al., 2021; Weiberg et al., 2019). Additional biases incorporated in this radiocarbon dataset are the distance of sampled sites to large cities with multiple archaeological research institutes (Prague, Brno, Olomouc) and specific long-term interest of archaeologists in particular sites (Tkáč and Kolář, 2021b). Due to these reasons, we did not analyse the SPDs from separate regions and kept the SPD for the Czech Republic in the most robust form possible.

We decided to use the unnormalized SPDs, which do not have the artificial peaks. When using the whole radiocarbon dataset, we observe the most significant increases in the SPD during the Neolithic, Eneolithic and Bronze Age (Figure 2: A). The same pattern is clearly visible also the density of barcodes visualising the bins. For exploring the effects of samples from short-lived organisms and samples of wood and charcoal, we created SPDs from these subsets too (Figure 2: B). The SPD based on short-lived samples has a very similar shape to the SPD curve based on all samples, as it is confirmed by Pearson correlation coefficient ($r=0.91$, $p<0.01$), whereas the wood/charcoal SPD differs significantly ($r=0.51$). The so-called old wood effect does not seem to have a significant effect on the probability densities, therefore we use the whole dataset for further analyses. Interestingly, both SPDs seem to be complementary in this long-term perspective, therefore the SPD during the Mesolithic is based mostly on wood/charcoal samples originating from hearths. Both of the SPDs are very similar during the Neolithic when cereal grains, bones of domestic animals and more frequent human burials became a standard part of archaeological evidence. The short-lived organisms contributed the most to the SPD during the periods of the Eneolithic and Early Bronze Age (4300-1500 BCE). The validity (and usability) of the current SPD based on both short-lived organisms and wood, after 1500 BCE is at least questionable due to a general lack of $^{14}C$ dates from that period.

As a last step, we compared the observed SPD with an exponential null model (Figure 3). The observed SPD shows several positive and negative deviations from the 95% confidence interval (global p=0.042). Negative deviation of the SPD can be observed during the second half of the 4$^{th}$ and the beginning of the 3$^{rd}$ millennium BCE (3352-2972 BCE). The demographic trends show significant positive departures from the null model during the Early Neolithic (5298-5279 BCE, 5265-5174 BCE, 5172 BCE, 4830-4676 BCE).

Interestingly, the radiocarbon proxy roughly matches the site-based proxy (Figure 4). The important difference is, of course, the temporal precision. The site-based human activity model works with time-blocks of 500 years; therefore, many details cannot be grasped. However, this match between the two demographic proxies is not general and works only between the Mesolithic and Early Bronze Age. Although subsequent periods have even more sites than the Early Bronze Age, the number of radiocarbon dates is significantly lower. Therefore, further analyses, especially the spatial clustering and comparison with pollen data, are based on more abundant site data.

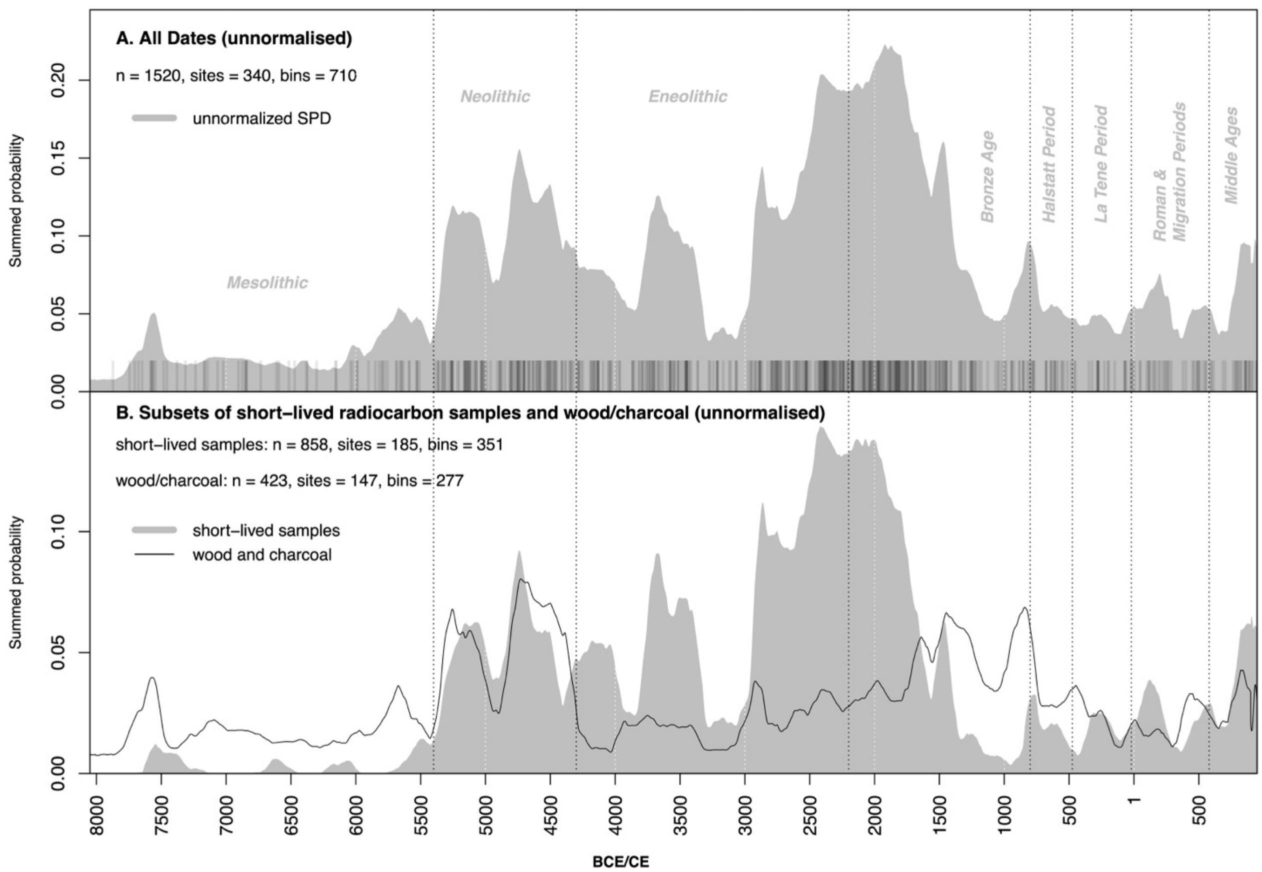


Figure 2. Patterns in archaeological radiocarbon dates: A. SPD of all dates (unnormalized) with barcodes showing the estimated median date for bins, B. SPDs (unnormalized) of subsets of short-lived radiocarbon samples and wood and charcoal.

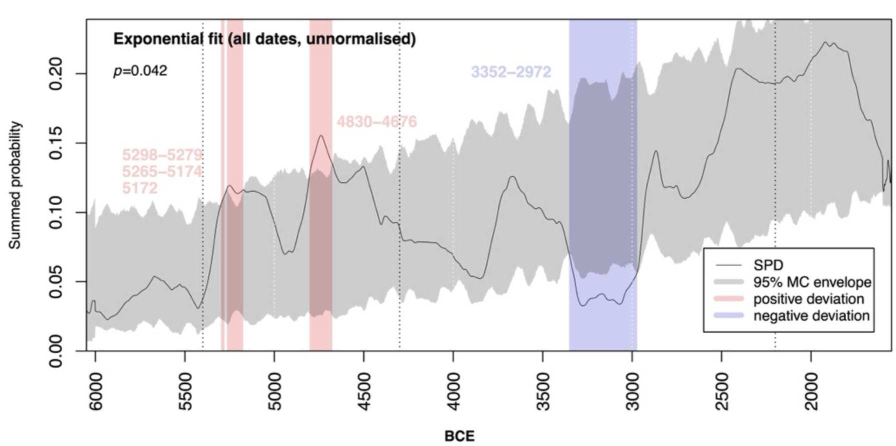


Figure 3. SPD (unnormalized) of all radiocarbon dates and exponential null model (95% confidence grey envelope).

### *3.2. Human activity model based on archaeological sites*

In total, 65,691 archaeological components were retrieved from the two databases. Further, we worked with time-blocs of 500 years, therefore the timeline for the analysis was set between 10,000 BCE and 1000 CE. The human activity model provides us with three parameters: the number of categorised archaeological components assigned to time-blocks in regularised spatial grid cells; occupancy probability for these spatial and temporal units; and the summed mean estimate of the spatial extent of human activity over the whole study area or regions.

Firstly, the human activity model provides us with categorised components whose dating was modelled according to the 500-year time-blocks (Figure 4). In the pre-Neolithic era (time-blocks before 5500 BCE), numbers of archaeological components per time unit are very low in the whole region and no significant temporal changes are observed. The start of the Neolithic – the period between 5500 and 5000 BCE – is coupled with a rapid increase in archaeological evidence, consisting mostly of settlements and single finds. This increase also continues during the subsequent time-block, but is followed by a rapid decrease in the available archaeological evidence after 4500 BCE. The model shows that the numbers of archaeological components between 4000 and 3000 BCE are at their lowest levels during the whole timespan under investigation. The period after 3000 BCE is characterised by an increase in the volume of archaeological evidence; moreover, the functional character changes too, and the archaeological evidence shows more burial sites. This trend continues even more strongly after 2500 BCE, resulting in a period between 1500 BCE and 1 CE (covering the Late and Final Bronze Age, Hallstatt and La Tène Periods) with the highest numbers of archaeological components, mostly categorised as settlements. The time-block 1–500 CE once more shows a rapid decrease in the amount of the available archaeological evidence, roughly very similar to the period 2500–2000 BCE. The last time-block (500–1000 CE) is again characterised by very abundant archaeological evidence.

Settlement and single finds without contextual information constitute most of the archaeological records for agricultural prehistory and the Early Mediaeval Period. Burial sites are relatively rare during the Neolithic and for most of the Eneolithic, and they become archaeologically visible just after 3000 BCE. From then onwards, they comprise a significant part of the archaeological evidence. Hoards seem to be mostly dated between 2500 and 500 BCE, covering the Bronze Age and several centuries before and after. All other functionally determined contexts (production and extraction, ritual, etc.) seem to be found and recognized by archaeologists only occasionally.

Secondly, the occupancy probability of the whole country, calculated based on the same dataset, shows similar temporal development (Figure 4, Figures S1 and S2 in Supplementary Materials). The area with archaeological evidence of human presence was very low during the Mesolithic (until 5500 BCE), then rapidly increased with the start of the Neolithic. The spatial expansion continued until 4500 BCE, and after that it was followed by a decrease lasting until 3000 BCE. Between 2500 and 1500 BCE, the occupied area was again approximately at the same levels as the Neolithic, only slightly lower. The largest area with archaeological evidence was registered during the three time-blocks covering the Late and Final Bronze Age, Hallstatt and La Tène Periods (1500 BCE–1 CE). This period was followed by a decrease in the occupied area (1–500 CE) and an increase again between 500 CE and 1000 CE.

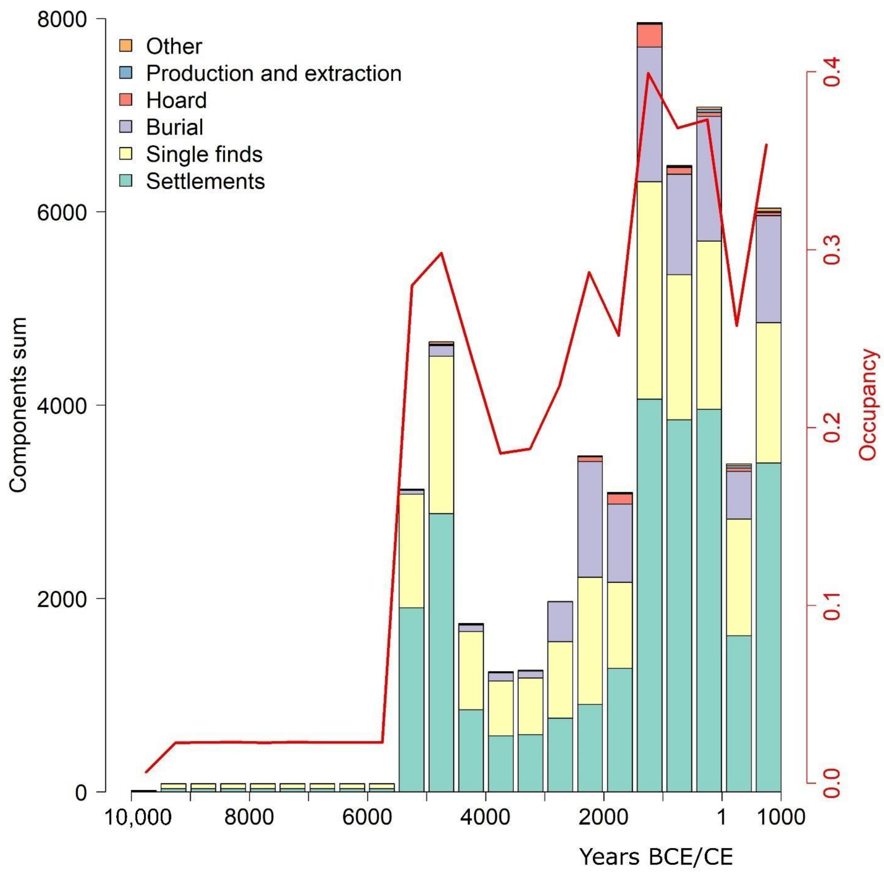


Figure 4. Temporal trends in archaeological evidence summarised over the whole study region: Bars represent the weighted sum of components belonging to a particular 500-year period (left axis) and the red line represents spatial occupancy calculated as an average fraction of occupied grid cells in a given period from the bootstrapped occupancy model (right axis).

### *3.2. Regionalization*

To explore regionally specific demographic trajectories, we clustered the quadrants according to the temporal development of occupancy. In both approaches, spatially constrained and unconstrained clustering, we decided *a priori* to cut the clustering hierarchy at the level which defines ten clusters. This number enables us to capture enough details and to describe and interpret the differences between clusters sufficiently. The detailed characteristics and descriptions of temporal developments of the spatially constrained clustering with ten classes (Figure 5) (PERMANOVA: $R2 = 0.72$; pseudo-$F = 719.82$; $p = 0.001$) is provided by Figure S3 and Table S1 in Supplementary materials. Our additional analysis shows a large overlap of centroids in ordination space for several classes implying similar temporal occupancy probability trajectory in these classes (Supplementary Figure S4). This was the case for regions 7, 8 and 9 (the peripheral regions in the east) and partially also for regions 3, 6 and 10 (lowland regions with relatively continuous settlement trajectories). The spatially constrained classification of regions provides us with larger segments of landscapes with similar demographic development for millennia, therefore we used these (more generalised) results for comparison with pollen sequences (see section 3.3. Pollen data).

For capturing a more detailed and nuanced picture of possible settlement histories, we also employed spatially unconstrained clustering with ten classes capturing more differences in temporal development of occupancy probability (PERMANOVA: $R2 = 0.87$; pseudo-$F = 1837.7$; $p = 0.001$), with classes clearly separated in ordination space (Suppl. Figure S6 and S7). Ten regions were chosen as the resulting classification was highly fragmented in space (Figure 6, Table S2 in Supplementary Materials).

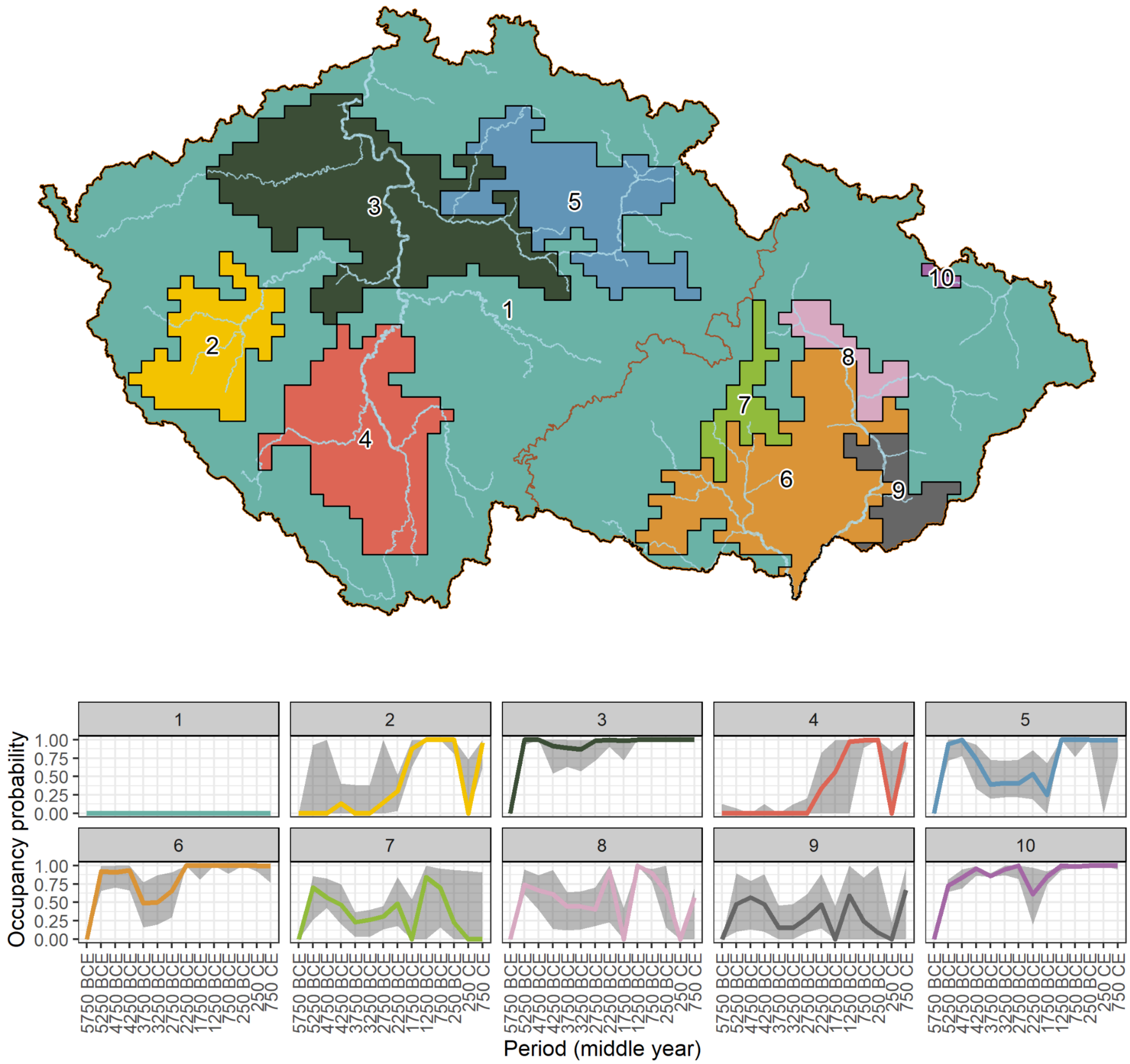


Figure 5. Ten coherent regions delimited by spatially constrained hierarchical classification according to the temporal development in the intensity of human activity between 6000 BCE and 1000 CE. Panels below the map show temporal trends in occupancy probability within each region: line represents median and shaded area represents interquartile range of occupancy probability values in quadrants belonging to particular region and time-period.

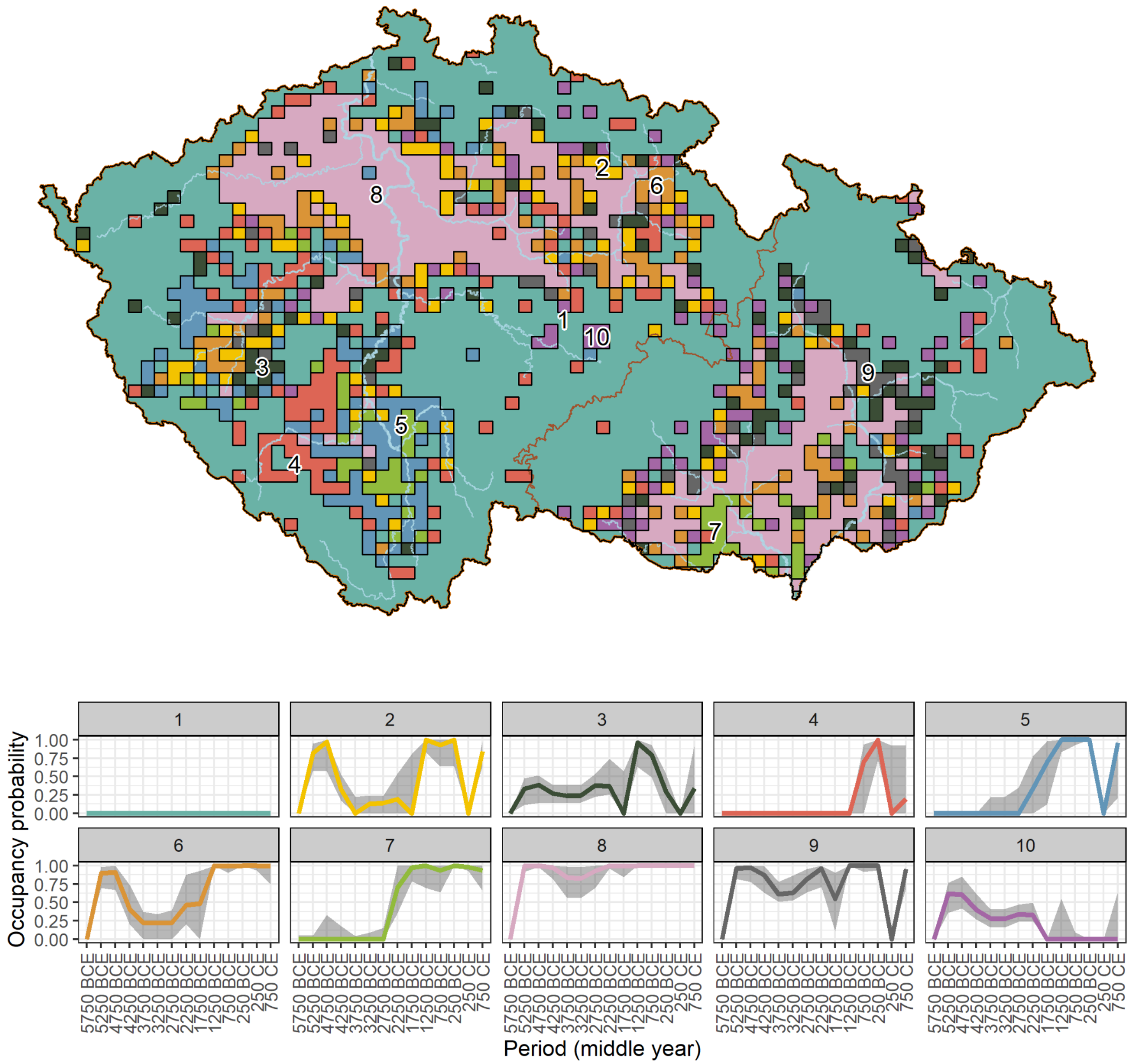


Figure 6. Ten regions delimited by spatially unconstrained hierarchical classification according to temporal development in the intensity of human activity between 6000 BCE and 1000 CE. Panels below the map show temporal trends in occupancy probability within each region: line represents median and shaded area represents interquartile range of occupancy probability values in quadrants belonging to particular region and time-period. Line colour and region number in the heading corresponds with the map representation. When the spatial constraint is not applied, then the core of the lowland area with high occupancy levels (region 8; pink) is classified as the same cluster, while the classification of quadrants on the transition between the 'core' settlement area and sparsely occupied area (green) is fragmented both spatially and qualitatively.

As a last procedure helping to understand population developments and characterise the stability of past settlement, we calculated and mapped the average occupancy probability over the whole study period and settlement stability as the sum of changes in occupancy probability between consecutive 500-year periods – i.e., long-term colonisation and abandonment processes (Figure S9). On the map of average occupancy probability, we can observe several areas inhabited nearly continuously – mainly in central and north-west Bohemia, east Bohemia, and regions in south and central Moravia. Interestingly, the area continuously inhabited is more fragmented in Moravia and seems to be more spatially continuous in Bohemia (Figure S9). The map summarising changes in occupancy probability over the period of interest shows several situations (Figure S9): (i) no changes are visible in areas without archaeological evidence of human activity (typically montane and highland areas on the borders and between Bohemia and Moravia, (ii) quadrants with low changes logically overlap with the areas of mostly continuous settlement, (iii) high changes in occupancy are visible at the peripheries of continuously settled regions and in regions colonised hundreds or thousands of years after the start of the Neolithic.

To sum up these results, we classified the area using arbitrary thresholds for average occupancy and its temporal stability, and visualised the resulting map with five categories reflecting current archaeological knowledge on human settlement (Figure 7): (i) continuous settlement (settlement expected in more than 75% of periods), (ii) stable periphery (settlement expected in 25% to 75% of time-blocks and a max. of four colonisation/abandonment events), (iii) pulsing periphery (settlement expected in 25% to 75% of time-blocks and more than four colonisation/abandonment events), (iv) minimal settlement activity (for areas with less than 25% occupied time-blocks) and (v) zero evidence of settlement. We can see that 'continuous settlement activity' during prehistory and early history is registered in a limited number of quadrants. Moreover, as previous analyses indicate, these cores of continuous past settlement activity are not present in all regions: southern and western Bohemia have only a few areas with archaeological evidence of continuous settlement. Settlement in 'stable peripheries' shows indications of settlement stability;

however, human settlement started there later than the Neolithic (typically Early Bronze Age). Additionally, these regions do not show evidence of multiple or long-term abandonment processes. These processes are characteristic for regions defined in our results as a 'pulsing periphery', which show patterns of several expansions and abandonment.

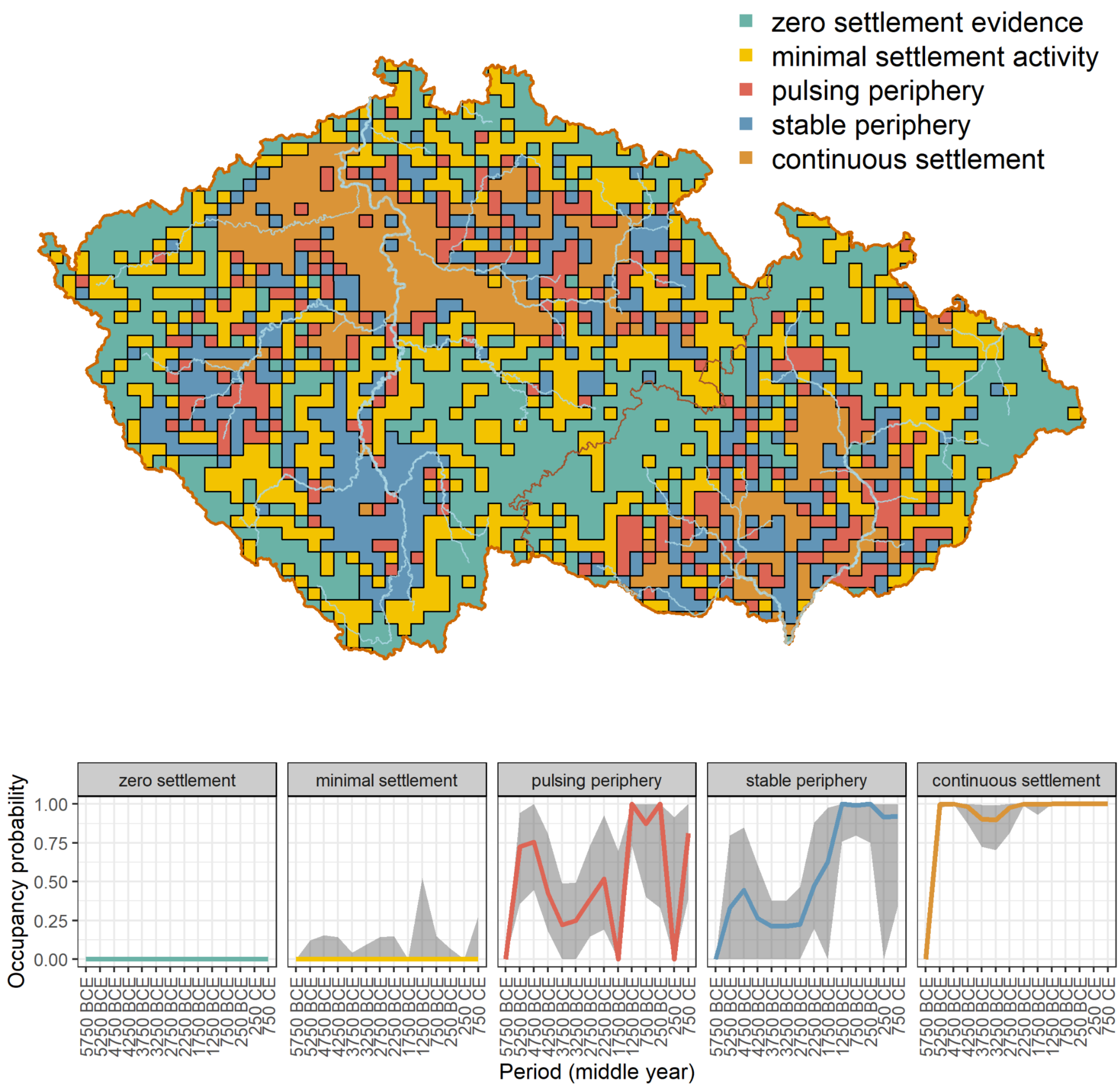


Figure 7. Categorization of regions according to the continuity of population developments and settlement stability. Panels below the map show temporal trends in occupancy probability within each region: line represents median and shaded area represents interquartile range of occupancy probability

values in quadrants belonging to particular region and time-period. Line colour corresponds with the map representation.

### *3.3. Pollen data*

For exploring whether the observed demographic trends correspond with vegetation changes, we selected five regions (regions 3, 4, 6, 8 and 1 at Figure 5), defined through spatially constrained clustering, which have distinct demographic trajectories and abundant palaeoecological data.

We found 94 pollen sequences; however, 66 of them fall in the sparsely occupied (mostly highland) area (region 1, Table S3). Pollen indication in the four densely settled archaeological regions (central and north-west Bohemia - region 3, south Bohemia - region 4, south Moravia - region 6, and central Moravia - region 8) is based on only a few natural archives. Nevertheless, the amount of available pollen sequences is sufficient. Our analyses distinguished six vegetation clusters (Figure 8: d and e). Clusters 3 and 5 appear in the Early and Middle Holocene in all regions studied; both are dominated by *Pinus* (>60%) with a higher abundance of wild grasses (10%). Cluster 3 contains *Corylus, Ulmus* and *Quercus*, whereas cluster 5 contains *Betula* (Figure S10 and S11). The rest of the clusters appear during the Middle and Late Holocene. Cluster 2 has a mixture of *Pinus* and *Picea*, whereas cluster 1 is dominated by *Picea, Fagus* and *Abies*. Clusters 4 and 6 show higher signals of human impact (cereals 1%, *Plantago lanceolata* 5%). Cluster 6 is characterised by a high abundance of *Tilia, Carpinus, Fraxinus* and a low abundance of wild grasses (<5%). Cluster 4 shows maxima of *Artemisia*, Chenopodiaceae and wild grasses (15%).

According to the preliminary analysis, the total variance of pollen data was influenced by the sparsely occupied area, especially from 7000 BCE when *Picea* increases and *Pinus-Corylus* forest (cluster 3) changes to *Pinus-Picea* forest (cluster 2, Figure 8: d). Since we focus on the impact of population fluctuations on vegetation, we excluded the sparsely occupied area from the further calculation of total variance. The total variance of pollen within the four archaeological regions rises from 4500 to 3500 BCE. This is given by the high contribution of the pollen archives located in central and north-west Bohemia to the total variance of pollen (Figure 8: c). This is the first area where vegetation changes from *Pinus-Picea* forest (cluster 2) to a landscape covered with more anthropogenic vegetation (cluster 4; see the high percentage of anthropogenic indicators). However, with regards to the two main groups of the most different clusters, the vegetation change from *Pinus-Corylus* (cluster 3) and *Pinus-Betula* (cluster 5) to all other clusters occurs between 5000 and 3000 BCE, depending on the region. Both warm lowland areas – central and north-west Bohemia and south Moravia – develop into anthropogenic vegetation (cluster 4). Central Moravia develops into a hardwood riverine forest (*Caprinus-Quercus-Tilia*; cluster 6) given by the location of the sites, and south Bohemia oscillates between *Pinus-Picea* forest (cluster 2) and montane forest (*Picea-Fagus-Abies*; cluster 1). Even though the increase in pollen variance has a delay of 1000–1500 years after the increase of variance of occupancy probability, both variances are significantly and positively correlated considering the Holocene as a whole. If we include time windows only from agricultural prehistory, the correlation becomes negative.

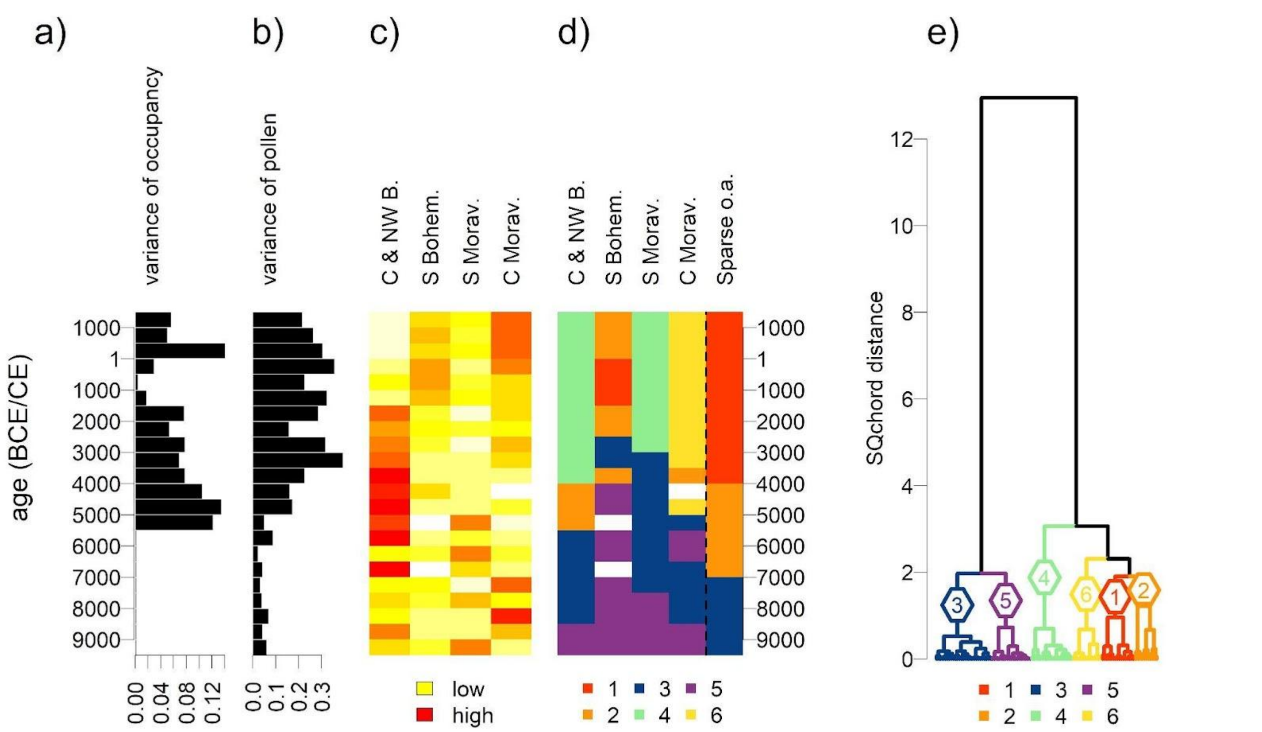

Figure 8. Comparison of human and vegetation development. a) variance of occupancy b) total variance of pollen c) contributions of individual areas to the total variance of pollen and d) vegetation groups based on pollen clustering, e) dendrogram of pollen clustering.

## 4. Discussion

In the following section, we interpret our results in a comprehensive way, i.e., we put the outcomes of our analyses into social, technological, economic and environmental contexts in a long-term perspective in the wider region of Central Europe. Subsequently, we utilise the archaeological results and discuss their significance for the study of human-vegetation interactions. The last section is more reflective and discusses the usability of large archaeological datasets, multi-proxy approaches in palaeodemography and some future directions.

### *4.1. The Mesolithic and transition to the Neolithic*

The beginning of the Holocene (ca. 9700 BCE) meant significant environmental changes, including rapid warming and long-term forest succession (Kuneš and Abraham, 2017). From previous research we know that the local hunters and gatherers used seasonally available resources in very diverse landscapes: their sites have been registered in lowlands, lakes and marshy landscapes, abris, caves, and mountains in southern, eastern and northern Bohemia (Figure S1; Kapustka et al., 2020; Ptáková et al., 2021). Both of our demographic proxies provide us with low values for the human population (Figures 2 and 4). In the case of the human activity model based on sites, the value is constant throughout the entire Mesolithic. This is caused by the low temporal accuracy of components usually being set at the level of the period as a whole. There were no other options, as most of the sites are known only as surface scatters of microlithic artefacts. This leads to unclarity in the absolute dating of hunting and gathering communities. However, we also know that the European foraging populations were probably relatively stable, i.e., without significant growths or declines over long periods (Downey et al., 2014; cf. Zahid et al., 2016).

Transition to an agro-pastoral economy was not sudden, indeed, it took a long time. Such economic and social overlaps or delayed agro-pastoral transitions have been registered in peripheral regions such as the Bohemian Paradise or southern Bohemia (Ptáková et al., 2021, 2020) that have higher altitudes, a colder regional climate, or less favourable soils. Here, the yields given by Early Neolithic farming systems could be less predictable, meaning that farmers may have relied more on foraging and actively establishing closer contact with hunters and gatherers, a strategy that persisted for several centuries (cf. Galeta and Bruzek, 2009; Nikitin et al., 2019; Vondrovský et al. 2018).

Farming and animal herding occurred in most of Czech territory during the time-block 5500–5000 BCE and is connected to the spread of the Linearbandkeramik (LBK), which has its earliest radiocarbon dates around 5400 BCE. The start of the Neolithic meant a significant transformation of lifestyle. The first farmers within the territory built longhouses (Květina and Hrnčíř, 2013; Vondrovský, 2018), intensively extracted greenschist for adze production (Prostředník et al., 2005; Ramminger, 2009; Šída, 2007), buried their dead more regularly at cemeteries (Masclans Latorre et al., 2020; Podborský, 2002; Šmíd, 2012), produced ceramic vessels for cooking and storage, and dug wells (Vostrovská et al., 2021, 2020). The combination of economic, technological, and social transformations, intertwined with immigration (Hofmanová et al., 2016), led to a significant increase in population numbers and density. This is visible in all lowland regions and is in stark contrast to the previous time-block (Figure S1). During these first centuries of agro-pastoral economies, the cores of prehistoric settlement with continuous settlement activity (Figure 7) were established.

The period after 5000 BCE provides us with evidence for several demographic events. The occupied area was only slightly larger than in the previous time-block (Figure 4), but the number of archaeological components (especially settlements) is larger. This can be interpreted in two ways. Firstly, in the case of settlements being contemporaneous, their density – and therefore also the population density – became higher. Secondly, if those settlements were not contemporaneous, this pattern could suggest higher settlement mobility. Thus one community could be traced in the archaeological evidence through several settlement sites and by multiple components.

The radiocarbon proxy gives us more detailed insight into the population dynamics during the Neolithic (Figures 2 and 3). Between the phases of demographic growth we can observe a period when the local farming populations did not rise (around 5000 BCE). From a cultural point of view, this is the moment when the pan-European LBK transformed into more regionalized cultural groups. In the case of the Czech Republic, we see the transition process into Stichbandkeramik Culture. Although we have evidence for the continuity of Neolithic settlement at several sites (e.g. Vondrovský et al., 2016; for Saxony, see Link, 2015), there was a demographic decrease at the end of the LBK in other European regions, which is related to diverse scenarios such as climate change (Gronenborn et al., 2014; Schmidt et al., 2004) and increased social inequality and tensions, occasionally resulting in violent acts (Furholt et al., 2020; Meyer et al., 2014; Müller-Scheeßel et al., 2021; Shennan, 2018; Zeeb-Lanz, 2014). The Neolithic population recovered and increased after 4830 BCE, and later we observe a similar population level in the area of interest. At this time, the partial reset of Neolithic society is connected to the rondel builders of the Stichbandkeramik and Lengyel Cultures (Řídký et al., 2019). However, even this phase of high population levels did not last for long.

### *4.2. The Eneolithic and transition to the Early Bronze Age*

The transition from the Neolithic to the Eneolithic, specifically the period after 4500 BCE, is characterised by a significant demographic decrease. Moreover, this situation continued until ca. 3000 BCE. The low population numbers, observed in the SPD (Figure 2) seem to be interrupted by a short rise around 3600 BCE, which falls within the temporal range of the Funnel Beaker Culture (Trichterbecher Culture, TRB). Recent archaeogenetic research has identified an immigration event from modern Saxony-Anhalt into Bohemia (Papac et al., 2021). However, it seems that this event was followed between 3500 and 3000 BCE

(3352-2972 BCE; Figure 3) by the lowest population numbers in the area of interest at any point in prehistory. While the Neolithic populations did not significantly fluctuate everywhere, this drop in population following several centuries of successful agro-pastoral subsistence strategy and demographic growth or stability has been registered in many regions in Europe and south-west Asia (e.g., Hinz et al., 2012; Müller, 2013; Palmisano et al., 2021; Timpson et al., 2014; Torfing, 2015; Weiberg et al., 2019; Weninger and Harper, 2015; Whitehouse et al., 2014). So far, there is no direct evidence for large-scale pandemics in Central Europe for the period (Fuchs et al., 2019), therefore the cause for the population decrease must lie elsewhere. The population dynamics is closely intertwined with subsistence strategies and climate fluctuations (Bevan et al., 2017), and it seems that the then populations in the Czech Republic modified their lives similarly to adaptive changes made in other regions. Zooarchaeological assemblages point to the increased importance of hunting (Kyselý, 2012). At the same time, the Eneolithic populations intentionally started barley cultivation (Dreslerová and Kočár, 2013) and switched to extensive farming practices, probably utilising the large-scale burning of woodland, leading to more pastures and more secure yields (Kolář et al., 2018).

The 4th millennium BCE is a time when animal traction for ards and carts was used for the first time in European prehistory; from ca. 4000 BCE, the local Lengyel communities started to produce copper artefacts; from the TRB onwards, new architectural forms – hillforts and burial mounds – were built. All these innovations can be very closely related to the rise of social inequality (Ebersbach, 2002; Bogaard et al., 2019; Halstead, 2014; Kolář et al., 2018; Mischka, 2014). The differentiation of agricultural work through the possession of an ard changed land ownership patterns, which was signified by large monuments. Such changes could indicate a period of social tension similar to the one just after 5000 BCE.

The Eneolithic population started to recover after 3000 BCE. This population increase continued even more strongly after 2500 BCE, when average occupancy reached levels comparable to the onset of the Neolithic. Interestingly, this is evidenced by a lower number of components, which indicates that the population was more dispersed over space. This is confirmed by the fact that we have observed more intense colonisation processes in the peripheral regions of southern and western Bohemia (stable and pulsing peripheries, Figure 7). SPD (Figure 2) confirms an analogous population increase during the 3rd millennium BCE, showing an increase around 2900 BCE at the time of the emergence of Corded Ware (CW), and then after 2600 BCE with the Bell Beaker (BB) and Únětice Culture communities. We know that this millennium was characterised by a higher proportion of highly mobile people with steppe-related ancestry (Allentoft et al., 2015) whose lineages transformed the burial rite into (regular) single burial inhumations (Furholt, 2019). In Bohemia, these genetic shifts were related to several social changes, including what were probably strict mating rules during the CW and BB, and significant population turnover during the subsequent Early Bronze Age (Papac et al., 2021).

### *4. 3. From the Bronze Age to the Early Middle Ages*

After 2000 BCE, the population continued to moderately increase. More interesting are the subsequent periods between 1500 BCE and 1 CE, which seem to be the time when population numbers rose higher than at any stage during the rest of Czech prehistory. According to the site-based proxy (Figure 4), the population from 1500 BCE onwards was stable and not fluctuating as strongly as before. From the literature, we know that the end of the Early Bronze Age is connected with population decline, and that from the Middle Bronze Age (ca. 1650–-1300 BCE) we register a considerably lower number of settlements in the Czech Republic and Central Europe generally (Jiráň et al., 2013; Kneisel, 2012; Kneisel et al., 2019; Parma, 2015). In contrast to the human activity model, our SPD reflects this population decline; however, this is certainly biased by the lack of radiocarbon-dated samples from the Middle Bronze Age onwards. This population decline – registered in the study of Parma (2015) – is masked in our results by the temporal resolution (500 years) and overlap with two time-blocks.

During the Bronze Age, humans not only densely settled the lowland areas (Figure 5 and 6, S5 and S8), but there is clear evidence of expansion to the peripheries and highlands as well (Dreslerová et al., 2020). In the case of southern Bohemia, where a dense and continuous settlement started at the beginning of Bronze Age, this expansion process was probably closely related to the Alpine Foreland (Šálková et al., 2019). Further development of settlement and regional population increase after 1500 BCE also coincided with the relocation of extracted copper ore sources, connected to continental exchange networks, from the Slovakian Carpathians to the Eastern Alps and Italy (Nørgaard et al., 2021)**.** The colonisation of south Bohemia gradually continued and culminated during the La Tène Period, when this region became an important extraction area for gold (Dreslerová and Demján, 2015; Waldhauser and Fröhlich, 2007)**.**

Feeding the larger populations was possible through a set of agricultural innovations which were part of the Bronze Age 'third food revolution' (Kneisel et al., 2015). Barley (*Hordeum vulgare*), which gives more secure yields, became more important from the Early Bronze Age (Dreslerová and Kočár, 2013). Important for sustaining the larger populations was most likely the introduction of broomcorn millet (*Panicum miliaceum L.*) to Central Europe shortly after 1500 BCE (Filipović et al., 2020). This resilient and fast-growing crop, enabling a second yield in combination with winter cereals, allowed for intense colonisation of agriculturally less favourable areas at the peripheries (Šálková et al., 2019). Subsequent Iron Age communities already had at their disposal 13 different crops and several technological innovations (iron ploughshare, scythe) that played a significant role in ensuring secure food availability for dense population in both lowland and highland regions (Dreslerová et al., 2020).

The social transformation related to the transition from the La Tène to the Roman Period involved significant depopulation. It seems that human communities abandoned the peripheries and concentrated within the most fertile lowlands of central Bohemia and southern Moravia. However, population dynamics during the first five centuries CE were probably much more complex, as we need to take into account not only the local inhabitants but also considerable numbers of Roman military units beyond the Roman *Limes*

(Vlach, 2018a, 2018b). During the last time-block of interest (500–1000 CE), the population increased again and re-populated previously abandoned regions in southern and western Bohemia and the peripheral zones surrounding the settlement cores. Recent finds attest to partial population continuity between the last two time-blocks under investigation (Macháček et al., 2021). Within the period 500–1000 CE two political formations emerged in the investigated region – Great Moravia and the Přemyslid Principality, later Kingdom of Bohemia (Boháčová, 2011; Macháček, 2012, 2010).

### *4.4. Population dynamics and vegetation changes*

The fluctuating intensity of human activity caused by demographic changes was reflected in vegetation. The variance of pollen and occupancy probability are correlated positively when measured throughout the Holocene. This is especially due to the steep increase in both proxies after the Mesolithic/Neolithic transition (Figure 8). This result would appear to show a positive match between archaeological periods and changes in alpha diversity (Roleček et al., 2021; Šizling et al., 2016) were it not for the fact that the rise of pollen variance has an approx. 1000–1500-year delay after the increase in archaeological variance. This produces a negative, though insignificant, correlation between both variables when only agricultural prehistory is considered.

The low population density of Mesolithic hunters and gatherers did not have a significant large-scale impact on land cover. However, they were able to bring about small-scale disturbances in the *Pinus* dominated forest, manifested through the spread of *Corylus avellana* (Kuneš et al., 2008). Vegetation at the Mesolithic/Neolithic transition shows compositional homogeneity across the four lowland areas (Figure 8). Relatively weak human impact at the beginning of agricultural prehistory diversified vegetation by disturbance regimes in the different environments. The spontaneous spread of natural and anthropogenic species in different landscapes produced quite divergent successional trajectories which are increasingly evident in the pollen after 5000 BCE. Interestingly, the highest variance in pollen occurred during the population decline in the 4th millennium BCE, when human societies adapted to climate fluctuations. The highest variance in pollen is probably caused by several factors. Firstly, due to the population decline, many areas had been abandoned by humans and succession could start there. The surroundings of human settlements were dominated by *Quercus* throughout agricultural prehistory; however, the anthropogenic environment in the Neolithic also hosted the first populations of late Holocene trees (*Abies, Carpinus* and *Fagus*; Novák et al. 2021), thus abandonments provided a unique ecological opportunity for their spread. Therefore, vegetation of the 4th millennium BCE was probably more diverse, including inhabited and regularly managed landscapes, abandoned landscapes in diverse succession stages and with apparent signs of land use legacies, and landscapes with no or only minimum (including episodic) human impact. Secondly, this period is characterised by a set of agricultural and technological innovations which probably have an impact on land cover. Vegetation with a strong anthropogenic impact signalling farming (*Cerealia*) and animal herding (*Plantago lanceolata*) occurred after 4000 BCE, resp. 3000 BCE, primarily in the two settlement cores with long-term demographic continuity (central and north-west Bohemia, south Moravia, i.e. regions 3 and 6 at Figure 5). This is supported by the fact that pollen profiles from the continuously populated central and north-west Bohemia contributed most to the total variance of pollen. In our study we identified a vegetation change (transformation into a '*well-tended garden*') similar to the study of Šizling et al. (2016). However, our unique combination of archaeological and pollen data enabled us to locate these changes within densely and continuously populated areas of prehistoric Central Europe.

We also identified different trajectories of human-vegetation interactions in different regions. First, the warmest lowlands of south Moravia and central and north-west Bohemia (regions 3 and 6 at Figure 5), with continuous and dense human settlement, show land cover with indications of fields, open pastures, and trampled areas with ruderals. Second, the area in central Moravia was also occupied by prehistoric farmers, but apart from evidence of fields, it looks like there was more involvement with woodland management due to the area's location within riverine forest. In contrast to these regions, the anthropogenic impact on land cover in south Bohemia, located in slightly poorer soils and at a somewhat higher elevation, has a different character. The most important impact of local farmers and herders was on forest species composition and the fairly restricted openness of the landscape for agro-pastoral land use. This is visible from the Bronze Age onwards, when both the local population and the contribution of this region to the total variance of pollen increased (Figure 8: c). Therefore, we can hypothesise about a smaller population density, smaller fields, and woodland pastures of the communities securing the copper exchange networks between the Alps and Central Bohemia. These differences in vegetation development between the Czech lowlands and uplands have already been identified and discussed (Roleček et al., 2021), but without the support of archaeological data. Similar regional aspects in human-vegetation interaction have been recently identified in the Czech archaeo-anthracological assemblages as well (Novák et al., 2021).

During the first millennia of the agricultural prehistory, the effectiveness of agro-pastoral land use was weaker, thus successional trajectories given by anthropogenic disturbance could integrate anthropogenic (winter cereals with respective weeds) and natural set of taxa, given by local environmental conditions and we observe rising alpha- and beta- diversity of pollen. After 1 CE, archaeobotanical (Pokorná et al., 2018) and pollen alpha diversity (Roleček et al., 2021) steeply increase in all areas with different settlement history and at the same time, we observe a decline in both variance in occupancy probability and variance of pollen (Figure 8: a, b). This points to increased homogenization of the land cover, caused by the spread of human settlement with similar land use and resulting species pool across the different regions, which might overshadow the natural ecological response and species pools given by local environmental conditions. This continued until the Early Mediaeval Period, a time that was previously proposed as the historical baseline for present naturalness in the Czech Republic (Abraham et al., 2016).

### *4.5. Validity and usability of archaeological SPDs and the site-based proxy for prehistoric population estimates*

Nowadays, SPDs are commonly used for estimating populations in the past; however, our study has clearly shown that this proxy cannot be utilised for all periods and regions. The number of radiocarbon dates from the Czech Republic is strongly biased towards the Neolithic, Eneolithic, and Early Bronze Age. The most up-to-date radiocarbon dataset shows that periods after the Early Bronze Age are not routinely dated by $^{14}$C: archaeologists instead tend to rely mostly on typo-chronological schemes of material culture, with only little external evidence for its precise position in time. This is clear from the comparison of the site-based proxy and the SPD. Whereas the site-based proxy shows the highest amount of archaeological components after 1500 BCE, the number of $^{14}$C samples (and therefore the values of SPD) is very low. Additionally, the radiocarbon proxy is biased towards internationally recognized units of archaeological classification which also have relatively rich burial evidence in the Czech Republic, such as LBK, TRB, CW, BB and Únětice Cultures.

The site-based human activity model is not accurate enough for fine-grained reconstructions of population dynamics. Previously, we showed that the average temporal accuracy of an archaeological component in one of our datasets is around 400–500 years (Kolář et al., 2016) and therefore we used 500-year time-blocks. For several reasons, this low temporal accuracy does not disqualify the site-based proxy from usage. Its most important advantage is the spatial and temporal coverage it provides – all archaeological sites from all periods within the whole country are covered. Due to heritage management laws, all archaeological sites under threat should be excavated, documented, and registered in the digital archives, therefore any research interest bias towards a period is much lower than in the case of radiocarbon dating.

Our spatially constrained approach to defining areas with different demographic trajectories proved to be crucial for identification of the demographic events on a regional spatial scale. These regions can be then relatively easily compared with vegetation dynamics inferred from the available palaeoarchives located directly in these regions. Nevertheless, the regional spatial scale in palaeodemography does not always sufficiently capture the details in population dynamics. The human activity model used in our spatially unconstrained demographic regionalization, and the subsequent categorization according to the population and settlement stability, proved to be useful for capturing the local colonisation-and-abandonment processes, which can be subtle, episodic, short-term, or even unsuccessful. We identified several phases in the spread of farming, and it is clear that the transition from foraging to an agro-pastoral lifestyle even in Central Europe was not unilinear. Outside of the continuous settlement areas, humans tried to inhabit additional zones. In Moravia, Neolithic and Eneolithic farmers subtly occupied the peripheral zones surrounding the core and abandoned these areas with the start of the Bronze Age. Interestingly, at the same time, colonisation of the previously uninhabited inner peripheries in southern Moravia started. Whether these processes of abandonment and colonisation were in close relation is a matter of future research. Southern Bohemia represents another story – a region spatially detached from the core of the continuous settlement in the Elbe lowlands. A story in which sporadic farming communities shared the same landscapes with hunters and gatherers up to the beginning of the Bronze Age, when the farming economy prevailed in the region, and later allowed for further expansion to the highlands.

On the other hand, site-based proxies are also problematic. The size of the dataset and its apparent homogeneity do not in themselves guarantee the absence of biases, which may be based on the behaviour of past populations, but are also influenced by the structure of modern settlement, land use, and local research practices. These biases can be partially removed by a high degree of generalisation, but when trying to understand palaeodemographic processes, these can be key factors that greatly influence interpretative possibilities, especially with regards to population density (cf. Demján and Dreslerová, 2016;

Kuna, 2015). The spatial distribution of archaeological sites can be distorted by the uneven distribution of archaeological research institutes, museums, heritage management offices, and universities. Additional bias could be caused by recent population dynamics. In the case of the Czech Republic, we can think of the expulsion of the German-speaking population after WWII leading to the abandonment of peripheral regions, large-scale reforestation, and a decline locally in the number of educated archaeologists. The site-based proxy also relies on the possibility to distinguish the material culture and the professional training of the respective excavating archaeologist. Some periods or archaeological classification units have a very specific, and therefore easily recognizable material culture, while others are really difficult to determine without additional scientific methods. Moreover, results can be influenced by the way fieldwork results are recorded in databases; the relationship between the quality and quantity of evidence, and demography still needs to be explored.

Our study shows that the combination of different archaeological proxies for population does reveal important details. By comparing average occupancy with the number of components we identified several phases of changes in settlement organisation or human mobility. Average occupancy is similar in the time-blocks 5500–4500 BCE and 2500–1500 BCE, but the character and sum of the sites significantly differ. Thus the first millennium of the Neolithic (5500-4500 BCE) can possibly be characterised by a higher density of human communities, whereas the end of the Eneolithic and the Early Bronze Age (2500-1500 BCE) by dispersal and lower density. Nevertheless, this phase was followed by a stark multiplication of settlement evidence, whereas average occupancy increased by only a third, and therefore settlements became denser again. The question is whether these changes in settlement organisation were related to changes in land use. Did human communities need to intensify their food production? Did they need to expand to previously less occupied areas? Or is this only a secondary effect of the generally good archaeological visibility of Late Bronze Age settlement? Interestingly, the phase of higher settlement density correlates with the introduction of millet into farming. Nevertheless, correlation is not causation, and we need to explore more about the relationship between spatial expansion, demography, land use, and the character of archaeological evidence.

Settlement density can also be significantly influenced by the mobility of human communities. Therefore, in situations when we mostly have only typo-chronologically dated settlements within a region, we cannot determine whether the archaeological evidence left behind comes from the settlement activity of a lower number of more mobile communities or a higher number of more sedentary ones. In contrast to wetland archaeology (Hofmann et al., 2016), the usual dryland archaeology provides us with only less precise information on settlement duration.

Another problem stems from the unknown number of inhabitants within a settlement or community. There are some estimates based on ethnographic observations or economic models (Schmidt et al., 2021), but absolute demographic estimates for a period without any written records is still a major challenge for archaeology (French et al., 2021). Be that as it may, radiocarbon dates-based methods do provide us with slightly more detailed insight into population numbers. This derives from the fact that one sample usually originates from only one organism (in most cases humans). The combination of different proxies potentially provides us with a more detailed perspective, and we can better evaluate whether or not a specific demographic proxy is in fact useful (cf. Carleton and Groucutt, 2021).

## 5. Conclusions

Through complex quantitative analyses of archaeological sites and radiocarbon dates, we identified four major demographic events and processes between 10,000 BCE and 1000 CE – the beginning of the Neolithic at 5400 BCE, the Eneolithic/Bronze Age transition in the 3rd millennium BCE, Bronze Age expansion after 1500 BCE, and mediaeval expansion after 500 CE. Comparison of two archaeological demographic proxies showed us their advantages and limitations; however, the relationship between absolute population numbers and the surviving archaeological evidence still needs more research. We identified two settlement cores in the lowlands, with additional inner and outer peripheries with different demographic histories. Our study clearly shows that prehistoric and early historic population dynamics were not a homogenised process, rather they were regionalized according to the local environmental and social conditions. The comparison of archaeological results with pollen-based vegetation proxies also showed regional aspects in human-vegetation interactions. Thus agro-pastoral communities dwelling in the lowlands had a major impact on the openness of the landscape used for fields and pastures, whereas contemporary communities with a similar economic mode residing in a different region are more visible in pollen records through species and structural changes in woodlands. We have therefore proved that the land use of contemporary prehistoric communities need not necessarily be the same.

We demonstrated that there was no unilinear development of human communities towards agricultural lifestyles. This subsistence strategy did not start everywhere with the onset of the Neolithic, in some regions it failed during the Eneolithic, in others, the foraging lifestyle persisted significantly longer and farming became a major economic strategy much later (during the Bronze Age or even Iron Age). To understand the underlying processes of these socio-economic changes, we need to include into our future research more quantified archaeological (both demographic and non-demographic) and non-archaeological proxies, and to evaluate the archaeological evidence in closer detail. Our study clearly shows the importance of combined quantitative archaeological and palaeoecological data for research on human-vegetation interactions. Additionally, we need to incorporate perspectives from social archaeology – discussing modes of social organisation or available technologies with a significant impact on land use (Kolář, 2019). Only such a broad interdisciplinary perspective will help us to fully understand the complex interactions between humans and vegetation during the distant past.

## Data availability statement

The archaeological and pollen datasets and R codes that we used are available at the following link via the repository Zenodo: https://doi.org/10.5281/zenodo.5810757.

## Authors' contribution statement

Jan Kolář: conceptualization, methodology, data curation, writing, reviewing and editing, quantitative analyses and visualisations, funding acquisition; Martin Macek: methodology, writing, reviewing and editing, quantitative analyses and visualisations; Peter Tkáč: data curation, reviewing and editing; David Novák: data curation, reviewing and editing; Vojtěch Abraham: methodology, writing, reviewing and editing, quantitative analyses and visualisations.

## Declaration of competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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